UNIVERSITA' DEGLI STUDI DI BARI ALDO MORO

Dipartimento di Scienze del Suolo, della Pianta e degli Alimenti DOTTORATO DI

RICERCA IN

Biodiversità, Agricoltura e Ambiente Curriculum: Agricoltura Sostenibile CICLO

XXXVIII SSD AGRI-03/A: SCIENZE E TECNOLOGIE DEI SISTEMI

ARBOREI E FORESTALI

Plant-based indices for the determination and monitoring of plant functional status in a context of climate change

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ESAME FINALE 2026

Summary

Perennial fruit crops are central to agricultural systems in Mediterranean and semi-arid regions, where climate change is progressively intensifying water scarcity, atmospheric evaporative demand, and drought frequency. In this context, water limitation is no longer episodic but structural, affecting not only seasonal productivity but also long-term carbon allocation, reserve dynamics, canopy development, and recovery capacity. These carry-over effects highlight the need for approaches that interpret plant responses in functional terms rather than relying exclusively on environmental descriptors or fixed water-status thresholds. This PhD thesis adopts the concept of plant functional status as an integrative framework to describe plant responses to water limitation. Plant functional status is defined as the capacity of plants to sustain coordinated hydraulic, stomatal, photosynthetic, and thermal processes along a stress gradient. Within this perspective, stress is interpreted as a progressive shift in the coordination among physiological processes. For instance, moderate reductions in stem water potential and stomatal conductance may reflect regulated adjustment, whereas the concurrent decline of gas exchange and increased leaf temperature may signal a loss of hydraulic– photosynthetic coordination. Functional transitions are therefore identified through integrative plant-based variables rather than relying exclusively on single absolute thresholds. The thesis is structured as an article-based dissertation composed of four chapters. Chapter I establishes the conceptual foundation through a comprehensive review of almond physiology and irrigation management, emphasizing the limitations of fixed physiological thresholds and soil-based approaches. Chapter II investigates almond responses to regulated deficit irrigation under field conditions, demonstrating how coordinated changes in water status, gas exchange, and thermal behaviour allow functional transitions to be identified along an irrigation gradient. This study allowed the identification of stomatal conductance, the carboxylative activity index ($P_{KO/KC}$), and stem

water potential as promising plant- based indicators in almond. Chapter III extends the analysis to grapevine, confirming the broader applicability of the integrative framework across perennial species subjected to different irrigation regimes. Chapter IV explores cultivar-dependent variability under controlled stress dynamics, showing how genotype-specific regulatory strategies influence the expression of functional responses. Across experimental contexts, classical variables such as stem water potential and stomatal conductance proved essential, but their interpretative value increased when integrated with photosynthetic and thermal information. Integrative indices derived from the combined analysis of chlorophyll fluorescence and leaf temperature enabled the inclusion of photosynthetic functionality within plant- based monitoring frameworks. In this study, these proxies were strongly associated with gas-exchange- derived assimilation rates, while requiring substantially shorter acquisition times than direct photosynthetic measurements, thereby increasing operational efficiency under field conditions.

Overall, the thesis demonstrates that plant functional status can be meaningfully assessed through coordinated plant-based measurements interpreted within a context-aware framework that accounts for phenology, environmental demand, stress trajectory, and genotype. By combining conceptual analysis, field experimentation, and controlled phenotyping, the work advances physiology-based approaches for the sustainable management and functional characterization of perennial fruit crops under climate- driven water limitation.

Sommario

Le colture frutticole perenni rappresentano una componente strutturale dei sistemi agricoli nelle regioni mediterranee e semi-aride, dove il cambiamento climatico sta progressivamente intensificando la scarsità idrica, la domanda evaporativa atmosferica e la frequenza degli eventi siccitosi. In questo contesto, la limitazione idrica non è più un

fenomeno episodico, ma una condizione strutturale che incide non solo sulla produttività stagionale, bensì anche sull'allocazione del carbonio nel lungo periodo, sulla dinamica delle riserve, sullo sviluppo della chioma e sulla capacità di recupero della pianta. Questi effetti, accumulabili in stagioni successive, rendono necessario un approccio interpretativo fondato sulla funzionalità dell'albero, piuttosto che basato esclusivamente su descrittori ambientali o su soglie fisse di stato idrico. La presente tesi di dottorato adotta il concetto di stato funzionale della pianta come quadro interpretativo integrato per descrivere le risposte alla limitazione idrica. Lo stato funzionale è definito come la capacità della pianta di mantenere coordinati, lungo un gradiente di stress, i processi idraulici, stomatici, fotosintetici e di dissipazione termica. In questa prospettiva, lo stress non è inteso come il superamento di una soglia assoluta, ma come una progressiva modificazione del grado di coordinazione tra processi fisiologici. Ad esempio, riduzioni moderate del potenziale idrico del fusto e della conduttanza stomatica possono determinare un aggiustamento regolato che non comporta grosse modifiche nelle performance fotosintetiche e produttive; al contrario, la concomitante riduzione degli scambi gassosi e l'aumento della temperatura fogliare possono indicare una perdita di coordinazione tra sistema idraulico e fotosintesi. Le transizioni funzionali vengono pertanto identificate attraverso variabili integrate su base pianta, anziché tramite il solo ricorso a soglie assolute isolate. La tesi è strutturata come dissertazione articolata in quattro articoli scientifici. Il capitolo I definisce il quadro concettuale mediante una revisione approfondita della fisiologia del mandorlo in diverse condizioni di disponibilità idrica e della gestione irrigua, evidenziando i limiti delle soglie fisiologiche fisse e degli approcci esclusivamente basati sul suolo. Il capitolo II analizza la risposta del mandorlo a strategie di stress idrico controllato in condizioni di campo, mostrando come le variazioni coordinate di stato idrico, scambi gassosi e comportamento termico consentano di individuare transizioni funzionali lungo un gradiente irriguo. In questo contesto,

conduttanza stomatica, indice di attività carbossilativa ($P_{KO/KC}$) e potenziale idrico del fusto sono emersi come indicatori promettenti su base pianta. Il capitolo III estende l'analisi alla vite, confermando l'applicabilità del quadro integrativo a specie perenni differenti sottoposte a regimi irrigui diversificati. Il capitolo IV approfondisce, in mandorlo, la variabilità dipendente dal genotipo in condizioni di limitazione idrica costante o crescente, dimostrando come strategie regolatorie specifiche di diverse cultivar influenzino l'espressione delle risposte funzionali. Nei diversi contesti sperimentali, variabili classiche quali il potenziale idrico del fusto e la conduttanza stomatica si sono confermate fondamentali; tuttavia, il loro valore interpretativo è risultato significativamente rafforzato quando integrate con informazioni fotosintetiche, termiche e di funzionalità dei fotosistemi. Indici integrativi derivati dall'analisi combinata della fluorescenza della clorofilla e della temperatura fogliare hanno consentito di includere la funzionalità fotosintetica nei sistemi di monitoraggio su base pianta. Nel presente studio, tali proxy hanno mostrato una stretta associazione con i tassi di assimilazione stimati tramite scambi gassosi, richiedendo però tempi di acquisizione significativamente inferiori rispetto alle misure fotosintetiche dirette e aumentando così l'efficienza operativa in condizioni di campo. Nel complesso, la tesi dimostra che lo stato funzionale della pianta può essere valutato in modo robusto attraverso misurazioni coordinate su base fisiologica, interpretate all'interno di un quadro contestualizzato che tenga conto di fenologia, domanda evaporativa, traiettoria dello stress e variabilità genotipica. Integrando analisi concettuale, sperimentazione in campo e fenotipizzazione in ambiente controllato, il lavoro contribuisce allo sviluppo di approcci fisiologici avanzati per la gestione sostenibile e la caratterizzazione funzionale delle colture frutticole perenni in condizioni di limitazione idrica indotta dal cambiamento climatico.

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INTRODUCTION

Climate change and abiotic stress in perennial fruit crops

Climate change is progressively reshaping the environmental conditions under which perennial fruit crops are cultivated, particularly in Mediterranean and semi-arid regions. Rising air temperatures, increasing atmospheric evaporative demand, and a higher frequency of drought events are intensifying abiotic stress and exacerbating water scarcity, with direct consequences for orchard sustainability and irrigation management (Lionello and Scarascia, 2018; Gambetta et al., 2020; IPCC, 2021; Freitas et al., 2023). Under these conditions, water limitation is no longer episodic but structural, requiring adaptive strategies that explicitly account for plant physiological responses.

In perennial cropping systems, abiotic stress cannot be regarded solely as a short-term constraint affecting yield within a single growing season. Recurrent or prolonged stress events may induce cumulative and carry-over effects by altering carbon allocation, reserve dynamics, canopy development, leaf longevity, and recovery capacity, thereby influencing productivity over multiple years (Hsiao, 1973; Torrecillas et al., 1996; Klein et al., 2001; Goldhamer and Fereres, 2017). From a physiological perspective, stress should therefore be considered as a process acting across time scales, whose effects may not be fully captured by instantaneous measurements but emerge through progressive changes in plant functioning. In this context, water deficit represents an external environmental constraint, whereas physiological stress reflects the internal functional state of the plant, shaped by regulatory processes that mediate the relationship between environment and performance (Passioura, 1996; Flexas et al., 2004).

This long-term and process-based view of stress highlights the need for approaches capable of interpreting plant responses in functional terms, rather than relying exclusively on environmental descriptors or water balance metrics.

Limits of traditional irrigation scheduling under water scarcity

Irrigation scheduling in fruit trees has traditionally relied on climate-driven approaches, such as reference and crop evapotranspiration combined with soil water balance models. These methods provide a robust framework for estimating potential crop water requirements, yet they primarily describe external forcing variables and do not necessarily reflect the actual physiological status of the plant (Jones, 2004; Fereres and Soriano, 2007). However, under heterogeneous field conditions characterized by localized wetting patterns and fluctuating atmospheric demand, plant responses to similar soil water levels may differ substantially within the same orchard (Vanella et al., 2022).

These limitations become particularly evident under deficit irrigation strategies, where mild to moderate water stress is intentionally imposed to improve water use efficiency while maintaining productivity (Fereres and Soriano, 2007; Shackel, 2011). In this context, the central management challenge is not the detection of water deficit per se, but the identification of the point at which stress shifts from adaptive physiological regulation to functionally limiting conditions. Operationally, this translates into the difficulty of defining when and to what extent irrigation should be applied to prevent irreversible functional impairment while still allowing controlled stress (Shackel, 2011; Fernández, 2017). This distinction reflects a fundamental physiological principle: plant performance is constrained not simply by resource availability, but by the emergence of limiting processes that disrupt the coordination among water transport, stomatal regulation, and carbon assimilation (Passioura, 1996).

Soil- and climate-based indicators alone are often insufficient to resolve this transition, as they do not account for how plants regulate internal processes in response to environmental constraints.

Plant-based monitoring approaches: opportunities and limitations

For this reason, increasing attention has been directed toward plant-based monitoring

approaches, which treat the plant as an integrative sensor of soil, atmosphere, genotype, and management conditions (Jones, 2004; Fernández, 2017; De Swaef et al., 2022). Physiological variables such as stem water potential (Ψstem), stomatal conductance (gs), leaf or canopy temperature (ΔT), and gas exchange variables have been widely used to describe plant water status and stress responses in woody crops (Shackel, 2011; De Swaef et al., 2022; Kisekka et al., 2024). Midday stem water potential integrates soil water availability and atmospheric demand and has been widely adopted as a reference indicator of plant water status in fruit trees (Naor, 2000). Stomatal conductance represents an early and sensitive response to water stress, directly linking transpiration control to carbon assimilation (Flexas et al., 2004; Cifre et al., 2005). Thermal indicators, such as leaf or canopy temperature and derived indices like the Crop Water Stress Index, reflect reductions in transpirational cooling under stomatal closure and offer potential for spatially explicit monitoring (Idso et al., 1981; Jackson et al., 1981; Jones, 2004).

Despite their physiological relevance, these indicators are strongly influenced by short-term environmental variability, phenology, and genotype. As a consequence, absolute threshold values are often poorly transferable across environments and cultivars, leading to ambiguous interpretations (Naor, 2000; Damour et al., 2010; Fernández, 2017). Importantly, this limitation is not merely technical, but interpretative: similar indicator values may correspond to different functional states depending on stress history, developmental stage, and regulatory strategy adopted by the plant. This ambiguity limits the direct use of single indicators for decision-making under field conditions.

From plant-based indicators to plant functional status

These limitations support a shift from indicator-based diagnostics toward the concept of plant functional status, defined as the capacity of the plant to sustain coordinated hydraulic, stomatal, photosynthetic, and thermal functioning under increasing water

limitation. Plant functional status is not directly measurable as a single variable but is inferred from the regulation and interaction among multiple physiological processes. From this perspective, stress is interpreted as a dynamic process, and functional thresholds emerge when the balance among these processes progressively deteriorates rather than when individual indicators reach fixed values.

This view is consistent with physiological frameworks emphasizing that plant performance declines when the integration among key processes weakens, rather than when a single variable exceeds a predefined limit (Passioura, 1996; Flexas et al., 2004; Flexas et al., 2013). Recent integrative studies further support the idea that plant responses to water stress arise from adjustments among hydraulic function, stomatal behaviour, and carbon metabolism, and that vulnerability develops when this integration can no longer be sustained (Meinzer et al., 2009; Meinzer et al., 2014; Chen et al., 2022).

Physiological indicators commonly used in plant-based monitoring can therefore be interpreted as partial descriptors of a broader functional state. Variables related to plant water relations describe the hydraulic component of stress, stomatal conductance reflects regulatory control over water loss and carbon gain, and thermal and photosynthetic indicators provide information on energy balance and biochemical performance. However, none of these variables alone is sufficient to capture the complexity of plant functioning under stress, particularly in heterogeneous field environments (Passioura, 1996; Flexas et al., 2004; Meinzer et al., 2014; Fernández, 2017).

Integrative plant-based indices and functional interpretation

Photosynthetic measurements offer direct insight into plant carbon assimilation and functional performance under stress, but their application in field conditions is constrained by time requirements and operational complexity (von Caemmerer, 2000; Flexas et al., 2002). This limitation has stimulated interest in alternative approaches

capable of capturing photosynthetic functionality through faster and less invasive measurements.

The integration of chlorophyll fluorescence and thermal information has been proposed as a promising avenue to describe photosynthetic functioning under stress. Fluorescence-derived variables provide information on photochemical efficiency and the partitioning of absorbed energy (Losciale et al., 2010), while leaf temperature reflects transpirational cooling and stomatal regulation (Genty et al., 1989; Niyogi, 1999; Jones, 2004). Multivariate approaches integrating chlorophyll fluorescence variables and temperature to assess leaf photo-assimilation performance have been previously proposed (Losciale et al., 2015). Building upon this integrative perspective, the combination of photochemical and thermal signals allows photosynthetic responses to be interpreted within the broader framework of plant energy balance (Losciale et al., 2023). Within this context, the transition from individual plant-based indicators to integrative indices represents a conceptual shift toward a coordination-based interpretation of stress responses. By integrating information from multiple variables, indices reduce sensitivity to short-term fluctuations and enhance comparability across conditions (Shackel, 2011; Fernández, 2017). Rather than defining universal thresholds, such indices support context-dependent diagnosis of functional stress by linking physiological responses to coordinated changes in plant functioning along a stress gradient. In this sense, plant-based indices are not conceived as prescriptive tools, but as interpretative frameworks capable of informing adaptive management decisions under variable environmental conditions.

Functional variability, stress dynamics, and genotype-dependent responses

Genotype-dependent variability further complicates the interpretation of plant-based indicators under field conditions. Differences among cultivars in stomatal sensitivity, hydraulic regulation, and photosynthetic response to stress can lead to contrasting

functional behaviours under similar environmental constraints (Torrecillas et al., 1996; Cifre et al., 2005; Karimi et al., 2015; Álvarez- Maldini et al., 2022). While such variability limits the applicability of fixed thresholds, it also provides valuable information on alternative functional strategies for coping with water limitation. Beyond its implications for irrigation monitoring, genotype-dependent variability is central to functional phenotyping under water-limited conditions. Genetic variability and phenotypic plasticity in almond have been shown to influence hydraulic regulation, stomatal behaviour, and the capacity to maintain carbon assimilation under stress (Fernández i Martí et al., 2009; Delplancke et al., 2013). Differences in drought-response strategies, including contrasting iso- and anisohydric behaviours, reflect alternative regulatory coordination among hydraulic transport, stomatal control, and carbon metabolism (Tardieu and Simonneau, 1998; Tyree and Zimmermann, 2002; Cochard et al., 2008). The identification of morphological and physiological traits associated with stress tolerance has therefore been proposed as a key step in breeding and selection programs aimed at improving adaptation to water scarcity (Valliyodan and Nguyen, 2006; Lauri et al., 2016). In this context, differences in stomatal sensitivity, hydraulic vulnerability, and photosynthetic regulation can be interpreted as functional traits rather than as experimental variability, providing a mechanistic basis for discriminating tolerant and more vulnerable cultivars under progressive water limitation.

Within a functional framework, genotypic variability can therefore be interpreted not as noise, but as an integral component of plant responses to stress, reflecting differences in how coordination among physiological processes is regulated (Passioura, 1996; Chen et al., 2022). In addition to stress intensity, the temporal development of water limitation may influence how plant responses are expressed and interpreted. The trajectory of stress imposition, whether static or progressively intensifying, could affect the coordination among physiological processes and the detectability of functional transitions. However,

the implications of stress dynamics for plant-based monitoring remain insufficiently explored, particularly under perennial cropping systems exposed to variable environmental conditions.

Almond as a model species and cross-crop generalization

Among perennial fruit crops, almond (*Prunus dulcis* Mill.) represents a particularly suitable model system for investigating plant functional status under climate change. Although traditionally considered a drought-tolerant species, modern almond production has become increasingly irrigation-dependent due to orchard intensification and yield-oriented management practices (Fereres and Goldhamer, 1990; Goldhamer and Fereres, 2017). This apparent contradiction makes almond an informative system for investigating how functional transitions emerge under water-limited conditions.

Field studies have shown that almond trees can sustain moderate water limitation through coordinated physiological regulation, while more severe or prolonged stress leads to progressive impairment of gas exchange and photosynthetic performance (Romero et al., 2004; Espadafor et al., 2017; Sperling et al., 2023). At the same time, pronounced variability among cultivars in physiological behaviour highlights the relevance of almond for investigating genotype-dependent functional strategies under stress. While almond constitutes the primary focus of this thesis, the inclusion of grapevine as a model perennial crop provides a complementary perspective. Grapevine has long been used as a reference species in deficit irrigation research, owing to its economic relevance and extensive physiological characterization. Studies conducted under Mediterranean conditions show that moderate water restriction can preserve physiological performance and yield while altering fruit and wine quality, whereas more severe deficits lead to functional impairment and reduced productivity (Escalona et al., 1999; Flexas et al., 2002; Losciale et al., 2024). The convergence of responses observed across almond and grapevine indicates that plant

functional status can be interpreted using common physiological principles, despite differences in phenology, canopy structure, and management objectives. This comparative perspective supports the transferability of plant-centred approaches for monitoring and interpreting plant responses to water stress across perennial cropping systems exposed to climate-driven constraints. Within this framework, the present thesis investigates plant-based indicators and integrative indices to interpret functional transitions under deficit irrigation and to analyse genotype-dependent variability in plant functional responses. By integrating conceptual analysis, field experimentation, and controlled phenotyping, the thesis advances a physiology-based and context-aware framework for interpreting and managing plant responses to climate-driven water limitation.

References

Álvarez-Maldini, C., Acevedo, M., Estay, D., Aros, F., Dumroese, R. K., Sandoval, S., & Pinto, M. (2022). Examining physiological, water relations, and hydraulic vulnerability traits to determine anisohydric and isohydric behavior in almond (*Prunus dulcis*) cultivars: Implications for selecting agronomic cultivars under changing climate. *Frontiers in Plant Science, 13*, 974050. https://doi.org/10.3389/fpls.2022.974050

Chen, Z., Li, S., Wan, X., & Liu, S. (2022). Strategies of tree species to adapt to drought from leaf stomatal regulation and stem embolism resistance to root properties. *Frontiers in Plant Science, 13*, 926535. https://doi.org/10.3389/fpls.2022.926535

Cifre, J., Bota, J., Escalona, J. M., Medrano, H., & Flexas, J. (2005). Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.): An open gate to improve water-use efficiency? *Agriculture, Ecosystems & Environment, 106*(2–3), 159–170. https://doi.org/10.1016/j.agee.2004.10.005

Cochard, H., Barigah, T. S., Kleinhentz, M., & Eshel, A. (2008). Is xylem cavitation resistance a relevant criterion for screening drought resistance among *Prunus* species? *Journal of Plant Physiology, 165*(9), 976–982. https://doi.org/10.1016/j.jplph.2007.07.020

Damour, G., Simonneau, T., Cochard, H., & Urban, L. (2010). An overview of models of stomatal conductance at the leaf level. *Plant, Cell & Environment, 33*(9), 1419–1438. https://doi.org/10.1111/j.1365-3040.2010.02181.x

De Swaef, T., Pieters, O., Appeltans, S., Borra-Serrano, I., Coudron, W., Couvreur, V.,

Garré, S., Lootens, P., Nicolaï, B., Pols, L., Saint Cast, C., Šalagovič, J., Van Haeverbeke, M., Stock, M., & Wyffels, F. (2022). On the pivotal role of water potential to model plant physiological processes. *in silico Plants, 4*(1), diab038. https://doi.org/10.1093/insilicoplants/diab038

Delplancke, M., Alvarez, N., Benoit, L., Espíndola, A., Joly, H. I., Neuenschwander, S., & Arrigo, N. (2013). Evolutionary history of almond tree domestication in the Mediterranean basin. *Molecular Ecology, 22*(4), 1092–1104. https://doi.org/10.1111/mec.12129

Escalona, J. M., Flexas, J., & Medrano, H. (1999). Stomatal and non-stomatal limitations of photosynthesis under water stress in field-grown grapevines. *Australian Journal of Plant Physiology, 26*(5), 421–433. https://doi.org/10.1071/PP99019

Espadafor, M., Orgaz, F., Testi, L., Lorite, I. J., González-Dugo, V., & Fereres, E. (2017). Responses of transpiration and transpiration efficiency of almond trees to moderate water deficits. *Scientia Horticulturae, 225*, 6–14. https://doi.org/10.1016/j.scienta.2017.06.028

Fereres, E., & Goldhamer, D. A. (1990). Deciduous fruit and nut trees. In B. A. Stewart & D. R. Nielsen (Eds.), *Irrigation of agricultural crops* (Agronomy Monograph No. 30, pp. 987–1017). ASA-CSSA-SSSA.

Fereres, E., & Soriano, M. A. (2007). Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany, 58*(2), 147–159. https://doi.org/10.1093/jxb/erl165

Fernández, J. E. (2017). Plant-based methods for irrigation scheduling of woody crops. *Horticulturae, 3*(2), 35. https://doi.org/10.3390/horticulturae3020035

Fernández i Martí, À., Alonso, J. M., Espiau, M. T., Rubio-Cabetas, M. J., & Socias i Company, R. (2009). Genetic diversity in Spanish and foreign almond germplasm assessed by molecular characterization with simple sequence repeats. *Journal of the American Society for Horticultural Science, 134*(5), 535–542. https://doi.org/10.21273/JASHS.134.5.535

Flexas, J., Bota, J., Cifre, J., Escalona, J. M., Galmés, J., Gulías, J., Lefi, E. K., Martínez-Cañellas, S. F., Moreno, M. T., Ribas-Carbó, M., Riera, D., Sampol, B., & Medrano, H. (2004). Understanding down-regulation of photosynthesis under water stress: Future prospects and searching for physiological tools for irrigation management. *Annals of Applied Biology, 144*(3), 273–283. https://doi.org/10.1111/j.1744-7348.2004.tb00343.x

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. *Functional Plant Biology, 29*(4), 461–471. https://doi.org/10.1071/PP01119

Flexas, J., Escalona, J. M., & Medrano, H. (1998). Down-regulation of photosynthesis by drought under field conditions in grapevine leaves. *Australian Journal of Plant Physiology, 25*(8), 893–900. https://doi.org/10.1071/PP98054

Flexas, J., Scoffoni, C., Gago, J., & Sack, L. (2013). Leaf mesophyll conductance and

leaf hydraulic conductance: An introduction to their measurement and coordination. *Journal of Experimental Botany, 64*(13), 3965–3981. https://doi.org/10.1093/jxb/ert319

Freitas, T. R., Santos, J. A., Silva, A. P., & Fraga, H. (2023). Reviewing the adverse climate change impacts and adaptation measures on almond trees (*Prunus dulcis*). *Agriculture, 13*(7), 1423. https://doi.org/10.3390/agriculture13071423

Gambetta, G. A., Herrera, J. C., Dayer, S., Feng, Q., Hochberg, U., & Castellarin, S. D. (2020). The physiology of drought stress in grapevine: Towards an integrative definition of drought tolerance. *Journal of Experimental Botany, 71*(16), 4658–4676. https://doi.org/10.1093/jxb/eraa245

Goldhamer, D. A., & Fereres, E. (2001). Irrigation scheduling protocols using continuously recorded trunk diameter measurements. *Irrigation Science, 20*(3), 115–125. https://doi.org/10.1007/s002710000034

Goldhamer, D. A., & Fereres, E. (2017). Establishing an almond water production function for California using long-term yield response to variable irrigation. *Irrigation Science, 35*(3), 169–179. https://doi.org/10.1007/s00271-016-0528-2

Hsiao, T. C. (1973). Plant responses to water stress. *Annual Review of Plant Physiology, 24*, 519–570. https://doi.org/10.1146/annurev.pp.24.060173.002511

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. *Agricultural Meteorology, 24*, 45–55. https://doi.org/10.1016/0002-1571(81)90032-7

Intergovernmental Panel on Climate Change. (2021). *Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/9781009157896

Jackson, R. D., Idso, S. B., Reginato, R. J., & Pinter, P. J. (1981). Canopy temperature as a crop water stress indicator. *Water Resources Research, 17*(4), 1133–1138. https://doi.org/10.1029/WR017i004p01133

Jones, H. G. (2004). Irrigation scheduling: Advantages and pitfalls of plant-based methods. *Journal of Experimental Botany, 55*(407), 2427–2436. https://doi.org/10.1093/jxb/erh213

Karimi, S., Yadollahi, A., Arzani, K., Imani, A., & Aghaalikhani, M. (2015). Gas-exchange response of almond genotypes to water stress. *Photosynthetica, 53*(1), 29–34. https://doi.org/10.1007/s11099-015-0070-0

Kisekka, I., Peddinti, S. R., Savchik, P., Yang, L., Culumber, M., Bali, K., Milliron, L., Edwards, E., Nocco, M., Reyes, C. A., Mahoney, R. J., Shackel, K., & Fulton, A. (2024). Multisite evaluation of microtensiometer and osmotic cell stem water potential sensors in almond orchards. *Computers and Electronics in Agriculture, 227*, 109547. https://doi.org/10.1016/j.compag.2024.109547

Klein, I., Esparza, G., Weinbaum, S. A., & DeJong, T. M. (2001). Effects of irrigation deprivation during the harvest period on leaf persistence and function in mature almond trees. *Tree Physiology, 21*(14), 1063–1072. https://doi.org/10.1093/treephys/21.14.1063

Lauri, P.-É., Barigah, T. S., Lopez, G., Martinez, S., Losciale, P., Zibordi, M., Manfrini, L., Corelli Grappadelli, L., Costes, E., & Regnard, J. L. (2016). Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. *Trees, 30*(5), 1893–1908. https://doi.org/10.1007/s00468-016-1408-3

Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change, 18*(5), 1481–1493. https://doi.org/10.1007/s10113-018-1290-1

Losciale, P., Chow, W. S., & Corelli Grappadelli, L. (2010). Modulating the light environment with the peach "asymmetric orchard": Effects on gas exchange performances, photoprotection, and photoinhibition. *Journal of Experimental Botany, 61*(4), 1177–1192. https://doi.org/10.1093/jxb/erp387

Losciale, P., Manfrini, L., Morandi, B., Pierpaoli, E., Zibordi, M., Stellacci, A. M., Salvati, L., & Corelli Grappadelli, L. (2015). A multivariate approach for assessing leaf photo-assimilation performance using the IPL index. *Physiologia Plantarum, 154*(4), 609–620. https://doi.org/10.1111/ppl.12328

Losciale, P., Gaeta, L., Corsi, M., Galeone, C., Tarricone, L., Leogrande, R., & Stellacci, A. M. (2023). Physiological responses of apricot and peach cultivars under progressive water shortage: Different crop signals for anisohydric and isohydric behaviours. *Agricultural Water Management, 286*, 108384. https://doi.org/10.1016/j.agwat.2023.108384

Losciale, P., Conti, L., Seripierri, S., Alba, V., Mazzone, F., Rustioni, L., di Leo, G., Tarricone, F., & Tarricone, L. (2024). Effect of different deficit irrigation regimes on vine performance, grape composition and wine quality of the "Primitivo" variety under Mediterranean conditions. *Irrigation Science, 42*, 877–890. https://doi.org/10.1007/s00271-024-00956-0

Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A., & Woodruff, D. R. (2009). Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology, 23*(5), 922–930. https://doi.org/10.1111/j.1365-2435.2009.01577.x

Meinzer, F. C., Woodruff, D. R., Marias, D. E., McCulloh, K. A., & Sevanto, S. (2014). Dynamics of leaf water relations components in co-occurring iso- and anisohydric conifer species. *Plant, Cell & Environment, 37*(11), 2577–2586. https://doi.org/10.1111/pce.12327

Naor, A. (2000). Midday stem water potential as a plant water stress indicator for irrigation scheduling in fruit trees. *Acta Horticulturae, 537*, 447–454. https://doi.org/10.17660/ActaHortic.2000.537.52

Passioura, J. B. (1996). Drought and drought tolerance. *Plant Growth Regulation, 20*, 79–83. https://doi.org/10.1007/BF00024003

Romero, P., Navarro, J. M., García, F., & Botía Ordaz, P. (2004). Effects of regulated deficit irrigation during the pre-harvest period on gas exchange, leaf development and crop yield of mature almond trees. *Tree Physiology, 24*(3), 303–312. https://doi.org/10.1093/treephys/24.3.303

Shackel, K. A. (2011). A plant-based approach to deficit irrigation in trees and vines. *HortScience, 46*(2), 173–177. https://doi.org/10.21273/HORTSCI.46.2.173

Sperling, O., Gardi, I., Ben-Gal, A., & Kamai, T. (2023). Deficit irrigation limits almond trees' photosynthetic productivity and compromises yields. *Agricultural Water Management, 289*, 108562. https://doi.org/10.1016/j.agwat.2023.108562

Tardieu, F., & Simonneau, T. (1998). Variability among species of stomatal control under fluctuating soil water status and evaporative demand: Modelling isohydric and anisohydric behaviours. *Journal of Experimental Botany, 49*(Special Issue), 419–432. https://doi.org/10.1093/jxb/49.Special_Issue.419

Torrecillas, A., Alarcón, J. J., Domingo, R., Planes, J., & Sánchez-Blanco, M. J. (1996). Strategies for drought resistance in leaves of two almond cultivars. *Plant Science, 118*(2), 135–143. https://doi.org/10.1016/0168-9452(96)04434-2

Tyree, M. T., & Zimmermann, M. H. (2002). *Xylem structure and the ascent of sap* (2nd ed.). Springer. https://doi.org/10.1007/978-3-662-04931-0

Valliyodan, B., & Nguyen, H. T. (2006). Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Current Opinion in Plant Biology, 9*(2), 189–195. https://doi.org/10.1016/j.pbi.2006.01.019

Vanella, D., Peddinti, S. R., & Kisekka, I. (2022). Unravelling soil water dynamics in almond orchards characterized by soil heterogeneity using electrical resistivity tomography. *Agricultural Water Management, 269*, 107652. https://doi.org/10.1016/j.agwat.2022.107652

von Caemmerer, S. (2000). Chlorophyll fluorescence and oxygen exchange during C_3 photosynthesis. In S. von Caemmerer (Ed.), *Biochemical models of leaf photosynthesis* (pp. 42–65). CSIRO Publishing. https://doi.org/10.1071/9780643103405

AIMS OF THE STUDY

The overarching aim of this PhD thesis was to develop and critically evaluate plant-based indices for the assessment and monitoring of plant functional status in a context of climate change, with particular reference to perennial fruit crops exposed to increasing water and thermo-evaporative stress. The thesis was grounded on the premise that, under current and projected climatic scenarios, orchard sustainability increasingly depends on identifying stress levels at which physiological coordination begins to deteriorate. Within this framework, plant-based indices were considered interpretative tools that link environmental constraints to plant functioning, supporting a physiology-oriented understanding of stress dynamics rather than a purely descriptive assessment of water deficit.

The first aim to identify the most informative plant-based physiological indicators for describing plant responses to water deficit in almond and grapevine, with particular attention to plant water status, stomatal regulation, thermal behaviour, and photosynthetic performance. This objective was addressed mainly in Chapters II and III, where these variables were examined under different irrigation conditions and in two perennial crop systems. A second objective was to evaluate how robust and transferable these indicators were across different experimental contexts and stress dynamics. In particular, the thesis examined whether their interpretation remained consistent under field and controlled conditions, and under different patterns of water limitation, including progressive and more static stress. This aspect was developed across Chapters II, III, and IV. A further aim was to characterize functional transitions along the stress gradient, distinguishing conditions in which plant responses still reflected coordinated physiological adjustment from those in which functional integrity began to deteriorate. Rather than defining universal thresholds, the thesis sought to identify context-dependent and phenology-

dependent ranges within which plant processes remained coordinated. This objective was addressed primarily in Chapter II.

The thesis also aimed to test whether combining multiple plant-based variables into integrative indices could improve the assessment of plant functional status compared with the use of single indicators alone. In this sense, Chapters II and III explored the added value of composite approaches for capturing the coordination among hydraulic, stomatal, thermal, and photosynthetic processes.

Finally, the work aimed to analyse genotype-dependent variability in almond under different water stress regimes, with particular reference to differences in stomatal behaviour, thermal regulation, and sensitivity to water limitation. By doing so, Chapter IV evaluated the potential of plant-based indices not only for stress assessment, but also as tools for functional phenotyping.

Overall, by integrating conceptual analysis, field experimentation, and controlled phenotyping, this thesis aimed to contribute to the development of a physiology-based and decision-oriented framework for monitoring plant functional status, with potential applications in adaptive irrigation management and genotype selection under climate-driven water limitation.

CHAPTER I

This chapter establishes the theoretical basis of the thesis by reframing plant responses to water deficit in terms of functional coordination rather than fixed water-status thresholds. Through a critical review of almond physiology and irrigation strategies, it highlights the limits of soil-based approaches and single-variable interpretations, and introduces plant functional status as an integrative framework grounded in hydraulic, stomatal, photosynthetic, and thermal coupling.

BACKGROUND

Almond is increasingly cultivated in arid and semi-arid environments, where irrigation has become essential to sustain yield, nut quality, and orchard profitability. Although the species retains several drought-adaptive traits, such as deep rooting and early phenology, its physiological response to water deficit is highly variable and depends on cultivar, phenological stage, atmospheric demand, and management conditions. Current irrigation approaches still rely largely on soil-based estimates or on the isolated interpretation of single plant variables, such as stem water potential, stomatal conductance, or canopy temperature. However, these indicators often show context-dependent thresholds, limiting their transferability across environments and reducing their effectiveness as universal decision criteria.

AIMS

This chapter aims to provide a critical and integrative synthesis of almond anatomical and ecophysiological responses to water availability, with specific emphasis on how hydraulic function, stomatal regulation, photosynthetic activity, and canopy thermal behaviour interact under deficit conditions. It also aims to examine the limits of threshold-based and soil-centered irrigation approaches, and to propose plant functional status as a more robust conceptual framework for interpreting physiological signals and supporting adaptive, phenology-driven irrigation strategies.

RESULTS

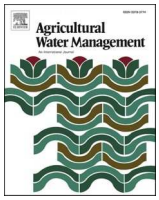
The chapter shows that almond responses to water deficit cannot be reliably interpreted through fixed physiological thresholds applied uniformly across cultivars and environments. Instead, the literature supports a functionally coordinated view in which water potential, stomatal conductance, photosynthesis, and leaf or canopy temperature must be interpreted jointly and in relation to phenological stage and atmospheric demand. This synthesis highlights why single-variable approaches are often insufficient and supports the development of integrated, plant-based decision frameworks for irrigation scheduling, with the goal of improving water-use efficiency while preserving yield, nut quality, and long-term orchard resilience.

Agricultural Water Management 325 (2026) 110162

Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat



Linking anatomy and physiology of almond to irrigation strategies: Towards standardized thresholds and decision-support tools for water-limited environments

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A R T I C L E I N F O

Handling Editor - Dr. Brent Clothier

Keywords:
Leaf functionality
Water stress
Physiological indicators
Drought tolerance
Water potential
Stomatal conductance
Canopy temperature

A B S T R A C T

Almond (*Prunus dulcis* (Mill.) D.A. Webb) is one of the most important nut crops cultivated in arid and semi-arid regions, where water availability is a key factor determining yield and nut quality. Its domestication in dry environments has favoured traits such as deep rooting and early phenology, which confer a moderate tolerance to drought. However, under prolonged or severe water stress, these adaptations become insufficient, leading to declines in yield. Understanding the balance between tolerance and vulnerability is therefore essential for developing irrigation strategies that ensure yield stability, nut quality and long-term orchard resilience under climatic conditions and modern cultivation systems increasingly dependent on irrigation. This review provides an integrative overview of almond's anatomical and ecophysiological responses to water availability, emphasizing key physiological indicators, such as water potential, stomatal conductance, and leaf temperature, as tools to guide irrigation management. The reliability of these variables depends on environmental conditions, phenological stages, and cultivar-specific traits, which complicates the definition of universal thresholds. By integrating anatomical and physiological evidence with recent advances in monitoring technologies, this review aims to support the development of standardized, adaptive irrigation protocols that enhance water use efficiency of almond trees while preserving yield and nut quality. Understanding cultivar adaptation and physiological thresholds is critical to ensure resilient almond production under increasing climate and water challenges.

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https://doi.org/10.1016/j.agwat.2026.110162
Received 16 August 2025; Received in revised form 14 January 2026; Accepted 14 January 2026
Available online 20 January 2026

1. Introduction

Almonds (*Prunus dulcis* (Mill.) D.A. Webb) can be grown under rainfed conditions in some areas; however, irrigation is considered essential to achieve optimal yield and fruit quality. Notably, almonds are not drought-resistant but drought-tolerant (Gradziel, 2017), meaning they can withstand moderate and seasonal water deficits without substantial physiological damage or yield penalties. Nonetheless, when water shortages become prolonged or severe, productivity declines markedly due to higher water stress experienced compared with fully irrigated (FI) trees (Miras-Ávalos et al., 2023). Following its expansion into highly productive irrigated regions during the 20th century, almond cultivation progressively shifted from predominantly rainfed systems to irrigation-dependent production. Breeding efforts have historically emphasized yield maximization, indirectly increasing almond dependence on irrigation for sustained productivity (Paudel et al., 2020; Egea et al., 2010). In semi-arid environments, irrigation strategies adapted to water scarcity have increased yields by up to tenfold compared with non-irrigated conditions (Goldhamer and Fereres, 2004). Several studies have shown that regulated deficit irrigation (RDI), supplying approximately 40–70 % of crop water requirements, can sustain yield with only minor reductions when water deficits are carefully timed and applied during specific phenological stages (Goldhamer et al., 2006; Egea et al., 2010). For this reason, almonds are considered a promising crop for improving water-use efficiency in water-limited regions. Efficient irrigation management in almond orchards relies on understanding and monitoring physiological variables that reflect tree water status and responses to water availability (Fernández, 2017). Several plant-based indicators have been identified as effective tools for irrigation management, particularly under water-limited conditions (Goldhamer and Fereres, 2001). Among the most widely used indicators in almond orchards are leaf and stem water potential ($\Psi_{leaf/stem}$), stomatal conductance (g_s) and leaf temperature (T_{leaf}) (Girona et al., 2005). Despite their widespread use, there is still no consensus on robust or universally applicable physiological thresholds. Published thresholds for stem water potential, gas exchange parameters and thermal indices vary widely among studies, reflecting strong dependencies on environmental conditions, soil type, cultivar-specific traits and, critically, phenological stage (Goldhamer et al., 2006). This variability complicates the development of standardized irrigation protocols and limits the transferability of research findings across growing conditions. A key unmet need is therefore a unified, physiologically grounded framework that hierarchically integrates these indicators across phenology and atmospheric demand, translating heterogeneous thresholds into operational and comparable decision rules.

Integrating plant-based indicators into decision support systems (DSS) and irrigation practices offers a pathway to translate physiological measurements into operational irrigation decisions, improving water management under semi-arid conditions while maintaining almond productivity.

Several reviews have addressed specific aspects of almond production, including breeding (Gradziel et al., 2013), irrigation and yield responses (Miras-Ávalos et al., 2023), and nut quality (Massantini and Frangipane, 2022). However, none provides an integrated synthesis linking almond origin and adaptation, anatomical and ecophysiological responses, irrigation management and nut quality within a single, physiologically grounded framework. The aim of this review is to bridge this gap by synthesizing current knowledge on almond anatomy and ecophysiology under water-limited conditions and by integrating plant-based indicators into a phenology-driven decision-support framework. This framework is intended to support the interpretation of physiological thresholds, the use of monitoring technologies and the development of adaptive irrigation strategies that enhance water-use efficiency while maintaining yield, nut quality and long-term orchard resilience under a changing climate.

2. Origin, adaptation, and relevance of almond in water-limited environments

Almonds are native to the arid and semi-arid regions of Central Asia and the Near East, where wild relatives such as *Prunus fenzliana* evolved under conditions of prolonged drought, high thermal amplitude, and low precipitation (Grasselly, 1976; Ladizinsky, 1999). Domestication likely occurred in the eastern Mediterranean (Casas-Agustench et al., 2011), with human-mediated dispersal and agroecological selection shaping the genetic structure of current cultivars (Delplancke et al., 2013).

The species expresses key traits favourable to dry environments, including early phenology, low chilling requirements, deep rooting systems, and strong tolerance to high temperatures and summer drought (Kester et al., 1994). However, modern high-yielding genotypes, particularly those bred under irrigated conditions, often show greater sensitivity to water deficits (Paudel et al., 2020). This contrast between ancestral drought-adaptive traits and the response of modern cultivars highlights almonds as a suitable model to analyse plant-based indicators under contrasting water-use strategies. Still, several studies have demonstrated that when deficits are timed during phenologically tolerant stages, yield losses are minimal (Goldhamer et al., 2006; Egea et al., 2010; Mirás-Ávalos et al., 2023), supporting the potential of RDI strategies for increasing water use efficiency. In addition to stage-based deficit strategies, partial rootzone drying (PRD) has been experimentally evaluated in almond as a complementary approach to water scarcity; however, its adoption in commercial orchards remains limited (Egea et al., 2011; Gutiérrez-Gordillo et al., 2020c, 2021).

Almond exhibits broad genetic variability due to its allogamous nature and historical selection under diverse environments (Fernández i Martí et al., 2009; Delplancke et al., 2013). This variability translates into cultivar-specific differences in flowering time, stomatal behaviour, osmotic regulation, and water-use efficiency, critical factors in designing physiologically informed irrigation protocols (Torrecillas et al., 1996; Álvarez-Maldini et al., 2022; Álvarez et al., 2023). This genotypic diversity is associated with contrasting stomatal strategies, hydraulic plasticity, and phenological sensitivity, which strongly condition the interpretation of water-status indicators across cultivars. The main characteristics of widely studied cultivars, including flowering, compatibility, productivity, and seed traits, are reported in Supplementary Table 1 (Pérez-Sánchez and Morales-Corts 2021; Calle et al., 2024).

Almonds are currently the most widely cultivated nut tree worldwide, with production concentrated in California, Spain, Australia, and Turkey (INC, 2021; FAO, 2023). An overview of global production trends, yield dynamics, and harvested area (2013–2023) is provided in Supplementary Table 2 (FAO, 2023; Freitas et al., 2023).

As agroclimatic zones shift due to ongoing global warming, driven by changes in temperature and precipitation patterns, the integration of ecophysiological understanding, genotype selection, and irrigation scheduling becomes essential to define cultivar-specific physiological thresholds and support the development of decision-support tools for water-efficient almond production (Di Lena et al., 2018; Lorite et al., 2020). In this context, almond represents a particularly informative system for linking phenology, physiology and irrigation management, providing a conceptual bridge to the indicator-based framework developed in subsequent sections.

In addition to cultivar-related traits, rootstock selection plays a central role in almond adaptation to water-limited environments. Rootstocks largely determine rooting depth, hydraulic conductivity, and tolerance to drought and hypoxia, thereby modulating tree water status and physiological responses to water deficit. Differences among widely used rootstock families, including peach × almond hybrids (e.g. GF677, Garnem), plum-based rootstocks (e.g. Rootpac®) and peach-based materials, lead to contrasting ecophysiological strategies that directly affect the interpretation of plant-based indicators such as stem water potential

(Ψ_{stem}), stomatal conductance (g_s), net photosynthesis (A_n) and canopy temperature. These aspects are analysed in detail in Section 4.1 ("Root system and rootstocks").

3. Soil, water and climatic requirements

3.1. Soil requirements for almond cultivation

Almond trees are grown on well-drained soils that possess certain physical and chemical characteristics favorable for their growth and production. In terms of soil texture, sandy loam or loamy soils are the best for almond cultivation (Viveros, 1999). Table 1 summarizes the principal soil physical and chemical thresholds reported in the literature for productive almond orchards.

3.2. Water requirements of almond

In modern orchards, seasonal water demand is primarily a function of how much photosynthetically active radiation (PAR) is intercepted by the canopy. As interception rises, so does crop evapotranspiration (ETc); each +10 % of intercepted PAR (measured around solar noon) adds roughly 40–50 mm to seasonal ETc, up to ~80 % interception; beyond that, water use keeps increasing while the marginal yield response flattens (Goldhamer and Fereres, 2017; Jin et al., 2020). This is why high-yield orchards under Mediterranean climates typically require 850–1300 mm year^{-1} (Jofre-Čekalović et al., 2022).

In practice, growers: (i) estimate ETc from interception (and/or crop coefficient (Kc)) and reference evapotranspiration (ETo), (ii) decide to apply a variable fraction of ETc as a function of almond phenology, and (iii) aim to adjust irrigation amounts using plant-based signals (Ψ_{stem}, Crop Water Stress Index (CWSI), g_s) to remain within safe physiological ranges; however, in commercial orchards this approach is still rarely implemented due to limited practical knowledge among growers and the absence of clear, standardized criteria for interpreting ecophysiological measurements.

We distinguish three operational paradigms for managing irrigation in almond orchards, all anchored to interception-based ETc: full irrigation (FI), regulated or sustained deficit irrigation (RDI/SDI), and partial rootzone drying (PRD).

1. FI. Where water is plentiful, irrigation returns ~100 % of the crop's total water requirements throughout the season. In California – Australia this translates to ~12500 m^3 ha^{-1} and can support up to 3900 kg kernel ha^{-1} when high interception is achieved (Abdelmoneim, 2024). The interception rule matters here because once the canopy nears ~ 80 %, further increases in leaf area index (LAI) keep raising ETc while yield gains taper (Jin et al., 2020).
2. RDI. Under RDI, irrigation is expressed as a variable fraction of the total crop water requirement (considering ETc, the effective rainfall and other sources of water input or output) adjusted as a function of tree phenology. During sensitive periods (bloom and early fruit growth), irrigation is maintained near full crop water requirement, while during less sensitive stages such as mid-summer kernel-filling, reductions to around 35 % can save 30–40 % of seasonal water with minimal yield penalties, provided stress remains moderate (Prgomet et al., 2020).
3. Allocation-limited systems (e.g., Spain). When seasonal water budgets are fixed (~2000–2500 m^3 ha^{-1}), interception-based ETc provides the reference demand, and the deficit must be allocated across phenological stages in accordance with water availability. Under such constraints, maintaining a sustained deficit throughout the season may be more practical than applying strict stage-based RDI, since irrigation timing is often determined by local water authorities or irrigation communities and may occur when water becomes available rather than when it is agronomically optimal (Egea et al., 2013).

Deficit during kernel-filling can depress hull-split and leaf area (Yang et al., 2023), yet moderate stress levels maintain yield (Egea et al., 2009a). Post-harvest drought is most detrimental, reducing next-year flowering (Goldhamer and Viveros, 2000). The correct choice of the phenological stage in which is possible to impose the water restriction as well as the use of sensor-based scheduling Ψ_{stem} probes, thermal/Near-Infrared Imaging (NIR) has cut water use by 22 % in Spanish trials (García-Tejero et al., 2018a).

Table 2 presents irrigation recommendations based on different percentages of the crop irrigation requirement (IR) and seasonal water availability. Here, 100 % IR equals the full ETc and indicates conditions where soil moisture is maintained near field capacity, avoiding water stress. Lower percentages represent RDI strategies that apply controlled stress at specific phenological stages. For example, with a seasonal water availability of 600 mm, irrigation could be scheduled as 100 % IR in stage I, 65 % IR in stage II, and 100 % IR in stage III (Gutiérrez-Gordillo, 2022). These recommendations should be interpreted as non-exhaustive, experience-based guidelines derived from accumulated field knowledge rather than as prescriptive or physiologically validated

Table 1
Principal soil physical and chemical thresholds for almond cultivation as reported in the literature.

Parameter	Threshold	Agronomic implication	References
Bulk density	≤ 1.4 Mg m^{-3}	Promotes water infiltration and root penetration	Weil and Brady, (2017); Fenster et al. (2021)
Organic matter	≥ 2 % (typical orchards < 1 %)	Improves structure and microbial activity	López et al., (2014); Martínez-Mena et al., (2020)
Soil pH	6.0–7.5	Maximises nutrient availability	Gordon et al., (2024)
Soil salinity (ECe)	≤ 1.5 dS m^{-1} (yield decline above)	Moderate sensitivity; avoid high-Na soils	Maas and Hoffman, (1977)
Mineral N	0.11–0.20 %	Adequate vegetative growth	Arquero, (2013)
Olsen-P	10–17 mg kg^{-1}	Supports flowering and nut set	Arquero, (2013)
Exchangeable K	150–300 mg kg^{-1}	Kernel-filling and drought tolerance	Arquero, (2013)
Available B	25–50 μg kg^{-1}	Gas exchange and kernel quality	Silva et al., (2022)
Soil Quality Index (SQI)	0.54–0.75 reported for almond orchards higher values generally indicate better soil conditions	Assessing site suitability and management performance in almond orchards	Miras-Ávalos et al., (2022)

Table 2
Non-exhaustive irrigation recommendations for adult almond orchards based on total seasonal water availability, expressed as a percentage of the full irrigation requirement (IR).

	Phenological stages of almond		
Availability of irrigation water (mm·year^{-1})	*Stage I Vegetative*	*Stage II Kernel-filling*	*Stage III Post-harvest*
600–400	100	65	100
400–300	100	50	75
300–200	75	40	50
< 200	50	50	50

irrigation thresholds. They are intended to provide a general framework for allocating limited seasonal water resources under Mediterranean conditions, acknowledging that cultivar, rootstock, soil and climatic variability strongly condition irrigation decisions.

4. Anatomical traits and crop development as a function of water availability

Almond trees exhibit xeromorphic characteristics that confer an ability to withstand drought conditions (Fereres et al., 1981; Ruiz-Sánchez, 1993). These traits, which influence intrinsic water use efficiency (WUEi)—defined as the ratio between photosynthetic CO_2 assimilation (A_n) and g_s to water vapor, are particularly relevant in regions with limited water availability. The almond tree is considered a highly plastic and adaptable species in relation to water requirements, as demonstrated by its wide cultivation range. Almonds can be grown in arid drylands under rainfed conditions with low planting densities (<100 trees ha^{-1}) and annual rainfall around 300 mm, yielding less than 100 kg of kernel ha^{-1} due to their inherent drought tolerance (Castel and Fereres, 1982; Girona et al., 2005). Conversely, under optimal agronomic conditions, including intensive irrigation practices with volumes up to 9000 m^3 ha^{-1}, almond yields can reach up to 3000 kg of kernel ha^{-1} (Goldhamer and Fereres, 2017).

While almonds were traditionally cultivated under rainfed conditions in some Mediterranean countries, this practice is increasingly abandoned due to poor profitability. Newly established orchards are almost exclusively irrigated, reflecting the well-documented sensitivity of almond yield to water scarcity (Goldhamer and Fereres, 2017).

Under drought or severe water restriction, almond trees undergo a series of phenological, morphological, physiological, and biochemical changes. For instance, at the end of summer, non-irrigated almond trees often shed their leaves earlier, a response believed to reduce canopy size and thus minimize transpirational water loss (Prgomet et al., 2020).

Plant responses to drought typically fall into two major categories: tolerance and avoidance. Tolerance mechanisms include the synthesis of phenolic compounds, protective proteins, proline, osmolyte compounds and specific enzymes that contribute to osmotic adjustment and turgor maintenance during water limitation. Avoidance mechanisms, conversely, involve suppression of growth and developmental processes, inducing a quiescent or dormancy-like state to conserve energy and protect vital structures (Mundree et al., 2002).

4.1. Root system and rootstocks

The root system, largely determined by the rootstock, is a primary driver of almond water acquisition and drought performance. Almond roots can explore deep soil profiles, with water uptake commonly concentrated in the upper 0.5 m but with substantial extraction reported from 0.5 to 1.0 m and occasionally below 1.2 m (Micke, 2005; Koumanov et al., 2006; Liu et al., 2015; Vanella et al., 2022). This vertical plasticity can buffer seasonal water deficits and interacts with management strategies such as partial root-zone drying (Ben-Asher et al., 1994). Under drip deficit irrigation, rooting tends to concentrate within the wetted bulb beneath emitters (Romero et al., 2004), which can increase capture of applied water but may reduce access to deeper reserves when surface layers dry.

Because rootstocks shape root system architecture (depth distribution, lateral exploration and fine-root dynamics), they influence whole-tree hydraulic conductance, vulnerability to hydraulic dysfunction, tolerance to hypoxia, and downstream stomatal regulation under water limitation. A key distinction is between seedling ("franco") and clonal rootstocks, which differ in genetic uniformity, vigour, hydraulic architecture, and drought/hypoxia responses (Rubio-Cabetas et al., 2016; Vahdati et al., 2021). Within seedling rootstocks, almond, peach and plum lineages have been used historically in almond orchards and represent contrasting functional strategies.

Seedling almond rootstocks are traditionally associated with rainfed or strongly water-limited conditions, consistent with deep exploratory rooting and broad edaphic adaptation in dry environments (Rubio-Cabetas et al., 2016; Álvarez et al., 2020). Their limitations are high vigour and genetic heterogeneity (reduced orchard uniformity) and poor suitability to hypoxia-prone sites, where sensitivity to root asphyxia and disease pressure can constrain performance (Wani et al., 2012; Rubio-Cabetas et al., 2016). Peach seedling rootstocks (*Prunus persica*) are historically linked to irrigated systems; they can perform adequately under regular water supply but generally lack the "rainfed" drought-survival profile attributed to almond seedlings, and may be constrained by poor drainage and root-zone stress in fine-textured soils (Rubio-Cabetas et al., 2016; Vahdati et al., 2021). Plum seedling rootstocks and plum selections (e.g., Myrobalan, *Prunus cerasifera*) are primarily relevant where soil aeration is limiting: compared with almond- and peach-based seedlings, plum backgrounds show higher tolerance to heavy soils and hypoxia, but often exhibit lower adaptation to prolonged drought or non-irrigated management and may require frequent irrigation; compatibility issues can also arise depending on cultivar and plum background (Wani et al., 2012; Rubio-Cabetas et al., 2016; Reig et al., 2019).

Modern orchards are dominated by clonal materials, particularly almond × peach and almond × plum hybrids, which differ in root depth distribution, fine-root deployment and tolerance to deficit irrigation versus hypoxia-prone conditions (Rubio-Cabetas et al., 2016; Vahdati et al., 2021). Almond × peach hybrids (e.g., GF-677 and the G×N series such as 'Garnem', 'Felinem' and 'Monegro') are widely used because of high vigour and broad adaptation and are commonly characterized as drought-capable in well-drained soils (Rubio-Cabetas et al., 2016; Vahdati et al., 2021). A consistent constraint, however, is their relatively low tolerance to waterlogging and root-zone hypoxia, which can be agronomically decisive in fine-textured or poorly drained sites (Vahdati et al., 2021). In such contexts, excess irrigation and limited aeration can rapidly impair root metabolism and reduce functional hydraulic supply to the canopy, amplifying water-stress symptoms even when soil water is not limiting.

Almond × plum hybrids and related plum-based clonal materials were developed to mitigate the hypoxia limitation of almond × peach materials and are typically positioned for heavy soils, replant situations and drainage-limited sites (Rubio-Cabetas et al., 2016; Vahdati et al., 2021). Under these conditions, plum-derived materials may tolerate transient waterlogging through root morphological responses and shifts in anaerobic metabolism (Habibi et al., 2023). Their trade-off under deficit irrigation is that plum heritage often corresponds to a shallower, more fibrous rooting pattern and higher dependence on frequent irrigation when topsoil dries rapidly, and graft compatibility remains a practical constraint in some backgrounds (Wani et al., 2012; Rubio-Cabetas et al., 2016).

Within plum-derived stocks, a useful functional refinement is the contrast between vigorous, fast-growing materials and slower-growing or size-controlling backgrounds. These phenotypes may differ in canopy demand and water extraction patterns under deficit irrigation and can show distinct water-status indicators (e.g., Ψ_{stem} and stomatal conductance) across environments and scion combinations (Reig et al., 2022). Importantly, such differences are often site- and scion-dependent; therefore, they are best treated as a framework for classification and hypothesis testing rather than a universal ranking across all conditions.

Dwarfing clonal rootstocks (e.g., Rootpac® series) have been introduced mainly to enable high-density and "super-intensive" orchard designs, where canopy size control and uniformity are central objectives (Rubio-Cabetas et al., 2016; Ben Yahmed et al., 2016). Their relevance to deficit irrigation or drought adaptation should be treated cautiously because these systems are typically managed under full or near-full irrigation, and robust validation under sustained water stress remains limited. Available evidence is largely context-specific: Rootpac-20 has

been associated with more negative Ψ_{stem} and stress symptoms under warm Mediterranean conditions (Ben Yahmed et al., 2016), and controlled experiments indicate more severe drought stress in young grafted plants on Rootpac-20 compared with self-rooted plants, alongside differences in allocation patterns relevant to drought performance (Álvarez et al., 2020). Rootpac-40 may show comparatively better water status than more extreme dwarfing materials in the same environment (Ben Yahmed et al., 2016), but this does not constitute broad validation under deficit irrigation. Accordingly, the current literature does not support presenting any single dwarfing genotype—including R-40—as a validated candidate for water-limited environments in terms of hydraulic performance, Ψ_{stem} dynamics, stomatal behaviour, or yield stability under water shortage; dwarfing rootstocks are most appropriately discussed as a functional category primarily relevant to irrigated high-density systems (Reig et al., 2022). In addition, other low- to moderate-vigour genotypes are also used in practice (e.g., Rootpac-20 and other Rootpac materials such as Rootpac-R), and their performance can vary with scion, soil constraints and irrigation regime (Vahdati et al., 2021; Connell and Milliron, 2024).

Overall, rootstock choice should be explicitly aligned with the dominant constraint: almond-based and almond × peach materials are generally most defensible where soils are well drained and drought/deficit irrigation is the primary stressor, whereas plum-based and almond × plum materials are preferentially positioned where drainage is constrained and hypoxia risk is high, provided compatibility and disease pressures are managed (Wani et al., 2012; Rubio-Cabetas et al., 2016; Vahdati et al., 2021).

4.2. Impact of water availability on shoot development

Shoot development reflects the balance between water supply, carbohydrate availability and reproductive demand. Under adequate water availability, trees sustain high turgor, vigorous shoot growth and bud formation, exploiting morphological plasticity in leaf traits to optimize light interception (Egea et al., 2012). Deep soil water reserves recharged in autumn–winter can partially substitute for early spring irrigation, as most vegetative growth occurs in spring and early summer (Hawker and Buttrose, 1980; Moldero et al., 2021). When water becomes limited, the timing of stress is critical. Spring coincides with intense reproductive effort; if hydraulic constraints limit photosynthesis, carbon availability becomes a bottleneck, and trees may reallocate resources towards root growth at the expense of canopy expansion (Álvarez et al., 2020). Late-season water deficits generally have limited impact on current-season shoot elongation, as most shoot growth has already ceased by late summer. However, the associated reduction in carbon assimilation markedly impairs the replenishment of non-structural carbohydrates (NSC), which are essential for tree maintenance during dormancy, for early cytokinesis in the following season, and for vegetative growth in late winter (Goldhamer and Viveros, 2000). Water stress during hull-split to post-harvest reduces carbohydrate availability and disrupts meristem transitions, lowering the number and quality of floral buds in the following season (Goldhamer and Smith, 1995). Several studies indicate that moderate water stress can accelerate or alter canopy development patterns. Under carbon-limited conditions, trees may transiently prioritize leaf expansion over reproductive investment (Freitas et al., 2023). After recovery from severe mid- to late-season stress, a vigorous post-stress vegetative flush is often observed, especially in light-crop years, which can compete with bud differentiation for assimilates and signaling, amplifying carry-over effects (Saa and Brown, 2014). In contrast, over-irrigation reduces WUEi by raising transpiration without proportional increases in carbon gain (Goldhamer and Fereres, 2017) and favors excessive vegetative growth at the expense of reproductive development. Overall, the evidence supports a management rule: early-season irrigation can be moderately reduced where deep soil reserves are sufficient for the correct leaf functionality and fruit growth, but water status from hull-split to post-harvest should be protected to ensure NSC replenishment and stable return bloom. Quantitative thresholds for "safe" early deficits are still uncertain and likely cultivar- and soil-specific.

4.3. Leaves, canopy, and light interception

Leaf and canopy traits determine how trees balance light capture with water utilization under variable soil moisture. Almond leaves are lanceolate with a thick, waxy cuticle, a xeromorphic combination that reduces cuticular water loss and supports adaptation to Mediterranean climates. Cultivars vary widely in canopy architecture (upright *vs* spreading *vs* prostrate) and leaf morphology (Palasciano and Catalano, 2022), and under well-hydrated conditions they adjust leaf traits to optimize photosynthetic activity throughout the canopy (Egea et al., 2012). When water availability declines, leaf expansion slows, early defoliation increases and productive leaf area is reduced (Romero et al., 2004).

Stomatal and mesophyll traits further modulate gas exchange. Stomatal size (24–30 μm length, 0.5–1 μm pore width) and stomatal density ($\approx$ 98–215 stomata mm^{-2}) show both genetic and environmental variability (Palasciano et al., 2005). Under drought, stomatal density often decreases, interpreted as a structural adjustment to reduce transpirational demand (Camposeo et al., 2011; Hernandez-Santana et al., 2016; Barl et al., 2025), though the magnitude and direction of change differ among genotypes. Higher mesophyll density is associated with lower g_s and A_n, contributing to genotypic differences in WUEi (Tomás et al., 2013; Eichi et al., 2014). At the canopy scale, increasing leaf area index (LAI) enhances light interception and potential carbon gain but accelerates soil water depletion and can constrain late-season productivity under drought (Wu et al., 2019).

These patterns suggest that intermediate canopy vigor is desirable under DI. Moderate-vigor rootstocks such as Root-PAC 40 can reduce excessive vegetative growth and support higher planting densities, potentially improving water-use efficiency at orchard scale, although their performance under Mediterranean drought is not yet well established (Rubio-Cabetas et al., 2024). Cultivars with higher capacity to store and remobilize carbon in woody and leaf tissues gain resilience when photosynthesis is restricted by stomatal closure (Hartmann et al., 2020). While robust functional relationships between LAI, stomatal traits and yield under DI remain to be quantified across climates, current evidence supports breeding and management strategies that avoid overly dense canopies in water-limited environments.

4.4. Flowers and pollination

Reproductive development from bud initiation to bloom is highly sensitive to water status and largely determines yield potential. When water deficits coincide with bud differentiation or flowering, flower number, flower quality and fruit set decline, with immediate reductions in current season yield and carry-over effects on orchard productivity (Girona et al., 2005). Flower size, density and viability generally track plant water status, indicating that water stress can compromise the crop before fruit growth starts. Tolerance to floral water stress varies among cultivars: drought-tolerant genotypes shed fewer flowers and maintain higher fruit set under moderate deficits, whereas sensitive genotypes show pronounced floral abscission. Properly timed RDI can mitigate the impact of moderate water shortages in less critical windows, likely by stabilizing resource allocation and hormonal signaling around bloom (Girona et al., 2005). However, when water stress overlaps with key reproductive phases, including bud initiation and early fruit set, negative effects on return bloom and fruit set are consistently reported (McMichael, 2009).

Water stress during fruit development and pre-dormancy also leaves "memory" effects. Reduced irrigation has been associated with higher tree mortality and long-term productivity losses (Moldero et al., 2022), while drought-induced disruptions in metabolism and reserves during

fruit development can persist into dormancy, altering bud differentiation and bloom quality in the subsequent season (Martinelli et al., 2012). At the organ level, water deficits may impair pistil development, reduce floral organ size, increase abortion and compromise fertilization success (Descamps et al., 2018). Drought during dormancy and ecodormancy can further delay blooming, particularly when stress coincides with or follows bud swell, indicating that winter water status modulates flowering phenology and synchrony with favorable conditions (Zamora, 2020).

Overall, the available evidence supports a clear management implication: water status should be safeguarded from bud initiation through flowering, whereas DI should be confined to later, less sensitive stages. Quantitative thresholds for acceptable stress (e.g., in terms of Ψ_{stem} or % ETc) during reproductive phases remain poorly defined and require phenology-specific studies across cultivars and climates. This stage-specific approach is consistent with the physiological thresholds discussed in Section 5.

4.5. Water availability effects on yield, crop load and kernel quality

Reproductive output in almond is strongly modulated by water availability, with the highest sensitivity typically occurring from fruit set through the rapid fruit growth phase, and a secondary sensitivity during kernel-filling and postharvest reserve replenishment. Water stress immediately after fruit set reduces turgor-driven cell expansion and limits assimilate transport, leading to smaller fruits, lighter kernels and greater crop-load instability (Egea et al., 2009b; Espadafor et al., 2015). When drought is prolonged or severe, the impacts extend beyond the current crop: carbohydrate reserves are depleted and floral induction can be inhibited, compromising both current and subsequent-year yield potential (Goldhamer and Viveros, 2000; Esparza et al., 2001). Conversely, several recent studies indicate that moderate, well-managed deficit irrigation (DI) can maintain yields close to those under full irrigation (FI) while improving selected aspects of kernel quality, although responses remain cultivar-dependent (Gutiérrez-Gordillo et al., 2020a; Lipan et al., 2020a).

Across regions, a broadly consistent relationship has been reported between irrigation volume and productivity, with water productivity (WP) on the order of ~1 kg dry kernels per 5 m^3 of irrigation water. This aligns with irrigated yields of approximately ~3000 kg ha^{-1} at ~1500 mm irrigation in Australia (Wirthensohn, 2020), ~2500 kg ha^{-1} at ~1250 mm in California (Goldhamer and Fereres, 2017), and ~1600–1700 kg ha^{-1} at 250–600 mm in Spain (Miras-Ávalos et al., 2023), noting that total seasonal water supply also includes winter precipitation and soil water storage. In terms of timing, early-season water scarcity before fruit set often has limited impact on final set (Esparza et al., 2001), whereas deficits imposed immediately after set are consistently critical because they restrict photosynthetic assimilation and carbon and nitrogen transport to developing sinks, ultimately reducing fruit growth and yield (Egea et al., 2009b). These patterns support DI strategies that minimize substantial stress from fruit set through the rapid fruit growth period, while allowing greater flexibility later in the season, provided tree water status does not decline to levels that jeopardize postharvest carbohydrate replenishment and subsequent bud formation (Goldhamer and Viveros, 2000; Esparza et al., 2001). Quantitative thresholds remain largely site- and cultivar-specific and are discussed in Section 5 in relation to Ψ_{stem} and fractional ETc.

Beyond yield and size, water availability also modulates kernel composition and nutritional quality. Severe water deficits are frequently associated with reduced kernel size and lower protein and lipid content, whereas controlled moderate stress under DI (e.g., RDI or SDI) can enhance specific quality traits. Lipan et al. (2020b) reported that 'Vairo' almonds under RDI had higher concentrations of sugars and organic acids, increased monounsaturated and polyunsaturated fatty acids (MUFA, PUFA), and an improved oleic/linoleic acid ratio compared with fully irrigated and over-irrigated treatments. In a multi-cultivar evaluation, Gutiérrez-Gordillo et al. (2020a) reported that SDI enhanced kernel biochemical composition in 'Guara', 'Marta' and 'Lauranne', with genotype-dependent responses: total fatty acids increased by 5–9 % across cultivars, while sugars rose markedly in 'Guara' (+46 %) and 'Marta' (+21 %), and organic acids increased particularly in 'Guara' (+17 %) and 'Lauranne' (+10 %). Fatty-acid profiles also shifted under SDI, with 'Marta' showing the greatest MUFA enrichment (+8 %), while 'Lauranne' and 'Guara' exhibited higher PUFA accumulation (+14 % and +18 %, respectively) (Gutiérrez-Gordillo et al., 2020a). These compositional changes have nutritional and functional implications and are consistent with sensory improvements previously documented: Lipan et al. (2019) found that almonds from moderately water-stressed trees received higher consumer acceptance, associated with greater sweetness, enhanced aroma and richer volatile profiles. Overall, the evidence supports moderate DI as a tool to maintain commercially acceptable yields while improving kernel value, provided that stress is carefully timed and controlled and does not compromise reserve dynamics and return bloom (Goldhamer and Viveros, 2000; Esparza et al., 2001).

4.6. Vessels: xylem structure and hydraulic vulnerability in almond

Xylem structure underpins the trade-off between hydraulic efficiency and safety in almond. Larger vessels increase water transport capacity but are more vulnerable to cavitation as soil dries, whereas smaller and more numerous vessels confer greater resistance to embolism at the expense of maximum conductivity (Tyree and Zimmermann, 2002; Cochard et al., 2008; Paudel et al., 2020). Once cavitation occurs, hydraulic conductivity declines and recovery after rewetting may be incomplete, with consequences for long-term WUEi and tree survival (Rockwell et al., 2014).

Marked genotypic differences in xylem hydraulic vulnerability have been documented. The water potential at which 50 % loss of hydraulic conductivity occurs (P_{50}), a standard metric of embolism resistance, varies substantially among almond genotypes and related Prunus species. Anisohydric cultivars such as 'Soleta' and 'Isabelona' exhibit more negative P_{50} values (–3.7 to –3.8 MPa), enabling stomatal conductance and carbon assimilation to be maintained at more negative water potentials. In contrast, isohydric genotypes such as 'Avijor' show higher P_{50} (–2.97 MPa) and close stomata earlier under water deficit (Álvarez-Maldini et al., 2022). Wild relatives can display even greater embolism resistance; for example, *Prunus ramonensis* combines small vessel diameters with thicker pit membranes, resulting in P_{50} values near –3.2 MPa (Paudel et al., 2020). These findings indicate that cultivars and rootstocks with "safer" xylem architectures, smaller vessels, higher vessel density and reinforced pit membranes, are better suited to water-limited environments, albeit with potential trade-offs in growth under non-limiting water. Incorporating anatomical and hydraulic traits (e.g., vessel size distribution, P_{50}) into breeding and selection programmes offers a promising pathway to improve drought resilience in almond.

5. Physiological variables and thresholds to manage irrigation

The growth and productivity of almond trees are closely linked to water availability, as both are influenced by the timing and severity of water deficits. To ensure efficient irrigation management, it is crucial to identify reliable indicators of plant water status that reflect tree physiological responses under variable soil moisture conditions. In this context, several ecophysiological variables are commonly measured to evaluate tree performance, including trunk diameter change, Ψ_{stem} and Ψ_{leaf} (MPa) in both stems and leaves, temperature of the leaf (T_{leaf}), A_n (μmol m^{-2} s^{-1}), and g_s (μmol m^{-2} s^{-1}) (Velazquez-Chavez et al., 2024).

5.1. Plant water potential as an indicator for irrigation management in almond

Plant water potential has long been used in almonds to assess plant water status and support irrigation management (Torrecillas et al., 1988; Girona et al., 1997; Gomes-Laranjo et al., 2006; Meyers et al., 2019). Among the available metrics, Ψ_{stem} is generally preferred to Ψ_{leaf} due to its greater stability and integrative nature (Shackel, 2011; Kisekka et al., 2024). Midday Ψ_{stem} is less affected by short-term atmospheric fluctuations and easier to measure than predawn water potential, making it suitable for routine monitoring at the orchard scale.

Under FI conditions, Ψ_{stem} (Table 3) usually ranges between –0.4 and –1.0 MPa, occasionally declining to –1.5 MPa during periods of high vapor pressure deficit (VPD) without indicating actual water stress (Klein et al., 2001; Espadafor et al., 2017; Fernandes de Oliveira et al., 2023). Sperling et al. (2023) and Conti et al. (2025) reported Ψ_{stem} values around –1.1 MPa in May, decreasing to –1.5 MPa in midsummer and –1.7 MPa late in the season. Midday Ψ_{leaf} (Table 4) follows a similar pattern, ranging from –1.0 to –1.5 MPa, with transient declines to –1.8 MPa even under non-limiting conditions (Torrecillas et al., 1996; Gutiérrez-Gordillo et al., 2023).

As soil water availability declines, both Ψ_{stem} and Ψ_{leaf} decrease in response to increasing water stress. Moderate stress is generally associated with Ψ_{stem} values below –1.7 MPa, while severe stress occurs between –2.6 and –3.0 MPa, depending on cultivar, phenological stage, and environmental conditions (Klein et al., 2001; Sperling et al., 2023). However, absolute Ψ_{stem} values have limited standalone interpretive value, as they are strongly influenced by evaporative demand. Therefore, irrigation scheduling based solely on fixed Ψ_{stem} thresholds can be misleading unless integrated with baseline relationships between Ψ_{stem} and VPD (Goldhamer and Fereres, 2001). In Prunus species, including almond, a well-established midday Ψ_{stem}–VPD baseline has been reported under non-limiting soil moisture conditions, described by the linear relationship $\Psi_{stem} = -0.12 \times VPD - 0.41$ MPa. This baseline implies that fully irrigated almond trees typically exhibit Ψ_{stem} values around −0.5 MPa at VPD ≈ 1 kPa and approximately −1.0 MPa at VPD ≈ 5 kPa, even in the absence of soil water limitation (McCutchan and Shackel, 1992; Shackel, 2011). Such baselines provide the necessary reference against which field Ψ_{stem} measurements should be interpreted, allowing separation of atmospheric effects from true soil water constraints (Shackel, 2011; Shackel et al., 2021). These reference relationships vary with species, cultivar, and measurement conditions and must therefore be explicitly considered when defining irrigation thresholds, including under RDI.

The interpretation of Ψ_{stem} should also account for soil heterogeneity and irrigation method, as localized deficits may not be fully reflected in Ψ_{stem}, particularly under micro-irrigation. Integrating Ψ_{stem} with complementary indicators such as soil water content, canopy temperature, or remote-sensing indices can enhance diagnostic reliability (Vanella et al., 2022). Moreover, varietal tolerance differs substantially: some cultivars maintain yield at Ψ_{stem} values below –2.0 MPa, while others show yield reductions at less negative potentials (Conti et al., 2025; Goldhamer and Viveros, 2000; Sperling et al., 2023).

Across the cultivar comparisons reported in Tables 3 and 4, differences in the seasonal Ψ_{stem} trajectory and the yield response suggest contrasting levels of tolerance to DI among cultivars (e.g., stables yield under moderate deficits in Guara and Lauranne versus greater yield sensitivity reported for cv. Marta under comparable conditions). Although a formal classification is beyond scope of this review, these patterns are consistent with cultivar-specific hydraulic regulation that range from more conservative (isohydric) to less conservative (anisohydric) responses.

Overall, Ψ_{stem} remains one of the most robust physiological indicators for managing irrigation in almond. When interpreted through Ψ_{stem}–VPD baselines and adjusted for cultivar and phenological variability, it provides a reliable basis for balancing water savings with yield stability and long-term orchard performance.

5.2. Leaf gas exchange and photosynthetic regulation under water stress

Almond trees exhibit a broad range of stomatal responses to soil and atmospheric water deficits, which are central to their drought-tolerance strategies (Torrecillas et al., 1996; Fernandes De Oliveira et al., 2023) (Table 5). Stomatal conductance (g_s) is typically one of the first physiological variables to decline under drought, restricting both transpiration and CO_2 diffusion (Torrecillas et al., 1988; Romero et al., 2004). This regulation plays a pivotal role in balancing water conservation and photosynthetic performance. Cultivar behavior differs substantially. Isohydric genotypes such as Guara close stomata early to maintain higher Ψ_{leaf}, thus conserving water but limiting carbon assimilation (Álvarez et al., 2023). Conversely, anisohydric cultivars such as Texas maintain higher g_s values despite decreasing Ψ_{leaf}, sustaining photosynthesis during moderate stress but increasing the risk of hydraulic failure (Tardieu and Simonneau, 1998).

Under well-watered conditions, g_s typically ranges between 0.4 and 0.7 mol m^{-2} s^{-1} prior to kernel-filling, decreasing to 0.25–0.15 mol m^{-2} s^{-1} during and after kernel-filling (June–August), even in FI trees (Romero et al., 2004; Gutiérrez-Gordillo et al., 2019, 2023; Prgomet et al., 2020). Under severe drought, values as low as 0.05–0.09 mol m^{-2} s^{-1} have been reported (Fernandes de Oliveira et al., 2023; Ranjbar et al., 2021). These trends have been consistently confirmed across cultivars and rootstocks in both pot and field conditions.

Because almond exhibits a strong stomatal regulation of photosynthesis, reductions in A_n closely parallel declines in g_s during mild to moderate water stress (Girona et al., 1997; Romero et al., 2006). However, the proportionality between A_n and g_s progressively weakens as drought intensifies, reflecting the increasing contribution of biochemical and photochemical limitations to CO_2 assimilation. These include pigment degradation, reduced Rubisco activity, mesophyll conductance (g_m) decline, and impairment of electron transport (Flexas et al., 2008; Álvarez et al., 2023). Under severe stress, the combined stomatal and biochemical constraints can reduce A_n by 55–70 % (Karimi et al., 2015; Conti et al., 2025).

Field evidence indicates a transition zone where A_n begins to decline disproportionately relative to g_s, marking the onset of metabolic limitation. This threshold typically occurs at $g_s \approx 0.10$–0.15 mol H_2O m^{-2} s^{-1} or $\Psi_{stem} \leq -2.0$ MPa. Meta-analyses by Flexas and Medrano (2002) suggest that reductions in RuBP regeneration and ATP synthesis emerge when g_s approaches 0.15 mol m^{-2} s^{-1}, whereas strong inhibition of photochemistry and Rubisco activity becomes evident below 0.10 mol m^{-2} s^{-1}.

Several studies have reported wide ranges of A_n under different irrigation regimes (Table 6). Sperling et al. (2023) observed a reduction in A_n from approximately 20–12 μmol CO_2 m^{-2} s^{-1} under FI and from 20 to 10 μmol CO_2 m^{-2} s^{-1} under DI. Fernandes de Oliveira et al. (2023) reported a decline from 16 to 4–5 μmol CO_2 m^{-2} s^{-1} under RDI, while Romero et al. (2004) documented values ranging from 14 to 7–9 μmol CO_2 m^{-2} s^{-1} under FI and from 10 to 4 μmol CO_2 m^{-2} s^{-1} under RDI. Under extreme drought, A_n values can drop to 2.4–2.6 μmol CO_2 m^{-2} s^{-1} (Prgomet et al., 2020), at which point photosynthesis becomes predominantly limited by metabolic and oxidative constraints. Overall, these studies show that declines in A_n under deficit irrigation are mainly driven by stomatal limitation at moderate stress levels, whereas biochemical constraints become increasingly important under severe drought. The magnitude of the response depends on stress intensity, duration, and phenological timing, highlighting the need to interpret A_n dynamics within both hydraulic and metabolic frameworks.

The phenological stage further modulates these physiological thresholds. During vegetative growth and early fruit development, well-watered almond trees typically reach A_n of 16–20 μmol CO_2 m^{-2} s^{-1}, whereas during kernel-filling, A_n commonly declines to 8–10 μmol CO_2 m^{-2} s^{-1} even under full irrigation (Klein et al., 2001; Ranjbar et al., 2021;

Table 3
Approximate ranges of stem water potential (Ψ_{stem}, MPa) in almond trees under different irrigation conditions, compiled from previously published studies. The reported values are approximate (~), as they have been estimated from published tables and graphical representations. Unless otherwise specified, the values correspond to midday measurements. When a single value is reported, it represents the mean, whereas ranges indicate the minimum and maximum values observed.

Reference	Plant material	Water conditions (mm)	Ψ_{stem}(MPa)	Yield
Klein et al., (2001)	7-year-old, Nonpareil grafted Nemaguard	**FI:** 675 (1995), 838 (1996), 746 (1997) before the harvest period, plus an additional 178 (1995–1996), 124 (1997) after harvest. During harvest (**August** to late **September**), irrigation was suspended for 18–53 days depending on treatment: **MS** trees received 71–152, while **SS** and **SS2** trees received between 0 and 53	**1995** **FI: July**: −0.7; **August**: −0.7/-1.5; **MS**: **July**: −0.7/-0.8; **August**: −0.8/-1.8; **SS**: **July**: −0.7/-1.5; **August**: −1.5/-2 **1996** **FI: August**: −1/-1.5; **September**: −1/-1.5 **MS**: **August**: −1/-2.25; **September**: −1/-1.8 **SS**: **August**: −1/-2.5; **September**: −1/-1.8 **SS2**: **August**: −1/-2.5; **September**: −2.3/-2.5 **1997** **FI: July**: −1; **August**: −1/-1.5; **September**: −1.5 **MS**: **August**: −1.5/-2.5; **September**: −1.5 **SS**: **July**: −1/-1.2; **August**: −1.5/-2.5 **SS2**: **July**: −1/-1.2; **August**: −1.5/-2.5; **September**: −2.5	**No data**
Fereres and Goldhamer, (2003)	4 years old Price	**CTRL: 100 % ETc,** 899 of water (June–**November** **RDI**: no irrigation from 6 **July**- 19 **August**	**CTRL**: **June**: −0.6/1.1; **July**: −0.8/-1.1; **August**: −0.7/-1.1; **September**: −0.8/-0.1; **October**: −0.8/-1.1; **November**: −0.7/-0.9 **Stress**: **August**: −1.4/-1.9	**No data**
Shackel, (2011)	Nonpareil and Carmel	Three irrigation regimes (**wet**, **medium**, **dry**) for 3 years (1991–1993)	**June**: **WET**: −1.1; **MED**: −1.1; **DRY**: −1.1 **July**: **WET**: −0.9/-1.1; **MED**: −1/-1.3; **DRY**: −1/-1.4 **August**: **WET**: −0.9/-1.1; **MED**: −1.1/-1.2; **DRY**: −1.3/-1.4 **September**: **WET**: −0.9/-1.2; **MED**: −1.2/-1.4; **DRY**: −1.4/-1.7 **October**: **WET:** −0.8/-1; **MED:** −1/-1.3; **DRY:** −1.4/-1.8	RDI maintained or slightly improved yields compared to grower irrigation across 4 years (2001–2004), with up to 50 % water savings and improved hull split uniformity. No yield penalties were observed under well-managed stress conditions
Espadafor et al., (2017)	Guara, grafted GF-677	**ETc: 475** **FI**: 100 %; 489 **MS**: 55 %; 262 **SS**: 40 % of water applied to FI: 188 **RF**: no irrigation	**FI**: −0.8/-1 all season **MS**: **June**: −0.8/-1.1; **July**: −1/-1.4; **August**: −1.1/-1.4; **September**: −0.8/-1 **SS**: **June**: −0.8/-1.1; **July**: −1.1/-1.2; **August**: −1.2/-1.5; **September**: −0.9/-1 **RF1**: **June**: −0.9/-1.2; **July**: −1.4/-1.5; **August**: −1.1/-1.5; **September**: −1/-1.1 **RF2**: **June**: −1/-1.4; **July**: −1.4/-1.5; **August**: −1.1/-1.5; **September**: −1/-1.3 **RF3**: **July**: −1.6/-1.9; **August**: −1.4/-2; **September**: −1.4/-1.5	**No data**
Moldero et al., (2022)	Guara grafted GF-677	**2017** (stress season): **FI**: 764 mm of seasonal irrigation **DI**: 191 (25 % ETc) **RF**: 0 **2018**: 772 applied to all treatments **2019**: 985 mm applied to all treatments	**FI**: **May**: around –1.0 (well hydrated); **June**: stable around –1.0; **July:** slight dip to –1.3 to –1.5; **August:** recovery toward –1.0 to –1.1; **September:** close −1 **DI**: **May:** Similar to FI (~–1.0); **June:** mild decline below –1.0; **July d**rops to –3.3 by end of month; **August:** partial recovery to around –2.0; **September:** close −2 **RF: May:** similar to FI (~–1.0); **June:** sharper decline; **July:** falls to –4.0, with defoliation; **August:** Not measured (defoliated)	A single season of severe deficit or no irrigation caused lasting yield losses. RF trees suffered major dieback, while DI trees survived but needed years to recover. Minimal irrigation is crucial to maintain productivity and avoid long-term damage
Fernandes De Oliveira et al., (2023)	Arr, Cos, Tuo and Tx grafted GF-677	**Returned ETc %** **2020: April-May**: 150 %; **May-June**: 70 %; **June-July**: 55 %; **August-September**: 65 % **2021: April-May**: 170 %; **May-June**: 80 %; **June-July**: 80 %; **August-September**: 70 % **2020**: **April-June**: 175; **July**	**2020** **May**: Tx: −0.4; Arr: −1.1; Cos: −0.8; Tuo: −0.6; **June**: Tx: −1.2; Arr: −1.4; Cos: −1.2; Tuo: −1.3; **July**: Tx: −1.6; Arr: −2; Cos: −1.2;	In 2020, yields were high for all cultivars, with Tx (7.3 kg plant^{-1}) and Arr (6.1 kg plant^{-1}) performing best. Significant yield decreases in 2021.

(*continued on next page*)

Table 3 (*continued*)

Reference	Plant material	Water conditions (mm)	Ψ_{stem}(MPa)	Yield
		September:1972021: **April-June**: 175; **July-September**:320	Tuo: −1.6; **August**: Tx: −1.5; Arr: −2.1; Cos: −1.5; Tuo: −1.4; **September**: Tx: −1.5; Arr: −1.6; Cos: −1.6; Tuo: −1.2; **2021** **June**: Tx: −1.5; Arr: −1.5; Cos: −1.2; Tuo: −1.2; **June-July:** Tx: −1.3; Arr: −1.7; Cos: −1; Tuo: −1; **July**: Tx: −1.3; Arr: −1.9; Cos:-1.2; Tuo: −1.2; **July**: Tx: −1.3; Arr: −1.3; Cos:-1.2; Tuo: −1.2; **July-August**: Tx: −1; Arr: −1.2; Cos: −1; Tuo: −1.2;	
Sperling et al., (2023)	UmElFahem	**2021**:(**FI**): **April**: 125; **May**: 195; **June**: 220; **July**: 260; **August**: 255; **September**: 190; **October**: 150 (**DI**): **April**: 120; **May**: 155; **June**: 120; **July**: 120; **August**: 95; **September**: 70; **October**: 35 (**Adaptive**): **April**: 120; **May**: 170; **June**: 160; **July**: 185; **August**: 150; **September**: 110; **October**: 85 **2022**:(**FI**): **April**: 125; **May**: 190; **June**: 205; **July**: 235; **August**: 230; **September**: 195; **October**: 135 (**DI**): **April**: 100; **May**: 125; **June**: 105; **July**: 105; **August**: 90; **September**: 50; **October**: 30 (**Adaptive**): **April**: 110; **May**: 150; **June**: 155; **July**: 170; **August**: 150; **September**: 120; **October**: 105	**FI**: **April**: −0.9; **May**: −1.1; **June-August**: −1.5; **October**: −1.7 **DI**: **April**: −0.9; **May**: −1.1; **June**: −2.0; **July-August**: −2.3; **August-September**: −2.6 **Adaptive**: **June**: −1.5; **July-September**: −1.9; **October**: −2.1	In 2021, yields were uniform across irrigation treatments. In 2022, 18 % yield reduction and a decrease in average kernel weight with deficit irrigation. Adaptive irrigation yields comparable to full irrigation.

FI: Full Irrigation; MS: moderately stressed; SS: severely stressed; RDI: Regulated deficit irrigation; ETc: Evapotranspiration of the crop; RF: Rainfed; DI: Deficit irrigation; MD: Moderate deficit; SD: Severe deficit; Arr: Arrubia; Coss: Cossu; Tuo: Tuono; Tx: Texas; CTRL: Control; PRD: Partial rootzone drying.

Álvarez-Maldini et al., 2022). This seasonal decline reflects a reduction in sink strength and metabolic demand later in the growing season. Recent findings by Gutiérrez-Gordillo et al. (2023) showed that this phase is characterized by progressive limitations in triose phosphate utilization (TPU) and a downregulation of the maximum rate of electron transport (J_{max}). This supports RuBP regeneration in the Calvin cycle and is consistent with reduced sink activity and lower photoassimilates demand. Consequently, similar g_s or Ψ_{stem} values may correspond to different stress intensities depending on the phenological stage.

Significant genotypic variability also influences gas-exchange dynamics. Isohydric cultivars such as Guara, Ferragnès, and Tuono tend to close stomata rapidly, preserving water status but limiting CO_2 uptake, whereas anisohydric genotypes such as Texas and Filippo Cea sustain higher g_s and A_n under moderate drought, delaying biochemical limitation but increasing vulnerability to hydraulic dysfunction (Tardieu and Simonneau, 1998; Conti et al., 2025). Consequently, the threshold g_s or Ψ_{stem} for a sharp photosynthetic decline varies among cultivars, reflecting distinct water-use strategies.

Complementary insights into the transition from stomatal to biochemical limitation are provided by chlorophyll fluorescence and oxidative markers. In almond leaves, Fv/Fm, Φ_{PSII} and ETR (maximum quantum yield of PSII and effective PSII efficiency, and electron transport rate, respectively) remain stable until g_s falls below ~ 0.10–0.15 mol m^{-2} s^{-1} , beyond which photochemical efficiency declines rapidly (Conti et al., 2025). Moderate drought typically maintains Fv/Fm ≈ 0.80, whereas severe stress reduces it below 0.75, indicating photoinhibition. Concurrent increases in non-photochemical quenching (NPQ) reflect enhanced thermal energy dissipation. At advanced stress levels, surplus excitation energy not used for carbon fixation promotes the formation of reactive oxygen species (ROS) causing oxidative damage to photosynthetic pigments and PSII reaction centers (Mittler, 2017). In almond leaves, drought stress induces a marked upregulation of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX). However, antioxidant activity is tightly linked to the photosynthetic state of the leaf, implying that when oxidative pressure exceeds the plant's detoxification capacity, photosynthetic performance declines (Bakhtiari et al., 2025).

In summary, almond's gas-exchange and photosynthetic dynamics follow a biphasic pattern: an initial phase dominated by stomatal regulation, followed by a phase in which biochemical and oxidative processes constrain assimilation. The magnitude and timing of this transition depend on cultivar, phenological stage, and drought severity. Understanding these physiological thresholds arises great interest for defining irrigation targets and improving the predictive capacity of stress–yield relationships in almond orchards.

Translating physiology into irrigation scheduling in almond requires reading g_s, A_n, and midday Ψ_{stem} as complementary rather than interchangeable signals. Stomatal conductance (g_s) is ideal for detecting incipient stress but is highly responsive to VPD and time of day; Ψ_{stem} integrates whole-tree hydration and filters short-term atmospheric noise, yet may under-represent stress where wetting is localized (drip, heterogeneous soils) and could be less informative on isohydric genotypes; A_n becomes most informative when interpreted alongside g_s to separate predominantly stomatal from emerging biochemical limitation (Fereres and Goldhamer, 2003; Goldhamer and Fereres, 2004; Shackel, 2011; Shackel et al., 2021; Romero et al., 2004; Flexas et al., 2008). Evidence from Mediterranean orchards further indicates that the timing and temporal pattern of water reduction determine how these indicators shift within the reversible physiological domain described in Section 5.2

At a semi-arid site (annual ETo ≈ 1400 mm; rainfall ≈ 540 mm, mainly October–April), season-long moderate deficits (SDI_{75}≈75 % ETc; SDI_{65}≈65 % ETc) applied to 'Guara', 'Marta' and 'Lauranne' resulted in substantial water savings (FI ≈ 770 mm; SDI_{75} ≈ 574 mm; SDI_{65} ≈ 516 mm) without significant yield penalties (Gutiérrez-Gordillo et al., 2023). Net photosynthesis (A_n) remained within typical seasonal ranges across phenological stages; in 'Guara' values around ~17–18 μmol CO_2 m^{-2} s^{-1} were maintained during vegetative growth across FI/SDI treatments, followed by and a predictable decline post-harvest decline (to ~8–11), while 'Lauranne' showed similarly stable values and 'Marta' displayed slightly greater sensitivity late in the season. These outcomes

Table 4
Approximate ranges of leaf water potential (Ψ_{leaf}, MPa) in almond trees under different irrigation conditions, compiled from previously published studies. The reported values are approximate (~) as they have been estimated from published tables and graphical representations. Unless otherwise specified, the values correspond to midday measurements. When a single value is reported, it represents the mean, whereas ranges indicate the minimum and maximum values observed.

Reference	Plant material	Water conditions (mm)	Ψ_{leaf} (MPa)	Yield
Torrecillas et al., (1988)	Six-year-old Garrigues grafted Atocha	**Wet treatment**: daily drip irrigation **Dry treatment**: natural rainfall	**Pre-dawn/midday values** Spring (21 **May**): **WET**: –0.56 / –1.86 MPa **DRY**: –0.93 / –2.19 MPa Summer (18 **July**): **WET**: –0.59 / –2.36 MPa **DRY**: –1.06 / –2.70 MPa Autumn (22 **October**): **WET**: –0.74 / –1.50 MPa **DRY**: –2.03 / –3.28 MPa	**No data**
Torrecillas et al., (1996)	One year-old Garrigues and Ramillete grafted Atocha	**CTRL**: drip irrigated daily for 6 months; the soil matric potential maintained at about −30 kPa **Deficit**: withholding irrigation for 28 days (from 5 June until 3 July). Then plants were irrigated to run off and subsequently were maintained as control for 8 days (until 11 July).	**June-July** **Predawn** Garrigues: **CTRL**: −0.2/-0.3; **Deficit**: −0.2/-0.8 Ramillete: **CTRL**: −0.2/-0.4; **Deficit**: −0.2/-0.98 **Midday** Garrigues: **CTRL**: −0.8/-1.6; **Deficit**: −0.7/-2.39 Ramillete: **CTRL**: −1/-1.8; **Deficit**: −0.6/-2.57	**No data**
Romero et al., (2004)	13-year-old almond Cartagenera grafted 'Franco'	**CTRL**: 100 %, 619.4 **RDI**: **June** to early **August** (kernel-filling stage) = 20 % 457.6	**Predawn** **CTRL**: −0.5; **RDI**: June: −0.5/-1; July: −1.2/-1.8; August: −2/-2.5; September-November: −0.5	Annual kernel yield decreased in RDI, the reduction was not significant (16 % and 4 % in 1999 and 2000, respectively) Increased hull tight percentage in 1999 but not 2000.
Girona et al., (2005)	Ferragnes grafted GF-677	**T-100:** 100 % ETc, 608 **T-130:** 130 % ETc, 746 **T-70:** 65 % Etc, 396 **RDI:** T100, from June to September: 20 % ETc, 236	**Predawn** **1991** **T-100 / T-130**: **June:** –0.2; **July**: −0.3; **August:** -0.5 **T-70**: **June:** –0.2; **July**: −0.4; **August:** –0.6 **RDI**: **June:** –0.2; **July**: −0.6; **August:** –0.1 **1993** **T-100: June:** –0.3; **July**: −0.4; **August:** –0.8 **T-130**: **June:** –0.2; **July**: −0.4; **August:** –0.6 **T-70**: **June:** –0.4; **July**: −0.6; **August:** –1.4 **RDI**: **June:** –0.3; **July**: −0.6; **August:** –1.6	RDI strategy (20 % ETc during kernel-filling) saved ~60 % of irrigation water, with only a 20 % reduction in yield. The decline in productivity under RDI appeared only after prolonged stress (3rd year). RDI is viable in the short-term, but may compromise long-term orchard productivity if not adjusted seasonally.
Egea et al., (2010)	Marta grafted GF-677	**CTRL:** 100 % ETc; 600 **RDI:** 50 % ETc kernel-filling; 332 **PRD70:** 50 % ETc; 358 **PRD50:** 50 % ETc; 256 **PRD30:** 30 % ETc; 168	**Predawn** **2004** **FI:** Apr–May: –0.31; Jun–Aug: –0.41; Sep–Oct: – **RDI:** Apr–May: –0.38; Jun–Aug: –0.63; Sep–Oct: – **PRD70:** Apr–May: –0.34; Jun–Aug: –0.56; Sep–Oct: – **PRD50:** Apr–May: –0.39; Jun–Aug: –0.61; Sep–Oct: – **PRD30:** Apr–May: –0.40; Jun–Aug: –0.73; Sep–Oct: – **2005** **FI:** Apr–May: –0.26; Jun–Aug: –0.37; Sep–Oct: –0.31 **RDI:** Apr–May: –0.26; Jun–Aug: –0.62; Sep–Oct: –0.34 **PRD70:** Apr–May: –0.40; Jun–Aug: –0.60; Sep–Oct:	Over three seasons, almond trees under full irrigation (FI) produced the highest kernel yield (4318 kg ha^{-1}). DI (RDI and PRD) reduced yields proportionally to water applied: PRD70 and RDI (≈60 % of FI water) reduced yield by 11–16 %. PRD50 showed an 18 % reduction, PRD30, the most stressed treatment, showed a 29 % yield loss. Individual kernel weight declined significantly only in PRD30. Kernel fraction remained stable (~30 %) across treatments. Despite lower yields, water productivity increased, reaching + 123 % in PRD30.

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Table 4 (*continued*)

Reference	Plant material	Water conditions (mm)	Ψ_{leaf} (MPa)	Yield
			–0.37 **PRD50:** Apr–May: –0.38; Jun–Aug: –0.69; Sep–Oct: –0.41 **PRD30:** Apr–May: –0.46; Jun–Aug: –0.84; Sep–Oct: –0.47	
Gutierrez-Gordillo et al., 2019	Guara, Marta and Lauranne; grafted on GN15.	**Annual ET_0**: 1400 **Rainfall**: 540 (mainly October to April) **2017: FI**: 750 **150-ETc**: 1250 **RDI65**: 500 **2018: FI**: 850 **150-ETc**: 1300 **RDI65**: 650 **FI:** 100 % ETc **Over-irrigated treatment (150-ETc)**: 150 % ETc **Regulated deficit irrigation (RDI65)**: 100 % ETc, during the kernel-filling stage: 65 % ETc	**2017** **Guara**: **FI**: −1/-2.5; **150-ETc**: −1/-1.5; **RDI65**: −1/-3 **Marta**: **FI**: −1/-2.5; **150-ETc**: −1/-1.6; **RDI65**: −1/-2.8 **Lauranne**: **FI**: −1/-2.7; **150-ETc**: −1/-1.7; **RDI65**: −1/-3.3 **2018** **Guara**: **FI**: −0.6/-1.7; **150-ETc**: −1/-1.4; **RDI65**: −0.6/-1.7 **Marta**: **FI**: −0.7/-2; **150-ETc**: −0.5/-1.9; **RDI65**: −0.6/-2.25 **Lauranne**: **FI**: −0.6/-1.9; **150-ETc**: −0.6/-1.5; **RDI65**: −0.6/-2	Guara and Lauranne showed no significant yield differences across irrigation treatments, indicating good adaptation to moderate water deficits. In contrast, cv. Marta exhibited significantly higher yields under 150 % ETc, suggesting greater sensitivity to drought. Despite reduced water input, RDI65 achieved similar yields to FI in Guara and Lauranne, and the highest IWP across all cultivars, making it an efficient strategy in semi-arid conditions.
Álvarez-Maldini et al., (2022)	Avijor, Isabelona, and Soleta grafted rootpac 20	**WW** **PD**	**Predawn** **CTRL**: Avijor: −0.7; Isabelona: −1; Soleta: −0.95 **Stress**: Avijor –2.93; Isabelona –2.39; Soleta –3.38 **MMV**: Avijor –2.94; Isabelona –2.83; Soleta –3.24	**No data**
Gutierrez-Gordillo et al., 2023	Guara, Marta and Lauranne grafted onto GN15	Vegetative period: **March-May** Kernel-filling: **June-July** Post harvest: **August** **SDI75**: 75 % ETc **SDI65**: 65 % ETc **FI: 100 %** **ETo**: 1400 **Rainfall**: 540 distributed mainly from **October** to **April**. **FI**: 770 **SDI75**: 574 **SDI65**: 516	**Guara** Vegetative stage: **FI:** - 0.7/-1.5; **SD75:** - 0.7/-1.5; **SD65:** - 0.7/-1.5; Kernel-filling: **FI:** −1.5/-1.7; **SD75:** −1.5/-2; **SD65**: −1.5/-2.1; Post-harvest: **FI**: −1.5/-1.7; **SD75**: −1.5/-1.8; **SD65**: −1.5/-1.8; **Marta** Vegetative stage: **FI:** - 0.6/-1.5; **SD75:** - 0.8/-1.5; **SD65:** - 0.78/-1.5; Kernel-filling: **FI:** −1.2/-1.8; **SD75:** −1.3/-1.8; **SD65:** −1.3/-2; Post-harvest: **FI**: −1.4/-1.6; **SD75:** −1.5/-1.7; **SD65:** −1.5/-1.7; **Lauranne** Vegetative stage: **FI** - 0.8/-1.5; **SD75** - 1/-1.5; **SD65** −1/-1.5; Kernel-filling: **FI** −1.5/-1.7; **SD75** −1.5/-2; **SD65** −1.5/-2; Post-harvest: **FI**: −1.5/-1.7; **SD75** −1.6/-2.1; **SD65** −1.6/-2.1;	No significative differences: Moderate water reductions of 25–35 % did not negatively affect yield, indicating that under certain pedoclimatic conditions, almond trees are relatively tolerant to reduced irrigation, especially when applied during phenologically less sensitive stages.

CTRL: Control; RDI: Regulated deficit irrigation; ET_o: Reference evapotranspiration; FI: Full irrigation; ETc: Evapotranspiration of the crop; IWP: irrigation water productivity; WW: Well-watered; PD: Pot desiccation; MMV: Minimum midday values; SDI: Sustained deficit irrigation; DI: Deficit irrigation.

illustrate that, under favorable pedoclimatic conditions, moderate SDI can be kept within the reversible, mostly stomatal-limitation range of water stress without compromising production. When phenology is explicitly considered, targeted RDI consistently preserves performance. In the same environment, a RDI treatment limiting irrigation to ~65 % ETc only during kernel-filling matched FI yields and delivered the highest irrigation water productivity across cultivars, whereas over-irrigation (150 % ETc) conferred no benefit for 'Guara' and 'Lauranne' but improved the yield of the more sensitive 'Marta' (Gutiérrez-Gordillo et al., 2019). Seasonal midday gas-exchange

Table 5
Approximate ranges of stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) in almond trees under different irrigation conditions, compiled from previously published studies. The reported values are approximate (~) as they have been estimated from published tables and graphical representations. Unless otherwise specified, the values correspond to midday measurements. When a single value is reported, it represents the mean, whereas ranges indicate the minimum and maximum values observed.

Reference	Plant material	Water conditions (mm)	g_s (mol H_2O m^{-2} s^{-1})	Yields
Torrecillas et al., (1988)	Six-year-old Garrigues grafted Atocha	**Wet treatment**: daily drip irrigation **Dry treatment**: natural rainfall	**Spring**: **WET**: 0.38/0.095; **DRY**:0.24/0.07 **Summer**: **WET**: 0.28/0.14; **DRY**:0.16/0.05 **Autumn**: **WET**: 0.24/0.09; **DRY**:0.16/0.05	**No data**
Torrecillas et al., (1996)	One year-old scions Garrigues and Ramillete grafted Atocha	**CTRL**: drip irrigated daily for 6 months; the soil matric potential maintained at about −30 kPa; **Deficit**: withholding irrigation for 28 days (from 5 June until 3 July). Then plants were irrigated to run off and subsequently were maintained as control for 8 days (until 11 July).	**Midday**: **Garrigues**: **CTRL**: 0.4/0.28; **Deficit**: 0.35/0.1 **Ramillete**: **CTRL**: 0.4/0.3; **Deficit**: 0.4/0.08	**No data**
Klein et al., (2001)	7-year-old, Nonpareil grafted Nemaguard	**FI:** 675 (1995), 838 (1996), and 746 (1997) before the harvest period, plus an additional 178 (1995–1996) and 124 (1997) after harvest. During harvest (**August** to late **September**), irrigation was suspended for 18–53 days depending on treatment: **MS** trees received 71–152, while **SS** and **SS2** trees received between 0 and 53	**Midday** **1995** FI: **July**: 0.3/0.2; **August**: 0.3/0.18; **September**: 0.18 **MS**: **July**: 0.3/0.2; **August**: 0.3/0.1; **SS: July**: 0.3/0.25; **August**: 0.2/0.1; **September**: 0.12	**No data**
Romero et al., (2004)	13-year-old almond Cartagenera grafted 'Franco'	**CTRL**: 100 %, 619.4 **RDI**: **June** to early **August** (kernel-filling stage) = 20 % 457.6	**CTRL**: **June**: 0.15; **July**: 0.15/0.10; **August**: 0.17/0.1; **September**: 0.13/0.1 **RDI**: **June**:0.13/0.08; **July**: 0.06/0.04; **August**: 0.13/0.06; **September-November**:0.17/0.06	Annual kernel yield decreased in RDI, the reduction was not significant (16 % and 4 % in 1999 and 2000, respectively) Increased hull tight percentage in 1999 but not 2000.
Gutierrez-Gordillo et al., 2019	Guara, Marta and Lauranne; grafted on GN15	**Annual ET_0**: 1400 **Rainfall**: 540 (mainly October to April) **2017: FI**: 750 **150-ETc**: 1250 **RDI65**: 500 **2018: FI**: 850 **150-ETc**: 1300 **RDI65**: 650 **FI:** 100 % ETc **Over-irrigated treatment (150-ETc)**: 150 % ETc **RDI65**: 100 % ETc, during the kernel-filling stage: 65 % ETc	**2017** **Guara**: **FI**: 0.18/0.06; **150-ETc**: 0.18/0.06; **RDI65**: 0.18/0.07 **Marta**: **FI**: 0.15/0.05; **150-ETc**: 0.15/0.07; **RDI65**: 0.16/0.07 **Lauranne**: **FI:** 0.15/0.05; **150-ETc**: 0.16/0.05; **RDI65**: 0.16/0.06 **2018** **Guara: FI:** 0.27/0.1; **150-ETc:** 0.21/0.1; **RDI65:** 0.28/0.1 **Marta: FI:** 0.21/0.09; **150-ETc:** 0.21/0.1; **RDI65:** 0.23/0.07 **Lauranne: FI:** 0.23/0.05; **150-ETc:** 0.22/0.075; **RDI65:** 0.23/0.75	Guara and Lauranne showed no significant yield differences across irrigation treatments, indicating good adaptation to moderate water deficits. In contrast, cv. Marta exhibited significantly higher yields under 150 % ETc, suggesting greater sensitivity to drought. Despite reduced water input, RDI65 achieved similar yields to FI in Guara and Lauranne, and the highest IWP across all cultivars, making it an efficient strategy in semi-arid conditions
Prgomet et al., (2020)	Ferragnes grafted on GF-677	**T100 – FI (100 % ETc)** 310 **T70 – SDI (70 % ETc)** 206 **T35 – SDI (35 % ETc)** 103 **T100–35 – RDI (100 % ETc reduced to 35 % during kernel-filling)** 173 **T0 – RF**	**July** **2015**: **T100**: 0.12; **T70**: 0.14; **T35**: 0.08; T100–35: 0.11; **T0**: 0.02 **2016**: **T100**: 0.15; **T70**: 0.14; T35: 0.10; **T100–35**: 0.14; **T0**: 0.01 **August** **2015**: **T100**: 0.10; **T70**: 0.10; **T35**: 0.10; **T100–35**: 0.10; **T0**: 0.05 **2016**: **T100**: 0.12; **T70**: 0.15; **T35**: 0.12; **T100–35**: 0.10; **T0**: 0.02 **September** **2015**: **T100**: 0.08; **T70**: 0.09; **T35**: 0.09; **T100–35**: 0.08; **T0**: 0.02 **2016**: **T100**: 0.15; **T70**: 0.14; **T35**: 0.11; **T100–35**: 0.1; **T0**: 0.04	2015 (favourable year) Highest yields observed under T70, T35, and even T0, exceeding T100. 2016 (climatically adverse year) Only T100 maintained high yield (2.63 kg $tree^{-1}$). T0 experienced a yield drop of ~67 % compared to T100. T35 and T70 also underperformed compared to T100. T100–35 Yield was comparable to T100 in both years, despite receiving 44 % less water.
Ranjbar et al., (2021)	Su, Tx, Mr, Sh and K, rootstocks: GF677, GN22 and seedling bitter almond No.32	Four levels of predawn soil water potential: none (- 0.1 MPa), moderate (- 0.7 MPa), severe (- 1.1 MPa) and very severe (-1.8 MPa) drought stress	**CTRL**: **Max**: Sh on GN-22: 0.247; **Min**: Mr on No.32: 0.225 **MS**: **Max**: Sh on GN-22: 0.247; **Min**: Sh, on, K on No.32: 0.197 **SS**: **Max**: Sh on GF677: 0.207; **Min**: K on No.32: 0.04	**No data**

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Table 5 (*continued*)

Reference	Plant material	Water conditions (mm)	g_s (mol H_2O m^{-2} s^{-1})	Yields
			VS: **Max**: M on GF677: 0.11; **Min**: Tx on GN-22: 0.01	
Álvarez-Maldini et al., (2022)	Avijor, Isabelona, and Soleta grafted rootpac 20	**WW** **PD**	**CTRL**: **Avijor** 0.374; **Isabelona** 0.530; **Soleta** 0.531**Stress**: **Avijor** 0.051; **Isabelona** 0.042; **Soleta** 0.054	**No data**
Fernades De Oliveira et al., 2023	Arr, Cos, Tuo and Tx grafted on GF-677	**Returned ETc %** **2020: April-May**: 150 %; **May-June**: 70 %; **June-July**: 55 %; **August-September**: 65 % **2021: April-May**: 170 %; **May-June**: 80 %; **June-July**: 80 %; **August-September**: 70 % **2020**: **April-June**: 175; **July-September**:197 **2021**: **April-June**: 175; **July-September**:320	**Tx**: 0.7/0.05; **Arr**: 0.65/0.05; **Coss**: 0.4/0.05; **Tuo**: 0.5/0.05	In 2020, yields were high for all cultivars, with Tx (7.3 kg $plant^{-1}$) and Arr (6.1 kg $plant^{-1}$) performing best. Significant yield decreases in 2021.
Gutierrez-Gordillo et al., 2023	Guara, Marta and Lauranne grafted onto GN15	Vegetative period: **March-May** Kernel-filling: **June-July** Post harvest: **August** **SDI75**: 75 % ETc **SDI65**: 65 % ETc **FI:** 100 % ETc **ETo**: 1400 **Rainfall**: 540 distributed mainly from October to April. **FI**: 770 **SDI75**: 574 **SDI65**: 516	**Guara** **Vegetative stage**: **FI**: 0.2; **SD75**: 0.21; **SD65**: 0.3; **Kernel-filling**: **FI:** 0.2; **SD75:** 0.21; **SD65:** 0.3; **Post-harvest**: **FI**: 0.19; **SD75:** 0.19; **SD65:** 0.19; **Marta** **Vegetative stage**: **FI:** 0.21; **SD75:** 0.21; **SD65:** 0.21; **Kernel-filling**: **FI:** 0.17; **SD75:** 0.2; **SD65:** 0.3; **Post-harvest**: **FI**: 0.17; **SD75:** 0.16; **SD65:** 0.16; **Lauranne** **Vegetative stage**: **FI:** 0.21; **SD75:** 0.22; **SD65:** 0.31; **Kernel-filling**: **FI:** 0.17; **SD75:** 0.17; **SD65:** 0.31; **Post-harvest**: **FI**: 0.78; **SD75:** 0.6; **SD65:** 0.82	No significative differences: Moderate water reductions of 25–35 % did not negatively affect yield, indicating that under certain pedoclimatic conditions, almond trees are relatively tolerant to reduced irrigation, especially when applied during phenologically less sensitive stages.
Sperling et al., (2023)	UmElFahem	**2021**: (**FI**): **April**: 125; **May**: 195; **June**: 220; **July**: 260; **August**: 255; **September**: 190; **October**: 150 (**DI**): **April**: 120; **May**: 155; **June**: 120; **July**: 120; **August**: 95; **September**: 70; **October**: 35 (**Adaptive**): **April**: 120; **May**: 170; **June**: 160; **July**: 185; **August**: 150; **September**: 110; **October**: 85 **2022**:(**FI**): **April**: 125; **May**: 190; **June**: 205; **July**: 235; **August**: 230; **September**: 195; **October**: 135 (**DI**): **April**: 100; **May**: 125; **June**: 105; **July**: 105; **August**: 90; **September**: 50; **October**: 30 (**Adaptive**): **April**: 110; **May**: 150; **June**: 155; **July**: 170; **August**: 150; **September**: 120; **October**: 105	2021: **FI**: 0.4/0.2; **DI**: 0.3/0.07; **Adaptive**: 0.4/0.2; 2022: **FI**: 0.6/0.19; **DI**: 0.6/0.1; **Adaptive**: 0.6/0.1	In 2021, yields were uniform across irrigation treatments. In 2022, 18 % yield reduction and a decrease in average kernel weight with DI. Adaptive irrigation yields comparable to full irrigation.

CTRL: Control; FI: Full irrigation; MS: moderately stressed; SS: severely stressed; RDI: Regulated deficit irrigation; ETc: Evapotranspiration of the crop; ET_o: Reference evapotranspiration; IWP: irrigation water productivity; SDI: Sustained deficit irrigation; RF: Rainfed; Su; Supernova; Arr: Arrubia; Coss: Cossu; Tuo: Tuono; Tx: Texas; Mr: Marcona; Sh: Shokoufeh; K: K13–40; WW: Well-watered; PD: Pot desiccation; DI: Deficit irrigation.

measurements from those trials indicate that well-timed RDI can maintain stomatal conductance at levels comparable to FI during the kernel-filling period, despite lower irrigation inputs. This pattern is consistent with an effective limitation of cumulative stress within the deficit window and a rapid recovery once full irrigation is restored. Year-type effects are critical for uniform deficits: in Prgomet et al. (2020) on 'Ferragnès'/GF-677, severe season-long cuts (70 % or 35 % ETc) performed comparably or better than FI in a favorable year, but in an adverse year only FI sustained high yield; by contrast, a RDI treatment (35 % ETc confined to kernel-filling) produced FI-level yields in both years with ~44 % less water, underscoring the robustness of concentrating moderate stress in less-sensitive windows and allowing recovery outside them Romero et al. (2004) similarly reported non-significant annual yield penalties (≈4–16 %) and occasional shifts in hull tightness under RDI applied during low-sensitivity phenological stages, consistent with in-window, reversible stomatal limitation and limited carry-over effects.

Although PRD remains comparatively less studied in almond, the available field evidence indicates that PRD can improve leaf-level water-use efficiency and yield at less negative afternoon Ψ_{stem} than RDI when seasonal water inputs are equal, consistent with partial stomatal closure induced by root signaling (Egea et al., 2011). At the whole-season scale, PRD and RDI generally deliver similar yields when total applied water is equivalent, with fruit growth and quality showing no consistent PRD advantage and overall water productivity rising as deficit increases (Egea et al., 2009; Egea et al., 2010); any small differences tend to

Table 6
Approximate ranges of photosynthesis (A_n, μmol CO_2 m^{-2} s^{-1}) in almond trees under different irrigation conditions, compiled from previously published studies. The reported values are approximate (~) as they have been estimated from published tables and graphical representations. Unless otherwise specified, the values correspond to midday measurements. When a single value is reported, it represents the mean, whereas ranges indicate the minimum and maximum values observed.

Reference	Plant material	Water conditions (mm)	A_n (μmol CO_2 m^{-2} s^{-1})	Yields
Klein et al., (2001)	7-year-old, Nonpareil grafted Nemaguard	**FI:** 675 (1995), 838 (1996), and 746 (1997) before the harvest period, plus an additional 178 (1995–1996) and 124 (1997) after harvest. During harvest (August to late September), irrigation was suspended for 18–53 days depending on treatment: **MS:** 71–152, while **SS** and **SS2** trees received between 0 and 53	**Midday** **1995** **FI:** July: 14/10; August: 11/8; September: 8/4 **MS**: July: 10; August: 10/6; **SS**: July: 12/9; August: 5; September: 5/3.2	**No data**
Romero et al., (2004)	13-year-old almond Cartagenera grafted 'Franco'	**CTRL**: 100 %, 619.4 **RDI**: **June** to early **August** (kernel-filling stage) = 20 % 457.6	**CTRL**: June: 14/9; July: 10/7; August: 11/7; September: 9/7 **RDI**: June: 10/7; July: 6/4; August: 9/4; September 10/4	Annual kernel yield decreased in RDI, the reduction was not significant (16 % and 4 % in 1999 and 2000, respectively) Increased hull tight percentage in 1999 but not 2000.
Prgomet et al., (2020)	Ferragnes grafted on GF-677	**T100 – FI (100 % ETc)** 310 **T70 – SDI (70 % ETc)** 206 **T35 – SDI (35 % ETc)** 103 **T100–35 – RDI (100 % ETc reduced to 35 % during kernel-filling)** 173 **T0 – RF**	**July** **2015**: **T100**: 8; **T70**: 7; **T35**: 6; **T100-35**: 7; **T0**: 2 **2016**: **T100**: 10; **T70**: 9; **T35**: 8; **T100-35**: 10; **T0**: 1 **August** **2015**: **T100**:8; **T70**:8; **T35**:8; **T100-35**: 8; **T0**: 4 **2016**: **T100**:8; **T70**:9; **T35**: 8; **T100-35**:7; **T0**:1,5 **September** **2015**: **T100**: 7; **T70**: 8; **T35**: 8; **T100-35**: 6; **T0**: 3 **2016**: **T100**: 10; **T70**: 9; **T35**: 8; **T100–35**: 10; **T0:** 4	2015 (favourable year) Highest yields observed under T70, T35, and even T0, exceeding T100. 2016 (climatically adverse year) Only T100 maintained high yield (2.63 kg $tree^{-1}$). T0 experienced a yield drop of ~67 % compared to T100. T35 and T70 also underperformed compared to T100. T100–35 Yield was comparable to T100 in both years, despite receiving 44 % less water.
Ranjbar et al., (2021)	Su, Tx, Mr, Sh and K, rootstocks: GF677, GN22 and seedling bitter almond No.32	Four levels of predawn soil water potential: none (- 0.1 MPa), **MS** (- 0.7 MPa), **SS** (- 1.1 MPa) and **SS2** (-1.8 MPa) drought stress	**CTRL**: **Max**: on GN-22: 14.14; **Min**: Tx on No.32: 12.99 **MS**: **Max**: K on GF677: 13.97; **Min**: Tx on GN22: 11.13 **SS**: **Max**: Sh on GF677: 11.95; **Min**: on No.32: 2.25 **SS2**: **Max**: M on GF677: 7.97 **Min**: K on No.32: 0.16	**No data**
Álvarez-Maldini et al., (2022)	Avijor, Isabelona, and Soleta grafted rootpac 20	**WW** **PD**	**CTRL**: **Avijor**: 12.24; **Isabelona**: 11.24; **Soleta**: 13.22 **Stress**: **Avijor**: 8.44; **Isabelona**: 6.16; **Soleta**: 7.26	**No data**
Fernades De Oliveira et al., 2023	Arrubia, Cossu, Tuono and Tx grafted on GF-677	**Returned ETc %** **2020: April-May**: 150 %; **May-June**: 70 %; **June-July**: 55 %; **August-September**: 65 % **2021: April-May**: 170 %; **May-June**: 80 %; **June-July**: 80 %; **August-September**: 70 % **2020**: **April-June**: 175; **July-September**:197 **2021**: **April-June**: 175; **July-September**:320	**Tx**: 16/8; **Arrubia**: 16/5; **Cossu**: 16/4; **Tuono**: 17/7	In 2020, yields were high for all cultivars, with Tx (7.3 kg $plant^{-1}$) and Arrubia (6.1 kg $plant^{-1}$) performing best. Significant yield decreases in 2021.
Gutierrez-Gordillo et al., 2023	Guara, Marta and Lauranne grafted onto GN15	Vegetative period: **March-May** Kernel-filling: **June-July** Post harvest: **August** **SDI75**: 75 % ETc **SDI65**: 65 % ETc **FI:** 100 % ETc **ETo**: 1400 **Rainfall**: 540 distributed mainly from October	**Guara** Vegetative stage: **FI**: 17; **SD75**: 18; **SD65**: 18 Kernel-filling: FI: 16; **SD75:** 17; **SD65:** 18 Post-harvest: **FI**: 11; **SD75:** 10; **SD65:** 8	No significant differences: Moderate water reductions of 25–35 % did not negatively affect yield, indicating that under certain pedoclimatic conditions, almond trees are relatively tolerant to reduced irrigation, especially when applied during penologically fewer sensitive stages

(*continued on next page*)

Table 6 (*continued*)

Reference	Plant material	Water conditions (mm)	A_n (μmol CO_2 m^{-2} s^{-1})	Yields
		to April. **FI**: 770 **SDI75**: 574 **SDI65**: 516	**Marta** Vegetative stage: **FI:** 17; **SD75**: 15; **SD65**: 17 Kernel-filling: FI 14; **SD75:** 15; **SD65:** 17 Post-harvest: **FI**: 13; **SD75:** 11; **SD65:** 10 **Lauranne** Vegetative stage: **FI:** 18; **SD75:** 18; **SD65:** 18 Kernel-filling: FI 14; **SD75**: 15; **SD65**: 16 Post-harvest: **FI**: 12; **SD75:** 12; **SD65:** 13	
Sperling et al., (2023)	UmElFahem	**2021**: (**Deficit**): **April**: 120; **May**: 155; **June**: 120; **July**: 120; **August**: 95; **September**: 70; **October**: 35 (**Full**): **April**: 125; **May**: 195; **June**: 220; July: 260; **August**: 255; **September**: 190; **October**: 150 (**Adaptive**): **April**: 120; **May**: 170; **June**: 160; **July**: 185; **August**: 150; **September**: 110; **October**: 85 **2022**:(**Deficit**): **April**: 100; **May**: 125; **June**: 105; **July**: 105; **August**: 90; **September**: 50; **October**: 30 (**Full**): **April**: 125; **May**: 190; **June**: 205; **July**: 235; **August**: 230; **September**: 195; **October**: 135 (**Adaptive**): **April**: 110; **May**: 150; **June**: 155; **July**: 170; **August**: 150; **September**: 120; **October**: 105	2021: **Full**: 20/12; **Deficit**: 20/10; **Adaptive**: 20/11 2022: **Full**: 20/13; **Deficit**: 20/10; **Adaptive**: 20/11	In 2021, yields were uniform across irrigation treatments. In 2022, 18 % yield reduction and a decrease in average kernel weight with DI. Adaptive irrigation yields comparable to full irrigation.

CTRL: Control; FI: Full irrigation; MS: moderately stressed; SS: severely stressed; RDI: Regulated deficit irrigation; ETc: Evapotranspiration of the crop; ETo: Reference evapotranspiration; IWP: irrigation water productivity; SDI: Sustained deficit irrigation; RF: Rainfed; Su; Supernova; Tx: Texas; Mr: Marcona; Sh: Shokoufeh; K: K13–40; WW: Well-watered; PD: Pot desiccation; DI: Deficit irrigation.

depend on soil texture and switching frequency rather than the technique per se (Adu et al., 2018).

Transpiration responds dynamically to the balance between soil moisture and atmospheric demand. Under high VPD, g_s reduction limits transpiration and leaf cooling, increasing T_{leaf} and inducing thermal stress (Karimi et al., 2015; López-López et al., 2018). Stomatal closure under water stress promotes photorespiration, which protects the plant but limits net carbon gain (Losciale et al., 2023). At the leaf scale, transpiration rates can fall from 8 mmol H_2O m^{-2} s^{-1} (FI) to < 0.5 mmol m^{-2} s^{-1} under severe drought (Ranjbar et al., 2021). Rootstock choice affects this response: GN22 reduced transpiration by ~20 % under mild stress, compared to 40 % in 'GF677'-grafted trees. At the canopy level, cultivars such as Arrubia show consistently lower transpiration and Ψ_{stem} than Texas under commercial irrigation, without yield penalties (Fernades De Oliveira et al., 2023). Additionally, orchard architecture impacts whole-tree gas exchange: high-density hedgerow systems improved water productivity and reduced transpiration compared to traditional open-vase designs (Quintanilla-Albornoz et al., 2024).

6. Sensor-based indicators and biophysical proxies of tree water status

Beyond primary ecophysiological responses, several sensor-based approaches have been developed to capture indirect biophysical or structural signals associated with tree water stress. Canopy and leaf temperature, sap flow and trunk diameter variations do not represent physiological mechanisms per se, but rather integrative proxies that reflect the downstream consequences of plant water status regulation. When properly interpreted and combined with physiological indicators such as Ψ_{stem}, g_s or A_n, these tools can support irrigation scheduling and improve the temporal resolution of water-stress detection at the orchard scale.

6.1. Canopy and leaf temperature

Under water stress, stomatal closure reduces transpiration, causing T_{leaf} to approach or exceed air temperature (Hsiao, 1973). This increase in canopy temperature (Tc) can therefore serve as an indirect indicator of g_s and plant water status (Idso et al., 1977; Jackson et al., 1981). Although canopy temperature does not constitute a physiological response per se, it integrates the combined effects of stomatal regulation and atmospheric demand, making it a useful indicator of tree water status under field conditions.

In almond orchards, infrared thermal sensing using either thermoradiometers or thermal cameras has gained attention over the last decade as a non-invasive tool for monitoring tree water status, especially under DI regimes (Gutiérrez-Gordillo et al., 2020b). In this sense, many authors have stated that the Crop water stress index (CWSI) is a reliable tree water status indicator and have reported, for the major almond cultivars, threshold values related to the midday Ψ_{stem}, the reference indicator for almond trees' irrigation management (Table 7).

Apart from water status assessment, thermal indices have been successfully used for estimating yield in almond trees based on the strong relationship between transpiration and production. Thus, Gonzalez-Dugo et al. (2019) and Bellvert et al. (2021) reported for the cultivars Guara and Marinada robust correlations between almond yield and seasonal CWSI.

Recent advancements have also demonstrated the potential of high-resolution UAV thermal imaging for almond phenotyping and water

Table 7
Values of Crop Water Status Index (CWSI) reported for different almond cultivars and scenarios of water deficit.

Cultivar	Location	Tree Water Status			Reference
		No Water Stress	*Mild Water Stress*	*Severe Water Stress*	
		Ψ_{stem} > -1.0 Mpa*	Ψ_{stem} from −1.0 MPa to −1.5 MPa*	Ψ_{stem} from −1.5 MPa to −2.0 MPa*	
		CWSI	CWSI	CWSI	
Carmel	Madera, CA, USA	< 0	0 – 0.58	0.58–0.73	Bellvert et al., (2018)
Guara	Seville, Spain	-0.17 ± 0.08	0.27 ± 0.07		Gutierrez-Gordillo et al., 2021
Guara	Cordoba, Spain	< 0	0–0.42	0.42–0.58	Gonzalez-Dugo et al., (2019)
Lauranne	Seville, Spain	-0.18 ± 0.11	0.21 ± 0.05		Gutierrez-Gordillo et al., 2021
Lauranne	Albacete, Spain	0–0.23	0.23–0.47	0.47–0.7	Sánchez-Virosta et al., (2025)
Marcona	Seville, Spain	-0.18 ± 0.08	0.12 ± 0.05		Gutierrez-Gordillo et al., 2021
Marta	Seville, Spain	-0.15 ± 0.09	0.19 ± 0.07		Gutierrez-Gordillo et al., 2021
Nonpareil	Arbuckle, CA, USA	0–0.33	0.33–0.5	0.5–0.66	Drechsler et al., (2019)

* Indicative Ψs_{tem} thresholds; specific values may differ among cultivars due to genotypic variation in drought response

management. Sapkota et al. (2025) used aerial CWSI to delineate irrigation management zones more effectively than normalized difference vegetation index (NDVI) or ETc alone. Bellvert et al. (2021) employed UAV-derived actual (ETa) and potential (ETp) evapotranspiration to compute an alternative CWSI formulation (1-ETa/ETp), identifying drought-tolerant rootstocks. Similarly, Gutiérrez-Gordillo et al. (2021) confirmed the reliability of UAV-based CWSI but noted that Ψ_{stem} remains more sensitive during the initial stages of water stress.

Another innovative water stress indicator for almond trees is the thermal variability within the canopy. González-Dugo et al. (2012) showed that the standard deviation of Tc within the crown correlated with water status in almond trees. This intra-crown variability increased under moderate stress and decreased at extreme stress levels, suggesting its utility for early stress detection when mean Tc remains unchanged.

6.2. Sap flow

Sap flow techniques have emerged as valuable tools for assessing water use and transpiration in almond trees, providing crucial insights into tree water status and irrigation management. These methods offer continuous, non-destructive measurements of water movement within the tree, allowing researchers and growers to monitor plant water use with high temporal resolution (Smith and Allen, 1996; Fernández et al., 2006; López-Bernal et al., 2010; Fuentes et al., 2013; Vice, 2021; Quintanilla-Albornoz et al., 2024). However, there are also limitations to consider, including calibration requirements, potential measurement errors, and scaling challenges (Vice, 2021). Operationally, sap flow is most useful when linked to plant water status; in almond, the "onset" of transpiration decline typically appears as a pattern change in the diurnal curve and coincides with Ψ_{stem} around –1.1 to –1.2 MPa, providing an early trigger for irrigation adjustment (Fuentes et al., 2013; González-Dugo et al., 2020; Quintanilla-Albornoz et al., 2023)

Most almond studies employ heat-pulse systems, (e.g., CHP/HRM), often calibrated against lysimeters or water balance to ensure accuracy at low flows and at night (Fernández et al., 2006; López-Bernal et al., 2010; Espadafor et al., 2015; Vice, 2021)

Sap flow monitoring has been applied to support irrigation scheduling in almond orchards, particularly under DI scenarios (Moldero, et al., 2021; Quintanilla-Albornoz, et al., 2024). In general:

- FI: trees under FI typically exhibit high and stable sap flow rates, reflecting optimal transpiration and water status (Moldero et al., 2021). These conditions promote sustained physiological activity and maximize photosynthesis and carbon assimilation, which are critical for fruit development and yield formation (Goldhamer and Fereres, 2001).
- DI: under moderate to severe DI, sap flow rates decline, indicating reduced transpiration and water uptake (Fernández et al., 2006; Shackel et al., 2011). This response is linked to stomatal closure and decreased g_s, which conserves water but limits carbon fixation, potentially affecting nut size, kernel weight, and overall productivity (Goldhamer and Fereres, 2001).
- Prolonged Water Stress: chronic water deficits can cause drastic reductions in sap flow, leading to hydraulic failure, cavitation, and tissue damage (Martínez-Vilalta et al., 2002). Prolonged stress may induce canopy dieback, compromise root vitality, and reduce orchard lifespan, necessitating precise irrigation adjustments to prevent irreversible damage.

By monitoring transpiration dynamics in real time, sap flow can enable early detection of water stress and support irrigation adjustments before visible symptoms appear (Jones, 2004; Vice, 2021; Quintanilla-Albornoz et al., 2024). In practice, "pattern-based" triggers, such as sustained flattening of the morning peak or a drop of daily flow relative to a well-watered baseline, have proven robust across FI/RDI contrasts and training systems (Jones, 2004; Fuentes et al., 2013; Quintanilla-Albornoz et al., 2023).

Lopez-Lopez, et al. (2018) reported that sap flow measurements calibrated with lysimeters captured marked interannual variability in canopy conductance, with higher crop load increasing daily transpiration in cv. Guara.

One of the most promising applications of sap flow monitoring is pattern recognition for early stress detection. Changes in diurnal sap flow patterns can precede visible drought symptoms, allowing growers to act before physiological damage occurs (Quintanilla-Albornoz et al., 2024). For example:

- Reduced Morning Surge: A smaller morning sap flow peak suggests restricted water uptake, possibly indicating early water stress (Shackel et al., 2011).
- Flattened Diurnal Curve: Under severe stress, the typical bell-shaped diurnal sap flow curve flattens, reflecting limited transpiration throughout the day (Fernández et al., 2006).
- Delayed Peak Flow Time: A delayed sap flow peak may signal impaired root water extraction or reduced hydraulic conductivity, requiring immediate irrigation adjustments (Jones, 2004).

Quintanilla-Albornoz, et al. (2023) compared estimates of almond crop (cv. Marinada) transpiration under three different production systems and irrigation treatments using sap flow measurements, concluding that the Two-Source Energy Balance (TSEB) and CandN-R transmittance models used synergically (TSEB-2TR) improved transpiration estimations. Table 8 distils operational sap-flow thresholds and their correspondence with plant water status (Ψ_{stem}/CWSI) reported in almond studies.

Future advances will likely strengthen the integration of sap flow into decision-support systems and precision irrigation workflows (Vice, 2021).

Table 8
Sap-flow operational thresholds in almond and concurrent water status (Ψ_{stem}/CWSI) as reported in the literature.

Cultivar	Location	Sap flow method	Treatments	Sap flow threshold	CWSI/Ψ_{stem} (MPa) reference	Reference
Guara	Cordoba, Spain	Trunk sap-flow probes (IAS-CSIC custom)	FI RDI 15 % ETc kernel-filling SDI 75 % ETc	Onset of transpiration decline when CWSI ≈ 0.2; diurnal pattern starts flattening	CWSI ≈ 0.2 ≙ Ψ_{stem}≈ −1.2 MPa	González-Dugo et al., 2020
Nonpareil	Berri, Australia	CHP	T100 100 %ETc, T60 60 % ETc,	Marked decrease in Sn and flattened morning peak (absolute flow NR)	Parabolic relationship Sn-Ψ; severe stress with Ψ at midday ≲ −1.8 MPa; incipient stress range around −1.2 to −1.5 MPa	Fuentes et al., (2013)
Marinada	Les Borges Blanques, Spain	HRM/CHP	FI MD 50 % ETc SS 20 % ETc Tree production system: Open vase, Central Axis, Hedgerow	Relative loss of flow vs FI and flattening of morning peak under DI (absolute flow NR)	Open vase (Ψ_{stem}): FI: −0.6 to –0.9 MD: −0.6 to-1.2 SS: −0.5 to –1.6 Central axis (Ψ_{stem}): FI: −0.6 to –1.0 MD: −0.6 to-1.6 SS: −0.5 to –2.0 Hedgerow (Ψ_{stem}): FI: −0.6 to –1.0 MD: −0.6 to-1.5 SS: −0.5 to –1.9	Quintanilla-Albornoz et al., (2023)
Guara	Seville, Spain	Sap flow + lysimeter (kt vs fIPAR)	FI (calibration)	Baseline of transpiration vs interception (PAR) for detecting flow deficits relative to canopy light capture	-	Espadafor et al., (2015)

FI: Full irrigation; MS: Moderate stress; SS: Severe stress; ETc: Evapotranspiration of the crop; RDI: Regulated deficit irrigation; SDI: Sustained deficit irrigation; CWSI; Crop Water Stress Index; Sn: Nocturnal sap-flow threshold; CHP: Compensation heat pulse method; HRM: Heat ratio method.

In conclusion, sap flow techniques offer a powerful tool for understanding tree water dynamics, guiding irrigation strategies, and improving orchard sustainability. Crucially, tying pattern-based sap flow triggers to Ψ_{stem} (e.g. onset around –1.1 to –1.2 MPa) and CWSI (~0.2) enables stage-sensitive, water saving irrigation with minimal yield penalties (Fuentes et al., 2013; González-Dugo et al., 2020; Quintanilla-Albornoz et al., 2023, 2024).

6.3. Dendrometry-based indicators

The measurement of tree dimensions and growth patterns has emerged as a valuable tool for precision agriculture, particularly in precision irrigation management. In almond trees and other woody and herbaceous species, indicators derived from trunk diameter variations (TDV) have been successfully evaluated as indicators of plant water status (Goldhamer and Fereres, 2001). Rather than representing a primary physiological response, TDV-based metrics function as integrative monitoring tools that capture the cumulative effects of tree water balance, transpiration demand and growth constraints. TDV, recorded with high-resolution dendrometers, reflects daily and seasonal changes in tree hydration and growth cycles.

As in other woody species, almond trunks display a 24-hour oscillation pattern, reaching their maximum diameter shortly before sunrise and their minimum in the afternoon (Goldhamer and Fereres, 2001). Under water deficit, diurnal shrinkage increases due to the imbalance between water uptake and transpiration, forcing the plant to draw from internal water reserves. When nocturnal rehydration is incomplete, successive daily maxima may stabilize or decline, providing a continuous, indirect signal of increasing water stress intensity (Goldhamer and Fereres, 2001).

Among TDV-derived indices, maximum daily shrinkage (MDS) has been widely explored and is sensitive to water deficit, making it useful for adjusting irrigation to maintain target stress patterns (Fereres and Goldhamer, 2003; Goldhamer and Fereres, 2001, 2004). For operational use, MDS is often expressed as a signal intensity, the ratio between the MDS of a monitored tree and the MDS of a well-watered reference tree

Table 9
Operational thresholds for maximum daily shrinkage (MDS) and daily trunk growth rate (TGR) in almond trees, with associated stem water potential (Ψ_{stem}) ranges, stress levels, and phenological recommendations as reported in the literature.

Indicator	Threshold	Associated Ψ_{stem} (MPa)	Stress Level	Phenological Stage Recommendations	References
MDS signal intensity (MDS/MDSref)	1.3–1.6	−0.6 to −1.0	Mild	Early fruit development (Stage II)	Puerto et al., (2013)
	2.2–2.8	−1.3 to −1.9	Moderate	Kernel-filling (Stage III/IV) — apply RDI for water saving	Puerto et al., (2013); Goldhamer and Fereres, (2004)
	> 2.8	< −1.9	Severe	Avoid — risk of yield and quality loss	Puerto et al., (2013)
MDS signal intensity	1.75	−0.7 to −1.1	Mild	Post-harvest irrigation management	Goldhamer and Fereres, (2004)
	2.75	−0.8 to −1.7	Moderate	Mid-season RDI target for water saving	Goldhamer and Fereres, (2004)
TGR daily growth rate	> 0.3	−0.5 to −0.8	No/Mild stress	Maintain during sensitive stages (kernel-filling, nut hardening)	Martín-Palomo et al., (2022)
	0.1–0.3	−0.8 to −1.4	Mild/ Moderate	Controlled RDI periods	Martín-Palomo et al., (2022)
	0–0.1	< −1.4	Moderate/ Severe	Avoid prolonged periods, except in late post-harvest	Martín-Palomo et al., (2022)
Baseline MDSref equation	MDSref = a + b·VPDmax; stress if MDSobs/MDSref > 1	Variable (climate-adjusted)	Variable	Applicable to all stages; allows daily thresholds adapted to atmospheric demand	Egea et al., 2009

Thresholds are based on field studies under different cultivars, ages, and climatic conditions. Unlike fixed mm thresholds, the Egea et al. (2009a) baseline method adjusts reference MDS according to maximum daily vapor pressure deficit (VPDmax) under well-watered conditions. Stress is indicated when observed MDS exceeds this climate-adjusted reference by a given ratio (signal > 1), enabling robust comparisons across days and seasons.

under the same atmospheric conditions (Goldhamer and Fereres, 2001). Practical signal thresholds are summarized in Table 9, where values of 1.3–1.6 are associated with mild stress in early fruit development, 2.2–2.8 with moderate stress during kernel-filling, and > 2.8 with severe stress that should be avoided (Puerto et al., 2013). Goldhamer and Fereres (2004) also proposed post-harvest and mid-season RDI thresholds of 1.75 and 2.75, respectively. These thresholds should be interpreted as operational guidelines rather than fixed physiological limits, as they integrate climatic demand and tree-specific responses.

In addition to MDS, daily trunk growth rate (TGR) has been proposed as a complementary indicator of stress intensity and duration.

In young almond trees, Nortes et al. (2005) reported that TGR responded more strongly to DI than MDS, and Martín-Palomo et al. (2019) observed the same in mature cv. 'Vairo' orchards, where MDS showed no clear response to water deficit. These differences suggest that TDV responses may depend on cultivar, scion–rootstock combination and sensor placement. More recently, Martín-Palomo et al. (2022) proposed an operational TGR-based approach, using the frequency distribution of daily growth rates. As shown in Table 9, values $> 0.3\ mm{\cdot}day^{-1}$ are typical of non-stressed or mildly stressed trees, $0.1–0.3\ mm{\cdot}day^{-1}$ correspond to mild/moderate stress, and $0–0.1\ mm{\cdot}day^{-1}$ indicate moderate/severe stress. This classification supports the use of TGR as a practical, sensor-based proxy for monitoring stress progression over time.

Regardless of the chosen indicator, effective use of TDV in almond irrigation scheduling requires the establishment of baseline relationships between MDS and maximum daily VPD (MDSref) for well-watered trees (Egea et al., 2009a) and the definition of phenology-specific thresholds for RDI strategies. Unlike fixed mm thresholds, the baseline method proposed by Egea et al. (2009a) also detailed in Table 9 dynamically adjusts the reference MDS according to the atmospheric demand of the day (VPDmax). By comparing the observed MDS with this climate-adjusted baseline, the method yields the Signal Intensity of Maximum Daily Shrinkage (SIMDS), which quantifies the relative deviation of trunk diameter variation from the reference curve and thus indicates the intensity of water stress under varying climatic conditions. Puerto et al. (2013) further demonstrated the practical application of variable SIMDS thresholds to modulate stress intensity according to crop sensitivity at each phenological stage.

In summary, TDV-derived indicators provide high-resolution, continuous information on tree water status and function as integrative monitoring tools rather than direct measurements of physiological processes. When combined with baseline approaches and phenology-specific thresholds, dendrometry can support irrigation scheduling in almond orchards, although robust interpretation requires consideration of cultivar-specific responses and environmental conditions.

7. General discussion; framework for irrigation decision-making in almond

Expanding almond production into increasingly water-limited regions demands irrigation strategies grounded in plant physiology. This section translates the physiological evidence reviewed in Sections 5 and 6 into a concise, operational decision-support framework aimed at practical irrigation scheduling rather than further mechanistic explanation. The framework is organized around six key components: (i) the phenological dependence of water sensitivity, (ii) the hierarchy of plant indicators, (iii) operational thresholds per stage, (iv) escalation rules when indicators diverge, (v) contextual modifiers, and (vi) implementation guidelines.

7.1. Physiological rationale: why is water sensitivity phenology-dependent?

- Almond sensitivity to water deficit varies with phenological stage because growth, carbon allocation and reserve dynamics are not uniform across the season During budbreak, fruit set and leaf expansion, cell growth depends on turgor and sustained supply of photoassimilates. Water deficits at this stage reduce leaf area, shoot growth and final fruit size, with knock-on effects on light interception and next-season floral inductions (Goldhamer and Viveros, 2000; Nortes et al., 2009; Egea et al., 2010).
- During kernel-filling, carbon demand declines because of reduced TPU and sink strength; consequently, moderate RDI seldom penalizes yield if water potential does not reach into severe stress ranges (Romero et al., 2004; Monks et al., 2017; Gutiérrez-Gordillo et al., 2023).
- In the post-harvest period, trees replenish reserves and differentiate floral buds; deficits during this stage deplete reserves and reduce the following year's bloom, generating carry-over effects (Goldhamer and Viveros, 2000). These mechanisms explain the yield patterns summarized in Tables 3 and 4.

Almond sensitivity to water deficit varies with phenological stage because growth, carbon allocation and reserve dynamics are not uniform across the season

7.2. Indicator hierarchy and physiological rationale

Effective irrigation control requires integrating multiple physiological indicators that operate at different spatial and temporal scales. The proposed operational flow is: $\Psi_{stem} \rightarrow g_s/A_n \rightarrow$ sensor-based proxies → irrigation decision.

The primary variable is Ψ_{stem}, which integrates the soil-plant-atmosphere continuum and filters short-term VPD fluctuations more effectively than Ψ_{leaf} (Shackel, 2011; Kisekka et al., 2024). Under FI, Ψ_{stem} follows a VPD-dependent baseline (-0.4 to −1.7 MPa) without implying stress; interpretation must therefore consider the Ψ_{stem}-VPD baseline relationship rather than absolute values (Shackel et al., 2021). Nonetheless, attention should be given to isohydric cultivars, in which Ψ_{stem} may remain relatively high while stomatal conductance (g_s) and carbon assimilation decline rapidly.

The secondary indicator is canopy temperature, normalized as the CWSI. Because stomatal closure reduces evaporative cooling, increases in leaf or canopy temperature track decreases in g_s. Properly calibrated CWSI values provide a canopy-scale proxy of g_s (Idso et al., 1981; Jackson et al., 1981; García-Tejero et al., 2018b; Bellvert et al., 2021).

Complementary indicators serve as tiebreakers when signals diverge.

The g_s-A_n relationship distinguishes stomatal from non-stomatal limitation; under moderate deficit, g_s declines while A_n is partly maintained; under severe stress, biochemical and photochemical restrictions dominate (Klein et al., 2001; Romero et al., 2004; Prgomet et al., 2020; Ranjbar et al., 2021; Sperling et al., 2023).

Dendrometry measurements, MDS and TGR, record whole-tree responses to water balance (Goldhamer and Fereres, 2001; Fereres et al., 2003; Martín-Palomo et al., 2019) and are particularly sensitive in young trees (Nortes et al., 2005). Where available, sap-flow sensors can confirm whole-tree transpiration dynamics.

7.3. Operational thresholds across phenological stages

The operational thresholds presented below are indicative values derived from published studies and should be locally adjusted using Ψ_{stem}–VPD baselines. Their purpose is to guide decision-making rather than define universal physiological limits. During budbreak and early fruit growth, Ψ_{stem} should remain close to its baseline (typically > −1.2 MPa). Irrigation is advised if Ψ_{stem} falls by more than 0.2 MPa below the baseline for two or more consecutive days or if CWSI exceeds 0.15. Stomatal conductance below $0.15\ mol\ m^{-2}\ s^{-1}$ signals the onset of stress.

In the fruit-set to rapid growth phase, maintaining Ψ_{stem} above −1.3 MPa prevents fruit absorption and nut size reduction, particularly

under coincident heat events (Goldhamer and Viveros, 2000). Net photoshynthesis (A_n) should remain at least 70 % of the FI value under comparable PAR conditions (Tables 5–6).

During kernel-filling, moderate RDI can be safely applied with Ψ_{stem} between –1.7 MPa and –2.0 MPa while maintaining CWSI < 0.25–0.35. Irrigation should be increased if Ψ_{stem} drops below –2.2 MPa for more than two consecutive days or if CWSI > 0.35, and severe stress (< −2.6 MPa) should be avoided to prevent kernel-mass loss and hydraulic damage (Romero et al., 2004; Monks et al., 2017; Espadafor et al., 2017; Gutiérrez-Gordillo et al., 2019; Sperling et al., 2023). Stomatal conductance higher than 0.12 mol m^{-2} s^{-1} is advisable (Conti et al., 2025).

Before harvesting, a slight water deficit (Ψ_{stem} ~ −1.7 to –2.2 MPa) facilitates shell split and nut detachment (Goldhamer and Viveros, 2000; Romero et al., 2004).

After harvest, Ψ_{stem} should return to baseline within 7–10 days. Maintaining positive TGR and stable MDS avoids depletion of carbohydrate reserves and secures floral induction for the next season (Goldhamer and Viveros, 2000; Martín-Palomo et al., 2019).

A phenology-aligned synthesis of these operational thresholds, including their hierarchical interpretation across indicators, is provided in Fig. 1, which summarizes the logic decisions developed in Section 6.

7.4. Escalation rules when indicators diverge

Under field conditions, indicators rarely evolve synchronously, so consistent interpretation requires escalation rules.

To avoid misinterpretation, irrigation decisions should follow a hierarchical logic in which Ψ_{stem} acts as the primary trigger, canopy temperature (CWSI) as secondary confirmation, and gas exchange or trunk-based indicators as tiebreakers when signals diverge.

When Ψ_{stem} declines below baseline, but CWSI remains low (<0.25), the apparent stress is usually driven by transient atmospheric demand rather than soil depletion (Goldhamer and Viveros, 2000); verification through g_s-A_n, ETR measurement is recommended, and irrigation adjustments should be made only when g_s < 0.15 mol m^{-2} s^{-1} or A_n < 8 μmol m^{-2} s^{-1} at saturating PPFD (Romero et al., 2004; Prgomet et al., 2020). Conversely, if Ψ_{stem} is near baseline while CWSI > 0.35, the discrepancy likely reflects canopy heterogeneity or midday measurement timing, and confirmation at standardized times or with UAV imagery is advisable (Espadafor et al., 2017).

Situations in which MDS increases while Ψ_{stem} remains stable may indicate localized soil compaction or restricted rooting depth (Martín-Palomo et al., 2019). This hierarchical logic, primary Ψ_{stem}, secondary CWSI, tiebreakers (g_s-A_n, TDV), minimizes false positives and stabilizes irrigation decisions under variable weather. This escalation logic (Ψ_{stem} → CWSI → gs/Aₙ or TDV) minimizes false positives and stabilizes irrigation decisions under variable atmospheric conditions, reinforcing the operational character of the proposed framework.

7.5. Contextual modifiers

Interpreting thresholds requires considering external and genotypic context. All operational thresholds proposed in this framework should therefore be interpreted as flexible reference ranges rather than fixed values. The Ψ_{stem}-VPD baseline shifts with atmospheric demand (Shackel et al., 2021); thus, measurements should always be paired with concurrent VPD and interpreted relative to the expected baseline for the prevailing conditions, rather than using absolute Ψ_{stem} thresholds. Denser canopies or readings near midday tend to exaggerate stress signals because of microclimate gradients and increased boundary-layer resistance, and should be interpreted with caution. Cultivar and rootstock also modulate hydraulic behavior. Isohydric genotypes such as Guara maintain tighter stomatal control and require higher Ψ_{stem} targets, whereas anisohydric cultivars like Texas or Soleta tolerate lower potentials but with narrower safety margins (Tyree and Zimmermann, 2002; Álvarez-Maldini et al., 2022; Álvarez et al., 2023). Rootstocks further condition soil tolerance: peach-almond confer vigor under FI but are sensitive to hypoxia in heavy soils, while plum hybrids improve waterlogging tolerance though graft compatibility may vary (Cabetas, 2016; Habibi et al., 2023). These anatomical and hydraulic traits justify cultivar- and rootstock-specific adjustment of stress thresholds and

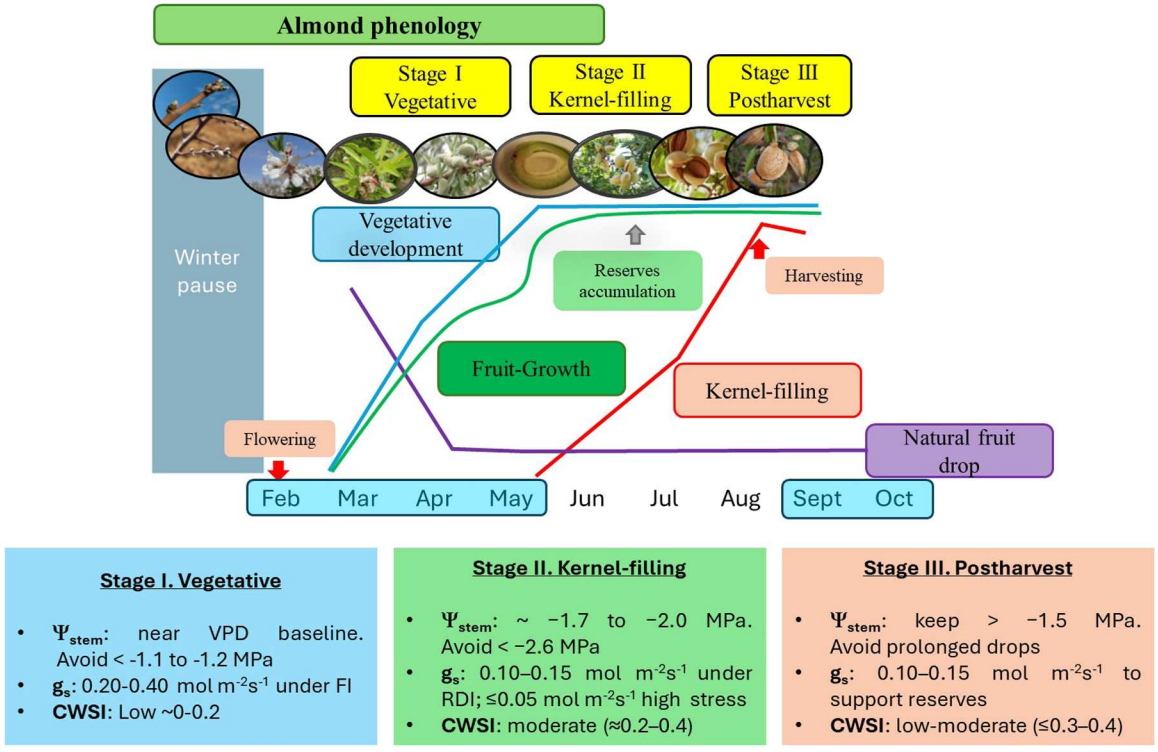

Fig. 1. Phenology-aligned thresholds for irrigation decisions in almond. (Modified from Gutiérrez-Gordillo et al., 2020c).

irrigation responses within the decision-support framework, rather than the application of universal trigger values across orchards.

7.6. Implementation guidance and decision chart

Consistent application of the proposed framework requires standardized measurement frequency and calibration of each sensor type. Ψ_{stem} should be measured once or twice per week per block at midday, increasing to daily during periods of extreme VPD (> 6 KPa). Thermal indicators must be calibrated for each season using non-stress and full-stress baseline established under local conditions. g_s-A_n spot checks are useful during phenological transitions or when other metrics provide conflicting information.

Continuous recording systems such as dendrometers (MDS/TGR) and sap-flow probes deliver high-resolution data with minimal maintenance, whereas UAV or fixed infrared thermography enable spatial analysis of canopy temperature. Table 2 presents irrigation recommendations for almonds according to seasonal water availability and phenological sensitivity, expressed as the percentage of the IR of the crop. Percentages lower than 100 % represent RDI intentionally applied during less sensitive stages to enhance water-use efficiency. These reference percentages function as the operational core of the decision framework proposed in this section and are consistent with previously validated RDI schemes for almonds (Gutiérrez-Gordillo, 2022).

Importantly, the framework is designed to guide the timing and relative intensity of irrigation adjustments rather than prescribing fixed irrigation doses. Absolute amounts should always be adapted to local irrigation system capacity, soil properties and root-zone characteristics.

This integration of physiological thresholds with water-allocation guidelines allows irrigation management to evolve from descriptive routines toward a real-time, evidence-based practice that links field instrumentation, crop physiology, and strategic resource planning.

7.6.1. Example decision logic

The integration of multiple indicators enables irrigation scheduling to follow a series of simple but physiologically meaningful rules.

When Ψ_{stem} remains more than 0.2 MPa below its baseline and CWSI exceeds 0.25 for two consecutive days, trees can be considered under moderate stress; a corrective irrigation equivalent to approximately 20–25 mm of net water applied to the effective root zone.

In practice, this amount should not be applied as a single continuous irrigation event but rather distributed over several irrigation pulses or consecutive days (e.g., 2–3 applications of 8–10 mm), depending on emitter discharge, soil infiltration capacity and root distribution. This approach minimizes deep percolation losses and avoids transient hypoxia in fine-textured soils.

The choice of this corrective range assumes a partially depleted root zone (approximately 25–40 % depletion of readily available water), a rooting depth of 0.6–1.0 m, and expected ETc rates over the subsequent days consistent with mid-season Mediterranean conditions. Smaller or larger adjustments may be required under different soil textures, irrigation layouts or climatic scenarios. If $g_s \leq 0.10$ mol m^{-2} s^{-1} or $A_n \leq 8$ μmol m^{-2} s^{-1} under non-heat-wave conditions, irrigation should be resumed immediately, as these thresholds indicate that stomatal closure has begun to limit carbon assimilation.

Following harvest, when the TGR approaches 0 for three or more days, rewatering before leaf fall is recommended to ensure replenishment of carbohydrate reserves for the next season (Girona et al., 1997).

Such rules translate the underlying physiological understanding into concrete operational steps and align with yield-neutral RDI windows previously demonstrated in almond (Goldhamer and Fereres, 2001; Romero et al., 2004; Gutiérrez-Gordillo et al., 2019).

7.6.2. Heat-wave safeguard

Exceptional atmospheric demand necessitates specific adjustments within deficit-irrigation programs. When forecasts indicate VPD > 6 kPa or unusually high maximum temperatures, temporary suspension of RDI is advised. Maintaining CWSI between 0.25 and 0.30 and ensuring that Ψ_{stem} does not fall more than 0.3 MPa below its baseline prevents irreversible hydraulic dysfunction and protects xylem integrity (Hsiao, 1973; Karimi et al., 2015; Losciale et al., 2023). In orchards equipped with microtensiometers or automated pressure chambers, these thresholds can serve as direct triggers for irrigation events, increasing the resilience of the proposed framework during climatic extremes.

8. Concluding remarks

Almond production is expanding into increasingly water-limited regions, making precision water management essential for both profitability and sustainability. This review integrates anatomical and physiological evidence to propose practical guidelines.

The decision framework developed here unifies physiological mechanisms with agronomic practice to guide irrigation under Mediterranean and semi-arid conditions. Central to this approach is the use of Ψ_{stem} interpreted through its VPD-dependent baseline, which provides a stable reference for identifying departures from the non-stress zone. Complementary indicators, including canopy-scale thermal indices (CWSI), leaf gas exchange (g_s–A_n), and dendrometry metrics (MDS/TGR), serve as secondary and tie-breaker variables when signals diverge.

Across phenological stages, maintaining Ψ_{stem} close to baseline during bloom and early nut development helps avoid reductions in fruit set and early kernel growth. During kernel-filling, moderate RDI can be safely applied (≈ –1.7 to –2.0 MPa), while values < –2.6 MPa or prolonged post-harvest stress should be avoided to protect carbon reserves and ensure adequate flower induction in the following season.

Cultivar–rootstock combinations with deeper rooting or higher hydraulic safety margins broaden the operational window under elevated VPD, whereas calibrated Ψ_{stem} and CWSI baselines allow timely, block-level adjustments when integrating in orchard and remote-sensing tools. Aligning irrigation decisions with these physiologically grounded thresholds enables improved water productivity without compromising nut quality. Continued integration of plant-based indicators with digital irrigation support systems will be essential for scaling these strategies across diverse almond-growing regions.

Beyond short-term irrigation optimization, almond production in Mediterranean and semi-arid regions increasingly requires a long-term adaptive perspective. Under current and projected climate scenarios, many orchards will operate recurrently, or almost permanently, under moderate deficit irrigation conditions. In this context, the objective of irrigation management should shift from maximizing annual yield toward maintaining stable, resilient and environmentally sustainable production systems over multiple seasons. Although such systems may function below their maximum productive potential in individual years, they can preserve hydraulic integrity, carbohydrate reserves and tree longevity, while reducing interannual yield variability. The decision-support framework proposed in this review is therefore intended not only as a tool for tactical irrigation scheduling, but also as a strategy to support long-term orchard resilience and predictability under increasing water scarcity and climatic uncertainty.

CRediT authorship contribution statement

S. Gutiérrez-Gordillo: Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Supervision. **L. Conti:** Conceptualization, Methodology, Investigation, Resources, Data

curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Supervision. **G. Egea:** Methodology, Investigation Data curation, Writing review – editing. **S. Vélez:** Methodology, Investigation Data curation, Writing – review & editing. **R. Martínez-Peña:** Methodology, Investigation Data curation, Writing – review & editing. **D. Andima:** Methodology, Investigation Data curation, Writing – review & editing. **V. Blanco:** Methodology, Investigation Data curation, Writing – review & editing. **M.A. Sarıdaş:** Methodology, Investigation Data curation, Writing – review & editing. **B. Kapur:** Methodology, Investigation Data curation, Writing – review & editing. **T.A. Paço:** Methodology, Investigation Data curation, Writing – review & editing. **E. Kullaj:** Methodology, Investigation Data curation, Writing – review & editing. **Ş.E. Aslan:** Methodology, Investigation Data curation, Writing – review & editing. **K. Vukićević:** Methodology, Investigation, Data curation, Writing – review & editing. **P. Losciale:** Methodology, Investigation, Resources, Data curation, Writing – review & editing, Project administration, Funding acquisition.

Funding

This work was supported by COST Action CA21142 (FruitCrews), funded by the European Cooperation in Science and Technology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The author Gutiérrez-Gordillo, S., currently holds a contract JDC2022–048551-I, funded by CIN/AEI/10.13039/501100011033 and by the European Union 'NextGenerationEU'/PRTR. The author Conti, L., holds a PhD scholarship financed by NextGenerationEU as part of the National Recovery and Resilience Plan (PNRR), Mission 4, component 2 "From research to business". The author Vélez, S., holds a Distinguished Researcher contract (Beatriz Galindo BG23/00073) is funded by the Spanish Ministry of Science, Innovation and Universities under the 2023 call, within the framework of the State Plan for Scientific, Technical, and Innovation Research (PEICTI) 2021–2023.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agwat.2026.110162.

Data availability

Data will be made available on request.

References

Abdelmoneim, Z.M., 2024. Deficit irrigation strategies on almond production in California: a brief review. Acta Hortic. (1406), 161–164. https://doi.org/10.17660/ActaHortic.2024.1406.23.

Adu, M.O., Yawson, D.O., Armah, F.A., Asare, P.A., Frimpong, K.A., 2018. Meta-analysis of crop yields of full, deficit, and partial root-zone drying irrigation. Agric. Water Manag 197, 79–90.

Álvarez, S., Martín, H., Barajas, E., Rubio, J.A., Vivaldi, G.A., 2020. Rootstock effects on water relations of young almond trees (cv. Soleta) when subjected to water stress and rehydration. Water 12, 3319. https://doi.org/10.3390/w12123319.

Álvarez, S., Núñez, L., Martín, H., Barajas, E., Miras-Ávalos, J.M., 2023. Differences in growth and water use efficiency in four almond varieties grafted onto Rootpac-20. Horticulturae 9, 295. https://doi.org/10.3390/horticulturae9030295.

Álvarez-Maldini, C., Acevedo, M., Estay, D., Aros, F., Dumroese, R.K., Sandoval, S., Pinto, M., 2022. Examining physiological, water relations, and hydraulic vulnerability traits to determine anisohydric and isohydric behaviour in almond (*Prunus dulcis*) cultivars: implications for selecting agronomic cultivars under changing climate. Front. Plant Sci. 13, 974050. https://doi.org/10.3389/fpls.2022.974050.

Arquero, O., 2013. Manual del almendro. Junta de Andalucía.

Bakhtiari, E.S., Mousavi, A., Yadegari, M., Haghighati, B., Martínez-García, P.J., 2025. Physiological and biochemical responses of almond (*Prunus dulcis*) cultivars to drought stress in semi-arid conditions in Iran. Plants 14, 734.

Barl, L., Debastiani Benato, B., Genze, N., et al., 2025. The combined effect of decreased stomatal density and aperture increases water use efficiency in maize. Sci. Rep. 15, 13804. https://doi.org/10.1038/s41598-025-94833-1.

Bellvert, J., Adeline, K., Baram, S., Pierce, L., Sanden, B., Smart, D., 2018. Monitoring crop evapotranspiration and crop coefficients over an almond and pistachio orchard through remote sensing. Remote Sens 10, 2001. https://doi.org/10.3390/rs10122001.

Bellvert, J., Nieto, H., Pelechá, A., Jofre-Cêkalovic, C., Zazurca, L., Miarnau, X., 2021. Remote sensing energy balance model for the assessment of crop evapotranspiration and water status in an almond rootstock collection. Front. Plant Sci. 12, 608967. https://doi.org/10.3389/fpls.2021.608967.

Ben Yahmed, J., Ghrab, M., Ben Mimoun, M., 2016. Eco-physiological evaluation of different scion-rootstock combinations of almond grown in Mediterranean conditions. Fruits 71 (3), 185–193. https://doi.org/10.1051/fruits/2016003.

Ben-Asher, J., Cardon, G., Phene, C.J., Hutmacher, R.B., Peters, D., Rolston, D.E., Biggar, J.W., 1994. Determining almond root zone from surface carbon dioxide fluxes. Soil Sci. Soc. Am. J. 58, 930–934. https://doi.org/10.2136/sssaj1994.03615995005800030041x.

Cabetas, M.J.R., 2016. Almond rootstocks: Overview. Options Méditerr 119, 133–143.

Calle, A., Aparicio-Durán, L., Batlle, I., Eduardo, I., Miarnau, X., 2024. Review of agronomic and kernel quality traits of 273 almond cultivars. Genet. Resour. Crop Evol. https://doi.org/10.1007/s10722-024-02183-0.

Camposeo, S., Palasciano, M., Vivaldi, G.A., Godini, A., 2011. Effect of increasing climatic water deficit on some leaf and stomatal parameters of wild and cultivated almonds under Mediterranean conditions. Sci. Hortic. 127, 234–241. https://doi.org/10.1016/j.scienta.2010.09.022.

Casas-Agustench, P., Salas-Huetos, A., Salas-Salvadó, J., 2011. Mediterranean nuts: Origins, ancient medicinal benefits and symbolism. Public Health Nutr. 14, 2296–2301. https://doi.org/10.1017/S1368980011002540.

Castel, J., Fereres, E., 1982. Responses of young almond trees to two drought periods in the field. J. Hortic. Sci. Biotechnol. 57, 175–187. https://doi.org/10.1080/00221589.1982.11515038.

Cochard, H., Tête, Barigah, S., Kleinhentz, M., Eshel, A., 2008. Is xylem cavitation resistance a relevant criterion for screening drought resistance among Prunus species? J. Plant Physiol. 165, 976–982. https://doi.org/10.1016/j.jplph.2007.07.020.

Connell, J.H., Milliron, L., 2024. Evaluation of rootstock cultivars for almond in California. Acta Hortic. (1406), 209–216. https://doi.org/10.17660/ActaHortic.2024.1406.32.

Conti, L., Gaeta, L., Giannini, M., D'Onghia, A., Montesano, F.F., Losciale, P., 2025. Scouting ecophysiological variables to monitor regulated deficit irrigation in almond. Sci. Hortic. 352, 114442. https://doi.org/10.1016/j.scienta.2025.114442.

Delplancke, M., Alvarez, N., Benoit, L., Espíndola, A., Joly, H.I., Neuenschwander, S., Arrigo, N., 2013. Evolutionary history of almond tree domestication in the Mediterranean basin. Mol. Ecol. 22, 1092–1104. https://doi.org/10.1111/mec.12129.

Descamps, C., Quinet, M., Baijot, A., Jacquemart, A.-L., 2018. Temperature and water stress affect plant–pollinator interactions in Borago officinalis. Ecol. Evol. 8, 3443–3456. https://doi.org/10.1002/ece3.3914.

Di Lena, B., Farinelli, D., Palliotti, A., Poni, S., DeJong, T.M., Tombesi, S., 2018. Impact of climate change on the possible expansion of almond cultivation area poleward: A case study of Abruzzo, Italy. J. Hortic. Sci. Biotechnol. 93, 209–215. https://doi.org/10.1080/14620316.2017.1357433.

Drechsler, K., Kisekka, I., Upadhyaya, S., 2019. A comprehensive stress indicator for evaluating plant water status in almond trees. Agric. Water Manag 216, 214–223. https://doi.org/10.1016/j.agwat.2019.02.003.

Egea, G., Dodd, I.C., González-Real, M.M., Domingo, R., Baille, A., 2011. Partial rootzone drying improves almond tree leaf-level water use efficiency and afternoon water status compared with regulated deficit irrigation. Funct. Plant Biol. 38, 372–385. https://doi.org/10.1071/FP10247.

Egea, G., González-Real, M.M., Baille, A., Nortes, P.A., Sánchez-Bel, P., Domingo, R., 2009b. The effects of contrasted deficit irrigation strategies on the fruit growth and kernel quality of mature almond trees. Agric. Water Manag 96, 1605–1614. https://doi.org/10.1016/j.agwat.2009.06.017.

Egea, G., González-Real, M.M., Baille, A., Nortes, P.A., Conesa, M.R., Ruiz-Salleres, I., 2012. Effects of water stress on irradiance acclimation of leaf traits in almond trees. Tree Physiol. 32, 450–463. https://doi.org/10.1093/treephys/tps016.

Egea, G., Nortes, P.A., Domingo, R., Baille, A., Pérez-Pastor, A., Gonzalez-Real, M.M., 2013. Almond agronomic response to long-term deficit irrigation applied since orchard establishment. Irrig. Sci. 31, 445–454.

Egea, G., Nortes, P.A., González-Real, M.M., Baille, A., Domingo, R., 2010. Agronomic response and water productivity of almond trees under contrasted deficit irrigation regimes. Agric. Water Manag 97, 171–181. https://doi.org/10.1016/j.agwat.2009.09.006.

Egea, G., Pagán, E., Baille, A., Domingo, R., Nortes, P., Pérez-Pastor, A., 2009a. Usefulness of establishing trunk diameter-based reference lines for irrigation scheduling in almond trees. Irrig. Sci. 27, 431–441. https://doi.org/10.1007/s00271-009-0157-0.

Eichi, V.R., Tyerman, S.D., Wirthensohn, M.G., 2014. Water relations and mesophyll anatomy in almond leaves. J. Am. Soc. Hortic. Sci. 139, 627–633. https://doi.org/10.21273/JASHS.139.6.627.

Espadafor, M., Orgaz, F., Testi, L., Lorite, I.J., Villalobos, F.J., 2015. Transpiration of young almond trees in relation to intercepted radiation. Irrig. Sci. 33, 265–275. https://doi.org/10.1007/s00271-015-0464-6.

Espadafor, M., Orgaz, F., Testi, L., Lorite, I.J., González-Dugo, V., Fereres, E., 2017. Responses of transpiration and transpiration efficiency of almond trees to moderate water deficits. Sci. Hortic. 225, 6–14. https://doi.org/10.1016/j.scienta.2017.06.028.

Esparza, G., DeJong, T.M., Weinbaum, S.A., 2001. Effects of irrigation deprivation during the harvest period on nonstructural carbohydrate and nitrogen contents of dormant, mature almond trees. Tree Physiol. 21, 1081–1086. https://doi.org/10.1093/treephys/21.14.1081.

FAO, 2023. FAOSTAT: Crops and livestock products.

Fenster, T.L.D., Oikawa, P.Y., Lundgren, J.G., 2021. Regenerative almond production systems improve soil health, biodiversity, and profit. Front. Sustain. Food Syst. 5, 664359. https://doi.org/10.3389/fsufs.2021.664359.

Fereres, E., Aldrich, T.M., Schulbach, H., Martinich, D.A., 1981. Responses of young almond trees to late-season drought. Calif. Agric. 35, 11–12.

Fereres, E., Goldhamer, D., 2003. Suitability of stem diameter variations and water potential as indicators for irrigation scheduling of almond trees. J. Hortic. Sci. Biotechnol. 78, 139–144. https://doi.org/10.1080/14620316.2003.11511596.

Fernandes De Oliveira, A., Mameli, M.G., De Pau, L., Satta, D., 2023. Almond tree adaptation to water stress: Differences in physiological performance and yield responses among four cultivars grown in Mediterranean environment. Plants 12, 1131. https://doi.org/10.3390/plants12051131.

Fernández, J.E., 2017. Plant-based methods for irrigation scheduling of woody crops. Horticulturae 3, 35. https://doi.org/10.3390/horticulturae3020035.

Fernández, J.E., Durán, P.J., Palomo, M.J., Díaz-Espejo, A., Chamorro, V., Girón, I.F., 2006. Calibration of sap flow measurements by the compensation heat-pulse method in olive, plum and orange trees: Relations with xylem anatomy. Tree Physiol. 26, 719–728. https://doi.org/10.1093/treephys/26.6.719.

Fernández i Martí, À., Alonso, J.M., Espiau, M.T., Rubio-Cabetas, M.J., Socias i Company, R., 2009. Genetic diversity in Spanish and foreign almond germplasm assessed by molecular characterization with simple sequence repeats. J. Am. Soc. Hortic. Sci. 134, 535–542. https://doi.org/10.21273/JASHS.134.5.535.

Flexas, J., Medrano, H., 2002. Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. Ann. Bot. 89, 183–189.

Flexas, J., Ribas-Carbó, M., Diaz-Espejo, A., Galmés, J., Medrano, H., 2008. Mesophyll conductance to CO_2: Current knowledge and future prospects. Plant Cell Environ. 31, 602–621. https://doi.org/10.1111/j.1365-3040.2007.01757.x.

Freitas, T.R., Santos, J.A., Silva, A.P., Fraga, H., 2023. Reviewing the adverse climate change impacts and adaptation measures on almond trees (*Prunus dulcis*). Agriculture 13, 71423. https://doi.org/10.3390/agriculture13071423.

Fuentes, S., Mahadevan, M., Bonada, M., Escalona, J.M., Bota, J., Medrano, H., Tyerman, S.D., 2013. Night-time sap flow is parabolically linked to midday water potential for field-grown almond trees. Irrig. Sci. 31, 1265–1276. https://doi.org/10.1007/s00271-013-0403-3.

García-Tejero, I.F., Gutiérrez-Gordillo, S., Ortega-Arévalo, C., Iglesias-Contreras, M., Moreno, J., Souza-Ferreira, L., Durán-Zuazo, V.H., 2018a. Thermal imaging to monitor the crop-water status in almonds by using the non-water stress baselines. Sci. Hortic. https://doi.org/10.1016/j.scienta.2018.04.045.

García-Tejero, I.F., Rubio, A.E., Viñuela, I., Hernández, A., Gutiérrez-Gordillo, S., Rodríguez-Pleguezuelo, C.R., Durán-Zuazo, V.H., 2018b. Thermal imaging at plant level to assess the crop-water status in almond trees (cv. Guara) under deficit irrigation strategies. Agric. Water Manag 208, 176–186. https://doi.org/10.1016/j.agwat.2018.06.002.

Girona, J., Marsal, J., Mata, M., Arbonés, A., Miravete, C., 1997. Evaluation of almond (*Amygdalus communis* L.) seasonal sensitivity to water stress. Acta Hortic. (449), 413–420. https://doi.org/10.17660/ActaHortic.1997.449.68.

Girona, J., Mata, M., Marsal, J., 2005. Regulated deficit irrigation during the kernel-filling period and optimal irrigation rates in almond. Agric. Water Manag 75, 152–167. https://doi.org/10.1016/j.agwat.2004.12.008.

Goldhamer, D.A., Fereres, E., 2001. Irrigation scheduling protocols using continuously recorded trunk diameter measurements. Irrig. Sci. 20, 115–125. https://doi.org/10.1007/s002710000034.

Goldhamer, D.A., Fereres, E., 2004. Irrigation scheduling of almond trees with trunk diameter sensors. Irrig. Sci. 23, 11–19. https://doi.org/10.1007/s00271-003-0088-0.

Goldhamer, D.A., Fereres, E., 2017. Establishing an almond water production function for California using long-term yield response to variable irrigation. Irrig. Sci. 35, 169–179. https://doi.org/10.1007/s00271-016-0528-2.

Goldhamer, D., Smith, T., 1995. Single-season drought irrigation strategies influence almond production. Calif. Agric. 49, 19–22.

Goldhamer, D.A., Viveros, M., 2000. Effects of preharvest irrigation cutoff durations and postharvest water deprivation on almond tree performance. Irrig. Sci. 19, 125–131. https://doi.org/10.1007/s002710000013.

Goldhamer, D.A., Viveros, M., Salinas, M., 2006. Regulated deficit irrigation in almonds: Effects of variations in applied water and stress timing on yield and yield components. Irrig. Sci. 24, 101–114. https://doi.org/10.1007/s00271-005-0014-8.

Gomes-Laranjo, J., Coutinho, J.P., Galhano, V., Cordeiro, V., 2006. Responses of five almond cultivars to irrigation: Photosynthesis and leaf water potential. Agric. Water Manag 83, 261–265. https://doi.org/10.1016/j.agwat.2005.11.007.

Gonzalez-Dugo, V., Lopez-Lopez, M., Espadafor, M., Orgaz, F., Testi, L., Zarco-Tejada, P., Lorite, I.J., Fereres, E., 2019. Transpiration from canopy temperature: Implications for the assessment of crop yield in almond orchards. Eur. J. Agron. 105, 78–85. https://doi.org/10.1016/j.eja.2019.01.010.

Gonzalez-Dugo, V., Zarco-Tejada, P., Berni, J.A.J., Suárez, L., Goldhamer, D., Fereres, E., 2012. Almond tree canopy temperature reveals intra-crown variability that is water stress-dependent. Agric. For. Meteor. 154–155, 156–165. https://doi.org/10.1016/j.agrformet.2011.11.004.

González-Dugo, V., Testi, L., Villalobos, F.J., López-Bernal, A., Orgaz, F., Zarco-Tejada, P. J., Fereres, E., 2020. Empirical validation of the relationship between the crop water stress index and relative transpiration in almond trees. Agric. For. Meteorol. 292, 108128.

Gordon, P.E., Ott, N.J., Brar, R.K., Holtz, B.A., Browne, G.T., 2024. Phosphorus fertilization can improve young almond tree growth in multiple replant settings. In: HortTechnology, 34, pp. 161–171. https://doi.org/10.21273/HORTTECH05143-22.

Gradziel, T.M., 2017. History of cultivation. In: Almonds: Botany, Production and Uses. CABI, pp. 43–69. https://doi.org/10.1079/9781780643540.0043.

Gradziel, T.M., Martínez-Gómez, P., 2013. Almond breeding. In: In: Plant Breeding Reviews, 37. Wiley, pp. 207–258. https://doi.org/10.1002/9781118358566.ch5.

Grasselly, C., 1976. Origine et évolution de l'amandier cultivé. Options Méditerr 32, 45–49.

Gutiérrez-Gordillo, S., 2022. New approaches to hydrosustainable almonds production: Agronomical, physiological and quality effects [PhD thesis, Universidad de Sevilla]. US Repository. https://idus.us.es/items/04985236-2cec-4117-a1e7-b1a7eae9edb4.

Gutiérrez-Gordillo, S., Durán-Zuazo, V., García-Tejero, I., 2019. Response of three almond cultivars subjected to different irrigation regimes in Guadalquivir river basin. Agric. Water Manag 222, 72–81. https://doi.org/10.1016/j.agwat.2019.05.031.

Gutiérrez-Gordillo, S., García-Tejero, I.F., Durán-Zuazo, V.H., Garcia Escalera, A., Ferrera Gil, F., Amores-Agüera, J.J., Hernández-Santana, V., 2020b. Assessing the water-stress baselines by thermal imaging for irrigation management in almond plantations under water scarcity conditions. Water 12, 1298. https://doi.org/10.3390/w12051298.

Gutiérrez-Gordillo, S., García-Tejero, I.F., Durán-Zuazo, V.H., Díaz-Espejo, A., Hernandez-Santana, V., 2023. The effect of nut growth limitation on triose phosphate utilization and downregulation of photosynthesis in almond. Tree Physiol. 43, 288–300. https://doi.org/10.1093/treephys/tpac122.

Gutiérrez-Gordillo, S., González-Santiago, J., Trigo-Córdoba, E., Rubio-Casal, A., García-Tejero, I., Egea, G., 2021. Monitoring of emerging water stress situations by thermal and vegetation indices in different almond cultivars. Agronomy 11, 1419. https://doi.org/10.3390/agronomy11071419.

Gutiérrez-Gordillo, S., Lipan, L., Durán-Zuazo, V.H., Sendra, E., Hernández, F., Hernández-Zazueta, M.S., Carbonell-Barrachina, Á.A., García-Tejero, I.F., 2020a. Deficit irrigation as a suitable strategy to enhance the nutritional composition of HydroSOS almonds. Water 12, 3336. https://doi.org/10.3390/w12123336.

Gutiérrez-Gordillo, S., Lipan, L., Durán-Zuazo, V.H., Carbonell-Barrachina, Á.A., Cárceles Rodríguez, B., Rubio-Casal, A.E., García-Tejero, I.F., 2020c. Linking sustainability and competitiveness of almond plantations under water scarcity and changing climate. In: Kumar, S., Meena, R.S., Jhariya, M.K. (Eds.), Resources Use Efficiency in Agriculture. Springer, pp. 695–728. https://doi.org/10.1007/978-981-15-6953-1_19.

Habibi, F., Liu, T., Shahid, M.A., Schaffer, B., Sarkhosh, A., 2023. Physiological, biochemical, and molecular responses of fruit trees to root zone hypoxia. Environ. Exp. Bot. 206, 105179. https://doi.org/10.1016/j.envexpbot.2022.105179.

Hartmann, H., Bahn, M., Carbone, M., Richardson, A.D., 2020. Plant carbon allocation in a changing world – challenges and progress: Introduction to a Virtual Issue on carbon allocation. N. Phytol. 227, 981–988. https://doi.org/10.1111/nph.16757.

Hawker, J.S., Buttrose, M.S., 1980. Development of the almond nut (*Prunus dulcis* (Mill.) D.A. Webb). Anatomy and chemical composition of fruit parts from anthesis to maturity. Ann. Bot. 46, 313–321. https://doi.org/10.1093/oxfordjournals.aob.a085922.

Hernandez-Santana, V., Fernández, J.E., Rodriguez-Dominguez, C.M., Romero, R., Diaz-Espejo, A., 2016. The dynamics of radial sap flux density reflects changes in stomatal conductance in response to soil and air water deficit. Agric. For. Meteor. 218–219, 92–101. https://doi.org/10.1016/j.agrformet.2015.11.013.

Hsiao, T.C., 1973. Plant responses to water stress. Annu. Rev. Plant Physiol. 24, 519–570. https://doi.org/10.1146/annurev.pp.24.060173.002511.

Idso, S.B., Jackson, R.D., Reginato, R.J., 1977. Remote sensing of crop yields: Canopy temperature and albedo measurements have been quantitatively correlated with final harvests of wheat. Science 196, 19–25. https://doi.org/10.1126/science.196.4285.19.

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

INC (International Nut and Dried Fruit Council Foundation), 2021. Nuts and dried fruits statistical yearbook 2019/2020.

Jackson, R.D., Idso, S.B., Reginato, R.J., Pinter, P.J., 1981. Canopy temperature as a crop water stress indicator. Water Resour. Res. 17, 1133–1138. https://doi.org/10.1029/WR017i004p01133.

Jin, Y., Chen, B., Lampinen, B.D., Brown, P.H., 2020. Advancing agricultural production with machine learning analytics: Yield determinants for California's almond orchards. Front. Plant Sci. 11, 290. https://doi.org/10.3389/fpls.2020.00290.

Jofre-Čekalović, C., Nieto, H., Girona, J., Pamies-Sans, M., Bellvert, J., 2022. Accounting for almond crop water use under different irrigation regimes with a two-source energy balance model and Copernicus-based inputs. Remote Sens 14, 2106. https://doi.org/10.3390/rs14092106.

Jones, H.G., 2004. Irrigation scheduling: Advantages and pitfalls of plant-based methods. J. Exp. Bot. 55 (407), 2427–2436. https://doi.org/10.1093/jxb/erh213.

Karimi, S., Yadollahi, A., Arzani, K., Imani, A., Aghaalikhani, M., 2015. Gas-exchange response of almond genotypes to water stress. Photosynthetica 53, 29–34. https://doi.org/10.1007/s11099-015-0070-0.
Kester, D.E., Gradziel, T.M., Micke, W.C., 1994. Identifying pollen incompatibility groups in California almond cultivars. J. Am. Soc. Hortic. Sci. 119, 106–109. https://doi.org/10.21273/JASHS.119.1.106.
Kisekka, I., Peddinti, S.R., Savchik, P., Yang, L., Culumber, M., Bali, K., Milliron, L., Edwards, E., Nocco, M., Reyes, C.A., Shackel, K., Fulton, A., 2024. Multisite evaluation of microtensiometer and osmotic cell stem water potential sensors in almond orchards. Comput. Electron. Agric. 227, 109547. https://doi.org/10.1016/j.compag.2024.109547.
Klein, I., Esparza, G., Weinbaum, S.A., DeJong, T.M., 2001. Effects of irrigation deprivation during the harvest period on leaf persistence and function in mature almond trees. Tree Physiol. 21, 1063–1072. https://doi.org/10.1093/treephys/21.14.1063.
Koumanov, K., Hopmans, J.W., Schwankl, L.W., 2006. Spatial and temporal distribution of root water uptake of an almond tree under microsprinkler irrigation. Irrig. Sci. 24, 267–278. https://doi.org/10.1007/s00271-005-0027-3.
Ladizinsky, G., 1999. On the origin of almond. Genet. Resour. Crop Evol. 46, 143–147. https://doi.org/10.1023/A:1008690409554.
Lipan, L., Cano-Lamadrid, M., Collado-González, J., López-Lluch, D., Moriana, A., Carbonell-Barrachina, Á.A., 2020b. Correlation between water stress and phenolic compounds of hydrosustainable almonds. J. Sci. Food Agric. 101, 3065–3070. https://doi.org/10.1002/jsfa.10896.
Lipan, L., García-Tejero, I.F., Gutiérrez-Gordillo, S., Demirbas, N., Sendra, E., Hernández, F., Durán-Zuazo, V.H., Carbonell-Barrachina, Á.A., 2020a. Enhancing nut quality parameters and sensory profiles in three almond cultivars by different irrigation regimes. J. Agric. Food Chem. 68, 2316–2328. https://doi.org/10.1021/acs.jafc.9b06854.
Lipan, L., Martín-Palomo, M.J., Sánchez-Rodríguez, L., Cano-Lamadrid, M., Sendra, E., Hernández, F., Burló, F., Vázquez-Araújo, L., Andreu, L., Carbonell-Barrachina, Á.A., 2019. Almond fruit quality can be improved by means of deficit irrigation strategies. Agric. Water Manag 217, 236–242. https://doi.org/10.1016/j.agwat.2019.02.041.
Liu, W., Li, R.-J., Han, T.-T., Cai, W., Fu, Z.-W., Lu, Y.-T., 2015. Salt stress reduces root meristem size by nitric oxide-mediated modulation of auxin accumulation and signaling in *Arabidopsis*. Plant Physiol. 168, 345–356. https://doi.org/10.1104/pp.15.00030.
López, R., Burgos, P., Hermoso, J.M., Hormaza, J.I., González-Fernández, J.J., 2014. Long term changes in soil properties and enzyme activities after almond shell mulching in avocado organic production. Soil Tillage Res 143, 155–163. https://doi.org/10.1016/j.still.2014.06.004.
López-Bernal, Á., Alcántara, E., Testi, L., Villalobos, F.J., 2010. Spatial sap flow and xylem anatomical characteristics in olive trees under different irrigation regimes. Tree Physiol. 30, 1536–1544. https://doi.org/10.1093/treephys/tpq095.
López-López, M., Espadafor, M., Testi, L., Lorite, I.J., Orgaz, F., Fereres, E., 2018. Water requirements of mature almond trees in response to atmospheric demand. Irrig. Sci. 36, 271–280. https://doi.org/10.1007/s00271-018-0582-z.
Lorite, I.J., Cabezas-Luque, J.M., Arquero, O., Gabaldón-Leal, C., Santos, C., Rodríguez, A., Lovera, M., 2020. The role of phenology in the climate change impacts and adaptation strategies for tree crops: a case study on almond orchards in Southern Europe. Agric. For. Meteor. 294, 108142. https://doi.org/10.1016/j.agrformet.2020.108142.
Losciale, P., Gaeta, L., Corsi, M., Galeone, C., Tarricone, L., Leogrande, R., Stellacci, A.M., 2023. Physiological responses of apricot and peach cultivars under progressive water shortage: different crop signals for anisohydric and isohydric behaviours. Agric. Water Manag 286, 108384. https://doi.org/10.1016/j.agwat.2023.108384.
Maas, E., Hoffman, G., 1977. Crop salt tolerance—Current assessment. J. Irrig. Drain. Div. 103, 115–134. https://doi.org/10.1061/jrcea4.0001137.
Martinelli, F., Basile, B., Morelli, G., D'Andria, R., Tonutti, P., 2012. Effects of irrigation on fruit ripening behaviour and metabolic changes in olive. Sci. Hortic. 144, 201–207. https://doi.org/10.1016/j.scienta.2012.07.012.
Martínez-Mena, M., Carrillo-López, E., Boix-Fayos, C., Almagro, M., Franco, N.G., Díaz-Pereira, E., Montoya, I., De Vente, J., 2020. Long-term effectiveness of sustainable land management practices to control runoff, soil erosion, and nutrient loss and the role of rainfall intensity in Mediterranean rainfed agroecosystems. Catena 187, 104352. https://doi.org/10.1016/j.catena.2019.104352.
Martínez-Vilalta, J., Piñol, J., Beven, K., 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. Ecol. Model 155, 127–147.
Martín-Palomo, M.J., Andreu, L., Pérez-López, D., Centeno, A., Galindo, A., Moriana, A., Corell, M., 2022. Trunk growth rate frequencies as water stress indicator in almond trees. Agric. Water Manag 271, 107765. https://doi.org/10.1016/j.agwat.2022.107765.
Martín-Palomo, M.J., Corell, M., Girón, I., Andreu, L., Trigo, E., López-Moreno, Y., Torrecillas, A., Centeno, A., Pérez-López, D., Moriana, A., 2019. Pattern of trunk diameter fluctuations of almond trees in deficit irrigation scheduling during the first seasons. Agric. Water Manag 218, 115–123. https://doi.org/10.1016/j.agwat.2019.03.033.
Massantini, R., Frangipane, M.T., 2022. Progress in almond quality and sensory assessment: an overview. Agriculture 12, 710. https://doi.org/10.3390/agriculture12050710.
McCutchan, H., Shackel, K.A., 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (Prunus domestica L. cv. French). J. Am. Soc. Hortic. Sci. 117, 607–611. https://doi.org/10.21273/jashs.117.4.607.
McMichael, P., 2009. All About Almonds Fact Sheet 07 – Almond Bud Initiation and Development. Almond Board of Australia.
Meyers, J.N., Kisekka, I., Upadhyaya, S.K., Michelon, G., 2019. Development of an artificial neural network approach for predicting plant water status in almonds. Trans. ASABE 62, 19–32. https://doi.org/10.13031/trans.12970.
Micke, W.C., 2005. Almond production manual (Ed.). Univ. Calif. Agric. Nat. Res. Publ. 3364.
Miras-Ávalos, J.M., González-Dugo, V., García-Tejero, I.F., López-Urrea, R., Intrigliolo, D.S., Egea, G., 2023M. Quantitative analysis of almond yield response to irrigation regimes in Mediterranean Spain. Agric. Water Manag 279, 108208. https://doi.org/10.1016/j.agwat.2023.108208.
Miras-Ávalos, J.M., Marco, P., Sánchez, S., Bielsa, B., Cabetas, M.J.R., González, V., 2022M. Soil quality index of young and differently managed almond orchards under Mediterranean conditions. Sustainability 14, 14770. https://doi.org/10.3390/su142214770.
Mittler, R., 2017. ROS are good. Trends Plant Sci. 22, 11–19.
Moldero, D., López-Bernal, Á., Testi, L., Lorite, I.J., Fereres, E., Orgaz, F., 2021. Long-term almond yield response to deficit irrigation. Irrig. Sci. 39, 409–420. https://doi.org/10.1007/s00271-021-00720-8.
Moldero, D., López-Bernal, Á., Testi, L., Lorite, I.J., Fereres, E., Orgaz, F., 2022. Almond responses to a single season of severe irrigation water restrictions. Irrig. Sci. 40, 1–11. https://doi.org/10.1007/s00271-021-00750-2.
Monks, D., Taylor, C., Sommer, K., Treeby, M.T., 2017. Deficit irrigation of almond trees did not decrease yield. Acta Hortic. (1150), 251–260. https://doi.org/10.17660/ActaHortic.2017.1150.35.
Mundree, S.G., Baker, B., Mowla, S., Peters, S., Saberi Marais, S., Vander Willigen, C., Govender, K., Maredza, A., Muyanga, S., Farrant, J., Thomson, J.A., 2002. Physiological and molecular insights into drought tolerance. Afr. J. Biotechnol. 1, 28–38.
Nortes, P.A., Gonzalez-Real, M.M., Egea, G., Baille, A., 2009. Seasonal effects of deficit irrigation on leaf photosynthetic traits of fruiting and non-fruiting shoots in almond trees. Tree Physiol. 29, 375–388. https://doi.org/10.1093/treephys/tpn032.
Nortes, P., Pérez-Pastor, A., Egea, G., Conejero, W., Domingo, R., 2005. Comparison of changes in stem diameter and water potential values for detecting water stress in young almond trees. Agric. Water Manag 77, 296–307. https://doi.org/10.1016/j.agwat.2004.09.034.
Palasciano, M., Camposeo, S., Godini, A., 2005. Stomatal size and frequency in wild (*A. webbii*) and cultivated (*A. communis*) almonds. Options Méditerr. Ser. A 63, 305–310.
Palasciano, M., Catalano, L., 2022. Mandorlo. In: Arboricoltura Speciale. Edagricole.
Paudel, I., Gerbi, H., Wagner, Y., Zisovich, A., Sapir, G., Brumfeld, V., Klein, T., 2020. Drought tolerance of wild versus cultivated tree species of almond and plum in the field. Tree Physiol. 40, 454–466. https://doi.org/10.1093/treephys/tpz134.
Pérez-Sánchez, R., Morales-Corts, M.R., 2021. Agromorphological characterization and nutritional value of traditional almond cultivars grown in the Central-Western Iberian Peninsula. Agronomy 11, 1238. https://doi.org/10.3390/agronomy11061238.
Prgomet, I., Pascual-Seva, N., Morais, M., Aires, A., Barreales, D., Ribeiro, A., Gonçalves, B., 2020. Physiological and biochemical performance of almond trees under deficit irrigation. Sci. Hortic. 261, 108990. https://doi.org/10.1016/j.scienta.2019.108990.
Puerto, P., Domingo, R., Torres, R., Pérez-Pastor, A., García-Riquelme, M., 2013. Remote management of deficit irrigation in almond trees based on maximum daily trunk shrinkage: Water relations and yield. Agric. Water Manag 126, 33–45. https://doi.org/10.1016/j.agwat.2013.04.013.
Quintanilla-Albornoz, M., Bellvert, J., Pelechá, A., Miarnau, X., 2024. Agronomic response, transpiration and water productivity of four almond production systems under deficit irrigation regimes. Sci. Hortic. 334, 113335. https://doi.org/10.1016/j.scienta.2024.113335.
Quintanilla-Albornoz, M., Miarnau, X., Pelechá, A., Casadesús, J., García-Tejera, O., Bellvert, J., 2023. Evaluation of transpiration in different almond production systems with two-source energy balance models from UAV thermal and multispectral imagery. Irrig. Sci. https://doi.org/10.1007/s00271-023-00888-1.
Ranjbar, A., Imani, A., Piri, S., Abdoosi, V., 2021. Drought effects on photosynthetic parameters, gas exchanges and water use efficiency in almond cultivars on different rootstocks. Plant Physiol. Biochem 26, 95–108. https://doi.org/10.1007/s40502-021-00568-2.
Reig, G., Iglesias, I., Zazurca, L., Torguet, L., Martinez, G., Miarnau, X., 2022. Physiological and agronomical responses of 'Vairo'almond and 'Big Top'nectarine cultivars grafted onto different prunus rootstocks and grown under semiarid Mediterranean conditions. Agronomy 12 (4), 821.
Reig, G., Salazar, A., Zarrouk, O., i, Forcada, C.F., Val, J., Moreno, M.Á., 2019. Long-term graft compatibility study of peach-almond hybrid and plum based rootstocks budded with European and Japanese plums. Sci. Hortic. 243, 392–400.
Rockwell, F.E., Wheeler, J.K., Holbrook, N.M., 2014. Cavitation and its discontents: Opportunities for resolving current controversies. Plant Physiol. 164, 1649–1660. https://doi.org/10.1104/pp.113.233817.
Romero, P., Botia, P., Garcia, F., 2004. Effects of regulated deficit irrigation under subsurface drip irrigation conditions on vegetative development and yield of mature almond trees. Plant Soil 260, 169–181. https://doi.org/10.1023/B:PLSO.0000030193.23588.99.
Romero, P., García, J., Botía, P., 2006. Cost–benefit analysis of a regulated deficit-irrigated almond orchard under subsurface drip irrigation conditions in Southeastern Spain. Irrig. Sci. 24, 175–184. https://doi.org/10.1007/s00271-005-0008-6.
Rubio-Cabetas, M.J. (2016). Almond rootstocks: overview. In O. Kodad, A. López-Francos, M. Rovira, & R. Socias i Company. XVI GREMPA Meeting on Almonds and Pistachios. Zaragoza, Spain (pp. 133-143).

Rubio-Cabetas, M.J., Bielsa, B., Espiau, M.T., 2024. Origin, genetic diversity and evolution in almond tree. In: Uthup, T.K., Karumamkandathil, R. (Eds.), Economically Important Trees. Springer, pp. 357–389. https://doi.org/10.1007/978-981-97-5940-8_10.

Ruiz-Sanchez, M.C., Sanchez-Blanco, M.J., Planes, J., Alarcon, J.J., Torrecillas, A., 1993. Seasonal changes in leaf water potential components in two almond cultivars. J. Agric. Sci. 120, 347–351. https://doi.org/10.1017/S0021859600076504.

Saa, S., Brown, P., 2014. Fruit presence negatively affects photosynthesis by reducing leaf nitrogen in almond. Funct. Plant Biol. 41, 884–891. https://doi.org/10.1071/FP13343.

Sánchez-Virosta, Á., Sánchez, J.M., Montoya, F., Gómez-Candón, D., González-Piqueras, J., Molina-Medina, A.J., López-Urrea, R., 2025. Assessment of different remote sensing techniques to estimate the CWSI of almond trees using canopy temperature. Int. J. Appl. Earth Obs. Geoinf. 142, 104737. https://doi.org/10.1016/j.jag.2025.104737.

Sapkota, A., Roby, M., Rao Peddinti, S., Fulton, A., Kisekka, I., 2025. Comparative analysis of ET, CWSI and NDVI to delineate site-specific irrigation management zones in almond orchards. Sci. Hortic. 339, 113860. https://doi.org/10.1016/j.scienta.2024.113860.

Shackel, K., 2011. A plant-based approach to deficit irrigation in trees and vines. HortScience 46, 173–177. https://doi.org/10.21273/HORTSCI.46.2.173.

Shackel, K., Moriana, A., Marino, G., Corell, M., Pérez-López, D., Martin-Palomo, M.J., Searles, P., 2021. Establishing a reference baseline for midday stem water potential in olive and its use for irrigation management. Front. Plant Sci. 12, 791711. https://doi.org/10.3389/fpls.2021.791711.

Silva, A.P., Aires, A., Barreales, D., Rodrigues, M.Á., Ribeiro, A.C., Gonçalves, B., Morais, M.C., 2022. Effects of foliar and soil boron fertilization on yield, leaf physiological traits and fruit attributes in rainfed almond orchards. Agronomy 12, 2005. https://doi.org/10.3390/agronomy12092005.

Smith, D.M., Allen, S., 1996. Measurement of sap flow in plant stems. J. Exp. Bot. 47, 1833–1844. https://doi.org/10.1093/jxb/47.12.1833.

Sperling, O., Gardi, I., Ben-Gal, A., Kamai, T., 2023. Deficit irrigation limits almond trees' photosynthetic productivity and compromises yields. Agric. Water Manag 289, 108562. https://doi.org/10.1016/j.agwat.2023.108562.

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.

Tomás, M., Flexas, J., Copolovici, L., Galmés, J., Hallik, L., Medrano, H., Ribas-Carbó, M., Tosens, T., Vislap, V., Niinemets, Ü., 2013. Importance of leaf anatomy in determining mesophyll diffusion conductance to CO_2 across species: quantitative limitations and scaling up by models. J. Exp. Bot. 64, 2269–2281. https://doi.org/10.1093/jxb/ert086.

Torrecillas, A., Alarcón, J.J., Domingo, R., Planes, J., Sánchez-Blanco, M.J., 1996. Strategies for drought resistance in leaves of two almond cultivars. Plant Sci. 118, 135–143. https://doi.org/10.1016/0168-9452(96)04434-2.

Torrecillas, A., Ruiz-Sanchez, M.C., del Amor, F., Leon, A., 1988. Seasonal variations on water relations of *Amygdalus communis* L. under drip irrigated and non-irrigated conditions. Plant Soil 106, 215–220. https://doi.org/10.1007/BF02371216.

Tyree, M.T., Zimmermann, M.H., 2002. Xylem structure and the ascent of sap, second ed. Springer.

Vahdati, K., Sarikhani, S., Arab, M.M., Leslie, C.A., Dandekar, A.M., Aletà, N., Bielsa, B., Gradziel, T.M., Montesinos, Á., Rubio-Cabetas, M.J., Sideli, G.M., Serdar, Ü., Akyüz, B., Beccaro, G.L., Donno, D., Rovira, M., Ferguson, L., Akbari, M., Sheikhi, A., Sestras, A.F., Kafkas, S., Paizila, A., Roozban, M.R., Kaur, A., Panta, S., Zhang, L., Sestras, R.E., Mehlenbacher, S.A., 2021. Advances in rootstock breeding of nut trees: objectives and strategies. Plants 10, 2234. https://doi.org/10.3390/plants10112234.

Vanella, D., Peddinti, S.R., Kisekka, I., 2022. Unravelling soil water dynamics in almond orchards characterized by soil-heterogeneity using electrical resistivity tomography. Agric. Water Manag 269, 107652. https://doi.org/10.1016/j.agwat.2022.107652.

Velazquez-Chavez, L.J., Daccache, A., Mohamed, A.Z., Centritto, M., 2024. Plant-based and remote sensing for water status monitoring of orchard crops: systematic review and meta-analysis. Agric. Water Manag 303, 109051. https://doi.org/10.1016/j.agwat.2024.109051.

Vice, H.K., 2021. Irrigation indices in almond: A comparison with an improved sap flow method. PhD Diss., Univ. California, Davis.

Viveros, M., 1999. Soil modifications: A must for almond orchards. Univ. Calif. Coop. Ext., Kern County.

Wani, I.A., Ahanger, R.A., Bhat, H.A., Lone, A.A., Bhat, T.A., Malik, I.A., Hassan, G.I., 2012. Rootstocks of almond. J. Plant Dev. Sci. Vol. 4 (2), 137–150.

Wani, I.A., Ahanger, R.A., Bhat, H.A., Lone, A.A., Bhat, T.A., Malik, I.A., Hassan, G.I., 2012. Rootstocks of almond. J. Plant Dev. Sci. Vol. 4 (2), 137–150.

Weil, R.R., Brady, N.C., 2017. The nature and properties of soils, fifteenth ed. Pearson.

Wirthensohn, M., 2020. New cultivars from the Australian almond breeding program. HortScience 55, 738–740. https://doi.org/10.21273/HORTSCI14716-19.

Wu, A., Hammer, G.L., Doherty, A., von Caemmerer, S., Farquhar, G.D., 2019. Quantifying impacts of enhancing photosynthesis on crop yield. Nat. Plants 5, 380–388. https://doi.org/10.1038/s41477-019-0398-8.

Yang, H., San, Y., Chen, Y., Ma, Y., Wang, X., Shoukat, M.R., Zheng, Y., Hui, X., 2023. Monitoring and investigating the change patterns of major growth parameters of almond trees under different irrigation conditions. Water 15, 3731. https://doi.org/10.3390/w15213731.

Zamora, G.G., 2020. Winter drought stress and bloom delay in almond: Evidence for an increased sensitivity during eco-dormancy. PhD Diss., Univ. California, Davis.

CHAPTER II

This chapter evaluates almond responses along an irrigation gradient under field conditions, identifying coordinated shifts in water status, gas exchange, and canopy temperature. It demonstrates that functional transitions emerge from progressive modifications in process coupling and identifies stem water potential, stomatal conductance, and $P_{KO/KC}$ a carboxylation index derived from chlorophyll fluorescence and leaf temperature measurements, as robust plant-based indicators of functional state.

BACKGROUND

Almond cultivation in semi-arid environments increasingly depends on irrigation management strategies that can improve water-use efficiency without compromising productivity. Conventional scheduling based mainly on soil moisture or microclimatic data does not always capture the actual functional state of the tree, because plant responses vary with pedoclimatic conditions, phenological stage, and atmospheric demand. For this reason, plant-based indicators such as stem water potential, stomatal conductance, thermal traits, and fluorescence-derived variables have been proposed as more integrative tools for assessing almond water status under deficit irrigation.

AIMS

This chapter aims to analyse how key ecophysiological variables describing tree functionality respond under different irrigation regimes in field-grown almond trees, and to identify the most informative indicators for defining future irrigation thresholds in cv. Guara. More specifically, it evaluates the coordinated behaviour of water status, gas exchange, and thermal–photochemical variables along a regulated deficit irrigation gradient during kernel filling.

RESULTS

The study showed that almond responses along the irrigation gradient were expressed as coordinated shifts in stem water potential, stomatal conductance, photosynthesis, and thermal/fluorescence-related variables. Under kernel filling, MRDI (80% ETc) maintained intermediate values between the fully irrigated control and SRDI (60% ETc), while SRDI caused the strongest decline in canopy functionality, with photosynthesis dropping to about 5.5 μmol m^{-2} s^{-1} and stomatal conductance to about 0.08 mol m^{-2} s^{-1} at peak stress. Strong relationships were observed between photosynthesis and stomatal conductance (R^2 = 0.94), photosynthesis and $P_{KO/KC}$ (R^2 = 0.77), and stomatal conductance and stem water potential (R^2 = 0.76), supporting the interpretation of functional transitions as changes in process coupling rather than isolated responses. Yield, fruit fresh weight, and seed dry weight did not differ significantly among treatments, although SRDI increased the proportion of tight-hull fruits. Overall, stem water potential, stomatal conductance, and $P_{KO/KC}$ emerged as the most robust plant-based indicators of functional state, while thermal variables helped capture the interaction between plant response and atmospheric demand.

Scientia Horticulturae 352 (2025) 114442

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Research Paper

Scouting ecophysiological variables to monitor regulated deficit irrigation in almond

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ARTICLE INFO

Keywords:
Water stress
Stomatal conductance
Photosynthesis
Stem water potential
Chlorophyll fluorescence
Plant-based indices
Prunus dulcis Mill

ABSTRACT

In semi-arid regions, almond orchards face significant challenges from climate change, necessitating sustainable irrigation strategies and advanced monitoring methods to enhance water use efficiency. This study investigated key ecophysiological variables to identify the most relevant physiological variables for future threshold definition in irrigation management (Prunus dulcis Mill., cv. Guara). The experiment included three irrigation treatments during the kernel-filling phase: 100 % (CTRL), 80 % (MRDI), and 60 % (SRDI) of crop evapotranspiration (ETc), with full irrigation provided during fruit growth and post-harvest periods. Key physiological variables, including stomatal conductance (gs), stem water potential (Ψ_s), photosynthesis (Pn), and $P_{KO/KC}$ (reflecting electron flux from PSII and RuBisCO carboxylative activity) were monitored weekly during a single growing season and showed clear seasonal dynamics: peaking during fruit growth, declining during kernel filling, and partially recovering post-harvest. During kernel filling, MRDI values for gs, Ψ_s, Pn, and $P_{KO/KC}$ were lower than CTRL but higher than SRDI. Strong correlations were observed between Pn and gs, $P_{KO/KC}$, as well as between gs and Ψ_s. Pn, gs, and $P_{KO/KC}$ were significantly influenced by air temperature and vapor pressure deficit, whereas Ψ_s was more closely linked to soil water content. Yield, fruit fresh weight, and seed dry weight were similar across treatments, although SRDI produced a higher proportion of tight-hull fruits. Variables such as gs, Ψ_s, Pn, and $P_{KO/KC}$ effectively captured plant water status and microclimatic variations. The MRDI treatment achieved significant water savings while maintaining yield and fruit quality, suggesting that Ψ_s, Pn, gs, and $P_{KO/KC}$ are reliable indicators of plant performance under reduced irrigation, with potential to inform the development of simplified, decision-support tools for growers. Advances in sensor technologies could facilitate the adoption of plant-based irrigation thresholds, improving water resource efficiency.

1. Introduction

Drought is the main problem in contemporary agriculture, threatening many fruit species in several countries, especially those in the Mediterranean Basin (Lopez et al., 2014). The Climate and Health Country Profile - Italy highlighted the increase in water scarcity conditions, particularly in southern areas, due to low rainfall and the growing demand for water from other sectors such as civil and industrial use (World Health Organization, 2015).

The main producers of almonds worldwide are the United States, Australia, Spain, Iran, and Italy (FAOSTAT), where production is essentially concentrated in two regions: Sicily and Apulia. Almond (*Prunus dulcis* Mill. (D.A. Webb)) is often described as moderately adapted to water-limited environments, primarily due to its long-standing cultivation in semi-arid rainfed systems. However, this resilience is relative and context-dependent, as almond productivity is highly sensitive to deficits during key phenological stages and requires precise irrigation scheduling to maintain yield and fruit quality (Girona et al., 2005). While not considered among the most drought-tolerant woody species, almond can perform adequately under moderate water stress. In contrast, other nut species such as pistachio (*Pistacia vera* L.) have exhibited more conservative water use strategies and maintained higher

Web references: FAO: https://www.fao.org/faostat/en/#data/QCL/visualize

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https://doi.org/10.1016/j.scienta.2025.114442
Received 13 January 2025; Received in revised form 13 September 2025; Accepted 10 October 2025
Available online 15 October 2025

stem water potential and water use efficiency under similar environmental constraints, highlighting the need to interpret almond's drought tolerance within a comparative physiological framework (Bellvert et al., 2018; Durán-Zuazo et al., 2020). Rational management of water resources appears necessary to achieve ecologically and economically sustainable production. The use of Decision Support Systems (DSS) based on monitoring soil water content and/or microclimate variables is becoming very common for proper irrigation management (Sadiq et al., 2021). However, a limitation of these approaches lies in their inability to directly investigate the functional state of the plant, which can respond variably to different pedoclimatic conditions. In field conditions, soil moisture sensors often show variability in their readings due to their limited sensing volume and sensitivity to local soil characteristics, such as gravel content, density, and salinity (Nolz and Loiskandl, 2017). Additionally, factors like soil temperature and electrical conductivity, which change over time, can also influence the sensors' accuracy (Domínguez-Niño et al., 2020). These challenges make it difficult to obtain consistent and reliable data from such sensors in agricultural settings. The use of plant-based sensors (PBS) offers a valuable complement to traditional approaches such as soil moisture monitoring, addressing some of their limitations—particularly when the goal is to enhance water use efficiency or optimize crop yields (Fernández, 2017; Millán et al., 2019).

Historically, plant water stress and irrigation needs were assessed mainly through soil measurements (Campbell and Campbell, 1982) and environmental data (Doorenbos and Pruitt, 1977). However, these approaches alone could be limiting for capturing the plant's actual physiological status (Ma et al., 2022) and lack the simplicity required for widespread, routine application. Consequently, there is growing interest in the development of plant-based indicators and sensors that integrate soil and environmental factors into a reliable index of tree functionality, defined as the integrated capacity to sustain water transport, stomatal regulation, and photosynthetic activity under variable water availability. This framework is consistent with the physiological strategies described by Chen et al. (2022), emphasizing the coordination between hydraulic function, stomatal control, and root traits in drought adaptation. Among these variables, stem water potential (Ψ_s) and stomatal conductance (gs) have emerged as key indicators, reflecting the plant's hydraulic status and the canopy's transpiration and photosynthetic capacity, respectively (De Swaef et al., 2022; Leuschner et al., 2022).

While midday leaf water potential (Ψ_{ml}) was initially considered a promising indicator across various species (Naor, 2000), it falls short in accurately reflecting plant stress due to factors such as stomatal regulation of transpiration mediated by environmental and root signals, as well as osmotic adjustments (Jones et al., 1985; Fereres and Goldhamer, 1990). Predawn leaf water potential, despite being more closely correlated with irrigation treatments than midday values (Xiloyannis et al., 1980), does not account for midday environmental stress; additionally, practical constraints (such as the requirement to measure leaf water potential before sunrise or to cover the leaf for 2–3 h prior the measurements) have likely hindered the widespread adoption of these methods for irrigation management in commercial orchards. In contrast, midday stem water potential (Ψ_{ms}) has been shown to correlate strongly with soil water potential, stomatal conductance (gs), and key yield parameters such as final fruit size (McCutchan and Shackel, 1992; Naor et al., 1995). As a result, Ψ_{ms} served as a reliable indicator, integrating the plant's responses to both soil moisture and environmental conditions (Nortes et al., 2005), making it one of the most suitable variables describing the tree water status across various species. Research has demonstrated its sensitivity to irrigation levels in apple, nectarine, peach (Garnier and Berger, 1985; Berman and DeJong, 1996), and pear (Ramos et al., 1994). Several studies have also established thresholds for Ψ_{ms}. For example, almond trees irrigated at field capacity exhibited midday stem water potential values between −0.7 and −1.0 MPa, depending on the evapotranspiration demands of the environment (Girona et al., 2005; Goldhamer and Girona, 2012). Additionally, Ψ_{ms} showed a strong correlation with stomatal conductance, which directly influences the rates of transpiration and photosynthesis, processes that ultimately impact yield (Naor, 2000). Although the measurement of midday stem water potential (Ψ_{ms}) is more technically demanding and labour-intensive than other plant water status indicators (Naor, 2000), it remains one of the most robust and reliable methods for diagnosing water stress in woody fruit species. Indeed, its adoption is supported by both research and practical extension, with tools such as pressure chamber thresholds, grower guidelines, and decision-support systems already in use for crops like prune and peach (McCutchan and Shackel, 1992; Shackel et al., 1997). Recent technological advances now allow continuous monitoring of Ψ_{stem} using embedded sensors like microtensiometers (Blanco and Kalcsits, 2021; González-Nieto et al., 2023; Kisekka et al., 2024) and stem psychrometers, based on dew point hygrometry (Dixon and Tyree 1984). Although still expensive, these technologies offer promising tools to support precision irrigation in water-limited environments.

Stomatal conductance measurements are highly informative regarding the plant's response to water stress; gs is considered one of the most effective water stress indicators in terms of earliness and sensitivity (Cifre et al., 2005; Jones, 2004). Like stem water potential, measurements of gs made with porometers and IRGAs require manual operation, which constrains the use of gs in precision irrigation. Accordingly, despite the variety of irrigation scheduling criteria that exist, none is completely satisfactory for managing high-frequency irrigation systems in tree crops (Jones, 2004). Nevertheless, recent advancements may address this issue. Advancements in sensor technologies have enabled the rapid acquisition of key physiological and environmental variables. Technological developments have enabled the commercialization of increasingly fast and accurate instruments capable of measuring multiple variables (i.e. stomatal conductance, leaf to air temperature difference, PAM chlorophyll fluorescence variables, leaf transpiration etc.) in just a few seconds. Although direct measurements of stomatal conductance (gs) are still difficult for routine orchard management due to their complexity and high sensitivity to fluctuating conditions (Damour et al., 2010), proxy-based approaches have been proposed. Hernández-Santana et al. (2016) estimated gs using sap flux density and vapor pressure deficit (VPD), while Losciale et al. (2023) employed the leaf-to-air temperature difference (ΔT) and VPD. These methods, relying on continuously measurable variables, may support gs estimation in research and technologically advanced orchards.

For broader implementation, the Crop Water Stress Index (CWSI; Idso et al., 1981; Jackson et al., 1981) represents a practical alternative. CWSI quantifies water stress based on canopy-to-air temperature differences and empirical baselines, with proven applications in almond orchards. However, accurate calibration is required, as reference baselines are influenced by environmental and genotypic factors (Egea et al., 2017; Gutiérrez-Gordillo et al., 2020; Blanco et al., 2023). Thermal imagery and CWSI thus offer scalable, grower-oriented tools for spatial stress monitoring in precision irrigation.

In parallel, improvements in chlorophyll fluorescence techniques have enabled rapid, non-invasive assessment of leaf photosynthetic status under field conditions (Losciale et al., 2015). Parameters such as PSII effective quantum yield (ΦPSII) and electron transport rate (JPSII) inform on the photochemical phase of photosynthesis, although their correlation with net CO_2 assimilation (Pn) may become decoupled under stress due to the engagement of alternative electron sinks, including photorespiration and cyclic electron flow (Genty et al., 1989; Niyogi, 1999). Integrating fluorescence metrics with variables such as ΔT and biochemical indicators of Rubisco efficiency (e.g., $P_{KO/KC}$) can enhance diagnostic capacity for both water status and photosynthetic performance (Losciale et al., 2015; 2023).

In addition to crop monitoring, water-stress-induced strategies have shown promising yet sometimes discordant results in reducing irrigation inputs without limiting production and quality. Regulated Deficit Irrigation (RDI) involves imposing water restrictions during specific

phenological stages when plants are least susceptible (Girona et al., 2005; Gutiérrez-Gordillo et al., 2019; Mañas et al., 2014 ; Prgomet et al., 2020; Stewart et al., 2011). Stress during fruit cytokinesis and after hull dehiscence could negatively affect seed size and bud differentiation in the following year (Goldhamer and Viveros, 2000; Goldhamer et al., 2006). The seed maturity period appears to be the least susceptible to water stress (Girona et al., 2005; Gutiérrez-Gordillo et al., 2019; Mañas et al., 2014; Prgomet et al., 2020); however, it is essential to correctly identify this period and determine the intensity of stress to apply (Monks et al., 2017; Razouk et al., 2020; Romero et al., 2004). Considering the current trend of expanding almond cultivation, particularly in semi-arid regions, it is of utmost importance to improve our understanding of the crop's water use, especially under water stress conditions.

The aims of this study were: (i) to analyse the behaviour of ecophysiological variables describing tree functionality under different water conditions and (ii) to select the most informative variables usable in the future to set optimal thresholds for managing irrigation in almond cv. "Guara."

2. Materials and methods

2.1. Experimental site

The trial was conducted in 2021 in a commercial almond orchard, "Tenute GUIDOTTI," on 7-year-old almond trees (cv. "Guara") grafted onto GF-677 rootstock, located in Casamassima, Bari, Italy (40°57′23″ N, 16°55′14″ E). The trees, spaced 5 × 5 m, were trained as an open vase system. Irrigation was supplied through a drip system with emitters delivering a flow rate of 3.4 L h^{-1} each, positioned every 0.7 m along the drip line. The irrigation system wetted approximately 30 % of the soil surface, concentrated along the rows.

The soil was classified as clay, consisting of 51.8 % clay, 32.6 % silt, and 15.6 % sand, with the rooting system extending to a depth of approximately 0.5 m. The soil water content at field capacity and wilting point was 0.31 and 0.21 m^3 m^{-3}, respectively. The study area had a Mediterranean climatic classification, with an annual reference evapotranspiration (ET_o) of 1055 mm and an accumulated rainfall of 673 mm, based on average data from the past 10 years (Ministry of Agriculture, Food Sovereignty, and Forests).

2.2. Irrigation treatments

The study covered the vegetative-reproductive period of 2021, starting from early fruit development in April (cell division stage), through the kernel-filling stage in June, up to harvest in August and post-harvest stages in September. Starting from the cell division stage, trees were irrigated to maintain soil moisture close to field capacity, with irrigation events triggered when approximately 40 % of the available water (AW) was depleted. This percentage corresponded to the readily available water, RAW namely the fraction that could be depleted without inducing significant water stress in almond (Allen et al., 1998).

The wetted area provided by the drip irrigation system was estimated to cover approximately 30 % of the surface and a rooting depth of 0.45 m was assumed based on previous inspection of the root zone expansion.

Irrigation scheduling was based on the water balance using the microclimatic approach (Allen et al., 1998). Crop evapotranspiration was calculated as

$$ETc = Kc \times ET_0$$

where ETc is the crop evapotranspiration, Kc is the single-crop coefficient, and ET_o is the reference evapotranspiration calculated using the Penman-Monteith equation. Microclimatic data were obtained from a weather station located within the experimental orchard (Winet srl, Italy). The crop coefficients (Kc) used during the experimental period were 0.85, 0.98, 1.02, 1.03, and 0.95 for May, June, July, August, and September, respectively. These values were derived by averaging the coefficients reported in several studies on almonds (Fereres et al., 1981; Girona, 2006; Sanden, 2007).

During the kernel-filling stage, three irrigation regimes were applied: full irrigation (CTRL), receiving 100 % of crop evapotranspiration (ETc), maintaining the soil within the range of the readily available water; mild deficit irrigation (MRDI), supplying 80 % of ETc; and severe deficit irrigation (SRDI), receiving 60 % of ETc. After harvest, all treatments were restored to full irrigation, receiving 100 % ETc. The kernel-filling stage was defined as the period starting with the rapid increase in seed dry weight. The irrigation season lasted from the end of May to the end of September. Soil moisture was monitored in all three irrigation treatments using soil moisture probes (10HS, Decagon Devices Inc., USA) installed at depths of 0.15 m, 0.30 m, and 0.45 m below the soil surface. Each treatment included three replicate plots, and one set of probes (at the three depths) was installed per replicate, totalling three sets of sensors per treatment. Soil water content (m^3 ha^{-1}) was estimated assuming a root zone depth of 0.45 m and a wetted area of 30 %, corresponding to the surface covered by the drip irrigation system.

2.3. Experimental design and plant measurements

The three treatments were arranged in a completely randomized 3-block experimental design. Each treatment within each block included approximately 75 trees, distributed across three rows (25 trees per row), with the two outer rows serving as guard rows. Within the middle row, three trees uniform in vigour, productive load, and phytosanitary status were selected for detailed monitoring, resulting in a total of nine monitored trees per treatment (three trees per block). Leaf functionality was assessed throughout the vegetative-reproductive season using an open-circuit infrared gas analyser equipped with a fluorometer and LED light source (Li-COR 6400XT, LI-COR, Lincoln, Nebraska, USA). The measured variables included net photosynthesis (Pn, μmol m^{-2} s^{-1}), stomatal conductance (gs, mol m^{-2} s^{-1}), leaf temperature (T_{leaf}, °C), leaf-to-air temperature difference (ΔT, °C), electron transport rate exiting Photosystem II (J_{PSII}, μmol m^{-2} s^{-1}), electron transport rate directed toward non-net carboxylative processes (J_{NC}, μmol m^{-2} s^{-1}; Losciale et al., 2010), and $P_{KO/KC}$, a variable describing the electron flux exiting PSII and the carboxylative activity of RuBisCO (Losciale et al., 2015; 2023). Measurements were taken three times a day (morning, noon, and afternoon) on well-exposed leaves. For each monitored tree, nine fully expanded and sun-exposed leaves were selected for gas exchange and chlorophyll fluorescence measurements; light intensity was standardized across the three treatments by adjusting the LED light source to match the levels naturally intercepted by the leaves. Reference temperature was maintained at ambient conditions while the reference CO_2 concentration was controlled and maintained at 400 ppm, with a flow rate set at 500 μmol s^{-1} to ensure adequate air mixing and measurement stability. Simultaneously, stem water potential (Ψ_s, MPa) was measured on the same trees by sampling two leaves per plant using a Scholander-type pressure chamber (Naor et al., 1995), following the same daily measurement schedule as gas exchange. Data collected at the three time points were averaged to obtain a representative daily value for each tree. From fruit-set to the harvest fruit growth was monitored on 10 fruits for each tree measuring fresh and dry weight of fruits and seeds. At harvest, the potential seed yield (t ha^{-1}), the production of fruits with adherent hulls (t ha^{-1}), and water productivity (kg of seeds per cubic meter of irrigation water supplied) were evaluated using trees from the middle row of each treatment. while fruit growth and weight and yield components were assessed on a sample of eighteen fruits for volume measurements. Soil moisture probes were installed along the monitored rows to continuously track soil water content throughout the season.

2.4. Experimental design and statistical analysis

Physiological and agronomic data were analysed separately for each

measurement date. After assessing the normality and homogeneity of variances by means of Shapiro–Wilk and Levene's tests, respectively, each variable was subjected to a one-way analysis of variance (ANOVA) considering the irrigation treatments as factor; mean separation was performed using the Tukey post-hoc test. Relationships among ecophysiological, microclimatic, and pedological variables were analysed through linear regressions, Pearson's correlation analyses and Principal Component Analysis (PCA).

ANOVA, Tukey HSD, regression analyses, and correlation matrices were performed in Python 3.11.6 using the packages pandas, statsmodels, scipy.stats, seaborn, and matplotlib.

Principal component analysis (PCA) was performed separately using Statistica software (version 7.0; TIBCO Software Inc., Palo Alto, CA, USA).

3. Results

3.1. Pedo-climatic conditions and irrigation

Meteorological conditions differed markedly during the irrigation season from May to September (Table 1). The climatic conditions in 2021 were particularly dry, as evidenced by the air temperature (T_{air}), vapour pressure deficit (VPD) trends, and the low number of rainfall events. As temperatures rose from spring to summer, the average temperature increased from 17.3 °C in May to a peak of 26.5 °C in July, before dropping to 21.1 °C in September. The minimum and maximum temperatures, both reported as monthly averages, followed a similar trend, with the lowest values in May and the highest in July and August, reflecting the seasonal heat increase. The average vapour pressure deficit (VPD) mirrored the trend of air temperature, showing values of 0.8 kPa in May, peaking at 1.8 kPa in July, and dropping back to 0.8 kPa in September (Table 1). Reference evapotranspiration (ET_0) closely followed the temperature and VPD trends, peaking its maximum in July and decreasing during the cooler months; crop evapotranspiration (ETc) mirrored this pattern.

The irrigation season started on May 5th. The control treatment received around 280 mm of water over the season, while MRDI and SRDI received 244 and 210 mm, respectively. These differences were particularly notable in June and July, when irrigation volumes were differentiated among the treatments (Table 1). May experienced the least rainfall, necessitating an early start to the irrigation season compared to the usual irrigation schedule for this area. The seasonal pattern of soil water content recorded for the treatments under investigation showed peaks in SWC corresponding to irrigation events (Fig. 1). From early June, when the irrigation regimes were imposed, the three treatments became differentiated, with SRDI reaching values below the lower threshold of readily available water (Fig. 1).

3.2. Fruit growth dynamics

Full bloom occurred on March 1st Fruit growth dynamics were monitored across the season to track phenological development under the different irrigation regimes (Fig. 2). During the first phase of fruit development, approximately up to 86 days after full bloom (DAFB), a rapid increase in fruit fresh weight was observed across all treatments. This phase corresponds to the rapid cell division. After 86 DAFB, the increase of fruit weight slowed significantly while seed dry weight exhibited a marked increase from 100 DAFB onward, reflecting the accumulation of dry matter within the seed tissues. Fruit growth variables were not significantly affected by the irrigation treatments.

3.3. Impact of water deficit on canopy functionality and water status

Following the beginning of the differentiated irrigation treatments, ecophysiological measurements were carried out on 15/06, 01/07, 13/07, 29/07, 24/08, and 23/09, corresponding to 106, 122, 134, 150, 176, and 206 days after full bloom (DAFB), respectively. Excluding 176 DAFB, the soil water content of CTRL was always within the range of readily available water (between 418.5 and 364.5 m^3 ha^{-1}, Fig. 3A). At 176 DAFB, one day before harvest, all the treatments experienced a 10-day irrigation withdrawal to allow bark dehydration and prevent potential damage during trunk shaking.

In MRDI, the soil water content was slightly lower than CTRL, with values below the threshold of readily available water recorded at 134 and 176 DAFB. SRDI showed the lowest SWC throughout the kernel-filling period, with values below the threshold of readily available water at both 134 and 176 DAFB (Fig. 3A).

During the measurement period, both T_{air} and VPD followed a similar trend throughout the season, increasing from 106 DAFB and peaking at 42 °C and 7 kPa at 150 DAFB. After this date, both variables began to decline, reaching their minimum values by the end of the season at 206 DAFB (Fig. 3B).

At 106 DAFB, the differentiated irrigation regimes had been established for just one day; net photosynthesis (Pn) and stomatal conductance (gs) were the highest of the season (Fig. 4A, B). CTRL, reaching the highest values, was statistically different from SRDI and MRDI for stomatal conductance (Fig. 4A, B). By 122 DAFB, a decline in both variables was observed across all treatments, with SRDI showing the steepest

Table 1
Monthly average microclimate data and irrigation treatments applied during the year. Data include monthly averages of air temperature (T_{av}, T_{min}, T_{max}, °C) and average vapor pressure deficit (VPD, kPa), as well as reference evapotranspiration (ET_0, mm), crop evapotranspiration (ETc, mm), and precipitation (mm). Considering that the orchard was irrigated with a micro-irrigation system and that the fraction of the soil surface wetted and explored by the greater part of the rooting system was 30 %, ET_0, ETc and the rainfall were dimensioned accordingly. Irrigation treatments are categorized as control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI), with total irrigation amounts listed for each treatment over the season. ETc for January, February, November and December were not considered as the trees were in dormancy without leaves.

Month	T_{av} (°C)	T_{MIN}	T_{MAX}	VPD (kPa)	ET_0 (mm)	ETc	$IRR_{(CTRL)}$	$IRR_{(MRDI)}$	$IRR_{(SRDI)}$	Rainfall
January	7.04	3.92	10.01	0.20	10.09	–	0.00	0.00	0.00	39.94
February	8.39	4.60	12.70	0.22	14.85	–	0.00	0.00	0.00	9.98
March	8.42	3.90	12.45	0.30	22.91	10.31	0.00	0.00	0.00	27.27
April	10.67	6.00	15.00	0.34	31.22	21.86	0.00	0.00	0.00	23.66
May	17.30	11.70	22.80	0.80	53.34	45.36	49.80	47.00	44.20	3.00
June	23.90	16.50	29.90	1.60	68.71	67.34	50.76	39.48	28.20	8.43
July	26.50	19.60	32.60	1.80	73.01	74.52	81.80	67.70	53.60	8.91
August	26.20	20.50	32.10	1.60	63.56	65.49	56.40	50.80	45.10	8.07
September	21.10	16.30	26.10	0.80	41.34	39.27	39.48	39.48	39.48	19.95
October	15.16	11.94	19.26	0.37	21.59	16.84	0.00	0.00	0.00	24.54
November	13.99	11.37	16.77	0.18	12.54	–	0.00	0.00	0.00	69.69
December	9.52	6.81	12.32	0.24	9.51	–	0.00	0.00	0.00	68.67
Total					422.65	340.97	278.24	244.46	210.58	321.09

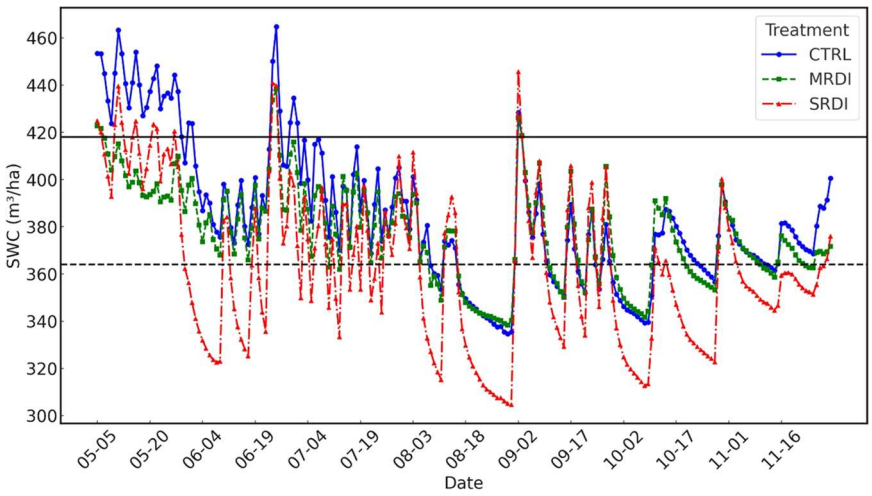

Fig. 1. Temporal trends of soil water content (SWC, m^3/ha) under three irrigation treatments: CTRL (control, blue), MRDI (moderate deficit, green), and SRDI (severe deficit, red) over the observation season. Horizontal lines represent the thresholds of the readily available water reserve: 418 m^3/ha (solid black line) and 364 m^3/ha (dashed line).

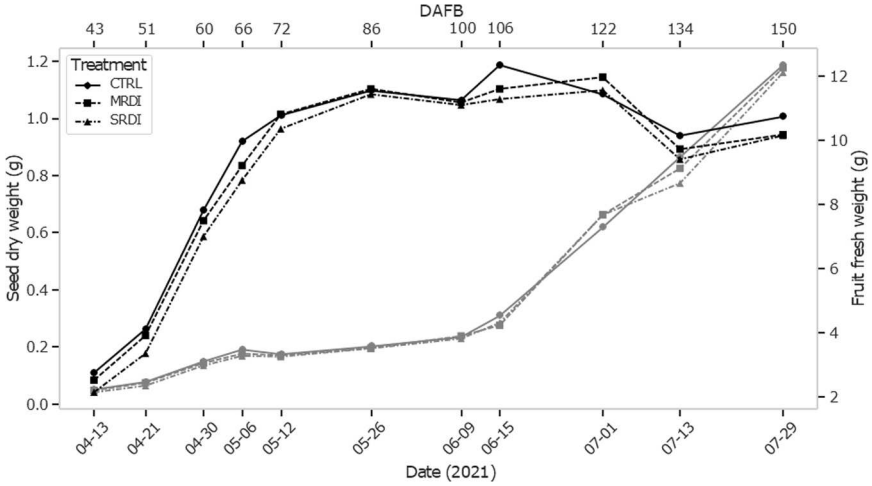

Fig. 2. Seasonal progression of seed dry weight (left axis, g) and fruit fresh weight (right axis, g) measured at different sampling dates during the 2021 growing season. Numbers at the top indicate days after full bloom (DAFB).

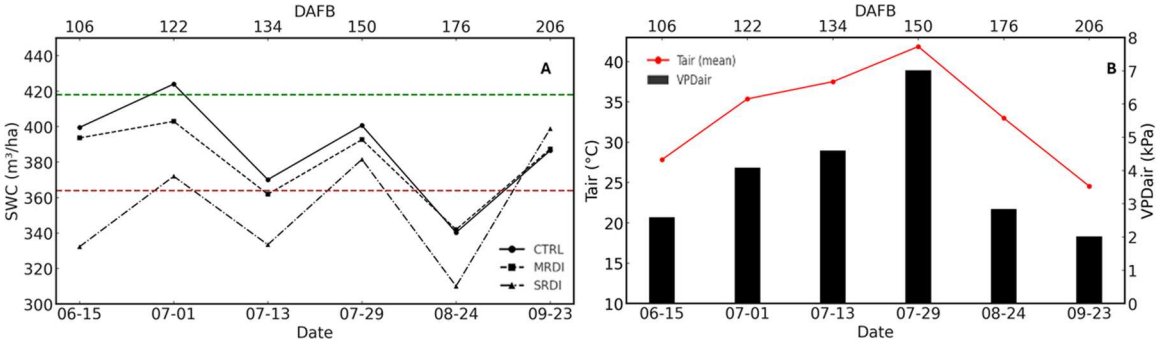

Fig. 3. Microclimatic variables and soil moisture during ecophysiological measurements under different irrigation regimes: control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI). Panel A shows soil water content (SWC, m^3/m^3), while Panel B illustrates average air temperature (T_{air}) and vapor pressure deficit (VPD_{air}). Measurements were performed on multiple dates (days after full bloom, DAFB). Horizontal lines represent the thresholds of the readily available water reserve: 418 m^3/ha (green line) and 364 m^3/ha (brown line).

reduction. By 134 DAFB, Pn and gs continued to decline in the severe water-stressed treatment, which recorded the lowest values of 5.5 μmol m^{-2} s^{-1} for net photosynthesis and 0.08 mol m^{-2} s^{-1} for stomatal conductance at 150 DAFB (Fig. 4A, B). At 176 DAFB, Pn in SRDI began to increase again (~9 μmol m^{-2} s^{-1}), reaching similar values to MRDI, while CTRL maintained almost the same level of Pn . After the harvest, all

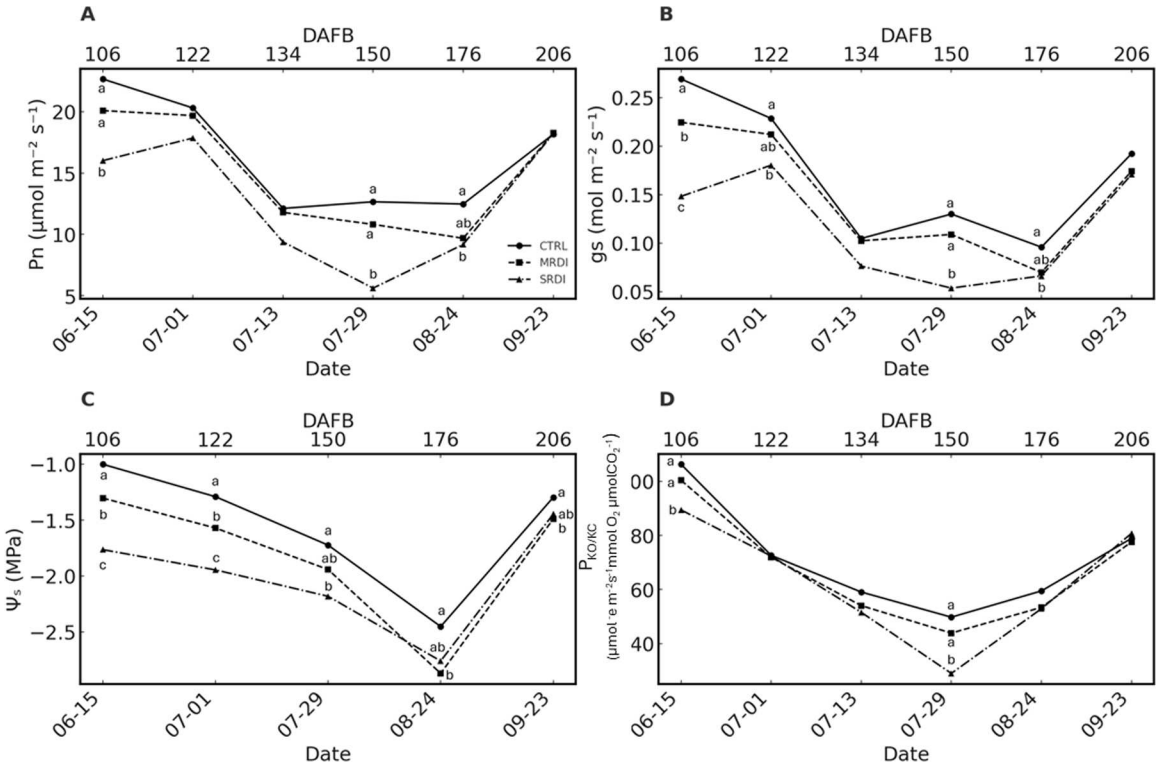

Fig. 4. Seasonal dynamics of key ecophysiological variables in almond trees under different irrigation treatments performed on multiple dates (days after full bloom, DAFB): control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI). Panel A shows net photosynthesis (Pn, μmol m^{-2} s^{-1}); Panel B displays stomatal conductance (gs, mol m^{-2} s^{-1}); Panel C illustrates stem water potential (Ψ_s, MPa); and Panel D presents the electron flux from PSII and the carboxylative activity of RuBisCO ($P_{KO/KC}$). Significant differences among treatments are denoted by different letters ($p = 0.05$).

treatments were fully irrigated, and at 206 DAFB, net photosynthesis increased to around 18 μmol m^{-2} s^{-1}. Although not statistically significant at 206 DAFB, the water-stressed treatments showed a gs slightly lower than the control (Fig. 4B). Comparing Pn and gs values at 106 and 206 DAFB, those recorded at 206 DAFB did not fully reach the levels observed in June, despite similar environmental conditions such as light intensity, air temperature, and VPD (Fig. 3). At the beginning of the differentiated water supply, stem water potential (Ψ_s) was the highest in CTRL (−1.0 MPa), followed by MRDI and SRDI, with Ψ_s values of −1.3 MPa and −1.7 MPa, respectively. This difference among the three treatments was maintained throughout the season until 150 DAFB, during which a general decline in Ψ_s was observed, culminating at 176 DAFB (Fig. 3C). At 176 DAFB, all treatments showed their most negative Ψ_s values, with differences between CTRL (−2.45 MPa) and the other treatments (~−2.78 MPa). Following full irrigation after harvest, Ψ_s increased, with CTRL showing the most significant recovery, reaching approximately −1.3 MPa, followed by SRDI and MRDI, which exhibited stem water potentials of around −1.5 MPa (Fig. 4C).

$P_{KO/KC}$, a new variable accounting for both the electron flux exiting PSII and the carboxylative activity of RuBisCO, displayed a trend similar to that observed for Pn, gs, and Ψ_s(Fig. 4D). At 106 DAFB, $P_{KO/KC}$ values were initially high, with significant differences between CTRL and SRDI. Like the other variables, $P_{KO/KC}$ declined over the following dates, reaching minimum levels at 150 DAFB. In contrast, Ψ_s showed its lowest values at 176 DAFB (Fig. 4D). Following full irrigation after harvest, $P_{KO/KC}$ increased, with no significant differences observed among treatments (Fig. 4D).

The fluorescence data analysis enabled the evaluation of differences in photochemical parameters across various irrigation treatments over the season. Specifically, J_{PSII} and J_{NC} represented the electron transport

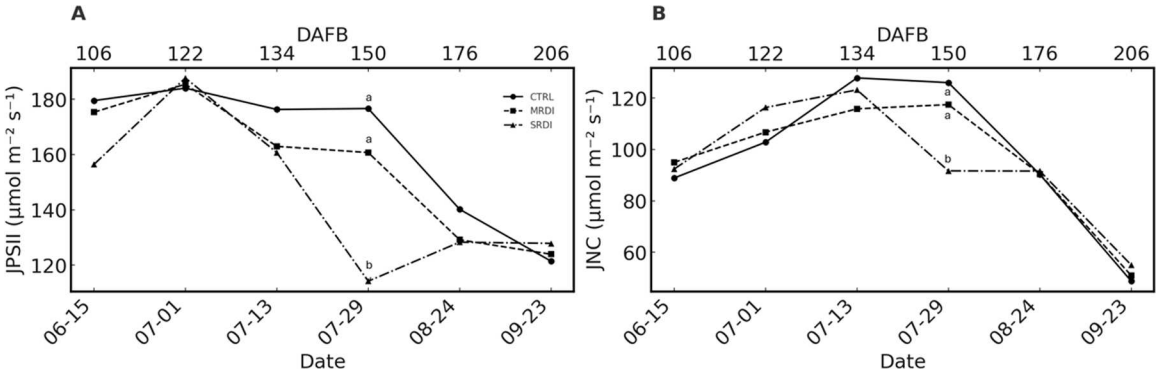

Fig. 5. Seasonal trends of electron transport rate exiting from PSII (J_{PSII}, panel A) and directed to non-net carboxylative pathways (J_{NC}, panel B) under different irrigation treatments: control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI). Measurements were performed on multiple dates (days after full bloom, DAFB). Significant differences among treatments are denoted by different letters ($p = 0.05$).

rates exiting from PSII and directed to photoprotective non-net carboxylative pathways, respectively (Fig. 5). In CTRL, J_{PSII} remained relatively stable until 150 DAFB; after this date, a decrease was observed (Fig. 5A). The same trend was observed in MRDI; however, after 122 DAFB, J_{PSII} began to decline more sharply, reaching its lowest value at 206 DAFB (124 μmol e^- m^{-2} s^{-1}). SRDI exhibited the most dramatic reduction, reaching its minimum at 150 DAFB (114 μmol e^- m^{-2} s^{-1}). The electron transport rate directed to photorespiration and alternative electron pathways (J_{NC}) was similar among treatments until 134 DAFB (Fig. 5B). For CTRL and MRDI, J_{NC} increased until 150 DAFB, corresponding to stable J_{PSII} (Fig. 5A) and declining Pn (Fig. 4A). In SRDI, J_{NC} decreased from 134 to 150 DAFB, corresponding to the lowest levels of J_{PSII} (Fig. 5A) and Pn (Fig. 4A), with values significantly lower than the other treatments. Afterward, J_{NC} decreased similarly among the three treatments (Fig. 5B).

At the beginning of the differentiated irrigation regime, ΔT values for the CTRL and MRDI treatments were close to zero, while SRDI exhibited a significantly positive ΔT of approximately 0.25 °C (Fig. 6A). As the season progressed (DAFB 134), ΔT increased, particularly in SRDI, where the temperature difference reached around 1 °C. At DAFB 150, following an increase in SWC due to irrigation and in correspondence with the highest values of T_{air} and VPD (Fig. 3B), ΔT decreased in the CTRL and MRDI treatments, while SRDI showed another peak, reaching approximately 1.25 °C. On this date, leaf temperature (T_{leaf}) also increased, exceeding 40 °C, with significant differences between CTRL, MRDI, and SRDI (Fig. 6B). At DAFB 176, when all treatments experienced water shortage, ΔT values for CTRL and MRDI increased, reaching 0.75 °C and 1 °C, respectively, while SRDI remained relatively stable (Fig. 6A). By the end of the season (DAFB 206), ΔT values remained high, peaking at 1.3 °C, 1.5 °C, and 1.4 °C for CTRL, MRDI, and SRDI, respectively.

3.4. Relationship among the variables

The correlation analysis revealed strong relationships among key ecophysiological variables, particularly gs, Pn, Ψ_s, and $P_{KO/KC}$ (Fig. 7A). Pn and gs were the most strongly correlated variables (r = 0.97), followed by $P_{KO/KC}$ with Pn (r = 0.89), gs with Ψ_s (r = 0.87), and Ψ_s with Pn (r = 0.82). Among plant functionality-related variables, Ψ_s and E showed the highest correlation with soil water content (r = 0.69 and 0.71, respectively), followed by gs (r = 0.65) and Pn (r = 0.58). Pn, gs, and $P_{KO/KC}$ exhibited negative correlations with vapor pressure deficit (VPD_{air}), with r values of −0.55, −0.42, and −0.72, respectively. A negative correlation was observed between T_{leaf} and Pn, gs, and $P_{KO/KC}$. Additionally, ΔT showed a strong negative correlation with both J_{PSII} and the transpiration rate (E), with r values of −0.85 in both cases. There was a moderate positive correlation between J_{PSII} and Pn (r = 0.49) and between E and gs (r = 0.60). Furthermore, J_{NC} displayed a strong positive correlation with air temperature (r = 0.79).

Although the full set of daily stem water potential (Ψ_s) measurements was used in statistical analyses, we also evaluated the relationship between midday values (Ψ_{ms}) and the daily average. As shown in Supplementary Figure S1, Ψ_{ms} was strongly correlated with the daily average Ψ_s (R^2 = 0.88), suggesting that midday measurements can serve as a reliable proxy for daily water status in operational irrigation monitoring.

The PCA revealed that Factor 1 and Factor 2 explained >87 % of the variance (Fig. 7B). J_{PSII}, J_{NC}, E, and ΔT were closely aligned with each other and strongly associated with Factor 2. Pn, gs, $P_{KO/KC}$, and Ψ_s were grouped together and associated with Factor 1. Pedo-climatic variables such as SWC, VPD, and T_{air} contributed equally to the determination of both factors (Fig. 7B).

The regression analysis revealed a strong linear relationship between Pn and gs (R^2 = 0.94), Pn and $P_{KO/KC}$ (R^2 = 0.77), and Pn and Ψ_s (R^2 = 0.66). Additionally, a direct linear relationship was observed between stomatal conductance and Ψ_s (R^2 = 0.76) (Fig. 8). While Pn declined almost linearly with decreasing stomatal conductance (Fig. 8A), J_{PSII} remained nearly constant up to gs ≈ 0.11 mol m^{-2} s^{-1} and then decreased (Fig. 9), in agreement with a breakpoint at gs = 0.110 mol m^{-2} s^{-1} derived by the application of a segmented-regression model (95 % confidence interval (CI) 0.087–0.153).

3.5. Irrigation and yields

Yields components under MRDI and SRDI treatments showed no statistically significant differences from the control (Table 2). SRDI resulted in higher hull tight yields compared to CTRL and MRDI, hence yield per hectare of regular fruit was slightly lower under SRDI (0.98 t ha^{-1}). Both deficit irrigation treatments achieved water savings, with MRDI showing an 12.1 % reduction in water use and SRDI achieving a 24.3 % reduction relative to the control. During the kernel filling period, SRDI received and MRDI received 41.4 % and 20.7 % less water than the control. Water productivity (kg m^{-3}) was slightly higher in SRDI and MRDI in comparison with CTRL (Table 2).

4. Discussion

4.1. Seasonal gas exchange dynamics and phenological constraints

In June, Ψ_s values around –1.0 MPa were recorded in the CTRL treatment, consistent with fully irrigated almond orchards as reported in previous studies (Espadafor et al., 2017; Fereres and Goldhamer, 2003; Shackel, 2011; Sperling et al., 2023). In kernel filling stage a general decline in Pn, gs, and Ψ_s was observed (Fig. 4), indicating that gas exchange in almond trees may be regulated by concurring factors such as atmospheric conditions (Palma and Novello, 1996) and plant

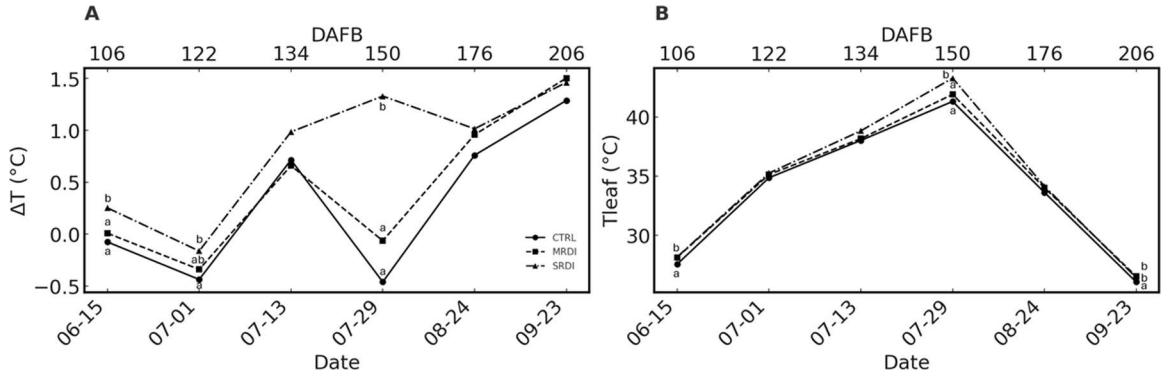

Fig. 6. Seasonal variations in leaf-to-air temperature difference (ΔT, panel A) and leaf temperature (T_{leaf}, panel B) under different irrigation treatments in almond trees: control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI). Measurements were performed on multiple dates (days after full bloom, DAFB). Significant differences among treatments are denoted by different letters (p = 0.05).

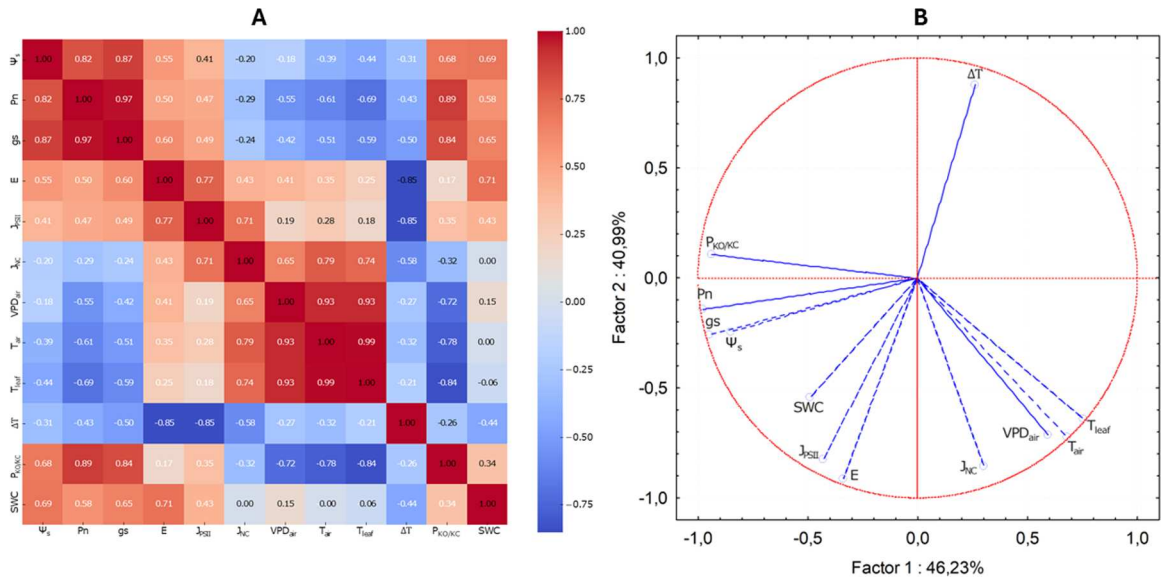

Fig. 7. Correlation matrix (A) and principal component analysis (PCA) biplot (B) of ecophysiological and environmental variables measured during the growing season under different irrigation treatments. The correlation matrix illustrates the strength and direction of relationships among variables, with warmer colours indicating positive correlations, cooler colours indicating negative correlations, and white numbers representing significant correlations ($p = 0.05$). The PCA biplot displays the distribution of variables along two principal components (Factor 1 and Factor 2), which explain 46.23 % and 40.99 % of the variance, respectively. Vectors indicate the contribution of each variable to the principal components, highlighting patterns and associations that characterize plant responses to water stress.

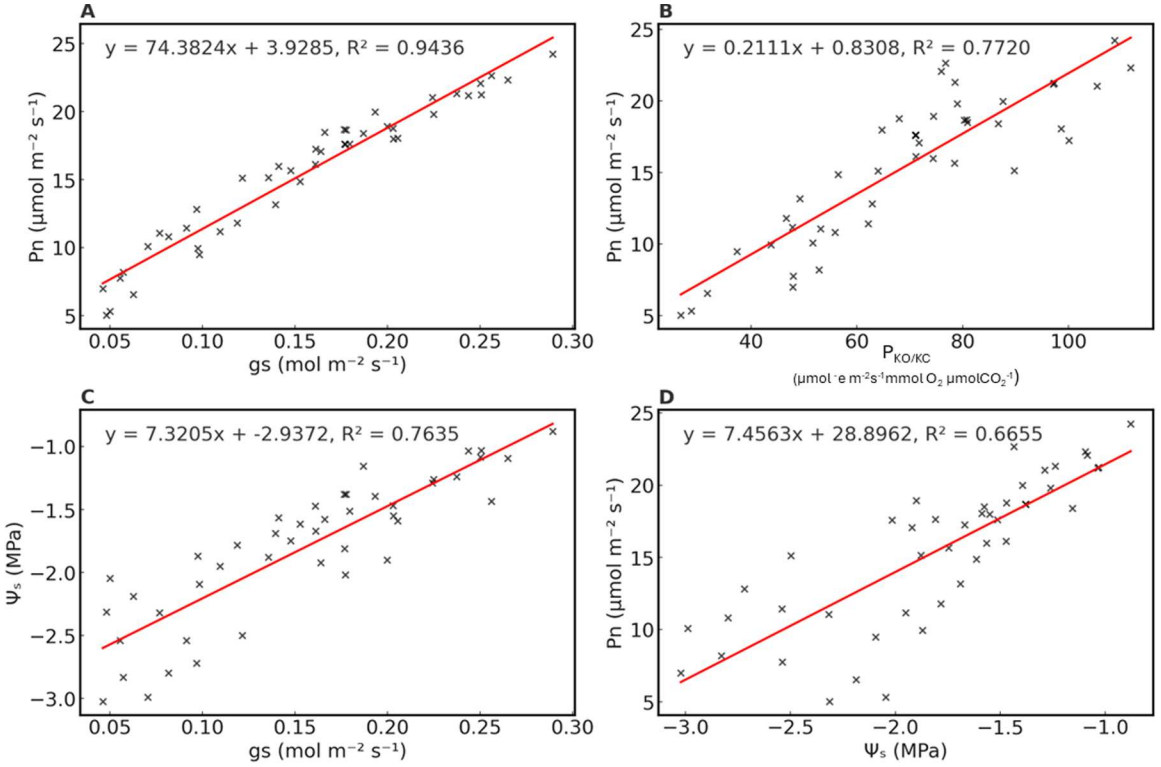

Fig. 8. Linear regressions showing the relationships between physiological variables measured on almond leaves during the kernel-filling stage. (A) Relationship between net photosynthetic rate (Pn, µmol m^{-2} s^{-1}) and stomatal conductance (gs, mol m^{-2} s^{-1}). (B) Relationship between Pn and the $P_{KO/KC}$ index (µmol $^{-}$e $m^{-2}s^{-1}$mmol O_2 µmolCO_2^{-1}), which expresses the efficiency of carboxylative use of electrons exiting from PSII based on chlorophyll fluorescence and leaf temperature. (C) Relationship between gs and stem water potential (Ψ_s, MPa. (D) Relationship between Pn and Ψ_s. All regressions were highly significant ($p < 0.001$), with R^2 values indicating strong correlations in each case.

developmental stage (Ruiz-Sánchez et al., 1988). Excluding August 24th (when all the treatments were subjected to a severe water restriction), Ψ_s in CTRL declined although the soil water content was always within the range of the readily available water (Fig. 3), likely due to extremely high VPD conditions (> 5–7 kPa). However, the physiological variables related to leaf functionality showed values close to the optimal range

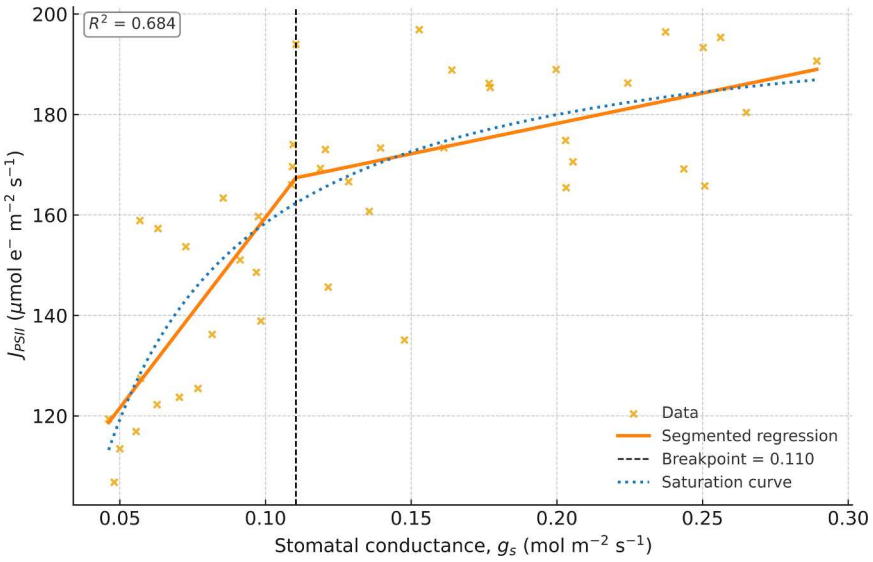

Fig. 9. Relationship between stomatal conductance (g_s; mol m^{-2} s^{-1}) and the electron-transport rate through PSII (J_{PSII}; µmol e^- m^{-2} s^{-1}) in almond leaves. A segmented regression (solid line) identifies a breakpoint at gs ≈ 0.11 mol m^{-2} s^{-1} (vertical dashed line), indicating a transition to a flatter response of J_{PSII}. Data were fitted using a saturation model (red line). The coefficient of determination (R^2) indicates the goodness of fit of the model to the observed data.

Table 2
Yield components, water savings, and water productivity under different irrigation treatments (CTRL, MRDI, SRDI) for almond production. Variables include total seed yield (t ha^{-1}), tight hull yield (t ha^{-1}), and net yield (t ha^{-1}). Water saving (%) represents the reduction in water supply compared to the control treatment, with additional water savings specifically during the kernel filling period. Water productivity is expressed as kg of yield per m^3 of water supplied (kg m^{-3}). Significant differences among treatments are indicated by different letters ($p = 0.05$).

TRT	Tot. seed		Hull tight		Yield	Water saving		Water saving at kernel filling		Water productivity
	(t ha^{-1})					(%)				(kg m^{-3})
CTRL	1.20	b	0.05	b	1.15	0	c	0	c	0.41
MRDI	1.15	b	0.04	b	1.11	12.1	b	20.7	b	0.45
SRDI	1.28	a	0.31	a	0.98	24.3	a	41.4	a	0.46

typically reported for this phenological stage in other studies conducted under similar environmental conditions (Gutierrez Gordillo et al., 2019 Klein et al., 2001; Romero et al., 2004). It is reported that during seed filling, even well-irrigated trees showed a reduction in canopy photosynthetic activity and stomatal conductance due to a shift in source–sink relationships and a progressive canopy senescence (Ruiz-Sánchez et al., 1988; Torrecillas et al., 1996). The overall seasonal decline in gas exchange variables during the kernel-filling stage can be partly attributed to phenological changes . Recent findings by Gutiérrez-Gordillo et al. (2023) demonstrated that in almond trees, including cv. 'Guara', a progressive limitation in triose phosphate utilization (TPU) and a downregulation of J_{max} (the maximum rate of electron transport driving RuBP regeneration in the Calvin cycle) occurred during this stage, reflecting a reduced sink strength and photoassimilates demand. The significantly stronger decline in gs and Pn observed during the kernel filling in MRDI and SRDI compared to CTRL demonstrated that water shortage, lead to earlier and more severe reductions in canopy functionality (Fig. 4).

4.2. *The role of soil and atmospheric factors in limiting tree functionality*

Comparing the date of 122 and 150 DAFB the soil water conditions were quite similar and within the range of the readily available water (Fig. 3A). However, the very high VPD and air temperature recorded at 150 DAFB induced the plant to close the stomata reducing the CO_2 intake (Fig. 4A,B). In addition, high temperature could have produced nonstomatal limitation to the photosynthetic process as it was more favourable to photorespiration rather than carbon assimilation (Karimi et al., 2015). At 150 DAFB, SRDI showed a consistent reduction of the electron transport rate exiting from PSII (Fig. 5A) due to the photosynthetic limitation. The absorbed energy no longer funnelled to the photochemistry was reasonably dissipated by the non-photochemical processes (J. Flexas et al. 2002). The reduction of the electron transport rate exiting from the PSII caused a consequent decrease in J_{NC} (electron transport rate exiting from the PSII but funnelled to non-net carbonylative transports; Losciale et al., 2010) in absolute terms (Fig. 5B). At 122 DAFB the percentage of electrons exiting from PSII and funnelled to photorespiration and the alternative electron transports (J_{NC} / J_{PSII}), was around 57 %, it for CRTL and MRDI, and 62 % for SRDI, respectively; it reached to ~73 % and 82 % at 150 DAFB, highlighting that the net carbon assimilation was even worsened by the increase of decarboxylation processes (Adams and Demmig-Adams, 2004). These results suggested that it would be desirable to couple atmospheric and plant measures to soil water content monitoring as the same soil water content could be appropriate in one case and limiting in another one. Water restriction induced a reduction of Ψ_s in MRDI and SRDI in comparison with CTRL; however, excluding at 176 DAFB, in moderate regulated deficit irrigation (MRDI), Pn and gs were not statistically affected (Fig. 4). Stomatal opening sustained carboxylation (Fig. 4A) as well as leaf thermoregulation (Fig. 6B) and the photochemistry balance (Fig. 5). In SRDI the high level of water restriction increased the potential imbalance between water absorption and loss, with the consequent reduction of Ψ_s, stomatal opening and Pn (Fig. 4). A midday stem water potential of −1.8 MPa was found as a safe threshold below which lower photosynthetic rates and leaf abscission was observed in Nonpareil variety (Klein et al., 2001). The severe water stress in SRDI by DAFB 150 reduced Pn and gs by approximately 55 % and 60 %, respectively. Karimi et al. (2015) similarly found that in drought-sensitive genotypes,

Pn and gs were reduced by 70 % and 97 %, respectively, under water deficiency. These findings align with other studies reporting the effects of drought stress on Pn in almonds (De Herralde et al., 2003; Romero et al., 2004; Isaakidis et al., 2004; Karimi et al., 2015). Leaf functionality, namely Pn, gs, $P_{KO/KC}$, was dependent by several factors and not exclusively by the soil water content (Velazquez-Chavez et al., 2024). The correlation analysis as well as the PCA results showed a significant correlation of these variables with the pedo-climatic conditions and with the level of hydration of the tree (Ψ_s), both concurring at determining the Factor 1 (Fig 7B). Comparing 122 with 150 DAFB in SRDI, it was possible to observe that a similar SWC, within the range of the readily available water, was enough to maintain the leaf gas exchanges at the same level of CTRL at 122 DAFB but not at 150 DAFB where air temperature and VPD became the main limiting factors (Fig. 3B, Fig. 4A).

4.3. Photoprotective responses and electron partitioning under stress

From a bioenergetic perspective, the reduction in the photosynthetic rate (one of the electron-consuming processes) in SRDI induced feedback inhibition of the electron flux density exiting from PSII (Fig. 5A), likely in favour of Non-Photochemical Quenching (Adams and Demmig-Adams, 2004). The importance of the photoprotective action of non-net carboxylative transports (Fig. 5B) progressively increased, quenching approximately 82 % of the electrons exiting from PSII at 150 DAFB. The weak relationship between Pn and J_{PSII} was showed by the correlation analysis and by PCA (Fig. 7), also depicting the weak contribution of this variable in determining the Factor 1, representing the functionality features of the canopy (Pn, gs, Ψ_s). In almond trees subjected to moderate water stress, reductions in Pn and gs did not significantly affect the electron transport rate (J_{PSII}), which was likely sustained by alternative non-net carboxylative processes (J_{NC}) such as photorespiration and alternative electron transports (Fig. 9). This behaviour has been observed in other fruit species, including grapevine, apple, pear, peach and apricot (J. Flexas et al., 2002; Losciale et al., 2015, 2023). The negative influence of high temperatures on the carboxylation efficiency of the leaves was also revealed by the correlation with Pn and J_{NC}, negative with the former ($r = -0.61$) and positive with the latter variable ($r = 0.79$) (Fig. 7A). The optimum temperature for carboxylative activity of RuBisCO is around 27–30 °C, above this range photorespiration (J_{NC}) was more facilitated at the expense of carboxylation (von Caemmerer, 2000). This photoprotective shift was also reported in other C_3 fruit trees (Noctor et al., 2002) and across the *Prunus* genus (Losciale et al., 2023), indicating that non-net carboxylative processes such as photorespiration play a crucial role in dissipating excess energy under stress conditions. Consistent with the hypothesis of a threshold-type response, the relationship between gs and J_{PSII} exhibited a distinct breakpoint. The segmented regression (continuous piecewise linear fit) identified a threshold at gs = 0.110 mol m^{-2} s^{-1}. Below this threshold, the slope was steep, whereas above it the response flattened markedly. Thus, while Pn declined almost linearly with decreasing stomatal conductance (Fig. 8A), J_{PSII} remained comparatively stable until gs ≈ 0.10–0.11 mol m^{-2} s^{-1} thanks to the activity of the non-net carboxylative transports (J_{NC}), after which it decreased (Fig. 9). This change in slope is consistent with an enhanced diversion of absorbed energy towards non-photochemical dissipation under stress, as previously reported for C_3 fruit trees.

4.4. Stomatal conductance as an indicator of tree water status

Stomatal conductance variation is one of the earliest physiological responses to stress and represents a primary limitation to photosynthesis under mild to moderate drought conditions (J Flexas et al., 2002). It is regulated by a complex interplay of factors, including soil water content, plant water potential, light intensity, atmospheric CO_2 concentration, humidity, temperature, wind, leaf water status, intercellular CO_2 levels, and chemical signals such as abscisic acid and cytokinins (Assmann and Shimazaki, 1999). The lowest values of Pn (5.62 μmol m^{-2} s^{-1}) and gs (0.05 mol m^{-2} s^{-1}) were observed in the SRDI treatment at 150 DAFB, whereas in the CTRL and MRDI treatments, these reductions occurred at 176 DAFB caused by the decrease in SWC imposed during the harvest period (Fig. 4A,B). This behaviour suggested that trees under severe water stress closed their stomata earlier to mitigate the risk of cavitation caused by the high vapor pressure deficit conditions (~7 kPa) of 150 DAFB (Fig. 3B). The photosynthetic rate is widely regarded as a key physiological indicator of stress tolerance (Ashraf, 2004), as it is genetically dependent and strongly correlated with both transpiration and stomatal conductance. This study found similar correlations, reflecting patterns observed in previous research on almond, where reductions in Pn and gs were observed as water restriction increased (Romero and Botía, 2006; Rouhi et al., 2007). This trend is common in drought-adapted species (Romero et al., 2004). The close relationship observed between Pn and gs (Fig. 7A), suggested that stomatal closure was a primary limiting factor for photosynthesis in almond (Prgomet et al. 2020), a relationship similarly observed in other studies on the same specie (Girona et al., 1993; Marsal et al., 1997). Romero and Botía (2006) reported that the key factors influencing gs are Ψ_s and VPD, consistent with the findings of the present study, where the correlations of gs with VPD, Ψ_s, and SWC were significant (Fig. 7). Drought stress limits stomatal conductance, restricting CO_2 transport to the chloroplasts (Flexas et al., 2008) and affecting mesophyll mechanisms, including the synthesis of the RuBisCO enzyme, thereby reducing photosynthetic capacity (Mahajan and Tuteja, 2005). This explains why SRDI consistently exhibited the lowest values for gs, Pn, throughout the growing season, particularly during the mid-season. The relation between gs and Ψ_s was linear (Fig. 8C), in contrast with specie or cultivar showing a drought avoidance strategy (Lauri et al., 2016; Losciale et al., 2023; Massonnet et al., 2007). In those cases, water shortage induced the rapid closure of stomata allowing the maintenance of water potential at a safe level to prevent the risk of cavitation (Álvarez-Maldini et al. 2022).

Although stomatal conductance (gs) typically represents one of the earliest physiological responses to water deficit (J. Flexas et al., 2002), in almond trees exposed to mild to moderate water stress (approximately –1.5 to –2.0 MPa), the decline in gs was often less marked than the concurrent decrease in water potential (Fig. 4B, C). This pattern suggests a limited stomatal sensitivity to declining Ψ in this species (Egea et al., 2011; Wartinger et al., 1990), with almonds frequently exhibiting substantial reductions in leaf or stem water potential before a sharp decline in gs becomes evident (García-Tejero et al., 2012, 2015). As a result, almond trees may sustain relatively high gs under moderate stress, supporting continued carbon assimilation and photosynthetic activity, thereby maintaining higher intrinsic water-use efficiency (McCutchan and Shackel, 1992; Rouhi et al., 2007).

In the present study, gs values at around 0.05 mol H_2O m^{-2} s^{-1} observed during the summer months indicated severe stress (Flexas et al., 2012). as well as in other drought-adapted species like grapevines (Escalona et al., 1999). In addition, in our study other concurring factors, such as photorespiration, emphasized by elevated leaf temperatures (> 40 °C), may have contributed to the observed limitations in photosynthesis (Yi et al., 2022; Losciale et al., 2014).

Given its strong correlations with both photosynthetic performance and plant water potential, and its rapid and non-invasive measurability we hypothesized that stomatal conductance (gs) represents a central variable for assessing plant response to deficit irrigation, due to its strong link with both photosynthetic activity and plant water status, and its rapid responsiveness to environmental conditions. These features support its use as a central variable in irrigation management strategies.

4.5. Recovery dynamics post-drought stress

Despite the significant reduction in photosynthesis during peak stress, the recovery of Pn in SRDI was relatively rapid, reaching

approximately 100 % of CTRL values within <30 days of resuming full irrigation (Fig. 4A). This rapid recovery of plant water status after drought stress has also been observed in young almond trees (Torrecillas et al., 1996) and other fruit trees, such as peaches (Goldhamer et al., 1999) and olive (Ahumada-Orellana et al., 2023). However, the speed of recovery may depend on the severity and the duration of the water stress imposed (Han et al. 2016). Various responses have been observed in water-stressed almond trees, ranging from partial recovery (Klein et al., 2001) to a swift recovery of photosynthetic capacity (Alvarez et al., 2020), with the specific response largely depending on the almond variety. Like other drought-tolerant plants, almonds possess a photosynthetic apparatus that is resistant to dehydration and capable of recovering after periods of severe drought (Ni and Pallardi, 1992). In contrast to the rapid recovery of photosynthesis (Pn), stomatal conductance (gs) exhibited a slower response, reaching approximately 90 % of control values only by 206 DAFB—a delayed recovery pattern consistent with observations in other almond cultivars under water stress (Rouhi et al., 2007; Torrecillas et al., 1996). This lag suggests that the reopening of stomata and the restoration of gas exchange were likely modulated not only by improvements in leaf water status but also by root-derived chemical signals, as previously proposed (Wartinger et al., 1990).

4.6. *Implications for irrigation scheduling and functional monitoring*

The strong correlations between $P_{KO/KC}$ and both gs ($r = 0.84$) and Pn ($r = 0.89$) suggests that this variable, related to the electron transport rate and to the biochemical limitations of carboxylation efficiency, was closely tied to the regulation of stomatal conductance and photosynthesis. The relationship of $P_{KO/KC}$ with Pn ($R^2 = 0.77$) and gs ($R^2 = 0.79$) hints its possible use as an alternative variable to rapidly estimate the leaf functionality since its detection is based on the measure of chlorophyll fluorescence and leaf temperature (Coupel-Ledru et al., 2019).

This integrated framework improves the reliability of physiological assessments and offers promising avenues for developing advanced tools for irrigation management under deficit conditions. Moreover oxidative stress-related variables could be valuable for advancing our knowledge of drought-induced physiological processes and for characterizing genotype-specific responses at the biochemical level.

The fruit growth pattern revealed a certain decoupling between the increase of fruit weight and the accumulation of dry matter in the seed (Fig. 2), allowing the identification of the kernell filling stage. While the water restriction strongly affected the leaf functionality, the absence of difference in fruit growth among the three treatments indicated that mild and even severe deficit irrigation regimes applied during the kernel-filling stage did not compromise fruit and seed development under the environmental conditions of the current year. Despite SRDI receiving 41 % less irrigation than CTRL during the stress phase, there was no significant reduction in yield (Table 2). This suggests that almond trees are adapted to endure periods of water stress without affecting annual production. These findings align with other studies that reported no yield changes in the initial years of irrigation deficit imposition (Girona et al., 2005; Klein et al., 2001). This resilience could be attributed to the almond tree's ability to accumulate reserve substances for use in the following season (Gutiérrez-Gordillo et al., 2020). However, as observed in the present study (Table 2), intense stress during the seed filling phase could have led to an increase in adherent hulls, reducing the commercial productivity (Doll, 2017). The results confirmed that stomatal conductance (gs) seems to be a highly sensitive indicator of tree water status in almond. Based on the strong relationship observed between stomatal conductance, photosynthetic performance, and plant water status, gs was used as a dynamic indicator to guide irrigation during the kernel-filling phase in the 2023 trial. Irrigation was triggered when gs fell below 75 % (MRDIgs) or 50 % (SRDIgs) of CTRL values. This approach enabled the maintenance of gs within the desired physiological range for most of the stress period, confirming its sensitivity to soil water availability and its suitability for supporting regulated deficit irrigation strategies.

From 112 DAFB onwards, gs values in both MRDIgs and SRDIgs treatments declined toward ~0.1 mol m^{-2} s^{-1} (Fig. 10), a level that—based on 2021 observations—had been previously identified as a tentative threshold below which water stress might begin to constrain gas exchange processes. While no significant differences in yield were observed at harvest, a high incidence of adherent hull almonds (>90 %) was again recorded in the gs-based treatments, in line with prior findings.

Although a direct causal relationship cannot be established, this recurring pattern suggests that crossing this gs level could be associated with physiological conditions predisposing to impaired hull dehiscence. Future work should aim to validate this tentative threshold across seasons and genotypes, and to clarify its specific contribution from the cumulative effects of prolonged water stress. Nonetheless, these results highlight the potential of gs as a functional tool for irrigation scheduling, and its promise for anticipating fruit quality risks under deficit conditions.

5. Conclusion

The integration of results about stomatal conductance, photosynthetic rate, fluorescence and stem water potential, provided a complex picture of plant ecophysiological behaviour under different water regimes. Almond showed a drought tolerant behaviour as the reduction of stomatal opening was less rapid than the drought avoiding species/cultivars. This aptitude allowed the tree to sustain the carboxylation and thermoregulation even under moderate water shortage. Monitoring soil or microclimatic variables alone was insufficient to explain tree performance, as leaf functionality also depended on phenology and atmospheric conditions. A multivariate approach that includes plant-based indicators proved more informative. Stem water potential (Ψ_s) emerged as the most sensitive early indicator of water stress, while stomatal conductance (gs) acted as a dynamic regulator of gas exchange and photosynthesis (Pn) reflected downstream metabolic limitations. Together, these variables provided a coherent picture of plant responses, from early stress perception to functional decline.

Among irrigation strategies, SRDI imposed the strongest stress, whereas MRDI offered a more sustainable compromise, preserving functionality while reducing water use. This highlights the importance of multi-parameter approach for assessing and managing drought stress.

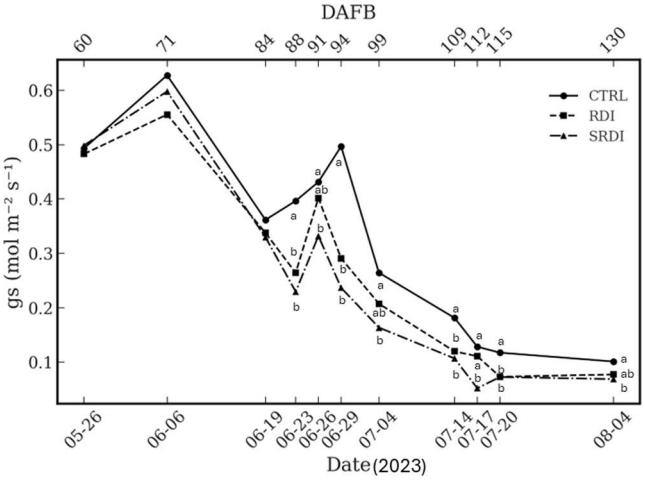

Fig. 10. Trends of stomatal conductance (gs) in 2023 under different irrigation treatments: control (CTRL), mild deficit irrigation (MRDI), and severe deficit irrigation (SRDI). Measurements were performed on multiple dates (days after full bloom, DAFB). Significant differences among treatments are denoted by different letters ($p = 0.05$).

Overall, gs represents a key integrative trait linking hydraulic status (Ψ_s) and carbon assimilation (Pn). Although direct measurement is impractical at field scale, it remains a valuable reference for developing indirect estimation models through remote sensing or physiological proxies such as the $P_{KO/KC}$ ratio.

Future research should expand the range of irrigation deficits tested, identify rapid and cost-effective indicators (including biochemical markers) of cultivar-specific drought responses, and integrate these into decision-support tools for irrigation scheduling and water-use optimization.

CRediT authorship contribution statement

Leonardo Conti: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Liliana Gaeta:** Investigation, Formal analysis, Data curation. **Michele Giannini:** Writing – original draft, Investigation, Data curation. **Anna D'Onghia:** Investigation. **Francesco Fabiano Montesano:** Formal analysis, Data curation. **Pasquale Losciale:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by Almond Management Innovation (AMì project): PSR PUGLIA 2014/2020 Sub-measure 16.2 Support for pilot projects and the development of new products, practices, processes and technologies. The opinions expressed in this work are the sole responsibility of the authors. The research was carried out under the project VALO.RE. I.N. CA.M.P.O. with financial support from the Italian Ministry of Agriculture, Food Sovereignty and Forestry (D.M. n. 667521; 12.30.2022).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2025.114442.

Data availability

Data will be made available on request.

References

Ahumada-Orellana, L., Ortega-Farias, S., Searles, P.S., Zúñiga, M., 2023. Leaf gas exchange, water status, and oil yield responses to rewatering after irrigation cut-off periods in a superintensive drip-irrigated olive (cv. Arbequina) orchard. Irrig. Sci. 41 (4), 557–570. https://doi.org/10.1007/s00271-022-00817-8.

Álvarez-Maldini, C., Acevedo, M., Estay, D., Aros, F., Dumroese, R.K., Sandoval, S., Pinto, M., 2022. Examining physiological, water relations, and hydraulic vulnerability traits to determine anisohydric and isohydric behaviour in almond (*Prunus dulcis*) cultivars: implications for selecting agronomic cultivars under changing climate. Front. Plant Sci. 13, 974050. https://doi.org/10.3389/fpls.2022.974050. Article.

Álvarez, S., Martín, H., Barajas, E., Rubio, J.A., Vivaldi, G.A., 2020. Rootstock effects on water relations of young almond trees (cv. Soleta) when subjected to water stress and rehydration. Water (Basel) 12 (12), 3319. https://doi.org/10.3390/w12123319.

Ashraf, M., 2004. Some important physiological selection criteria for salt tolerance in plants. Flora - Morphol. Distrib. Funct. Ecol. Plants 199 (5), 361–376. https://doi.org/10.1078/0367-2530-00165.

Assmann, S.M., Shimazaki, K., 1999. The multisensory guard cell: stomatal responses to blue light and abscisic acid. Plant Physiol. 119 (3), 809–816. https://doi.org/10.1104/pp.119.3.809.

Adams, W.W., Demmig-Adams, B., 2004. Chlorophyll fluorescence as a tool to monitor plant response to the environment. In: Papageorgiou, G.C., Govindjee (Eds.), *Chlorophyll a Fluorescence* (Advances in Photosynthesis and Respiration, *Chlorophyll a Fluorescence* (Advances in Photosynthesis and Respiration, 19. Springer, Dordrecht, pp. 583–604. https://doi.org/10.1007/978-1-4020-3218-9_22.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration. Guidelines for computing crop water requirements. FAO Irrig. Drain. Pap. 56.

Bellvert, J., Adeline, K., Baram, S., Pierce, L., Sanden, B.L., Smart, D.R., 2018. Monitoring crop evapotranspiration and crop coefficients over an almond and Pistachio orchard through remote sensing. Remote Sens. (Basel) 10 (12), 2001. https://doi.org/10.3390/rs10122001.

Berman, M.E., DeJong, T.M., 1996. Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*). Tree Physiol. 16, 859–864.

Blanco, V., Kalcsits, L., 2021. Microtensiometers accurately measure stem water potential in Woody perennials. Plants 10 (12), 2780. https://doi.org/10.3390/plants10122780.

Blanco, V., Willsea, N., Campbell, T., Howe, O., Kalcsits, L., 2023. Combining thermal imaging and soil water content sensors to assess tree water status in pear trees. Front. Plant Sci. 14, 1197437. https://doi.org/10.3389/fpls.2023.1197437.

Campbell, G.S., Campbell, M.D., 1982. Irrigation scheduling using soil moisture measurements: theory and practice. In: Hillel, D. (Ed.), Advances in Irrigation, Advances in Irrigation, 1. Academic Press, pp. 25–42.

Chen, Z., Li, S., Wan, X., Liu, S., 2022. Strategies of tree species to adapt to drought from leaf stomatal regulation and stem embolism resistance to root properties. Front. Plant Sci. 13, 926535. https://doi.org/10.3389/fpls.2022.926535.

Cifre, J., Bota, J., Escalona, J.M., Medrano, H., Flexas, J., 2005. Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.): an open gate to improve water-use efficiency? Agric. Ecosyst. Env. 106 (2–3), 159–170. https://doi.org/10.1016/j.agee.2004.10.005.

Coupel-Ledru, A., Pallas, B., Delalande, M., Boudon, F., Carrié, E., Martinez, S., Regnard, J.-L., Costes, E., 2019. Multi-scale high-throughput phenotyping of apple architectural and functional traits in orchard reveals genotypic variability under contrasted watering regimes. Hortic. Res. 6, 52. https://doi.org/10.1038/s41438-019-0137-3, 2019.

Damour, G., Simonneau, T., Cochard, H., Urban, L., 2010. An overview of models of stomatal conductance at the leaf level. Plant Cell Env. 33 (9), 1419–1438. https://doi.org/10.1111/j.1365-3040.2010.02181.x.

De Herralde, F., Biel, C., Savé, R., 2003. Leaf photosynthesis in eight almond tree cultivars. Biol. Plant 46 (4), 557–561. https://doi.org/10.1023/A:1024867612478.

De Swaef, T., Pieters, O., Appeltans, S., Borra-Serrano, I., Coudron, W., Couvreur, V., Garré, S., Lootens, P., Nicolaï, B., Pols, L., Saint Cast, C., Šalagovič, J., Van Haeverbeke, M., Stock, M., Wyffels, F., 2022. On the pivotal role of water potential to model plant physiological processes. In. Silico Plants. 4 (1), diab038. https://doi.org/10.1093/insilicoplants/diab038.

Dixon, M.A., Tyree, M.T., 1984. A new stem hygrometer, corrected for temperature gradients and calibrated against the pressure bomb. Plant Cell Env. 7 (9), 693–697. https://doi.org/10.1111/1365-3040.ep11572454.

Doll, D. (2017). Almond water requirements. In *Almonds: Botany, Production and Uses* (pp. 279–290). https://doi.org/10.1079/9781780643540.0279.

Domínguez-Niño, J.M., Oliver-Manera, J., Arbat, G., Girona, J., Casadesús, J., 2020. Analysis of the variability in soil moisture measurements by capacitance sensors in a drip-irrigated orchard. Sensors 20 (18), 5100. https://doi.org/10.3390/s20185100.

Doorenbos, J., Pruitt, W.O., 1977. Crop Water requirements. Irrigation and Drainage. FAO Irrigation and Drainage Paper No, p. 24.

Durán-Zuazo, V.H., Cárceles Rodriguez, B., Gutiérrez-Gordillo, S., Bilbao Benítez, M., Cermeño Sacristán, P., Pérez Parra, J.J., García-Tejero, I.F., 2020. Rethinking irrigated almond and pistachio intensification: a shift towards a more sustainable water management paradigm. Rev. Ciênc. Agrár. 43 (2), 24–49. https://doi.org/10.19084/rca.19651.

Egea, G., Dodd, I.C., González-Real, M.M., Domingo, R., Baille, A., 2011. Partial rootzone drying improves almond tree leaf-level water use efficiency and afternoon water status compared with regulated deficit irrigation. Funct. Plant Biol. 38 (5), 372–385. https://doi.org/10.1071/FP10247.

Egea, G., Padilla-Díaz, C.M., Martínez, J., Fernández, J.E., Pérez-Ruiz, M., 2017. Assessing a crop water stress index derived from aerial thermal imaging and infrared thermometry in super-high density olive orchards. Agric, Water Manag. 187, 210–221.

Escalona, J.M., Flexas, J., Medrano, H., 1999. Stomatal and non-stomatal limitations of photosynthesis under water stress in field-grown grapevines. Funct. Plant Bio. 26, 421–433. https://doi.org/10.1071/PP99019.

Fereres, E., Goldhamer, D., 2003. Suitability of stem diameter variations and water potential as indicators for irrigation scheduling of almond trees. J. Horticul. Sci. and Biotech. 78, 139–144. https://doi.org/10.1080/14620316.2003.11511596.

Fereres, E., Kitlas, P., Goldfien, R., Pruitt, W.O., Hagan, R.M., 1981. Simplified But Scientific Irrigation Scheduling, 35. California Agriculture, pp. 19–21.

Espadafor, M., Orgaz, F., Testi, L., Lorite, I.J., González-Dugo, V., Fereres, E., 2017. Responses of transpiration and transpiration efficiency of almond trees to moderate water deficits. Scientia Horticulturae 225, 6–14. https://doi.org/10.1016/j.scienta.2017.06.028.

Fereres, E., Goldhamer, D.A., 1990. Deciduous fruits and nuts. In: Stewart, B.A., Nielsen, D.R. (Eds.), *Irrigation of Agricultural Crops* (ASA Monograph, *Irrigation of Agricultural Crops* (ASA Monograph, 30. American Society of Agronomy, Madison, WI, pp. 987–1017.

Fernández, J.E., 2017. Plant-based methods for irrigation scheduling of Woody Crops. Horticulturae 3 (2), 35. https://doi.org/10.3390/horticulturae3020035.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002a. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and

mesophyll limitations. Funct. Plant Biol. 29 (4), 461–471. https://doi.org/10.1071/PP01119.
Flexas, J., Ribas-Carbó, M., Díaz-Espejo, A., Galmés, J., Medrano, H., 2008. Mesophyll conductance to CO_2: current knowledge and future prospects. Plant Cell Env. 31 (5), 602–621. https://doi.org/10.1111/j.1365-3040.2007.01757.x.
Flexas, J., Escalona, J.M., Evain, S., Gulías, J., Moya, I., Osmond, C.B., Medrano, H., 2002b. Steady-state chlorophyll fluorescence (Fs) measurements as a tool to follow variations of net CO2 assimilation and stomatal conductance during water-stress in C3 plants. Physiol. Plant. 114 (2), 231–240. https://doi.org/10.1034/j.1399-3054.2002.1140209.x. Feb.
Flexas, J., Gallé, A., Galmés, J., Ribas-Carbo, M., Medrano, H., 2012. The response of photosynthesis to soil water stress. In: Aroca, R. (Ed.), Plant Responses to Drought Stress. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-32653-0_5.
García-Tejero, I., Durán-Zuazo, V.H., Arriaga, J., Hernández, A., Vélez, L.M., Muriel-Fernández, J.L., 2012. Approach to assess infrared thermal imaging of almond trees under water-stress conditions. Fruits 67 (6), 463–474. https://doi.org/10.1051/fruits/2012040.
García-Tejero, I.F., Hernández, A., Rodríguez, V.M., Ponce, J.R., Ramos, V., Muriel, J.L., Durán-Zuazo, V.H., 2015. Estimating almond crop coefficients and physiological response to water stress in semiarid environments (SW Spain). J. Agric. Sci. Technol. 17 (5), 1255–1266.
Garnier, E., Berger, A., 1985. Testing water potential in peach trees as an indicator of water stress. J. Hortic. Sci. 60, 47–56.
Girona, J., Marsal, J., Cohen, M., Mata, M., Miravete, C., 1993. Physiological, growth and yield responses of almond (Prunus dulcis L.) to deficit irrigation regimes. Acta Horticul. 335, 389–398. https://doi.org/10.17660/ActaHortic.1993.335.47.
Girona, J., Mata, M., Marsal, J., 2005. Regulated deficit irrigation during the kernel-filling period and optimal irrigation rates in almond. Agric. Water Manag. 75 (2), 152–167. https://doi.org/10.1016/j.agwat.2004.12.008.
Genty, B., Briantais, J.-M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Bioch. et Biophys. Acta (BBA) - Gen. Sub. 990 (1), 87–92. https://doi.org/10.1016/S0304-4165(89)80016-9.
Girona, J., 2006. La respuesta del cultivo del almendro al riego. Vida Rural 234, 12–16.
Goldhamer, D.A., Fereres, E., Mata, M., Girona, J., Cohen, M.B., 1999. Sensitivity of continuous and discrete plant and soil water status monitoring in peach trees subjected to deficit irrigation. J. Am. Soc. Hortic. Sci. 124 (4), 437–444. https://doi.org/10.21273/JASHS.124.4.437.
Goldhamer, D., Viveros, M., 2000. Effects of preharvest irrigation cutoff durations and postharvest water deprivation on almond tree performance. Irrig. Sci. 19 (2), 125–131. https://doi.org/10.1007/s002710000013.
Goldhamer, D.A., Viveros, M., Salinas, M., 2006. Regulated deficit irrigation in almonds: effects of variations in applied water and stress timing on yield and yield components. Irrig. Sci. 24 (2), 101–114. https://doi.org/10.1007/s00271-005-0014-8.
Goldhamer, D.A., Girona, J., 2012. Crop yield response to water: almond. In: Steduto, P., Hsiao, T.C., Fereres, E., Raes, D. (Eds.), FAO Irrigation and Drainage Paper No. 66. Food and Agriculture Organization of the United Nations, Rome, pp. 358–373.
Gonzalez Nieto, L., Huber, A., Gao, R., Biasuz, E.C., Cheng, L., Stroock, A.D., Lakso, A.N., Robinson, T.L., 2023. Trunk water potential measured with microtensiometers for managing water stress in "Gala" apple trees. Plants (Basel) 12 (9), 1912. https://doi.org/10.3390/plants12091912.
Gutiérrez-Gordillo, S., Durán-Zuazo, V., García-Tejero, I., 2019. Response of 1624 three almond cultivars subjected to different irrigation regimes in Guadalquivir 1625 river basin. Agric. Water Manag. 222, 72–81. https://doi.org/10.1016/j.agwat.2019.05.031, 1626.
Gutiérrez-Gordillo, S., Durán Zuazo, V.H., Hernández-Santana, V., Ferrera Gil, F., García Escalera, A., Amores-Agüera, J.J., García-Tejero, I.F., 2020. Cultivar dependent impact on yield and its components of young almond trees under sustained-deficit irrigation in semi-arid environments. Agronomy 10 (5), 733. https://doi.org/10.3390/agronomy10050733. Article.
Gutiérrez-Gordillo, S., García-Tejero, I.F., Durán Zuazo, V.H., Díaz-Espejo, A., Hernandez-Santana, V., 2023. The effect of nut growth limitation on triose phosphate utilization and downregulation of photosynthesis in almond. Tree Physiol. 43 (2), 288–300. https://doi.org/10.1093/treephys/tpac122.
Han, J.-M., Meng, H.-F., Wang, S.-Y., Jiang, C.-D., Liu, F., Zhang, W.-F., Zhang, Y.-L., 2016. Variability of mesophyll conductance and its relationship with water use efficiency in cotton leaves under drought pretreatment. J. Plant Physiol. 194, 61–71. https://doi.org/10.1016/j.jplph.2016.03.014.
Hernandez-Santana, V., Fernández, J.E., Rodriguez-Dominguez, C.M., Romero, R., Diaz-Espejo, A., 2016. The dynamics of radial sap flux density reflects changes in stomatal conductance in response to soil and air water deficit. Agric. Meteorol. 218–219, 92–101. https://doi.org/10.1016/j.agrformet.2015.11.013.
Idso, S.B., Jackson, R.D., Pinter Jr, P.J., Reginato, R.J., Hatfield, J.L., 1981. Normalizing the stress degree day for environmental variability. Agric, Meteorol. 24, 45–55. https://doi.org/10.1016/0002-1571(81)90032-7.
Isaakidis, A., Sotiropoulos, T.E., Almaliotis, D., Therios, I.N., Stylianidis, D., 2004. Response to severe water stress of the almond (Prunus amygdalus) 'Ferragnès' grafted on eight rootstocks. N. Z. J. Crop Hortic. Sci. 32, 355–362.
Jackson, R.D., Idso, S.B., Reginato, R.J., Pinter, P.J., 1981. Canopy temperature as a crop water stress indicator. Water Resour. Res. 17 (4), 1133–1138. https://doi.org/10.1029/WR017i004p01133.
Jones, H.G., Lakso, A.N., Syvertsen, J.P., 1985. Physiological control of water status in temperate and subtropical fruit trees. Hortic. Rev. (Am. Soc. Hortic. Sci.) 7, 301–344. https://doi.org/10.1002/9781118060726.ch9.
Jones, H.G., 2004. Irrigation scheduling: advantages and pitfalls of plant-based methods. J. Exp, Bot 55 (407), 2427–2436. https://doi.org/10.1093/jxb/erh213.
Karimi, S., Yadollahi, A., Arzani, K., Imani, A., Aghaalikhani, M., 2015. Gas-exchange response of almond genotypes to water stress. Photosynthetica 53 (1), 29–34. https://doi.org/10.1007/s11099-015-0070-0.
Kisekka, I., Peddinti, S.R., Savchik, P., Yang, L., Culumber, M., Bali, K., Milliron, L., Edwards, E., Nocco, M., Reyes, C.A., Mahoney, R.J., Shackel, K., Fulton, A., 2024. Multisite evaluation of microtensiometer and osmotic cell stem water potential sensors in almond orchards. Comput. Electron. Agric. 227 (1), 109547. https://doi.org/10.1016/j.compag.2024.109547.
Klein, I., Esparza, G., Weinbaum, S.A., DeJong, T.M., 2001. Effects of irrigation deprivation during the harvest period on leaf persistence and function in mature almond trees. Tree Physiol. 21 (14), 1063–1072. https://doi.org/10.1093/treephys/21.14.1063.
Lauri, P.É., Barigah, T.S., Lopez, G., Martinez, S., Losciale, P., Zibordi, M., Manfrini, L., Corelli-Grappadelli, L., Costes, E., Regnard, J.L., 2016. Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. Trees - Struct. Funct. 30 (5), 1893–1908. https://doi.org/10.1007/s00468-016-1408-3.
Leuschner, C., Schipka, F., Backes, K., 2022. Stomatal regulation and water potential variation in European beech: challenging the iso/anisohydry concept. Tree Physiol. 42 (2), 365–378. https://doi.org/10.1093/treephys/tpab104.
Lopez, G., Behboudian, M.H., Girona, J., Marsal, J., 2014. Yield and quality responses of deciduous fruit trees to drought and strategies for its mitigation. Acta Hortic. 1058, 221–227. https://doi.org/10.17660/ActaHortic.2014.1058.25.
Losciale, P., Chow, W.S., Corelli-Grappadelli, L., 2010. Modulating the light environment with the peach 'asymmetric orchard': effects on gas exchange performances, photoprotection, and photoinhibition. J. Exp, Bot. 61, 1177–1192. https://doi.org/10.1093/jxb/erp387.
Losciale, P., Manfrini, L., Morandi, B., Novak, B., Pierpaoli, E., Zibordi, M., Corelli Grappadelli, L., Anconelli, S., Galli, F., 2014. Water restriction effect on pear rootstocks: photoprotective processes and the possible role of photorespiration in limiting carbon assimilation. Acta Hortic. 1058, 237–244. https://doi.org/10.17660/ActaHortic.2014.1058.27.
Losciale, P., Manfrini, L., Morandi, B., Pierpaoli, E., Zibordi, M., Stellacci, A.M., Salvati, L., Corelli Grappadelli, L., 2015. A multivariate approach for assessing leaf photo-assimilation performance using the IPL index. Physiol. Plant 154 (4), 609–620. https://doi.org/10.1111/ppl.12328.
Losciale, P., Gaeta, L., Corsi, M., Galeone, C., Tarricone, L., Leogrande, R., Stellacci, A.M., 2023. Physiological responses of apricot and peach cultivars under progressive water shortage: different crop signals for anisohydric and isohydric behaviours. Agric. Water Manag. 286, 108384. https://doi.org/10.1016/j.agwat.2023.108384.
Ma, Y., Liu, H., Yu, Y., Guo, L., Zhao, W., Yetemen, O., 2022. Revisiting soil water potential: towards a better understanding of soil and plant interactions. Water (Basel) 14 (22), 3721. https://doi.org/10.3390/w14223721.
Mahajan, S., Tuteja, N., 2005. Cold, salinity and drought stresses: an overview. Arch. Biochem. Biophys. 444 (2), 139–158. https://doi.org/10.1016/j.abb.2005.10.018.
Mañas, F., López, F.P., López, U.R., 2014. Effects of different regulated and sustained deficit irrigation strategies in almond production. Acta Hort. 1028, 391–394. https://doi.org/10.17660/ActaHortic.2014.1028.64.
Marsal, J., Girona, J., Mata, M., 1997. Leaf water relation parameters in almond compared to hazelnut trees during a deficit irrigation period. J. Am. Soc. Hortic. Sci. 122 (4), 582–587. https://doi.org/10.21273/JASHS.122.4.582.
Massonnet, C., Costes, E., Rambal, S., Dreyer, E., Regnard, J.L., 2007. Stomatal regulation of photosynthesis in apple leaves: evidence for different water-use strategies between two cultivars. Ann. Bot. 100 (6), 1347–1356. https://doi.org/10.1093/aob/mcm222.
McCutchan, H., Shackel, K.A., 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). J. Am. Soc. Hortic. Sci. 117, 607–611.
Millán, S., Casadesús, J., Campillo, C., Moñino, M.J., Prieto, M.H., 2019. Using soil moisture sensors for automated irrigation scheduling in a plum crop. Water (Basel) 11 (10), 2061. https://doi.org/10.3390/w11102061.
Monks, D.P., Taylor, C., Sommer, K., Treeby, M.T., 2017. Deficit irrigation of almond trees did not decrease yield. Acta Hortic. 1150, 251–260. https://doi.org/10.17660/ActaHortic.2017.1150.35.
Naor, A., Klein, I., Doron, I., 1995. Stem water potential and apple size. J. Am. Soc. Hortic. Sci. 120, 577–582.
Naor, A., 2000. Midday stem water potential as a plant water stress indicator for irrigation scheduling in fruit trees. Acta Hortic. 537, 447–454. https://doi.org/10.17660/ActaHortic.2000.537.52.
Ni, B.-R., Pallardy, S.G., 1992. Stomatal and nonstomatal limitations to net photosynthesis in seedlings of woody angiosperms. Plant Physiol. 99 (4), 1502–1508. https://doi.org/10.1104/pp.99.4.1502.
Niyogi, K.K, 1999. PHOTOPROTECTION REVISITED: genetic and molecular approaches. Annu. Rev. Plant Physiol. Plant Mol. Biol. 50, 333–359. https://doi.org/10.1146/annurev.arplant.50.1.333. JunPMID: 15012213.
Noctor, G., Veljovic-Jovanovic, S., Driscoll, S., Novitskaya, L., Foyer, C.H., 2002. Drought and oxidative load in the leaves of C3 plants: a predominant role for photorespiration? Ann. Bot. 89, 841–850. https://doi.org/10.1093/aob/mcf096. Spec No.
Nolz, R., Loiskandl, W., 2017. Evaluating soil water content data monitored at different locations in a vineyard with regard to irrigation control. Soil Water Res. 12 (3), 152–160. https://doi.org/10.17221/9/2016-SWR.
Nortes, P.A., Pérez-Pastor, A., Egea, G., Conejero, W., Domingo, R., 2005. Comparison of changes in stem diameter and water potential values for detecting water stress in

young almond trees. Agric. Water Manag. 77 (1–3), 296–307. https://doi.org/10.1016/j.agwat.2004.09.034.
Palma, L., Novello, V., 1996. Caratteristiche dell'attività fotosintetica di mandorlo e pistacchio. Riv, Frutt. 1, 55–56.
Prgomet, I., Pascual-Seva, N., Morais, M.C., Aires, A., Barreales, D., Castro Ribeiro, A., Silva, A.P., Barros, A.I.R.N.A., Gonçalves, B., 2020. Physiological and biochemical performance of almond trees under deficit irrigation. Sci. Hortic. 261, 108990. https://doi.org/10.1016/j.scienta.2019.108990.
Ramos, D.E., Weinbaum, S.A., Shackel, K.A., Schwankl, L.J., Mitcham, E.J., Mitchell, F. G., Snyder, R.G., Mayer, G., McGourty, G., 1994. Influence of tree water status and canopy position on fruit size and quality of Bartlett pears. Acta Hortic. 367, 192–200. https://doi.org/10.17660/ActaHortic.1994.367.24.
Razouk, R., Kajji, A., Hamdani, A., Charafi, J., Hssaini, L., Bouda, S., 2020. Yield and Fruit Quality of almond, Peach and Plum Under Regulated Deficit Irrigation. Frontiers of Agricultural Science and Engineering.
Romero, P., Botia, P., Garcia, F., 2004. Effects of regulated deficit irrigation under subsurface drip irrigation conditions on vegetative development and yield of mature almond trees. Plant Soil 260, 169–181. https://doi.org/10.1023/B:PLSO.0000030193.23588.99.
Romero, P., Botía, P., 2006. Daily and seasonal patterns of leaf water relations and gas exchange of regulated deficit-irrigated almond trees under semiarid conditions. Env. Exp. Bot. 56 (2), 158–173. https://doi.org/10.1016/j.envexpbot.2005.01.012.
Rouhi, V., Samson, R., Lemeur, R., Van Damme, P., 2007. Photosynthetic gas exchange characteristics in three different almond species during drought stress and subsequent recovery. Env. Exp. Bot. 59 (2), 117–129. https://doi.org/10.1016/j.envexpbot.2005.10.001.
Ruiz-Sánchez, M.C., Torrecillas, A., Del Amor, F., León, A., Abrisqueta, J.M., 1988. Leaf water potential and leaf conductance during the growing season in almond trees under different irrigation regimes. Biol. Plant 30, 327–332.
Sadiq, Md & Rahman, S.M. & Kayes, Shakiyen & Sumaita, Afnan & Chisty, Nafiz. (2021). A review on the imaging approaches in agriculture with crop and soil sensing methodologies. 1–7. https://doi.org/10.1109/ICDS53782.2021.9626711.
Sanden, B., 2007. Fall Irrigation Management in Drought Year For almonds, pistachios, and Citrus. Kern Soil Water Newsl, pp. 1–8.
Shackel, K., 2011. A plant-based approach to deficit irrigation in trees and vines. HortScience 46 (2), 173–177. https://doi.org/10.21273/HORTSCI.46.2.173.
Shackel, K.A., Ahmadi, H., Biasi, W., Buchner, R., Goldhamer, D.A., Gurusinghe, S.H., Hasey, J., Kester, D., Krueger, B., Lampinen, B., McGourty, G., Micke, W., Mitcham, E., Olson, B., Pelletrau, K., Philips, H., Ramos, D., Schwankl, L.J., Sibbett, S., Yeager, J., 1997. Plant water status as an index of irrigation need in deciduous fruit trees. Horttechnology 7 (1), 23–29. https://doi.org/10.21273/HORTTECH.7.1.23.
Sperling, O., Gardi, I., Ben-Gal, A., Kamai, T., 2023. Deficit irrigation limits almond trees' photosynthetic productivity and compromises yields. Agricul. Water Manag. 289, 108562. https://doi.org/10.1016/j.agwat.2023.108562.
Stewart, W., Fulton, A., Krueger, W., Lampinen, B., Shackel, K., 2011. Regulated deficit irrigation reduces water use of almonds without affecting yield. Calif. Agric. (Berkeley) 65 (2), 90–95. https://doi.org/10.3733/ca.v065n02p90.
Torrecillas, A., Alarcón, J.J., Domingo, R., Planes, J., Sánchez-Blanco, M.J., 1996. Strategies for drought resistance in leaves of two almond cultivars. Plant Sci. 118 (2), 135–143. https://doi.org/10.1016/0168-9452(96)04434-2.
Velazquez-Chavez, L.J., Daccache, A., Mohamed, A.Z., Centritto, M., 2024. Plant-based and remote sensing for water status monitoring of orchard crops: systematic review and meta-analysis. Agric. Water Manag. 303, 109051. https://doi.org/10.1016/j.agwat.2024.109051.
Von Caemmerer, S., 2000. Biochemical Models of Leaf Photosynthesis. CSIRO Publishing. https://doi.org/10.1071/9780643103405.
Wartinger, A., Heilmeier, H., Hartung, W., Schulze, E.D., 1990. Daily and seasonal courses of leaf conductance and abscisic acid in the xylem sap of almond trees [*Prunus dulcis* (Miller) D. A. Webb] under desert conditions. New Phytol. 116 (4), 581–587. https://doi.org/10.1111/j.1469-8137.1990.tb00542.x.
World Health Organization, 2015. *Operational Framework For Building Climate Resilient Health Systems* (No. WHO/FWC/PHE/EPE/15.52). World Health Organization. https://www.who.int/publications/i/item/WHO-FWC-PHE-EPE-15.52.
Xiloyannis, C., Uriu, K., Martin, G., 1980. Seasonal and diurnal variation in abscisic acid, water potential, and diffusive resistance in leaves from irrigated and non-irrigated peach trees. J. Am. Soc. Hortic. Sci. 105 (4), 412–415.
Yi, X.-P., Yao, H.-S., Fan, D.-Y., Zhu, X.-G., Losciale, P., Zhang, Y.-L., Zhang, W.-F., Chow, W.S., 2022. The energy cost of repairing photoinactivated photosystem II: an experimental determination in cotton leaf discs. New. Phytol. 235, 446–456. https://doi.org/10.1111/nph.18165.

CHAPTER III

Extending the framework to grapevine, this chapter tests the generality of the integrative approach across species and irrigation regimes. The interspecific comparison reveals that early functional decoupling may occur along different physiological axes, supporting a multidimensional interpretation of plant responses to water deficit.

BACKGROUND

To test whether the integrative interpretation of plant functional status can be extended beyond almond, this chapter examines grapevine responses to deficit irrigation under Mediterranean conditions. In grapevine, water shortage and heat interact strongly to affect gas exchange, plant water status, carbon allocation, yield components, grape composition, and wine quality. Existing irrigation strategies therefore require a framework able to connect leaf functionality with whole-vine performance, rather than relying on a single variable or on productivity alone.

AIMS

This chapter aims to evaluate the effects of different deficit irrigation regimes on *Vitis vinifera* cv. Primitivo by integrating ecophysiological responses with vegetative performance, starch reserves, yield, grape composition, and wine quality. Within the broader thesis logic, the chapter serves to test the generality of the integrative approach across species and to verify whether early functional disruption in grapevine emerges through coordinated changes in plant water status, stomatal behaviour, photosynthesis, and photochemical regulation under different irrigation intensities.

RESULTS

The results show that the integrative framework is transferable to grapevine, but that functional decoupling emerges along partially different physiological axes than in almond. Mild deficit irrigation at 85% ETc did not significantly affect leaf functionality, starch reserves, vigour, or yield, and produced the most favourable balance between water saving and wine quality. Stronger deficits, especially at 55% and 29% ETc, reduced photosynthesis, stomatal conductance, stem water potential, starch accumulation, vegetative growth, and yield, with T29 also reducing cluster number. At the same time, the study showed that decreases in carbon assimilation were not always matched by proportional declines in photochemical electron transport, indicating an early decoupling between gas exchange and photochemistry mediated by increased photoprotective and non-net carboxylative processes. This supports a multidimensional interpretation of water-deficit responses, in which plant function cannot be inferred from a single indicator but must be read through the joint behaviour of hydraulic, stomatal, photosynthetic, and carbon-allocation variables.

Irrigation Science
https://doi.org/10.1007/s00271-024-00956-0

ORIGINAL PAPER

Effect of different deficit irrigation regimes on vine performance, grape composition and wine quality of the "Primitivo" variety under mediterranean conditions

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Received: 15 February 2024 / Accepted: 15 July 2024

Abstract
Climate change represents one of the current major challenges and the improper use of water resources is an impeding threat. Agricultural research can play a crucial role by developing innovative strategies and techniques to reduce water use without affecting crop productivity and quality, particularly in grapevine growing in Mediterranean areas, as both productivity and wine quality are quintessential for the economic and ecologic sustainability of this crop. The present study aimed to define a deficit irrigation strategy for the "Primitivo" grapevine cultivar, taking into account the overall pathway of the vineyard performance in terms of leaf functionality, starch reserves, vine productivity, and wine quality. The trial was carried out in Southern-Italy on a three year-old, drip irrigated vineyard, imposing four deficit irrigation regimes for two consecutive seasons, consisting of 29 (T29), 55 (T55), 85 (T85) and 100% (T100) of crop evapotranspiration (ET_C). Mild water restriction (T85) did not affect vegetative nor reproductive vine performance. Deficit irrigation at 55% ET_C lowered leaf functionality, starch accumulation, vine vigour and yield, due to a reduction of cluster weight; however, wine acidity and phenolic compounds were increased. T29 further decreased yield, as also the number of clusters was reduced. The most water-stressed treatment revealed a low concentration of malic acid in the must and a consequent increase of the ethanol sensation in the wine. After 9 months ageing, T85 had the highest wine colour intensity suggesting this treatment as the most promising in terms of quality and quantity of wine as well as for water saving.

Keywords Water stress · Leaf functionality · Water use efficiency · Sensorial analysis · Starch reserves · Bud fertility malic acid

Introduction

According to the European Environment Agency (EEA), 20% of the European territory and 30% of EU population are affected by water scarcity every year. Drought causes economic damage of up to EUR 9 billion annually and additional unquantified damage to ecosystems and their services (EEA, 2021). Agricultural activities, which use around 70% of all human water withdrawals (Santos et al. 2020; Schultz 2017), are impacted by the water shortages and heat waves. In grapevine, water stresses coupled to heat waves negatively affect vine and leaf physiology, fruit growth and ripening, and wine quality (Gambetta et al. 2020). High temperature, for example, could enhance soluble solids content but, at the same time, can cause a decrease of anthocyanins and titratable acidity (Gutiérrez–Gamboa et al. 2021). The effects of water stress on plant physiology have been widely studied, as well as their impact on grape production and quality (Oliver-Manera et al. 2023). The expected temperature increase, of 0.3–1.7 °C in the near future (Drappier et al. 2019), the reduction of precipitation, and the occurrence of extreme events enhance the process of desertification in the Mediterranean Region (Safriel 2009),

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Published online: 24 July 2024

which is considered a hotspot of climate change (Cos et al. 2022; Lionello and Scarascia 2018). Many areas in Southern Italy are subjected to water shortages and the Apulia region has experienced a consistent decrease in annual rainfall in recent years, limiting its agricultural water resource (Gentilesco et al. 2023; Zollo et al. 2016). Modern irrigation technologies and strategies can help to improve water use efficiency (WUE) whilst benefitting grape and wine quality (Romero et al. 2022). Moderate and controlled water stress, achieved through deficit irrigation, reduced vine vigour and the competition for carbohydrates, promoting the production of secondary metabolites in the berries (Bonfante et al. 2017; Munitz et al. 2017; Romero et al. 2022), and enhancing the anthocyanin content and aroma precursors in the wine. Controlled water stress improved sensory traits, like higher astringency, better colour intensity (Intrigliolo and Castel 2011), improved aromatic profile and higher fruity and floral sensory hints, gaining persistence and balance (Gamero et al. 2014a, b). Appropriate irrigation strategies aiming at reducing water supply, matching quality and productivity, are key to make this practice economically and environmentally sustainable (Ruiz-Sanchez et al. 2010). The use of water-stress-induced strategies such as deficit irrigation, also called "sustained" deficit irrigation (DI), regulated deficit irrigation (RDI) and partial rootzone drying (PRD) (Conesa et al. 2018) represents one of the pivotal approaches. Deficit irrigation consists of a fixed reduction of water supply during the growing season so that the amount supplied is less than the water lost by the vineyard (Ruiz-Sanchez et al. 2010). The proper application of DI requires a deep knowledge of the plant response to water deficit and the economic impact of this type of management on vineyard performance (Tomás et al. 2014; Torres et al. 2021). The soil water content decreases progressively during the vegetative season due to a combination of the constant reduction of water supply and the depletion of the soil water reserve (Fereres and Soriano 2007). The intensity of water restriction to impose may vary as a function of the cultivar and the yield target (Sadras and Schultz 2012; Romero et al. 2022). In grapevine cv. "Bobal", a reduction of 35% of crop evapotranspiration (ET_C) during the growing season was suggested for optimizing grape skin, seed, and volatile composition in comparison with full irrigation, allowing at the same time a yield increase in comparison to rainfed vines (Lizama et al. 2021). Water restriction, bringing the predawn leaf water potential at -1.0 MPa, negatively affected "Sauvignon Blanc" aroma, which was instead enhanced under mild water deficit (Des Gachons et al. 2005). It has been reported that only severe water stress can significantly affect starch reserves. In cv. "Malbec" subjected to deficit irrigation, no significant differences were observed between fully irrigated treatment and a 60% DI; while a water reduction to 38% and 25% of the control significantly impacted starch accumulation (Dayer et al. 2013). Another interesting strategy is the regulated deficit irrigation (RDI), which offers greater potential to save water, reduce excessive vine vigour, increase WUE and to improve berry and wine quality; however, the identification of the phenological stages in which to impose the water restriction and the intensity of the water deficit are crucial decisions (Barbagallo et al. 2021; Costa et al. 2007; García-Esparza et al. 2018; Iglesias and Garrote 2015; Intrigliolo et al. 2016). In partial root-zone drying irrigation (PRD), water is supplied alternately only to a part of the root system, while the rest is left dry. This promotes the production of chemical signals in the dry roots (e.g. abscisic acid, ABA), triggering partial stomatal closure that improves water use efficiency (Romero et al. 2022; Sadras 2009; Wang et al. 2012).

Although Italy is one of the main wine exporters in the world, producing around 50.3 million hl per year (OIV 2022), and Apulia is the second national producer (ISTAT, 2021), there are only a few studies about the effects of deficit irrigation on vine performance and wine quality in this region (Storchi et al. 2005; Tarricone et al. 2017), although it could be a suitable approach to improve berry quality and WUE without affecting yields and could more easily be adopted by farmers than PRD and RDI (Buesa et al. 2017; Pérez-Álvarez et al. 2021; Shellie and King 2020; Zarrouk et al. 2016). Only a few studies have considered the effects of varying irrigation inputs in terms of vineyard performance, grape composition and wine quality, to get information about the most appropriate irrigation strategies to apply (Romero et al. 2022). The present research evaluated the impact of different deficit irrigation regimes imposed for two consecutive years on canopy functionality, vegetative performances, productivity, and wine quality of grapevine cv. "Primitivo" under semi-arid conditions.

Materials and methods

Experimental set up and irrigation regimes

The trial was carried out in 2020 and 2021, in a commercial vineyard of *Vitis vinifera* L. cv. "Primitivo" UBA 47/B clone, grafted on 775 Paulsen rootstock (*Vitis berlandieri* x *Vitis rupestris*) located in the Castel del Monte area, within the Denomination of Controlled and Guaranteed Origin of Corato (Apulia region, Southern Italy), 353 m above sea level (41°05'36" N 16°20'22" E) on a shallow, gravel, silty-clay soil, with sub-alkaline reaction and 1.8% organic matter. Vines (3 years old) were spaced 2.3 m between rows and 1.1 m within row (3.952 vines ha^{-1}). The alley-row was left to a natural grass cover, which was mowed three times per

year, in Spring and early Summer; the rows were tilled in a 70 cm wide strip underneath the vines.

The area has been characterized as a Mediterranean climate (Csa) (Pinna 1970), following the Köppen-Geiger classification system (Koppen 1936). Meteorological data, collected from a weather station close to the vineyard, were utilized to classify the vineyard, using the multicriteria climatic classification system for grape-growing regions developed by Tonietto and Carbonneau (2004). The vineyard exhibited a Huglin Index (HI) (Huglin 1978) of 2631, in 2020, and 2803 in 2021, being classified as Warm ($HI + 2$; $2400 > HI \leq 3000$). The Cool night Index (CI) (Tonietto 1999) ranged from 16.1 °C, in 2020, to 16.4 °C in 2021, thus indicating Temperate nights ($CI - 1; 14 > CI \leq 18$). Additionally, the Dryness Index (DI) (Riou et al. 1994) was 47.7 mm, in 2020, and −72.6 mm in 2021, classifying the vineyard as moderately dry ($-100 > DI > 50$ mm). The Winkler Index (WI) (Winkler et al. 1974) was 2127, in 2020, and 2296 in 2021, placing the vineyard on the boundary between regions IV and V.

Vines were trained as vertical shoot positioned (VSP) training system and pruned as double Guyot, with 16–18 buds per vine, taking in account wood maturity. Canopy management practices included shoot positioning in the month of June, followed by mechanical shoot topping soon after.

The vineyard was outfitted with drip-irrigation, and water supply was managed through the evapotranspiration approach with ET_0 (Pennman-Monteith estimation), given by the microclimatic station located close to the vineyard site, and ET_C obtained estimating the crop coefficient (K_C) according to the canopy size (Allen and Pereira 2009). The latter was estimated by NDVI derived for the vineyard by Sentinel 2 satellite data (Hornbuckle et al. 2016; Mzid et al. 2023; Trout and Johnson 2007). Water (pH: 7.8; electrical conductivity: 0.253 dS m^{-1}) was extracted from groundwater at a depth of about 800 m and the pump was powered by photovoltaic panels. Vines were subjected to four irrigation strategies in the two years: T100 (full irrigation, no water deficit) and three deficit irrigation regimes T85, T55 and T29 with a water restitution of 85, 55 and 29% of ET_C, respectively, using self-compensating drippers with different flow rates: 3.8, 3.2, 2.1 and 1.1 L h^{-1} for the four treatments, respectively. Soil water content values at field capacity and wilting point were 0.219 and 0.097 m^3m^{-3}, respectively; the available water content was 0.122 m^3m^{-3}. Water was supplied when 40% of the available water in T100 (readily available water) had been lost. Soil water content was monitored on T100 treatment by one soil moisture probe per replicate (Sentek's EnviroSCAN) at various depths (5, 15, 25, 35, 45 and 55 cm); the data were used to cross check whether the water supplied using the evapotranspiration approach was appropriate to bring the soil water content of the first 50 cm (active root zone) at field capacity.

The four treatments were arranged according to a randomized complete block design with three blocks. Within each block, each treatment had 30 vines arranged on 3 rows, with 10 plants each. Vines of the central part of the central row were used for determinations while the remaining vines served as guards.

Leaf functionality and water relations

Ecophysiology measures were performed only in 2021. On June 21st, July 27th and August 27th, corresponding to berry cell division, cell expansion and close to harvest, midday leaf gas exchanges, temperature and chlorophyll fluorescence were measured with an integrated fluorometer and gas exchange system fitted with an artificial and adjustable light source (iFL, ADC BioScientific Ltd., Global House, Geddings Road, Hoddesdon, United Kingdom). Light intensity (PPFD) was maintained constant across the treatments by setting the LED light source to the natural irradiance experienced by the leaves immediately before the measurements (PPFD of 1000, 1900 and 1700 µmol $m^{-2}s^{-1}$ on June 21st, July 27th and August 27th, respectively); the reference CO_2 was set at 400 ppm. The following measures were taken on 3 vines of the central row for each block and treatment, at solar noon: leaf net photosynthesis (Pn, µmol m^{-2} s^{-1}); stomatal conductance (gs, mol m^{-2} s^{-1}); transpiration (E, mmol m^{-2} s^{-1}); effective efficiency of PSII (Φ_{PSII} = [Fm'-Fs] / Fm'); electron transport rate exiting PSII ($J_{PSII,}$ µmol m^{-2} s^{-1}); leaf and air temperature (T_{leaf}, T_{air}, °C). Midday stem water potential (Ψs, MPa) was measured on the same vines using a Scholander chamber (3005F01, Soil Moisture Equipment Corp., Santa Barbara CA, USA), following Naor et al. (1995).

Starch reserves and bud fertility

During the 2020 Winter, one-year pruning wood was collected from the same vines. Five woody sections were obtained in 3 internodes (3rd, 5th, 7th) from each stem. A total of 180 woody sections were analysed following the method described by Rustioni et al. (2017). Reflectance spectra of the tissues were collected by a Jaz System spectrometer (Ocean Optics, B.V., Dunedin, USA) before and after on-solid starch iodine complexation obtained by Lugol stain, according to Rustioni et al. (2016). The starch index was calculated as:

$$Starch\ Index = \frac{R_{Re(900)}}{R_{Re(555)}} - \frac{R_{t0(900)}}{R_{t0(555)}}$$

$R_{x(w)}$ = Reflectance (% calibrated on the reference blank).

x = spectrum type: t0 = before reaction; Re = after Lugol reaction.

w = wavelength of interest (nm): 900 = normalization reference; 555 = starch-iodine complex absorption maximum.

To investigate the effect of water deficit on the next vegetative season, during the bud break period of 2021 and 2022, the number of buds, clusters and shoots, as well as the bud fertility (number of clusters per bud) were calculated for the four treatments on the same vines.

Vegetative and productive performances

At the end of each vegetative season, the number and weight of clusters and the pruning weight were measured for each vine. In addition, the average cluster weight (g), yield (t ha^{-1}) and Water Productivity (WP), expressed as kg of clusters per m^3 of supplied water irrigation (Fernández et al. 2020), were calculated. The Ravaz index (Ravaz 1903) was calculated as kg of grape per kg of pruning weight for each vine under investigation.

Quality and wine sensorial analysis

The quality of must was evaluated by measuring: soluble sugar residues (SSR, °Brix), pH, titratable acidity (g l^{-1}) and malic acid (g l^{-1}) according to standard procedures (EEC2676). In 2021, micro-vinifications were carried out from the grapes of all treatments: about 100 kg of grapes were manually harvested and vinified at the experimental winery of CREA-VE according to the procedure described by Gambacorta et al. (2022). The grapes were crushed and de-stemmed with a stainless-steel crusher-destemmer and placed in 100 L vertical stainless-steel vats. Potassium metabisulphite (6 g/100 kg), yeast (Saccharomyces cerevisiae var. Bayanus, Mycoferm CRU05, 20 g/100 kg, Ever, Pramaggiore, Italy) and yeast activator (Enovit, AEB, Venice, Italy) were added. Maceration was performed for 9 days with 2 punch-downs per day. Then, free-run wine was recovered by draining, and the grape pomace was gently pressed to recover press-run wine using a 80 L stainless-steel hydropress. The free-run and press-run wines were blended and raked after 2 weeks to eliminate gross lees. The wines were bottled after 6 months, without any additional treatment, and analyzed for ethanol concentration (%v/v), pH, titratable acidity as tartaric acid (TA, g L^{-1}), malic acid (g L^{-1}), and dry reduced extract (DRE, gL^{-1}). Total polyphenols as gallic acid (TP, mgL^{-1}) and anthocyanins, as malvidin-3-glucoside (A, mgL^{-1}), were assayed according to Di Stefano et al. (1989).

A first round of sensorial analysis was conducted after 6 months of wine aging and a second round, aimed at evaluating the evolution of wines in time, was replicated three months later. Thirteen expert panellists performed the sensorial analysis; 30 ml of each wine, labelled with four random numbers and covered with plastic film were served at 20 °C in 250 ml ISO goblets. The evaluation entailed two sections: the first consisted of a list of descriptors related to visual, olfactory and taste aspects to be scored by using a structured 10-point scale; the second one reported a list of specific sensorial notes to be flagged by the panellists.

Statistical analysis

The four irrigation regimes were compared for leaf functionality, starch reserves, bud fertility, productivity, must and wine quality by means of ANOVA considering the randomized complete block design; mean separation was performed with post-hoc SNK test. For those variables tested for the two consecutive years a 2-way ANOVA was performed, considering the year and the water regime as factors. A non-parametric approach was used for sensorial analysis data. Kruskal-Wallis test was performed to compare medians of each descriptor, Mann Whitney test was used to verify differences in the perception of each descriptor between the first and the second round of sensorial analysis. Furthermore, a chi-square test was conducted on each individual note perceived by the 13 panellists for each wine to assess its statistical significance, as follows:

$$x^2 = \frac{(observed - expected)^2}{(expected)} = \frac{(Nr\ panelists\ perceiving\ hint - Total\ Nr\ panelists)^2}{(Total\ Nr\ panelists)}$$

Specifically, the threshold value for 12 degrees of freedom (GL) and $\alpha < 0.05$ was 5.23. Therefore, a note was considered significantly perceived by the panel when indicated by at least 5 tasters on a total of 13.

Results

Microclimate and irrigation regimes

Climate patterns in 2020 and 2021 were in line with average Mediterranean climate (Koppen 1936). The Winter and the initial part of the Spring 2021 were characterized by rains; at the beginning of the Spring air temperature increased and rainfall frequency and intensity diminished. The highest air temperatures were recorded from June to August with maximum values often exceeding 33 °C. In the same period rainfalls amounted to 90 and 52.2 mm in 2020 and 2021, respectively. The vapor pressure deficit (VPD) increased

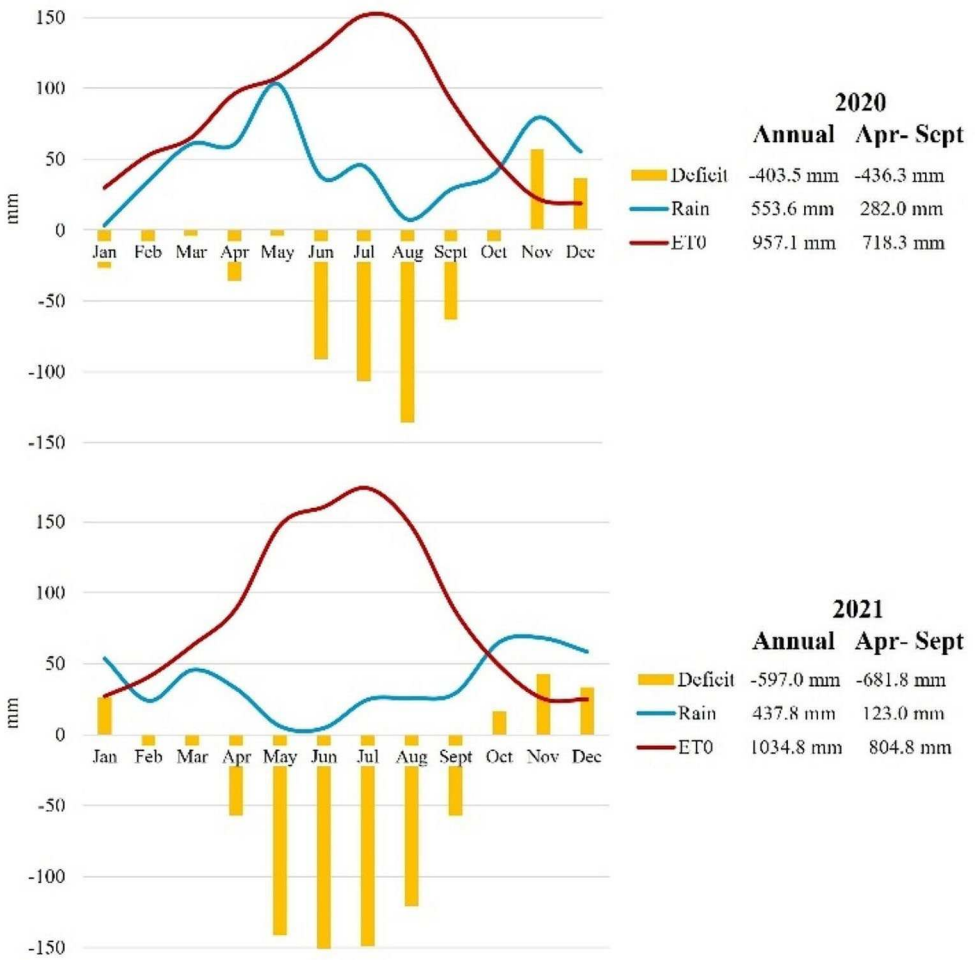

Fig. 1 Seasonal water deficit in 2020 and 2021, calculated as the difference between the reference Evapotranspiration (ETo) and rainfall, during the entire year and from April to September

Table 1 Water supplied to the four irrigation regimes in 2020 and 2021 seasons

Year	Treatment	Water supply (m^3 ha^{-1})
2020	T29	174.2
	T55	330.4
	T85	510.6
	T100	600.7
2021	T29	222.1
	T55	421.2
	T85	651
	T100	765.9

during the year reaching the maximum values during Summer, with average daily VPDs of 1.5 and 2.17 kPa in 2020 and 2021, respectively. The seasonal water deficit, calculated as the difference between the reference Evapotranspiration (ETo) and rainfall, was higher in 2021 than 2020; it increased approaching Summer and from June to August it was 333 and 425 mm in 2020 and 2021, respectively (Fig. 1). Despite this, the vineyard area was classified in both years as warm, with temperate nights and a moderate dryness, in line with previous studies (Alba et al. 2021; Gentilesco et al. 2023) and compliant with an area in the Mediterranean basin. Water was supplied from July 24th to September 2nd in 2020 and from June 21st to August 2nd in 2021, with seasonal volumes in T100 of 600 and 765 m^3ha^{-1}, respectively. Seasonal water supply in T29 was 174 and 222 m^3h^{-1} for 2020 and 2021, respectively (Table 1).

Leaf functionality and water relations

Leaf functionality was first measured on June 21st, 2021, two days after the onset of the treatments. Air temperature and VPD were 38.6 °C and 3.64 kPa, respectively; net photosynthesis (Pn) and stomatal conductance (gs) were generally low and T100 and T85 showed higher values than the remaining treatments (Table 2). Leaf temperature exceeded 40 °C with the highest values recorded on T55 and T29. The electron transport rate exiting from PSII (J_{PSII}) was higher in T100 and T85 than T55 and T29 (Table 2). The second measurement was performed on July 27th during cell expansion. Midday air temperature and VPD were 37.4 °C and 4.98 kPa. No differences were observed for all the ecophysiology variables even if T29 showed a slightly lower

Table 2 Net photosynthesis (pn), stomatal conductance (gs), leaf transpiration (E), leaf temperature (T_{leaf}), electron transport rate exiting PSII (J_{PSII}) and stem water potential (Ψs), recorded on the four treatments during fruit cell division (21/6), fruit cell expansion (27/7) and close to the harvest (27/8) in 2021. Within each date and for each variable, different letters indicate a statistical difference at $p = 0.05$

Date	Treatment	Pn		gs		E		T_{leaf}		J_{PSII}		Ψs
		(μmol m^{-2} s^{-1})		(mol m^{-2} s^{-1})		(mmol m^{-2} s^{-1})		(°C)		(μmol e^{-} m^{-2} s^{-1})		(MPa)
21/6	**T29**	1.26	b	0.013	b	0.67	b	41.15	b	98.52	b	-
	T55	1.14	b	0.013	b	0.83	b	43.15	b	80.61	b	-
	T85	3.61	a	0.027	a	1.48	a	40.59	a	148.41	a	-
	T100	2.83	a	0.023	a	1.33	a	40.60	a	140.70	a	-
27/7	**T29**	3.61		0.051		3.33		44.21		119.03		-1.28
	T55	5.42		0.087		5.17		45.18		119.01		-1.17
	T85	3.28		0.043		2.71		44.14		96.06		-1.04
	T100	6.40		0.093		5.73		44.34		137.25		-1.05
27/8	**T29**	7.59	b	0.108	c	2.89	b	34.39		158.86	b	-1.20 b
	T55	7.62	b	0.127	bc	3.31	ab	34.82		174.72	b	-0.97 a
	T85	9.55	a	0.141	b	3.32	ab	33.85		180.22	b	-0.86 a
	T100	10.62	a	0.176	a	3.93	a	34.24		232.33	a	-0.83 a

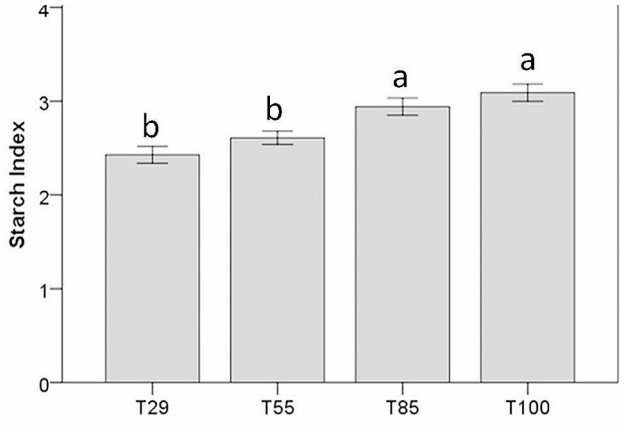

Fig. 2 Starch content quantified by means of the Starch Index recorded on canes of the four treatments under investigation in 2020. Different letters indicate a statistical difference at $p = 0.05$

midday stem water potential, close to -1.3 MPa; the average Pn, gs and Ψs were 4.7 μmol m^{-2} s^{-1}, 0.07 mol m^{-2} s^{-1} and − 1.18 MPa, respectively (Table 2). Close to harvest, air and leaf temperature recorded at midday were 27.8 and 34.2 °C, respectively. Pn values in T100 and T85 were higher than in T55 and T29; the highest gs was recorded in T100 followed by T85, T55 and T29. Leaf temperature was similar among the treatments and the highest and the lowest values of J_{PSII} were recorded on T100 and T29, respectively. The minimum midday stem water potential was observed in T29 with Ψs of -1.20 MPa (Table 2).

Starch reserves and bud fertility

DI significantly impacted starch reserve accumulation in woody canes, with similar values of starch index in T100 and T85, decreasing in the treatments receiving less water (Fig. 2).

No year by treatment interaction was recorded for number of buds, clusters, shoots, and bud fertility. The former three variables showed lower values in 2021 than in 2022 (Table 3). The number of buds and shoots was lower in T29 and T55 in comparison with T85 and T100. Bud fertility, expressed as the number of clusters per bud, was slightly lower in T29 than in the remaining treatments (Table 3); the lowest number of clusters was recorded in T29. No difference for the percentage of budbreak was observed, suggesting that the lower number of shoots of T29 was dependent by the lower number of buds rather than a higher level of closed buds (Table 3).

Vegetative and productive performances

The interaction between year and irrigation regime was not significant. Excluding the average cluster weight, the

Table 3 Number of buds left with Winter pruning, and the derived number of clusters, shoots and bud fertility detected on the four irrigation treatments in the two years of trial. Within each experimental factor, (*) or different letters indicate a statistical difference at $p = 0.05$

Experimental factor	Buds (number vine^{-1})		Clusters		Shoots		Bud fertility (cluster bud^{-1})
Year							
2021	10.18	*	12.06	*	8.98	*	1.32
2022	17.11		25.17		15.89		1.44
TRT							
T29	11.89	b	14.56	b	10.56	b	1.19
T55	13.22	ab	20.22	a	12.17	ab	1.54
T85	15.31	a	20.33	a	13.56	a	1.42
T100	14.72	a	20.28	a	13.94	a	1.39

second year of investigation revealed a general reduction of productivity, attributable to the lower number of buds left with the Winter pruning and the related number of clusters (Table 4). The heaviest clusters were observed in T100 and T85, followed by T55 and T29 (Table 4); T29 showed the lowest number of clusters per vine (Table 4). Yield was not different between T100 and T85 (~7 t ha^{-1}), while it was reduced in T55 and T29 showing values of 4.21 and 2.86 t ha^{-1}, respectively (Table 4). Water productivity did not differ among the treatments while the pruning weight was different between T100, T85 and T55, T29. The Ravaz index decreased progressively passing from T100 to T29 (Table 4).

Wine quality and sensorial analysis

Harvest was performed at the same time for all the treatments according to the "Primitivo" appellation guidelines: when the Total Soluble Solids (TSS) were at least 19.5–20.0 °Brix. Harvest occurred on October 3rd and on September 2nd in 2020 and 2021, respectively. There was no interaction between year and irrigation regime for must quality (Table 5). TSS and malic acid (mal) values were lower in 2020 than in 2021, probably due to the higher cropload recorded in 2020; pH and titratable acidity were quite similar in the two years. T100 and T85 had the lowest TSS (~21.5 °Brix) and T55 the highest (23.1 °Brix); T29 showed an intermediate level of total soluble solids (Table 5). No difference for pH was observed, while the concentration of TA was reduced in T29 in comparison with T100 and T85. A decrease of malic acid concentration was observed in T29 (Table 5).

Chemical analysis on the 2021 wines was performed after 6 months ageing. The lowest ethanol content was observed in T29 and T85 in comparison with the remaining water regimes. Total acidity decreased in the severe water stress treatment, while T55 revealed a malic acid concentration higher than the other treatments as well as the dry reduced extract (DRE). T55 had the highest phenolic compounds content with T85 recording an anthocyanins content lower than the remaining treatments (Table 6).

The first sensory analysis was conducted after 6 months ageing on wines derived from the four treatments. No difference was found for all the descriptors (Fig. 3a). The notes perceived by at least 5 panellists on a total of 13 showed a prevalence of hints of berries, fresh and sour cherry in spirit, and spicy notes of black pepper, cloves, cinnamon. The ethanol sensation was particularly high in T29 (Fig. 3b). The second sensory analysis was performed after 9 months ageing on the same wines. A difference was found on the descriptor "Color Intensity", highest in T85 (Fig. 4a). The notes perceived by panellists resulted similar to the previous sensory analysis, with red fruits hints, alcoholic sensation. In addition, notes of black pepper and liquorice emerged clearly after 9 months ageing. During this analysis the ethanol sensation in T29 was reduced in comparison with the previous tasting (Fig. 4b). No differences emerged for descriptors between the first and second tasting both in T29 and in T100. T55 showed a decrease of "sweetness" with the ageing of the wine. The same was observed for T85 and in addition the perception of viscosity increased in the second tasting (Fig. 5).

Discussion

Water restriction below 45% ET_C (T55, T29) progressively decreased yield, due to the reduction of cluster weight, probably caused by water shortage, decreased sugar synthesis and accumulation (Chaves et al. 2010; Lovisolo et al. 2010). The lower number of clusters in T29, further decreased productivity (Table 4). Water restriction in T55 and T29 in 2020 affected annual wood starch accumulation (Fig. 2); consequently, the already short Winter pruning performed for the four treatments was made even more severe for the less irrigated treatments, leaving less buds (Table 3). However, T55 compensated this limitation with more clusters per bud, 1.54 (Tables 3 and 4). Severe DI may have modified vine source/sink balance by reducing the gas exchanges

Table 4 Vegetative-reproductive performance and Water Productivity (WP) recorded on the four irrigation treatments in the two years of trial. Within each experimental factor, (*) or different letters indicate a statistical difference at $p = 0.05$

Experimental factor	Clusters		Cluster weight		Yield		WP		Pruning weight		Ravaz Index	
	(number vine^{-1})		(g)		(t ha^{-1})		(kg m^{-3})		(g vine^{-1})		kg grapes/kg pruning weight	
Year												
2020	25.23	*	89.67		8.94	*	19.29	*	373.35	*	6.06	*
2021	12.06		79.33		3.80		7.77		237.10		4.03	
TRT												
T29	12.97	b	56.05	b	2.86	c	11.61		228.29	b	3.18	b
T55	15.77	ab	67.85	b	4.21	b	10.27		277.82	b	3.85	b
T85	15.66	ab	112.75	a	6.83	a	11.50		361.81	a	4.88	a
T100	18.21	a	96.07	a	7.10	a	10.56		352.98	a	4.96	a

through the closure of stomata (Müller et al. 2011), which was reflected in a reduced allocation of non-structural carbon reserves to perennial organs (Dayer et al. 2013; Herrera et al. 2015; Rustioni et al. 2019). On the other hand, mild drought conditions did not impact significantly the starch accumulation in canes. Water restriction also reduced vegetative activity in T55 and, above all, T29 showing the lowest pruning weight (Chaves et al. 2010; Matthews et al. 1990; Smart and Coombe 1983). WP was maintained stable among the treatments with a parallel reduction of reproductive and vegetative activity in the most stressed treatments (Table 4), suggesting a good plasticity of this variety as other grapevine cultivars (Intrigliolo et al. 2008).

Excluding T29, all the treatments showed a midday stem water potential between −0.8 to -1.1 MPa, considered as mild stress for grapevine. Ψs in T29 was ≤ -1.20 MPa, within the range of moderate-severe water stress for this species (Sadras and Shultz 2012). The generally low values of net photosynthesis recorded during the first and the second measurements could be attributable to the high VPD and air temperature encountered in this period. VPD was 3.64 and 4.98 kPa during the first and the second date, respectively, and the vines coped with the high evapotranspirative demand of the environment closing their stomata. In addition, air temperature was excessive (38.6 and 37.4 °C on June 21st and July 27th, respectively) for optimum RuBisCO carboxylative activity, and led to more photorespiration (von Caemmerer 2000; Foyer et al. 2009). Water restriction can affect carbon assimilation (Oliver-Manera et al. 2023) due to stomatal and non-stomatal limitations (Cifre et al. 2005; Flexas et al. 2002; Osmond and Grace 1995; Seaton and Walker 1990). Stomatal closure reduced CO_2 intake lowering carboxylation in T29 and T55 (Table 2). At the same time the reduction of leaf transpiration would have affected leaf thermoregulation increasing leaf temperature and the photoprotective (but dry matter consuming) pathways, i.e. photorespiration and the alternative electron transports (Escalona et al. 1999). At the very low gs levels, recorded on June 21st, for example, the rate of electrons exiting PSII (J_{PSII}) was proportional to the rate of net photosynthesis, indicating that the plant funnelled more energy to non-photochemical quenching processes instead of moving electrons no longer usable by RuBisCO (Table 2). On August 28th gs levels were higher; stomatal conductance and Pn were reduced passing from T85 to T55, however J_{PSII} remained quite stable as the electrons that could not be used for carboxylation were used by photorespiration and the alternative electron processes. These mechanisms are quite common in C3 plants, including fruit crops such as apple, pear, peach and apricot (Losciale et al. 2008, 2011, 2023), as well as in grapevine where Pn decreased with gs while J_{PSII} remained stable till a threshold of around 0.1 mol

Table 5 Total soluble solids (TSS), pH, Titratable Acidity (TA) and malic acid (mal), recorded on the must obtained from the four irrigation treatments in the two years of trial. Within each experimental factor, (*) or different letters indicate a statistical difference at $p = 0.05$

Experimental factor	TSS (°Brix)		pH	TA (g L^{-1})		mal (g L^{-1})	
Year							
2020	19.83	*	3.71	4.75		1.26	*
2021	24.27		3.75	4.59		3.09	
TRT							
T29	22.14	ab	3.74	3.90	b	1.72	b
T55	23.13	a	3.80	4.63	ab	2.40	a
T85	21.71	b	3.75	4.99	a	2.40	a
T100	21.23	b	3.63	5.17	a	2.19	a

Table 6 Chemical characteristics of Primitivo wines as a function of four irrigation regimes. E ethanol; TA-titratable acidity as tartaric acid; Mal-malic acid; DRE-dry reduced extract; TP-total polyphenols as gallic acid; A-anthocyanins as malvidin-3-glucoside. For each variable, different letters indicate a statistical difference at $p = 0.05$

YEAR	TREATMENT	E (% v/v)	pH	TA (g L^{-1})	Mal (g L^{-1})	DRE (g L^{-1})	A (mg L^{-1})	TP (mg L^{-1})
	T29	13.58 b	3.94	4.94 b	0.19 b	33.10 c	404.77 a	1762.67 b
	T55	14.90 a	3.91	5.91 a	0.67 a	36.56 a	438.67 a	2001.33 a
2021	**T85**	13.21 b	3.66	5.93 a	0.25 b	31.79 d	398.71 b	1569.33 d
	T100	14.77 a	3.73	5.73 a	0.27 b	34.07 b	410.33 a	1664.10 c

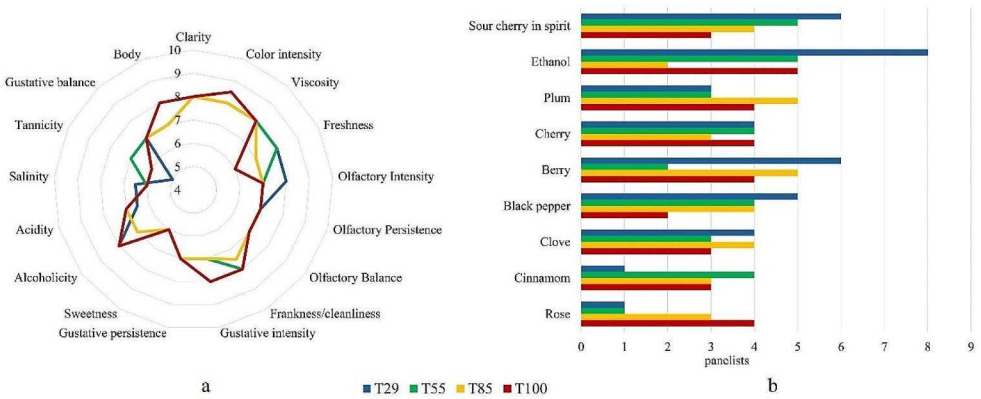

Fig. 3 Sensory evaluation in wines obtained from full irrigation (T100) and deficit irrigation (T25, T50, T85) of Primitivo grapevines after 6 months ageing (**a**) and sensorial perceived hints (**b**). Hints indicated by at least 5 tasters are significatively perceived at $\alpha < 0.05$

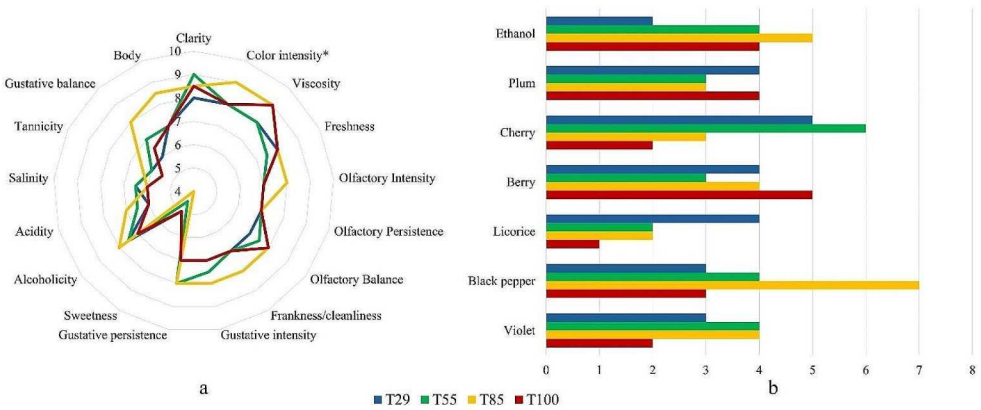

Fig. 4 Sensory evaluation in wines obtained from full irrigation (T100) and deficit irrigation (T25, T50, T 85) of Primitivo grapevines after 9 months ageing (**a**) and sensorial perceived hints (**b**). Hints indicated by at least 5 tasters are significatively perceived at $\alpha < 0.05$

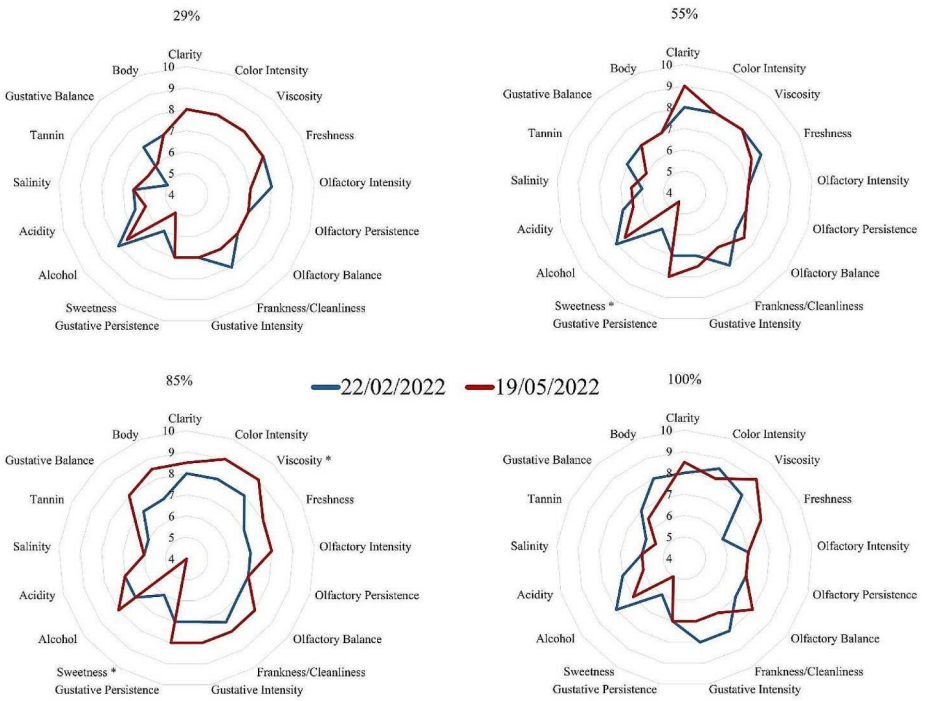

Fig. 5 Comparison of the sensory profiles of wines obtained from full irrigation (T100) and deficit irrigation (T25, T50, T 85) of Primitivo grapevines and tasted at two different aging stages: after 6 months (22/02/2022) and 9 months (19/05/2022)

$m^{-2}s^{-1}$. Below this value also the electron transport rate (J_{PSII}) dropped with a consequent increase of the photoprotective non-photochemical quenching (Flexas et al. 2002).

After seed hardening the water flux into the berries mainly occurs through the phloem (Düring et al. 1987; Findlay et al. 1987; Greenspan et al. 1996), which in turn depends on the concentration of sugars downloaded by leaves after the carboxylation process. The reduction in photosynthesis in T29 and T55 could have limited the phloem flux, contributing to the reduction of cluster weight (Table 4). Moderate DI (T85) did not affect leaf functionality as well as the productive and vegetative performances of vines, in accordance with previous studies on other grapevine cultivars, which report yield decreases when water restitution was lower than 80% ET_C (Du et al. 2006; Grimes and Williams 1990; Intrigliolo et al. 2008; Messaoudi and El-Fellah 2004).

A general reduction of the must quality was observed in T29 (Table 5). Sugar content slightly increased while the concentration of TA and malic acid declined. The low vigour of these vines probably exposed berries at a high level of direct light with a consequent increase of their temperature, leading to malic acid degradation (Buttrose et al. 1971; Ruffner et al. 1976). Wine quality did not always follow the same trend as the must, revealing the importance of the wine making process on the quality of the final product (Iorio et al. 2022). In general, a good wine quality, according to the standard of the variety, was achieved for all the treatments (Suriano et al. 2016). High water deficit (T29) decreased alcohol content, titratable acidity, malic acid and the dry reduced extract. Water supply of about half of evapotranspiration (T55) induced a higher alcohol content, titratable acidity, dry reduced extract, total polyphenols and anthocyanins of wines, associated with low yields per hectare. This water shortage could provide positive qualitative effects in terms of acidity and phenolic compounds (Greven et al. 2009). Sensorial analysis suggested that the paradigm "less quantity more quality" is confirmed within a certain range. After 6 months, wines were quite similar even if the ethanol sensation was higher in T29 (Fig. 3), maybe caused by the low concentration of malic acid, which could not compensate this sensation (Table 6). After 9 months, the colour intensity increased in T85, together with viscosity (Fig. 5). Considering the sensorial analysis, T85 can be considered a favourable compromise between high productivity, wine quality and water saving.

Conclusions

The Deficit Irrigation strategy, supplying 85% of ET_C along the season, led to a satisfactory result from a quantitative and qualitative point of view, on grapevine cv. "Primitivo", while allowing to save water resources. Water shortages higher than 45% ET_C affected whole vine behaviour in terms of reproductive and vegetative activity, limiting carbon fixation and plant water status. Water supply of 55% ET_C had a positive effect on wine quality with a considerably negative impact on yield, cluster weight, as well as on the vegetative

activity, lowering the starch reserve accumulation, the quality of wood, the number of shoots and the general vigour of the plant. Severe water stress further reduced the plant vigour and productivity also lowering the number of clusters in addition to their weight. Particularly interesting are the results of T55 where the wine quality, assessed by chemical analysis after 6 months, was increased but to the cost of a severe loss of productivity. Further studies aiming at investigating the effect of an intermediate DI, between 85 and 55 ET_C, on the general behaviour of Primitivo grapevine, as well as the long-term effects on the quantitative and qualitative performances of the vines are needed.

Acknowledgements The authors would like to thank Melis S., Puppi E., Carpino A., and Bene A. for their contribution in data collection, Torrevento Wineries, Corato (BA) for hosting the trial, and professors Stellacci A.M. and Corelli-Grappadelli L. for enhancing the quality of the text.

Author contributions Conceptualization and methodology, L.P. and T.L.; data curation, C.L., S.S., M. F., T. F., R. L., D.G.; formal analysis, L.P., A.V; investigation, C.L., S.S., M.F., T.F., R.L.; supervision, L.P., T.L.; writing original draft, L.P., C.L., S.S.; Writing review and editing, R.L., A.V., T.L. All authors have read and agreed to the published version of the manuscript.

Funding Open access funding provided by Università degli Studi di Bari Aldo Moro within the CRUI-CARE Agreement.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

References

Alba V, Gentilesco G, Tarricone L (2021) Climate change in a typical apulian region for table grape production: spatialisation of bioclimatic indices, classification and future scenarios. OENO One 55(3):317–336. https://doi.org/10.20870/oeno-one.2021.55.3.4733

Allen RG, Pereira LS (2009) Estimating crop coefficients from fraction of ground cover and height. Irrig Sci 28(1):17–34. https://doi.org/10.1007/s00271-009-0182-z

Barbagallo MG, Vesco G, Di Lorenzo R, Lo Bianco R, Pisciotta A (2021) Soil and regulated deficit irrigation affect growth, yield and quality of 'nero d'avola' grapes in a semi-arid environment. Plants 10(4):641. https://doi.org/10.3390/PLANTS10040641/S1

Bonfante A, Alfieri SM, Albrizio R, Basile A, De Mascellis R, Gambuti A, Giorio P, Langella G, Manna P, Monaco E, Moio L, Terribile F (2017) Evaluation of the effects of future climate change on grape quality through a physically based model application: a case study for the Aglianico grapevine in Campania region, Italy. Agric Syst 152:100–109. https://doi.org/10.1016/J.AGSY.2016.12.009

Buesa I, Pérez D, Castel J, Intrigliolo DS, Castel JR (2017) Effect of deficit irrigation on vine performance and grape composition of Vitis vinifera L. Cv. Muscat of Alexandria. Aust J Grape Wine Res 23(2):251–259. https://doi.org/10.1111/AJGW.12280

Buttrose MS, Hale CR, Kliewer WM (1971) Effect of temperature on the composition of 'Cabernet Sauvignon' Berries. Am J Enol Viticult 22(2):71–75. https://doi.org/10.5344/AJEV.1971.22.2.71

Chaves MM, Zarrouk O, Francisco R, Costa JM, Santos T, Regalado AP, Rodrigues ML, Lopes CM (2010) Grapevine under deficit irrigation: hints from physiological and molecular data. Ann Botany 105(5):661–676. https://doi.org/10.1093/AOB/MCQ030

Cifre J, Bota J, Escalona JM, Medrano H, Flexas J (2005) Physiological tools for irrigation scheduling in grapevine (Vitis vinifera L.): an open gate to improve water-use efficiency? Agric Ecosyst Environ 106(2):159–170. https://doi.org/10.1016/j.agee.2004.10.005

Conesa MR, Dodd IC, Temnani A, De la Rosa JM, Pérez-Pastor A (2018) Physiological response of post-veraison deficit irrigation strategies and growth patterns of table grapes (cv. Crimson Seedless). Agric Water Manage 208:363–372. https://doi.org/10.1016/J.AGWAT.2018.06.019

Cos J, Doblas–Reyes F, Jury M, Marcos R, Bretonnière PA, Samsó M (2022) The Mediterranean climate change hotspot in the CMIP5 and CMIP6 projections. Earth Syst Dynam 13:321–340

Costa JM, Ortuño MF, Chaves MM (2007) Deficit irrigation as a strategy to save water: physiology and potential application to horticulture. J Integr Plant Biol 49:1421–1434. https://doi.org/10.1111/j.1672-9072.2007.00556.x

Dayer S, Prieto JA, Galat E, Perez Peña J (2013) Carbohydrate reserve status of Malbec grapevines after several years of regulated deficit irrigation and crop load regulation. Aust J Grape Wine Res 19(3):422–430. https://doi.org/10.1111/ajgw.12044

Des Gachons C, Van Leeuwen C, Tominaga T, Soyer JP, Gaudillère JP, Dubourdieu D (2005) Influence of water and nitrogen deficit on fruit ripening and aroma potential of Vitis vinifera L Cv Sauvignon Blanc in field conditions. J Sci Food Agric 85(1):73–85. https://doi.org/10.1002/JSFA.1919

Di Stefano R, Cravero MC, Gentilini N (1989) Metodi per lo studio dei polifenoli dei vini. L'Enotecnico, (5): 83–89

Drappier J, Thibon C, Rabot A, Geny–Denis L (2019) Relationship between wine composition and temperature: impact on Bordeaux wine typicity in the context of global warming—review. Crit Rev Food Sci Nutr 59:14–30

Du T, Kang S, Zhang J, Li F, Hu X (2006) Yield and physiological responses of cotton to partial root-zoneirrigation in the oasis field of northwest China. Agric Water Manage 84:41–52

Düring H, Lang A, Oggionni F (1987) Patterns of water flow in Riesling berries in relation to developmental changes in their xylem morphology. Vitis 26:123–131

EEA EEA Report No 12/2021Water resources across Europe-confronting water stress: an updated assessment. Available online: https://www.eea.europa.eu/publications/water-resources-across-europe-confronting

Escalona JM, Flexas J, Medrano H (1999) Contribution of different levels of plant canopy to total carbon assimilation and intrinsic water use efficiency of manto negro and tempranillo grapevines. Acta Hort 493:141–148. https://doi.org/10.17660/ACTAHORTIC.1999.493.13

Fereres E, Soriano MA (2007) Deficit irrigation for reducing agricultural water use. J Exp Bot 58(2):147–159. https://doi.org/10.1093/jxb/erl165

Fernández JE, Alcon F, Diaz-Espejo A, Hernandez-Santana V, Cuevas MV (2020) Water use indicators and economic analysis for on-farm irrigation decision: a case study of a super high density olive tree orchard. Agric Water Manage 237:106074. https://doi.org/10.1016/j.agwat.2020.106074

Findlay N, Oliver KJ, Nil N, Coombe BG (1987) Solute Accumulation by grape pericarp cells: IV. Perfusion of pericarp apoplast via the pedicel and evidence for xylem malfunction in ripening berries. J Exp Bot 38(4):668–679. https://doi.org/10.1093/JXB/38.4.668

Flexas J, Bota J, Escalona JM, 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(4):461–471. https://doi.org/10.1071/PP01119

Foyer CH, Bloom AJ, Queval G, Noctor G (2009) Photorespiratory metabolism: genes, mutants, energetics, and redox signaling. Annu Rev Plant Biol 60:455–484

Gambacorta G, Faccia M, Natrella G, Noviello M, Masi G, Tarricone L (2022) Early basal Leaf removal at different sides of the Canopy improves the quality of Aglianico Wine. Foods 11(19):3140. https://doi.org/10.3390/foods11193140

Gambetta GA, Herrera JC, Dayer S, Feng Q, Hochberg U, Castellarin SD (2020) The physiology of drought stress in grapevine: towards an integrative definition of drought tolerance. J Exp Bot 71(16):4658–4676. https://doi.org/10.1093/JXB/ERAA245

Gamero E, Moreno D, Talaverano I, Prieto MH, Guerra MT, Valdés ME (2014a) Effects of irrigation and cluster thinning on tempranillo grape and wine composition. S Afr J Enol Vitic 35(2):196–204. https://doi.org/10.21548/35-2-1006

Gamero E, Moreno D, Vilanova M, Uriarte D, Prieto MH, Valdés ME (2014b) Effect of bunch thinning and water stress on chemical and sensory characteristics of tempranillo wines. Aust J Grape Wine Res 20(3):394–400. https://doi.org/10.1111/AJGW.12088

García-Esparza MJ, Abrisqueta I, Escriche I, Intrigliolo DS, Álvarez I, Lizama V (2018) Volatile compounds and phenolic composition of skins and seeds of Cabernet Sauvignon grapes under different deficit irrigation regimes. VITIS - J Grapevine Res 57(3):83–91. https://doi.org/10.5073/VITIS.2018.57.83-91

Gentilesco G, Coletta A, Tarricone L, Alba V (2023) Bioclimatic characterization relating to temperature and subsequent future scenarios of Vine growing across the Apulia Region in Southern Italy. Agriculture 13:644. https://doi.org/10.3390/agriculture13030644

Greenspan MD, Schultz HR, Matthews MA (1996) Field evaluation of water transport in grape berries during water deficit. Physiol Plant 97:55–62. https://doi.org/10.1111/j.1399-3054.1996.tb00478.x

Greven MM, Raw V, West BA (2009) Effects of timing of water stress on yield and berry size. Water Sci Technol 60(5):1249–1255. https://doi.org/10.2166/wst.2009.553

Grimes DW, Williams LE (1990) Irrigation effects on plant water relations and productivity of Thompson Seedless grapevines. Crop Sci 30:255–260

Gutiérrez–Gamboa G, Zheng W, Martínez de Toda F (2021) Current viticultural techniques to mitigate the effects of global warming on grape and wine quality: a comprehensive review. Food Res Int 139:109946

Herrera JC, Bucchetti B, Sabbatini P, Comuzzo P, Zulini L, Vecchione A, Peterlunger E, Castellarin SD (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(2):254–265. https://doi.org/10.1111/AJGW.12143/SUPPINFO

Hornbuckle J, Ballester C, Vlesshouwer J, Hoogers B, Montgomery J, Hoogers R (2016) IrriSAT Technical Reference.

Huglin P (1978) Nouveau mode d'évaluation des possibilités héliothermiques d'un milieu viticole. Comptes Rendus De L'académie D'agriculture De France 64:1117–1126

Iglesias A, Garrote L (2015) Adaptation strategies for agricultural water management under climate change in Europe. Agric Water Manage 155:113–124. https://doi.org/10.1016/J.AGWAT.2015.03.014

Intrigliolo DS, Castel JR (2011) Interactive effects of deficit irrigation and shoot and cluster thinning on grapevine cv. Tempranillo. Water relations, vine performance and berry and wine composition. Irrig Sci 29(6):443–454. https://doi.org/10.1007/S00271-010-0252-2

Intrigliolo DS, Castel JR, Cárcel S (2008) Effects of crop level and irrigation on yield and wine quality of tempranillo grapevines in a dry year. Acta Hort 792:371–378. https://doi.org/10.17660/ActaHortic.2008.792.43

Intrigliolo DS, Lizama V, García-Esparza MJ, Abrisqueta I, Álvarez I (2016) Effects of post-veraison irrigation regime on Cabernet Sauvignon grapevines in Valencia, Spain: yield and grape composition. Agric Water Manage 170:110–119. https://doi.org/10.1016/J.AGWAT.2015.10.020

Iorio D, Gambacorta G, Tarricone L, Vilanova M, Paradiso VM (2022) Effect of early basal Leaf removal on phenolic and Volatile Composition and Sensory Properties of Aglianico Red Wines. Plants 11:591. https://doi.org/10.3390/plants11050591

Koppen W (1936) Das Geographisca System Der Klimate. In: Koppen W, Geiger G (eds) Handbuch Der Klimatologie, Gebr. Borntraeger, Berlin, pp 1–44

Lionello P, Scarascia L (2018) The relation between climate change in the Mediterranean region and global warming. Reg Environ Chang18:1481–1493

Lizama V, Pérez-Álvarez EP, Intrigliolo DS, Chirivella C, Álvarez I, García-Esparza MJ (2021) Effects of the irrigation regimes on grapevine cv. Bobal in a Mediterranean climate: II. Wine, skins, seeds, and grape aromatic composition. Agric Water Manage 256:107078. https://doi.org/10.1016/J.AGWAT.2021.107078

Losciale P, Zibordi M, Manfrini L, Corelli-Grappadelli L (2008) Effects of rootstock on pear photosynthetic efficiency. Acta Hort 800:241–247. https://doi.org/10.17660/actahortic.2008.800.28

Losciale P, Zibordi M, Manfrini L, Morandi B, Bastias RM, Corelli-Grappadelli LC (2011) Light management and photoinactivation under drought stress in Peach. Acta Hort 922:341–348. https://doi.org/10.17660/actahortic.2011.922.44

Losciale P, Gaeta L, Corsi M, Galeone C, Tarricone L, Leogrande R, Stellacci AM (2023) Physiological responses of apricot and peach cultivars under progressive water shortage: different crop signals for anisohydric and isohydric behaviours. Agric Water Manage 286:108384. https://doi.org/10.1016/j.agwat.2023.108384

Lovisolo C, Perrone I, Carra A, Ferrandino A, Flexas J, Medrano H, Schuber 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. Funct Plant Biol 37(2):98–116. https://doi.org/10.1071/FP09191

Matthews MA, Ishii R, Anderson MM, O'Mahony M (1990) Dependence of wine sensory attributes on vine water status. J Sci Food Agric 51(3):321–335. https://doi.org/10.1002/JSFA.2740510305

Messaoudi Z, El-Fellah A (2004) Optimisation de l'irrigation de la vigne dans le plateau de Meknès (Maroc). Cah Options Méditer 62:197–201

Müller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, amd Gibon Y (2011) Water deficits uncouple growth from photosynthesis,

increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot 62:1715–1729
Munitz S, Netzer Y, Schwartz A (2017) Sustained and regulated deficit irrigation of field-grown merlot grapevines. Aust J Grape Wine Res 23(1):87–94. https://doi.org/10.1111/AJGW.12241
Mzid N, Boussadia O, Albrizio R, Stellacci AM, Braham M, Todorovic M (2023) Salinity Properties Retrieval from Sentinel-2 Satellite Data and Machine Learning algorithms. Agronomy 13:716. https://doi.org/10.3390/agronomy13030716
Naor A, Klein I, Doron I (1995) Stem water potential and apple size. J Am Soc Hortic Sci 120(4):577–582. https://doi.org/10.21273/JASHS.120.4.577
OIV (2022) State of the World Vine and Wine Sector in 2022. Available online: https://www.oiv.int/sites/default/files/documents/2023_SWVWS_report_EN.pdf
Oliver-Manera J, García-Tejera O, Mata M, Girona J (2023) Cumulative response of Tempranillo vines to the crop forcing technique and pre-forcing and post-veraison water stress in terms of yield and grape and wine quality. Irrig Sci 41:571–587. https://doi.org/10.1007/S00271-023-00855-W
Osmond CB, Grace SC (1995) Perspectives on photoinhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis? J Exp Bot 46(specialissue):1351–1362. https://doi.org/10.1093/JXB/46.SPECIAL_ISSUE.1351
Pérez-Álvarez EP, Intrigliolo DS, Almajano MP, Rubio-Bretón P, Garde-Cerdán T (2021) Effects of Water Deficit Irrigation on Phenolic composition and antioxidant activity of Monastrell grapes under Semiarid conditions. Antioxidants 10(8):1301. https://doi.org/10.3390/ANTIOX10081301
Pinna M (1970) Contributo alla classificazione del clima d'Italia. Rivista Geografica Italiana 77(2):129–152 ISSN 0035-6697
Ravaz L (1903) Sur La Brunissure De La Vigne. Comptes rendus de l'Académie des Sci 136:1276–1278
Riou CH, Becker N, Sotes Ruiz V, Gomez-Miguel V, Carbonneau A, Panagiotou M, Calo A, Costacurta A, Castro de R, Pinto A, Lopes C, Carneiro L, Climaco P (1994) Le déterminisme climatique de la maturation Du raisin: application Au Zonage De La Teneur em sucre dans la communauté européenne. Office des Publications Officielles des Communautés Européennes, Luxembourg, p 322
Romero P, Navarro JM, Ordaz PB (2022) Towards a sustainable viticulture: the combination of deficit irrigation strategies and agroecological practices in Mediterranean vineyards. A review and update. Agric Water Manage 259:107216. https://doi.org/10.1016/J.AGWAT.2021.107216
Ruffner HP, Hawker JS, Hale CR (1976) Temperature and enzymic control of malate metabolism in berries of Vitis vinifera. Phytochemistry 15(12):1877–1880. https://doi.org/10.1016/S0031-9422(00)88835-4
Ruiz-Sanchez MC, Domingo R, Castel JR (2010) Review. Deficit irrigation in fruit trees and vines in Spain. Span J Agricultural Res 8(2):5–20. https://doi.org/10.5424/SJAR/201008S2-1343
Rustioni L, Ciacciulli A, Grossi D, Brancadoro L, Failla O (2016) Stem xylem characterization for Vitis drought tolerance. J Agric Food Chem 64:5317–5323
Rustioni L, Ciacciulli A, Zulini L, Zuliani E, Sivilotti P, Herrera JC (2017) Starch quantification in woody tissues by reflectance spectroscopy and on-solid iodine complexation. Sci Hortic 226:117–121
Rustioni L, Herrera JC, Failla O, Peterlunger E, Sivilotti P (2019) Stem starch reserves studied by on-solid reactions coupled with reflectance detections in water stressed grapevines Vitis. 58:47–51
Sadras VO (2009) Does partial root-zone drying improve irrigation water productivity in the field? A meta-analysis. Irrig Sci 27(3):183–190. https://doi.org/10.1007/S00271-008-0141-0/FIGURES/4
Sadras VO, Shultz H (2012) Grapevine In: Crop yield response to water; Steduto, P., Hsiao, T., Fereres, E., Raes, D. (ed.s), pp.460–485, FAO-Rome
Safriel UN (2009) Status of Desertification in the Mediterranean Region. In Water Scarcity, Land Degradation and Desertification in the Mediterranean Region In: Rubio JL, Safriel UN, Daussa R, Blum W, Pedrazzini F (eds). Part of NATO Science for Peace and Security Series C: Environmental Security; Springer: Berlin, Germany
Santos JA, Fraga H, Malheiro AC, Moutinho-Pereira J, Dinis LT, Correia C, Moriondo M, Leolini L, Dibari C, Costafreda-Aumedes S, Kartschall T, Menz C, Molitor D, Junk J, Beyer M, Schultz HR (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
Schultz HR (2017) Issues to be considered for strategic adaptation to climate evolution – is atmospheric evaporative demand changing? OENO One 51(2):107–114. https://doi.org/10.20870/OENO-ONE.2017.51.2.1619
Seaton GGR, Walker DA (1990) Chlorophyll fluorescence as a measure of photosynthetic carbon assimilation. Proc Royal Soc B: Biol Sci 242(1303):29–35. https://doi.org/10.1098/rspb.1990.0099
Shellie KC, King BA (2020) Application of a daily crop water stress index to Deficit Irrigate Malbec Grapevine under Semi-arid conditions. Agriculture 10(11):492. https://doi.org/10.3390/AGRICULTURE10110492
Smart RE, Coombe BG (1983) Water relations in grapevine. Water deficit and plant growth, vol VII. Academic (London, UK; New York, USA), pp 136–196
Storchi P, Giorgessi F, Valentini P, Tarricone L, Bonello F, Tamborra P (2005) Effect of irrigation on vegetative and reproductive behaviour of 'Sauvignon Blanc' in Italy. Acta Hort 689:349–356
Suriano S, Alba V, Di Gennaro D, Basile T, Tamborra M, Tarricone L (2016) Major phenolic and volatile compounds and their influence on sensorial aspects in stem-contact fermentation winemaking of Primitivo red wines. J Food Sci Technol 53:3329–3339. https://doi.org/10.1007/S13197-016-2310-0
Tarricone L, Alba V, Di Gennaro D, Amendolagine AM, Gentilesco G, Masi G (2017) Grape and wine quality of Vitis vinifera 'Nero Di Troia' in response to moderate deficit irrigation. Acta Hort 1150:485–492
Tomás M, Medrano H, Escalona JM, Martorell S, Pou A, Ribas-Carbó M, Flexas J (2014) Variability of water use efficiency in grapevines. Environ Exp Bot 103:148–157. https://doi.org/10.1016/J.ENVEXPBOT.2013.09.003
Tonietto J (1999) Les macroclimats viticoles Mondiaux et l'influence du mésoclimat sur la typicité de la Syrah et du Muscat de Hambourg dans le sud de la France: méthodologie de caráctérisation. Thèse Doctorat. Ecole Nationale Supérieure Agronomique, Montpellier, p 233
Tonietto J, Carbonneau A (2004) A multicriteria climatic classification system for grape-growing regions worldwide. Agric for Meteorol 124:81–97. https://doi.org/10.1016/j.agrformet.2003.06.001
Torres N, Yu R, Martínez-Lüscher J, Kostaki Eand Kurtural SK (2021) Effects of Irrigation at different fractions of Crop Evapotranspiration on Water Productivity and Flavonoid composition of Cabernet Sauvignon Grapevine. Front Plant Sci 12:1858. https://doi.org/10.3389/FPLS.2021.712622/BIBTEX
Trout TJ, Johnson LF (2007) Estimating crop water use from remotely sensed NDVI, Crop Models and Reference ET. USCID Fourth International Conference on Irrigation and Drainage, The Role of Irrigation and Drainage in a sustainable Future. Clemmens, AJ and Anderson SS (eds.), Sacramento, California, October 3–6, 2007
von Caemmerer S (2000) Chlorophyll fluorescence and oxygen exchange during C3 photosynthesis. In: CSIRO (ed) Biochemical

models of Leaf Photosynthesis. CSIRO Publishing (Australia), pp 42–65

Wang Y, Liu F, Jensen CR (2012) Comparative effects of deficit irrigation and alternate partial root-zone irrigation on xylem pH, ABA and ionic concentrations in tomatoes. J Exp Bot 63(5):1907–1917. https://doi.org/10.1093/JXB/ERR370

Winkler AJ, Cook J, KliewerWM, Lider LA (1974) General Viticulture; University of California Press: Berkeley, CA, USA, 1974

Zarrouk O, Brunetti C, Egipto R, Pinheiro C, Genebra T, Gori A, Lopes CM, Tattini M, Chaves MM (2016) Grape ripening is regulated by deficit irrigation/elevated temperatures according to cluster position in the canopy. Front Plant Sci 7:1640. https://doi.org/10.3389/FPLS.2016.01640

Zollo AL, Rillo V, Bucchignani E, Montesarchio M, Mercogliano P (2016) Extreme temperature and precipitation events over Italy: Assessment of high-resolution simulations with COSMO-CLM and future scenarios. Int J Climatol 36(2):987–1004. https://doi.org/10.1002/JOC.4401

CHAPTER IV

This chapter investigates cultivar-specific regulatory strategies under controlled stress dynamics. It shows how genotypic differences modulate the trajectory and expression of functional responses, reinforcing the importance of context-aware interpretation when defining functional boundaries under water limitation.

BACKGROUND

Improving almond performance under water limitation requires not only optimized irrigation strategies but also the identification of cultivar-specific drought-response traits. Because stomatal regulation, thermal response, and carbon assimilation are strongly modulated by genotype and stress dynamics, drought tolerance cannot be inferred from a single measurement or from a single stress scenario. Controlled phenotyping under progressive soil drying offers a useful framework to distinguish short-term physiological strategies among cultivars and to evaluate which indicators are most informative for comparative screening.

AIMS

This chapter aims to evaluate whether progressive soil water depletion improves the discrimination of drought responses among almond cultivars under controlled conditions, and to assess the suitability of selected physiological variables for describing cultivar-specific adjustment to water deficit. More specifically, it compares five cultivars under control, static stress, and dynamic stress conditions, with particular emphasis on stomatal conductance, leaf-to-air temperature difference, and related functional traits as comparative indicators of short-term drought response.

RESULTS

The study showed clear genotype-dependent differences in the trajectory and expression of functional responses to water limitation. Dynamic stress was more effective than static stress in separating cultivar behaviour over time. Filippo Cea and Texas maintained higher stomatal conductance over a broader range of available water content and generally showed lower leaf overheating, whereas Ferragnes, Makako, and Tuono exhibited earlier stomatal closure accompanied by larger increases in leaf-to-air temperature difference. Transpiration closely mirrored stomatal conductance, while $P_{KO/KC}$ declined later than gs, indicating that early stomatal regulation preceded stronger carboxylative limitation. The Physiological Resistance Index further supported lower relative stomatal sensitivity in Filippo Cea, and to a lesser extent in Texas, compared with the other cultivars. Recovery after rehydration was variable among genotypes, confirming that cultivar identity modulates both stress progression and post-stress recovery. Overall, the results reinforce that functional boundaries under water deficit are cultivar-specific and must be interpreted in relation to stress dynamics and indicator coupling rather than through fixed universal thresholds.

Phenotypic characterization of 5 almond cultivars under drought stress

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Abstract

Developing drought-resilient almond cultivars is crucial for sustainable farming in Mediterranean climates. We evaluated five cultivars (Texas, Filippo Cea (syn Filippo Ceo), Makako, Ferragnes, Tuono) under three irrigation regimes: full irrigation (CTRL, 100% AWC (available water content), static stress (SS, 45% AWC), and dynamic stress (DS, gradual reduction to 15% AWC). Both SS and DS followed a recovery period. Growth traits and physiological variables, stomatal conductance (gs), transpiration (Tr), relative water content (RWC), PSII electron transport (J_{PSII}), leaf-to-air temperature difference (ΔT), and carboxylation index ($P_{KO/KC}$), were measured. Stomatal conductance and ΔT showed consistent and coordinated responses to soil water depletion (r = –0.84). The dynamic stress protocol resulted in clearer temporal differentiation among cultivars compared with static deficit. During progressive soil drying, Filippo Cea and Texas maintained higher gs over a broader range of AWC, whereas Ferragnes, Makako and Tuono exhibited earlier reductions in gs accompanied by increases in ΔT. Differences among cultivars were also reflected in the calculated Physiological Resistance Index (PhyResIx), which provided a comparative description of relative stomatal sensitivity under the imposed conditions.

The combined assessment of gs and ΔT allowed characterization of cultivar-specific physiological responses to short-term soil water depletion in this experimental system. Further validation under field conditions and evaluation of long-term agronomic performance are required before extrapolating these findings to orchard management.

Keywords: Prunus dulcis, drought tolerance, stomatal conductance, phenotyping.

INTRODUCTION

Drought is one of the main abiotic stresses threatening global agriculture, particularly in Mediterranean regions (Fernández et al., 2013). Two complementary adaptation strategies are being developed: (i) advanced irrigation techniques to mitigate yield loss, and (ii) breeding of cultivars capable of maintaining productivity under water scarcity (Gabaldón-Leal et al., 2017). Almond has become increasingly profitable due to market demand, with new orchards established in areas with suitable soils and irrigation. However, as a perennial crop, almond has limited adaptive flexibility compared with annuals (Parker & Abatzoglou, 2016, 2017). Adaptation strategies include the selection of drought-tolerant cultivars (Gabaldón-Leal et al., 2017), identification of new growing regions (Parker & Abatzoglou, 2016, 2017), and irrigation practices such as regulated deficit irrigation (RDI) (Fereres & Soriano, 2007; Girona et al., 2005). Although almonds tolerate drought, adequate irrigation improves yield and nut quality (Egea et al., 2013; García-Tejero et al., 2018). Deficit irrigation (DI), providing water below evapotranspiration demand, balances conservation with productivity (Fereres & Soriano, 2007). Under water stress, plants typically reduce stomatal conductance (gs) and photosynthesis, a strategy observed in almonds (Flexas et al., 2004, 2013; Romero et al., 2004). Stomatal behavior is influenced by environmental conditions, leaf water status, circadian rhythms, and hormonal signals such as abscisic acid (ABA) (Bacon, 2004; Webb & Hetherington, 1997). Stomatal conductance peaks between 20–40 °C,

while extremes (<5 °C, >45 °C) limit function (Jarvis, 1976). Vapor pressure deficit (VPD) strongly regulates stomata, with higher VPD reducing gs to prevent excessive transpiration (Maroco et al., 1997; Monteith, 1995). These responses help prevent dehydration and cavitation, sometimes independently of leaf water content (Álvarez-Maldini et al., 2022; Franks et al., 1997; Maherali et al., 2003). Stomatal sensitivity may be reduced under elevated CO_2 but intensified under water stress (Bunce, 1997; Eamus & Shanahan, 2002). Improving almond drought tolerance requires understanding almond responses across morphological (rooting, leaf area), biochemical (osmolytes), and physiological (stomatal regulation) traits. Combining ecophysiology, transcriptomics, and genetics provides reliable targets for resistance (Lauri et al., 2016; Valliyodan & Nguyen, 2006). The present study aimed to evaluate whether progressive soil water depletion enhances discrimination among almond cultivars under controlled conditions and to assess the suitability of selected physiological variables for describing cultivar-specific responses to drought.

Specifically, the study investigated the responses of five almond cultivars subjected to different irrigation regimes, with particular attention to stomatal conductance (gs) and leaf-to-air temperature difference (ΔT) as potential indicators of short-term physiological adjustment to soil water depletion.

The additional objective was to identify traits that may support comparative phenotyping of young trees under controlled stress conditions, without directly addressing long-term agronomic performance or field-level drought tolerance.

MATERIALS AND METHODS

The experiment was conducted from early spring to late summer 2024 at ALSIA, Metaponto (Southern Italy), using ninety potted almond trees grafted on Garnem rootstock and supplied by Vivai Fortunato (Sammichele di Bari, Italy). Five cultivars (Ferragnes, Filippo Cea, Makako, Texas and Tuono) were selected based on reported differences in drought response.

The experiment was arranged in a completely randomized design with a 5 × 3 factorial combination of cultivars and irrigation regimes. Eighteen plants per cultivar were used, with six plants randomly assigned to each irrigation treatment. The individual plant was considered the experimental unit.

To standardize canopy structure, all plants were pruned to a single shoot before the trial. Initial shoot growth and leaf traits were recorded. Specific leaf area (SLA) was determined on dried samples after leaf area measurement using the Easy Leaf Area application, previously validated against a LI-COR 3100 area meter.

Irrigation thresholds were established from gravimetrically determined soil hydrological constants. Three irrigation regimes were imposed: CTRL (100% AWC), SS (45% AWC), and DS, in which soil water content was progressively reduced from 100% to 15% AWC, with plants maintained for about one week at each intermediate level. After reaching 15% AWC, plants were rehydrated to 100% AWC to assess recovery.

The experimental phase lasted from June 6 to July 11. The trial was carried out on the Lamnatech phenotyping platform at Metapontum Agrobios, integrating automated weighing and irrigation systems that ensured precise maintenance of soil moisture thresholds.

Weekly physiological measurements were performed at midday under saturating light using a LI-COR 600 poro-fluorometer. Stomatal conductance (gs), transpiration rate (Tr), leaf-to-air temperature difference (ΔT), and chlorophyll fluorescence were measured on three fully expanded leaves per plant. PSII electron transport rate (J_{PSII}) was estimated from chlorophyll fluorescence according to Genty et al. (1989), whereas the carboxylation index ($P_{KO/KC}$) was derived as a fluorescence-based proxy of carboxylative activity following the integrative approach described by Losciale et al. (2015, 2023). Measurements from the three leaves were averaged prior to statistical analysis to avoid pseudoreplication. Relative water content (RWC) was determined in the DS treatment at 15% AWC and after rehydration (100% AWC), using fresh, turgid, and dry weights.

For the DS treatment, a Physiological Resistance Index based on stomatal conductance (PhyResIx) was calculated as a comparative indicator of stomatal sensitivity to soil water depletion, expressing the proportional reduction in gs relative to the proportional reduction in available water content (AWC).The index expresses the proportional reduction in gs relative to the proportional reduction in available water content (AWC). Values close to zero indicate limited relative stomatal sensitivity, whereas higher positive values indicate stronger stomatal limitation in response to decreasing soil water availability.

The index should be interpreted as a comparative indicator under the specific experimental conditions of this study.

Data were analysed separately for each sampling date, namely 06/06, 11/06, 18/06, 25/06, 02/07, 05/07, 09/07, and 11/07, in order to describe treatment effects along the progression of soil water

depletion. For each date, one-way ANOVA was performed (i) to compare cultivars within each irrigation treatment and (ii) to compare irrigation treatments within each cultivar. When significant effects were detected, means were separated using Tukey's HSD test ($p \leq 0.05$).
Assumptions of normality and homogeneity of variances were verified prior to analysis using residual inspection and Levene's test.
Since measurements were repeated over time on the same experimental units, the date-wise analysis should be interpreted as descriptive of temporal dynamics rather than as a fully integrated longitudinal model. Therefore, results are discussed considering consistency of patterns across dates rather than isolated single-date significances.
Pearson correlation coefficients were calculated using pooled data across cultivars and irrigation treatments. Correlation analysis was exploratory and did not account for the hierarchical structure of the experimental design.

RESULTS AND DISCUSSION

At the onset of the experiment, Makako, Tuono, and Ferragnes showed the greatest shoot growth and leaf production, while Texas and Filippo Cea developed smaller canopies. Leaf area did not vary significantly among cultivars, but fresh and dry weights were highest in Texas and lowest in Makako. Specific leaf area (SLA) was greatest in Makako and lowest in Texas and Filippo Cea. Low SLA, usually linked to thicker leaves with higher structural investment, has been associated with enhanced drought tolerance in Mediterranean species (Poorter et al., 2009; Wright et al., 2005), suggesting that Texas and Filippo Cea may possess stronger structural adaptations to cope with water scarcity (Fig.1).

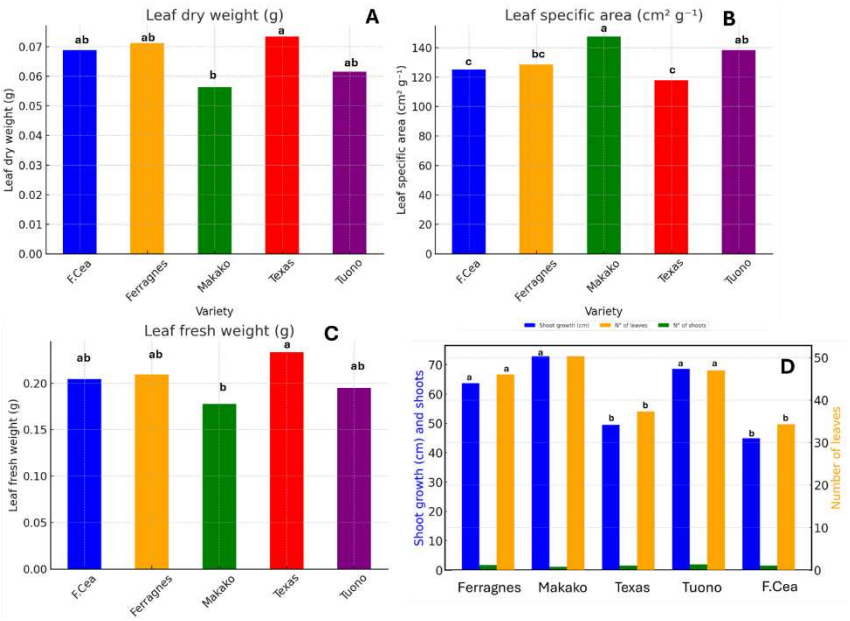

Figure 1. Initial vegetative traits of five almond cultivars (Ferragnes, Makako, Texas, Tuono, Filippo Cea) before stress imposition: (A) leaf dry weight, (B) specific leaf area (SLA), (C) leaf fresh weight, and (D) shoot growth and leaf number. Values represent means ± SE (n = 6 plants per cultivar). Different letters indicate significant differences among cultivars according to one-way ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

The three water treatments affected functionality trends differently across varieties. These trends reflected the decline in soil water content (AWC), with the SS treatment dropping first, followed by DS. When both DS and SS reached 45% AWC, no significant differences were observed, suggesting that progressive water depletion and a sudden cut-off in AWC induce a similar response in plant functionality, at least within a short time window (Fig. 2). Under static stress, gs dropped rapidly, while under dynamic stress cultivars diverged: Filippo Cea and Texas maintained higher gs until 60% AWC afterwards gs drastically decreased in DS for Texas in comparison with Filippo Cea. Makako, Tuono, and Ferragnes decreased earlier. After rehydration, recovery was incomplete, but Makako and Ferragnes regained near-control levels. Rapid recovery of plant water status has been noted in young almond trees (Torrecillas et al., 1996) and other fruit trees, such as peaches (Goldhamer et al., 1999) and citrus (Fereres et al., 1979). However, recovery speed depends on the

severity of the stress: DS recovery after reaching 15% AWC was generally slower than SS for Texas and Makako (Fig. 2). Klein et al. (2001) reported immediate water potential recovery in moderately stressed almond trees but slower recovery under severe stress.

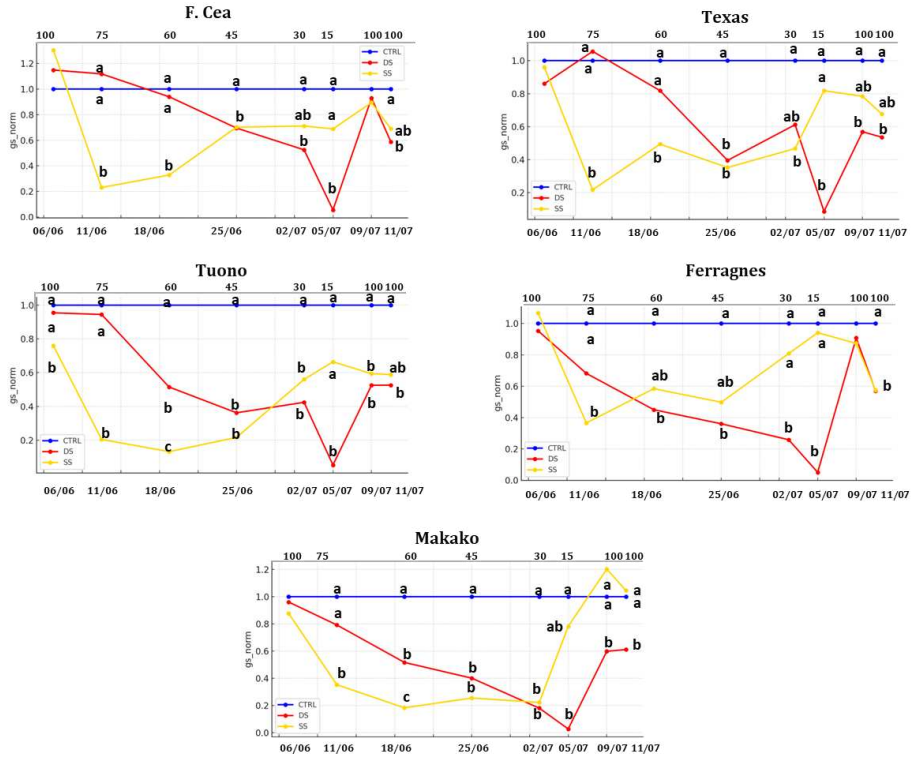

Figure 2. Stomatal conductance (gs) trends over time in five almond cultivars under control (CTRL), static stress (SS, 45% AWC), and dynamic stress (DS, progressive reduction to 15% AWC). Values were normalized to the corresponding control treatment at each date. Data represent means (n = 6 plants per treatment × cultivar). Within each sampling date, different letters indicate significant differences according to one-way ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

Transpiration (Tr) mirrored gs patterns showing a strong correlation (Fig.3); leaf-to-air temperature difference (ΔT) increased under drought, especially in Makako and Tuono, but remained lower in Texas and Filippo Cea. A strong negative correlation between gs and ΔT ($r = -0.85$) was observed when data were pooled across cultivars and treatments, indicating a consistent association between stomatal regulation and leaf thermal response under the imposed stress conditions.

Since correlation analysis was conducted on pooled data without explicitly modelling the hierarchical structure of the experiment, results should be interpreted as indicative of functional association rather than as evidence of direct causality (Karimi et al., 2015; Ahmad et al., 2018). The correlation between gs and the carboxylation index $P_{KO/KC}$ was weaker than the previous variable even if it was positive and significative (Fig. 3, $r = 0.72$). $P_{KO/KC}$ declined when AWC fell below 45%, with sharper reductions in Makako and Tuono. Filippo Cea and Texas maintained higher values under stress (data not shown). The late decline of carboxylation in comparison with stomatal conductance suggested that the initial stomatal closure, recorded at high AWC, did not limit the leaf carboxylation that was affected later (Losciale et al., 2023).

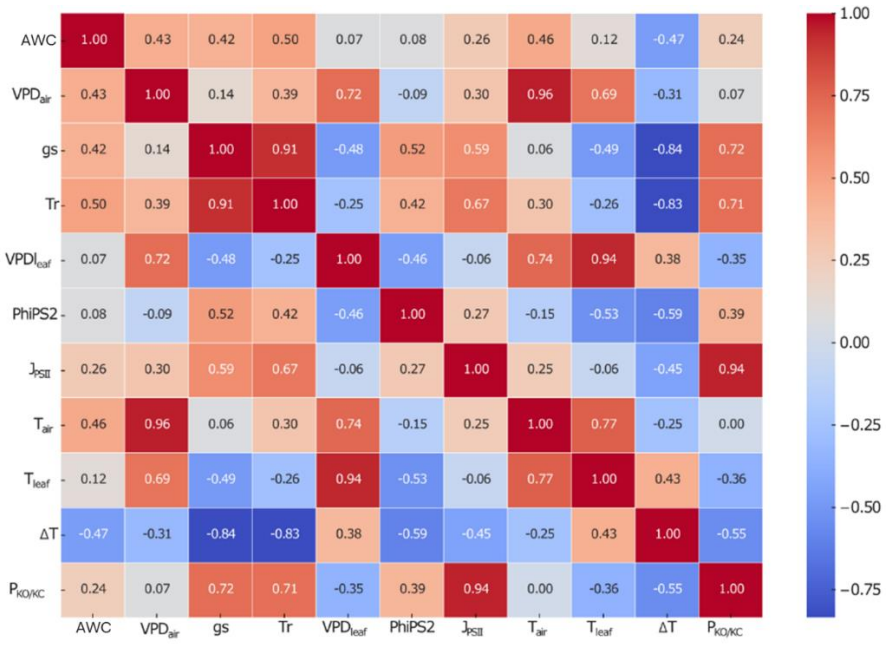

Figure 3. Correlation matrix between various ecophysiological and environmental variables, including available water content (AWC), vapor pressure deficit in the air (VPD_{air}), stomatal conductance (gs), transpiration rate (Tr), leaf-to-air vapor pressure deficit (VPD_{leaf}), quantum efficiency of PSII (PhiPS2), photosynthetic electron transport rate (J_{PSII}), air temperature (T_{air}), leaf temperature (T_{leaf}), leaf-to-air temperature difference (ΔT), and photosynthetic performance index ($P_{KO/KC}$). The strength and direction of correlations are represented by color intensity, with red indicating strong positive correlations and blue indicating strong negative correlations.

The Physiological Resistance Index (PhyResIx) indicated lower relative stomatal sensitivity in Filippo Cea and, to a lesser extent, in Texas, compared with the other cultivars. The index provides a comparative description of stomatal behaviour during progressive soil drying under controlled pot conditions. Given that the index assumes a proportional relationship between gs and AWC, its interpretation should be limited to the experimental context and not considered a direct measure of hydraulic resistance (Fig. 4). These findings are in agreement with those of Fernandes de Oliveira et al. (2023) and Maldera et al.(2024), where Filippo Cea and Texas showed better photosynthetic performance and, consequently, superior vegetative growth compared to other varieties such as Tuono.

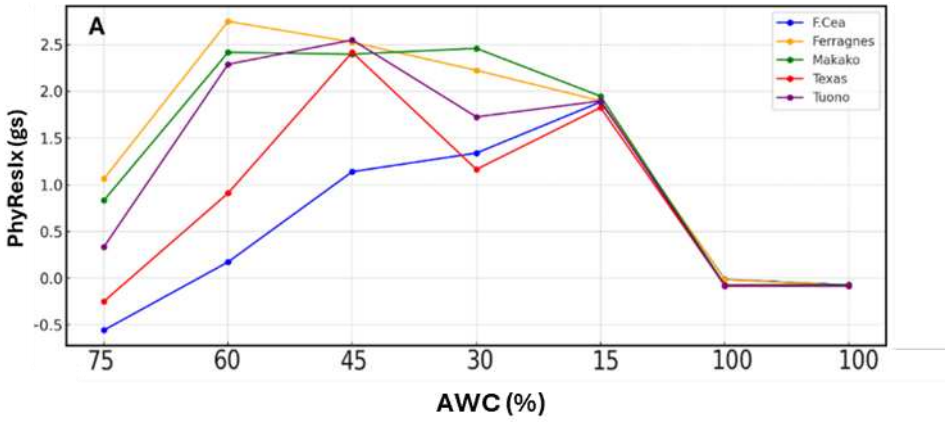

Figure 4. Physiological Resistance Index based on stomatal conductance (PhyResIx_gs) calculated during the dynamic stress (DS) treatment as a function of soil water depletion. Lower values indicate reduced stomatal sensitivity to decreasing soil water content. Values represent means of six plants per cultivar.

Figure 5 showed the relative water content (RWC) under drought stress (DS), when available water content (AWC) reached 15%, and after recovery, when AWC was restored to 100%. After rewatering, RWC increased significantly in 'Texas' and 'Tuono', whereas the other cultivars did not show significant differences between stress and recovery conditions. The restoration of leaf hydration may involve physiological mechanisms such as osmotic adjustment (Karimi et al., 2012); however, osmotic potential was not directly measured in the present study.

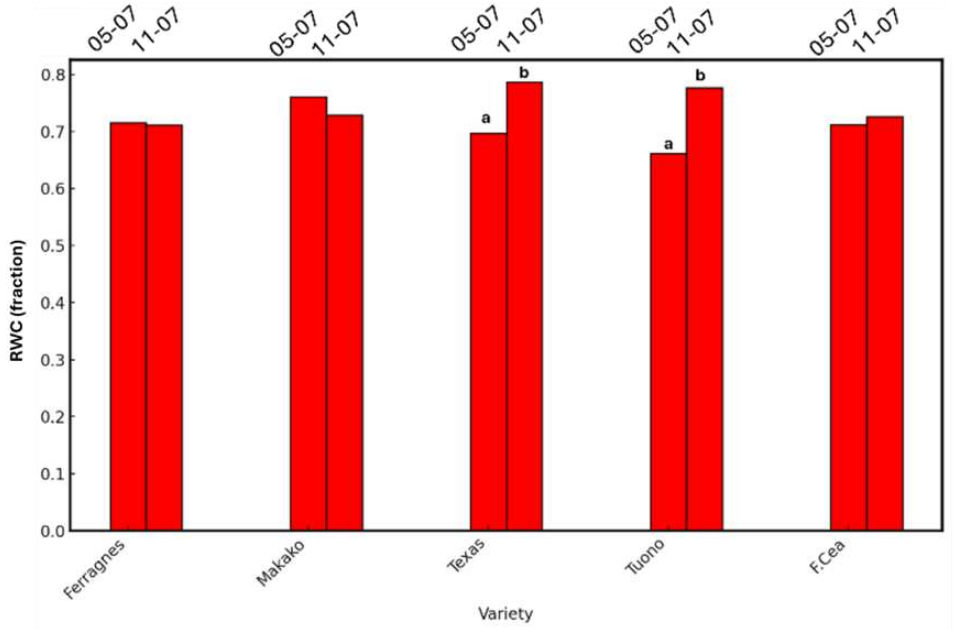

Figure 5. Relative water content (RWC) of five almond cultivars (Ferragnes, Makako, Texas, Tuono and Filippo Cea) for DS. Measurements were taken on two dates, July 5th and July 11th, 2024. The AWC was at 15% on July 5th and 100% July 11th. Different letters indicate significant differences between dates within each cultivar according to one-way ANOVA followed by Tukey's HSD test ($p \leq 0.05$).

CONCLUSIONS

In this study gs and ΔT emerged as sensitive and informative indicators of water deficit and the dynamic stress protocol was more effective in differentiating cultivar behaviour. Overall, Filippo Cea and Texas demonstrated tolerance to water stress, sustaining gs, Tr, and photosynthesis longer while maintaining lower ΔT. Ferragnes, Makako, and Tuono adopted early stomatal closure, conserving water but reducing photosynthetic capacity and increasing overheating risk. Recovery capacity varied, with Makako, Filippo Cea and Ferragnes showing better recovery once rehydrated. The combined use of gs and ΔT proved highly effective to distinguish the course of the stress. Since ΔT can be remotely monitored, it could offer a promising tool for high-throughput phenotyping and irrigation management. Integrating gs, ΔT, and PhyResIx provides a robust framework for evaluating drought tolerance as well as to set plant-based irrigation strategies.

Literature Cited

Ahmad, Z., Waraich, E. A., Akhtar, S., Anjum, S., Ahmad, T., Mahboob, W., Abdul Hafeez, O. B., Tapera, T., Labuschagne, M., & Rizwan, M. (2018). Physiological responses of wheat to drought stress and its mitigation approaches. *Acta Physiologiae Plantarum, 40*, 80. https://doi.org/10.1007/s11738-018-2651-6

Álvarez-Maldini, C., Acevedo, M., Estay, D., Aros, F., Dumroese, R. K., Sandoval, S., & Pinto, M. (2022). Examining physiological, water relations, and hydraulic vulnerability traits to determine anisohydric and isohydric behavior in almond (*Prunus dulcis*) cultivars: Implications for selecting agronomic cultivars under changing climate. *Frontiers in Plant Science, 13*, 974050. https://doi.org/10.3389/fpls.2022.974050

Bacon, M. A. (Ed.). (2004). *Water use efficiency in plant biology*. Blackwell Publishing.

Barzegar, K., Yadollahi, A., Imani, A., & Ahmadi, N. (2012). Influences of severe water stress on photosynthesis, water use efficiency and proline content of almond cultivars. *Journal of Applied Horticulture, 14*(1), 33–39. https://doi.org/10.37855/jah.2012.v14i01.06

Bunce, J. A. (1997). Does transpiration control stomatal responses to water vapour pressure deficit? *Plant, Cell & Environment, 20*(1), 131–135. https://doi.org/10.1046/j.1365-3040.1997.d01-3.x

Eamus, D., & Shanahan, S. T. (2002). A rate equation model of stomatal responses to vapour pressure deficit and drought. *BMC Ecology, 2*, 8. https://doi.org/10.1186/1472-6785-2-8

Egea, G., Nortes, P. A., Domingo, R., Baille, A., Pérez-Pastor, A., & González-Real, M. M. (2013). Almond agronomic response to long-term deficit irrigation applied since orchard establishment. *Irrigation Science, 31*, 445–454. https://doi.org/10.1007/s00271-012-0322-8
Fereres, E., Martinich, D. A., Aldrich, T. M., Castel, J. R., Holzapfel, E., & Schulbach, H. (1982). Drip irrigation saves money in young almond orchards. *California Agriculture, 36*(9–10), 12–13.
Fereres, E., & Soriano, M. A. (2007). Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany, 58*(2), 147–159. https://doi.org/10.1093/jxb/erl165
Fernandes de Oliveira, A., Mameli, M. G., De Pau, L., & Satta, D. (2023). Almond tree adaptation to water stress: Differences in physiological performance and yield responses among four cultivar grown in Mediterranean environment. *Plants, 12*(5), 1131. https://doi.org/10.3390/plants12051131
Fernández, J. E., Perez-Martin, A., Torres-Ruiz, J. M., Cuevas, M. V., Rodriguez-Dominguez, C. M., Elsayed-Farag, S., Morales-Sillero, A., García, J. M., Hernandez-Santana, V., & Diaz-Espejo, A. (2013). A regulated deficit irrigation strategy for hedgerow olive orchards with high plant density. *Plant and Soil, 372*(1–2), 279–295. https://doi.org/10.1007/s11104-013-1704-2
Flexas, J., Bota, J., Cifre, J., Escalona, J. M., Galmés, J., Gulías, J., Lefi, E. K., Martínez-Cañellas, S. F., Moreno, M. T., Ribas-Carbó, M., Riera, D., Sampol, B., & Medrano, H. (2004). Understanding down-regulation of photosynthesis under water stress: Future prospects and searching for physiological tools for irrigation management. *Annals of Applied Biology, 144*(3), 273–283. https://doi.org/10.1111/j.1744-7348.2004.tb00343.x
Flexas, J., Scoffoni, C., Gago, J., & Sack, L. (2013). Leaf mesophyll conductance and leaf hydraulic conductance: An introduction to their measurement and coordination. *Journal of Experimental Botany, 64*(13), 3965–3981. https://doi.org/10.1093/jxb/ert319
Franks, P. J., Cowan, I. R., & Farquhar, G. D. (1997). The apparent feedforward response of stomata to air vapour pressure deficit: Information revealed by different experimental procedures with two rainforest trees. *Plant, Cell & Environment, 20*(1), 142–145. https://doi.org/10.1046/j.1365-3040.1997.d01-14.x
Gabaldón-Leal, C., Ruiz-Ramos, M., de la Rosa, R., León, L., Belaj, A., Rodríguez, A., Santos, C., & Lorite, I. J. (2017). Impact of changes in mean and extreme temperatures caused by climate change on olive flowering in southern Spain. *International Journal of Climatology, 37*(2), 940–957. https://doi.org/10.1002/joc.5048
García-Tejero, I. F., Gutiérrez-Gordillo, S., Souza, L., Cuadros-Tavira, S., & Durán-Zuazo, V. H. (2019). Fostering sustainable water use in almond (*Prunus dulcis* Mill.) orchards in a semiarid Mediterranean environment. *Archives of Agronomy and Soil Science, 65*(2), 164–181. https://doi.org/10.1080/03650340.2018.1492113
Girona, J., Mata, M., & Marsal, J. (2005). Regulated deficit irrigation during the kernel-filling period and optimal irrigation rates in almond. *Agricultural Water Management, 75*(2), 152–167. https://doi.org/10.1016/j.agwat.2004.12.008
Goldhamer, D. A., Viveros, M., & Salinas, M. (2006). Regulated deficit irrigation in almonds: Effects of variations in applied water and stress timing on yield and yield components. *Irrigation Science, 24*(2), 101–114. https://doi.org/10.1007/s00271-005-0014-8
Jarvis, P. G. (1976). The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 273*(927), 593–610. https://doi.org/10.1098/rstb.1976.0035
Karimi, S., Yadollahi, A., Nazari-Moghadam, R., Imani, A., & Arzani, K. (2012). In vitro screening of almond (*Prunus dulcis* (Mill.)) genotypes for drought tolerance. *Journal of Biological and Environmental Sciences, 6*(18), 263–270.
Karimi, S., Yadollahi, A., Arzani, K., Imani, A., & Aghaalikhani, M. (2015). Gas-exchange response of almond genotypes to water stress. *Photosynthetica, 53*(1), 29–34. https://doi.org/10.1007/s11099-015-0070-0
Klein, I., Esparza, G., Weinbaum, S. A., & DeJong, T. M. (2001). Effects of irrigation deprivation during the harvest period on leaf persistence and function in mature almond trees. *Tree Physiology, 21*(14), 1063–1072. https://doi.org/10.1093/treephys/21.14.1063
Lauri, P.-É., Barigah, T. S., Lopez, G., Martinez, S., Losciale, P., Zibordi, M., Manfrini, L., Corelli Grappadelli, L., Costes, E., & Regnard, J. L. (2016). Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. *Trees, 30*(5), 1893–1908. https://doi.org/10.1007/s00468-016-1408-3
Losciale, P., Manfrini, L., Morandi, B., Pierpaoli, E., Zibordi, M., Stellacci, A. M., Salvati, L., & Corelli Grappadelli, L. (2015). A multivariate approach for assessing leaf photo-assimilation performance using the IPL index. *Physiologia Plantarum, 154*(4), 609–620. https://doi.org/10.1111/ppl.12328
Losciale, P., Gaeta, L., Corsi, M., Galeone, C., Tarricone, L., Leogrande, R., & Stellacci, A. M. (2023). Physiological responses of apricot and peach cultivars under progressive water shortage: Different crop signals for anisohydric and isohydric behaviours. *Agricultural Water Management, 286*, 108384. https://doi.org/10.1016/j.agwat.2023.108384
Maherali, H., Johnson, H. B., & Jackson, R. B. (2003). Stomatal sensitivity to vapour pressure difference over a subambient to elevated CO_2 gradient in a C_3/C_4 grassland. *Plant, Cell & Environment, 26*(8), 1297–1306. https://doi.org/10.1046/j.1365-3040.2003.01054.x
Maldera, F., Vivaldi, G. A., Iglesias-Castellarnau, I., & Camposeo, S. (2021). Two almond cultivars trained in a super-high density orchard show different growth, yield efficiencies and damages by mechanical harvesting. *Agronomy, 11*(7), 1406. https://doi.org/10.3390/agronomy11071406
Maroco, J. P., Pereira, J. S., & Chaves, M. M. (1997). Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. *Australian Journal of Plant Physiology, 24*(3), 381–387. https://doi.org/10.1071/PP96062
Monteith, J. L. (1995). A reinterpretation of stomatal responses to humidity. *Plant, Cell & Environment, 18*(4), 357–364. https://doi.org/10.1111/j.1365-3040.1995.tb00371.x
Parker, L. E., & Abatzoglou, J. T. (2016). Projected changes in cold hardiness zones and suitable overwinter ranges of perennial crops over the United States. *Environmental Research Letters, 11*(3), 034001. https://doi.org/10.1088/1748-

9326/11/3/034001
Parker, L. E., & Abatzoglou, J. T. (2017). Comparing mechanistic and empirical approaches to modeling the thermal niche of almond. *International Journal of Biometeorology, 61*(9), 1593–1606. https://doi.org/10.1007/s00484-017-1338-9
Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist, 182*(3), 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x
Romero, P., Navarro, J. M., García, F., & Botía Ordaz, P. (2004). Effects of regulated deficit irrigation during the pre-harvest period on gas exchange, leaf development and crop yield of mature almond trees. *Tree Physiology, 24*(3), 303–312. https://doi.org/10.1093/treephys/24.3.303
Torrecillas, A., Alarcón, J. J., Domingo, R., Planes, J., & Sánchez-Blanco, M. J. (1996). Strategies for drought resistance in leaves of two almond cultivars. *Plant Science, 118*(2), 135–143. https://doi.org/10.1016/0168-9452(96)04434-2
Valliyodan, B., & Nguyen, H. T. (2006). Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Current Opinion in Plant Biology, 9*(2), 189–195. https://doi.org/10.1016/j.pbi.2006.01.019
Webb, A. A. R., & Hetherington, A. M. (1997). Convergence of the abscisic acid, CO_2, and extracellular calcium signal transduction pathways in stomatal guard cells. *Plant Physiology, 114*(4), 1557–1560. https://doi.org/10.1104/pp.114.4.1557
Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., & Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography, 14*(5), 411–421. https://doi.org/10.1111/j.1466-822X.2005.00172.x

CONCLUSIONS

This PhD thesis investigated how plant-based variables and integrative indices can be used to interpret plant functional status in perennial fruit crops exposed to increasing water and thermo-evaporative stress. The central premise was that, under climate-driven environmental variability, sustainable orchard management depends on the capacity to interpret plant responses in functional terms rather than relying solely on descriptive measures of water deficit.

The conceptual framework, established through a comprehensive review of almond physiology and irrigation management, highlighted a central limitation of plant-based approaches: while numerous physiological indicators are available, their operational use is constrained by the difficulty of defining thresholds that remain valid across environments, phenological stages, and cultivars. This analysis led to the adoption of plant functional status as a dynamic and context-dependent property emerging from the interaction among hydraulic regulation, stomatal behavior, carbon assimilation, and bioenergetic balance.

Across the experimental contexts, classical variables such as stem water potential and stomatal conductance proved indispensable for stress monitoring. However, their interpretative value increased when considered together with gas exchange, thermal behaviour, and photosynthetic performance. Rather than identifying stress through isolated values, functional transitions were more clearly detected through changes in the coordination among physiological processes.

In almond subjected to regulated deficit irrigation, moderate water restriction induced coordinated reductions in stomatal conductance and net photosynthesis without compromising yield, indicating controlled functional adjustment. Under more severe restriction, stem water potential declined markedly from early stages, whereas stomatal

conductance and carbon assimilation showed a more gradual decrease, reflecting limited stomatal sensitivity to declining Ψ_{stem} under mild-to-moderate stress. In parallel, photosynthetic electron transport remained comparatively buffered by non-net carboxylative processes, with J_{PSII} remaining stable until stomatal conductance approached a breakpoint around 0.10–0.11 mol m^{-2} s^{-1}, below which electron transport also declined and photoprotective dissipation became increasingly dominant. Thus, as shown in Chapter II, functional impairment was not associated with a single absolute water-potential threshold but with a progressive loss of functional coordination along the irrigation gradient. Within this coordinated range, net photosynthesis remained tightly linked to stomatal conductance, $P_{KO/KC}$, and stem water potential, and both deficit irrigation treatments achieved water savings without significant yield penalties. The grapevine experiment provided a complementary context for evaluating the same framework. Under severe deficit irrigation, reductions in gas exchange were largely driven by stomatal closure under high evaporative demand, while midday stem water potential remained comparatively stable across most treatments, indicating an apparent capacity to buffer plant water status under severe deficit. In this case, functional limitation was primarily expressed through coordinated downregulation of carbon assimilation and vegetative growth rather than through abrupt hydraulic collapse. The comparison between species therefore showed that the first detectable loss of coordination may occur along different process axes, hydraulic–stomatal decoupling in almond and gas-exchange-driven source limitation in grapevine, reinforcing the need for a multidimensional interpretation of plant responses. In practical terms, a multidimensional interpretation can be implemented in irrigation scheduling by using climate- and phenology-based estimates of crop water requirement as the operational baseline, and then refining irrigation decisions with selected plant-based indicators when greater physiological resolution is needed. In this framework, stem water potential, stomatal conductance, and thermal or

photosynthetic proxies should be regarded as complementary sources of information rather than as measurements that must always be collected simultaneously. This approach is intended to improve the interpretation of plant responses within the relevant phenological stage, evaporative demand, and genotype, rather than to replace conventional scheduling with a measurement-intensive protocol.

A relevant methodological contribution of the work concerns the incorporation of photosynthetic functionality into plant-based monitoring. The $P_{KO/KC}$ index, obtained from the integration of chlorophyll fluorescence and leaf temperature measurements, provided a rapid proxy of photosynthetic performance that complemented traditional water status and gas exchange assessments. Although it does not replace detailed gas-exchange analysis, $P_{KO/KC}$ demonstrates how functional information can be integrated into monitoring protocols, improving the sensitivity of stress detection without substantially increasing measurement complexity.

The controlled phenotyping study further demonstrated that plant functional trajectories are strongly cultivar-dependent. Under equivalent soil water depletion, genotypes differed in their capacity to sustain stomatal conductance, transpiration-mediated thermal regulation (ΔT), and carboxylation-related performance ($P_{KO/KC}$). Filippo Cea and Texas emerged as the cultivars showing the most stable overall behaviour under dynamic stress, particularly in terms of stomatal conductance and thermal response, while Makako, Tuono, and Ferragnes exhibited earlier stomatal limitation and stronger thermal responses. Consequently, identical soil water conditions did not correspond to equivalent functional states across cultivars. Plant-based indices should therefore be interpreted within a genotype-aware framework. This means that they should not be read against a single universal threshold, because cultivars differ in their baseline physiological behaviour and in the way they respond to progressive soil water depletion. Under equivalent soil water conditions, different genotypes may maintain different levels of

stomatal conductance, transpirational cooling, and photosynthetic functionality, and therefore may not correspond to the same functional state. In practical terms, plant-based indices should be interpreted relative to genotype-specific baselines and response trajectories, so that they can be used not only for stress monitoring, but also for comparative phenotyping and cultivar-specific irrigation management. Several limitations should be acknowledged. The stress dynamics evaluated under controlled conditions require validation under multi-year field scenarios, and the transferability of functional transitions across diverse climatic contexts remains to be established. Moreover, the physiological determinants of cultivar-specific behaviour deserve further investigation, particularly in relation to hydraulic traits and long-term resilience. Future research should therefore combine plant-based monitoring with structural and trait-based analyses to refine the interpretation of plant functional status under climate change.

Overall, this thesis advances a physiology-based and context-aware framework for interpreting plant responses to water limitation in perennial fruit crops. By integrating conceptual analysis, field experimentation, and controlled phenotyping, the work demonstrates that plant functional status can be meaningfully assessed through coordinated plant-based approaches across experimental scales. Accordingly, this thesis provides a practical foundation for irrigation management strategies not by proposing fixed universal thresholds, but by offering a decision framework for identifying when water limitation remains functionally sustainable and when it becomes functionally restrictive. Within this framework, irrigation scheduling can remain anchored to phenology- and climate-based estimates of crop water requirement, while plant-based indicators and integrative indices help refine decisions by identifying the maintenance or loss of coordination among hydraulic regulation, stomatal behaviour, photosynthetic performance, and thermal balance. Thus, the practical contribution of the thesis lies in supporting adaptive irrigation management through a context-aware interpretation of

plant responses, rather than through isolated thresholds alone.