

Seeking almond cultivars response to irrigation and soil-management systems using eco-physiological behaviour and its connections to productivity

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Abstract

Water scarcity is the most limiting factor in many Mediterranean regions, making the implementation of sustainable irrigation and soil-management strategies essential for sustainable production. Almond (*Prunus dulcis* Mill.) represents the second woody crop in Andalusia (S Spain). This study integrates the physiological and yield responses of four almond cultivars (Marcona, Guara, Lauranne, and Marta) grown under different management strategies: two irrigation regimes [full irrigation (FI) and regulated-deficit irrigation (RDI)] and two soil-management systems [cover crop (CC) and bare soil (BS)]; during two monitoring seasons (2024–2025). The net photosynthesis (A_n), stomatal conductance (g_{sw}), transpiration (E), intercellular CO₂ concentration (C_i), and stem-water potential (Y_{Stem}) were monitored throughout the three key phenological stages (vegetative growth, kernel filling, and post-harvest). At the end of each season, the yield (in-shell almonds, kernel, and single fruit weight) was measured for each treatment and cultivars. The RDI reduced irrigation volumes ~ 50% compared with FI, without significant declines in kernel yield, revealing an improvement in water-use efficiency. The cultivar strongly influenced the physiological behaviour, since cvs. Marta and Marcona required higher g_{sw} to reach the maximum A_n rates. The analysis revealed that g_{sw} exerted the main control over A_n , particularly during mid-summer and kernel-filling stage, showing its key regulatory role in almond photosynthetic performance under drought conditions. In relation to the soil-management systems, CC did not affect the gas exchange activity and yield, compared with BS. Singularly, the combination of RDI x CC proved fully compatible, encouraging water-use efficiency and physiological stability without compromising almond yield. Here we show that the cultivar selection is crucial, when coupled with RDI and vegetative soil cover, which potentially provides an effective strategy for improvement water-irrigation management and soil health, and therefore, fostering the sustainable almond cultivation in Mediterranean agroecosystems.

Highlights

Regulated deficit irrigation combined with cover crops improved resource use efficiency without important yield losses

Almond cultivar determined contrasting physiological and productive responses to water stress

Gas exchange patterns highlighted genotype-dependent drought resilience

Stomatal conductance drove photosynthetic responses throughout phenological stages

1.- Introduction

Mediterranean agriculture faces escalating pressure to secure water supplies as water scarcity and climate change increasingly threaten its availability, which is exacerbated with the frequency and intensity of drought events for agricultural crops (Claro et al. 2024; IPCC 2023). Within this context, almond (*Prunus dulcis* Mill.) has become a strategic woody crop due to its high market demand, nutritional value, and relative drought tolerance (Safavi et al. 2025). As response, the irrigated almond area in Andalusia (S Spain) has sharply increased, rising from less than 10% of the total almond surface around 2010 to over 35,000 ha in 2023/24, accounting for approximately 16% of orchards in production. Most of this expansion occurred since 2017, driven by the establishment of new intensive plantations, many of them in the Guadalquivir River basin, where irrigation already covers more than 45% of the Andalusian almond area (CAPDR 2024; MAPA 2024).

Over the last ten years, the average irrigation water allocation for almond orchards in Andalusia has generally ranged between 2,300 and 2,500 m³ ha⁻¹ year⁻¹ (net), according to regional hydrological planning documents, although in dry years, allocations have often been reduced to around 2,000 m³ ha⁻¹, whereas in average years, effective applications

may approach 2,700–3,500 m³ ha⁻¹, depending on system efficiency (CHG 2022). These values remain well below the potential crop water requirements for high-yielding orchards, estimated at 8,000–9,000 m³ ha⁻¹, reflecting a predominance of regulated deficit irrigation strategies (RDI) in commercial orchards (IFAPA 2023). In this agreement, RDI has been proved as one of the most efficient water-saving techniques for woody crops (Chen et al. 2023), consisting of applying higher water stress at specific phenological phases less sensitive to drought, while maintaining full irrigation (FI) or lower water stress conditions during critical periods as flowering or postharvest. Several works in almond have reported water savings of 30–50% with no significant yield reduction, and even improvements in kernel quality when stress is carefully controlled (Lipan et al. 2019; Mirás-Avalos et al. 2023).

From a physiological standpoint, RDI induces a moderate decline in stomatal conductance (g_{sw}) and transpiration (E), partially limiting the carbon assimilation (A_n) but enhancing intrinsic water-use efficiency (WUE_i) (Goldhamer et al. 2006; Egea et al. 2010), although the response magnitude varies markedly among cultivars (Gutiérrez-Gordillo et al. 2020a, Paudel et al. 2020).

Soil-management practices can further influence the performance of RDI (González-Gómez et al. 2022). Traditionally, Mediterranean orchards have been managed under bare soil (BS) conditions to minimise competition for water resources. However, this practice promotes erosion, degrades soil organic matter, and reduces microbial activity, and infiltration capacity (Macci et al. 2012). In contrast, the use of cover crops (CC) improves soil structure, enhances organic carbon, reduces runoff, and buffers soil temperature and evaporation (Montanaro et al. 2017; Repullo-Ruibérriz et al. 2021; García-Tejero et al. 2024).

The implementation of CC is not only an agronomic choice but also a policy-driven requirement under the European Green Deal and the Common Agricultural Policy (CAP 2023–2027). Within this framework, the new eco-schemes incentivise to implement agro-environmental practices aimed at mitigating climate impacts, improving biodiversity, and increasing soil carbon sequestration (European Commission, 2021). Among the eligible practices, the establishment of permanent vegetative covers in woody crops is one of the most widely promoted measures, although under drought conditions achieving compatibility between CC and the main woody crop remains challenging due to their seasonal competition for water and nutrients (Montanaro et al. 2017; Novara et al. 2021).

Few studies have examined the combined effects of irrigation regime, CC, and cultivar on almond yield and eco-physiological response and it limits the understanding of how RDI and CC jointly influence the efficiency of the whole orchard system. We hypothesised that implementing moderate RDI combined with CC can sustain almond yield and improve WUE_i through enhanced physiological regulation, without compromising productivity. Furthermore, we expected that the magnitude and direction of these responses would be genotype-dependent, reflecting intrinsic differences in physiological plasticity among cultivars.

By integrating ecophysiological, agronomic, and policy perspectives, this work aims to provide a comprehensive understanding of how the interaction RDI and CC can be implemented to enhance the sustainability of almond production systems under the constraints imposed by the European Green Deal and ongoing climatic challenges. The specific objectives of this study were therefore to: (i) evaluate the physiological responses (A_n , g_{sw} , E , and C_i) of four almond cultivars (Marcona, Guara, Lauranne, and Marta) under contrasting irrigation (FI and RDI) and soil-management systems (CC and BS); (ii) quantify the impact on yield components (kernel weight, in-shell yield, and kernel-to-shell ratio); and (iii) analyse the interaction among phenological period, cultivar, and soil-management to identify key drivers of adaptation to water stress under Mediterranean conditions.

2. Material and Methods

2.1. Site description

The trial was conducted during two consecutive seasons (2024–2025) at the experimental farm IFAPA “Las Torres” (Alcalá del Río, Seville, SW Spain, 37° 30' 38.55" N; 05° 57' 44.98" W, 11 m a.s.l.). Trees, corresponding to four cultivars (Guara, Marta, Lauranne, and Marcona) are grafted onto GN15 rootstock, and 7 x 6 m spaced. Trees are drip irrigated using two pipelines with emitters of 2.3 L h⁻¹ at 0.75 m intervals.

The soil of the experimental plots is a silty loam typical Fluvisol, that is more than 2.5 m deep; with a field capacity of 0.42 m³ m⁻³, a permanent wilting point of 0.18 m³ m⁻³, and organic matter content around 1%. The climatology in the study area is attenuated meso-Mediterranean, with an annual ET₀ rate of 1,400 mm and an annual rainfall of 540 mm, which is mainly distributed from October to April, and with the months of June to August having the highest evapotranspiration rates and little or no rainfall. All cultural practices (fertilisation, pruning, pest control) were conducted according to standard recommendations for integrated production for almond in Andalusia (BOJA 2012).

2.2. Irrigation and soil-management system

Irrigation requirements (II.RR.) based on crop evapotranspiration (ET_c) were calculated according to the FAO methodology (Allen et al. 1998). Crop coefficients specific to almond and local conditions were taken from García-Tejero et al. (2015). Two irrigation strategies were imposed: i) a full irrigation (FI) treatment; supplying 100% of II.RR. throughout the season; and ii) a regulated deficit irrigation (RDI): applying 75% of II.RR. during vegetative growth and post-harvest, and 35% during kernel-filling. Irrigation scheduling was weekly calculated, using meteorological data from a nearby automated weather station.

In addition, two soil-management systems were applied: cover crop (CC) and bare soil (BS). The cover crop consisted of a mixture of 25% oat (*Avena sativa* L.) and 75% vetch (*Vicia sativa* L.). The mixture was allowed to develop through winter and early spring, achieving more than 80% ground coverage by mid-April, when it was mown and left on the surface as mulch to reduce soil evaporation. Although a reseeding of the cover crop was carried out at the beginning of autumn to ensure its proper establishment, a central strip was maintained throughout the entire growing season to facilitate natural reseeding. The BS plot was maintained weed-free by chemical mowing following the recommendations of the Integrated Almond Production Manual for Andalusia (BOJA 2012). All other management practices, including tillage depth and fertilisation schedule, were the same for all treatments.

In summary, the four studied almond cultivars were subjected to four different management strategies (MS): FI×CC, FI×BS, RDI×CC, and RDI×BS.

2.3. Physiological and yield measurements

Leaf gas-exchange parameters were determined using a portable infrared gas analyser (LI-6800, LI-COR Inc., Lincoln, NE, USA). The measured variables were net photosynthesis (A_n), stomatal conductance (g_{sw}), transpiration (E), and intercellular CO₂ concentration (C_i). Measurements were taken under standardised conditions commonly adopted for Mediterranean woody crops: a photosynthetic photon flux density (PPFD) of approximately 1300–1500 μmol m⁻² s⁻¹, a reference CO₂ concentration of 400 μmol mol⁻¹, leaf temperature of 25–28°C, and relative humidity between 50–60%. Measurements were performed bi-weekly throughout the three main phenological periods: vegetative growth, kernel filling, and post-harvest. All readings were made at solar midday (12:00–14:00 h) under clear-sky conditions to minimise diurnal variability. One fully expanded, healthy, sun-exposed leaf per monitored tree was selected from the mid-canopy level for each controlled tree. Stem-water potential (Ψ_{Stem}) was determined concurrently using a Scholander-type pressure chamber (PMS Model 1000, Albany, OR, USA). For these measurements, shaded leaves were enclosed in aluminium foil and covered with plastic bags for at least two hours prior to sampling to allow equilibration

between leaf and stem water potential. Measurements were taken at solar midday on the same days as the gas-exchange analyses.

At maturity, all monitored trees were mechanically harvested using a trunk shaker with umbrella and integrated dehulling unit. Harvest dates varied among cultivars according to their phenological cycle: 'Guara' – late July to early August; 'Marta' – early to mid-August; 'Lauranne' – mid August; and 'Marcona' – mid September. After harvesting, all nuts were air-dried naturally until they reached approximately 6% moisture content. Kernels were manually separated from shells for determination of yield and kernel weight. The following variables were recorded: total almond yield with shell (kg ha^{-1}); kernel yield (kg ha^{-1}), kernel and nut unit weight (g), and kernel/shell ratio (yield ratio) expressed as a decimal fraction (0–1). For unit-weight determinations, a representative subsample of 100 nuts per tree was used. All yield data were corrected for moisture content and expressed on a per-hectare basis.

2.4. Experimental design and statistical analysis

The experimental layout followed a randomised complete block design, with a factorial arrangement of treatments ($2 \times 2 \times 4$). The factors were: (i) Irrigation regime – full irrigation (FI) and regulated deficit irrigation (RDI); (ii) Soil-management system – cover crop (CC) and bare soil (BS); and (iii) Cultivar – "Guara", "Marta", "Lauranne", and "Marcona". Each combination was replicated three times, with each replication consisting of a group of four homogeneous trees within the same row.

Data were subjected to factorial analysis of variance (ANOVA) to evaluate the effects of irrigation regime, soil-management system, and cultivar, as well as their interactions. Prior to analysis, assumptions of normality and homogeneity of variance were verified by the Shapiro–Wilk and Levene tests, respectively. Since all data met these assumptions, no transformation was required. Separate analyses were performed for each experimental season (2024 and 2025). Means were compared using Tukey's Honest Significant Difference (HSD) test at a confidence level of $p < 0.05$.

To explore the relationships among physiological variables and their temporal stability, a correlation analysis was first conducted separately for each experimental year (2024 and 2025) and for each phenological period. Pearson correlation coefficients were calculated among gas-exchange variables (A , g_{sw} , E), internal CO_2 concentration (C_i) and stem-water potential (Ψ_{stem}). Correlation matrices were generated independently for each year and period in order to avoid confounding seasonal effects. Subsequently, correlations were compared between years to identify relationships that remained consistent in sign and significance throughout seasons, which were interpreted as robust functional associations, versus relationships that varied between years, indicating context-dependent physiological responses.

To further integrate physiological traits and production variables in an unconstrained multivariate framework, Principal Component Analysis (PCA) was applied. PCA was performed separately for each phenological period using standardized physiological variables and then extended to include productive traits (kernel yield, kernel unit weight and kernel-to-shell ratio). This approach allowed visualization of coordinated patterns among variables, assessment of cultivar-specific physiological strategies, and evaluation of the degree of overlap between irrigation regimes and soil-management systems without imposing the experimental design on the ordination structure.

Finally, Redundancy Analysis (RDA) was used as a constrained ordination technique to quantify the proportion of physiological variability is explained by the experimental factors. Physiological variables throughout periods were standardized and used as response variables, while "Year", "Irrigation regime", "Soil-management system" and "Cultivar" were included as explanatory factors. Significance of the RDA models and individual terms was assessed using permutation tests. Together, these complementary multivariate approaches enabled an integrated interpretation of physiological functioning, its temporal robustness, and its linkage to genotype and resource management.

All analyses were conducted using R statistical software (4.3.1 version). The base stats package was used for ANOVA computation, while *emmeans* and *multcompView* were applied for post-hoc comparisons and letter assignment. The *Hmisc* and *corrplot* packages were used for correlation analyses and graphical representation of physiological interactions.

3. Results and Discussion

3.1. Weather conditions and irrigation water applied

Table 1 Weather conditions and irrigation water applied for each season and phenological period								
Phenological period	DOY	Rainfall	ET ₀	ET _C	II.RR.	FI	RDI	WS
		(mm)						(%)
2024								
Winter dormancy	1–60	174.8	81.1	8.1	0	0	0	
Vegetative growth	61–152	179	382.3	276.2	134.9	122.7	85.9	30
Kernel filling	153–223	15.6	515.7	491.5	479	417.1	168.1	59.7
Postharvest	224–295	133.2	382.2	369.2	322.6	306.7	214.7	30
Seasonal	1-295	502.6	1361.3	1153.3	751.4	846.4	468.6	
2025								
Winter dormancy	1–60	199.4	73.8	6.6	0	0	0	
Vegetative growth	61–152	337.1	322.8	225.9	0	61.3	49.1	20
Kernel filling	153–223	3	418.4	393.9	391.5	349.6	143.5	58.9
Postharvest	224–295	3.6	280.7	262.1	259.4	245.3	171.7	30
Seasonal	1-295	543.1	1095.7	888.4	454.1	656.3	364.3	

DOY, day of the year; II.RR., irrigation requirements; ET₀, Reference evapotranspiration; ET_C, Crop evapotranspiration; FI, full-irrigated treatment; RDI, regulated deficit irrigation; WS, water saving.

Table 1 summarizes the seasonal weather conditions and irrigation water applied during each phenological period for each treatment. According to this, it is remarkable the strong interannual variability typical of Mediterranean environments, with marked effects on water demand and irrigation during the months with highest evapotranspirative demand. In 2024, the total ET₀ reached 1,361 mm, while rainfall barely exceeded 500 mm, resulting in a pronounced atmospheric demand and clear seasonal imbalances. By contrast, the 2025 season presented a milder evaporative environment (ET₀ ≈ 1,096 mm) and higher rainfall accumulation (543 mm), which moderated the II.RR. and reduced the overall water stress intensity during the vegetative period. Nevertheless, for both years the kernel-filling stage (June–August) remained the most critical period, with negligible precipitation and ET_C values exceeding 490 and 394 mm in 2024 and 2025, respectively.

The total water applied for FI treatment amounted to 846 and 656 mm, while the RDI supplied 469 and 364 mm for 2024 and 2025, respectively—representing average annual water savings close to 45%. The largest deficit was

concentrated during kernel filling, when RDI reached around 35–40% of FI doses, while moderate reductions (about 70–75% of FI) were imposed during the vegetative and postharvest phases. Relating to the interannual comparisons, the higher rainfall and lower evaporative demand in 2025 reduced irrigation requirements by nearly 100 mm relative to 2024, yet the proportional water savings achieved through RDI were practically identical (~44–45%).

3.2. Crop physiological response to water stress during the studied season

3.2.1. Season 2024

Tables 2 summarizes the analysis of variance of the studied physiological variables, the factors considered and their interactions during 2024 season. ANOVA revealed that the phenological stage and cultivar were the main factors significantly affecting gas exchange variables (A_n , g_{sw} , and E), while Ψ_{Stem} was strongly influenced by both stage and irrigation. In contrast, soil management showed no significant effects on any variable, either alone or in interaction with other factors. Most two- and three-way interactions were non-significant, except for a combined effect of irrigation $\times$ soil management $\times$ cultivar, which influenced photosynthetic activity, stomatal regulation and stem water potential. These results indicate that physiological performance was primarily governed by phenological stage and genotype, with irrigation exerting a notable influence on crop water status.

Table 2
ANOVA summary with the significance of main factors and their interactions on gas-exchange parameters and stem-water potential during 2024.

Factors	A_n	g_{sw}	E	C_i	Ψ_{Stem}
Phenological stage	***	***	***	NS	***
Irrigation	NS	NS	NS	NS	***
Soil-management system	NS	NS	NS	NS	NS
Cultivar	**	***	***	**	NS
Irrigation x Soil-management system	NS	NS	NS	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	**	*	*	NS	*

A_n , net photosynthesis; g_{sw} , stomatal conductance; E , transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential; NS, not significant; *, **, and *** significant differences for $p < 0.05$, $p < 0.001$, and $p < 0.001$, respectively.

The post-hoc comparisons provided further insights into the eco-physiological responses of almond trees across different phenological stages, irrigation regimes, soil-management systems, and cultivars (Table 3). As expected, phenology emerged as the most influential factor, significantly affecting A_n , g_{sw} , E , C_i , and Ψ_{Stem} . Photosynthetic activity reached its maximum during the vegetative period, decreasing moderately during kernel filling, and dropped sharply in postharvest. This progressive decline highlights the strong ontogenic control of gas exchange, particularly after harvest, when trees shift from carbon assimilation to storage metabolism (Egea et al. 2011; Gutiérrez-Gordillo et al. 2023).

Table 3
Mean values of gas exchange and water potential parameters as affected by phenological stage, irrigation regime, soil-management system, and cultivar. Season 2024

	A_n	g_{sw}	E	C_i	Y_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	$\mu\text{mol mol}^{-1}$	(MPa)
Phenological period					
Vegetative growth	15.25a	0.207a	0.005a	245a	-1.05a
Kernel filling	12.44b	0.160b	0.005a	233b	-1.28c
Post harvest	7.66c	0.101c	0.004b	246a	-1.15b
Irrigation regime					
FI	11.8a	0.155a	0.004a	241a	-1.08a
RDI	11.7a	0.157a	0.005a	242a	-1.27b
Soil-management system					
CC	11.9a	0.158a	0.005a	242a	-1.15a
BS	11.7a	0.154a	0.005a	241a	-1.20a
Cultivar					
Guara	11.8a	0.152b	0.004c	238b	-1.17a
Marta	10.1b	0.125c	0.004b	238b	-1.17a
Lauranne	12.7a	0.163b	0.005ab	237b	-1.17a
Marcona	12.6a	0.184a	0.005a	252a	-1.19a
Interactions					
FI x CC x Guara	13.36ab	0.174abc	0.005abcd	237a	-1.10ab
FI x CC x Marta	9.35b	0.112c	0.003d	236a	-1.08ab
FI x CC x Lauranne	13.90ab	0.170abc	0.005abc	230a	-1.09ab
FI x CC x Marcona	12.43ab	0.195ab	0.005abc	260a	-1.11ab
FI x BS x Guara	12.27ab	0.154abc	0.004bcd	237a	-1.05ab
FI x BS x Marta	9.92ab	0.125bc	0.004cd	237a	-1.02a
FI x BS x Lauranne	13.05ab	0.164abc	0.005abc	236a	-1.09ab
FI x BS x Marcona	14.57a	0.203a	0.006ab	243a	-1.08ab
RDI x CC x Guara	12.24ab	0.153abc	0.005abc	232a	-1.29b
RDI x CC x Marta	11.03ab	0.141abc	0.005abc	242a	-1.31b
RDI x CC x Lauranne	13.06ab	0.177abc	0.006ab	238a	-1.29b
RDI x CC x Marcona	14.43a	0.200a	0.006a	242a	-1.29b
RDI x BS x Guara	12.22ab	0.161abc	0.005abc	235a	-1.23ab

	A_n	g_{sw}	E	C_i	Ψ_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	$\mu\text{mol mol}^{-1}$	(MPa)
RDI x BS x Marta	11.21ab	0.141abc	0.005abcd	235a	-1.27ab
RDI x BS x Lauranne	12.57ab	0.163abc	0.005abc	238a	-1.21ab
RDI x BS x Marcona	11.18ab	0.169abc	0.005abc	257a	-1.26ab

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential; FI, full irrigation; RDI, regulated deficit irrigation, CC, cover crops, BS, bare soil

In addition, irrigation factor did not significantly influence for A_n , g_{sw} , or E but had a strong effect on Ψ_{Stem} , RDI trees showing lower values in comparison to FI. This pattern suggests that although the RDI was promoting a water-stress situation, trees were able to maintain gas exchange through partial stomatal and metabolic adjustments, reflecting a degree of drought tolerance (Romero et al. 2004; Ruiz-Sánchez et al. 1993). Moreover, soil-management management showed no significant effect on most variables, reinforcing the idea that, under the studied conditions, soil cover or bare soil did not markedly constrain physiological performance.

The cultivar effect was particularly striking: cvs. Lauranne and Marcona exhibited higher A_n and g_{sw} values compared with cv. Marta, which consistently displayed lower activity for both physiological parameters. This suggests an intrinsic genetic variability in stomatal behaviour and photosynthetic capacity, which has been reported for almond cultivars differing in drought tolerance (Torrecillas et al. 1996; Gutiérrez-Gordillo et al. 2019; 2023).

Taking into consideration that the highest differences were observed as response to phenological stage, it was developed a similar analysis for each period. During the vegetative growth, water availability was not limiting, as indicated by relatively stable stem-water potential ($\Psi_{Stem} \approx -1.0$ MPa) and the absence of irrigation or soil-management effects. The A_n and g_{sw} were high across all treatments, with significant differences driven primarily by cultivar. The cv. Marta consistently displayed lower values compared to cvs. Guara, Lauranne, and Marcona, suggesting inherent genetic constraints in g_{sw} behaviour and A_n capacity (Tables 4 and S1).

By contrast, the kernel filling stage emerged as the period where treatments reflected the highest differences. Thus, Ψ_{Stem} dropped substantially (down to -1.45 MPa in RDI plots), indicating that the RDI and CC strategies effectively imposed a moderate to water stress (Tables 4 and S1). This was accompanied by significant reductions in A_n ($\approx 10\text{--}15 \mu\text{mol m}^{-2} \text{s}^{-1}$), with relevant differences depending on the almond cultivar. Thus, cv. Marcona maintained relatively higher values of gas exchange even under RDI (less conservative), while cv. Marta again showed the lowest performance.

This stage was also characterized by strong stomatal control of transpiration ($E \sim g_{sw}$), confirming that stomatal limitations dominated photosynthetic regulation in almond (Egea et al., 2011). Some authors have confirmed that some almond cultivars (*i.e.* cv. Avijor) differ in their water-use strategy, with some genotypes exhibiting more conservative responses to water deficit—characterized by earlier stress avoidance—than others (*i.e.* cvs. Soleta and Isabelona), which conditions their suitability to deficit irrigation strategies (Paudel et al. 2020; Álvarez-Maldini et al. 2022)

In the postharvest stage, A_n rates declined sharply ($\approx 4\text{--}9 \mu\text{mol m}^{-2} \text{s}^{-1}$) in all treatments, reflecting an ontogenic down-regulation of photosynthetic capacity. Although Ψ_{Stem} was still more negative under RDI (-1.25 to -1.35 MPa), the

impact on A_n and g_{sw} was minimal, and C_i tended to increase. This indicates that postharvest photosynthetic decline was not primarily driven by stomatal closure, but by non-stomatal metabolic limitations, consistent with a reallocation of resources towards reserve accumulation once fruit load is removed (Gutiérrez-Gordillo et al. 2023; Egea et al. 2011; Spinelli et al. 2016). Thus, while deficit irrigation imposed measurable water stress, its impact on gas exchange was attenuated by the intrinsic metabolic decline at this stage (Tables 4 and S1).

Table 4
ANOVA for main factors and interactions on physiological variables during the monitored phenological stages. Season 2024

Factors	A_n	g_{sw}	E	C_i	Ψ_{Stem}
Vegetative growth					
Irrigation	NS	NS	***	NS	NS
Soil-management system	NS	NS	NS	NS	NS
Cultivar	***	***	***	NS	NS
Irrigation x Soil-management system	NS	NS	*	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS
Kernel filling					
Irrigation	NS	NS	NS	NS	***
Soil-management system	NS	NS	NS	NS	*
Cultivar	***	***	***	**	NS
Irrigation x Soil-management system	NS	NS	NS	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	*	*	*	NS	NS
Post-harvest					
Irrigation	NS	NS	**	NS	***
Soil-management system	NS	NS	NS	NS	NS
Cultivar	NS	***	***	NS	NS
Irrigation x Soil-management system	NS	NS	*	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	*	*	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential. NS, not significant; *, **, and *** significant differences for $p < 0.05$, $p < 0.001$, and $p < 0.001$,

respectively.

Table S1

Mean values of gas exchange and stem-water potential during phenological stages for each irrigation strategy, soil-management system, and cultivar combinations. Season 2024.

	A_n	g_{sw}	E	C_i	Y_{Stem}
	$(\mu\text{mol m}^{-2} \text{s}^{-1})$	$(\text{mol m}^{-2} \text{s}^{-1})$	$\text{mol m}^{-2} \text{s}^{-1}$	$\mu\text{mol mol}^{-1}$	(MPa)
Vegetative growth					
FI x CC x Guara	16.3ab	0.223ab	0.005abc	248a	-1.04a
FI x CC x Marta	11.9b	0.153b	0.003c	249a	-0.99a
FI x CC x Lauranne	16.5ab	0.216ab	0.005abc	244a	-1.03a
FI x CC x Marcona	17.2ab	0.268a	0.005abc	261a	-0.96a
FI x BS x Guara	15.0ab	0.209ab	0.005abc	250a	-1.03a
FI x BS x Marta	12.4ab	0.158ab	0.004bc	245a	-1.01a
FI x BS x Lauranne	15.5ab	0.186ab	0.005abc	231a	-1.05a
FI x BS x Marcona	17.6a	0.246ab	0.006ab	245a	-0.98a
RDI x CC x Guara	16.2ab	0.217ab	0.006ab	241a	-1.09a
RDI x CC x Marta	15.5ab	0.185ab	0.005abc	229a	-1.14a
RDI x CC x Lauranne	15.4ab	0.220ab	0.006ab	245a	-1.15a
RDI x CC x Marcona	17.3ab	0.248ab	0.006a	260a	-1.18a
RDI x BS x Guara	13.4ab	0.182ab	0.005abc	248a	-1.08a
RDI x BS x Marta	13.0ab	0.160ab	0.005abc	233a	-1.10a
RDI x BS x Lauranne	16.1ab	0.220ab	0.006ab	245a	-0.99a
RDI x BS x Marcona	14.6ab	0.228ab	0.006ab	260a	-1.01a
Kernel filling					
FI x CC x Guara	14.61a	0.183abc	0.006ab	227a	-1.17abc
FI x CC x Marta	10.42a	0.107c	0.004c	217a	-1.17abc
FI x CC x Lauranne	14.51a	0.166abc	0.005abc	214a	-1.18abc
FI x CC x Marcona	11.84a	0.180abc	0.005abc	253a	-1.13ab
FI x BS x Guara	10.72a	0.150abc	0.005abc	215a	-1.05a
FI x BS x Marta	10.72a	0.127bc	0.004bc	235a	-1.02a
FI x BS x Lauranne	13.38a	0.164abc	0.005abc	229a	-1.34ab
FI x BS x Marcona	14.97a	0.216a	0.007a	245a	-1.13ab
RDI x CC x Guara	11.98a	0.138bc	0.005abc	221a	-1.48c
RDI x CC x Marta	10.42a	0.140abc	0.005abc	244a	-1.48c
RDI x CC x Lauranne	12.85a	0.177abc	0.006ab	242a	-1.45bc

	A_n	g_{sw}	E	C_i	Ψ_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	$\text{mol m}^{-2} \text{s}^{-1}$	$\mu\text{mol mol}^{-1}$	(MPa)
RDI x CC x Marcona	14.38a	0.189ab	0.007a	233a	-1.43bc
RDI x BS x Guara	13.48a	0.176abc	0.006ab	224a	-1.34abc
RDI x BS x Marta	9.88a	0.146abc	0.005abc	246a	-1.42bc
RDI x BS x Lauranne	11.78a	0.146abc	0.005abc	229a	-1.39bc
RDI x BS x Marcona	11.02a	0.160abc	0.006abc	249a	-1.42bc
Post harvest					
FI x CC x Guara	6.51a	0.08abc	0.003bc	242a	-1.06a
FI x CC x Marta	4.60a	0.06c	0.002c	254a	-1.04a
FI x CC x Lauranne	8.77a	0.11abc	0.004abc	241a	-1.02a
FI x CC x Marcona	6.50a	0.12abc	0.003bc	275a	-1.21a
FI x BS x Guara	5.93a	0.08abc	0.003bc	259a	-1.09a
FI x BS x Marta	6.98a	0.08abc	0.003bc	232a	-1.03a
FI x BS x Lauranne	8.65a	0.13ab	0.004ab	259a	-1.05a
FI x BS x Marcona	9.15a	0.12abc	0.004ab	236a	-1.12a
RDI x CC x Guara	6.91a	0.09abc	0.003bc	240a	-1.25a
RDI x CC x Marta	5.52a	0.07bc	0.003bc	258a	-1.22a
RDI x CC x Lauranne	9.97a	0.11abc	0.004ab	222a	-1.18a
RDI x CC x Marcona	10.18a	0.15a	0.005a	258a	-1.21a
RDI x BS x Guara	7.83a	0.10abc	0.003bc	238a	-1.23a
RDI x BS x Marta	9.95a	0.11abc	0.004ab	218a	-1.20a
RDI x BS x Lauranne	8.82a	0.11abc	0.004ab	244a	-1.20a
RDI x BS x Marcona	6.32a	0.10abc	0.003bc	267a	-1.35a

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential; FI, full irrigation; RDI, regulated deficit irrigation, CC, cover crops, BS, bare soil

3.2.2. Season 2025

The physiological behaviour of the almond trees during 2025 was clearly modulated by the phenological period (Tables 5 and 6). The seasonal evolution of gas-exchange parameters followed a consistent pattern, with the highest values of A_n ($15.8 \mu\text{mol m}^{-2} \text{s}^{-1}$) and g_{sw} ($0.235 \text{mol m}^{-2} \text{s}^{-1}$) taking place during the vegetative stage, coinciding with the most favourable climatic conditions and active canopy growth. As the season progressed, a growing decline was observed, reaching minimum values in post-harvest stage ($A_n = 3.9 \mu\text{mol m}^{-2} \text{s}^{-1}$; $g_{sw} = 0.117 \text{mol m}^{-2} \text{s}^{-1}$). This trend reflects a clear stomatal and non-stomatal limitation of photosynthesis at the end of the cycle, similar behaviour than that recorded in 2024.

Regarding to irrigation treatment, the results revealed moderate effects consistent with the water regime applied. Plants under RDI exhibited slightly lower (but not significant) A_n ($10.25 \mu\text{mol m}^{-2} \text{s}^{-1}$) compared with the FI ($A_n = 10.66 \mu\text{mol m}^{-2} \text{s}^{-1}$); these reductions being accompanied by a clear decline in Ψ_{Stem} (-1.49 MPa vs. -1.18 MPa , respectively), indicating an effective induction of controlled water stress.

Soil-management system showed no significant influence on the physiological variables, although slight tendencies were found. Trees grown under BS tended to display marginally higher g_{sw} and E than those with CC, particularly under FI strategy. This pattern may be associated with a reduced competition for water and a slightly greater soil evaporation contribution, but the magnitude of the effect was minimal. The stability of A_n and Ψ_{Stem} for both soil-management systems highlight the limited short-term physiological impact of cover cropping under these experimental conditions.

Moreover, differences among cultivars were more evident. The cvs. Lauranne and Marcona showed the highest A_n values (11.3 and $10.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) and maintained greater g_{sw} , showing higher photosynthetic capacity and greater diffusive control. By contrast, cv. Marta exhibited the lowest A_n and g_{sw} , which is consistent with a more conservative behaviour under water-limited environments. The cv. Guara displayed intermediate responses and relatively stable Ψ_{Stem} values (-1.31 MPa), confirming its balanced regulation between water saving and carbon assimilation.

Finally, the triple interaction (Irrigation $\times$ Soil-management system $\times$ Cultivar) displayed a limited significance, suggesting that cultivar performance was largely independent of soil-management system. The highest A_n values were observed in cvs. Lauranne and Guara under FI conditions, both in CC and BS plots, while cv. Marta under RDI + CC reached the lowest photosynthetic and conductance rates, along with the most negative Ψ_{Stem} values (-1.62 MPa). These results reinforce the notion that the physiological response to moderate water stress is primarily genotype-dependent, with irrigation strategy exerting a secondary influence, and soil-management system not causing relevant effects.

Table 5
ANOVA summary with the significance of main factors and their interactions on gas-exchange parameters and stem-water potential during 2025.

Factors	A_n	g_{sw}	E	C_i	Ψ_{Stem}
Phenological stage	***	***	***	***	***
Irrigation	NS	***	NS	***	***
Soil-management system	NS	*	NS	NS	NS
Cultivar	*	***	**	***	NS
Irrigation x Soil-management system	NS	NS	NS	*	NS
Irrigation x Cultivar	NS	NS	NS	*	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS

A_n , net photosynthesis; g_{sw} , stomatal conductance; E , transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential. NS, not significant; *, **, and *** significant differences for $p < 0.05$, $p < 0.001$, and $p < 0.001$, respectively.

Table 6
Mean values of gas exchange and water potential parameters as affected by phenological stage, irrigation regime, soil-management system, and cultivar. Season 2025

	A_n	g_{sw}	E	C_i	Y_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\mu\text{mol m}^{-1}$)	(MPa)
Phenological period					
Vegetative growth	15.78a	0.235a	0.004b	264c	-1.16a
Kernel filling	11.66b	0.204b	0.007a	280b	-1.49b
Post harvest	3.92c	0.117c	0.004b	331a	-1.35b
Irrigation regime					
FI	10.66a	0.200a	0.005a	298a	-1.18a
RDI	10.25a	0.171b	0.005a	286b	-1.49b
Soil-management system					
CC	10.28a	0.176b	0.005a	289a	-1.32a
BS	10.63a	0.195a	0.005a	294a	-1.35a
Cultivar					
Guara	10.86ab	0.197a	0.005ab	292ab	-1.31a
Marta	9.48b	0.155b	0.004b	289b	-1.33a
Lauranne	11.34a	0.187ab	0.005ab	284b	-1.31a
Marcona	10.13ab	0.202a	0.006a	302a	-1.38a
Interactions					
FI x CC x Guara	11.19a	0.213ab	0.005a	296ab	-1.16ab
FI x CC x Marta	9.79a	0.161ab	0.004a	298ab	-1.15a
FI x CC x Lauranne	11.07a	0.185ab	0.004a	286ab	-1.18ab
FI x CC x Marcona	9.70a	0.212ab	0.005a	313a	-1.19ab
FI x BS x Guara	11.14a	0.230a	0.006a	305ab	-1.17ab
FI x BS x Marta	10.30a	0.175ab	0.005a	291ab	-1.16ab
FI x BS x Lauranne	12.06a	0.209ab	0.005a	282ab	-1.18ab
FI x BS x Marcona	10.02a	0.215a	0.006a	313a	-1.22ab
RDI x CC x Guara	10.45a	0.163ab	0.005a	279b	-1.46ab
RDI x CC x Marta	8.15a	0.120b	0.004a	277b	-1.62ab
RDI x CC x Lauranne	11.70a	0.193ab	0.005a	285ab	-1.34ab
RDI x CC x Marcona	10.20a	0.164ab	0.005a	279b	-1.47ab
RDI x BS x Guara	10.67a	0.184ab	0.005a	289ab	-1.47ab

	A_n	g_{sw}	E	C_i	Ψ_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\mu\text{mol m}^{-1}$)	(MPa)
RDI x BS x Marta	9.69a	0.164ab	0.005a	288ab	-1.37ab
RDI x BS x Lauranne	10.53a	0.163ab	0.005a	283ab	-1.55ab
RDI x BS x Marcona	10.61a	0.219a	0.006a	304ab	-1.64b

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential; FI, full irrigation; RDI, regulated deficit irrigation, CC, cover crops, BS, bare soil

As the previous season, it was controlled the effects of irrigation strategy, soil-management system, cultivar and their interactions in the monitored variables within each phenological period. The physiological performance during 2025 was strongly driven by crop phenology, while the effects of irrigation, soil-management system, and their interactions were secondary and highly stage-dependent (Table 7). During the vegetative period, neither gas-exchange parameters (A_n , g_{sw} , E), just Ψ_{Stem} and C_i showed a detectable reaction to irrigation, indicating that irrigation strategy could be affecting the plant water status before than carbon assimilation. The soil-management system and cultivar effects were negligible at this early stage, and no interaction reached significance. Tukey's comparisons confirmed that all combinations formed a single statistical group for all variables, reflecting the naturally favourable environmental conditions characteristic of early spring as was shown in Table S2.

The physiological structure changed markedly during kernel filling stage (Table 7). During this period irrigation promoted a strong and consistent influence across the full set of variables (A_n , g_{sw} , E, C_i , and Ψ_{Stem}), reflecting a higher sensitiveness to water availability, probably because of the higher evapotranspirative demand. In addition, soil-management system showed a minor effect (just in E), while the cultivar exerted a significant influence on g_{sw} and C_i , and revealing intrinsic differences in stomatal regulation.

Finally, in post-harvest stage, the pattern shifted again. Irrigation no longer affected A_n , g_{sw} , E or C_i , but remained significant for Ψ_{Stem} , showing that water status continued reflecting differences among treatments, even when photosynthetic activity was already declining. Cultivar effects regained prominence, significantly influencing A_n , g_{sw} , E, and Ψ_{Stem} , and demonstrating that genetic differences dominate the late-season physiological behaviour. In summary, taking into consideration the obtained results in 2025, crop phenology was the primary driver of physiological behaviour, with marked shifts in sensitivity throughout stages. Irrigation strongly modulated gas-exchange and water status only during the kernel-filling stage, while soil-management system exerted modest, variable effects. The cultivar emerged as a robust and consistent factor, particularly in the mid and late season, highlighting stable genotypic differences in water-use traits and stomatal behaviour. High-order interactions were minimal, indicating that the crop eco-physiological response was largely structured by inherent phenological dynamics and cultivar-specific physiology, with water availability exerting its influence primarily during the period of greatest atmospheric demand.

Table 7
ANOVA for main factors and interactions on physiological variables during the
monitored phenological stages. Season 2025

Factors	An	g_{sw}	E	Ci	Ψ_{Stem}
Vegetative growth					
Irrigation	NS	NS	NS	***	**
Soil-management system	NS	NS	NS	NS	NS
Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system	NS	NS	NS	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS
Kernel filling					
Irrigation	*	***	*	**	***
Soil-management system	NS	NS	*	NS	NS
Cultivar	NS	**	NS	***	NS
Irrigation x Soil-management system	NS	NS	NS	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS
Post-harvest					
Irrigation	NS	NS	NS	NS	***
Soil-management system	NS	*	NS	NS	*
Cultivar	**	***	**	NS	*
Irrigation x Soil-management system	NS	NS	NS	NS	NS
Irrigation x Cultivar	NS	NS	NS	NS	NS
Soil-management system x Cultivar	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO₂ concentration; Ψ_{Stem} , stem-water potential. NS, not significant; *, **, and *** significant differences for $p < 0.05$, $p < 0.001$, and $p < 0.001$, respectively.

Table S2

Mean values of gas exchange and stem-water potential during phenological stages for each irrigation strategy, soil-management system, and cultivar combinations. Season 2025.

	A_n	g_{sw}	E	C_i	Y_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\mu\text{mol mol}^{-1}$)	(MPa)
Vegetative growth					
FI x CC x Guara	14.84a	0.24a	0.004a	269a	-1.08a
FI x CC x Marta	16.19a	0.23a	0.004a	265a	-1.06a
FI x CC x Lauranne	14.41a	0.24a	0.004a	284a	-1.12a
FI x CC x Marcona	14.60a	0.24a	0.004a	288a	-1.09a
FI x BS x Guara	15.75a	0.32a	0.006a	292a	-1.10a
FI x BS x Marta	14.48a	0.22a	0.004a	271a	-1.11a
FI x BS x Lauranne	16.13a	0.26a	0.005a	268a	-1.09a
FI x BS x Marcona	14.30a	0.21a	0.004a	278a	-1.19a
RDI x CC x Guara	18.37a	0.24a	0.005a	241a	-1.22a
RDI x CC x Marta	13.27a	0.17a	0.004a	249a	-1.35a
RDI x CC x Lauranne	18.96a	0.28a	0.005a	257a	-1.15a
RDI x CC x Marcona	14.56a	0.18a	0.004a	246a	-1.21a
RDI x BS x Guara	18.08a	0.23a	0.004a	237a	-1.19a
RDI x BS x Marta	15.53a	0.21a	0.004a	253a	-1.21a
RDI x BS x Lauranne	17.00a	0.20a	0.004a	238a	-1.15a
RDI x BS x Marcona	16.04a	0.28a	0.004a	282a	-1.22a
Kernel filling					
FI x CC x Guara	14.87a	0.31a	0.009a	299ab	-1.28a
FI x CC x Marta	11.37a	0.17bc	0.006ab	275ab	-1.32a
FI x CC x Lauranne	13.24a	0.22abc	0.007ab	275ab	-1.40a
FI x CC x Marcona	9.57a	0.23abc	0.007ab	313a	-1.37a
FI x BS x Guara	13.97a	0.26ab	0.008ab	287ab	-1.26a
FI x BS x Marta	12.54a	0.20abc	0.007ab	272ab	-1.30a
FI x BS x Lauranne	12.51a	0.20abc	0.007ab	268b	-1.34a
FI x BS x Marcona	11.91a	0.26ab	0.009ab	303ab	-1.33a
RDI x CC x Guara	10.29a	0.15bc	0.006ab	262b	-1.77a
RDI x CC x Marta	8.80a	0.12c	0.005b	260b	-1.75a
RDI x CC x Lauranne	11.07a	0.18abc	0.007ab	276ab	-1.64a

	A_n	g_{sw}	E	C_i	Y_{Stem}
	($\mu\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\text{mol m}^{-2} \text{s}^{-1}$)	($\mu\text{mol mol}^{-1}$)	(MPa)
RDI x CC x Marcona	10.49a	0.18abc	0.006ab	278ab	-1.51a
RDI x BS x Guara	11.74a	0.19abc	0.007ab	274ab	-1.64a
RDI x BS x Marta	10.56a	0.18abc	0.006ab	278ab	-1.56a
RDI x BS x Lauranne	12.06a	0.20abc	0.007ab	276ab	-1.72a
RDI x BS x Marcona	11.54a	0.22abc	0.007ab	288ab	-1.64a
Post-harvest					
FI x CC x Guara	3.87ab	0.09a	0.003a	321a	-1.12ab
FI x CC x Marta	1.82b	0.08a	0.003a	355a	-1.07ab
FI x CC x Lauranne	5.54ab	0.09a	0.003a	299a	-1.03a
FI x CC x Marcona	4.94ab	0.16a	0.004a	338a	-1.11ab
FI x BS x Guara	3.69ab	0.12a	0.003a	334a	-1.14ab
FI x BS x Marta	3.87ab	0.11a	0.003a	329a	-1.07ab
FI x BS x Lauranne	7.55a	0.17a	0.005a	310a	-1.12ab
FI x BS x Marcona	3.85ab	0.17a	0.005a	358a	-1.16ac
RDI x CC x Guara	2.68b	0.09a	0.004a	332a	-1.39bc
RDI x CC x Marta	2.39b	0.07a	0.003a	323a	-1.77de
RDI x CC x Lauranne	5.09ab	0.12a	0.005a	321a	-1.24ab
RDI x CC x Marcona	5.54ab	0.13a	0.005a	314a	-1.69cd
RDI x BS x Guara	2.19b	0.13a	0.004a	356a	-1.60cd
RDI x BS x Marta	2.99b	0.10a	0.004a	334a	-1.35abc
RDI x BS x Lauranne	2.53b	0.09a	0.003a	335a	-1.79ed
RDI x BS x Marcona	4.27ab	0.17a	0.005a	343a	-2.06e

A_n , net photosynthesis; g_{sw} , stomatal conductance; E, transpiration; C_i , intercellular CO_2 concentration; Ψ_{Stem} , stem-water potential; FI, full irrigation; RDI, regulated deficit irrigation, CC, cover crops, BS, bare soil

3.3. Integrative analysis of physiological response to RDI and cover crops

With the aim of providing an integrative interpretation of the almond eco-physiological response to the applied treatments, a correlation analysis was carried out among the main physiological variables studied (Fig. 1). Considering that the phenological period was a key factor and that previous results had shown temporal shifts in physiological behaviour throughout the year, this correlation analysis was conducted separately for each period. Subsequently, those relationships that remained consistent from one season to another – that is, those showing minimal interannual

variation — were identified as robust and considered to represent the core eco-physiological mechanisms governing almond performance under water stress conditions.

The correlation analysis provides an integrative view of the physiological coordination among photosynthetic, stomatal and hydraulic traits. Thus, by examining the associations between A_n , g_{sw} , E , C_i , and Ψ_{Stem} , the analysis captured the underlying functional structure of gas-exchange regulation throughout the season and across years. For both seasons, a coherent structure of strong and significant correlations emerged, concretely among the gas-exchange variables. Throughout all periods, A_n , g_{sw} , and E were tightly linked, evidencing a consistent physiological core that represents the diffusive and stomatal control of photosynthesis and transpiration. The relationships $A_n - g_{sw}$ and $E - A_n$ were highly significant, confirming the predominance of stomatal regulation in the coordination of carbon assimilation and water loss (Manzoni et al., 2011). In this agreement, in almond, mesophyll and stomatal conductance are tightly coupled, so that under moderate water stress, a coordinated reduction in internal (g_i) and stomatal (g_{sw}) CO_2 diffusion occurs, ultimately leading to a decline in net photosynthesis, primarily driven by diffusional limitations rather than biochemical impairment as was reported by Tomás et al. (2013) and Eichi et al. (2014).

Additionally, the strength of correlations varied slightly among phenological periods. During the vegetative and fruit-growth stages, the network of positive associations was particularly dense, reflecting vigorous gas exchange under favourable environmental conditions. During the kernel filling stage, a partial decoupling between diffusive and hydraulic traits was found: correlations involving Ψ_{Stem} became weaker or even negative (e.g. $A - \Psi_{Stem}$, $E - \Psi_{Stem}$), suggesting stronger water limitations and stomatal closure. Finally, for the post-harvest stage, these associations partially recovered, showing a relaxation of water constraints after kernel maturity.

Although the general structure was similar in 2024 and 2025, subtle differences were noted. That is, the 2025 season displayed slightly stronger linkages between Ψ_{Stem} and the gas-exchange variables, suggesting a closer hydraulic control during that year. Overall, both seasons revealed the same hierarchical organization of physiological relationships, with gas-exchange parameters forming a stable nucleus and water-status variables showing higher temporal sensitivity (Fernandes de Oliveira et al. 2023).

Across phenological stages, a consistent set of strong and positive correlations denoted, fostering a core functional network that remained stable between 2024 and 2025. The relationships $A_n - g_{sw}$ and $E - A_n$ were particularly robust, exhibiting minimal interannual variation ($\Delta r \approx 0$) and maintaining high significance throughout the three phenological periods as shown in Fig. 2. These stable associations indicate that the coordination between carbon assimilation and stomatal behaviour is structurally conserved, supporting the notion of a tightly coupled stomatal control of photosynthesis (Buckley et al. 2017). Similarly, the positive and recurrent correlation between g_{sw} and Ψ_{Stem} suggests that the stomatal response to plant water status was reproducible across contrasting environmental conditions, evidencing a consistent hydraulic feedback mechanism.

Red and blue circles represent, respectively, increases and decreases in correlation strength in 2025 compared with 2024. The size of each circle is proportional to the magnitude of Δr , and asterisks indicate statistically significant differences according to Fisher's z test ($p < 0.05$, $p < 0.01$, $p < 0.001$). Each panel corresponds to a phenological period (1: vegetative growth, 2: kernel filling, 3: post-harvest). Positive values indicate stronger functional coupling in 2025, whereas negative values denote weakened coordination between variables.

In contrast, other relationships displayed notable plasticity, indicating a higher sensitiveness to external variability. The correlations that involved Ψ_{Stem} and either A_n , E or C_i were the most variable across seasons and periods. For instance, $A_n - \Psi_{Stem}$ and $E - \Psi_{Stem}$ strengthened in 2025, revealing a tighter coupling between photosynthetic activity, transpiration and plant water status under drier conditions (Álvarez Maldini et al. 2022). These changes suggest that while the basic

stomatal–photosynthetic coordination remains stable, the sensitivity of these processes to water potential can vary because of the experimental conditions, representing a flexible adjustment to fluctuating environmental constraints (Torres-Ruiz et al. 2024).

Altogether, these findings illustrate a dual physiological strategy. On one hand, almond maintains a structurally conservative functional core—the stable coordination among A_n , g_{sw} and E —that underpins efficient gas exchange and water-use regulation. On the other hand, it exhibits plasticity in water-related linkages ($A_n-\psi_{Stem}$, $E-\psi_{Stem}$, $C_i-\psi_{Stem}$), enabling dynamic responses to variations in water supply and climatic conditions.

Given that the relationship between A_n and g_{sw} was the most robust and consistent across years, this pair of variables was selected to explore the intrinsic coordination between diffusive and biochemical processes under water-limited conditions. To further characterize inter-varietal differences in stomatal regulation, the A_n – g_{sw} response was fitted for each cultivar using an exponential model, combining data from both 2024 and 2025 campaigns. In addition, it was estimated the conductance threshold ($g_{sw_{50}}$) at which photosynthetic activity reaches 50% of its asymptotic maximum (A_{max}), a physiologically meaningful indicator of stomatal efficiency and water-use efficiency.

Varieties achieving high assimilation rates at lower g_{sw} values can be interpreted as exhibiting a more efficient behaviour — characterized by tighter stomatal control and higher intrinsic water-use efficiency — whereas those requiring higher conductance to attain similar assimilation levels tend to follow a more an-isohydric strategy, maintaining gas exchange at lower water potentials but at the expense of greater water loss. Among the cultivars evaluated, Guara and Lauranne exhibited the lowest $g_{sw_{50}}$ thresholds (≈ 0.17 – $0.19 \text{ mol m}^{-2} \text{ s}^{-1}$), indicating that they attained half of their photosynthetic potential at comparatively low stomatal opening. This pattern suggests a higher water-use efficiency and a tendency towards isohydric regulation, maintaining carbon uptake while restricting water loss. In contrast, cvs. Marta and Marcona showed higher conductance thresholds (≈ 0.23 – $0.27 \text{ mol m}^{-2} \text{ s}^{-1}$), requiring greater stomatal aperture to achieve comparable assimilation rates (Fig. 3, Table 8). Such behaviour enhances carbon gain under favourable conditions but may involve higher transpirational costs. These results reinforce the physiological basis for genotype-specific adaptation to water stress, positioning cvs. Guara and Lauranne as the most water-efficient trees, and cvs. Marta and Marcona as more opportunistic, less conservative genotypes.

The intervarietal variability observed in the A_n – g_{sw} response is consistent with previous reports describing substantial genotypic differences in stomatal regulation and water-use efficiency in almond and other Mediterranean fruit trees. In this line, Conti et al. (2025) observed that cv. Guara exhibit conservative gas-exchange behaviour, maintaining moderate assimilation at relatively low conductances — a feature now confirmed by the lower $g_{sw_{50}}$ threshold identified in the present experiment. Also, these authors observed that in cv. Guara almond trees under moderate water stress, reductions in A_n and g_{sw} did not significantly affect the electron transport rate, which was likely sustained by alternative non-net carboxylative processes such as photorespiration or alternative electron transports. Similarly, Álvarez-Maldini et al. (2022) highlighted that such isohydric responses allow almond trees to preserve leaf water potential and prevent hydraulic failure under drought conditions, albeit with reduced carbon gain. Conversely, the higher $g_{sw_{50}}$ values of cv. Marcona agree with the more “risk-taking” behaviour reported for other vigorous genotypes, which tend to maintain stomatal opening and photosynthesis even under declining Y_{Stem} . Thus, from an agronomic standpoint, cultivars with lower $g_{sw_{50}}$ thresholds (e.g., Guara and Lauranne) could sustain higher instantaneous water-use efficiency under limited irrigation, while those with higher thresholds (cvs. Marta and Marcona) may better exploit transient water availability during wetter periods.

Table 8
Parameters of the exponential $A_{\max}-g_{sw}$ model and conductance thresholds (50% A_{n50}) for four almond cultivars

Cultivar	$A_{\max}$	k	R^2	g_{sw50}	A_{n50}
Marcona	27.40	2.95	0.46	0.24	13.70
Guara	24.83	3.97	0.63	0.17	12.41
Marta	34.40	2.54	0.68	0.27	17.20
Lauranne	27.43	3.58	0.66	0.19	13.72

3.4. Yield response to irrigation strategies and cover crops

Table 9 displays the ANOVA for yield response based on different components (almond in shell, unit weight, and kernel-to-shell ratio) during both studied seasons. Throughout the monitored seasons, differences on shell yield, kernel yield and kernel unit weight were found exclusively by the cultivar effect, with no significant influence by irrigation strategy, soil-management system or their interaction were found. Rather than reflecting a lack of response, this pattern denotes a highly robust agronomic behaviour: moderate RDI did not reduce production, and the implementation of cover crops did not provoke any yield penalty. In practical terms, almond trees were able to maintain their productive capacity under moderate water limitations and did so equally well in the presence of groundcovers, even though these might be expected to compete for water or plant nutrients.

The fact that RDI combined with cover crops produced yields comparable to FI and BS underscores the resilience of the system and highlights the compatibility of groundcover-based management with sustainable almond production. This outcome is particularly relevant in Mediterranean environments, where water scarcity is structural and the adoption of conservation practices must not compromise productivity.

Finally, the kernel-to-shell ratio further supported this behaviour: although consistently driven by cultivar effects, it showed only a minor, year-specific interaction with management factors, showing that kernel allocation remained largely stable despite differences in water availability or soil cover.

Table 9
ANOVA for irrigation strategy, soil-management system, and cultivar effects on almond productivity during two-year monitoring seasons

	Yield (Shell)		Yield (Kernel)		UW		K-S ratio	
	2024	2025	2024	2025	2024	2025	2024	2025
Irrigation	NS	NS	NS	NS	NS	NS	NS	NS
Soil-management system	NS	NS	NS	NS	NS	NS	NS	NS
Cultivar	***	***	***	***	***	***	**	***
Irrigation x Soil-management system	NS	NS	NS	NS	NS	NS	NS	NS
Irrigation x Soil-management system x Cultivar	NS	NS	NS	NS	NS	NS	*	NS

UW, Unit weight; K-S ratio, kernel-to-shell ratio. NS, not significant; *, **, and *** significant differences for $p < 0.05$, $p < 0.001$, and $p < 0.001$, respectively.

Post-hoc comparisons for kernel yield showed a highly stable response throughout irrigation regimes in both seasons (Table S3). In 2024, FI and RDI produced very similar kernel yields (1,765 and 1,748 kg ha⁻¹, respectively), something alike occurring in 2025, when kernel yields under FI and RDI reached 1,978 and 2,065 kg ha⁻¹, respectively; confirming that the RDI strategy imposed in this experiment did not compromise kernel productivity in either season.

Cultivar differences were substantially larger and highly consistent over the monitored seasons. In 2024, kernel yield ranged from 1,355 kg ha⁻¹ for cv. Guara to 1,998 kg ha⁻¹ for cv. Lauranne, whereas in 2025 the range widened from 1,451 kg ha⁻¹ for cv. Marcona to 2,837 kg ha⁻¹ for cv. Marta. The cvs. Lauranne and Marcona were the most stable between years (variation of - 113 and - 184 kg ha⁻¹, respectively), while cv. Guara and especially cv. Marta showed greater year-to-year variability (+ 500 and + 928 kg ha⁻¹, respectively).

Irrigation × soil-management system combinations showed only minor differences in 2024, when kernel yield varied between 1,639 and 1,677 kg ha⁻¹. This variability increased in 2025, with yields ranging from 2,111 kg ha⁻¹ (FI × BS) to 1,845 kg ha⁻¹ (FI × CC), these differences were not significant. The UW and the kernel-to-shell ratio –both indicators of kernel development and commercial quality– also showed strong genotypic control with limited sensitivity to irrigation or soil-management system. The K-S ratio remained remarkably stable during the seasons, revealing that the proportional allocation between kernel and shell is driven predominantly by cultivar rather than by interannual variability. The cv. Guara consistently exhibited the highest value whereas cv. Marcona showed the lowest in both years, confirming its well-known tendency toward thicker shell development. On the other hand, the cv. Lauranne presented the most stable K-S ratio, with minimal year-to-year fluctuation, underscoring its suitability in systems where consistency in kernel proportion is desirable.

The kernel unit weight also showed clear genotypic differentiation with minimal influence from irrigation or soil-management system. Among cultivars, Marcona consistently exhibited the highest unit weights, clearly separating it from the rest, whereas cv. Lauranne showed the lowest values in both seasons. The cvs. Marcona and Lauranne were the most regular cultivars in terms of kernel size, displaying very small fluctuations between monitored years. An interesting pattern emerged when kernel unit weight was interpreted jointly with kernel yield: the years with the highest production were accompanied by lower unit weights, indicating that increases in total yield were primarily driven by a greater number of fruits per tree rather than by larger kernels. This inverse relationship between crop load and kernel size further reinforces the idea that production dynamics in almond are strongly mediated by fruit number, while kernel morphology remains mostly cultivar-dependent and relatively insensitive to moderate RDI or the introduction of cover crops.

The RDI strategies in almond have been shown to sustain productivity when irrigation reductions are moderate and applied during phenologically tolerant stages. Several studies report that reducing irrigation to 40–70% of crop water requirements result in only slight or negligible yield reductions, particularly when deficits are imposed during kernel filling (Goldhamer et al., 2006; Egea et al., 2009). Under these conditions, seasonal irrigation volumes can be reduced by 30–40% with minimal yield declines (Prgomet et al. 2020). In contrast, severe or prolonged water deficits lead to reductions in kernel dry weight and total yield and may induce carry-over effects on subsequent seasons (Goldhamer and Viveros, 2000; Gutiérrez-Gordillo et al. 2019). In addition, it is remarkable that cultivar-dependent water-use strategies underlie the differential productive response of almond to RDI. More conservative (isohydric) cultivars, characterized by early stomatal closure and enhanced hydraulic safety, tend to prioritize stress avoidance, which may limit their productive response under RDI. In contrast, less conservative or more productive cultivars maintain physiological activity under moderate water deficit and often show greater yield stability when RDI is properly timed. Mediterranean studies report that cultivars such as Guara exhibit higher yield resilience under RDI, whereas others, including cv. Marcona, are more sensitive to deficit intensity, with intermediate responses observed in cvs. Lauranne or Marta. These contrasting strategies highlight that the effectiveness of RDI depends not only on deficit intensity and

phenological timing, but also on the inherent water-use strategy of each cultivar, reinforcing the need for cultivar-specific irrigation thresholds (Gutiérrez-Gordillo et al. 2020a; Paudel et al. 2020; Álvarez-Maldini et al. 2022).

That is, the yield components in almond are defined by the fruit number and individual fruit weight, both of which are sensitive to water availability. Water stress during early fruit development affects fruit set and kernel growth, while prolonged or poorly timed deficits can alter carbohydrate reserves and reduce flower induction, thereby decreasing fruit number in the subsequent season. Moreover, crop load modulates fruit growth capacity, as differences in fruit set influence assimilate allocation and ultimately determine individual fruit size (Egea et al., 2009; Espadafor et al. 2015; Goldhamer and Viveros 2000).

Table S3
Post-hoc mean separation (Tukey CLD) for almond yield components subjected to irrigation regimes and soil-management systems throughout the studied seasons

Factor		Almond yield		Kernel yield		Unit weight		K-S	
		2024	2025	2024	2025	2024	2025	2024	2025
		(kg ha ⁻¹)				(g)			
Irrigation	FI	5,080a	5,793a	1,657a	1,978a	1.32a	1.28a	0.33a	0.34a
	RDI	5,133a	6,157a	1,659a	2,065a	1.30a	1.20a	0.33a	0.33a
Soil-management system	CC	5,083a	5,867a	1,659a	1,962a	1.32a	1.23a	0.33a	0.33a
	BS	5,130a	6,083a	1,658a	2,081a	1.30a	1.24a	0.33a	0.34a
Cultivar	Guara	3,741b	4,955b	1,355b	1,855b	1.29b	1.20b	0.36a	0.38a
	Lauranne	5,703a	5,558b	1,998a	1,942b	1.10c	1.10b	0.35a	0.35ab
	Marcona	5,277a	5,154b	1,371b	1,451b	1.55a	1.53a	0.26b	0.28c
	Marta	5,705a	823a	1,909a	2,837a	1.30b	1.12b	0.34a	0.34b
Irrigation x Soil-management system	FI x CC	5,102a	5,419a	1,676a	1,845a	1.32a	1.27a	0.33a	0.34a
	FI x BS	5,058a	6,167a	1,639a	2,111a	1.32a	1.29a	0.33a	0.34a
	RDI x CC	5,064a	6,316a	1,642a	2,079a	1.32a	1.20a	0.33a	0.33a
	RDI x BS	5,203a	5,998a	1,677a	2,050a	1.28a	1.20a	0.33a	0.34a
Guara	FI x CC	4,042a	3,519a	1,507a	1,350a	1.30a	1.20ab	0.37a	0.38a
	FI x BS	3,842a	4,272ab	1,416a	1,673a	1.31a	1.41a	0.37a	0.39a
	RDI x CC	3,499a	5,788ab	1,236a	2,003a	1.30a	1.05b	0.35a	0.34a
	RDI x BS	3,581a	6,242a	1,262a	2,395a	1.25a	1.14ab	0.35a	0.38a
Lauranne	FI x CC	6,610a	5,427a	2,308a	1,966a	1.14a	1.12a	0.35a	0.36a
	FI x BS	5,482a	5,579a	1,900a	1,930a	1.07a	1.10a	0.35a	0.34a
	RDI x CC	4,943a	6,086a	1,767a	2,142a	1.15a	1.05a	0.36a	0.35a
	RDI x BS	5,777a	5,142a	2,016a	1,729a	1.07a	1.15a	0.35a	0.34a
Marcona	FI x CC	4,981a	5,644a	1,252a	1,593a	1.58a	1.51a	0.25a	0.28a
	FI x BS	5,198a	5,458a	1,347a	1,561a	1.56a	1.52a	0.26a	0.29a
	RDI x CC	4,907a	4,856a	1,255a	1,304a	1.58a	1.61a	0.26a	0.27a
	RDI x BS	6,021a	4,659a	1,631a	1,348a	1.49a	1.48a	0.27a	0.29a
Marta	FI x CC	4,776a	7,085a	1,636a	2,470a	1.26a	1.26a	0.34a	0.35a

Factor		Almond yield		Kernel yield		Unit weight		K-S	
		2024	2025	2024	2025	2024	2025	2024	2025
	FI x BS	5,709a	9,362a	1,892a	3,279a	1.36a	1.14a	0.33a	0.35a
	RDI x CC	6,906a	8,535a	2,310a	2,869a	1.27a	1.08a	0.33a	0.34a
	RDI x BS	5,431a	7,950a	1,799a	2,730a	1.32a	1.03a	0.33a	0.34a
Cultivar x Irrigation x Soil-management system	Guara x FI x CC	4,042ab	3,519e	1,507a	1,350b	1.30c	1.20c	0.37a	0.38a
	Guara x FI x BS	3,842ab	4,272de	1,416a	1,673b	1.31c	1.41b	0.37a	0.39a
	Guara x RDI x CC	3,499b	5,788bcde	1,236a	2,003ab	1.30c	1.05e	0.35a	0.34abc
	Guara x RDI x BS	3,581b	6,242bcde	1,262a	2,395ab	1.25cd	1.14cd	0.35a	0.38a
	Marta x FI x CC	4,776ab	7,085abcd	1,252a	2,470ab	1.58a	1.26c	0.25b	0.35abc
	Marta x FI x BS	5,709ab	9,362a	1,347a	3,279a	1.56a	1.14cd	0.26b	0.35abc
	Marta x RDI x CC	6,906a	8,535ab	1,255a	2,869ab	1.58a	1.08de	0.26b	0.34abc
	Marta x RDI x BS	5,431ab	7,950abc	1,631a	2,730ab	1.49ab	1.03e	0.27b	0.34abc
	Lauranne x FI x CC	6,610ab	5,427bcde	1,636a	1,966ab	1.26cd	1.12d	0.34ab	0.36ab
	Lauranne x FI x BS	5,482ab	5,579bcde	1,892a	1,930ab	1.36bc	1.10d	0.33b	0.34abc
	Lauranne x RDI x CC	4,943ab	6,086abcd	2,310a	2,142ab	1.27cd	1.05e	0.33b	0.35abc
	Lauranne x RDI x BS	5,777ab	5,142bcde	1,799a	1,729ab	1.32c	1.15cd	0.33b	0.34abc
	Marcona x FI x CC	4,981ab	5,644bcde	2,308a	1,593b	1.14de	1.51a	0.35a	0.28bc
	Marcona x FI x BS	5,198ab	5,458bcde	1,900a	1,561b	1.07e	1.52a	0.35a	0.29bc
	Marcona x RDI x CC	4,907ab	4,856cde	1,767a	1,304b	1.15de	1.61a	0.36a	0.27c
	Marcona x RDI x BS	6,021ab	4,659cde	2,016a	1,348b	1.07e	1.48ab	0.35a	0.29bc

FI, full irrigation; RDI, regulated deficit irrigation, CC, cover crops, BS, bare soil

3.5. Eco-physiological and yield integration: genotypic determinism and the tree resilience to soil and water management

To integrate the eco-physiological observations obtained across phenological periods with the final productive performance of the trees, two complementary multivariate approaches were applied. First, a Principal Component Analysis (PCA) was used to explore the inherent structure of variation among physiological traits and to visualise how cultivars, irrigation regimes and soil-management systems were positioned in the multivariate space without imposing any a priori model structure. In addition, a Redundancy Analysis (RDA) was performed to quantify the extent to which the observed physiological variability could be statistically attributed to the experimental factors (year, irrigation, soil-management system, and cultivar). This approach allowed us to evaluate the relative importance of genotype, climatic year, soil-management system and irrigation regime in shaping physiological functioning, while also identifying the specific traits most associated with each driver.

The PCA performed separately for each phenological period revealed clear shifts in the multivariate physiological structure of the trees as the season developed, together with consistent cultivar-dependent patterns and minimal separation between irrigation or soil management treatments (Fig. 4). For the vegetative stage, the PCA explained 53,3% of total variability, and revealed a clear physiological gradient along PC1 (27,9%), mainly driven by net photosynthesis (A_{P1}), stomatal conductance (g_{sw_P1}) and transpiration (E_{P1}), which were positively associated with kernel yield. In contrast, PC2 (25,4%) was largely explained by intercellular CO_2 concentration (C_{i_P1}) and stem-water potential during this stage (Pot_{P1}), indicating a decoupling between carbon assimilation and internal CO_2 dynamics at this early stage. Overall, neither irrigation strategy nor cultivar showed a clear global multivariate separation, suggesting that water stress was still limited and that physiological functioning remained largely conservative over genotypes during the vegetative period. Nevertheless, a consistent intra-cultivar pattern emerged, as RDI trees tended to be displaced towards lower PC2 scores compared to FI trees for all cultivars. This systematic shift suggests early adjustments in plant water status under RDI. These adjustments would be primarily associated with water relation variables (Ψ_{Stem}), while gas exchange parameters remained largely unaffected, indicating that RDI induced subtle but detectable physiological regulation without impairing photosynthetic activity at this stage.

During the kernel filling stage, the PCA was able to explain 63% of total variability; and it was primarily structured by a strong gas-exchange gradient along PC1 (39,1%), with net assimilation (A_{P2}), stomatal conductance (g_{sw_P2}) and transpiration (E_{P2}) showing high and consistent loadings. The stem-water potential (Pot_{P2}) contributed to the same axis but with a lower weight, indicating that water status became more closely integrated with stomatal and photosynthetic functioning than in the vegetative period. Kernel yield followed the same general orientation as A_{P2} and g_{sw_P2} , although its shorter vector suggests that yield variability was only partially captured by the main physiological gradient during this stage. In contrast, PC2 (23,9%) was largely dominated by unit weight and C_{i_P2} , reflecting an orthogonal dimension associated with internal CO_2 dynamics and fruit size-related variation rather than with gas-exchange intensity per se.

Although kernel filling stage did not result in a clear multivariate clustering of irrigation regimes, cultivar-specific responses to RDI became apparent along the main gas-exchange axis (PC1). Under FI, cvs. Guara and Marta were positioned towards the same direction as A, g_{sw} and E, denoting a strong coupling between water availability and gas-exchange capacity. In contrast, under RDI, cvs. Guara and Lauranne showed the greatest displacement away from the gas-exchange vectors, triggering a stronger down-regulation of physiological activity. Conversely, cvs. Marta and Marcona under RDI remained close to the origin of PC1, reflecting a more buffered or conservative adjustment to water deficit rather than a marked departure from the dominant physiological gradient.

During postharvest stage, the PCA was able to explain 58,9% of total variability, and it was primarily driven by gas-exchange variables (A_P3, gsw_P3 and E_P3), which remained strongly aligned and thus defined the main axis of physiological activity (PC1, 34,2%). As opposed to the kernel filling stage, Ψ_{Stem} (Pot_P3) was oriented in the opposite direction to the gas-exchange vectors, indicating a clear decoupling between plant water status and photosynthetic functioning. This pattern suggests that the post-harvest decline in carbon assimilation was not primarily driven by water limitation, but rather by an intrinsic down-regulation of photosynthesis associated with phenological progression. Accordingly, variability in C_i along the orthogonal axis further supports the predominance of non-stomatal limitations during this stage. Thus, C_i contributed mainly to the orthogonal axis (PC2, 24,7%), indicating a progressive decoupling between internal CO_2 dynamics and stomatal regulation. Finally, irrigation and cultivar effects were not expressed as distinct multivariate clusters during post-harvest, implying that phenological control dominated tree physiology at this stage, while residual water-status differences played a comparatively secondary role.

P1, vegetative growth; P2, kernel filling; P3, post-harvest stage. Pot corresponds to stem-water potential

Redundancy analysis (RDA) was used to quantify how much of the variation in physiological traits over stages was associated with season, irrigation regime, soil-management system, and cultivar (Fig. 5). RDA explained a large proportion of the total physiological variance ($R^2 = 0.65$; adjusted $R^2 = 0.61$), indicating a strong association among physiological traits and experimental factors included in the model. The first constrained axis (RDA1) accounted for approximately 53% of the explained variance, while the second axis (RDA2) explained a further 23%, together capturing around 76% of the constrained variability. These findings indicate that the multivariate physiological response was primarily structured along a dominant gradient, with additional differentiation captured by the secondary axis. Thus, the ordination biplot clearly showed that the annual signal dominated the constrained space: the centroids for 2024 and 2025 were well separated along the first RDA axis, and several physiological variables projected towards one year or the other. Additionally, variables related to stomatal activity and gas exchange during kernel filling and post-harvest periods (A_P2, A_P3, gsw_P2, gsw_P3, E_P2, C_i _P3) were oriented towards 2025, whereas some traits measured earlier in the season (e.g., Pot_P1–P3, A_P3) loaded more in the direction of 2024. This pattern indicates that inter-annual differences in climatic conditions and tree status left a strong imprint on the multivariate physiological response, and hence, the campaign level exerted a primary influence on the overall intensity of physiological activity.

In contrast, RDA2 was dominated by Ψ_{Stem} throughout the phenological stages (Pot_P1, Pot_P2, and Pot_P3), and effectively separated irrigation strategies, highlighting water availability as a robust determinant of plant water status irrespective of year-to-year variability. The cultivar effects were also expressed along this second axis, with cv. Lauranne clearly positioned opposite to the remaining cultivars, suggesting a distinct water-use strategy and a stronger sensitivity to plant water status. These findings evidence a hierarchical control of almond physiology, with interannual climatic variability defining the physiological envelope, irrigation regulating internal water status, and cultivar modulating functional responses within these constraints. Also, this fact confirms that each cultivar follows a characteristic eco-physiological strategy when integrated over the three monitored phenological periods.

Conversely, soil-management systems produced only small shifts in ordination space. The centroids for BS and CC were located near the centre and only slightly separated, with no clear alignment of any physiological vector towards one irrigation regime. This agrees with the variance partitioning results, where cultivar and year explained most of the constrained variation, while irrigation and soil-management system contributed only a minor fraction.

P1, vegetative growth; P2, kernel filling; P3, post-harvest stage. Pot corresponds to stem-water potential

These RDA results were fully consistent with the patterns observed in the previous analyses and reinforce the integrative interpretation of the present experiment. The high proportion of physiological variance explained by the

model confirms that the combined effects of year and genotype, and to a lesser extent irrigation regime and soil-management system, adequately capture the main determinants of almond eco-physiological functioning. The dominance of RDA1 is in agreement with the strong interannual signal detected in the period-specific PCA and correlation analyses, where core physiological relationships remained stable, while their magnitude and expression varied between seasons in response to environmental conditions.

Likewise, the relevance of RDA2 was consistent with the cultivar separation observed in the PCA, particularly during the kernel-filling period, confirming that cultivars follow distinct eco-physiological strategies that are maintained throughout the growing cycle and seasons. In contrast, the relatively small contribution of RDI and soil-management systems to the multivariate space explains the strong overlap among treatments observed both in the PCA and in productive means, reinforcing the conclusion that these practices act as secondary modulators within an inherently stable physiological system. Overall, the convergence of correlation analyses, PCA and RDA demonstrates that almond production systems are dominated by a robust functional core, defined by the coordination of gas-exchange processes and regulated primarily by genotype and phenology. This multiscale coherence provides a solid basis for interpreting the absence of negative productive effects under moderate deficit irrigation and cover cropping, and supports the concept of high eco-physiological resilience of almond orchards under sustainability-oriented management strategies.

4. Conclusions

This study provides an integrated eco-physiological and agronomic assessment of almond response to regulated deficit irrigation and soil-management systems for different cultivars and seasons under Mediterranean environment.

Throughout monitored phenological stages and years, a stable functional core defined by the tight coordination among stomatal conductance, transpiration, and net photosynthesis was consistently preserved. This conservative coordination underpinned carbon assimilation and water-use regulation, even under moderate water deficit, while water-status-related relationships exhibited greater plasticity, allowing flexible adjustment to interannual climatic variability and seasonal demand. Kernel filling emerged as the key phenological window in which physiological activity was most strongly linked to final yield, confirming the central role of mid-season gas exchange in determining productive outcomes.

The almond cultivar and phenological stage were the dominant drivers of physiological variability, whereas irrigation regime and soil-management systems exerted only secondary, modulatory effects. In addition, the moderate RDI and the presence of a winter cover crop did not disrupt cultivar-specific physiological strategies nor alter the overall structure of the multivariate physiological space. As response, these management practices did not compromise kernel yield, unit weight or kernel-to-shell ratio, evidencing a high level of agronomic robustness. Also, the genotypic differences in stomatal efficiency further clarified contrasting water-use strategies among cultivars. The cvs. Guara and Lauranne showed higher stomatal efficiency and a more conservative regulation, achieving substantial carbon assimilation at lower stomatal conductance, whereas cvs. Marta and Marcona exhibited more opportunistic behaviour, maintaining higher gas exchange at the cost of greater water loss. Therefore, these intrinsic differences provide a physiological basis for cultivar-specific adaptation to deficit irrigation strategies. In conclusion, our findings demonstrate that almond production systems display strong functional resilience under moderate water limitation and conservation-oriented soil-management system, considering the significant implications of cover crops for soil health. That is, from a practical perspective, the combination of RDI with cover crops constitutes a viable and sustainable strategy for Mediterranean almond orchards, provided that cultivar selection is aligned with the intended water-management goals.

Declarations

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Author Contribution

I.F.G.-T. conceived and designed the study. I.F.G.-T., A.C.-P., J.F.H.-G., J.C.C.-G. and F.J.A.-N. conducted the field experiments and collected the data. I.F.G.-T. performed the statistical analyses and interpreted the results. I.F.G.-T. wrote the main manuscript text. A.C.-P. prepared all tables and figures. A.E.R.-C. and V.H.D.-Z. contributed to data interpretation and critically revised the manuscript. A.E.R.-C. and V.H.D.-Z. supervised the research. All authors reviewed and approved the final version of the manuscript.

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Figures



Figure 1

Correlation panels among the main physiological variables (A_n , g_{sw} , C_i , E , and Y_{Stem}) for each phenological period and monitored seasons

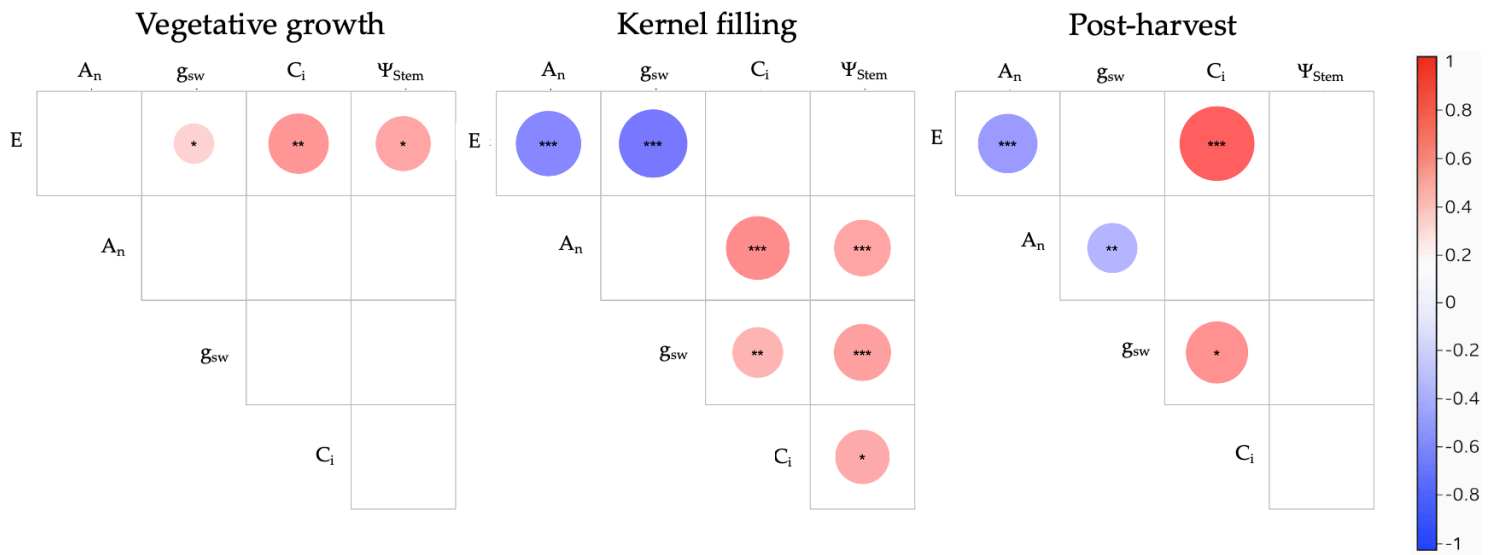


Figure 2

Interannual changes in physiological correlations ($\Delta r = 2025 - 2024$) throughout phenological periods.

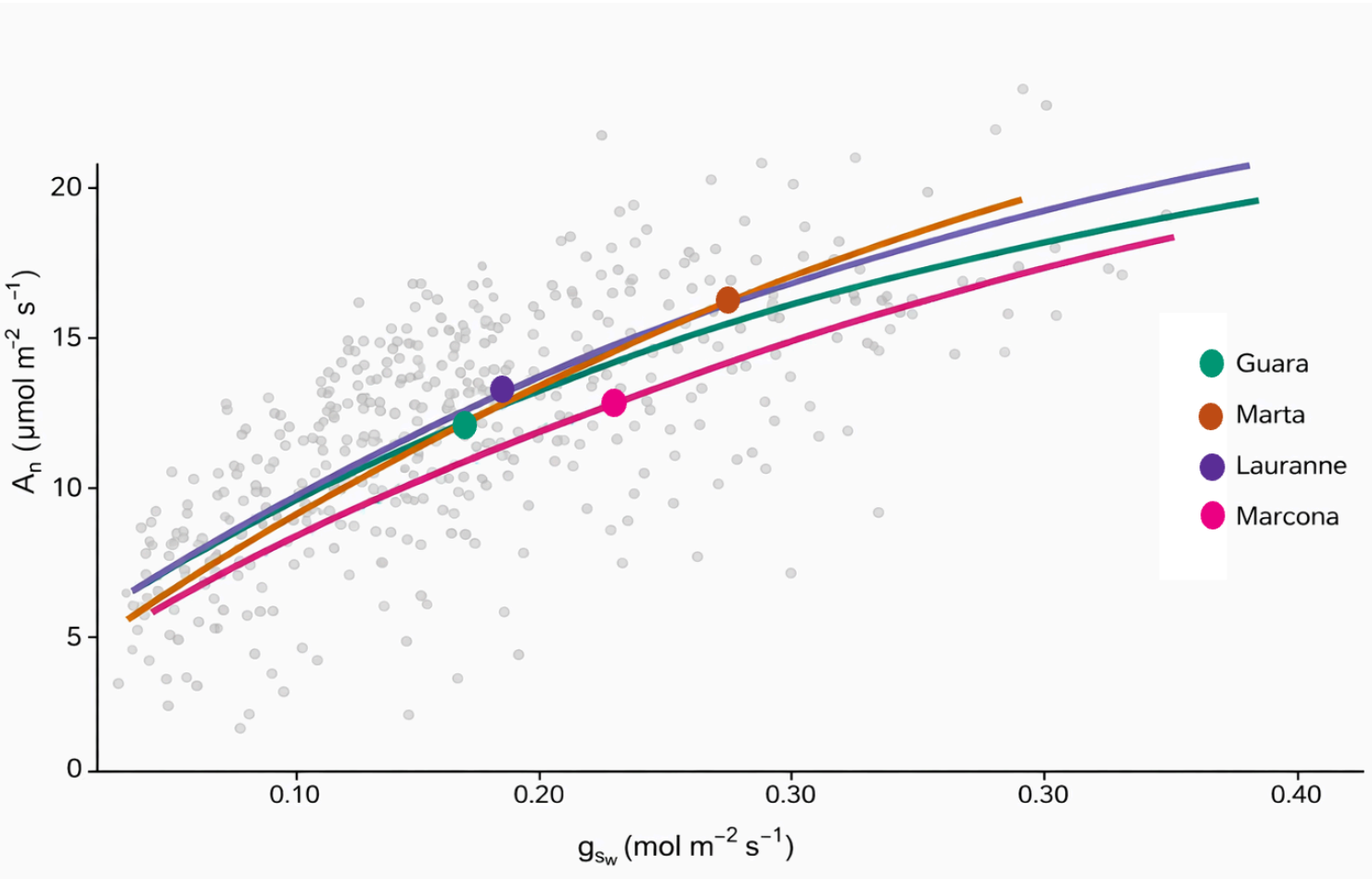


Figure 3

Varietal response of almond photosynthesis to stomatal conductance (A_n – g_{sw}) fitted with an exponential model and 50% A_n thresholds.

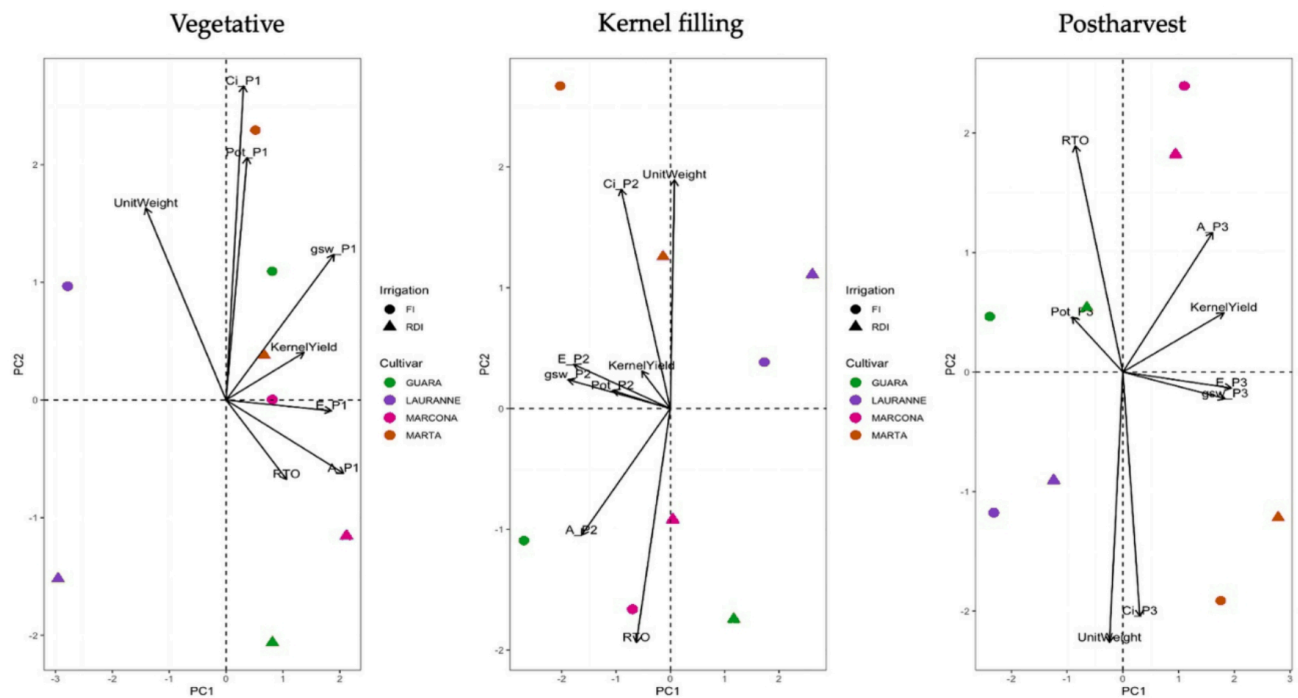


Figure 4

Principal component analysis (PCA) of physiological variables and production traits over studied phenological periods (P1–P3).

P1, vegetative growth; P2, kernel filling; P3, post-harvest stage. Pot corresponds to stem-water potential

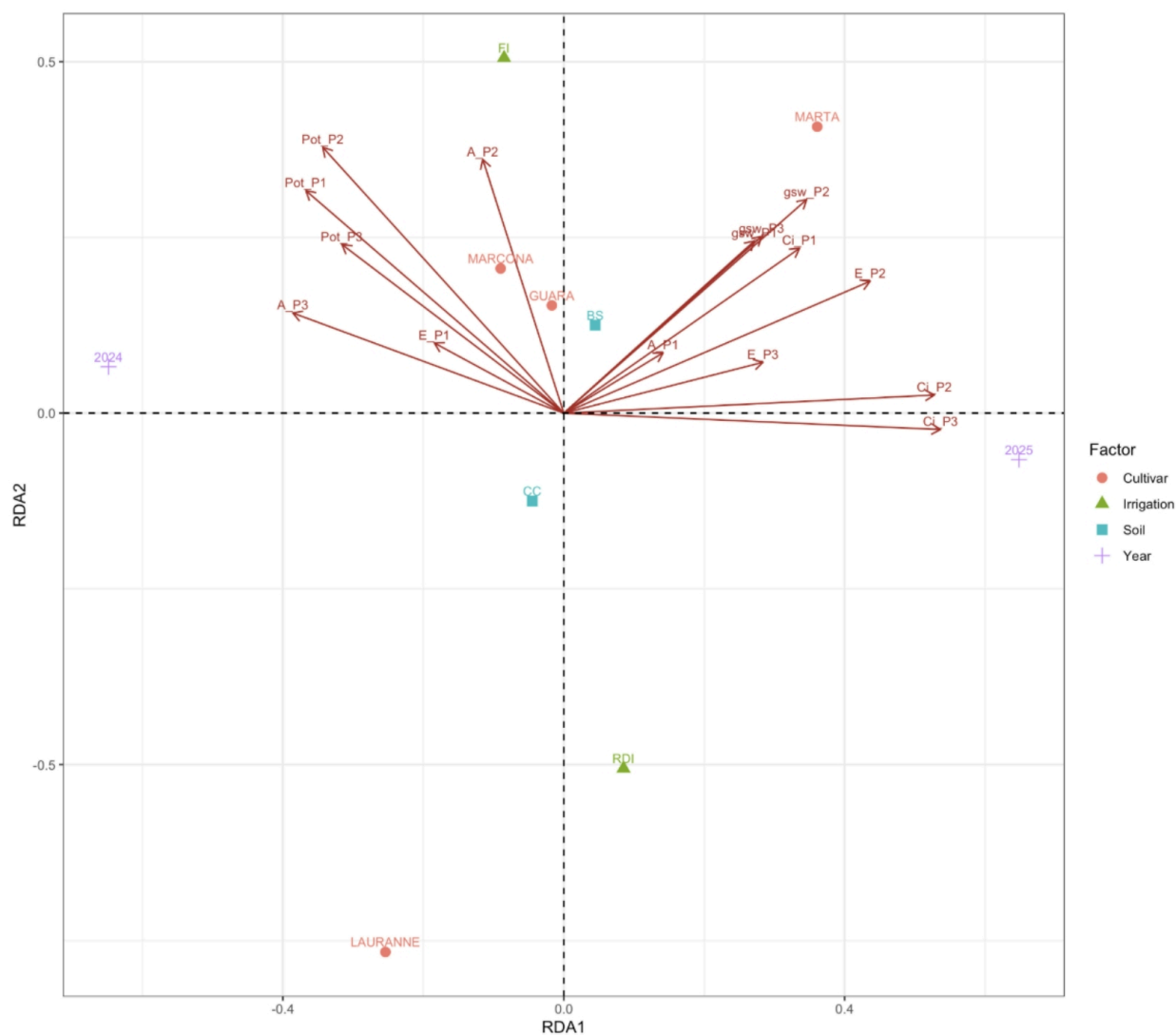


Figure 5

Redundancy Analysis (RDA) of physiological traits constrained by year, irrigation, soil-management system, and cultivar.

P1, vegetative growth; P2, kernel filling; P3, post-harvest stage. Pot corresponds to stem-water potential

Supplementary Files

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