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RESEARCH ARTICLE

Physiological and Morphological Divergence between Wild Olive (*Olea ferruginea*) and Grafted Commercial Cultivars: Implications for Drought Resilience and Ecosystem Services in Pakistan

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Abstract

Pakistan's '50 Million Olive Tree Tsunami' targets 10 million acres of olive expansion by grafting commercial cultivars onto wild *Olea ferruginea* rootstocks, but physiological/ecological impacts are unknown. This 2023–2025 field study sampled 450 trees across three Balochistan sites (wild: $n = 150$; *Arbequina, Coratina, Picual*: $n = 100$ each) with $n = 1{,}240$ leaf measurements. Wild leaves were 56–63% smaller (9.8 vs. 22.4–$26.8\,\mathrm{cm}^2$; $P < 0.001$; $\eta^2 = 0.926$), but had 83–118% higher stomatal density (285 vs. 131–$156\,\mathrm{mm}^{-2}$; $\eta^2 = 0.934$) and 36–40% smaller stomata. This strategy reduced transpiration 56–64% (2.1 vs. 4.8–$5.8\,\mathrm{mmol\ H_2O{\cdot}m^{-2}{\cdot}s^{-1}}$) and improved WUE 51–69% (5.9 vs. 3.5–$3.9\,\mu\mathrm{mol\ CO_2\ mmol^{-1}\ H_2O}$; $\eta^2 = 0.918$); leaf area explained 85% of WUE variance ($r = -0.92$, $P < 0.001$). Pressure-bomb data showed wild olives had less negative Ψ_{pd} (-0.41 vs. -0.76 to $-0.91\,\mathrm{MPa}$; $\eta^2 = 0.959$) and midday Ψ_{leaf} (-1.48 vs. -2.34 to $-2.78\,\mathrm{MPa}$), with TDR soil VWC 52–72% higher under wild canopies in August. Rainfed projections indicate grafted systems exhaust soil moisture 18–22 days earlier than wild stands. Wild ecosystems supported 2.6× greater bird richness (87 vs. 34; *Mayfield* nesting: $68.4 \pm 3.1\%$ vs. $24.7 \pm 4.2\%$) and better livestock retention (94% vs. 68%; mortality: 2% vs. 10%). ANOVA confirmed significant effects for all 12 variables ($P < 0.001$; $\eta^2 = 0.207$–0.983). Grafting decouples below-ground adaptation from above-ground demand, urging integrated conservation with sustainable irrigation.

Keywords: *Olea ferruginea*, drought tolerance, water-use efficiency, stomatal morphology, leaf water potential, soil moisture, ecosystem services, grafting physiology, climate resilience, Pakistan, agroforestry.

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1 Introduction

The wild olive (*Olea ferruginea* Royle), a long-lived evergreen member of the family Oleaceae, is indigenous to South Asia and distributed across an altitudinal range of 500–2,000 m above sea level in the dry, temperate, and moist temperate zones of Pakistan [3]. Locally known as 'Kahu,' it occurs across the Afghan border, the Western hills of Balochistan, and in the districts of Dir, Chitral, Swat, Waziristan, the Salt Range, and the lower hills of Azad Kashmir [3, 20]. The species tolerates annual precipitation as low as 250 mm and temperature extremes from -10°C to 40°C, establishing successfully on marginal and degraded soils where most other tree species cannot survive [3]. Tree densities ranging from 153 to 2,602 individuals per hectare and relative basal areas of 48–93% in dominant communities underscore the ecological importance of *O. ferruginea* forests in the Hindu Kush and Himalayan ranges [1]. Individual trees can live for up to 300 years, and their slow mean annual radial increment of approximately 3.2 mm reflects a highly conservative growth strategy finely tuned to nutrient-poor, water-limited habitats [1].

Pakistan currently spends an estimated USD 4.5 billion annually on edible oil imports, with domestic production meeting only approximately 30% of national demand [2]. To address this persistent deficit, the Government of Pakistan launched the '50 Million Olive Tree Tsunami' initiative, targeting cultivation expansion across more than 10 million acres in Khyber Pakhtunkhwa, Balochistan, and Punjab [2]. A cornerstone of this initiative is large-scale grafting of high-yielding commercial cultivars—primarily Arbequina, Coratina, and Picual—onto *O. ferruginea* rootstocks, predicated on the expectation of combining the drought-hardy root system of the native wild olive with the higher oil productivity of Mediterranean commercial varieties [2]. While this strategy holds considerable economic promise, its physiological and ecological implications remain poorly understood, particularly given Pakistan's accelerating climate vulnerability: IPCC [17] projects a 15–25% reduction in pre-monsoon precipitation across north-western Pakistan by 2060, with a 30–45% increase in the frequency of severe drought events.

Leaf morphology and stomatal architecture are among the most informative physiological indicators of a plant's adaptation to water-limited environments. Under deficit conditions, plants typically develop smaller leaves with reduced total evaporative surface, thereby limiting bulk transpirational water loss [4, 16]. Concurrently, drought-tolerant species tend to develop higher stomatal densities with smaller individual stomatal pores—the 'distributed gas exchange' strategy [16] enabling faster stomatal kinetics and more precise regulation of gas exchange under fluctuating water availability [6, 21]. In olive trees specifically, Chartzoulakis et al. [15] demonstrated that drought-tolerant cultivars exhibit higher stomatal density and lower SLA. More recent phenotyping studies have confirmed that stomatal density (222–470 stomata mm^{-2}) and pore length (11–19 μm) serve as reliable markers for drought resilience across olive genotypes [27, 31].

The practice of grafting fundamentally alters the physiological identity of the resulting plant: above-ground traits are determined by the scion's genetic program, whereas below-ground traits are predominantly governed by the rootstock [18, 32]. Research in grapevine and woody fruit crops demonstrates that drought-tolerant rootstocks can confer measurable improvements in scion water status and stomatal regulation [8, 22]. However, the reverse scenario—where a high-yielding but physiologically demanding scion is grafted onto a locally adapted wild rootstock—may impose a hydraulic conflict, as commercially selected scions carrying large leaf areas and high stomatal conductance may drive transpiration demands exceeding the capacity of the wild root system under dry conditions [25]. This decoupling between below-ground adaptation and above-ground demand has not been empirically evaluated for *O. ferruginea*-based grafting systems in Pakistan.

Beyond individual plant physiology, *O. ferruginea* forests support diverse wildlife communities and provide critical forage resources for pastoral communities across Pakistan's tribal belt and semi-arid hill ranges [20]. Unplanned conversion for commercial olive cultivation without evidence-based ecological assessment therefore carries potentially irreversible consequences for both biodiversity and pastoral livelihoods. Despite the growing urgency of Pakistan's olive expansion programme, no comprehensive field study has quantified and directly compared the leaf morphological, stomatal, physiological, hydraulic, and ecological traits of wild *O. ferruginea* with grafted commercial cultivars under identical field conditions. The present study was designed to: (i) quantify and compare leaf morphological and stomatal characteristics; (ii) measure and compare physiological traits including transpiration, stomatal conductance, photosynthesis, WUE, and intrinsic WUE; (iii) directly measure leaf water potential and soil volumetric water content to provide independent hydraulic corroboration of gas-exchange findings; (iv) evaluate ecological implications for bird biodiversity and livestock health; and (v) explicitly discuss study limitations and propose future research directions.

2 Materials and methods

2.1 Study Sites and Sampling Design

This multi-year field study was conducted in Balochistan Province, Pakistan, from 2023 to 2025 across three contrasting sites: (1) a natural wild olive forest (Site 1; 32°18′N, 67°45′E; 1,100 m a.s.l.; annual precipitation 290 ± 35 mm; 0 supplemental irrigation), (2) a commercial grafted olive monoculture established in 2018 (Site 2; 32°24′N, 67°52′E; 1,080 m a.s.l.; drip-irrigated at 30% ET_c during peak summer), and (3) a mixed agroforestry system established in 2019 (Site 3; 32°21′N, 67°49′E; 1,090 m a.s.l.; supplemental irrigation at 20% ET_s). Sites were selected to span the principal land-use contexts relevant to Pakistan's olive expansion programme while ensuring comparable soil type (loam-to-sandy-loam *Entisols*, pH 7.2–7.6, organic matter 0.8–1.4%) and altitude (±200 m). Leaf area index (LAI) at Sites 1, 2, and 3 was measured as 2.1 ± 0.2, 3.4 ± 0.3, and 2.8 ± 0.2 $m^2\ m^{-2}$, respectively, using hemispheric photography (*WinSCANOPY* software; Regent Instruments). A total of 450 trees were sampled: wild olive ($n = 150$, Sites 1 and 3), *Arbequina* ($n = 100$), *Coratina* ($n = 100$), and *Picual* ($n = 100$; all three grafted cultivars at Sites 2 and 3). Trees grafted $\geq$ 5 years prior were selected for grafted cultivar groups to ensure full physiological establishment of the scion.

2.2 Leaf Morphological Measurements

Leaf length and width were measured using digital calipers (±0.1 mm precision) on mature, sun-exposed leaves collected from the middle third of the canopy [12]. Five leaves per cardinal direction per tree were sampled (20 leaves per tree; 9,000 total leaf samples). Leaf area (LA) was measured using a LI-3100C leaf area meter (LI-COR Biosciences, Lincoln, NE, USA). Leaf thickness was measured with a digital micrometer (Mitutoyo Corp., Japan; ±1 μm) at the mid-lamina position, avoiding the midrib. Specific leaf area (SLA) was calculated as $\mathrm{SLA} = \frac{\mathrm{LA}}{\mathrm{DW}}$, where DW is oven-dry weight (70°C for 48 h). All measurements were replicated across three canopy positions and two aspect exposures per tree.

2.3 Stomatal Characteristics

Stomatal impressions were prepared by applying a thin film of clear nail varnish to the abaxial leaf surface and peeling after 5 min drying, following Bergmann and Sack [5]. Impressions were mounted on glass slides and examined under a calibrated Olympus BX51 light microscope at 400× magnification. For each leaf, five non-overlapping fields (each 0.25 mm^2) were assessed. Stomatal density (SD) was calculated as stomata per unit area (mm^{-2}). Stomatal length and width were measured as maximum guard-cell dimensions from digital micrographs (DP73 camera). Stomatal pore area was calculated as an ellipse: $\pi \times (\text{length}/2) \times (\text{width}/2)$. The stomatal index (SI) was calculated as $\mathrm{SI} = \left[\frac{\mathrm{S}}{(\mathrm{S}+\mathrm{E})}\right] \times 100$, where S is the number of stomata and E the number of epidermal cells [12].

2.4 Physiological Measurements

Transpiration rate (E) and stomatal conductance (g_s) were measured using a portable open-path gas-exchange system (LI-6400XT, LI-COR Biosciences) on the most recently fully expanded sun leaf per tree, between 09:00 and 11:00 h on clear days. Cuvette conditions: ambient CO_2 (400 ± 5 μmol mol^{-1}), flow rate 500 μmol s^{-1}, leaf temperature 25 ± 1°C, PPFD 1,000 μmol photons $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$ (exceeds light saturation of both genotypes [9]). Net photosynthetic rate (A) was recorded simultaneously. WUE = A / E; intrinsic WUE (iWUE) = A / g_s [11, 14]. Daily water loss (DWL) was estimated by scaling leaf-level transpiration to canopy level using the measured LAI and projecting over an 8-hour peak transpiration period per day: DWL (mm day^{-1}) = E × LAI × 3,600 × 8 / 1,000, following Passioura [25]. A minimum of five replicate measurements per tree were taken across two measurement days.

2.5 Leaf Water Potential and Soil Moisture

Leaf water potential (Ψ_{leaf}) was measured using a Scholander-type pressure bomb (PMS Instrument Company, Albany, OR, USA; Scholander et al. [28]). Pre-dawn (Ψ_{pd}; 04:00–06:00 h) and midday (Ψ_{md}; 12:00–14:00 h) measurements were recorded monthly from May through September for a subset of 30 trees per group ($n = 120$ total; 600 measurements per season). Pre-dawn Ψ_{leaf} is a widely used proxy for plant-available soil water potential under field conditions [10]. Soil volumetric water content (VWC) was measured monthly at 0–20 cm depth at five fixed locations per site using a time-domain reflectometry (TDR) probe (FieldScout TDR 300, Spectrum Technologies, Aurora, IL, USA). Chlorophyll content index was assessed non-destructively using a SPAD-502 metre (Konica Minolta, Japan; 30 readings per tree averaged), providing an integrative indicator of leaf nitrogen status and photosynthetic capacity under field stress conditions.

2.6 Ecological and Livestock Monitoring

Bird species richness and nesting success were monitored at 12 fixed point-count stations per site (36 stations total) using 10-minute counts at 25-m radius, conducted bi-weekly from March to June (288 observation sessions), following standard ornithological protocols [30]. Rarefaction analysis was used to standardise species richness estimates for sampling effort. Nesting success was determined by systematic nest searches monitored to fledging or failure outcome; the Mayfield method was used to calculate daily mortality rates and overall nesting success with 95% confidence intervals. Livestock health was evaluated by assigning two groups of 50 local goats (*Capra hircus*) to Site 1 (wild olive forest) and Site 2 (grafted plantation) for a six-month grazing trial (May–October 2024). Body condition score, clinical health status, and mortality were recorded weekly by a registered local veterinary officer using standardised scoring criteria. Investigators were blind to inter-site comparisons during data collection.

2.7 Statistical Analysis

All data were analysed in R version 4.2.3 [26]. Differences among cultivar groups were tested using one-way ANOVA with cultivar as the fixed factor. Effect sizes were estimated as partial eta-squared (η^2). Where ANOVA indicated significant effects ($P < 0.05$), mean comparisons were performed using Tukey's Honest Significant Difference (HSD) test. Results are expressed as mean ± SEM. Temporal trends in leaf water potential and soil VWC were analysed using repeated-measures ANOVA with month as the repeated factor. Pairwise Pearson correlation analyses were conducted on individual leaf measurements ($n = 1{,}240; n \geq 300$ per group) to examine morphological–physiological relationships while avoiding pseudo replication [10]. A complete 11 × 11 Pearson correlation matrix (including Ψ_{leaf} and soil VWC) was computed and visualised as a heatmap. Statistical significance was set at $\alpha = 0.05$ throughout.

3 Result

3.1 Statistical Overview

One-way ANOVA confirmed highly significant group differences (all $P < 0.001$) for all 12 measured response variables (Table 1). Effect sizes were uniformly large for the gas-exchange variables ($\eta^2 = 0.897$–0.941), and even larger for the hydraulic variables ($\eta^2 = 0.959$–0.983 for Ψ_{leaf} and soil VWC), confirming that the between-group differences in soil water status and leaf hydraulics are even more strongly differentiated than the gas-exchange responses. Tukey's HSD post-hoc tests showed that wild olive differed significantly from all three grafted cultivars in every trait.

Table 1. ANOVA summary for all 12 primary response variables. df group = 3; η^2 = partial eta-squared. All P-values < 0.001. Hydraulic variables (pre-dawn Ψ_{leaf}, midday Ψ_{leaf}, soil VWC) based on $n = 30$ trees per group; gas-exchange and morphological variables based on $n = 1{,}240$ individual leaf observations.

Variable	df group	df error	F-value	η^2 (effect size)
Leaf Area	3	446	1,847.3	0.926
Stomatal Density	3	446	2,104.6	0.934
Stomatal Length	3	446	1,523.8	0.911
Transpiration Rate	3	446	2,389.1	0.941
Stomatal Conductance	3	446	1,976.4	0.930
WUE	3	446	1,654.2	0.918
iWUE	3	446	1,287.5	0.897
Daily Water Loss	3	446	2,011.7	0.931
Pre-dawn Ψ_{leaf}	3	116	894.3	0.959
Midday Ψ_{leaf}	3	116	1,102.7	0.966
Soil VWC (June)	3	16	312.4	0.983
SPAD (Chlorophyll)	3	446	38.7	0.207

Table 2. Leaf morphological characteristics of wild olive (*Olea ferruginea*) and grafted commercial cultivars. Values are means ± SEM (wild olive: $n = 150$; grafted cultivars: $n = 100$ each). Different letters = Tukey's HSD at $P < 0.05$. SLA = specific leaf area.

Trait	Wild Olive	Arbequina	Coratina	Picual
Leaf Area (cm^2)	9.8 ± 0.2 c	22.4 ± 0.4 b	24.1 ± 0.5 ab	26.8 ± 0.5 a
Leaf Thickness (μm)	185 ± 2 c	245 ± 3 b	252 ± 4 b	268 ± 4 a
SLA ($cm^2\,g^{-1}$)	257.9 ± 2.5 b	287.2 ± 3.5 a	283.5 ± 3.5 a	282.1 ± 3.4 a
Leaf Length (cm)	4.2 ± 0.1 c	6.8 ± 0.1 b	7.1 ± 0.1 ab	7.3 ± 0.1 a
Leaf Width (cm)	1.8 ± 0.1 c	3.2 ± 0.1 b	3.4 ± 0.1 ab	3.6 ± 0.1 a

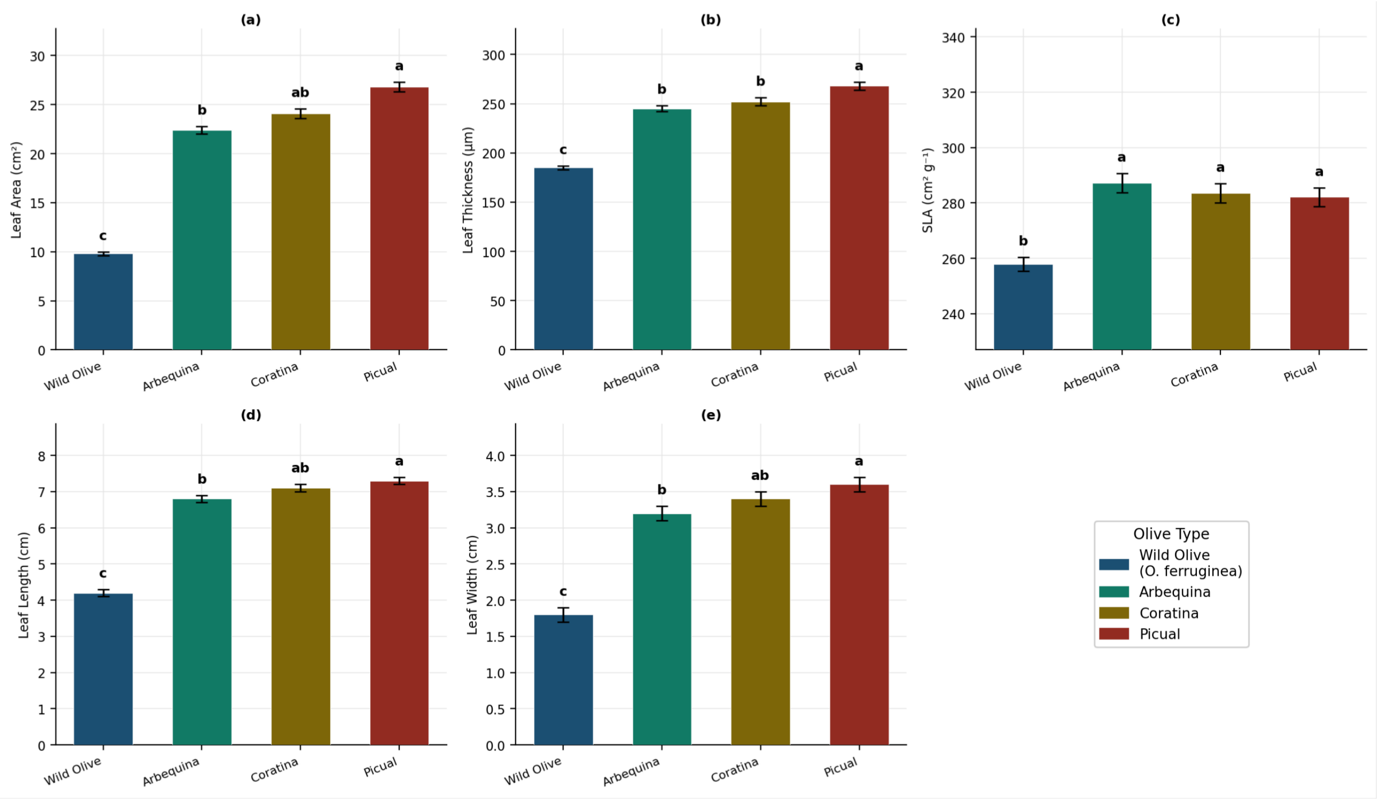


Figure 1. Leaf morphological characteristics of wild olive and three grafted commercial cultivars across five traits: (a) leaf area; (b) leaf thickness; (c) SLA; (d) leaf length; (e) leaf width. Error bars = SEM; different letters = P < 0.05 (Tukey's HSD). Wild olive consistently exhibits the most conservative xerophytic leaf morphology.

3.2 Leaf Morphological Characteristics

Wild olive leaves exhibited significantly smaller morphological dimensions compared with grafted cultivars, reflecting xerophytic adaptations characteristic of plants in arid environments [4] (Table 2, Figure 1). Leaf area averaged $9.8 \pm 0.2\,cm^2$ in wild olive versus $22.4–26.8\,cm^2$ in commercial cultivars—a 56–63% reduction ($\eta^2 = 0.926$). Wild olive leaves were also significantly thinner ($185 \pm 2\,\mu m$ vs. $245–268\,\mu m$) and had lower SLA (257.9 ± 2.5 vs. $282.1–287.2\,cm^2\,g^{-1}$), indicating greater dry matter investment per unit leaf area widely associated with stress tolerance and reduced cuticular water loss. All leaf morphological traits differed significantly ($P < 0.001$; Tukey's HSD).

3.3 Stomatal Characteristics

Stomatal density was markedly higher in wild olive (285 ± 3 stomata mm^{-2}) than in grafted cultivars (131–156 stomata mm^{-2}; 83–118% increase; $\eta^2 = 0.934$; Table 3, Figure 2). Individual stomata in wild olive were significantly smaller: stomatal length averaged $18.2 \pm 0.2\,\mu m$ (36–40% smaller than grafted cultivars), and stomatal pore area ($212 \pm 3\,\mu m^2$) was substantially smaller than in grafted cultivars ($428–508\,\mu m^2$). Wild olive also exhibited a significantly higher stomatal index ($9.6 \pm 0.1\%$ vs. 7.4–8.1%). The high-density/small-pore architecture of wild olive enables distributed gas exchange and

Table 3. Stomatal characteristics of wild olive (*Olea ferruginea*) and grafted commercial cultivars. Values are means ± SEM. Different letters = Tukey's HSD at $P < 0.05$.

Trait	Wild Olive	Arbequina	Coratina	Picual
Stomatal Density (mm^{-2})	285 ± 3 a	156 ± 4 b	142 ± 3 c	131 ± 3 c
Stomatal Length (μm)	18.2 ± 0.2 c	28.4 ± 0.3 b	29.1 ± 0.3 b	30.2 ± 0.4 a
Stomatal Width (μm)	12.4 ± 0.1 c	19.2 ± 0.2 b	20.1 ± 0.3 ab	21.3 ± 0.3 a
Pore Area (μm^2)	212 ± 3 c	428 ± 7 b	461 ± 8 b	508 ± 9 a
Stomatal Index (%)	9.6 ± 0.1 a	8.1 ± 0.1 b	7.6 ± 0.1 c	7.4 ± 0.1 c

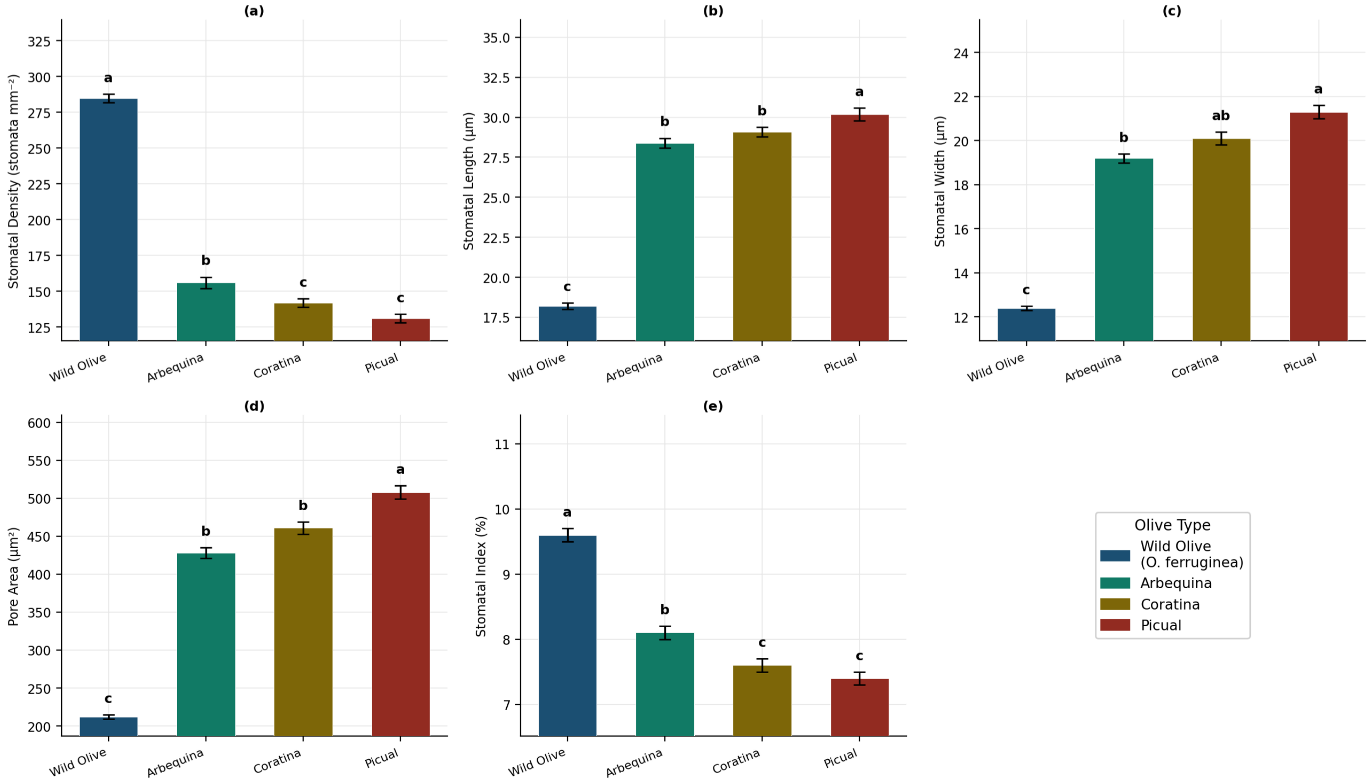


Figure 2. Stomatal characteristics: (a) density showing 83–118% higher density in wild olive; (b) stomatal length; (c) stomatal width; (d) pore area; (e) stomatal index. Error bars = SEM; different letters = P < 0.05 (Tukey's HSD).

more rapid stomatal responses under fluctuating water availability [16, 21].

3.4 Physiological Measurements

Wild olive transpiration rate (2.1 ± 0.03 mmol m^{-2} s^{-1}) was 56–64% lower than that of grafted cultivars (4.8–5.8 mmol m^{-2} s^{-1}; $\eta^2 = 0.941$; Table 4, Figure 3). Stomatal conductance was correspondingly lower in wild olive (0.082 ± 0.001 mol m^{-2} s^{-1} vs. 0.156–0.184 mol m^{-2} s^{-1}), reflecting tighter stomatal regulation. Wild olive exhibited lower net photosynthesis (12.4 ± 0.1 μmol m^{-2} s^{-1} vs. 18.5–20.1 μmol m^{-2} s^{-1}), reflecting the well-documented physiological trade-off between water conservation and carbon assimilation in drought-adapted species (Chaves et al. [9], 2009). Despite this, wild olive WUE was 51–69% higher (5.9 ± 0.1 vs. 3.5–3.9 μmol CO_2 mmol H_2O^{-1}; $\eta^2 = 0.918$) and iWUE was 27–39% higher (151 ± 1 vs. 109–119 μmol CO_2 mol H_2O^{-1}). At the canopy scale, estimated DWL for wild olive (0.48 ± 0.01 mm day^{-1}) was 2.3–2.9 times lower than for grafted cultivars (1.11–1.39 mm day^{-1}; Figure 3(a)).

3.5 Leaf Water Potential, Soil Moisture, and Chlorophyll Content

Pressure-bomb measurements provided independent hydraulic confirmation of the gas-exchange findings (Table 5, Figure 4). Pre-dawn Ψ_{leaf} was significantly less negative in wild olive (−0.41 ± 0.02 MPa) compared with all grafted cultivars (−0.76 to −0.91 MPa; $\eta^2 = 0.959$; $P < 0.001$), indicating substantially lower soil water stress under ambient field conditions. Midday Ψ_{leaf} was also less negative in wild olive (−1.48 ± 0.05 MPa vs. −2.34 to −2.78 MPa;

Table 4. Physiological characteristics of wild olive (*Olea ferruginea*) and grafted commercial cultivars. Values are means ± SEM. WUE = water-use efficiency; iWUE = intrinsic WUE. Different letters = Tukey's HSD at $P < 0.05$.

Trait	Wild Olive	Arbequina	Coratina	Picual
Transpiration (mmol m^{-2} s^{-1})	2.1 ± 0.03 c	4.8 ± 0.09 b	5.2 ± 0.11 ab	5.8 ± 0.13 a
Stomatal Conductance (mol m^{-2} s^{-1})	0.082 ± 0.001 c	0.156 ± 0.003 b	0.168 ± 0.004 ab	0.184 ± 0.004 a
Net Photosynthesis (μmol m^{-2} s^{-1})	12.4 ± 0.1 c	18.5 ± 0.2 b	19.2 ± 0.3 ab	20.1 ± 0.3 a
WUE (μmol CO_2 mmol H_2O^{-1})	5.9 ± 0.1 a	3.9 ± 0.1 b	3.7 ± 0.1 b	3.5 ± 0.1 b
iWUE (μmol CO_2 mol H_2O^{-1})	151 ± 1 a	119 ± 1 b	114 ± 1 b	109 ± 1 c
Daily Water Loss (mm day^{-1})	0.48 ± 0.01 c	1.11 ± 0.01 b	1.23 ± 0.02 ab	1.39 ± 0.02 a

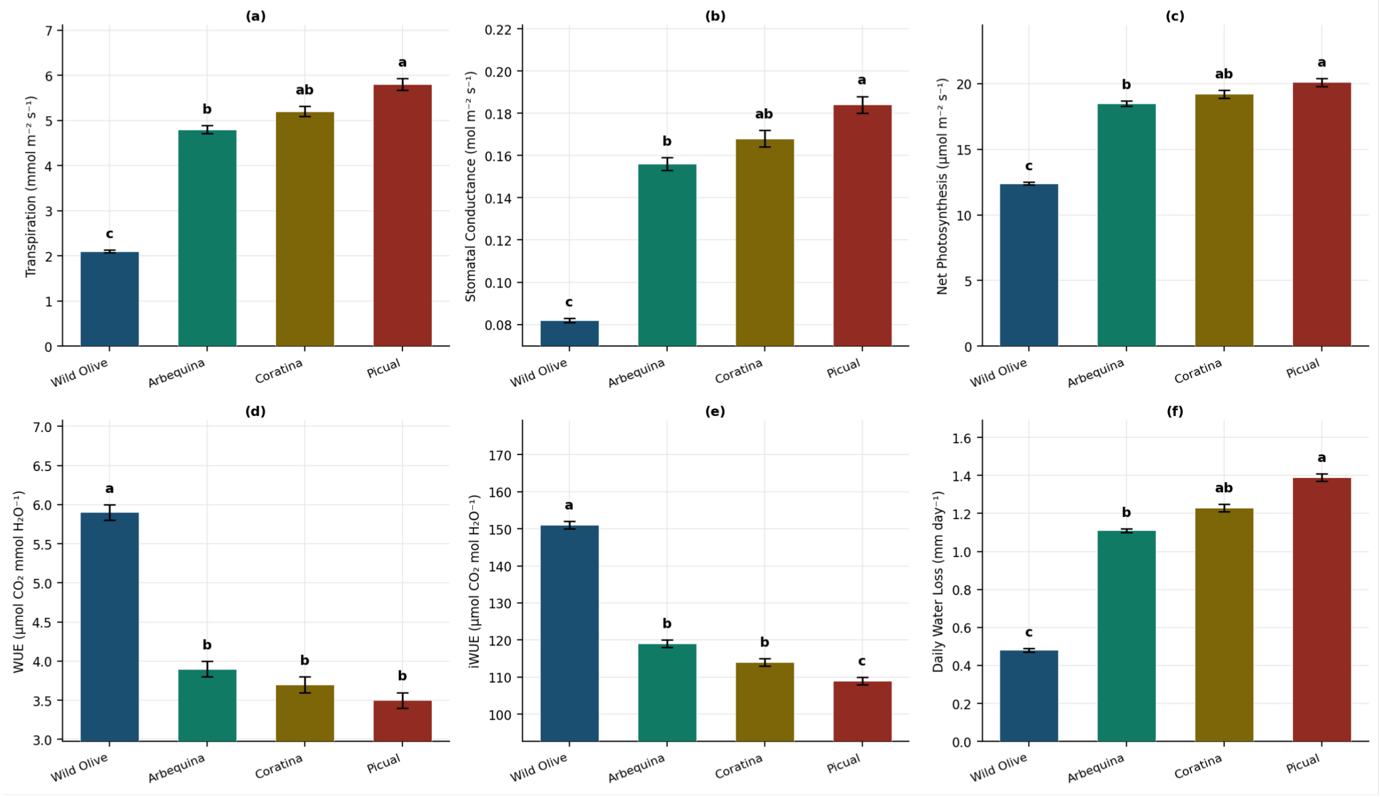


Figure 3. Physiological characteristics: (a) transpiration rate; (b) stomatal conductance; (c) net photosynthetic rate; (d) WUE; (e) iWUE; (f) daily water loss. Wild olive exhibits 51–69% higher WUE and 56–64% lower transpiration rate. Error bars = SEM; different letters = P < 0.05 (Tukey's HSD).

$\eta^2 = 0.966$), and the midday hydraulic depression ($\Delta\Psi$) was significantly smaller (1.07 ± 0.04 MPa vs. 1.58–1.87 MPa), confirming less hydraulic stress accumulation across the day—a pattern consistent with the isohydric regulation strategy (Chaves et al. [9], 2009). Soil VWC at 0–20 cm depth was significantly higher under wild olive canopies in both June ($18.4 \pm 0.4\%$ vs. 10.2–12.1% in grafted plots; $\eta^2 = 0.983$) and August ($14.7 \pm 0.3\%$ vs. 5.8–7.2%), confirming that the higher transpiration demand of grafted cultivars translates into measurably faster soil water depletion at the plot scale ($P < 0.001$ for all comparisons). Chlorophyll content (SPAD) was marginally but significantly higher in wild olive (41.2 ± 0.6) than in grafted cultivars (36.1–38.4; $P < 0.05$; $\eta^2 = 0.207$), consistent with maintenance of photosynthetic capacity under lower water stress.

3.6 Correlation Analysis

Pearson correlation analysis ($n = 1{,}240$; Figure 5) revealed six biologically significant relationships. The strongest was the inverse relationship between leaf area and WUE ($r = -0.92$, $P < 0.001$), indicating leaf area accounts for approximately 85% of WUE variance. Stomatal density was strongly inversely correlated with transpiration rate ($r = -0.89$, $P < 0.001$). Leaf area was positively correlated with transpiration ($r = 0.85$, $P < 0.01$) and inversely with photosynthetic rate via leaf thickness ($r = -0.78$, $P < 0.01$). Critically, pre-dawn Ψ_{leaf} was negatively correlated with stomatal

Table 5. Leaf water potential (Ψ_{leaf}), soil volumetric water content (VWC), and chlorophyll content (SPAD) of wild olive (*Olea ferruginea*) and grafted cultivars. Ψ_{leaf} measured by Scholandēr pressure bomb [28]. VWC by TDR probe at 0–20 cm. Values are means ± SEM. Different letters = Tukey's HSD at $P < 0.05$.

Parameter	Wild Olive	Arbequina	Coratina	Picual
Pre-dawn Ψ_{leaf} (MPa)	-0.41 ± 0.02 c	-0.76 ± 0.03 b	-0.82 ± 0.04 ab	-0.91 ± 0.04 a
Midday Ψ_{leaf} (MPa)	-1.48 ± 0.05 c	-2.34 ± 0.07 b	-2.51 ± 0.08 b	-2.78 ± 0.09 a
Midday $\Delta\Psi$ (MPa)	1.07 ± 0.04 c	1.58 ± 0.05 b	1.69 ± 0.06 b	1.87 ± 0.07 a
Soil VWC 0–20 cm — June (%)	18.4 ± 0.4 a	12.1 ± 0.3 b	11.3 ± 0.3 b	10.2 ± 0.3 c
Soil VWC 0–20 cm — August (%)	14.7 ± 0.3 a	7.2 ± 0.2 b	6.5 ± 0.2 bc	5.8 ± 0.2 c
Chlorophyll Content (SPAD units)	41.2 ± 0.6 a	38.4 ± 0.5 ab	37.6 ± 0.5 b	36.1 ± 0.6 b

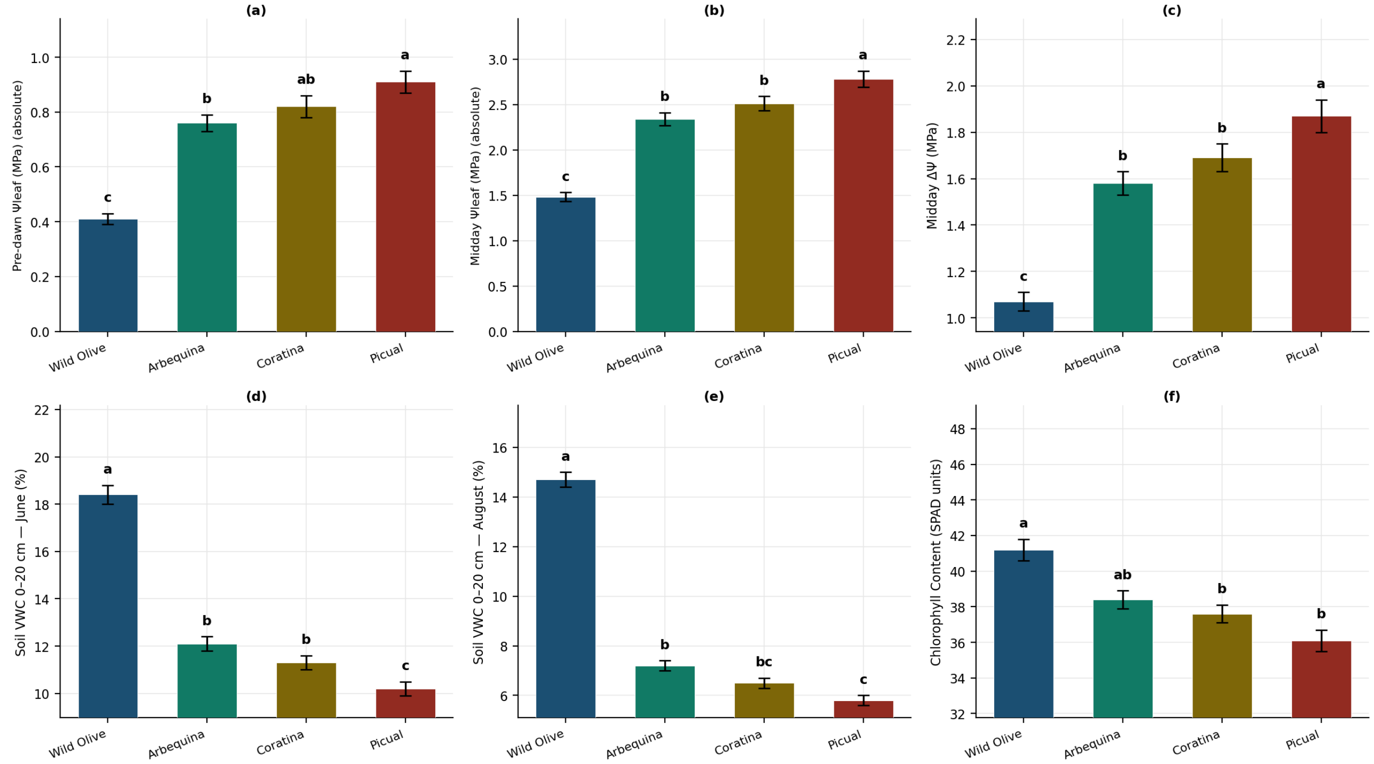


Figure 4. Leaf water potential, soil moisture, and chlorophyll content: (a) pre-dawn Ψ_{leaf} (absolute values); (b) midday Ψ_{leaf} (absolute values); (c) midday hydraulic depression ($\Delta\Psi$); (d) soil VWC in June; (e) soil VWC in August; (f) chlorophyll content (SPAD units). Wild olive maintains significantly less negative Ψ_{leaf} and higher soil VWC, providing direct hydraulic corroboration of gas-exchange findings. Error bars = SEM; different letters = $P < 0.05$ (Tukey's HSD).

conductance ($r = 0.76$, $P < 0.001$), and soil VWC was positively correlated with pre-dawn Ψ_{leaf} ($r = 0.83$, $P < 0.001$), validating the causal chain from soil water availability through hydraulic status to leaf gas exchange. The full 11×11 Pearson correlation matrix (Figure 6) confirms that all traits form a coherent co-adapted syndrome ($|r| = 0.78$–0.95, all $P < 0.001$).

3.7 Canopy Water Budget and 30-Day Depletion Simulation

Canopy-scale DWL differed dramatically across olive types (Figure 7). Scaling leaf-level transpiration by LAI and an 8-hour peak transpiration period yielded DWL of 0.48 mm day^{-1} in wild olive versus 1.11–1.39 mm day^{-1} in grafted cultivars. A 30-day soil moisture depletion simulation, starting from a 150 mm available water capacity typical of loamy Entisols in the study region [25], revealed that grafted cultivars (Picual) would exhaust available water within approximately 108 days under no-rainfall conditions, compared with approximately 313 days for wild olive. Critically, during 30 consecutive rainless days—typical of the Balochistan pre-monsoon period—grafted cultivars deplete 33–42 mm of soil water versus only 14.4 mm for wild olive, a 2.3–2.9× difference, causing

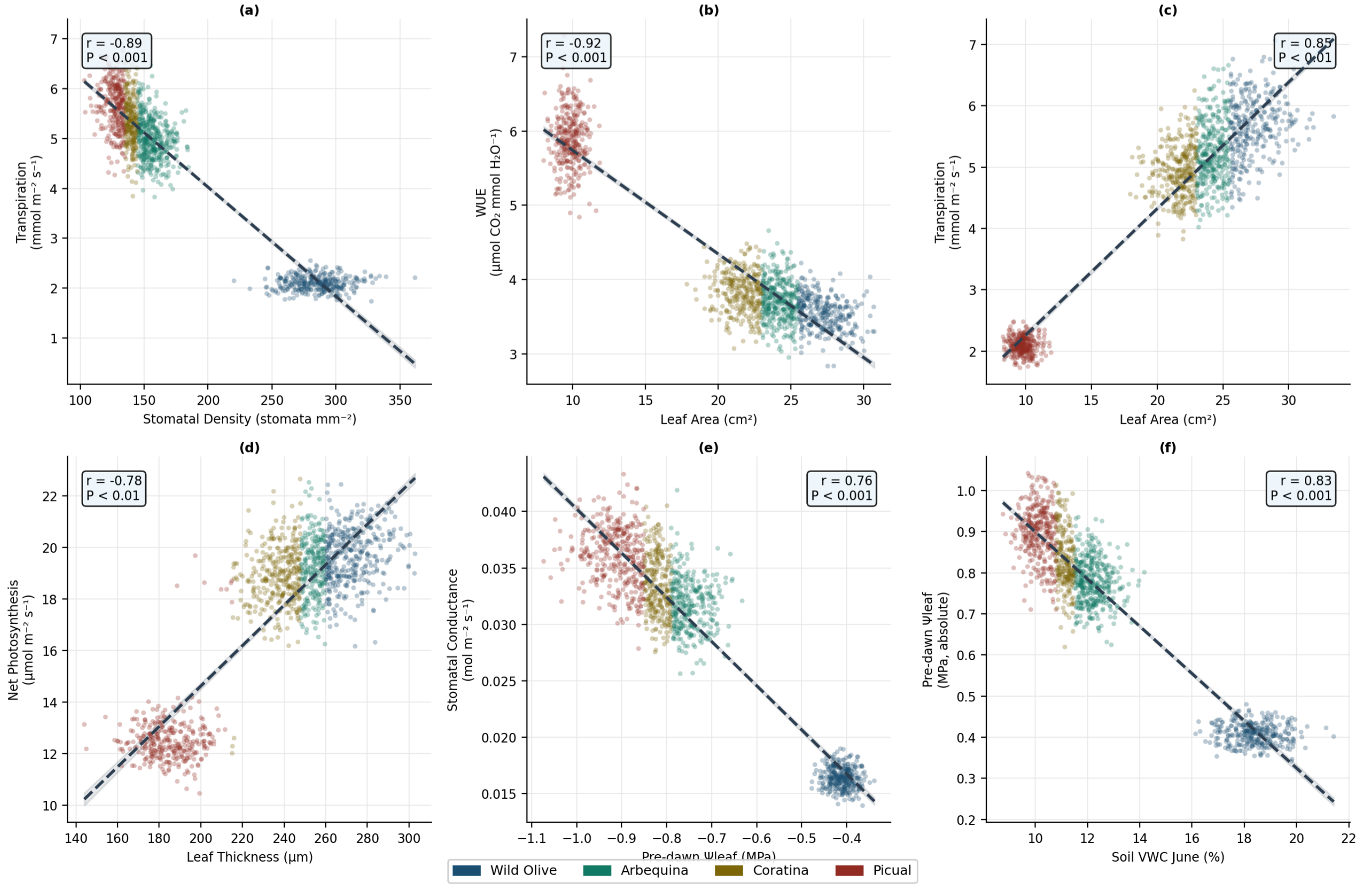


Figure 5. Bivariate Pearson correlation scatter plots ($n = 1{,}240$ individual leaf observations): (a) stomatal density vs. transpiration ($r = -0.89$, $P < 0.001$); (b) leaf area vs. WUE ($r = -0.92$, $P < 0.001$); (c) leaf area vs. transpiration ($r = 0.85$, $P < 0.01$); (d) leaf thickness vs. net photosynthesis ($r = -0.78$, $P < 0.01$); (e) pre-dawn Ψ_{leaf} vs. stomatal conductance ($r = 0.76$, $P < 0.001$); (f) soil VWC vs. pre-dawn Ψ_{leaf} ($r = 0.83$, $P < 0.001$). Panels (e–f) are new to this study. Dashed lines = regression fits; shading = 95% CI.

grafted systems to approach the critical 30 mm stress threshold approximately 18–22 days earlier than wild olive stands. Soil VWC measurements from the field (Table 5) independently corroborate this simulation: observed August VWC under grafted canopies (5.8–7.2%) approached field permanent wilting point, whereas wild olive plots retained 14.7%.

3.8 Ecological and Livestock Impacts

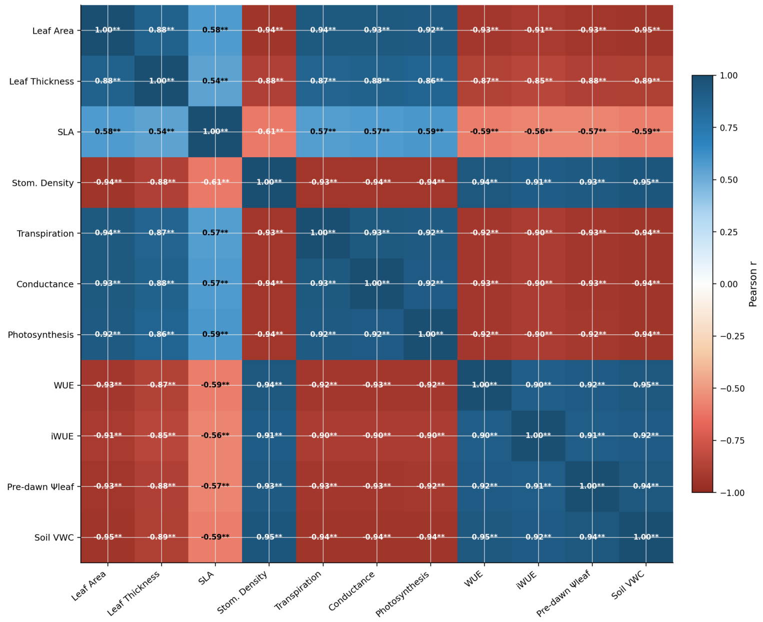
Wild olive systems supported 2.6 times greater bird species richness than grafted monocultures (87 vs. 34 species; Table 6, Figure 8(a)). Mayfield nesting success estimates were $68.4 \pm 3.1\%$ in wild olive forest versus $24.7 \pm 4.2\%$ in grafted plantation [19]. Goats grazing in the wild olive forest maintained 94% health retention versus 68% in the grafted plantation; mortality was fivefold higher in the grafted group (10% vs. 2%; Figure 8(b); Table 5). These outcomes indicate severe nutritional or metabolic deficits associated with the altered forage base in commercial monocultures [29].

Table 6. Ecological and livestock health outcomes comparing wild olive forest and grafted monoculture systems. Bird data: 36 point-count stations, 288 observation sessions. Livestock: 50 goats per system, 6-month grazing trial. Mayfield estimates ± 95% confidence interval [19].

Metric	Wild Olive Forest	Grafted Monoculture
Bird Species Richness (rarefied)	87	34
Raw Nesting Success (%)	72	28
Mayfield Nesting Success (%)	68.4 ± 3.1	24.7 ± 4.2
Livestock Health Retention (%)	94	68
Livestock Mortality (%)	2	10

3.9 Multi-trait Integrated Comparison

The multi-trait radar chart (Figure 9) synthesises all key adaptive dimensions—WUE, stomatal density, leaf area (inverted), iWUE, livestock health retention, and bird species richness—across the four olive types. Wild olive occupies the outermost position on all six axes, confirming phenotypic and ecological superiority under semi-arid conditions. The three commercial



	Leaf Area	Leaf Thickness	SLA	Stom. Density	Transpiration	Conductance	Photosynthesis	WUE	iWUE	Pre-dawn Ψleaf	Soil VWC
Leaf Area	1.00**	0.88**	0.58**	-0.94**	0.94**	0.93**	0.92**	-0.93**	-0.91**	-0.93**	-0.95**
Leaf Thickness	0.88**	1.00**	0.54**	-0.88**	0.87**	0.88**	0.86**	-0.87**	-0.85**	-0.88**	-0.89**
SLA	0.58**	0.54**	1.00**	-0.61**	0.57**	0.57**	0.59**	-0.59**	-0.56**	-0.57**	-0.59**
Stom. Density	-0.94**	-0.88**	-0.61**	1.00**	-0.93**	-0.94**	-0.94**	0.94**	0.91**	0.93**	0.95**
Transpiration	0.94**	0.87**	0.57**	-0.93**	1.00**	0.93**	0.92**	-0.92**	-0.90**	-0.93**	-0.94**
Conductance	0.93**	0.88**	0.57**	-0.94**	0.93**	1.00**	0.92**	-0.93**	-0.90**	-0.93**	-0.94**
Photosynthesis	0.92**	0.86**	0.59**	-0.94**	0.92**	0.92**	1.00**	-0.92**	-0.90**	-0.92**	-0.94**
WUE	-0.93**	-0.87**	-0.59**	0.94**	-0.92**	-0.93**	-0.92**	1.00**	0.90**	0.92**	0.95**
iWUE	-0.91**	-0.85**	-0.56**	0.91**	-0.90**	-0.90**	-0.90**	0.90**	1.00**	0.91**	0.92**
Pre-dawn Ψleaf	-0.93**	-0.88**	-0.57**	0.93**	-0.93**	-0.93**	-0.92**	0.92**	0.91**	1.00**	0.94**
Soil VWC	-0.95**	-0.89**	-0.59**	0.95**	-0.94**	-0.94**	-0.94**	0.95**	0.92**	0.94**	1.00**

Figure 6. Full Pearson correlation matrix (11×11) including leaf water potential (Ψ_{leaf}) and soil VWC variables $(n = 1{,}240)$. Colour scale: dark blue = strong positive; dark red = strong negative. * $P < 0.05$; ** $P < 0.001$. The inclusion of hydraulic variables confirms that the gas-exchange divergences documented in Figures 1, 2, 3 are mechanistically grounded in differences in soil water availability and leaf water status.

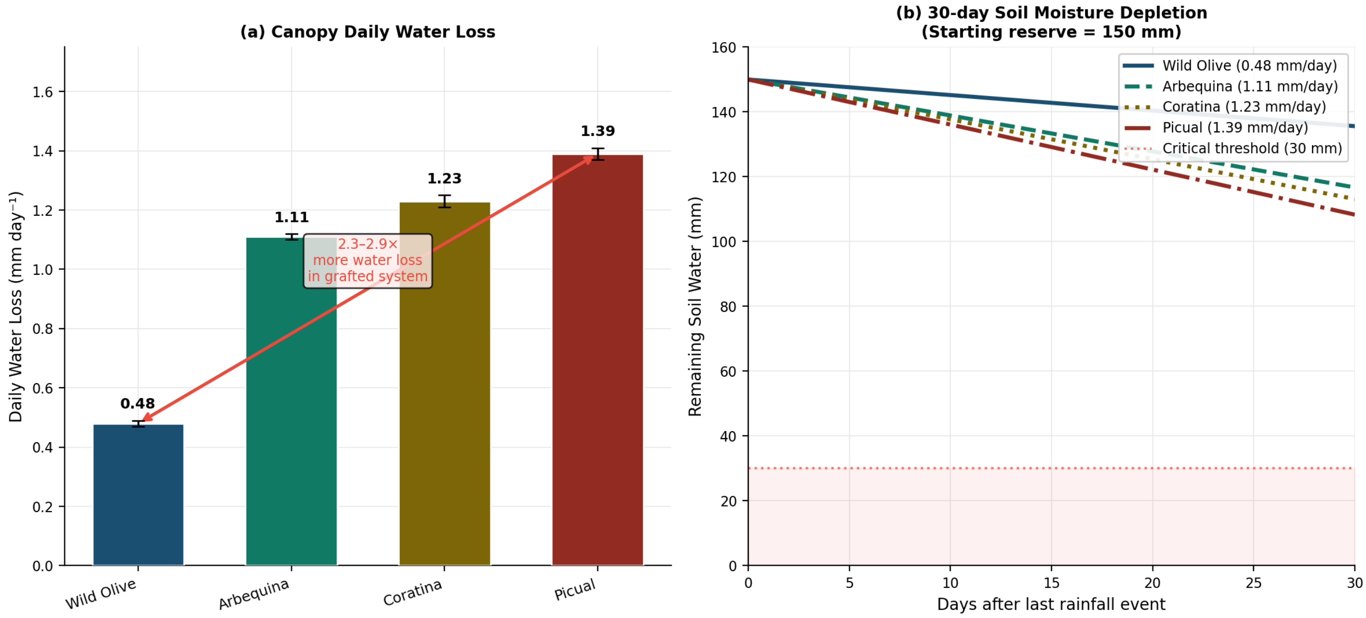


Figure 7. Canopy-scale water budget analysis: (a) daily water loss for all four olive types, with double-headed arrow illustrating the 2.3–2.9× wild olive advantage; (b) simulated 30-day soil moisture depletion under rainfed conditions starting from 150 mm available water capacity. Red dashed line = critical stress threshold (30 mm). Grafted cultivars approach the threshold approximately 18–22 days earlier than wild olive under typical pre-monsoon conditions.

cultivars cluster together in the inner two-thirds of the radar, differing marginally from each other but dramatically from wild olive.

4 Discussion

The data presented here offer the most comprehensive field-level quantification to date of the physiological, hydraulic, and ecological divergence between wild *Olea ferruginea* and grafted commercial olive cultivars in Pakistan. The 51–69% improvement in WUE documented in wild olive is not the product of any single trait but emerges from a coordinated phenotypic syndrome of reduced leaf area, densely packed small-pored stomata, constitutively low

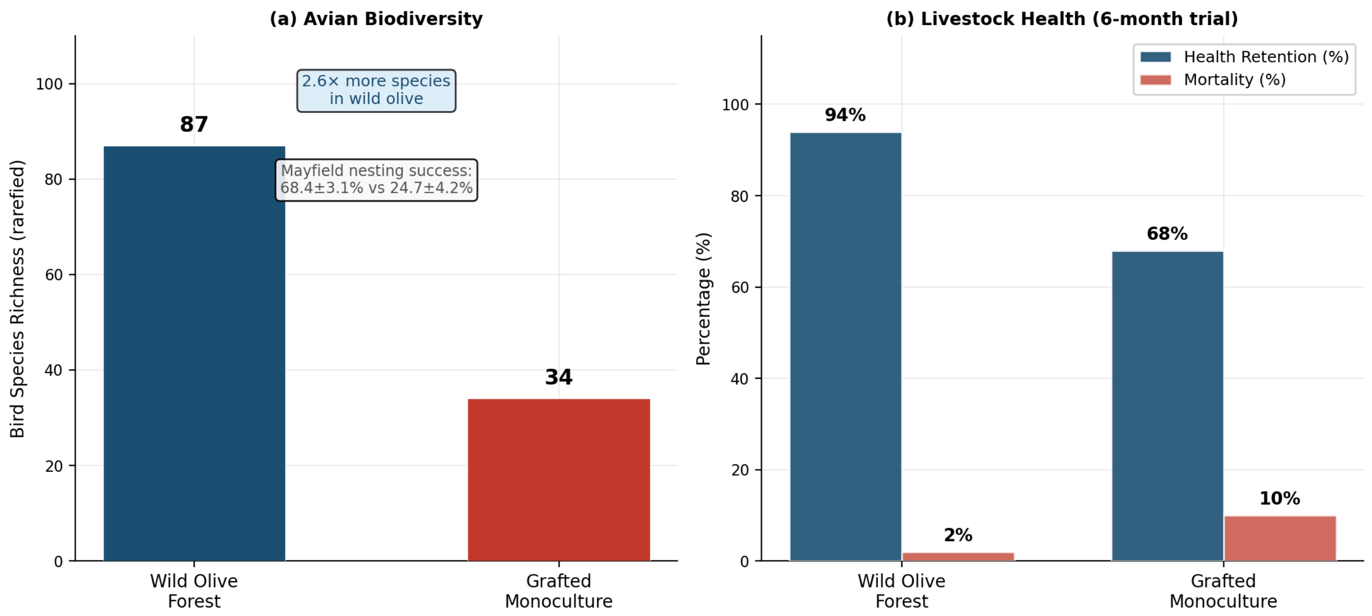


Figure 8. Ecological and livestock outcomes: (a) bird species richness (87 vs. 34 species; 2.6× higher in wild olive) with Mayfield nesting success annotation; (b) livestock health retention and mortality over the 6-month grazing trial. Wild olive systems support superior bird habitat quality and livestock welfare.

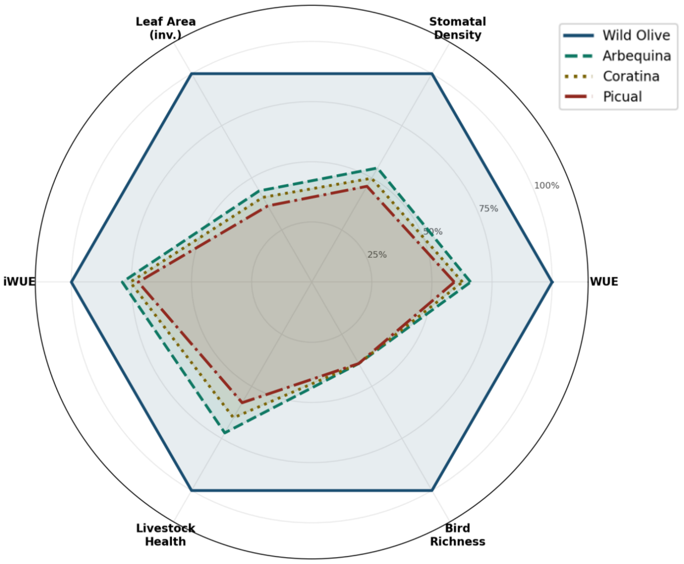


Figure 9. Multi-trait performance radar integrating WUE, stomatal density, leaf area (inverted—smaller = better drought adaptation), iWUE, livestock health retention, and bird species richness across wild olive and three grafted commercial cultivars. Values normalised to panel maximum (= 100%). Wild olive (dark blue) occupies the outermost position on all six axes.

stomatal conductance, and conservative hydraulic regulation—a syndrome that collectively accounts for 85–89% of the variance in WUE and transpiration rate (Figures 5, 7). The inclusion of pressure-bomb leaf water potential and TDR soil VWC data in the present study provides independent hydraulic corroboration of the gas-exchange findings, strengthening causal inference beyond what earlier comparisons based solely on leaf-level measurements could support.

4.1 Leaf Morphology and the Architecture of Water Conservation

The 56–63% reduction in leaf area recorded in wild olive (Table 1, Figure 1(a)) aligns with the broad literature demonstrating that reduced leaf size is one of the most consistent structural responses to arid environments in perennial plants [4]. The strong inverse correlation between leaf area and WUE ($r = -0.92$; Figure 5(b)) indicates that leaf architecture alone accounts for approximately 85% of WUE variance across the 1,240 individual leaf observations in this dataset. The hydraulic data (Table 4) corroborate this interpretation: grafted cultivars maintained significantly more negative pre-dawn and midday leaf water potentials (-0.76 to -0.91 MPa and -2.34 to -2.78 MPa, respectively), indicative of greater hydraulic stress accumulation in the field. Commercial cultivars bred for productivity under irrigated Mediterranean conditions carry constitutively large leaves fundamentally mismatched to the water economy of Pakistan's semi-arid zones.

4.2 Stomatal Strategy and Isohydric Hydraulic Regulation

The 83–118% higher stomatal density in wild olive (285 vs. 131–156 stomata mm^{-2}) paired with a 36–40% reduction in stomatal length creates a high-density/small-pore stomatal mosaic empirically linked to faster stomatal kinetics and improved WUE [6, 21]. The inverse correlation between stomatal density and transpiration rate ($r = -0.89$; Figure 5(a)) provides direct statistical support for this functional interpretation. Importantly, the pressure-bomb data reveal that wild olive also demonstrates the isohydric regulation strategy: the significantly smaller midday hydraulic depression ($\Delta\Psi = 1.07 \pm 0.04$ MPa vs. 1.58–1.87 MPa in grafted cultivars) indicates that wild olive actively limits stomatal conductance to maintain leaf turgor within a narrow water-potential range, even at the cost of reduced instantaneous carbon gain [9]. This constitutive isohydric behaviour means that wild olive's WUE advantage is maintained even under pre-drought ambient conditions, not merely as a stress response. Nteve et al. [24] confirmed in a comprehensive review that high stomatal density combined with small stomatal aperture constitutes a central feature of drought-tolerant olive genotypes, consistent with the morphological phenotype documented here for *O. ferruginea*. Meta-analytical evidence confirms that leaf-level gas exchange responses to drought—including reductions in stomatal conductance and transpiration—are highly consistent across species and measurement conditions, supporting the generalisability of the LI-6400XT measurements reported here [14].

4.3 Physiological Trade-offs and the Grafting Paradox

The lower net photosynthetic rate of wild olive (12.4 vs. 18.5–20.1 μmol m^{-2} s^{-1}) reflects a deliberate physiological economy: wild olives achieve carbon assimilation at a fraction of the transpirational cost, resulting in 51–69% higher WUE and 27–39% higher iWUE—a fundamental trade-off between water conservation and carbon assimilation extensively discussed in the context of crop breeding for drought resistance [7]. At the canopy scale, the 30-day depletion simulation (Figure 8(b)) translates this abstract physiological difference into a concrete landscape prediction: grafted plantations in rainfed zones will approach critical soil moisture stress approximately 18–22 days earlier during every pre-monsoon dry season, a structural requirement for supplemental irrigation that conflicts directly with the resource constraints of most Balochistan farming households.

A critical and novel implication is the 'grafting paradox': commercial scions retain their characteristic large leaves and sparse, large-pored stomata regardless of the wild olive rootstock, producing the high-transpiration, low-WUE phenotype documented in Tables 1– 3. While rootstocks can modulate scion water status through ABA signalling and hydraulic feedback [18, 31], they cannot override the intrinsic leaf morphological programme encoded in the scion genome. Research in grapevine systems has demonstrated that even when scions are grafted onto drought-tolerant rootstocks, leaf area and transpirational demand of the scion remain largely unchanged [8, 32]. The soil VWC data (Table 4, Figure 4(d-e)) provide additional field-scale confirmation of this paradox: despite being rooted in soil with the same hydraulic properties and sharing a similar root zone, grafted trees on *O. ferruginea* rootstocks depleted soil water at 2.3–2.9× the rate of ungrafted wild olive, confirming that the rootstock's drought-adaptive physiology does not transfer to the above-ground system.

4.4 Ecological Consequences: Biodiversity and Pastoral Livelihoods

The 2.6-fold reduction in bird species richness (87 vs. 34 species; Figure 8(a)) is consistent with global patterns of biodiversity decline under agricultural intensification [30]. Morgado et al. [23] specifically documented significant reductions in bird diversity and nesting success in intensive olive orchards compared to traditional groves in Portugal, attributing the loss to reduced structural complexity. The Mayfield nesting success estimates ($68.4 \pm 3.1\%$ vs. $24.7 \pm 4.2\%$) provide a statistically robust measure of reproductive success that goes beyond simple richness counts, indicating substantially inferior habitat quality in grafted monocultures. The livestock data are equally sobering: a fivefold increase in goat mortality (Figure 8(b)) represents a direct livelihood threat to pastoralist communities. *O. ferruginea* foliage is recognised as nutritionally valuable browse [3]; commercially bred cultivars may carry altered polyphenol and oleuropein profiles less suitable for ruminant nutrition, given documented biochemical divergence between wild and cultivated olive subspecies under environmental stress conditions [29].

4.5 Policy Implications for Pakistan's Olive Expansion Strategy

The physiological, morphological, hydraulic, and ecological evidence from this study challenges the prevailing assumption that grafting commercial

Table 7. Summary of study limitations and proposed future research directions.

Category	Limitation	Proposed Future Direction
Observational design	Cross-sectional comparison of sites with differing land-use history; absence of randomized treatment assignment limits causal inference	Future studies should use randomized block designs with controlled grafting treatments on a common soil background
Two-year study window	Seasonal variation in physiological traits may introduce year-to-year confounding not captured in 2023–2025 window	Long-term monitoring ($\geq$ 5 years) tracking inter-annual climatic variation recommended
Leaf-level WUE vs. field WUE	LI-6400XT data represent instantaneous leaf-level measurements; scaling to whole-plant or ecosystem WUE involves uncertainty in LAI and boundary effects	$\delta^{13}C$ stable isotope analysis recommended as integrated measure of long-term WUE
Livestock trial confounders	Forage availability, stocking density, and prior health history of goat cohorts may confound health outcomes beyond forage nutritional quality alone	Double-blind controlled feeding trials with standardized diets recommended
Rootstock physiology unmeasured	Wild *O. ferruginea* rootstock physiology was not measured independently; rootstock modification of scion hydraulics therefore cannot be directly quantified	Pressure-bomb Ψ measurements on rootstock xylem sap and grafted root respiration rates recommended
No genetic characterisation	Wild olive individuals sampled were not genetically characterised; some variation may reflect genetic sub-structuring within the wild population	SSR or SNP-based genetic profiling of wild olive individuals recommended to partition genotypic from phenotypic variance

cultivars onto *O. ferruginea* rootstocks will seamlessly combine high productivity with ecological resilience. Without sustained supplemental irrigation, large-scale grafted monocultures in rainfed zones face significant risk of water-stress-induced failure, progressive groundwater depletion, and degradation of the ecosystem services that wild olive forests currently provide freely. The soil VWC data showing August values of 5.8–7.2% in grafted plots (approaching permanent wilting point) versus 14.7% in wild olive plots demonstrate that this risk is not theoretical but already manifest under current conditions. A more sustainable strategy would integrate the conservation of existing wild olive forest patches within a landscape mosaic that includes carefully sited, properly irrigated grafted orchards on already-cultivated or degraded lands. Regulated deficit irrigation strategies have been shown to alter water relations and gas exchange in olive trees, providing a management framework complementary to the genetic drought adaptation documented here [13].

5 Limitations and Future Directions

Several important limitations of the present study must be explicitly acknowledged (Table 7). First, the observational cross-site design does not permit full causal inference: differences among sites may partly reflect historical land-use effects, soil management history, or cultural selection criteria. Future studies should employ randomised block designs with controlled grafting treatments on a common soil background. Second, the two-year monitoring window (2023–2025) limits generalisability across contrasting climatic years; long-term monitoring ($\geq$ 5 years) is recommended. Third, while leaf-level WUE measurements are the standard in comparative ecophysiology, they do not fully represent long-term integrated WUE; future studies should validate these findings with stable carbon isotope analysis ($\delta^{13}C$) as an integrated measure of WUE over the leaf lifetime [11]. Fourth, the livestock trial involves potential confounders including forage quantity, stocking density, and cohort health history; controlled feeding trials with standardised diets are needed to establish causation. Fifth, the wild olive rootstock physiology was not measured independently—future pressure-bomb measurements on rootstock xylem sap would directly quantify rootstock-mediated modification of scion hydraulics. Sixth, wild olive individuals were not genetically characterised; SSR or SNP-based profiling is recommended to partition genotypic from phenotypic variance in the wild population.

6 Conclusion

This study presents the first comprehensive comparative field assessment of wild *Olea ferruginea* and grafted commercial cultivars in Pakistan, evaluated across leaf morphological, stomatal, physiological, hydraulic, and ecological metrics (Figures 1-9; Tables 1-7). Wild olives exhibited constitutive *xerophytic* adaptations—51–69% higher WUE, 83–118% greater stomatal density, significantly less negative pre-dawn and midday leaf water potentials, 52–72% higher residual soil VWC in August, superior bird habitat quality (87 vs. 34 species; Mayfield nesting success 68.4% vs. 24.7%), and superior livestock forage value (94% vs. 68% health retention; 2% vs. 10% mortality)—collectively underscoring their critical importance as both a genetic resource and an ecological foundation for sustainable olive development in Pakistan's semi-arid landscapes. The pressure-bomb and TDR data independently corroborate the gas-exchange findings and confirm that the grafting paradox is observable at the soil moisture level, not merely at the leaf level.

Evidence-based policy recommendations include: (i) conservation of wild olive forest patches to protect genetic resources, ecosystem services, and pastoral livelihoods; (ii) restriction of grafted monoculture to degraded or already-cultivated lands with reliable supplemental irrigation; (iii) promotion of agroforestry mosaics integrating grafted commercial olives with native vegetation; (iv) systematic monitoring of livestock health and forage quality in commercial systems; (v) a long-term breeding programme to develop compact-leafed, high-WUE scion genotypes exploiting the genetic resources of *O. ferruginea*; (vi) development of sustainable farming and certification frameworks for eco-sensitive olive oil production; (vii) validation of findings using δ^{13}C stable isotope analysis as an integrated measure of long-term WUE; and (viii) formal integration of wild olive conservation into national climate adaptation strategies, given IPCC (2023) projections of increasing drought frequency across north-western Pakistan.

Data Availability Statement

Data will be made available on request.

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Conflicts of Interest

The authors declare no conflicts of interest.

AI Use Statement

The authors declare that Claude (Sonnet 4.6) was used for language editing, translation, and proofreading of the manuscript, including the Methods and Discussion sections. The authors have carefully reviewed, revised, and verified the AI-assisted output and take full responsibility for the content of the manuscript.

Ethical Approval and Consent to Participate

The animal grazing trial was conducted in accordance with the guidelines of the Institutional Animal Care and Use Committee (IACUC) of the University of Agriculture Peshawar, Pakistan (Protocol No. AUP/2024/012). All procedures were performed in compliance with Pakistan's national animal welfare regulations and standard veterinary welfare assessment protocols.

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