



Suitability of two different organic substrates as growing media for sustaining the productivity of mediterranean plant species in degraded sites

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Abstract

The degradation of natural and urban areas due to human activities has intensified in recent decades, leading to significant biodiversity loss and decline in ecosystem service. In this context, the revegetation with native Mediterranean sclerophyllous shrubs represents a promising strategy for the recovery of overexploited environments. This study evaluated the suitability of two organic substrates—compost (C) and a compost-poultry manure mix (CP)—obtained from domestic waste and green refuse, as growing media for three Mediterranean species (*Quercus ilex* L., *Phillyrea angustifolia* L., *Laurus nobilis* L.) to restore degraded sites. To assess the effects of substrate type and climate on primary production, three plant species were cultivated for one year in mesocosms containing limestone debris, which was amended with either C or CP, and leaf gas exchanges as well as key eco-physiological traits were monitored across seasons. Results showed that plants on CP exhibited higher photosynthetic rates compared to those on C substrate, with increases of 25%, 12%, and 20% for *Q. ilex*, *P. angustifolia*, and *L. nobilis*, respectively, accompanied by greater height and trunk diameter for all species. Notably, during the summer drought period, CP plants maintained enhanced carbon fixation—22%, 25%, and 37% higher than C plants for the respective species. One year after, organic matter (OM) in the CP substrate had decreased by 44%, compared to only 7% in the C substrate, suggesting more rapid utilization by the plants. The readily available OM and the higher water-holding capacity of CP substrate (+54% after one year), presumably contributed to the improved photosynthetic and transpiration rates during summer. Among species, *Q. ilex* demonstrated the highest resilience under challenging environmental conditions. Overall data suggests that the CP substrate is more effective than the C in promoting plant growth and offers significant potential for the recovery of degraded sites, such as disused quarries.

Keywords Compost · Poultry manure · Sclerophyllous species · Photosynthesis · Urban environment

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Introduction

Human activities are a significant driver of the degradation of both natural and urban environments, ultimately leading to the loss of biodiversity and essential ecosystem services. Among these activities, quarrying has a particularly significant environmental impact, as it alters the structure and functioning of ecosystems, especially in Mediterranean areas, where it not only accelerates soil erosion but also represents a significant threat to local biodiversity. In the Campania Region of southern Italy alone, it has been estimated that quarries occupy, approximately, 227 km² of land (Regione Campania 2017). Here, the extraction of limestone and other materials leads to the complete removal

of vegetation and topsoil, resulting in areas highly susceptible to erosion. Steep slopes, where the loss of protective vegetation and soil cover significantly increases erosion risks, undergo degradation that not only hampers natural regeneration processes but also poses substantial challenges for ecological restoration (Carabassa et al. 2020; Zhu et al. 2024).

The removal of native vegetation during quarrying activities disrupts the habitat structure of the Mediterranean maquis, leading to a decline in plant and animal diversity. In this context, it is crucial to find suitable solutions to mitigate the adverse effects of quarrying practices. Revegetation of exploited areas using native Mediterranean sclerophyllous shrubs is a promising strategy for restoring overexploited ecosystems, such as abandoned quarries. Previous studies have shown that the introduction of native species in limestone quarry rehabilitation promotes the establishment of diverse plant communities, thus contributing to soil stabilization and habitat restoration (Scotton and Andreatta 2021).

Several studies have also demonstrated the effectiveness of in-situ remediation technologies for refurbishing degraded areas and maintaining ecosystem services (Maisto et al. 2010; Oldfield et al. 2015; Zhang et al. 2019). In particular, the addition of organic amendments to the soil is particularly valuable because it reduces the metal availability for crops (Abad-Valle et al. 2016) and is also a cost-effective and environmentally friendly practice, supporting the circular economy and recycling of renewable resources (Islam et al. 2024).

A significant advantage of adding organic amendments to the soil is the improvement of soil-plant water relationships, which positively influences soil quality and plant productivity. However, it is noteworthy that the soil water retention capacity after the amendment application can vary over time, depending on the type of manure (Kallenbach et al. 2019). Generally, the addition of labile organic matter results in rapid decomposition, decreasing the long-term benefits associated with the good water retention. Besides soil-plant water dynamics, organic amendments also modify the soil carbon-to-nitrogen (C/N) ratio over time (Averett et al. 2017) either promoting nitrogen mineralization or its immobilization (Marzi et al. 2020). Initially, the nitrogen provided by organic amendments promotes rapid plant growth, also favoring decomposition and mineralization. In particular, a high nitrogen supply enhances the overall health status and photosynthesis of plants by increasing chlorophyll synthesis, Rubisco activity, photosystem II photochemical efficiency and electron transport rate (Arena et al. 2005; Mangalassery et al. 2019; Soualiou et al. 2023; Wei et al. 2024). However, nitrogen use efficiency tends to decrease in the long term as plants begin to compete with

soil microorganisms for nitrogen uptake, particularly in overexploited soils (Yang et al. 2015; Kitonyo et al. 2018).

Numerous experimental trials have demonstrated the benefits of adding compost to inert substrates or nutrient-poor soils for restoring urban areas and degraded sites, such as disused quarries (Maisto et al. 2010; McGrath et al. 2020). Previous research has shown that incorporating compost or a mixture of compost and poultry manure into quarry debris significantly alters the physical, chemical, and biological properties of the substrate, both in the short term and long term (Memoli et al. 2017). It is widely accepted that the use of compost from animal or plant origin, along with poultry manure enhances nutrient availability and improve soil structure, thus supporting plant growth, especially in overexploited agricultural or urban soils (Baldantoni et al. 2015, 2016; Forge et al. 2016; Tao et al. 2024). However, while most studies have focused on soil properties, less attention has been paid to the physiological response of plants to short and long-term amendment addition, particularly in sclerophyllous species of the Mediterranean maquis, which play a crucial role in ecosystem services and have significant potential for urban greening strategies (Vitale et al. 2024).

The benefits of organic amendments on plants can vary depending on the amendment type. Generally, substrates rich in humic substances release nutrients gradually, resulting in long-lasting positive effects on both plants physiological attributes and soil microorganism functions, while nitrogen-rich amendments tend to promote rapid plant growth (Memoli et al. 2017; da Silva Oliveira et al. 2017). Furthermore, intrinsic factors such as the plant ability to utilize available resources, and seasonal variations in growth and photosynthesis, can strongly influence plant physiological response to fertilizers and cannot be ignored.

This study evaluates the effectiveness of two organic substrates derived from recycled wastes in supporting the growth and physiological performance of three Mediterranean maquis representative species. The use of these substrates not only helps to restore degraded environments but also converts waste materials into valuable resources, addressing both ecological restoration and waste management challenges.

The specific goals of this research are: (1) to compare the efficacy of different organic substrates as growing media for native Mediterranean species (*Quercus ilex* L., *Phillyrea angustifolia* L., and *Laurus nobilis* L.) for ecological restoration and (2) to evaluate how long the potential benefits of organic substrates on plant productivity can be sustained. To achieve these aims, a mesocosm trial was established in an open area under typical Mediterranean climate conditions, utilizing two types of organic substrates: compost (C) and a mixture of compost and poultry manure (CP) both applied

over limestone debris. The photosynthetic performance and leaf functional traits of all species were monitored over one year, across all seasons to assess the effects of both seasonality and substrate type.

The employment of native species in this study ensures that the outcomes are directly applicable to the Mediterranean maquis ecosystem, as non-native species may respond differently in terms of water usage, competition, and ecological interactions. Furthermore, utilizing local species enhances the study's relevance for conservation efforts and restoration projects, also providing insights into how these species may react to climate change and other anthropogenic factors.

Materials and methods

Mesocosm setting up

Fourteen mesocosms (pot diameter: 1 m, pot height: 1 m) were set up for the experiment. Each mesocosm was filled with a bottom layer (0–60 cm depth) of limestone debris of different granulometry derived from abandoned quarries, and an upper layer (60–90 cm depth) consisting of organic matrices, either compost (C) or compost mixed with poultry manure (CP). More specifically, seven mesocosms were filled with compost mixed with expanded clay pellets (v: v=70:30) placed on limestone debris, and the remaining seven were filled with a mixture of compost, poultry manure, and expanded clay pellets (v: v:v=60:10:30), also placed above the limestone debris. Each mesocosm received 150 kg fresh weight (f.w.) of compost, corresponding to approximately 1900 t/ha. The compost used in the experiment was produced by a local company (Pomigliano Ambiente S.p.A., Pomigliano, Naples, Italy) and derived from the organic part of municipal waste and green waste from tree pruning.

The experimental setup did not include a control consisting only of limestone debris without organic substrate, as such settings would not have supported adequate plant rooting especially for sclerophyllous species, which are characterized by extensive root systems that represent the major portion of their total biomass (Sanesi et al., 2012). Therefore, this study compared the physiological performance of plants grown on C and CP substrate to assess which of the two is the most suitable for plant growth.

The mesocosms were placed outdoor in an open area at the Biology Department of the University of Naples Federico II (Naples, Italy) (40°51'40.89" N; 14°15'44.86" S) at temperature and rainfall conditions typical of the Mediterranean area (Fig. 1).

The two organic substrates were characterized at the beginning and at the end of the experiment (after one year) for organic matter content, water holding capacity, pH, carbon (C) and nitrogen (N) content and total and available nutrients (Table 1). The t-tests and confidence intervals are reported in Table 1S.

In each mesocosm, three native sclerophyllous shrubs of 2-year-old, typical of the Mediterranean maquis, were transplanted. These included two specimens each of *L. nobilis* L. (bay tree), *P. angustifolia* L. (jasmine box), and *Q. ilex* L. (holm oak), for a total of six specimens per mesocosm (Fig. 1S). Plants used in the experiment were provided by the garden center of the Corpo Forestale dello Stato in Sabaudia (Latina, Italy).

From March 2004 to March 2005, in vivo measurements of gas exchange and chlorophyll a fluorescence emission were conducted on all three species across the four seasons: spring, summer, autumn, and winter to evaluate their photosynthetic activity. Additionally, leaf water content (LWC), carbon (C) and nitrogen (N) concentration were measured on the same leaves used for gas-exchange analyses. As a proxy for plant growth, plant height and stem diameter were estimated at the beginning of the experiment and after one year of plant establishment on the different substrates (Table 2S).

Leaf water content, and C and N determination

For each mesocosm and season, five fully expanded green leaves of holm oak, bay tree, and jasmine box were collected to determine leaf water content (LWC). LWC was evaluated gravimetrically by weighing fresh leaves and reweighing them after oven-drying samples at 75 °C.

For carbon (C) and nitrogen (N) analysis, five leaves *per* species were pooled for each mesocosm. After the oven-dried samples were ground into a fine powder by an agate mortar and pestle (Fritsch Analysette Spartan 3 Pulverisette 0) and for each pooled sample four sub-samples were analysed using an elemental analyser (CNS analyser—Thermo Finnigan) as reported in De Marco et al. (2013).

Leaf gas exchange and chlorophyll a fluorescence analysis

Leaf gas exchange measurements were conducted using a portable gas-exchange system (HCM-1000, Heinz, Walz GmbH, Effeltrich, Germany) simultaneously with chlorophyll fluorescence analyses using a pulse amplitude modulated fluorometer (MINI-PAM, Heinz, Walz GmbH, Effeltrich, Germany), as reported in Vitale et al. (2012).

In the early morning (07:00–08:00 a.m.), leaves were darkened for 30 min to determine the dark respiration (R_d)

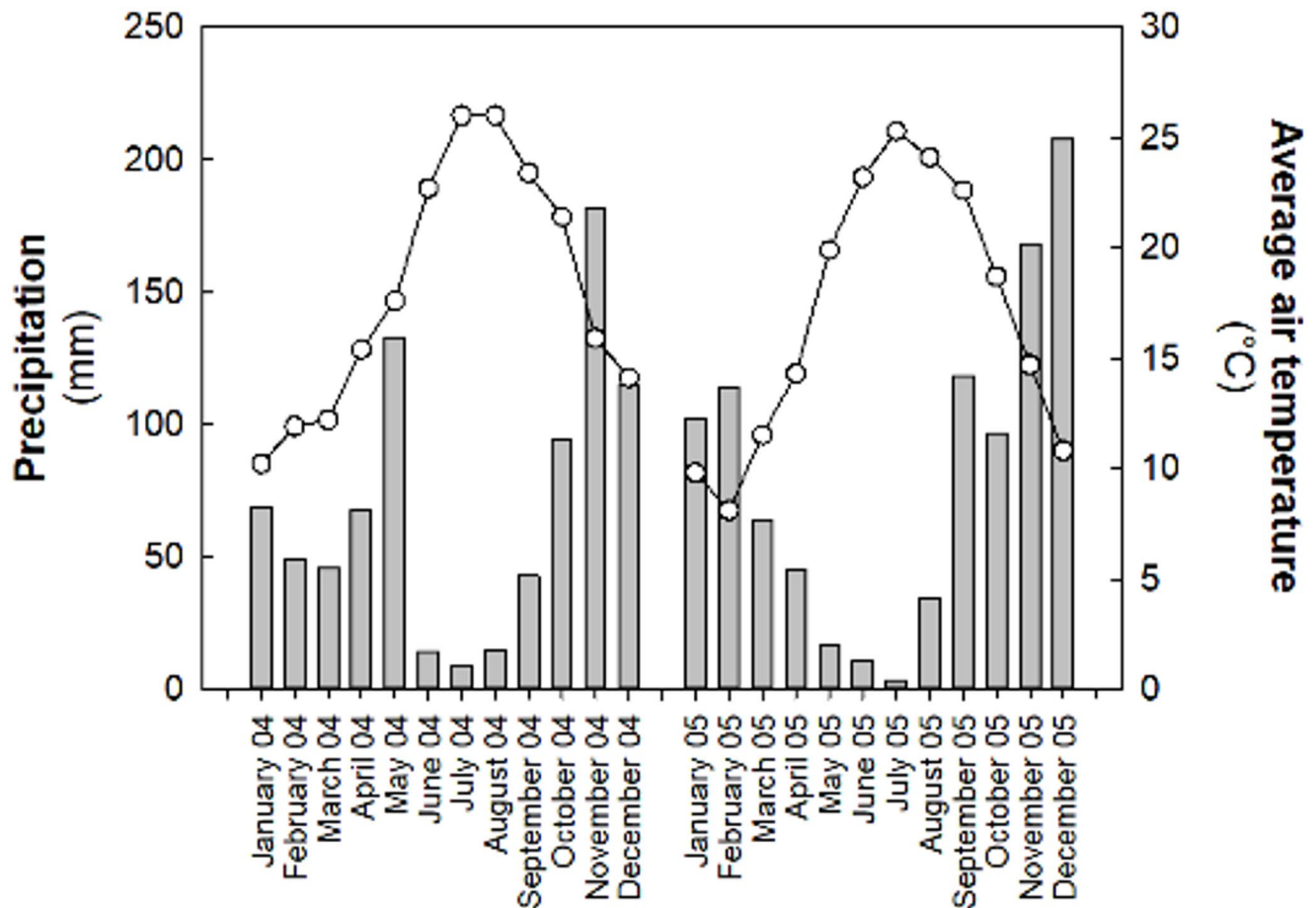


Fig. 1 Monthly mean of precipitations and temperatures in the experimental sampling period of one year

and the maximal PSII photochemical efficiency (F_v/F_m). For F_v/F_m calculation, the background fluorescence signal, F_0 , was induced by light of $0.5 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ at the frequency of 0.6 kHz, whereas a 1s saturating light pulse of $10,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ was applied to determine the maximal fluorescence level in the dark-adapted state, F_m . F_v/F_m was calculated according to Kitajima and Butler (1975) as the ratio between the variable fluorescence, F_v ($F_m - F_0$) and F_m .

Net photosynthesis (A_N), stomatal conductance (g_s -H₂O), transpiration rate (E), and quantum yield of PSII electron transport (Φ_{PSII}) were measured from 12:00 a.m. to 2:30 p.m. under seasonal conditions of temperature and relative humidity, and PPFD of $1,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Leaves were illuminated using an external light source (1050-H -Walz) placed on the cuvette plane. Photosynthetic light response curves were previously carried out to assess the light-saturated photosynthetic rate. This value corresponding to $1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for all three species, was utilized to determine light intensity during gas exchange measurements in the field (Maisto et al. 2010). The measurements were acquired after 8–10 min from leaf enclosure

in cuvette, at the reaching of the steady state for net CO₂ assimilation.

The steady-state fluorescence signal (F_t) and the maximal fluorescence (F_m') under illumination were measured by setting light measure at a frequency of 20 kHz. The quantum yield of PSII linear electron transport (Φ_{PSII}) was estimated according to Genty et al. (1989) and used for the calculation of linear electron transport rate (ETR) following Krall and Edwards (1990). Thermal dissipation of excess absorbed light was expressed by Stern-Volmer non-photochemical quenching (NPQ) and calculated as $(F_m - F_m')/F_m'$ following Bilger and Björkman (1990). Gas exchange parameters were calculated according with equations reported in von Caemmerer and Farquhar (1981). The water use efficiency, WUE, was calculated as the A_N/E ratio, while the apparent carboxylation efficiency as the A_N/C_i ratio, where C_i represents the intercellular CO₂ concentration. Furthermore, the ratio between linear electron transport rate and net photosynthesis (ETR/A_N) has been used to indicate the electron transport utilized by acceptors other than CO₂ (Krall and Edwards 1990; D'Ambrosio et al. 2006).

Table 1 Mean values ($\pm$ s.e.) of pH, organic matter (OM), water holding capacity (WHC), carbon (C) and nitrogen (N) content, total (tot) and available (ava) nutrients at the beginning and the end of the experiment (2004–2005) in the two substrates: compost (C) and Compost + Poultry manure (CP). Asterisks indicate the significant differences between substrates (C vs. CP) at each sampling time. Letters indicate the significant differences for C (lower letters) and CP (upper letters) substrates at different sampling times (2004 vs. 2005). The significant differences were assessed through t-test or signed rank test according normal or not normal data distribution

	2004		2005	
	C	CP	C	CP
pH	7.70 $\pm$ 0.00 ^a	6.80 $\pm$ 0.06 ^B	7.94 $\pm$ 0.14 ^a	8.06 $\pm$ 0.09 ^A
OM (% d.w.)	31.2 $\pm$ 1.71 ^a	39.1 $\pm$ 1.01 ^A	28.9 $\pm$ 1.21 ^a	21.8 $\pm$ 1.14 ^B
WHC (% d.w.)	33.09 $\pm$ 2.21 ^a	51.52 $\pm$ 15.49 ^{A*}	30.0 $\pm$ 0.37 ^a	46.3 $\pm$ 0.32 ^A
C (% d.w.)	17.8 $\pm$ 0.95 ^b	18.3 $\pm$ 2.79 ^{A*}	18.7 $\pm$ 2.48 ^{a*}	12.0 $\pm$ 0.72 ^B
N (% d.w.)	1.57 $\pm$ 0.10 ^b	1.62 $\pm$ 0.11 ^A	2.01 $\pm$ 0.22 ^{a*}	1.40 $\pm$ 0.07 ^A
Cd _{tot} (μ g g ⁻¹ d.w.)	0.39 $\pm$ 0.03 ^{a*}	0.27 $\pm$ 0.04 ^A	0.33 $\pm$ 0.03 ^{a*}	0.21 $\pm$ 0.04 ^A
Cu _{tot} (μ g g ⁻¹ d.w.)	139 $\pm$ 2.75 ^b	131 $\pm$ 4.92 ^B	203 $\pm$ 14.5 ^a	164 $\pm$ 6.03 ^A
Fe _{tot} (mg g ⁻¹ d.w.)	22.4 $\pm$ 1.29 ^a	22.0 $\pm$ 1.06 ^A	12.3 $\pm$ 0.42 ^b	17.1 $\pm$ 1.14 ^B
K _{tot} (mg g ⁻¹ d.w.)	23.5 $\pm$ 1.08 ^a	26.1 $\pm$ 1.02 ^{A*}	19.7 $\pm$ 1.06 ^b	23.5 $\pm$ 1.06 ^{B*}
Mg _{tot} (mg g ⁻¹ d.w.)	8.94 $\pm$ 0.52 ^a	8.81 $\pm$ 0.42 ^A	3.87 $\pm$ 0.52 ^a	7.81 $\pm$ 0.53 ^{A*}
Na _{tot} (mg g ⁻¹ d.w.)	5.27 $\pm$ 0.33 ^a	5.72 $\pm$ 0.33 ^A	4.48 $\pm$ 0.24 ^a	5.77 $\pm$ 0.15 ^A
Ni _{tot} (μ g g ⁻¹ d.w.)	25.2 $\pm$ 0.61 ^b	20.7 $\pm$ 1.01 ^B	30.1 $\pm$ 0.68 ^a	28.5 $\pm$ 1.54 ^A
Zn _{tot} (mg g ⁻¹ d.w.)	0.41 $\pm$ 0.01 ^b	0.40 $\pm$ 0.01 ^A	0.56 $\pm$ 0.05 ^{a*}	0.35 $\pm$ 0.02 ^A
Cd _{ava} (μ g g ⁻¹ d.w.)	0.20 $\pm$ 0.01 ^a	0.20 $\pm$ 0.01 ^A	0.25 $\pm$ 0.02 ^a	0.18 $\pm$ 0.01 ^A
Cu _{ava} (μ g g ⁻¹ d.w.)	19.5 $\pm$ 1.76 ^a	32.1 $\pm$ 0.80 ^{A*}	13.9 $\pm$ 0.99 ^b	14.8 $\pm$ 0.98 ^B
Fe _{ava} (μ g g ⁻¹ d.w.)	0.37 $\pm$ 0.04 ^a	0.44 $\pm$ 0.02 ^A	0.26 $\pm$ 0.02 ^b	0.16 $\pm$ 0.01 ^B
K _{ava} (μ g g ⁻¹ d.w.)	4.29 $\pm$ 0.26 ^a	5.72 $\pm$ 0.42 ^A	0.96 $\pm$ 0.02 ^b	3.46 $\pm$ 0.65 ^{B*}
Mg _{ava} (μ g g ⁻¹ d.w.)	0.88 $\pm$ 0.04 ^{a*}	1.18 $\pm$ 0.08 ^{A*}	0.69 $\pm$ 0.05 ^a	1.10 $\pm$ 0.11 ^A
Na _{ava} (μ g g ⁻¹ d.w.)	0.51 $\pm$ 0.04 ^a	0.63 $\pm$ 0.05 ^A	0.06 $\pm$ 0.00 ^b	0.32 $\pm$ 0.08 ^B
Ni _{ava} (μ g g ⁻¹ d.w.)	1.22 $\pm$ 0.20 ^a	2.46 $\pm$ 0.19 ^A	0.95 $\pm$ 0.11 ^b	0.62 $\pm$ 0.04 ^B
Zn _{ava} (μ g g ⁻¹ d.w.)	0.11 $\pm$ 0.01 ^a	0.14 $\pm$ 0.01 ^A	0.12 $\pm$ 0.01 ^{a*}	0.09 $\pm$ 0.01 ^B

Statistical analyses

The normality of the data distribution was performed by the Shapiro-Wilk test (for $\alpha=0.05$). When the data did not match the basic assumptions of normality and homoscedasticity required for parametric statistics, a Log₁₀ function was applied to normalize the data. Differences between treatments (compost vs. compost mixed with poultry manure) within the same plant species were analysed by paired t-tests (for $\alpha=0.05$), while differences among plant species within the same treatment were assessed by one-way ANOVA followed by the Duncan's post hoc test (for $\alpha=0.05$). The direct influences of plant species and treatment (compost vs. compost mixed to poultry manure) on leaf functional traits (N and C content, and LWC), photosynthetic (A_N , g_s -H₂O, E , Φ_{PSII} , NPQ) characteristics and on derived gas exchanges parameters (WUE, ETR/A_N , A_N/C_i), were assessed by linear-mixed effects (LME) models. For each leaf characteristic, the influence of plant species and treatment, considered as fixed effects, and of sampling season, regarded as a random effect, was calculated using restricted maximum likelihood (REML), the better estimation of variance components for the present dataset. The significant impacts and interactions among plant species, substrates and sampling seasons on leaf characteristics were calculated by comparing models, using the likelihood ratio test with the ANOVA function (for $\alpha=0.05$).

To evaluate significant differences ($\alpha=0.05$) in leaf traits in relation to substrates and plant species, permutational multivariate analyses of variance (PERMANOVA) was

applied using Bray–Curtis distance matrices. This analysis was carried out using the ADONIS function with 999 permutations, along with the pairwise.perm.manova function, also with 999 permutations, to assess the leaf characteristic values.

Furthermore, to investigate significant differences ($\alpha=0.05$) in leaf traits across the four sampling seasons in relation to substrate treatment and among different plant species within each season, PERMANOVA analyses was applied with Bray–Curtis distance matrices. Pairwise comparisons were conducted using the pairwise.perm.manova function, with 999 permutations applied to leaf trait values. Non-metric multidimensional scaling (NMDS) based on Bray–Curtis distance was performed to show leaf trait variation in relation to treatments, plant species and seasons.

All the statistical analyses, including one-way ANOVAs, paired t-tests, linear mixed models (using the lme4 package) and NMDS (using the vegan packages) were performed in the R3.6.2 programming environment (R Development Core Team), while the graphical representation was created using SigmaPlot12 software (Jandel Scientific, San Rafael, CA, USA).

Results

Overall trend of leaf analysis

The linear mixed effect model applied to data collected over one year revealed that leaf characteristics mainly depended

on sampling season (random effect) (Table 2), while plant species and treatment (fixed effects) had a significant impact on leaf properties. Specifically, the investigated plant characteristics, namely N and C leaf concentration, F_{PSII} , NPQ, E, g_s -H₂O, A_N , LWC exhibited significant variability based on species, while other plant traits, specifically N and C leaf concentration, ETR/ A_N , E, g_s -H₂O, A_N , WUE, A_N /Ci differed in response to the treatment (Table 2).

The effects of manure on plant physiological and functional traits revealed significant differences between the two treatments (PERMANOVA test, $P < 0.01$). More specifically, plants grown in substrate enriched with compost mixed with poultry manure (poultry) were primarily characterized by transpiration rate (E), stomatal conductance (g_s -H₂O), and net photosynthesis (A_N); in contrast, plants grown in substrate amended with compost were mainly defined by water use efficiency (WUE), and ratios electron transport to net photosynthesis (ETR/ A_N), and net photosynthesis to intercellular CO₂ concentration (A_N /Ci) (Fig. 2a). Additionally, the influence of plant species on physiological and functional traits also showed significant differences among the species (PERMANOVA test, $P < 0.05$). *Q. ilex* (Q) was primarily associated to E, g_s -H₂O, and A_N , while *P. angustifolia* (Ph) was mainly characterized by carbon (C) and nitrogen (N) content, and leaf water content (LWC). Lastly, *L. nobilis* (L) was primarily associated to WUE, ETR/ A_N , and A_N /Ci (Fig. 2b).

The growth on the two different substrates significantly impacted on plant physiological and functional traits across the seasons with PERMANOVA test showing strong differences ($P = 0.001$) between the two substrates during spring and summer (Fig. 3). Plants grown on substrate enriched with compost and poultry manure exhibited higher levels of E and g_s -H₂O in both spring and summer. In contrast, plants growing on substrate with sole compost were mainly characterized by C and N content, LWC, NPQ, and ETR/ A_N

during the spring, whereas in summer, they were primarily associated with N, NPQ, and ETR/ A_N (Fig. 3).

The effect of plant species on physiological and functional traits across seasons showed significant differences (PERMANOVA test, $P = 0.05$) among the species in all seasons (Fig. 4). In spring (Fig. 4a), Q plants were primarily characterized by high transpiration rate (E) and stomatal conductance to water vapor (g_s -H₂O), whereas Ph plants were mainly associated to carbon content (C) and leaf water content (LWC). In contrast, L plants were defined by higher nitrogen content (N), non-photochemical quenching (NPQ), and ratio of electron transport to net photosynthesis (ETR/ A_N). In summer (Fig. 4b), Q plants were mainly characterized by net photosynthesis (A_N), quantum yield of photosystem II (F_{PSII}), and water use efficiency (WUE), Ph plants remained associated with higher carbon content (C), while L plants were identified by elevated levels of nitrogen (N), leaf water content (LWC) and NPQ. >During fall (Fig. 4c), Q plants were associated with g_s -H₂O and A_N , Ph plants with F_{PSII} , while L plants were characterized by N, LWC, NPQ, and the ETR/ A_N ratio. Finally, during winter (Fig. 4d), Q plants were defined by LWC and E, Ph plants were predominantly identified by g_s -H₂O, whilst L plants were characterized by C, N, and WUE.

Differences in leaf functional and photosynthetic traits among sclerophyllous grown on compost and compost mixed with poultry manure for each season

Plant growth on different substrates significantly influenced leaf functional traits during the summer and fall seasons (Fig. 5). In summer, the leaf water content (LWC) of L plants grown on compost (C) was higher ($P < 0.05$) than that of plants grown on compost enriched with poultry manure (CP). In contrast, during the fall, LWC was significantly

Table 2 Statistical report on fixed (species and treatments) and random effect and fixed factors interaction for the investigated physiological and functional leaf traits. Nitrogen content (N), carbon content (C), quantum yield of PSII (F_{PSII}), non-photochemical quenching (NPQ), electron transport to net photosynthesis ratio (ETR/ A_N), transpiration (E), stomatal conductance (g_s -H₂O), net photosynthesis (A_N), water use efficiency (WUE), apparent carboxylation efficiency (A_N /Ci), leaf water content (LWC). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

		Fixed effect		Random effect	Residual	Interactions between fixed factors
		Species	Treatment	Season		Species x Treatment
N	F	29.1 ***	5.75 *	16.6 ***	61.9	0.36
C	F	15.5 ***	4.04 *	26.9 ***	70.9	0.36
F_{PSII}	F	5.91 **	3.58	59.1 ***	40.1	0.15
NPQ	F	14.3 ***	1.83	36.6 ***	66.3	0.53
ETR/ A_N	F	0.59	5.93 *	77.1 ***	22.9	1.82
E	F	9.49 ***	28.1 ***	49.2 ***	50.8	1.49
g_s -H ₂ O		17.3 ***	30.7 ***	66.1 ***	33.9	1.44
A_N		8.61 ***	10.4 ***	54.1 ***	48.9	0.48
WUE		0.52	4.72 *	13.7 ***	86.3	0.30
A_N /Ci		0.28	6.66 *	14.9 ***	85.1	0.55
LWC		20.3 ***	0.52	42.8 ***	52.2	0.11

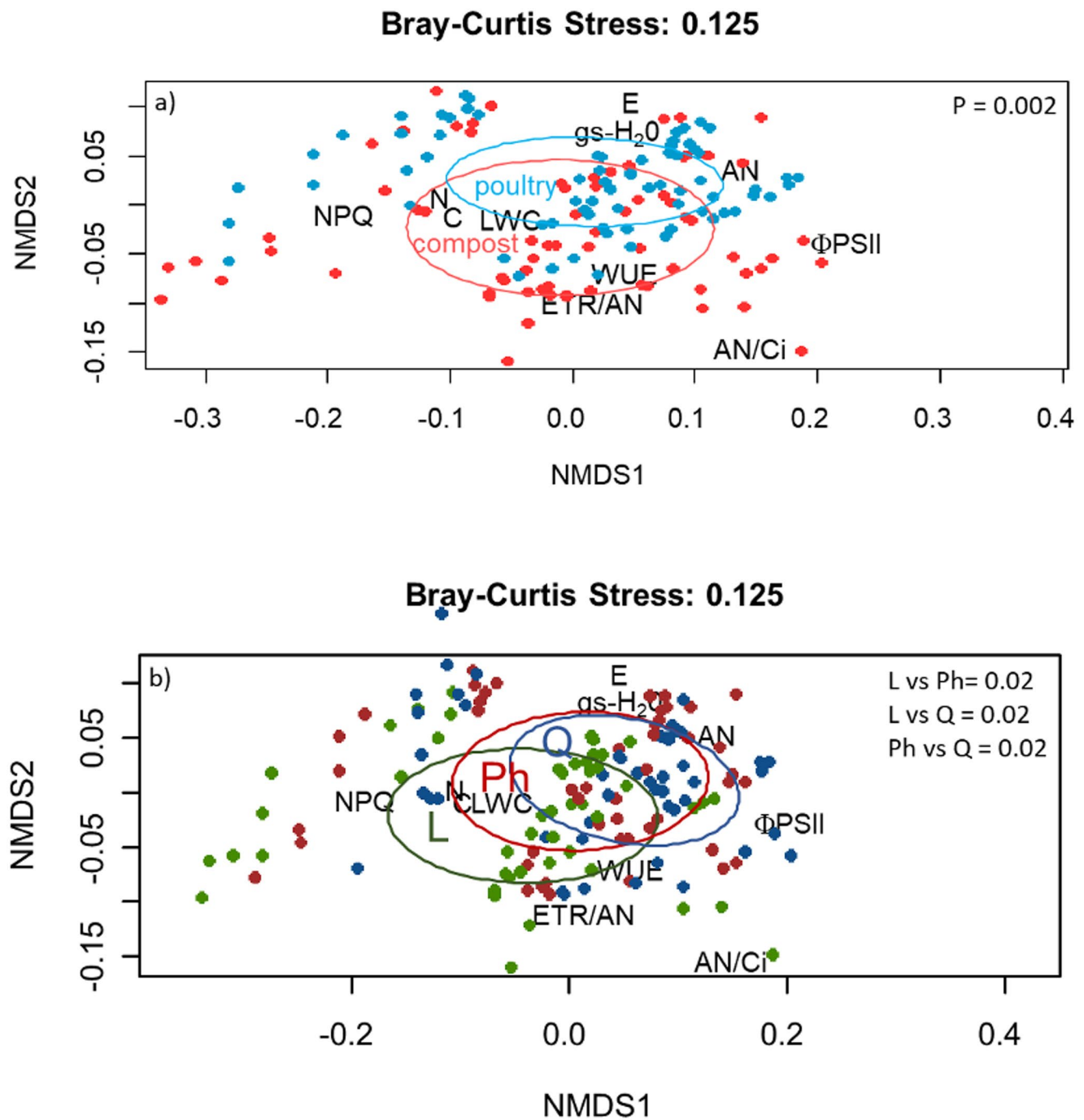


Fig. 2 Non-metric multidimensional scaling (NMDS) ordination plots (first two axes) based on Bray–Curtis distances showing variation in leaf characteristics in response to **(a)** substrate treatments (compost and compost mixed with poultry manure) and **(b)** plant species (*Phillyrea angustifolia* [Ph], *Quercus ilex* [Q], and *Laurus nobilis* [L]). The displayed leaf characteristics are: Non-photochemical quenching, NPQ; Transpiration, E; Nitrogen content, N; Carbon content C; Leaf water

content, LWC; Water use efficiency, WUE; Net photosynthesis, A_N ; quantum yield of PSII, Φ_{PSII} ; Stomatal conductance, g_s-H_2O ; Electron transport to net photosynthesis ratio, ETR/ A_N ; Apparent carboxylation efficiency, A_N/C_i . Significant differences among plant species and between treatments were reported as P-value in the graph (permutational multivariate analysis of variance - ADONIS)

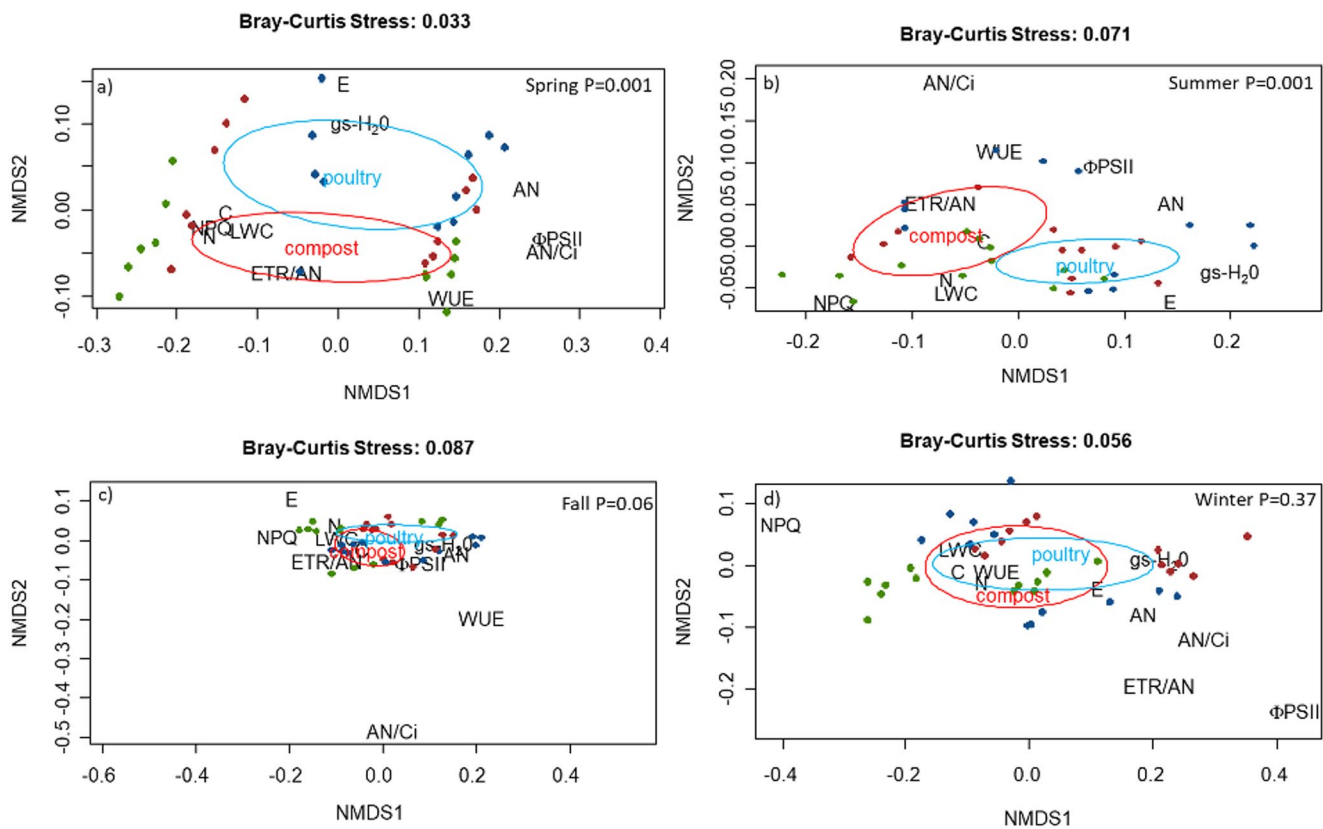


Fig. 3 Non-metric multidimensional scaling (NMDS) ordination plots (first two axes) based on Bray–Curtis distances, showing variation in plant leaf characteristics of plants grown on different substrates (compost vs. compost mixed with poultry manure) across seasons: spring (a), summer (b), fall (c), and winter (d). The displayed leaf characteristics are: Non-photochemical quenching, NPQ; Transpiration rate, E; Nitrogen content, N; Carbon content C; Leaf water content, LWC;

Water use efficiency, WUE; Net photosynthesis, A_N ; Quantum yield of PSII, Φ PSII; Stomatal conductance, g_s -H₂O; Electron transport to net photosynthesis ratio, ETR/ A_N ; Apparent carboxylation efficiency, A_N/C_i . Significant differences in leaf characteristics between substrates were reported as P-value in the graph (permutational multivariate analysis of variance - ADONIS)

higher ($P < 0.01$) in both L and Q plants grown on CP. Among the studied species, Q plants consistently exhibited the lowest LWC ($P < 0.05$), except in winter (Fig. 5A).

Conversely to LWC, the effect of substrate on leaf carbon (C) concentration was observed only in the spring for P species, where a significant decrease ($P < 0.01$) on CP compared to C substrate was evidenced. In winter, for both P and Q plants, there were significant changes: leaf carbon concentration (C) increased ($P < 0.001$) in P grown on CP, while it decreased ($P < 0.05$) in L compared to C (Fig. 5B). The highest leaf C concentration ($P < 0.05$) was found in P, except during winter.

The influence of substrate on leaf nitrogen (N) content was evident across all seasons except for summer, and its impact varied depending on species. Specifically, compared to C, N content decreased ($P < 0.05$) in P plants on CP during spring, while it increased ($P < 0.01$) in Q plants on CP during fall. In winter, leaf N content was higher ($P < 0.05$) in both P and Q plants grown on CP compared to C substrate (Fig. 5C).

The gas exchange measurements indicated that growth on C substrate did not result in a statistically significant difference in net photosynthesis (A_N) among species during spring, summer, and winter. On the contrary, during fall, A_N was significantly lower ($P < 0.01$) in Q compared to P and L plants (Fig. 6A). Stomatal conductance (g_s) and transpiration (E) were statistically higher ($P < 0.01$) in Q plants during spring and in P plants during winter, while no difference among the species was evidenced in summer and fall (see Fig. 6B, C). Plant growth on the CP substrate did not result in any differences in A_N among the diverse species (Fig. 6A). However, during spring and summer, both g_s and E were significantly lower ($P < 0.05$) in L compared to P and Q plants; conversely, these values were similar across all species in the fall and winter (Fig. 6B, C). Lastly, the water-use efficiency (WUE) did not show any statistically significant differences among the various sclerophyllous species across the seasons or between the different substrates (Fig. 6D).

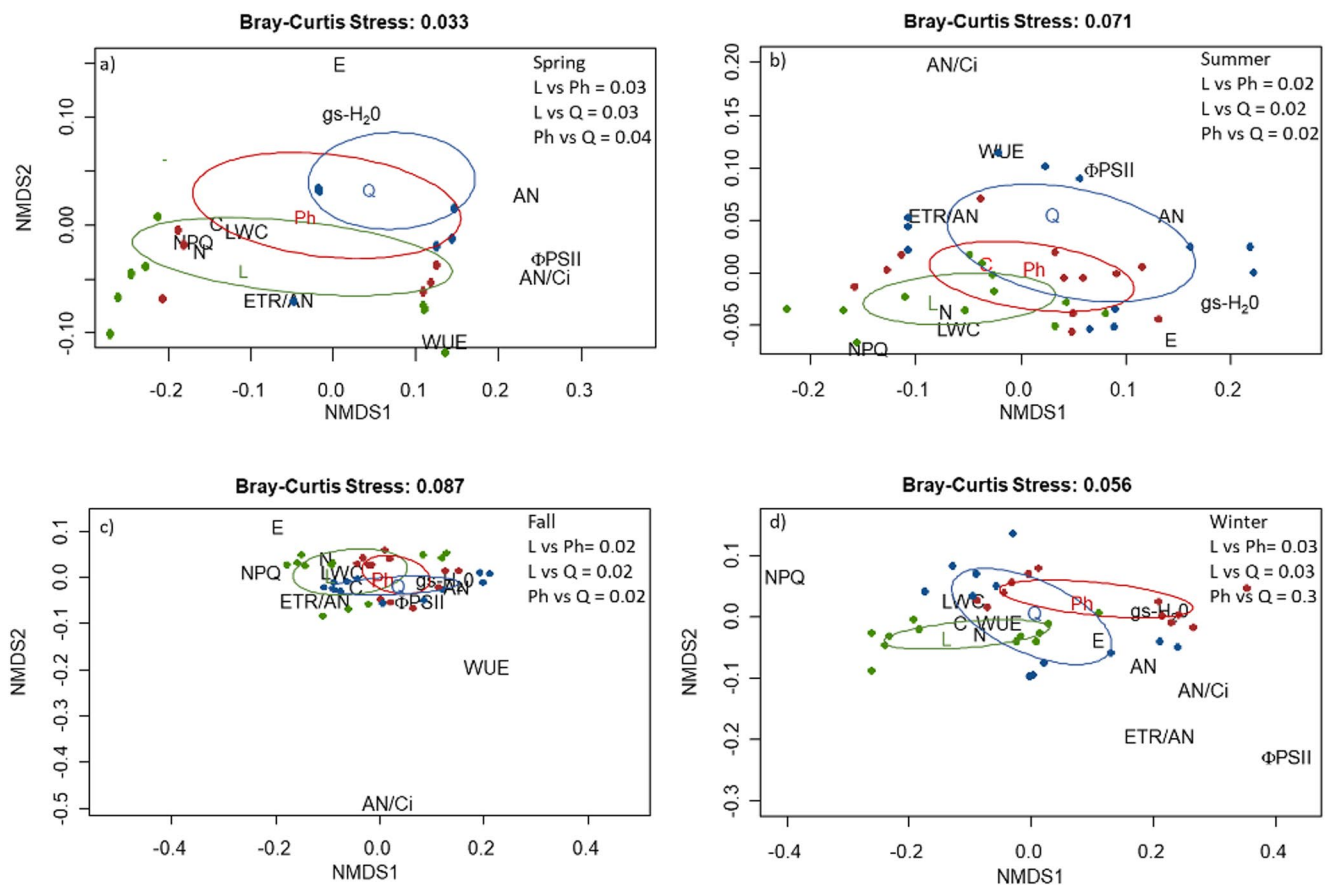


Fig. 4 Non-metric multidimensional scaling (NMDS) ordination plots (first two axes) based on Bray–Curtis distances, showing variation in leaf characteristics among plant species—*Phillyrea angustifolia* (Ph), *Quercus ilex* (Q), and *Laurus nobilis* (L) in the four seasons: spring (a), summer (b), fall (c), and winter (d). Considered leaf characteristics include: Non-photochemical quenching, NPQ; Transpiration rate, E; Nitrogen content, N; Carbon content C; Leaf water content, LWC;

On the C substrate, the effective quantum yield of photosystem II (Φ_{PSII}) significantly increased ($P < 0.01$) in Q compared to L and P plants, only during the summer and fall. At the same time, no significant differences were observed in spring and winter (Fig. 7A). Regarding the non-photochemical quenching (NPQ), levels were statistically higher ($P < 0.01$) only in L plants during the fall, with no difference among species in the other seasons (Fig. 7B). The ratio ETR/A_N was significantly higher ($P < 0.05$) in Q plants during the summer, and in both L and Q plants during the fall. No statistical difference was observed among the species in winter and spring (Fig. 7C). On the CP substrate, only L plants exhibited a significant decrease ($P < 0.05$) in Φ_{PSII} during the fall, along with a significant increase in NPQ in the summer (Fig. 7A, B). The ETR/A_N ratio showed no statistically significant differences among the species across all seasons (see Fig. 7C).

Water use efficiency, WUE; Net photosynthesis, A_N ; quantum yield of PSII, Φ_{PSII} ; Stomatal conductance, g_s-H_2O ; Electron transport to net photosynthesis ratio, ETR/A_N ; Apparent carboxylation efficiency, A_N/C_i . Significant differences in leaf characteristics among plant species were reported as P-value in the graph (permutational multivariate analysis of variance - ADONIS)

Seasonally variation in leaf functional and photosynthetic traits of sclerophyllous grown on compost and compost mixed with poultry manure

In summer, leaf water content (LWC) of L plants was significantly higher ($P < 0.05$) when grown on the C than CP substrate, while in fall, LWC was statistically higher ($P < 0.01$) in CP than C for both L and Q plants. No statistically significant difference was observed between C and CP substrates for the same species in winter and spring (Fig. 5A). Regarding leaf carbon concentration (C) P plants exhibited a significantly higher C level ($P < 0.01$) when grown on the C substrate during spring, and L plants showed higher C levels in winter on the C compared to CP substrate. Conversely, in winter, the C concentration in the leaves of P plants significantly increased ($P < 0.01$) when grown on CP compared to C substrate, and no difference was found between the same

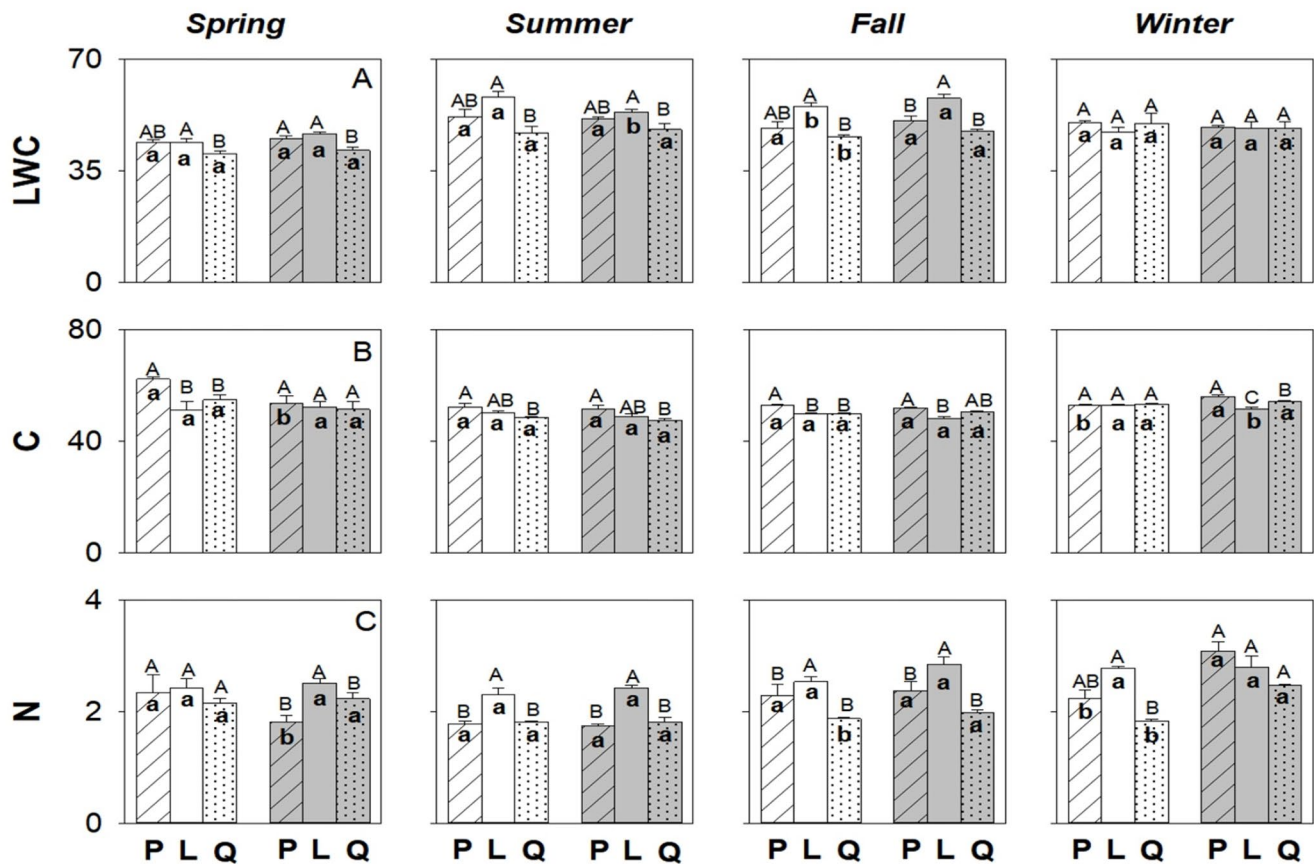


Fig. 5 Mean values ($\pm$ s.e.) of leaf water content (LWC) (A) and total C and N concentrations (B–C) in leaves of *P. angustifolia* (P, coarse bar), *L. nobilis* (L, empty bar) and *Q. ilex* (Q, dotted bar) grown on compost (white bars) and compost enriched with poultry manure (grey bars) in

different sampling seasons (Spring, Summer, Fall and Winter). Capital letters indicate the differences among the plant species within the same treatment. Lowercase letters indicate the differences between the treatments within the same plant species

species of plants grown on C and CP during the other two seasons (Fig. 5B).

For leaf nitrogen (N) concentration, significant differences were observed in P plants which showed higher values ($P < 0.05$) on C than on CP during spring. On the other hand, in autumn, L plants had a higher N concentration on CP compared to C, while in winter, both P and Q plant species exhibited higher N concentrations ($P < 0.05$) when grown on CP rather than on C (Fig. 5C).

The net photosynthesis (A_N) was significantly higher ($P < 0.01$) for all species grown on CP compared to C substrate during the spring and summer, while in the autumn, this was also true for L and Q plants (Fig. 6A). During spring, stomatal conductance (g_s) was statistically higher ($P < 0.01$) in all species grown on CP compared to C substrate, and this pattern continued in the summer for P and Q, as well as in the fall for Q plants. However, in autumn and winter, g_s did not show significant differences among the same species on different substrates (see Fig. 6B).

During spring the transpiration rate (E) was statistically higher ($P < 0.05$) on CP than C for all species and

this trend also persisted through summer, fall and winter (Fig. 6C). Water use efficiency (WUE) was statistically higher ($P < 0.001$) in Q plants grown on C compared to CP in winter, while no significant difference among species was observed during other seasons (Fig. 6D).

In autumn, the quantum yield of PSII electron transport (Φ_{PSII}) was statistically higher ($P < 0.05$) in all species grown on CP than on C. In summer a similar trend was observed in P and L plants (Fig. 7A). Moreover, neither non-photochemical quenching (NPQ) nor the ratio ETR/A_N varied significantly among different sclerophyllous species across all seasons. The only exception was represented by ETR/A_N ratio of Q species which was statistically higher ($P < 0.05$) in plants grown on C than on CP in both spring and summer (Fig. 7B, C).

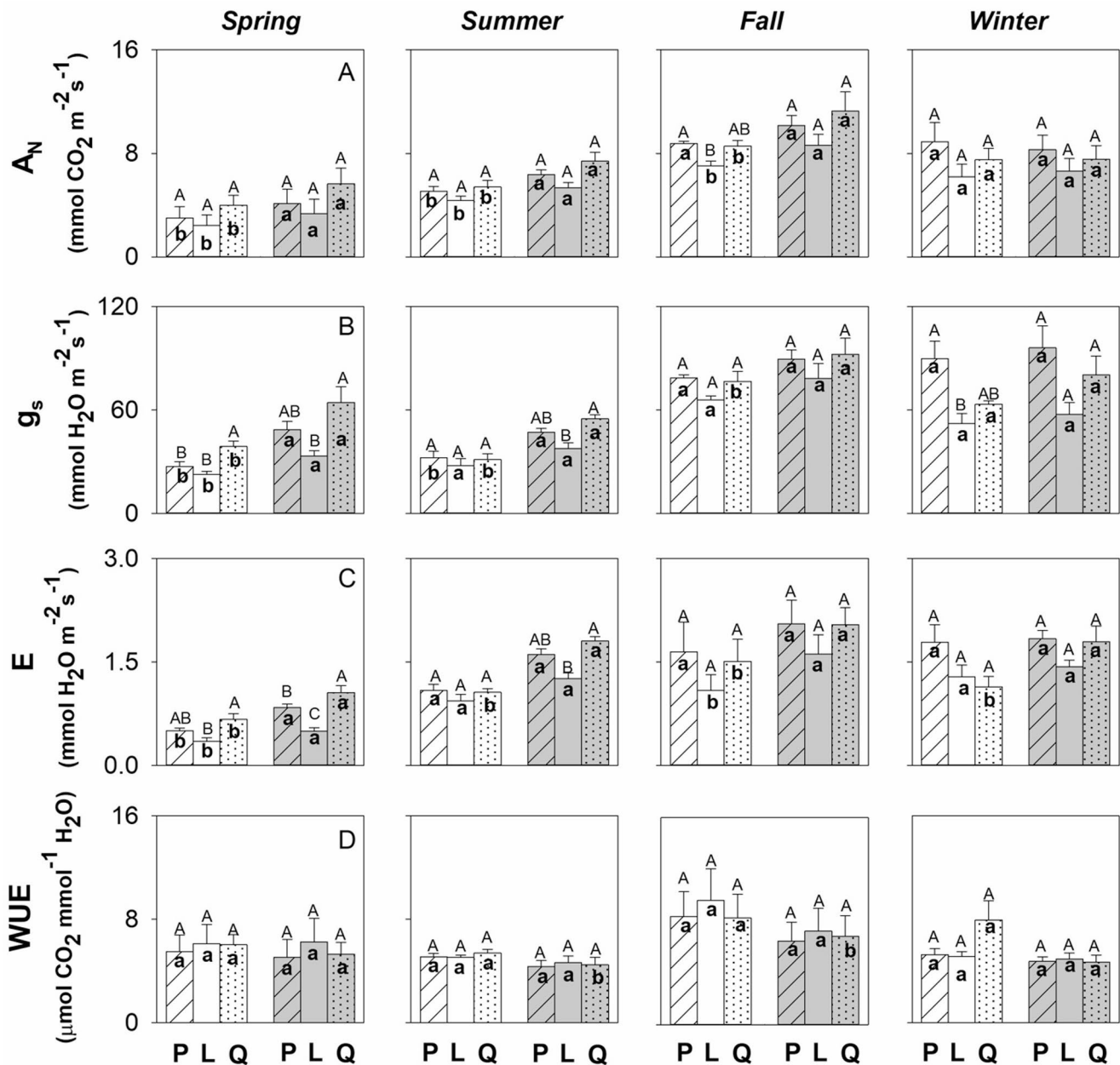


Fig. 6 Mean values ($\pm$ s.e.) of net photosynthesis (A_N)(A), stomatal conductance (g_s)(B), transpiration rate (E)(C), water use efficiency (WUE)(D) in leaves of *P. angustifolia* (P, coarse bar), *L. nobilis* (L, empty bar) and *Q. ilex* (Q, dotted bar) grown on compost (white bars) and compost enriched with poultry manure (grey bars) during differ-

ent sampling seasons (Spring, Summer, Fall and Winter). Capital letters indicate the differences among the plant species within the same treatment. Lowercase letters indicate the differences between the treatments within the same plant species

Discussion

In this study, we evaluated if three representative species of the Mediterranean maquis vegetation (*Q. ilex*, *P. angustifolia* and *L. nobilis*) could grow on waste-derived substrates (quarry debris) enriched with compost (C) and compost mixed with poultry manure (CP) with the primary aim to reusing waste materials as idoneous substrates for plant

cultivation. Plant functional and ecological traits monitored over one year evidenced that both seasonality and substrate type significantly influenced the physiological performance. Compared to C, plant growth on CP substrate significantly improved photosynthetic activity in all three species, with increases of 25%, 12%, and 20% for *Q. ilex*, *P. angustifolia*, and *L. nobilis*, respectively, indicating that the CP substrate is more idoneous for plant growth. This conclusion was further supported by greater trunk diameter and stem

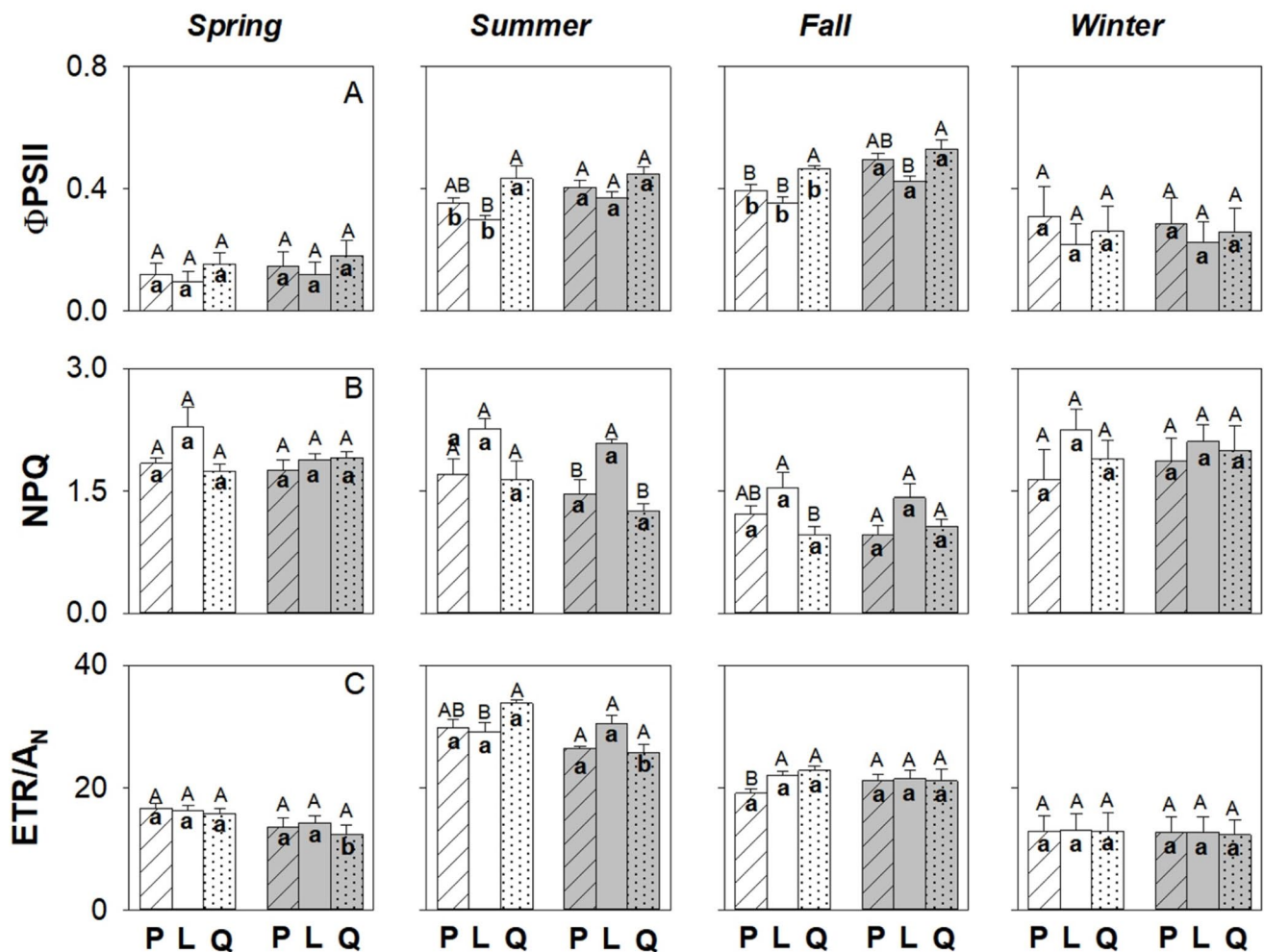


Fig. 7 Mean values ($\pm$ s.e.) of quantum yield of PSII electron transport (Φ PSII)(A), non-photochemical quenching (NPQ)(B), electron transport rate and net photosynthesis ratio (ETR/A_N)(C) in leaves of *P. angustifolia* (P, coarse bar), *L. nobilis* (L, empty bar) and *Q. ilex* (Q, dotted bar) grown on compost (white bars) and compost enriched with

poultry manure (grey bars) at different sampling times (Spring, Summer, Fall and Winter). Capital letters indicate the differences among the plant species within the same treatment. Lowercase letters indicate the differences between the treatments within the same plant species

height observed in plants of the three species grown on the CP substrate after one year. The different suitability of C and CP substrates was evident, especially during summer, when photosynthetic carbon fixation rate on CP was 22%, 25%, and 37% higher than on C substrate in *Q. ilex*, *P. angustifolia*, and *L. nobilis*, respectively.

The increased photosynthetic carbon fixation observed in plants grown on the CP compared to C substrate during the summer sustains the activity of the photosynthetic electron chain, by using all the reductive power (ATP and NADPH) in photochemistry. This efficient utilization of light energy in photochemical reactions helps reduce the risk of photo-inhibition to the photosynthetic apparatus, a typical constraint under high temperatures and light intensities typical of Mediterranean summer season (Dideran et al., 2024). Furthermore, changes in nutrient and organic matter content, detected after one year support the evidence of deep

interactions between plant metabolism and growth on the two different substrates. Specifically, after one year, both the C and CP substrates exhibited a significant decrease in total and available nutrient content; however, this decline was more pronounced in the CP medium, suggesting higher nutrient availability initially, followed by rapid uptake by plants during their growth.

Consistent with the hypothesis that the CP substrate provides a more readily available reservoir of nutrients for plant growth, the reductions in available nutrient and organic matter (OM) in the CP substrate were greater: Zn (-36%), Ni (-75%), Fe (-64%), Cu (-54%), and OM (-44%), than those found in the C substrate: Zn (-9%), Ni (-5%), Fe (-30%), Cu (-29%), and OM (-7%). This observation is supported by a study conducted on the same mesocosms by Memoli et al. (2017), which demonstrated that even 17 years after their

establishment, the CP substrate remained richer in available nutrients compared to C substrate.

The significant reduction in organic matter indicates a continuous release of nutrients to the plants, likely contributing to the increased productivity observed in the CP substrate (Gerke 2022). The enhanced photosynthetic activity in CP compared to C plants is consistent with the observed increase in plant height of +52%, +48% and +80% and in trunk diameter of +108%, +54% and +82% in *P. angustifolia*, *L. nobilis* and *Q. ilex*, respectively, after one year of growth on CP substrate, confirming the best fitness of CP substrate for plant development. It is ascertained that Zn, Ni, Fe, and Cu are essential enzyme cofactors involved in photosynthetic metabolism, including chlorophyll synthesis, light reactions, and electron transport activities (Adamczyk-Szabela and Wolf 2024).

The CP substrate also showed a higher water-holding capacity (WHC), which was retained after one year of plant growth. WHC is influenced by several factors including soil temperature, microbial respiration, substrate availability, root type, plant growth, stomatal conductance, transpiration, and belowground carbon allocation. Water dissolves nutrients and facilitates their absorption and movement through plants, sustaining vegetative growth throughout the year, particularly during the summer dry season, when maintaining an adequate water balance enhances plant tolerance to high temperatures (Farhad et al. 2018; Rockwell and Sage 2022). The higher water holding capacity of CP compared to C substrate may explain the increased transpiration rates (+26% in *P. angustifolia*, +31% in *L. nobilis* and +53% in *Q. ilex*) observed in CP plants compared to C across all seasons. This increase in transpiration is generally associated with higher photosynthetic gains (Asargew et al. 2024).

The utilization of CP substrate as a growing medium appears particularly promising during the summer, when Mediterranean ecosystems are subjected to drought and sclerophyllous species experience limitations in leaf gas exchange, which may compromise the functionality of photosynthetic apparatus (Pellegrini et al. 2021). It has been demonstrated that Mediterranean sclerophyllous species *P. angustifolia*, *L. nobilis* and *Q. ilex* are well adapted to drought conditions through morphological and physiological traits like small thick waxy leaves, deep root systems, and tight stomatal control to reduce water loss thereby maintaining water relationships and a positive carbon balance (Ramírez-Valiente et al., 2021; Kaproth et al. (2023). However, the increasing aridity due to environmental changes is starting to reveal the limitations of these adaptations (Miranda et al. 2023).

In this context, the elevated soil water-holding capacity, combined with a readily available reserve of organic matter in CP substrate, is a crucial attribute that allows plants

satisfy their evaporative demand and nutrient requirements helping them survive, especially during the summer drought periods typical of Mediterranean regions (Tramblay et al. 2020; Gerke 2022). The enhanced photosynthetic capacity of sclerophyllous species on CP substrate benefits both natural and urban ecosystems; indeed, Mediterranean maquis plants are often utilized to recover urban soils and mitigate urban heat islands through the transpiration process (Vitale et al. 2024). Using CP substrate for plant growth may increase transpiration rates favoring the cooling effect in an urban context, providing an important ecosystem service.

Prolonged dry summers, typical of Mediterranean areas and intensified by climate change, negatively impact the photosynthetic apparatus of sclerophyllous species, which retain leaves throughout the year, resulting in reduced carbon assimilation under drought. The photosynthetic decline leads to the overproduction of reactive oxygen species, which damages the photosystems (Pellegrini et al. 2021). Additionally, high temperatures and vapor pressure deficits induce stomatal closure and reduced transpiration, enhancing leaf temperature and photoinhibition (Marchin et al. 2023). Our study demonstrates that the benefits of plant growth on CP substrate, compared to C, are particularly evident during summer, when both gas exchanges and photochemical processes are promoted. Growth on CP substrates improves the efficiency of photosynthetic electron transport, which reduces the need to dissipate excess absorbed light photochemically or thermally to avoid photoinhibition (Murakami et al. 2024).

The higher photochemical efficiency observed during summer and maintained during fall is responsible for the elevated photosynthetic rate in these months compared to winter and spring, when the photochemical efficiency declined, making essential the activation of thermal (increase of NPQ) and photochemical (increase of ETR/A_N) dissipation processes as safety mechanisms against photoinhibition (Arena et al. 2008; Didaran et al. 2024). Our data also indicate that, even if all species on the CP substrate showed a better physiological performance than in C, they employ different photoprotective mechanisms to achieve it, especially in summer. For instance, *L. nobilis*, which exhibits the highest NPQ values, employs thermal dissipation as a preferred safe strategy.

Among species, *Q. ilex* grown on CP substrate exhibited significantly higher values of g_s (+32% vs. 23% in *P. angustifolia* and 20% in *L. nobilis*) and E compared to other species, suggesting a more efficient stomatal control in response to seasonal climatic variations. The higher stomatal conductance in CP than C plants, associated to the better water holding capacity of this substrate, can be considered a physiological advantage as the stomata opening guarantees a higher CO_2 supply at the carboxylation site and promote

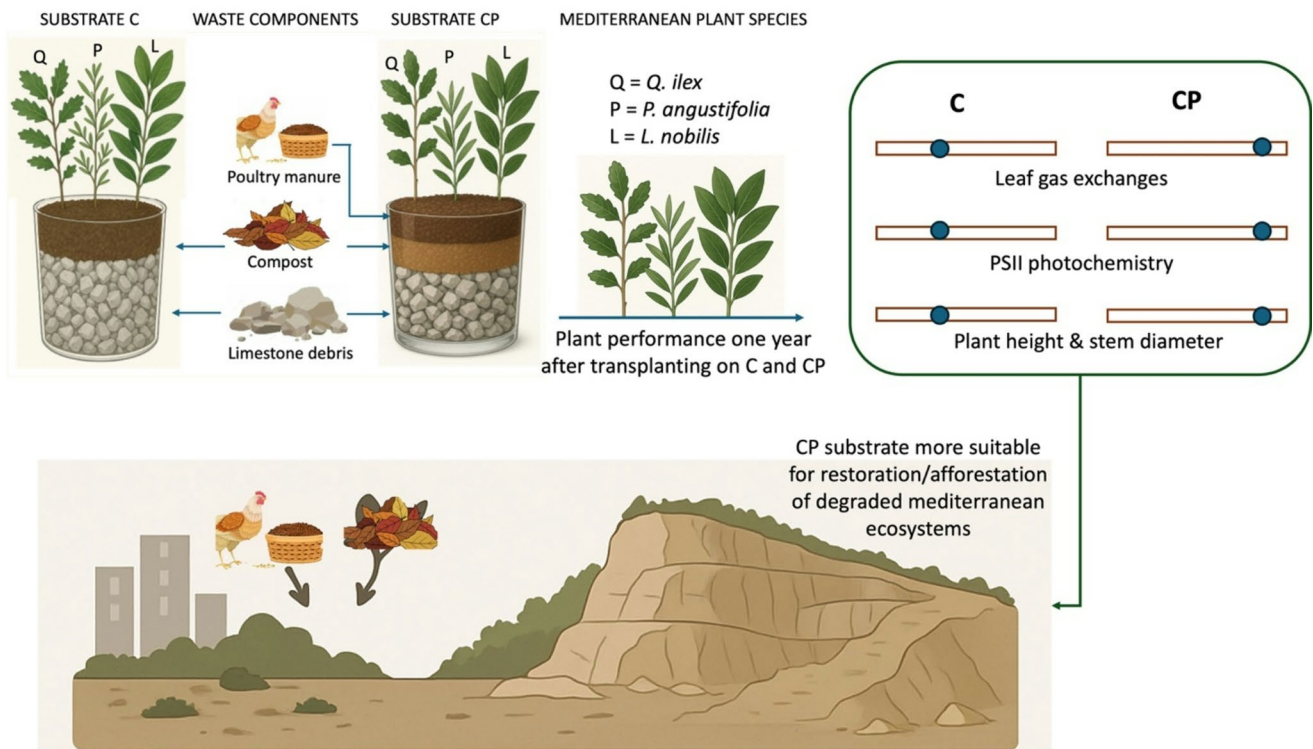


Fig. 8 Summary illustration of the main physiological (leaf gas exchanges, photochemistry of photosystem II - PSII) and morphological (plant height and stem diameter) outcomes after one year of growth

leaf cooling via transpiration, under hot summer conditions (Urban et al. 2017).

The adequate hydration status in both C and CP substrates may explain the stable values of WUE observed across all species and seasons. Furthermore, the maintenance of good plant-water relationships provides evidence that adding a mixture of compost and poultry manure to inert limestone debris can yield an idoneous substrate capable to sustain plant growth, even under summer drought conditions. The main results of this study are summarized in Fig. 8. The two substrates affected the primary production (leaf gas exchanges and PSII photochemistry) of the tree species differently. Overall, regardless of species, the CP substrate promoted higher photosynthesis and photochemical efficiency compared to the C substrate. This enhancement in physiological performance resulted in increased biomass production, as evidenced by the greater stem and plant diameter after one year of growth.

Conclusions

This study demonstrates the strong potential of compost–poultry manure (CP) substrate, derived from organic waste and quarry debris, as a sustainable alternative to conventional soils. One-year monitoring of plant on C and CP

on compost (C) and compost enriched with poultry manure (CP) in the Mediterranean species: *Q. ilex* (Q), *P. angustifolia* (P), and *L. nobilis* (L.)

substrates evidenced significantly higher photosynthetic activity, transpiration rates, and photochemical efficiency in CP compared to C plants. The physiological advantages of plant growth on CP substrate resulted in increased biomass, with greater plant height and trunk diameter across all tested species. During summer drought, especially *Q. ilex* takes advantage from higher water-holding capacity of CP substrate, which supports high transpiration rates for leaf cooling. The enhanced suitability of CP medium in sustaining plant productivity is likely ascribed to its greater reserve of essential nutrients, readily available organic matter, and higher water-holding capacity than C substrate. Our study indicates CP substrate as a low-cost solution for reforestation, urban greening, and ecological restoration—especially in degraded or post-industrial landscapes where traditional soils are scarce or overexploited. By repurposing agricultural and quarry by-products, the study supports a circular economy approach to land management. In the climate change scenario, which threatens soil fertility, water availability, and urban ecosystems, integrating such waste-based substrates can play a pivotal role in promoting long-term environmental sustainability.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42398-025-00365-9>.

Author contributions G.M., A.D.M. and C.A. contributed to study conceptualization and design. L.S., L.V., V.M., E.V. and C.A. conducted the formal analysis. C.A. and L.V. contributed to investigation and methodology. C.A., G.C., V.M., G.S., L.S. and E.V. curated data. L.S. validated data. G.M. provided founding and resources. C.A. supervised the project. L.S. and C.A. wrote the original draft. All authors revised, edited and approved the final version of the manuscript.

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Data availability Data are available upon reasonable request from the authors.

Declarations

Ethical approval The research work embodied in the MS does not involve Human Participants and/or Animals, and as such does not require Ethical Clearance.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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