

Cork oak seedling establishment following an exceptionally dry winter: Effects of container type in a Mediterranean forest restoration initiative

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ABSTRACT

Changing climatic conditions pose significant obstacles for reforestation and restoration, increasing the risk of planting failure. Following outplanting, seedlings face a critical stage where the root system is not yet fully developed to ensure adequate water uptake. In this context, container type influences nursery seedling traits and may affect establishment in Mediterranean forest restoration, where erratic drought events are becoming increasingly frequent. We evaluated the effects of four container types (Tray, Single pot, Small Air-pot and Big Air-pot) on nursery morphology and outplanting performance of *Quercus suber* 1-yr-old seedlings planted in December 2022 in a post-fire restoration site in central Italy, across two slopes with different aspects, which were characterised in terms of soil and spontaneous vegetation. Shortly after planting, an unusually dry winter led to complete defoliation of all seedlings, providing a rare opportunity to assess their response to unexpected post-planting drought in terms of resprouting, physiology, and stable isotope signatures. Container type strongly influenced nursery seedling morphology and post-planting performance under the unexpected winter drought conditions. Seedlings grown in the Big Air-pot, the largest container tested, exhibited greater nursery size, higher survival, faster early growth, and enhanced resprouting capacity after outplanting. Physiological traits of the dominant resprouting shoot did not reveal signs of stress during the growing season. In contrast, south-facing slopes imposed harsher environmental conditions, resulting in more constrained seedling responses, in agreement with plant ecological requirements observed across sites. These findings identify container design as a key determinant of seedling quality and early establishment success, highlighting its importance for Mediterranean forest restoration under increasing climatic stress.

1. Introduction

The Mediterranean basin is among the regions most vulnerable to climate change and has been identified by the Intergovernmental Panel on Climate Change (IPCC) as a climate hotspot, with projections of rising mean temperatures and more frequent extreme events (Ali et al., 2022; Jézéquel et al., 2025). Alongside increasingly prolonged and severe summer droughts, the region is experiencing unpredictable dry periods even during typically wetter seasons, with winter precipitation projected to decline by up to 40% (Caloiero et al., 2018; Tuel and Eltahir, 2020). Reduced rainfall combined with higher temperatures is altering soil

water balance and intensifying the risk of severe water shortages (Noto et al., 2023).

These changing climatic conditions add major challenges for reforestation and restoration, increasing the risk of planting failure (Vallejo et al., 2012; Peñuelas and Sardans, 2021). After outplanting, seedlings face a critical phase in which the root system is still insufficiently developed to ensure adequate water uptake (Grossnickle and Ivetić, 2022). Rapid development of new roots capable of penetrating deeper, moister soil layers is therefore essential (Grossnickle, 2012; Pinto et al., 2016; Andivia Muñoz et al., 2019). At this stage, limited soil hydraulic conductivity may induce drought stress even under relatively favourable soil moisture conditions

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(Grossnickle, 2005; Grossnickle and Ivetić, 2022), and water shortage remains a primary constraint to establishment in Mediterranean restoration projects (Mendoza et al., 2009; Puertolas et al., 2024). Post-planting stress is particularly severe in Mediterranean environments characterised by intense summer drought, making early root growth decisive for seedling survival (Castro et al., 2004; Villar-Salvador et al., 2012; Andivia Muñoz et al., 2019).

Rapid root growth after outplanting is shaped by both extrinsic factors and intrinsic seedling traits (Vallejo et al., 2012; Dumroese et al., 2016; Grossnickle and MacDonald, 2018), and survival in afforestation and reforestation projects depends on their interaction (Villar-Salvador et al., 2004, 2012). Clarifying these relationships is essential to improve plantation success (Ostertag et al., 2016; Andivia et al., 2021). Development of good practice protocols considering all phases of a reforestation project—from site preparation to planting timing and post-planting care—can assure root and shoot growth as well as enhance soil water availability, thereby influencing establishment, particularly under limiting site conditions (Ceacero et al., 2012; Ivetić and Devetaković, 2016; Del Campo et al., 2021).

In Mediterranean environments, planting is typically carried out in autumn or winter to take advantage of higher soil moisture during the cooler, wetter season (Mediavilla and Escudero, 2004; Villar-Salvador et al., 2012, 2026). After outplanting, rapid root growth and early soil exploration rely heavily on storage compounds accumulated within seedlings during nursery cultivation (Villar-Salvador et al., 2015, 2026; Toca et al., 2022). Accordingly, morphological and physiological traits of nursery-grown seedlings are critical indicators of plant functionality (Grossnickle and MacDonald, 2018; Toca et al., 2022; Villar-Salvador et al., 2026). These functional traits result from nursery practices—including stock type (container-grown or bare-root), growing density, age, nutrient management, irrigation, shading, and storage—which influence seedling size, shoot and root biomass, root architecture, and the accumulation of non-structural carbohydrates (NSC) and nutrients (Landis and Nisley, 1990; Landis et al., 1990; Cortina et al., 2013; Villar-Salvador et al., 2026; Grossnickle et al., 2020). By adjusting nursery practices, seedling traits can therefore be modulated to improve adaptability to planting conditions (Grossnickle, 2012).

The relationship between seedling size at planting and post-planting survival has long been debated. Some studies have suggested that smaller seedlings with a low shoot-to-root ratio may outperform larger ones, particularly under arid conditions. (i.e., Tuttle et al., 1988; Trubat, Cortina, and Vilagrosa, 2011), indicating that seedlings with a smaller transpiring shoot and a relatively larger root system (low shoot-to-root ratio, S/R) are better able to sustain growth (Villar-Salvador et al., 2026). These phenotypes have been typically associated with a conservative growth strategy that enhances resource-use efficiency, making seedlings more resilient under drought conditions (Villar-Salvador et al., 2026). However, it is well documented that larger seedlings - those with greater height, root collar diameter, or biomass - often exhibit higher survival rates than smaller ones (i.e., Mason et al., 1996; South et al., 2005; Cuesta et al., 2010a; Pinto et al., 2011; Villar-Salvador et al., 2012; Andivia et al., 2021, Villar-Salvador et al., 2026). Moreover, larger seedlings with a balanced S/R benefit from greater resource reserves and enhanced mobilization of nutrients and NSC accumulated during nursery cultivation (Cuesta et al., 2010b; Villar-Salvador et al., 2012; Andivia et al., 2021). This can improve growth potential, establishment, competitive ability, and drought resistance (Wagner, 2005; Villar-Salvador et al., 2012). However, this growth pattern also entails higher resource demand and may increase water loss through greater shoot transpiration (Grossnickle, 2012; Oliet et al., 2019).

Research has shown that the size and design of nursery containers can influence seedling growth, S/R, and post-planting survival (e.g., Landis et al., 1990; NeSmith, Duval, 1998; Aphalo and Rikala, 2003; Tsakalimi et al., 2005; Dominguez-Lerena et al., 2006; Pinto et al., 2011; Sun et al., 2018). Container characteristics can affect biomass allocation between shoots and roots (Tsakalimi et al., 2005; Mariotti

et al., 2015a) and shape root system architecture (Oddiraju et al., 1994; Heiskanen and Rikala, 1998; Chirino et al., 2008; Mariotti et al., 2015a). Consequently, container type can influence seedling establishment (South et al., 2005; Dominguez-Lerena et al., 2006; Villar-Salvador et al., 2026) and, ultimately, the effectiveness and cost of reforestation efforts (NeSmith and Duval, 1998; Pinto et al., 2011).

In this context, the present study was designed to evaluate whether four different container types – different in structure and volume – influence the size of evergreen cork oak (*Quercus suber*) nursery seedlings and, consequently, to assess their establishment within a forest restoration project implemented four years after a wildfire in a Mediterranean area. We hypothesized that different container types affect seedling morphological and physiological traits, leading to different establishment and performance. Planting was carried out in early December 2022, following local standard practices. However, the subsequent winter was characterized by an unexpected and prolonged dry period that markedly deviated from the typical Mediterranean conditions and caused the complete defoliation of the cork oak seedlings. By the onset of the first growing season in spring 2023, all planted seedlings had lost their entire canopy. This event prompted a reformulation of the study objectives to evaluate how four containers types may affect: (a) cork oak seedling morphology at the nursery stage (growth and biomass), and (b) the nursery seedlings' capacity to respond to post-planting winter drought, assessed through morphological (total height, dominant shoot length, root collar diameter, number of leaves of the dominant shoot and number of new shoots) and physiological parameters (chlorophyll content and fluorescence, leaf carbon and nitrogen concentration and isotopic composition). This atypical climatic event provided, to our knowledge, a rare opportunity to evaluate the performance of container-grown seedlings under field conditions that are projected to become increasingly frequent in Mediterranean environments due to climate change, particularly with respect to winter and spring droughts.

2. Materials and methods

2.1. Study area

The study area is located in the municipality of Vicopisano (43° 42' 26.1" N 10° 32' 32.0" E, Central Italy) at approximately 400 m a.s.l. The site burned during a wildfire in September 2018 (<https://www.regione.toscana.it>). Before the fire, the area was predominantly covered by a monospecific stand of *Pinus pinaster*. Currently, the surrounding vegetation consists mainly of *P. pinaster* and *Olea europaea*, with secondary growth of forest and shrub vegetation, as well as mixed coniferous and sclerophyll forests. A more restricted portion of deciduous forest is also present, mainly mixed forests of *Castanea sativa* with other broadleaved species (i.e., *Robinia pseudoacacia*, *Acer campestre*, *Ulmus minor*, *Alnus glutinosa*, *Quercus* spp.). The study site (0.6 ha) is part of a forest restoration project in the burned area characterized by scarce natural regeneration of tree species and consists of a hillside divided into two slopes with contrasting exposures. The south-facing (Side A) and northwest-facing (Side B) slopes were included as environmental factors in the experimental design due to their differing site conditions after preliminary visual assessment. The two site slopes were further characterized in terms of soil properties and vegetation.

2.1.1. Site climate and anomalous post-planting aridity

The climate of the study area is humid and temperate, with summer seasonal aridity. The mean annual air temperature is 14.3 °C, with an average annual rainfall of 1089 mm. During summer, the mean temperature reaches 23.4 °C, with total rainfall reaching 130 mm.

Following the unforeseen aridity event, we conducted a retrospective analysis of meteorological data from Climate Downscaling Tool (<https://climatedt.org/>) to characterize this anomalously dry period. Compared with the previous 30-year average, February and March 2023 experienced below-average precipitation (53.6 mm in 2023), maximum temperatures more than 1 °C above the long-term mean (11.3 °C in 2023),

and a negative Standardized Precipitation–Evapotranspiration Index (SPEI = −1.10 in 2023; Fig. 1). Such climatic conditions were corroborated by historical records by the meteorological Tuscany geoportal (Lamma; https://geoportale.lamma.rete.toscana.it/rischio_incendi/index.phtml): the Drought Code (DC; deep soil moisture >10 cm) and the Duff Moisture Code (DMC; litter moisture), both commonly used in wildfire risk assessment, reached unusually high values in February and March 2023, reflecting low moisture conditions.

2.1.2. Soil sampling and analysis

Three bulk soil samples were collected in Side A and Side B at two depths (i.e., 0–10 and 10–20 cm). Soil samples were collected to represent the seedling planting areas. Soil samples were collected in November 2022 (the day of planting), June 2023, September 2023, and November 2023. Samples were air-dried and sieved at 2 mm before physical, chemical and biological analysis. Size distribution of aggregates (0.02–2000 µm) was measured using a laser granulometer Mastersizer 3000 (Malvern Panalytical Ltd., UK), equipped with a wet sample dispersion unit. Afterwards, soil samples were sonicated in the granulometer recirculation system and measured again. Ultrasound was applied until the size distribution of dispersed particles was constant. The aggregate granulometric curve was compared to the curve obtained at the end of ultrasound application. Index of aggregate stability (ASI) were determined as the difference between the median diameter of soil samples before and after sonication. Soil pH and EC were measured in water extract 1:2.5 and 1:2, respectively, using specific electrodes (ASA-SSSA, 1996). Cation exchange capacity (CEC) was measured by the barium chloride method (Sumner and Miller, 1996). Total organic carbon (TOC) and total nitrogen (TN) were determined by dry combustion using a Flash Smart NC Soil elemental analyser (Thermo Fisher Scientific, Waltham, MA, USA). Soil samples for TOC measures were previously treated with HCl:H₂O (1:1 v:v). Soil sieved samples (0.3 g) were digested by a microwave (ETHOS 900, FKV, Torre Boldone, BG, Italy) using a HNO₃:H₂O₂ mixture (5:2 v:v), following the EPA Method 3051a. Then, the total concentration of Ca, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, Zn were determined using inductively coupled plasma spectrometry (ICP-OES 5900 Agilent, Santa Clara, CA, USA) and expressed as mg kg^{−1}. Olsen P was calorimetrically determined using the molybdenum blue method (ASA-SSSA, 1996). The available concentrations of macronutrients (Ca, K, Mg) for plants were also measured by ICP-OES after extraction with 1 M H₃COONH₄ at pH 7. The soil hydrolytic enzyme activities were determined following the methods proposed by Marx et al. (2001) and Vepsäläinen et al. (2001), using fluorogenic methylumbelliferyl (MUB)-substrates. The enzymes analysed were β-glucosidase (BG; EC 3.2.1.21), phosphatase (P; EC 3.1.3.2), N-acetyl-β-D-glucosaminidase (NAG, EC 3.2.1.14). Fluorescence was measured with an automated fluorometric plate reader (Infinite F200 pro, TECAN, Switzerland). The enzyme activities (BG, P and NAG) were normalized to TOC and expressed as µmol MUB g^{−1} TOC h^{−1}. The vector

analysis as a quantitative method based on the calculation of vector lengths and angles of plotted proportional enzyme activities (C:N vs C:P acquisition) was applied. The analysis quantifies the vector lengths as the relative investments in C vs N and P acquisitions and the vector angles as P vs N acquisition (Moorhead et al., 2016; Cui et al., 2020). The vector analysis was carried out using the method reported by Moorhead et al. (2016), for assessing the magnitude of microbial resource limitation. The vector length (VL) and vector degree (VD) were calculated as follows:

$$VL = \sqrt{(\ln BG / \ln BG + \ln NAG)^2 + (\ln BG / \ln BG + \ln P)^2}$$

$$D = \text{Degrees}(\text{ATAN2}(\ln BG / \ln BG + \ln NAG), (\ln BG / \ln BG + \ln P))$$

Greater values of VL indicate greater C-limitation vs N/P limitation; the VD < 45° refers to N-limitation, while > 45° to P limitation.

2.1.3. Vegetation survey

In summer 2023, vegetation surveys were conducted to characterize the plant communities and environmental conditions at the two slopes. Sixteen 5 × 5 m quadrats were established, centered on the experimental seedling plots (eight in Side A and eight in Side B, as described in Section 2.3). For each quadrat, the following variables were recorded: (i) total ground cover percentage; (ii) maximum vegetation height; and (iii) species identity and individual ground cover for all vascular plants (trees, shrubs, and herbs). Species identification followed Pignatti et al. (2017). These data were used as biological indicators of site severity to compare the two slopes.

2.2. Nursery seedlings cultivation

Sowing took place at the beginning of 2022, using local seed source. Indeed, close to the study area, there is a local population of *Q. suber*. Seeds were gathered from ten mother trees, each spaced at least 50 m apart, ensuring equal representation in the study. The acorns were stored in moist sand at 3 ± 0.5 °C to simulate natural overwintering conditions and prevent premature germination. In early April, acorns were weighed, and those with weights within ±5% of the seed lot meanweight were placed in moist sand at 18 °C. After one week of pre-germination, 96 acorns with radicles shorter than 5 mm were randomly chosen. The seedlings were grown in the nursery facilities at the Department of Agriculture, Food, Environment and Forestry (DAGRI), University of Florence (43°48'30.53"N; 11°12'01.46"E). Seedlings were grown using four different types of containers. Two types had a traditional design, whereas the other two were innovative for forest seedlings forest nursery production. The latter included two sizes of Air-Pot[®]; these containers have non-flat walls and perforated cones along with a grid at the bottom, designed to reduce root deformation and promote fine roots development

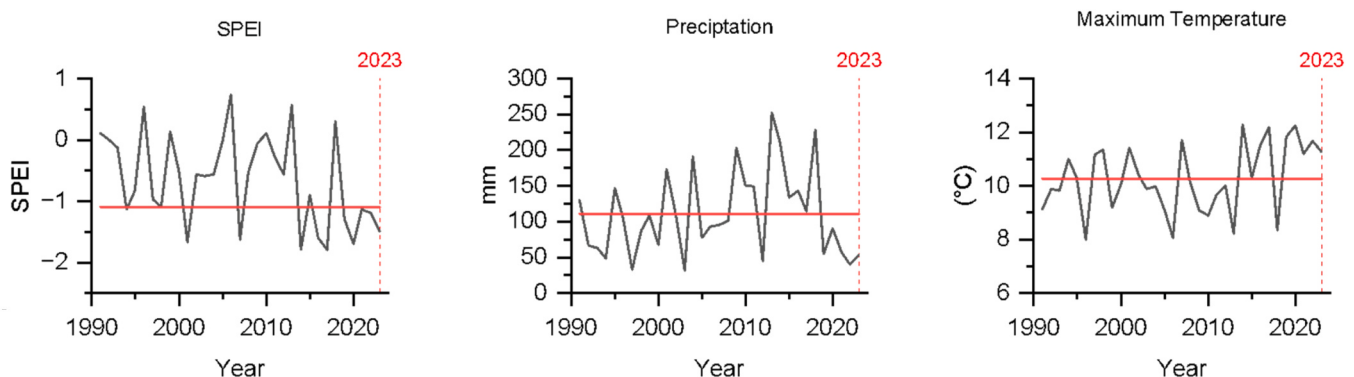


Fig. 1. Time series of February–March SPEI (left), cumulative precipitation (center), and mean maximum temperature (right). Gray lines show annual variability for the February–March period, the solid red horizontal line represents the 30-year mean (1994–2023) for each variable, and the dashed red vertical line marks the year 2023.

through air pruning. The 2 Air-Pot were: a) a Big Air-pot with a volume of 3617.3 cm³, circular top section with a diameter of 16 cm, depth 18 cm, growing density 25 seedlings/m²; and b) a Small Air-pot with a volume of 863.5 cm³, circular top section with a diameter of 10 cm, depth 11 cm, growing density 100 seedlings/m², which was included to evaluate a container volume comparable to those commonly used in forest nursery production. The other two types were: c) a Tray with 12 cavities, each with a volume of 558 cm³, depth 18 cm, top section of 7 × 7 cm, growing density 120 seedlings/m²; d) a Single pot with a volume of 3103.17 cm³, closer to the Big Air-pot, top section of 13 × 13 cm, depth 21.5 cm, growing density of 49 seedlings/m².

The growing medium was made of 0/40 peat and 3/8 fine pumice (3:1) and 1.5 kg m⁻³ calcium carbonate with the addition of NPK (Mg) 17–09–11 (2) fertilizer with microelements. The containers were daily irrigated to maintain the substrate at the field capacity (calculated by the gravimetric method per container type). At the end of the first growing season, the nursery stock was characterized by morphology and dry mass by destructive analysis. On eight seedlings per container type, we measured: root collar diameter, height, number of leaves and leaf area as well as the dry weight (DW) of the shoot system (stem and branches), of the leaves, and of the root system, separating the main root (taproot) and the first order lateral roots (FOLR). The shoot-to-root ratio (S/R) and Specific Leaf Area (SLA) were also calculated.

2.3. Field performance

Sixteen plots were established within the area (plots 1–7 on the south-facing slope, Side A, and 8–16 on northwest-facing slope, Side B), randomly distributed according to site morphology and spaced at least 2 m apart. Each plot was 1.5 × 1.5 m. Four seedlings - one for each type of container - were planted at the corners of each plot, for a total of 64 plantlets (32 in each side). The planting took place in early December 2022. No specific site preparation or post-planting treatments were applied to minimize additional variability. These conditions are also representative of standard practice in many Italian reforestation projects.

An initial assessment was conducted at the end of January 2023, when seedling height (H₀) was recorded. During the second survey at the end of March 2023, before the onset of the growing season, all the seedlings were completely leafless due to an erratic dry period. Following this unexpected condition, the monitoring protocol was revised and field measurements recalibrated. The first data collection was then moved to July 2023 on surviving seedlings (18 in Side A and 25 in Side B), when the plants had regrown their leaves. In Side A, the surviving seedlings comprised 4 Small Air-pot, 6 Big Air-pot, 4 Single pot, and 4 Tray seedlings, whereas in Side B they comprised 6 Small Air-pot, 8 Big Air-pot, 6 Single pot, and 5 Tray seedlings. This survival remained unchanged throughout the monitoring period until the final survey in December 2023, and all the measurements described below were performed on these surviving seedlings. The reaction to the post-transplant aridity event was evaluated through morphological and physiological measurements. Data were collected in July and August, and then in October (end of the growing season) and December (non-growing season). The morphological assessment focused on the new dominant shoot, considered an indicator of the plant's vigour and capacity to respond after a dry event. The dominant shoot was identified and marked in July to track it throughout the growing season, including any possible dieback. The dominant shoot length and number of leaves were recorded in each surviving seedling; in August, we measured the length (L) and width (W) of all leaves of the dominant shoot for all surviving seedlings. Leaf length (L) was measured along the main vein of the leaf, while leaf width (W) was measured at the point of maximum leaf expansion. Specific Leaf Area (SLA) was then determined from the leaf area (LA) and dry mass (DM) of one medium-sized leaf per seedling, selected relative to the other leaves on the dominant shoot. L and W of all leaves of the dominant shoot were used to derive the LA and DM from

the product LxW according to Liu et al. (2017), and to estimate the SLA of the dominant shoot per surviving seedling. Furthermore, total height, root collar diameter and the total number of new resprouting shoots and the occurrence of apical dieback were recorded on all surviving seedlings. Total seedling height was measured as the distance from the ground to the highest green shoot, regardless of its orientation.

Chlorophyll content and fluorescence were recorded in July, August and October. Chlorophyll content was determined on the first fully expanded mature leaf in each surviving seedling by measuring the transmittance of red (650 nm) and infrared (940 nm) light using the SPAD 502 Plus (Spectrum Technologies, Aurora, IL) (Uddling et al., 2007). On the same leaf, chlorophyll *a* fluorescence was assessed with a portable fluorimeter (Handy-PEA; Hansatech Instruments, Ltd, UK). Measurements were taken at ambient temperature following a 40-minute dark adaptation period at midday. Fluorescence changes were recorded during a 1-second light pulse with an intensity of 3500 μmol m⁻² s⁻¹. Based on these measurements, the maximum quantum efficiency of PSII photochemistry (Fv/Fm) and PSII photochemistry (PI) performance index were calculated.

Additionally, leaf carbon and nitrogen concentrations and isotopic composition (δ¹³C and δ¹⁵N) were determined to identify patterns related to plant stress and resource-use efficiency. Due to their sensitivity to environmental conditions, δ¹³C and δ¹⁵N are widely used to assess the effects of climate variability and nutrient availability on plant functional strategies and physiological performance (Farquhar and Lloyd, 1993; Flanagan, 1993). Leaf samples were oven-dried at a conservative temperature of 40 °C until constant weight, a threshold chosen to prevent any risk of thermal nitrogen volatilization and potential kinetic isotope fractionation. Complete desiccation was strictly verified by monitoring mass through consecutive weightings, and the dried material was subsequently ground to a fine powder with a mortar. An aliquot of dry powder (1–2 mg) was combusted into an elemental analyser (Model NA 1500, Carlo Erba, Milan, Italy) and carried by a He stream to an isotope ratio mass spectrometer (Isoprime Ltd., Cheshire, UK) to measure the concentration and isotope ratios of C (R = ¹³C/¹²C) and N (R = ¹⁵N/¹⁴N). The isotopic compositions were expressed as δ notation vs VPDB for δ¹³C and vs atmospheric N₂ for δ¹⁵N, according to the expression: δ = (R_s - R_{std})/R_{std} × 1000, where R_s is the isotope ratio of the sample and R_{std} is the isotope ratio of the international standard. IAEA-CH6 sucrose and IAEA-600 caffeine were used for scale normalization of measured δ¹³C values to the VPDB scale, while for δ¹⁵N we used IAEA-600 caffeine and USGS40 glutamic acid. The precision of isotopic measurements was better than 0.1‰ for both δ¹³C and δ¹⁵N.

2.4. Statistical analysis

Differences in soil parameters between A and B sides were assessed by unpaired *t*-test (*p* < 0.05).

Differences in plant community composition and structure between Side A and Side B were assessed using both univariate and multivariate approaches. Ground cover and ecological characteristics, the latter estimated via Ellenberg indicator values (Pignatti, 2005), were compared between the two sides using *t*-tests after verifying normality and homoscedasticity. Compositional differences of vegetation were evaluated through a PERMANOVA (999 permutations) based on a cover-weighted Bray-Curtis distance matrix (Oksanen et al., 2013), following a test for multivariate homogeneity of dispersions (betadisper; Anderson et al., 2006; Warton et al., 2012). All analyses were performed using the *vegan* package in R version 4.0.3 (R Core Team 2020).

For the nursery stock, container type was treated as the main factor (source of variation) in a one-way ANOVA (*p* < 0.05). Levene's test was used to verify the homogeneity of variances, and Fisher's LSD Test was applied for post-hoc comparisons. The effects of pot type and side on seedling survival and occurrence of dry apices were assessed using binary logistic regression. Survival (alive and dead) and dry apices (present/absent) were treated as a binary response variable, while pot type

and side were included as categorical predictors. The reference levels were set to Tray for the pot type and to Side B for the side factor. Model coefficients were estimated relative to these reference categories and are presented as odds ratios. At the beginning of the growing season, in March 2023, seedling mortality could not be assessed as the plants were leafless. Therefore, we postponed the survival assessment until the onset of new shoot resprouting. A two-way factorial ANOVA was carried out to evaluate the main effects of container type and slope aspect, and to test interaction effects between these two factors on seedling field performance and both biometric and morphophysiological plant traits. Again, Levene's test was used to verify the homogeneity of variances, and Fisher's LSD Test was applied for post-hoc comparisons. Linear regressions (statistics are reported in Table S1) were performed between leaf area (LA) and leaf length $\times$ width (L $\times$ W), and between dry mass (DM) and L $\times$ W, to predict LA and DM of all the leaves on the shoot based on their length and width (Liu et al., 2017). Seedlings' statistical analyses were performed using OriginPro (OriginLab Corporation, Northampton, MA, USA).

3. Results

3.1. Planting site characterization

3.1.1. Soil properties

Before the establishment, a full characterization of chemical and physical soil properties did not show any statistical differences between Sides A and B (Table 1). After one year of plant growth, only the soil properties expected to change over a short time scale were evaluated, not revealing any significant differences between sides, except for TOC. That had a higher value in Side A than in Side B (Table 2). Concerning the enzyme activities, monitored throughout the year, no significant differences were observed at 0–10 soil depth amongst sides (data not shown). Instead, at 10–20 cm soil depth, the BG had a higher activity in Side A than B in June and September, while the vector analysis revealed a higher VL in Side A than B in June and November (Fig. 2).

3.1.2. Vegetation

The multivariate analysis revealed a clear and significant separation in plant community composition between the two slopes (PERMANOVA, $p < 0.001$), as illustrated by the NMDS ordination (Fig. 3). This compositional divergence was supported by the Ellenberg ecological indices, which indicated that Side A (south-facing) was characterized by species with significantly higher light requirements (L values) compared to Side B. Despite the harsher exposure, Side A exhibited higher values for percentage cover than Side B ($64.5 \pm 20.2\%$ Vs $34.1 \pm 11.9\%$; $p = 0.002$).

3.2. Nursery seedlings

Container type significantly influenced root collar diameter, leaf area, leaf number, and the dry mass of different plant parts (stem, leaves, taproot, FOLR, and root system), while having no effect on seedling height or the S/R ratio (Fig. 4, Tab. S2). In general, Big Air-pot seedlings outperformed all morphological traits, excluding SLA, which was highest in Single pot seedlings.

3.3. Field performance

Binary logistic regression revealed that the Big Air-pot marginally increased seedling survival compared with Trays (odds ratio [OR] = 5.97), indicating an approximately six-fold increase in the odds of survival; however, this effect was only marginally significant ($p = 0.056$). No significant effects were detected for the Small Air-pot or Single pot ($p > 0.70$). Site exposure had no effect on survival. Regarding the presence of dry apex, no significant effects of container type were detected, although seedlings grown in the Big Air-pot tended to show reduced odds, even if not significant, of dry apex occurrence relative to tray-grown seedlings (OR = 0.16,

Table 1

Soil properties measured in 2022 in both sides (A, B) at different depths (0–10 and 10–20 cm). Unpaired *t*-test *p*-values between sides are reported in the tables. BD = bulk density; ASI = aggregate stability index; EC = electrical conductivity; CEC = cation exchange capacity.

Depth	Side	0–10 cm			10–20 cm		
		A	B	<i>p</i> -value	A	B	<i>p</i> -value
BD	g cm ⁻³	1.00 ± 0.11	1.01 ± 0.21	ns	1.28 ± 0.08	1.22 ± 0.10	ns
Coarse	%	46 ± 12	43 ± 10	ns	45 ± 16	42 ± 12	ns
ASI		534 ± 72	509 ± 183	ns	300 ± 111	269 ± 106	ns
pH		5.5 ± 0.3	5.6 ± 0.2	ns	5.7 ± 0.1	5.7 ± 0.1	ns
EC	dS m ⁻¹	0.42 ± 0.28	0.27 ± 0.02	ns	0.37 ± 0.18	0.23 ± 0.04	ns
CEC	meq (+) kg ⁻¹	12.1 ± 1.9	12.9 ± 0.7	ns	12.0 ± 0.7	16.1 ± 3.7	ns
Ca	g kg ⁻¹	1.35 ± 0.24	1.14 ± 0.28	ns	1.27 ± 0.56	0.74 ± 0.09	ns
Cr	mg kg ⁻¹	11.3 ± 2.4	9.1 ± 1.4	ns	11.8 ± 8.5	8.8 ± 4.8	ns
Cu	mg kg ⁻¹	16.8 ± 9.1	19.2 ± 13.4	ns	13.8 ± 5.4	9.6 ± 4.9	ns
Fe	g kg ⁻¹	10.8 ± 0.6	9.9 ± 0.5	ns	10.8 ± 1.1	10.0 ± 2.0	ns
K	g kg ⁻¹	0.81 ± 0.09	0.78 ± 0.20	ns	0.59 ± 0.28	0.62 ± 0.31	ns
Mg	g kg ⁻¹	3.76 ± 0.05	3.49 ± 0.06	**	3.85 ± 0.56	3.51 ± 0.60	ns
Mn	g kg ⁻¹	1.55 ± 0.80	1.21 ± 0.34	ns	1.53 ± 0.91	1.09 ± 0.29	ns
Na	g kg ⁻¹	0.08 ± 0.01	0.09 ± 0.02	ns	0.07 ± 0.02	0.08 ± 0.04	ns
Ni	mg kg ⁻¹	12.9 ± 1.8	11.8 ± 1.7	ns	13.8 ± 6.3	11.0 ± 4.7	ns
Zn	mg kg ⁻¹	76 ± 5	71 ± 1	ns	70 ± 15	65 ± 15	ns
Olsen P	mg kg ⁻¹	32.9 ± 7.6	34.5 ± 3.4	ns	28.1 ± 8.2	28.3 ± 5.8	ns

$p = 0.08$). In contrast, exposure significantly affected dry apex occurrence, with seedlings under Side A showing substantially higher odds of developing dry apex compared with Side B (OR = 6.73, $p = 0.040$), corresponding to an approximately six-fold increase in the odds of this condition.

Height was strongly affected by container type from the first measurement onward (Fig. 5, Tab S3). Seedlings grown in Big Air-pot showed the greatest values throughout most of the study period, whereas tray-grown seedlings exhibited the lowest height values. Toward the end of the growing season, the advantage of the Big Air-pot became less pronounced, and a marginal decrease in recorded height was observed in some individuals compared to previous measurements (Fig. 5). This reduction was associated with the occurrence of apical dieback, which was more frequent on Side A than on Side B, in seedlings grown in the Big Air-pot compared to those in the other. For dominant shoot elongation, no significant differences emerged (Fig. 5). Root collar diameter growth was consistent with height growth until August, seedlings plants grown in Big Air-pot generally reached larger diameter, and slope exposure had a minimal impact. By October, these differences diminished, and root collar diameter overlapped across all container types and slope exposures.

The number of leaves on the dominant shoot showed substantial overlap among container types and between slope exposures, with no clear or consistent differences (Fig. 5). Slope exposure did not produce marked patterns at any sampling date. The Big Air-pot showed the highest number of new resprouting shoots (Fig. 5) during the study period, while the tray showed the lowest; new shoot production in Big Air-pot treatments was approximately two- to three-fold higher than in the Tray.

Table 2

Soil properties measured in 2022 and 2023 in both sides (A, B) at different depths (0–10 and 10–20 cm). Unpaired *t*-test *p*-values between sides are reported in the tables. Exch = exchangeable; TOC = total organic carbon; TN = total nitrogen.

Year	Depth	Side	Exch Ca mg kg ⁻¹	Exch K mg kg ⁻¹	Exch Mg mg kg ⁻¹	TOC %	TN %
2022	0–10 cm	A	742 ± 174	143 ± 58	162 ± 42	5.8 ± 1.3	0.39 ± 0.13
		B	613 ± 1307	115 ± 31	163 ± 25	6.1 ± 1.5	0.32 ± 0.06
		<i>p</i> -value	ns	ns	ns	ns	ns
	10–20 cm	A	728 ± 306	93 ± 20	140 ± 32	4.0 ± 0.6	0.25 ± 0.06
		B	481 ± 105	79 ± 38	125 ± 33	3.7 ± 1.5	0.20 ± 0.01
		<i>p</i> -value	ns	ns	ns	ns	ns
2023	0–10 cm	A	949 ± 727	139 ± 87	260 ± 201	9.0 ± 3.5	0.61 ± 0.28
		B	652 ± 10	80 ± 12	185 ± 16	6.6 ± 1.9	0.46 ± 0.09
		<i>p</i> -value	ns	ns	ns	ns	ns
	10–20 cm	A	489 ± 348	84 ± 49	134 ± 95	5.4 ± 0.6	0.28 ± 0.06
		B	377 ± 66	43 ± 18	108 ± 18	3.5 ± 0.8	0.21 ± 0.05
		<i>p</i> -value	ns	ns	ns	*	ns

Regarding the SLA value, it was higher ($p < 0.0001$) in Side A ($75.47 \pm 2.95 \text{ cm}^2 \text{ g}^{-1}$) compared to Side B ($73.98 \pm 2.11 \text{ cm}^2 \text{ g}^{-1}$); the seedlings grown in the Tray ($75.32 \pm 3.35 \text{ cm}^2 \text{ g}^{-1}$) and in the Big Air-pot ($74.99 \pm 2.14 \text{ cm}^2 \text{ g}^{-1}$) showed a higher SLA ($p < 0.0001$) compared to ones grown in Single pot ($73.49 \pm 1.41 \text{ cm}^2 \text{ g}^{-1}$) and Small Air-pot ($73.44 \pm 1.54 \text{ cm}^2 \text{ g}^{-1}$). Chlorophyll content and chlorophyll fluorescence parameters (Fv/Fm and PI) assessed on fully expanded leaves showed no significant differences in July, August, and October

($p > 0.05$) (data not shown). These results were further supported by the analysis of leaf C and N stoichiometry (C/N ratio) and isotopic composition ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, Fig. 6). Leaf $\delta^{13}\text{C}$ averaged approximately -29‰ and did not differ significantly among slopes or container types. This was associated with the absence of significant differences in leaf C/N stoichiometry. In contrast, leaf $\delta^{15}\text{N}$ varied with both slope and container type, with generally higher values on the north-facing slope (Side B) than on the south-facing slope (Side A). On Side A, $\delta^{15}\text{N}$ values were lowest in the tray treatment, intermediate in the single pot and Big Air-pot, and highest in the Small Air-pot. On Side B, $\delta^{15}\text{N}$ values were higher across all container types, with the highest values observed in the single pot, followed by the tray and Big Air-pot, whereas the Small Air-pot showed the lowest values.

4. Discussion

Our results showed that container type influences nursery seedling morphology and field performance following the unexpected winter drought after outplanting. Seedlings grown in the Big Air-pot, the largest container tested, showed increased size at the nursery stage and, during the subsequent growing season, higher survival, faster early growth, and enhanced resprouting capacity. The physiological traits of the dominant resprouting shoot did not show stress symptoms during the growing season. The south-facing slope created more challenging conditions for seedling responses, consistent with patterns observed in the vegetation analysis. Although south-facing soil showed a different carbon cycling, the two exposures did not differ in soil chemistry, physics and nutrient availability, which not represent a limiting factor for plant establishment.

4.1. Nursery seedling morphology

Container type strongly influenced seedling morphological traits at the nursery stage, with container volume emerging as the main driver, and depth playing a secondary role. Seedlings grown in the Big Air-pot, the largest container tested (3617 cm^3), produced greater root collar diameter and higher above- and belowground biomass than in other container types. Although the Single pot had a comparable volume (only $\sim 14\%$ smaller than the Big Air-pot) and greater depth, it did not induce

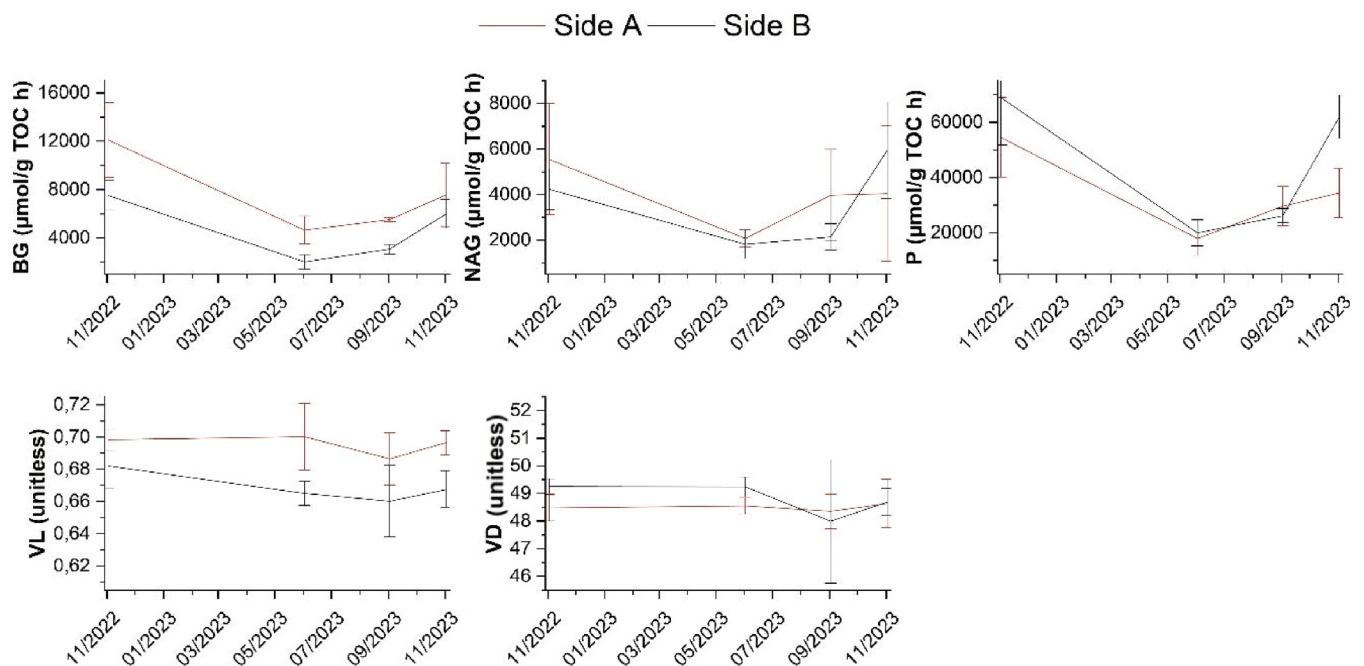


Fig. 2. Enzymes activities and vector analysis measured in each side (A, B). BG = β-glucosidase; NAG = N-acetylglucosaminidase; P = phosphatase; VL = vector length; VD = vector degree.

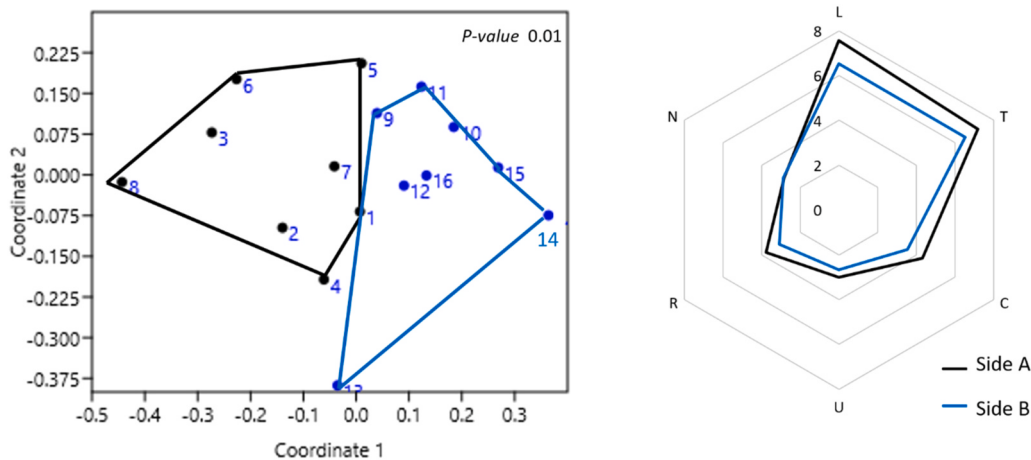


Fig. 3. Plant community characterization of the two experimental slopes. (a) Non-metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis distances; polygons represent the two slope aspects (Side A, south-facing in black; Side B, northwest-facing in blue), with the p-value indicating the significance of compositional differences (PERMANOVA). (b) Radar chart showing the mean Ellenberg indicator values for the species identified on each side: L (light), T (temperature), C (continentality), F (moisture), R (reaction), and N (nutrients).

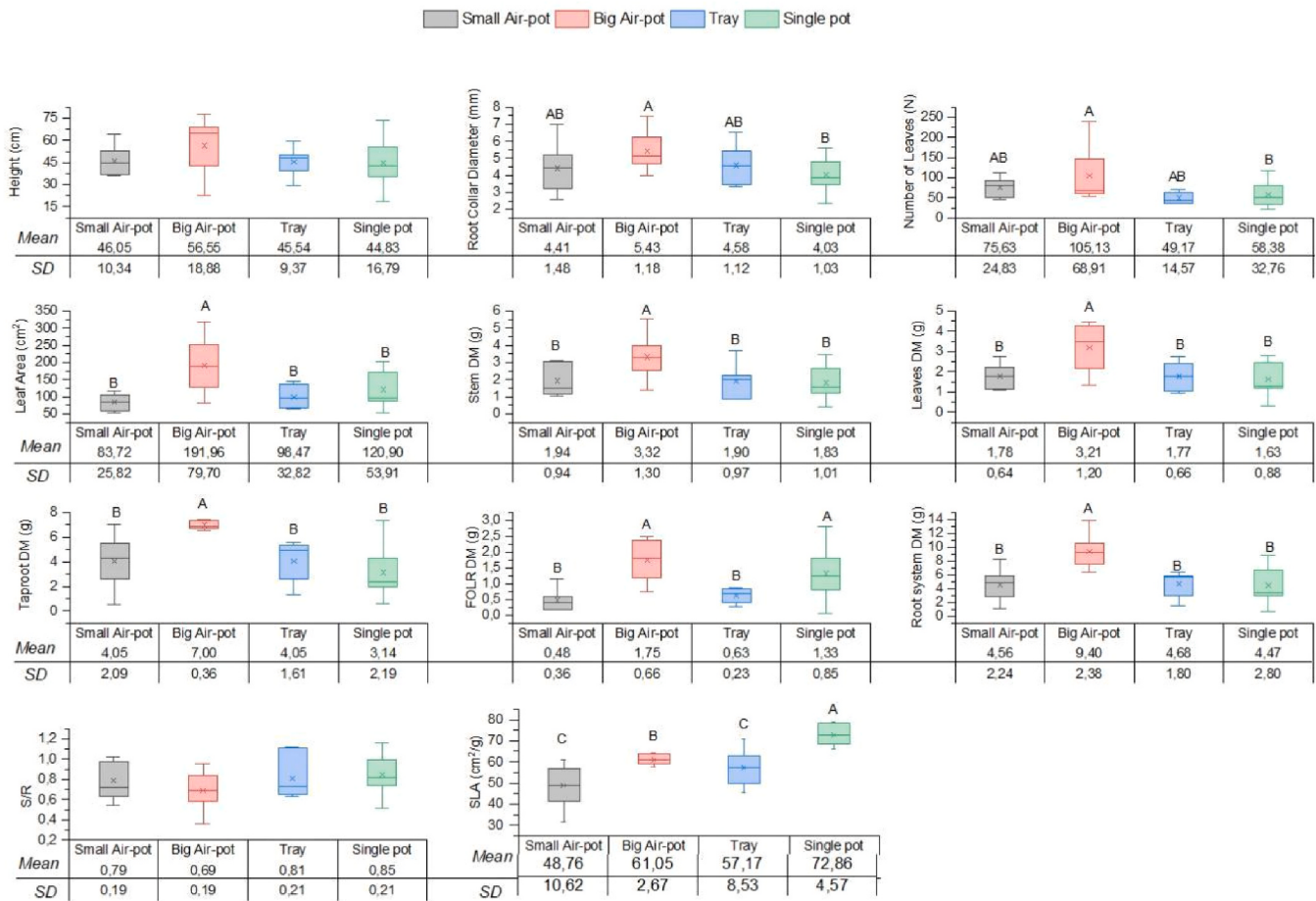


Fig. 4. Height, root collar diameter, number of leaves, leaf area, stem dry mass (DM), leaves dry mass (DM), taproot dry mass (DM), first order lateral roots dry mass (FOLR DM), root system dry weight (DM), shoot/root ratio (S/R), and specific leaf area (SLA) for plants grown in Small Air-pot, Big Air-pot, Tray, and Single pot containers. Within each box, the (x) represents the mean, while the horizontal line indicates the median; boxes represent the interquartile range and whiskers indicate variability. Mean and standard deviation (SD) are reported below each panel. Different uppercase letters indicate significant differences among container types ($p < 0.05$).

similar diameter growth or biomass accumulation. These results are consistent with the literature identifying container volume as a primary determinant of plant growth (i.e., Ortega et al., 2006; Dumroese et al., 2011; Mariotti et al., 2015b; Sun et al., 2018), as larger rooting

volumes enhance resource availability and root expansion (e.g., Landis et al., 1990; Dominguez-Lerena et al., 2006; Villar-Salvador et al., 2026). According to the global meta-analysis of Poorter et al. (2012), doubling the rooting volume of a container can increase total plant mass

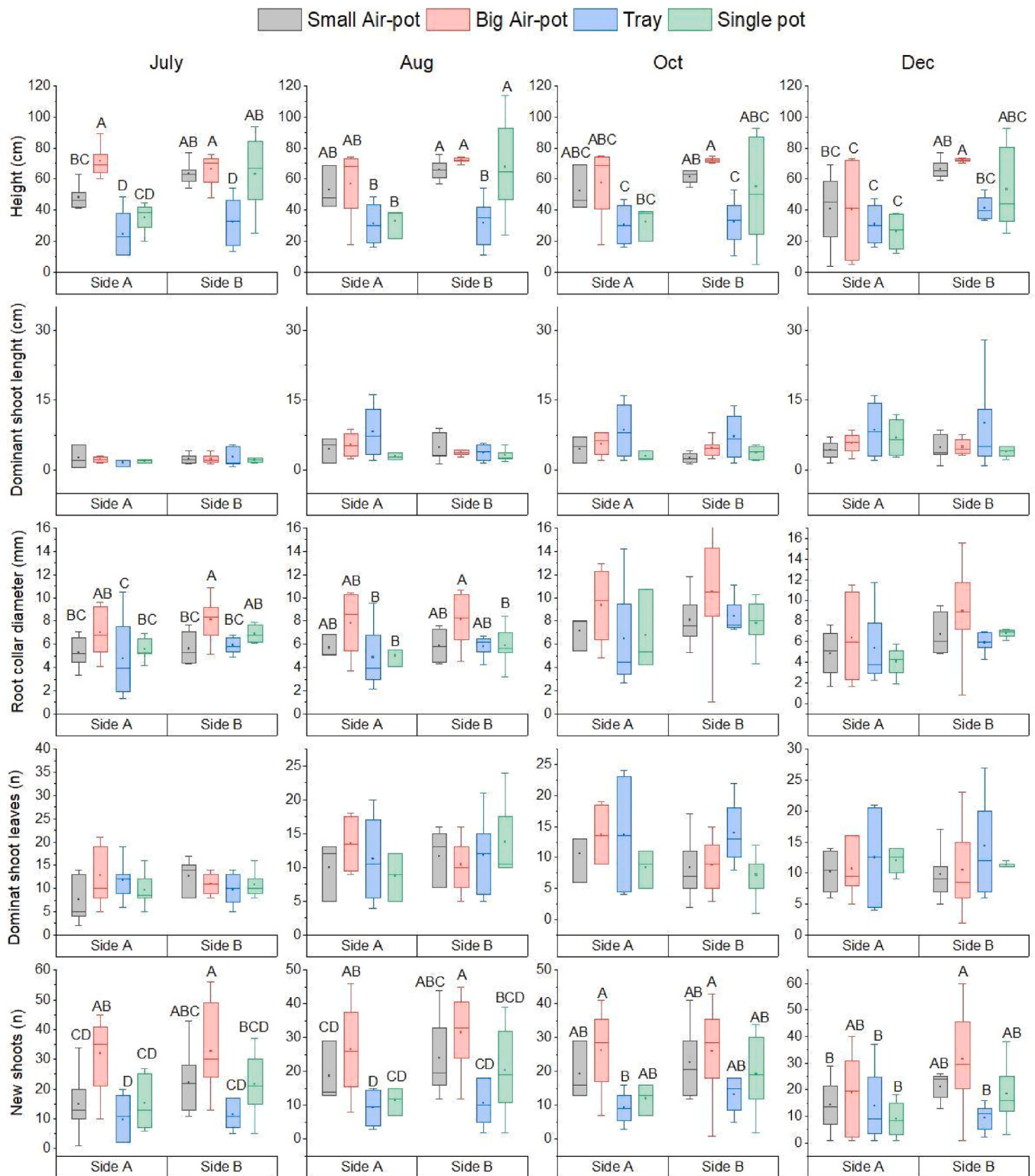


Fig. 5. Height, dominant shoot length, root collar diameter, number of leaves on the dominant shoot, and number of new shoots for plants grown in Small Air-pot, Big Air-pot, Tray, and Single pot containers, separately for Side A and Side B in July, August, October, and December. Within each box, the (x) represents the mean and the horizontal line represents the median; boxes indicate the interquartile range and whiskers represent variability. Different uppercase letters indicate significant differences among treatments within each month and side ($p < 0.05$).

by approximately 43%. Moreover, large-seeded, taproot-forming angiosperms respond positively to increased container size, thereby delaying root system saturation and enhancing belowground biomass accumulation (Passioura, 2006; Wilkinson et al., 2014; Turner, 2019). Nevertheless, container volume alone does not fully explain the

observed patterns. In fact, despite the relatively large volume and higher depth than the Big Air-pot, seedlings grown in the Single pot showed growth comparable to that observed in the other two much smaller containers, Tray and Small Air-pot (84.6% and 76.1% smaller than Big Air-pot, respectively). This suggests that factors other than size may also

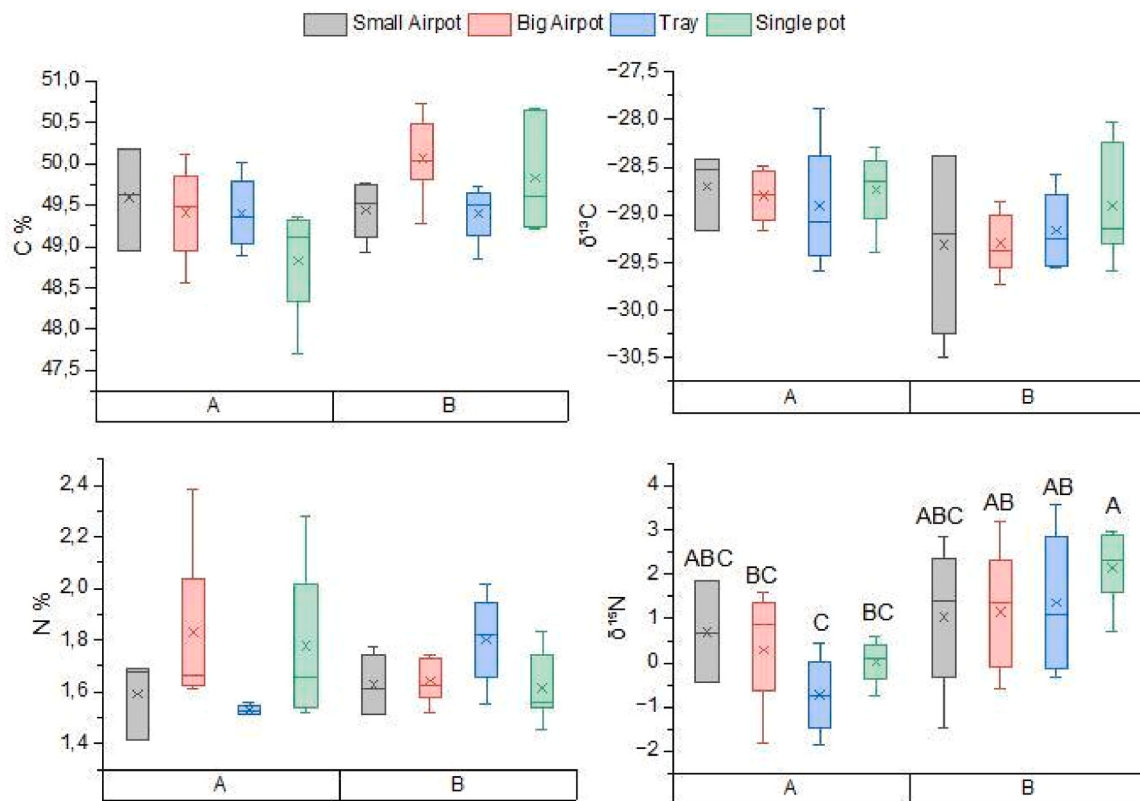


Fig. 6. Leaf C and N concentration and their isotope compositions ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of plants grown in Small Air-pot, Big Air-pot, Tray, and Single pot containers in Side A and Side B. Within each box, the (x) represents the mean and the horizontal line represents the median; boxes indicate the interquartile range and whiskers represent variability. Different uppercase letters indicate significant differences among treatments within each pot and side ($p < 0.05$).

play a role. Container depth contributed to taproot development, as shown by the higher taproot mass in the Big Air-pot (18 cm deep), in agreement with previous studies on taproot-forming species such as *Quercus* (Chirino et al., 2008; Mariotti et al., 2015a,b; Villar-Salvador et al., 2026). Nonetheless, our results showed that depth alone did not compensate for reduced effective growing conditions, as evidenced by the Tray (18 cm deep). Seedlings grown in the Tray and in the Small Air-pot—sizes commonly used in forest nursery practice worldwide—had a size comparable to that of seedlings usually grown in forest nursery (Benamirouche et al., 2019; Kholkhal and Benamar, 2021); however, they consistently exhibited lower shoot and root biomass than seedlings grown in the Big Air-pot, despite reaching comparable heights. This pattern reflects the effect of high nursery seedlings growing density, where competition for light promotes shoot elongation at the expense of diameter and biomass accumulation (Landis, 1990; Wilkinson et al., 2014; Villar-Salvador et al., 2026; Mariotti et al., 2026). Accordingly, container depth appears to be a less reliable indicator of nursery seedling development than shoot and root biomass or root collar diameter—variables related to root growth biomass and outplanting performance (Grossnickle, 2012; Tsakalimi et al., 2013; Andivia et al., 2021; Grossnickle and Ivetić, 2022), particularly when comparing stocktypes differing in species, cultivation practices, container type and density (Andivia et al., 2021; Mariotti et al., 2023; Puértolas et al., 2024). The absence of differences in the shoot-to-root ratio indicates that biomass allocation between above- and belowground compartments remained balanced in all container types, consistently with observed values (Bacher et al., 2022; Chahboub et al., 2025). The effect of the air-pruning design was limited. Although the Air-pot system is intended to promote lateral root proliferation through its structure, the biomass of first-order lateral roots did not differ between the two larger containers, the Big Air-pot and the Single pot. Moreover, no clear advantage was observed in the Small Air-pot, whose size is comparable to standard

forest nursery containers, suggesting that the benefits of air pruning may emerge above a certain container volume. In smaller Air-pot containers, increased water loss through the perforated walls may instead constrain growth and require careful irrigation planning, as previously observed for *Q. robur* and *Juglans regia* (Mariotti et al., 2015a,b).

4.2. Seedling field response to unexpected drought event

Measurements carried out in July were specifically aimed at capturing the initial response of seedlings to the unexpected climatic event and clarifying the resulting increase in mortality. The seedlings grown in the Big Air-pot had accumulated greater biomass at the nursery stage, subsequently showing the best early morphological response across most traits on both slopes. In July, these seedlings were taller and showed a higher total number of new shoots. Together, these traits indicate a stronger vegetative response, likely supported by greater availability of stored reserves. In line with our observations, *Quercus* seedlings can respond to drought stress with enhanced shoot formation following re-watering, which can be viewed as a compensatory mechanism offsetting the growth limitation experienced during the drought period (Spieß et al. 2012). Consistently, in reforestation and forest restoration projects under standard operational conditions, larger seedlings tend to show better outplanting performance, i.e., survival and growth, due to greater resource availability and more effective non-structural carbohydrate (NSC) remobilization supporting growth potential (Cuesta et al., 2010b; Uscola Fernández et al., 2014; Uscola et al., 2015; Villar-Salvador et al., 2015, 2026), particularly in stress-resistant species planted in dry sites (Cuesta et al., 2010b; Andivia et al., 2021). Accordingly, a recent global quantitative analysis has highlighted the positive role of container size in outplanting performance: increasing container size results in larger seedlings and can optimize the seedling outplanting performance under harsher conditions (Villar-Salvador et al., 2026; Mariotti et al.,

2026). Seedling mortality, at the end of the growing season, reflected the combined effect of slope exposure and container type. Although differences were not statistically significant, seedling mortality was markedly higher on the south-facing slope compared to the north-facing one, indicating that micro-site conditions strongly influenced seedling survival under harsher conditions. While dominant shoot length and physiological traits—including leaf $\delta^1\text{ }^3\text{C}$, used here as a proxy for intrinsic water-use efficiency (i.e., the ratio of CO_2 assimilation to stomatal conductance over the leaf expansion period; Hubick, Farquhar, 1989)—did not differ markedly among container types, this does not undermine the overall interpretation. Rather, it suggests that all surviving plants maintained a similar baseline of photosynthetic efficiency. The dominant resprouting shoot represents the primary axis of investment in young seedlings (Zeppel et al., 2015; Pietras et al., 2016; Turcsán et al., 2016), and it is therefore likely that all individuals prioritised its development under stress conditions. For this reason, the higher number of new shoots observed in Big Air-pot seedlings is particularly relevant, as it reflects whole-plant response beyond the dominant shoot, indicating greater canopy development and potentially higher photosynthetic capacity. Consistently, root collar diameter was also significantly greater in Big Air-pot seedlings in July, further supporting their superior response to the stress event (Grossnickle and MacDonald, 2026), given its close relationship with root system development (Grossnickle, 2000; Binotto et al., 2010; Bayala et al., 2009; Guimarães et al., 2024).

As the growing season progressed, differences among container types became less pronounced. Climatic conditions during the subsequent months were more consistent with the seasonal average, corresponding to the typical site conditions to which the species is adapted. By December, however, seedlings grown in the Big Air-pot generally maintained greater growth, particularly on the north-facing slope. North-facing slopes experience lower solar radiation and higher soil moisture availability, whereas south-facing slopes are characterized by higher temperatures and greater water limitation, resulting in more stressful conditions for seedling establishment (Castro et al., 2004; Ceacero et al., 2012; Cramer et al., 2018). Moreover, the observed reduction in stem height over time is explained by the occurrence of apical dieback, which was more frequent in seedlings grown in the Big Air-pot, especially on the south-facing slope.

Even though total organic carbon was higher in Side A than in Side B, enzyme activity related to C acquisition (BG) and vector length increased in Side A during the summer, reflecting a C limitation in the soil (Kunito et al., 2024). This could be related to a combined effect of plant composition, environmental temperature and soil texture. The higher temperature in Side A may affect microbial activities (Karhu et al., 2014), increasing microbial C demands and leading to the depletion of its easily available forms. The changes in plant litter input and the fine soil texture probably contributed to a chemical and physical protection of the organic C, reducing its bioavailability. Despite this C cycle alteration in Side A, the bioavailability of macronutrients did not decrease over time, suggesting that it did not affect oak seedling establishment. The higher foliar $\delta^1\text{ }^5\text{N}$ observed on the north-facing slope (Side B) likely reflects enhanced N turnover under wetter conditions, where accelerated nitrification and denitrification promote preferential ^{14}N losses. In contrast, the south-facing slope (Side A) supported higher plant cover and diversity, which may enhance nitrogen uptake and retention, contributing to a more closed N cycle and lower $\delta^1\text{ }^5\text{N}$ (Robinson, 2001; Craine et al., 2015). Within this environmental framework, nursery legacy effects appeared to modulate the isotopic response of seedlings. Despite initial differences in seedling biomass, $\delta^1\text{ }^5\text{N}$ values were broadly similar between Big and Small Air-pot seedlings across both slopes, suggesting that container type had a limited influence on nitrogen acquisition relative to site conditions. In contrast, seedlings grown in more constraining containers (trays and single pots) exhibited greater isotopic variability and stronger differences between slopes. These patterns may reflect persistent effects of nursery production on root system development and subsequent soil exploration following outplanting. Consistent with this interpretation, Zadworny et al. (2025) reported that regeneration-induced differences in root system

architecture and rooting depth were associated with differences in foliar $\delta^1\text{ }^5\text{N}$ in oaks, highlighting the long-term influence of early root development on plant physiological traits. The greater $\delta^1\text{ }^5\text{N}$ divergence between slopes observed in tray- and single pot-grown seedlings is consistent with the possibility that seedlings with more constrained root systems were more responsive to local environmental conditions, whereas Air-pot seedlings appeared less sensitive to slope-related variation. However, because root distribution was not directly assessed in the present study, the mechanisms underlying these isotopic differences remain speculative. Overall, slope-related variation in nitrogen cycling appears to be the primary driver of foliar $\delta^1\text{ }^5\text{N}$, whereas container-induced differences in root development may have contributed a secondary, context-dependent influence. Consistently, differences among container types became more evident within each slope, indicating that nursery-induced variation not only influenced $\delta^1\text{ }^5\text{N}$ patterns but also translated into field performance. Results on the species cover, composition and ecology of spontaneous plant communities suggest that the environmental conditions were more severe on the south-facing slope (Side A) as reflected by the higher light requirements (Ellenberg L values) of the local plant community. In these selective microenvironments, the higher percentage of plant cover on Side A likely intensified biological competition for scarce winter and summer water resources, a factor that significantly penalized seedlings in smaller containers with more restricted root systems (Pinto et al., 2012; Ceacero et al., 2012). Conversely, the greater soil volume and improved root architecture provided by the Big Air-pot allowed *Q. suber* to develop a deeper and more robust root system (Chahbaub et al., 2025). This architectural advantage likely enabled the seedlings to bypass the competitive pressure exerted by the shallower-rooted spontaneous vegetation, reaching more stable water sources in deeper soil layers (Grossnickle and Ivetić, 2022).

Seedlings grown in the Big Air-pot consistently showed higher survival, even under the more stressful conditions of the south-facing slope. This suggests that larger seedlings were better able to cope with the stress despite the absence of any pre- or post-planting supportive practices such as irrigation.

Although large containers, such as the Big Air-pot, are relatively uncommon in operational forestry due to higher costs and logistical constraints, their use may be justified under particularly adverse restoration scenarios. In such contexts, the production of larger seedlings can enhance their capacity to withstand post-planting stress, especially where environmental limitations constrain early establishment (Villar-Salvador et al., 2012; Andivia et al., 2021). It is also important to note that no pre- or post-planting treatments were applied in this study, despite their key role and widespread recommendation in restoration guidelines (Stanturf et al., 2026). The absence of practices such as irrigation, soil preparation, or post-planting care represents a severe constraint for seedling establishment; yet, it reflects a management approach that is still commonly adopted in some Mediterranean contexts, including Italy. Under these limiting conditions, differences among nursery stocktypes become more evident, highlighting the importance of seedling morphological attributes in supporting early field performance. Consequently, planting stock produced in larger containers should be considered for specialized applications under specific site conditions. In these selective environments, investing in functionally superior planting stock is fully justified to enhance establishment success under increasingly unpredictable climatic regimes.

5. Conclusions

This study highlights the central role of nursery-derived morphological traits in shaping seedling establishment under Mediterranean conditions. The unexpected post-planting winter drought experienced in our study provided a valuable opportunity to assess seedling establishment under field conditions that are projected to become increasingly frequent in the region due to climate change. Under these conditions, seedling performance was primarily driven by morphological attributes, with larger seedlings showing a greater capacity to withstand stress and

recover through resprouting. While large containers remain uncommon in operational forestry due to their higher production costs, their use may be justified in targeted Mediterranean forest restoration projects where enhanced seedling functionality is required to improve establishment success. Indeed, seedlings grown in Big Air-Pot containers exhibited greater growth, resulting in consistently higher survival across contrasting slope exposures.

Improved root system architecture and associated carbon reserves enabled seedlings to tolerate better water stress, prompting adaptive shoot dieback and rapid, robust resprouting.

These findings identify container design as one of the key determinants of seedling quality and early establishment success, emphasizing the importance of selecting appropriate nursery containers to enhance the resilience of Mediterranean forest restoration under increasing climatic stress.

CRedit authorship contribution statement

Lucia Mondanelli: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Barbara Mariotti:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Pietro Castellucci:** Writing – review & editing, Investigation, Data curation. **Claudia Coccozza:** Writing – review & editing, Supervision, Investigation, Funding acquisition. **Andrea Scartazza:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation. **Silvia Traversari:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Francesca Vannucchi:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Elisa Carrari:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Alessio Giovannelli:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition. **Alberto Maltoni:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.124227](https://doi.org/10.1016/j.foreco.2026.124227).

Data Availability

Data will be made available on request.

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