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REVIEW

Global Quantitative Review of Container Effects on Nursery Growth and Field Survival in Forest Seedlings

Barbara Mariotti[1] · Enrique Andivia[2] · Pedro Villar-Salvador[3] · Vladan Ivetić[4] · Alessandro Bizzarri[1] · Maurizio Ventura[5] · Roberto Tognetti[5] · Fabio Salbitano[6] · Claudia Cocozza[1] · Alberto Maltoni[1]

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Abstract

Purpose of review Container type, volume, depth, and cultivation density represent key and economically relevant decisions for forest nurseries, as they directly shape seedling traits and outplanting performance. Despite numerous studies, existing knowledge remains fragmented and context-specific, limiting the development of general, evidence-based guidelines. This review examines how these container variables influence seedling morphology in the nursery and outplanting survival across taxonomic plant groups, seedling ages, and planting environments.

Recent findings We found that larger container volume and depth increase proportionally more root than shoot growth resulting in reduced shoot-to-root mass ratio (S:R), whereas increasing cultivation density reduces seedling biomass and increases S:R. These patterns are more pronounced in cell containers and in ≤ 1 year-old seedlings. Container depth enhances root development particularly in angiosperms. Larger volume and deeper containers improve outplanting survival, especially in cell containers, in ≤ 1 year-old plants, angiosperms, and in harsher, forest planting sites. Planting site aridity does not modulate the effects of container properties on survival. Interestingly, outplanting survival is influenced by both direct effects of container characteristics and indirect pathways mediated by morphology, which differ between angiosperms and gymnosperms.

Summary Container characteristics are major drivers of seedling morphology in the nursery and early field survival. These findings support prioritizing larger containers and cell containers for ≤ 1 year-old stock to optimize performance under harsh planting sites. Increasing container depth promotes larger seedlings by enhancing root growth in large-seeded, taproot-forming angiosperms, whereas survival in gymnosperms appears to be more influenced by cultivation density. This review provides a quantitative basis for improving container selection and nursery decision-making in forest plantings.

Keywords Container volume · Container depth · Cultivation density · Tree planting · Outplanting performance · Seedling quality

Introduction

Forestation initiatives — whether for artificial regeneration, restoration projects, or productive plantations — predominantly rely on nursery-grown seedlings [1]. Seedling cultivation practices vary across regions, depending on species, climate, and the socioeconomic context [2–5]. Nursery factors, such as growing media, rooting volume, fertilization regime, and environmental conditions, interact with the ecological and functional characteristics of the species to shape seedling morphological and physiological attributes [6–9]. This interaction results in different seedling phenotypes that can strongly differ in outplanting survival and growth [6, 10–12]. Therefore, understanding the cultivation factors that promote early outplanting performance is essential for successful forest planting initiatives and for the consequent provision of ecosystem services [13, 14]. High quality seedlings show high survival and growth under field conditions, i.e., seedlings with functional traits that maximize establishment success under the specific conditions at each site. Matching seedling functional traits to the environmental conditions of the planting site is the cornerstone of the Target Plant Concept (TPC), a conceptual framework in which species, provenance, stocktype, seedling quality, site preparation, and post-planting practices meet local environmental

Extended author information available on the last page of the article

conditions and project goals [15, 16]. Applying the TPC requires extensive knowledge on how different nursery practices influence seedling outplanting performance under different environmental conditions and across species types. A plethora of nursery studies have addressed these questions; however, most have typically focused on specific site conditions, species and provenances, stocktypes, and planting practices. This precludes our ability to provide general science-based recommendations on how to tune nursery practices to match seedling functional attributes to specific sites and forestation goals. Therefore, one main scientific challenge of the forest nursery sector is to provide informed recommendations to forest managers and practitioners [14]. One tool for achieving this is performing quantitative synthesis of the existing nursery published scientific literature. To our knowledge, few global quantitative reviews have been published on the relationship between specific nursery practices, seedling attributes, and outplanting performance under different planting conditions [12, 17, 18].

The choice of the container to cultivate seedlings is a key decision in container nurseries due to its effect on seedling quality and cultivation costs [19]. Containers strongly affect seedling growth and functional attributes by determining the space and the availability of other resources for root and shoot development. A significant body of literature has underscored the influence of container characteristics on seedling morphology (e.g. [20–24]), and physiology (e.g. [10, 25, 26]),, and, to a lesser extent, on seedling outplanting performance [11, 25, 27]. The primary function of a nursery container is to provide a suitable environment for germination and seedling growth [19]. An effective container should be large enough to hold an appropriate amount of growing medium to support seedling growth during cultivation time and ensure sufficient space at full cultivation density for light capture and water availability. These growth requirements must be balanced with nursery operational considerations such as cost, durability, recyclability, and ease of handling [19]. Although factors related to operability are usually prioritized by nursery management, the selection of containers should be based also on its impact on seedling functional traits relevant to planting projects [28, 29].

Containers can be classified by a plethora of physical and material characteristics, such as the type (tray, pot, individual cells, polybags) or construction material (e.g., plastic, styrofoam, fabric), but container volume appears to have the strongest effect on seedling performance. Differences in container volume result from the combined effects of container width and depth [30] and its effects on seedling growth has been extensively evaluated across multiple species and nursery growing conditions [27, 31–37]. Overall, container volume positively correlates with shoot and root growth, but the outcome may depend on the study conditions. The first quantitative review on this subject [21] indicated that doubling rooting volume increased plant mass by 43%, suggesting that the reduced growth in containers with lower volumes is primarily linked to physiological constraints rather than changes in leaf morphology or mass allocation. The effect of other volume-related container characteristics, such as depth, has been less investigated. However, studies on *Quercus* species [38–40] also showed positive correlations between container depth and shoot and root mass. Seedlings cultivated in deeper containers can reach deeper soil layers faster after outplanting and exhibit higher root hydraulic and stomatal conductance under water stress [38]. Cultivation density (i.e., seedlings per m²) is another critical factor related to container volume. Containers of smaller volume are usually associated with higher cultivation densities, which increase aboveground competition and reduce irrigation efficiency and uniformity [19].

This body of evidence remains fragmented across studies involving different species, nursery practices, and environmental conditions. As a result, we lack a comprehensive quantitative synthesis to identify general patterns and provide evidence-based guidance on container selection that supports nursery management while enhancing forestation success. Understanding how container traits, including cultivation density, influence outplanting performance, and specifically whether these effects are modulated by container type, seedling age, species taxonomic group, and planting site conditions, can provide valuable and impactful insights for land managers and the entire forestry sector [27, 35, 41]. In this context, a quantitative analysis can help disentangle the mechanisms that directly and indirectly (mediated by ecophysiological mechanisms influenced by nursery and planting practices) drive seedling performance after outplanting. In this regard, we hypothesized that container characteristics and cultivation density directly affect outplanting survival and growth through modification of the dry weights of seedling shoots (SDW) and roots (RDW) and their ratio (S:R) in the nursery. Here, we conducted a systematic review of the globally published literature followed by a quantitative analysis to address the following questions: *(a)* How do container volume, depth, and cultivation density influence seedling morphological traits (i.e., SDW, RDW, S:R) in the nursery?) *(b)* Do container volume, depth, and cultivation density influence outplanting performance (i.e., survival and height growth)?; *(c)* Are these effects modulated by container type (cell containers, polybags, and compressed peat disks), seedling age (≤ 1 and > 1 year), taxonomic group (angiosperms and gymnosperms), planting site (forest and cropland), and aridity conditions at planting sites? Seedling age determines growth rate and sensitivity to stress factors [14, 42–44], while angiosperms generally grow faster and show larger leaves and higher transpiration rate than gymnosperms due to marked differences in xylem and leaf traits [45, 46]. Outplanting performance depends strongly on soil resources, which depend on climate aridity [12, 18] and soil properties, often more favorable in croplands than in typical forest sites [47, 48]. Finally, we asked *(d)* Are the effects of container volume, depth, and cultivation density on outplanting survival mediated by their effects on seedling morphology?

To the best of our knowledge, this is the first quantitative review on this topic and can contribute to an increase of global quantitative studies for the forest nursery sector (see [17]). Given that container choice has a significant impact on nursery costs [2], a deeper overall understanding of how container characteristics affect seedling morphology, and early outplanting performance, is essential to guide future research and practitioners´ container selection toward optimizing seedling performance under specific conditions.

Forest nursery terminology related to container types is often inconsistent across scientific and technical contexts. To improve clarity, we adopt the following classification according to Landis et al. [2, 49]. Cell containers refer to cavities, typically made of plastic or styrofoam, used either as individual containers or aggregated into trays (or blocks). Cell containers usually have rigid or semi-rigid walls and often include structural or chemical features to minimize root deformation. Polybags are small polyethylene sacks with highly flexible walls, mostly black, with smooth surfaces that do not prevent root deformations. They are widely used due to their low cost and commonly filled with field soil [4]. Compressed peat disks refer to small blocks of compressed dry peat that expand when watered and are enclosed in a degradable plastic net; this category includes both mini-plugs and larger stocks.

Materials and Methods

Literature Search

We conducted a systematic literature search in April 2024. The search included the following databases: Web of Science; Scopus; Reforestation, Nurseries, and Genetic Resources (USDA Forest Service, RNGR); SciELO; and the Sociedad Española de Ciencias Forestales (SECF), along with Google Scholar (using the first 300 results). Additional sources included non-indexed journals from Italy, Spain, France, Canada, and Eastern Europe. When available, the literature categories considered were Agricultural and Biological Sciences, Ecology, and Environmental Science. Search terms included "container*" AND "seedling*" AND "nursery" in Title, Keywords, and Abstract.

The literature search across the databases resulted in the following articles: Web of Science (986 articles), Scopus (1,749), RNGR (332), SciELO (552), SECF (27), and Google Scholar (300), totaling 3,946 articles. After removing duplicates and articles not relevant to the forest nursery sector, 3,034 articles were excluded. Topic screening was performed on the remaining 933 articles, including 21 from non-indexed journals, and 513 articles were excluded for not aligning with the research focus. Title and abstract screening was conducted on the remaining 420 articles, resulting in 64 exclusions. Thus, 356 articles underwent final vetting and selection (Fig. 1).

Study Vetting and Final Selection

A full-text screening was then done on the 356 articles. A study was selected if: (1) it included data about container characteristics (type, size, or both) and either seedling morphological characteristics after nursery cultivation, outplanting survival, or both; (2) it was published after 1985, to avoid outdated nursery practices; (3) nursery cultivation was conducted outdoors or in a greenhouse or under tunnels (i.e., not in growth chamber); (4) containers used were typical for forest nurseries (e.g. very large containers used for ornamental plants were excluded); (5) it included at least two cases of container type and/or volume (e.g., the same type with two different volumes); (6) it focused on trees (including hybrids) and shrubs inhabiting forest ecosystems (i.e., ornamental or fruit species, varieties, and related hybrids were excluded); (7) seedlings were grown from seeds, excluding cuttings, clones, and grafted plants; and (8) results reported at least the mean values and sample size for target seedling variables.

Moreover, a study was excluded if: (a) plants were transplanted into progressively larger containers as often occurs in fruit and ornamental nurseries (transplanting was allowed only in cases such as mini-plugs or other facilities used exclusively for seed germination); (b) treatments included radicle pruning after germination or any other root pruning during nursery cultivation; (c) the outplanting performance was not assessed under field conditions (i.e. seedlings transplanted into larger containers and/or in a greenhouse were excluded); (d) the duration of nursery cultivation was not considered standard, i.e., excluding the cases when it lasted only a few weeks or when the experiment ended significantly earlier than the typical readiness of seedlings for outplanting; (e) more than one seedling was grown within a single container. Using these criteria, we excluded 231 studies. Thus, 124 studies were selected (Fig. 1; reference list reported in SM1).

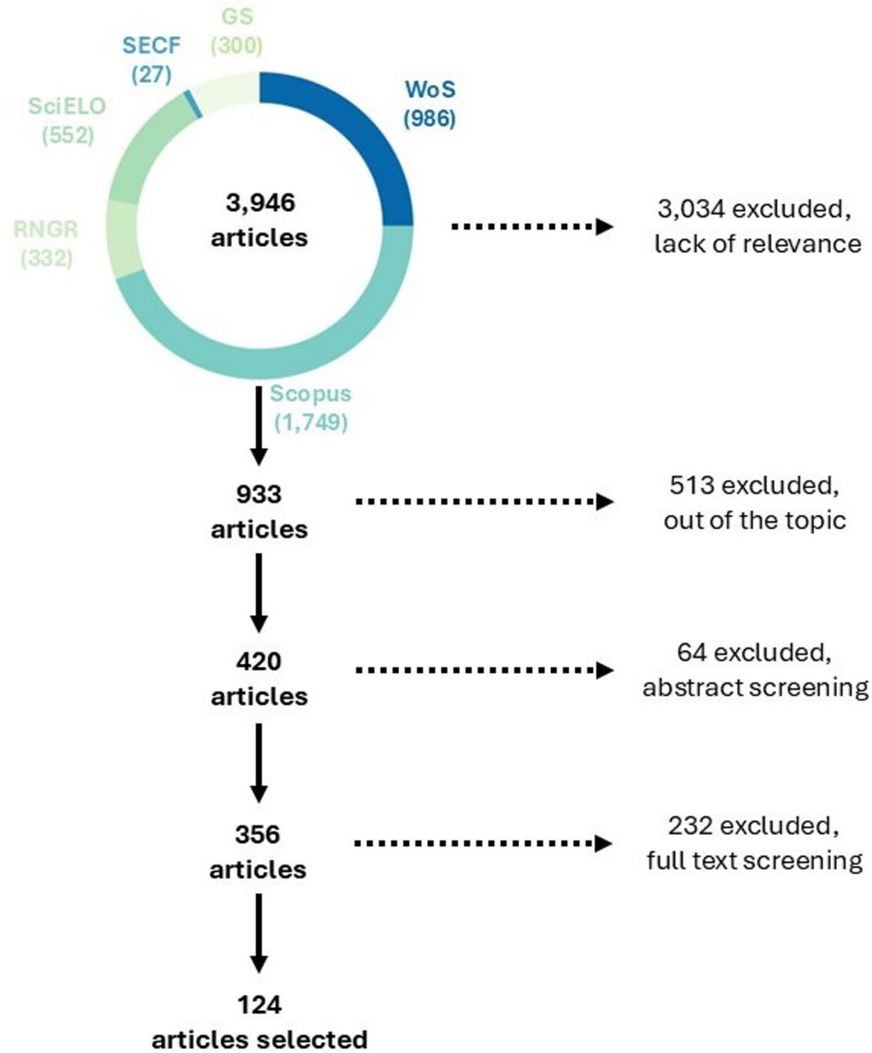

Fig. 1 Flowchart summarizing the article selection process adopted in the quantitative review. Selected references are listed in SM1

Study Cases and Data Extraction

For each selected study, we identified "study cases," discrete combinations of species, container type, container volume, nursery site, and seedling age. Therefore, many studies contained multiple study cases. When a study case was repeated within the same experiment under different nursery treatments (such as fertilization, irrigation, or other nursery practices, or combinations thereof), we averaged the mean values across all the treatments, or their combinations, and the sample size was given by the total number of treatments.

In the database, for each study case, we included or retrieved the following information.

- Container type and dimensions: container type (cell containers, polybags, compressed peat disks) and dimensions (volume, depth, width). When not reported, information was obtained from brand catalogs, related studies using the same model, or by contacting authors; where possible, dimensions were also calculated from available data. The number of study cases of cell containers and polybags is reported in the figures; compressed peat disks included 21 study cases.
- Cultivation density. When not reported in the study, it was calculated assuming that nursery production optimized the available space. The area occupied by the containers was considered as they were placed closely together, with their top sections used to calculate the number of containers per square meter.
- Location: when not reported in the article, coordinates of the nursery site and of studied field sites were approximated using Google Earth, which was also used to determine if field sites were cropland or a forest site. We also obtained the aridity index of the field site from the Global Aridity Index Geospatial Database [50], which is calculated from the WorldClim 2.0 data set [51] for the interval 1970–2000 at a resolution of 30 arc-sec, using precipitation and potential evapotranspiration data as follows:

$$Aridity\ index = Precipitation/Potential\ evapotranspiration \quad (1)$$

To facilitate the interpretation of the results we considered the moderator "Aridity" as the inverse of the Aridity index (1).

- Species, which were also classified according to taxonomic group (gymnosperms or angiosperms).
- Seedling size, age and field performance: seedling size was characterized by SDW, RDW, and the ratio of SDW to RDW (S:R). Seedling age at the end of nursery cultivation was classified as ≤1 year old, > 1 year old. Field performance data included survival and height growth 1 year after outplanting. If not explicitly reported, height growth was calculated as the difference between the final height of the seedlings in the nursery and their height measured in the field. When data was reported in figures we used ImageJ to retrieve the data [52].

The final database ultimately included 653 case studies, 100 species across 50 genera (66.6% angiosperms, 33.4% gymnosperms), and 27 countries worldwide (Fig. 2). From all study cases, 240 cases (in 44 papers) presented field data encompassing 64 planting sites distributed across five biomes as classified by Whittaker [53] (Fig. 3).

Data Analyses

Firstly, we used linear mixed models (LMM) to separately evaluate the effect of the different variables related to container characteristics and seedling cultivation in the nursery (i.e., container volume, container depth, and cultivation density) on seedling characteristics (SDW, RDW, and S:R) and height growth after outplanting. For evaluating the effect of these variables on the percentage of survival after outplanting we used generalized linear mixed models (GLMM). In all models, we considered the identity of primary studies as random term to account for lack of independence between case studies within each primary study [12]. Models were weighted by the number of measured seedlings (i.e., sample size), assuming that a higher sampling effort implies higher precision in estimating effects [54]. In LMMs, response variables were log-transformed to achieve homoscedasticity when needed.

Secondly, we evaluated whether the effect of container volume, container depth, and cultivation density on seedling characteristics and outplanting performance was modulated by container type, seedling age, taxonomic group, and planting site aridity. For that, we introduced each moderator interacting with seedling cultivation variables (container volume, container depth, and cultivation density) in the models described above, and tested significant differences between slopes for each level of variables (all variables are categorical with the exception of aridity) and whether the slopes were significantly different from zero (i.e., significant slope) by using a t-test ($P<0.05$). We also evaluated the effect of container characteristics and cultivation density in compressed peat disks. However, these analyses were performed separately for this type of container because its volume range (50 to 207 cm^3) was not comparable to that of polybags and cell containers (50 to 1500 cm^3). All models were fitted in R v4.3.1 using the packages *nmle* [55], *emmeans* [56], and *performance* [57].

Lastly, we used Structural Equation Modelling (SEM) to disentangle direct and indirect effects of container volume,

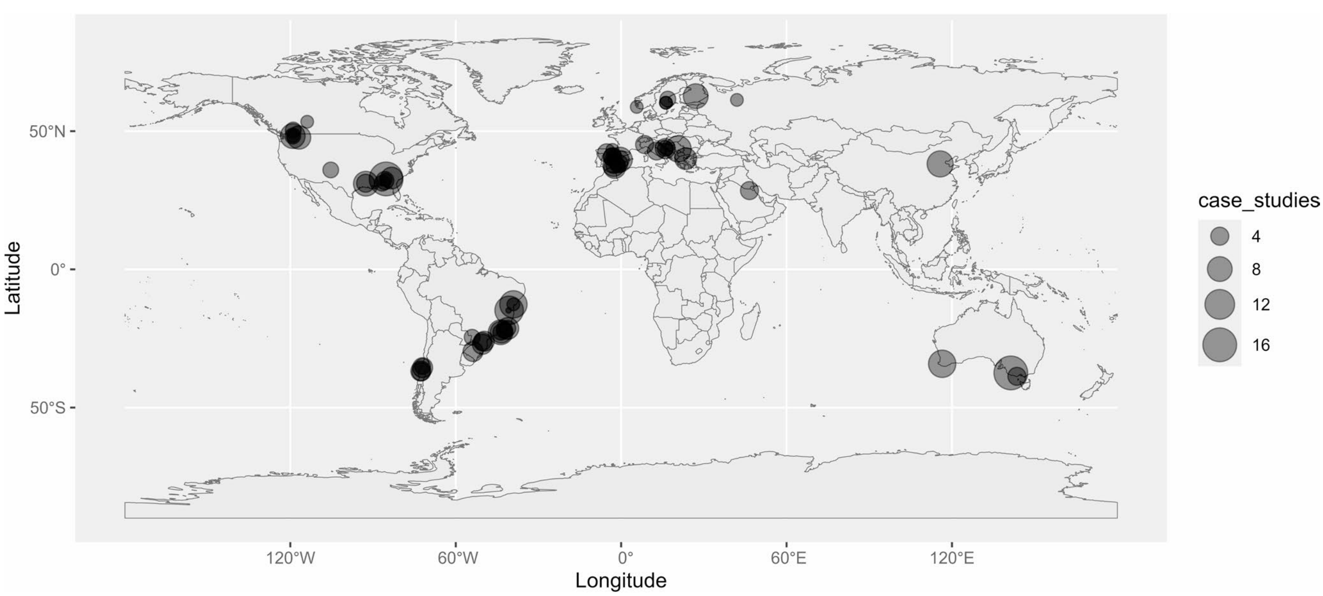

Fig. 2 Global distribution of case studies ($n=240$) with planting sites included in the quantitative review. Symbol size is proportional to the number of case studies at each location

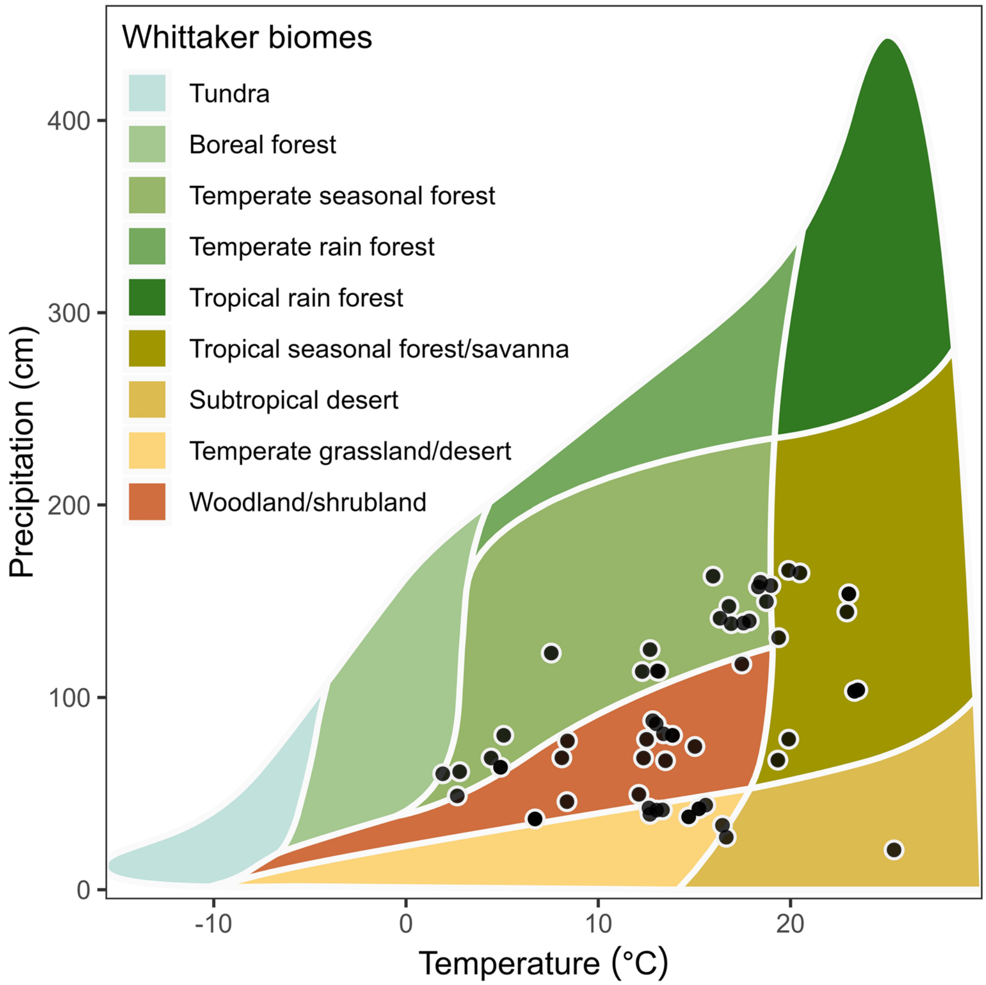

Fig. 3 Positioning of the case studies with field data within Whittaker biomes [53], according to mean annual temperature and precipitation conditions

container depth, and cultivation density on seedling characteristics and outplanting performance. SEM allows combining multiple causal relationships between variables from multiple separate linear models into a single causal network [58]. We created a SEM using a potential set of interconnected regression analyses in which arrows departing from container and growing characteristics have a direct effect on outplanting survival and an indirect effect through the modification of seedling morphological characteristics in the nursery (Fig. 4; Table 1). The initial model included SDW, RDW, S:R and outplanting survival as endogenous variables in four regression analyses: (i) SDW as a function of container volume, container, depth, and cultivation density; (ii) RDW as a function of container volume, container, depth, and cultivation density; (iii) S:R as a function of SDW and RDW; (iv) outplanting survival as a function of container volume, SDW, RDW, and S:R. As the correlations between container volume, container depth, and cultivation density were high, we considered correlations between the errors of these variables in our SEM. In all models, we considered the identity of primary studies as random term and weighted observations by the number of measured seedlings (i.e., sample size). We fitted the hypothesized SEM for all species and separately for angiosperms and gymnosperms because of functional differences between the taxonomic groups [59]. We tested the goodness of fit using a chi-squared test on the Fisher's C statistic [60]. This test evaluates whether potential missing paths should be considered in the initial SEM. Finally, we iteratively removed all non-significant missing paths, and each time re-tested the model's adequacy. SEM analyses were performed in R using the *piecewiseSEM* package [60]. Indirect effects were calculated as the product of the path coefficients along a mediating pathway.

Results

Do Container Volume, Depth, and Cultivation Density Influence Seedling Morphology in the Nursery?

Across the database, container volume significantly increased SDW ($P<0.001$, $n=455$) and RDW ($P<0.001$,

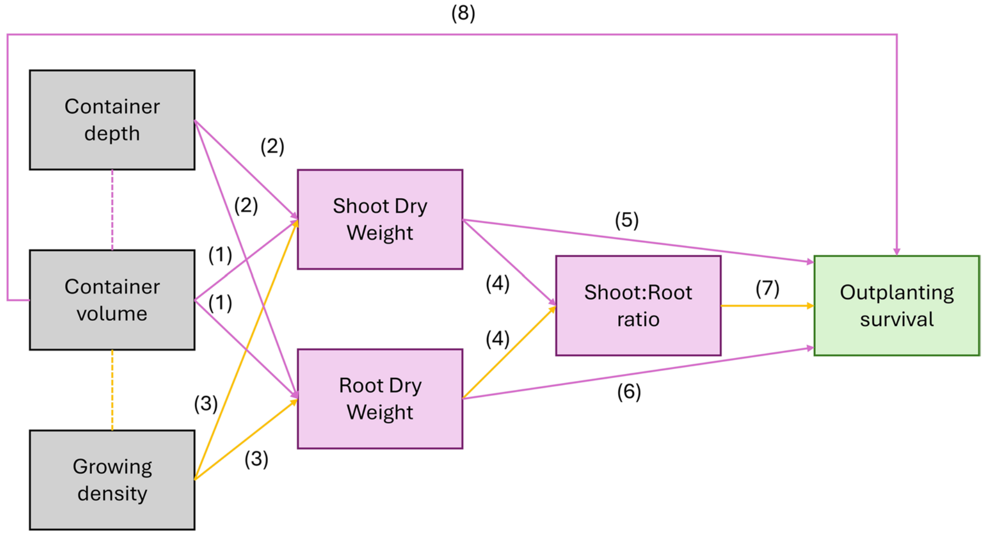

Fig. 4 Hypothesized structural equation model. Solid orange arrows denote negative causal effects whereas solid purple arrows depict positive effects. Dashed arrows represent correlations. The numbers represent the hypothesis underlying the effects, shown in Table 1

Table 1 Hypotheses supporting links in the hypothesized Structural Equation Model depicted in Fig. 4. References in this table are listed in SM2. Seedling size in the first three hypotheses refers to any variable indicating plant dimension, such as mass, root collar diameter, height, or stem volume

No#	Hypothesis	Reference
1	Container volume increases seedling size	Landis et al. 1990; Chirino et al. 2008; Pinto et al. 2011, 2012, 2016; Haywood et al. 2012; Jelić 2012; Poorter al 2012; Ivetić and Škorić2013; Regan et al. 2015; Mariotti et al. 2015a
2	Container depth increases seedling size	Chirino et al. 2008; Mariotti et al. 2015b; de la Fuente et al. 2017; Haywood et al. 2012; Jelić 2012; Pinto et al. 2011, 2012, 2016; Ivetić and Škorić 2013; Regan et al. 2015; Park et al. 2021
3	Cultivation density decreases seedling size through competition	Simpson et al. 1991; Shipman 1964; Menzies et al. 1985; Barnett and Brissette 1986; Nebgen and Mayer 1986; Rowan 1986; Ward and Johnston 1986; Mexal and South 1991; South 1993; Simpson 1994; Peterson 1997; Jinks and Mason 1998; South et al. 2005; Williams and Stewart 2006; Carneiro et al. 2007; Ivetić and Škorić 2013; Aghai et al. 2014
4	S:R is defined by the size of both compartments	Climent et al. 2011
5	Larger seedlings have higher outplanting survival	Andivia et al. 2021
6	Nursery root size increases outplanting survival	Thomson and Schultz 1995; Rose et al. 1997; Ward et al. 2000; Davis and Jacobs 2005; Jacobs et al. 2005; Wilson et al. 2007; Ivetić et al. 2016 Grossnickle and Ivetic 2022
7	Lower S:R increases outplanting survival	Larsen et al. 1986; Boyer and South 1987; van den Driessche 1991; Ivetić et al. 2016; Grossnickle 2012
8	Indirect effect of container volume on outplaning survival mediated by factors such as root deformations or plug nutrient content	Grossnickle and Ivetić 2022

$n=469$), but decreased S:R ($P=0.025$, $n=465$). Container depth also increased RDW ($P=0.001$, $n=357$) and decreased S:R ($P=0.012$, $n=368$), but had no effect on SDW ($P=0.260$, $n=346$). Cultivation density showed opposite results to container volume and depth, decreasing SDW ($P<0.001$, $n=329$) and RDW ($P<0.001$, $n=340$), while increasing S:R ($P=0.005$, $n=351$).

The effect of container volume and depth, and cultivation density on plant morphology differed among container types. Container volume had a positive effect on SDW and RDW in polybags and cell containers, while a negative effect of container volume on S:R was only observed in cell containers (Fig. 5). In compressed peat disks, volume had a negative effect on SDW and S:R, while it did not influence RDW (data not shown). Container depth increased RDW and reduced S:R only in cell containers (Fig. 6). Thus, results in cell containers suggest that variations in volume and depth influenced shoot and root biomass allocation. Cultivation density consistently decreased SDW and RDW in polybags and cell containers, but the positive relationship between cultivation density and S:R was only observed in cell containers (Fig. 7). Cultivation density did not affect morphology in seedlings grown in compressed peat disks (data not shown).

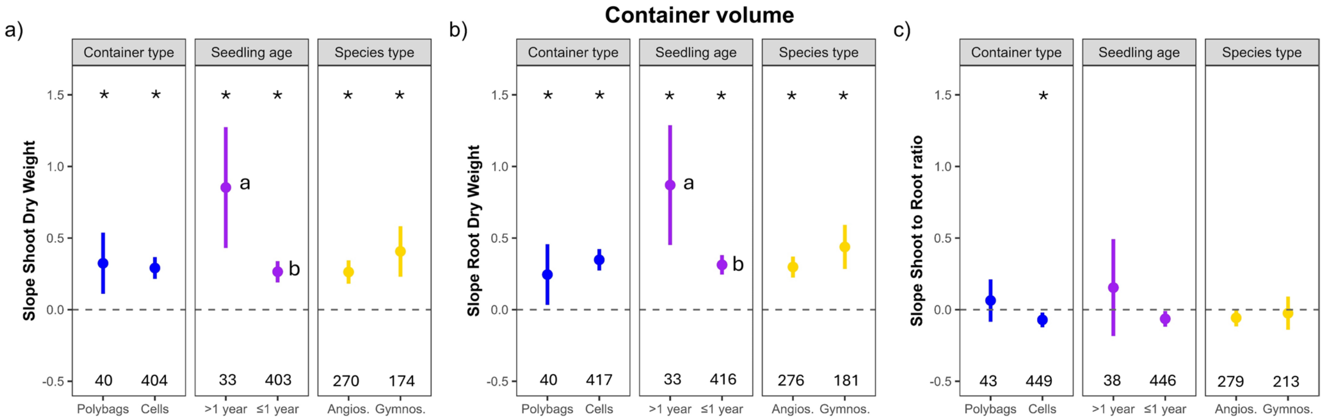

Fig. 5 Estimated slopes (±95% confidence interval) for the effect of container volume on the shoot dry weight (**a**), root dry weight (**b**), and shoot to root ratio (**c**) for each level of moderators (container type, seedling age, and taxonomic group). Stars (*) indicate a significant effect of the moderator at a specific level, while different letters indicate significant differences between the levels of the moderator on the examined parameter. Numbers inside the subfigures indicate the number of study cases of each moderator

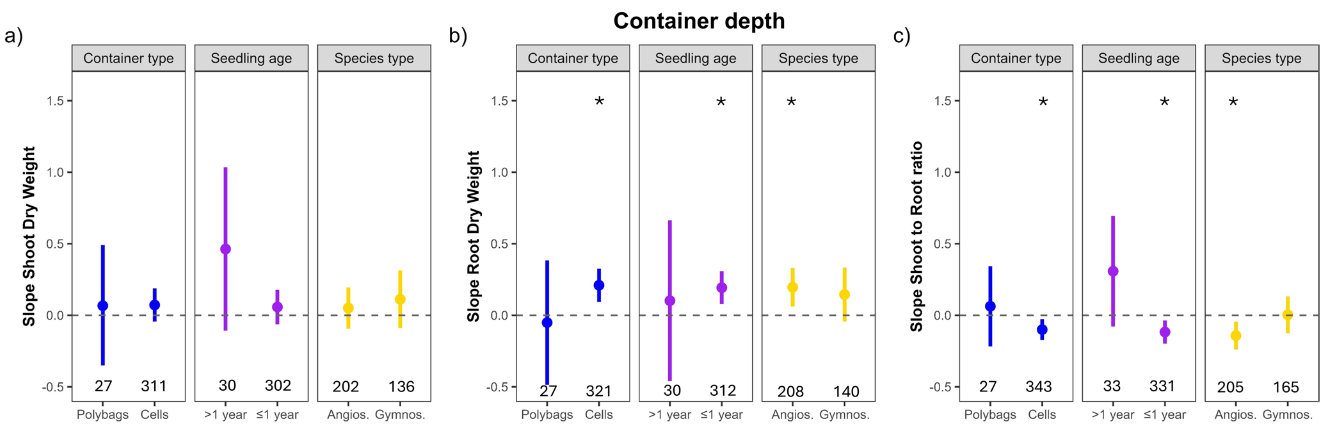

Fig. 6 Estimated slopes (±95% confidence interval) for the effect of container depth on shoot dry weight (**a**), root dry weight (**b**), and shoot to root ratio (**c**) for each level of moderators (container type, seedling age, and taxonomic groups). Stars (*) indicate a significant effect of the moderator at a specific level. Numbers inside the subfigures indicate the number of study cases of each moderator

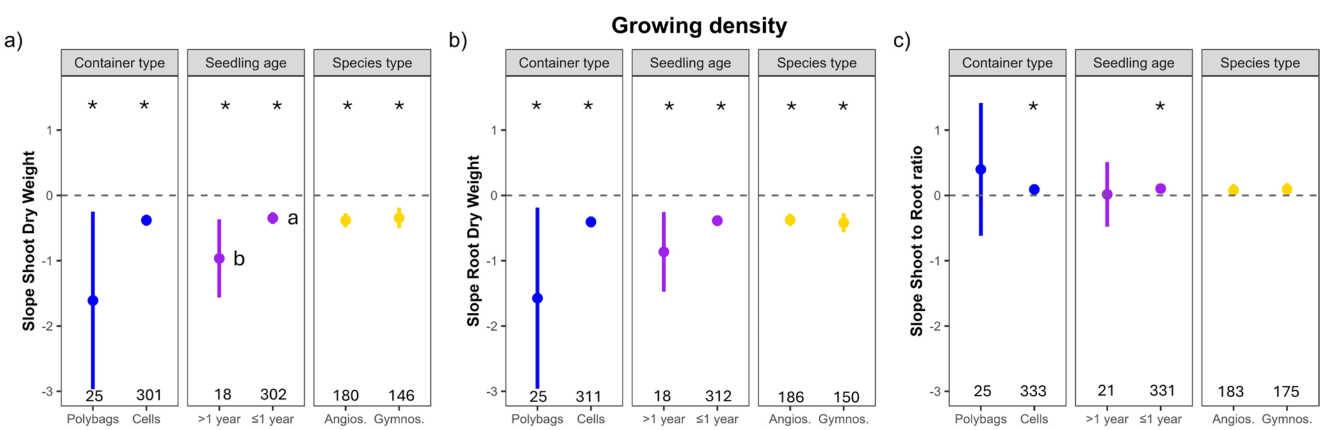

Fig. 7 Estimated slopes (±95% confidence interval) for the effect of cultivation density on shoot dry weight (**a**), root dry weight (**b**), and shoot to root ratio (**c**) for each level of moderators (container type, seedling age, and taxonomic groups). Stars (*) indicate a significant effect of the moderator at a specific level. Numbers inside the subfigures indicate the number of study cases of each moderator

Container volume increased SDW and RDW in both seedling age classes, but the effect was significantly higher in seedlings > 1 year-old (Fig. 5). However, container depth significantly increased RDW only in ≤ 1 year-old seedlings (Fig. 6). The negative effect of cultivation density on SDW and RDW was consistent for both seedling age classes, but the effect on SDW was higher in seedlings > than one year (Fig. 7). The negative effect of container volume and depth, and the positive one of cultivation density on S:R was only significant for ≤ 1 year-old seedlings.

The positive effects of container volume and the negative effects of cultivation density on SDW and RDW similarly affected both angiosperms and gymnosperms (Figs. 5 and 7). In contrast, the positive effect of depth on RDW and the negative effect on S:R were only significant for angiosperms (Fig. 6). We did not find, however, any significant effect of container volume and cultivation density on S:R for angiosperms and gymnosperms separately.

Do Container Size and Cultivation Density Influence Outplanting Performance?

Across all study cases, container volume and depth increased outplanting survival ($P<0.001$, $n=230$ and $P=0.002$, $n=181$, respectively), while cultivation density had a marginal negative effect ($P=0.053$, $n=162$). Container volume, depth, and cultivation density were not significant for outplanting height growth.

The positive effect of container volume and depth on survival was only significant for cell containers and ≤ 1 year-old seedlings (Fig. 8a, b) although these results must be interpreted with caution due to the limited number of study cases involving polybags and seedlings > 1 year-old. The effect of container characteristics was consistent for both taxonomic groups, but the relationship with container volume was more positive in angiosperms than in gymnosperms (Fig. 8a, b). We found no significant interaction between aridity and the effect of container volume or cultivation density on survival. The effects of container dimensions and growing density on survival were, however, observed in forest sites but not in cropland (Fig. 8).

Are the Effects of Container Characteristics and Cultivation Density on Outplanting Survival Mediated by Their Effects on Seedling Morphology?

We did not find evidence for indirect effects of container volume and depth, and cultivation density on outplanting survival mediated by seedling morphological traits in the nursery when all species were analyzed together (Fig. 9a). However, when angiosperms and gymnosperms were analyzed separately, we found that container volume and cultivation density influenced survival in both taxonomic groups through modifications of seedling morphology. In angiosperms, survival was negatively related to S:R (Fig. 9b), which was modified by positive effects of container volume on SDW and RDW, and by negative effects of container depth on SDW. In gymnosperms, outplanting survival was negatively related to SDW, which was also negatively related to cultivation density (Fig. 9c). In all analyses (Fig. 9a, b, and c), we found a direct positive effect of container volume on survival. In angiosperms, this direct effect was strengthened by positive indirect effects mediated by modifications in seedling morphology ($\beta=0.301$ and 0.012 for direct and indirect effects, respectively), while in gymnosperms it was weakened by negative indirect effects ($\beta=0.259$ and -0.058 for direct and indirect effects, respectively).

Discussion

Our results revealed that container volume, depth, and cultivation density are key drivers of nursery seedling growth. Compared to small-volume containers, large-volume containers yielded more root mass than shoot mass, reducing the S:R, whereas higher cultivation density, associated with the small-volume containers, produced the opposite effects. Increasing container depth specifically enhanced root development, contributing to the stronger influence of container volume on root than on shoot, as also supported by SEM analysis (Fig. 9). Containers with larger volume and greater depth also improved seedling outplanting survival, although they did not affect field growth, whereas the negative effect of the higher cultivation density was weaker and less consistent (Fig. 8). Overall, these trends were more pronounced in cell containers than in polybags, in ≤ 1 year-old seedlings than in older stock, and in angiosperms than in gymnosperms.

Container Volume, Depth, and Cultivation Density Influence Seedling Morphology in the Nursery

The positive influence of container volume on shoot and root mass is consistent with previous findings in different species and in a wide variety of regions (e.g. [21, 27, 32, 33, 35, 37, 39, 61, 62]). Larger containers provide more space for root growth and hold more water and nutrients [63, 64], resulting in higher tissue nutrient and carbohydrate content [27, 65–68]. This higher resource availability, however, cannot fully explain the greater growth of seedlings in large containers as reduced growth in smaller containers is primarily driven by lower photosynthesis per unit of rooting volume, rather than by changes in leaf morphology or mass allocation

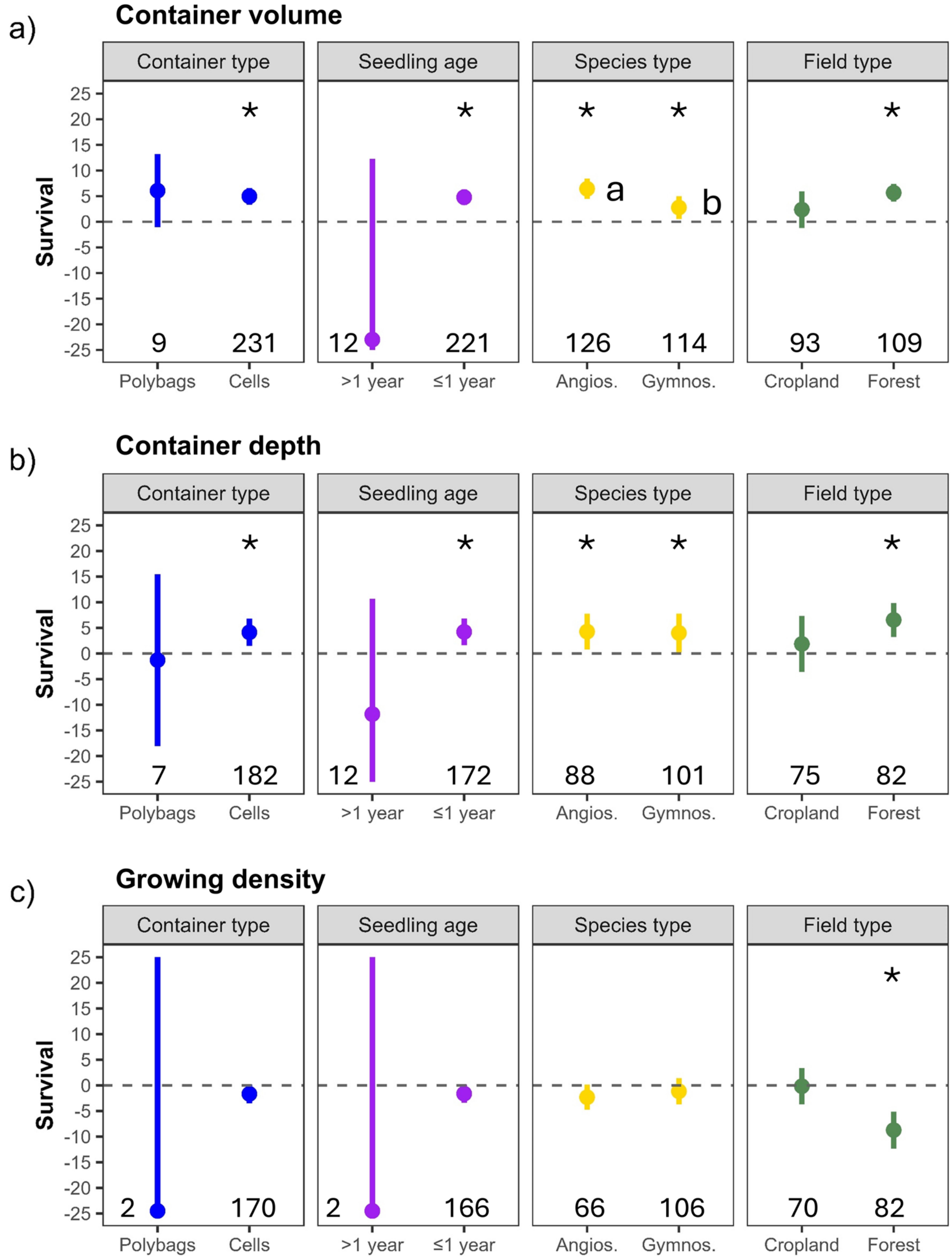

Fig. 8 Estimated slopes (±95% confidence interval) for the effect of container volume (**a**), container depth (**b**), and cultivation density (**c**) on outplanting survival for each level of moderators (container type, seedling age, taxonomic group, and field type). Model estimates for levels with less than five observations are not represented because of lack of model convergence. Stars (*) indicate a significant effect of the moderator at a specific level. Numbers inside the subfigures indicate the number of study cases of each moderator

[21]. Thereby, high plant mass relative to container volume enhances root confinement and can limit seedling growth [21]. In addition, the lower water-holding capacity of smaller containers can lead to faster substrate drying between irrigation events, potentially subjecting seedlings to short periods of increased water stress, especially for large plants [69, 70].

The positive effects of container volume on seedling growth occurred both in polybags and cell containers, the most used container types globally. This suggests that growth depends primarily on available space regardless of container wall rigidity (i.e., rigid vs. flexible walls). Therefore, flexibility of container walls, which could lead to changes in available space or substrate lateral compression by placing polybags tightly together in the nursery, does not appear to have a significant effect. This property, however, likely determines the limited volume range of compressed peat disks [30], whose use is often restricted to germination and early seedling development prior to transplanting into cavities or bareroot nursery beds [71, 72]. Additionally, the soft, fibrous walls of compressed peat disks can retain more salts and restrict salt redistribution within the growing medium [73]. This effect may be amplified by higher moisture loss through the plastic net walls, promoting greater salt accumulation compared to rigid-wall containers.

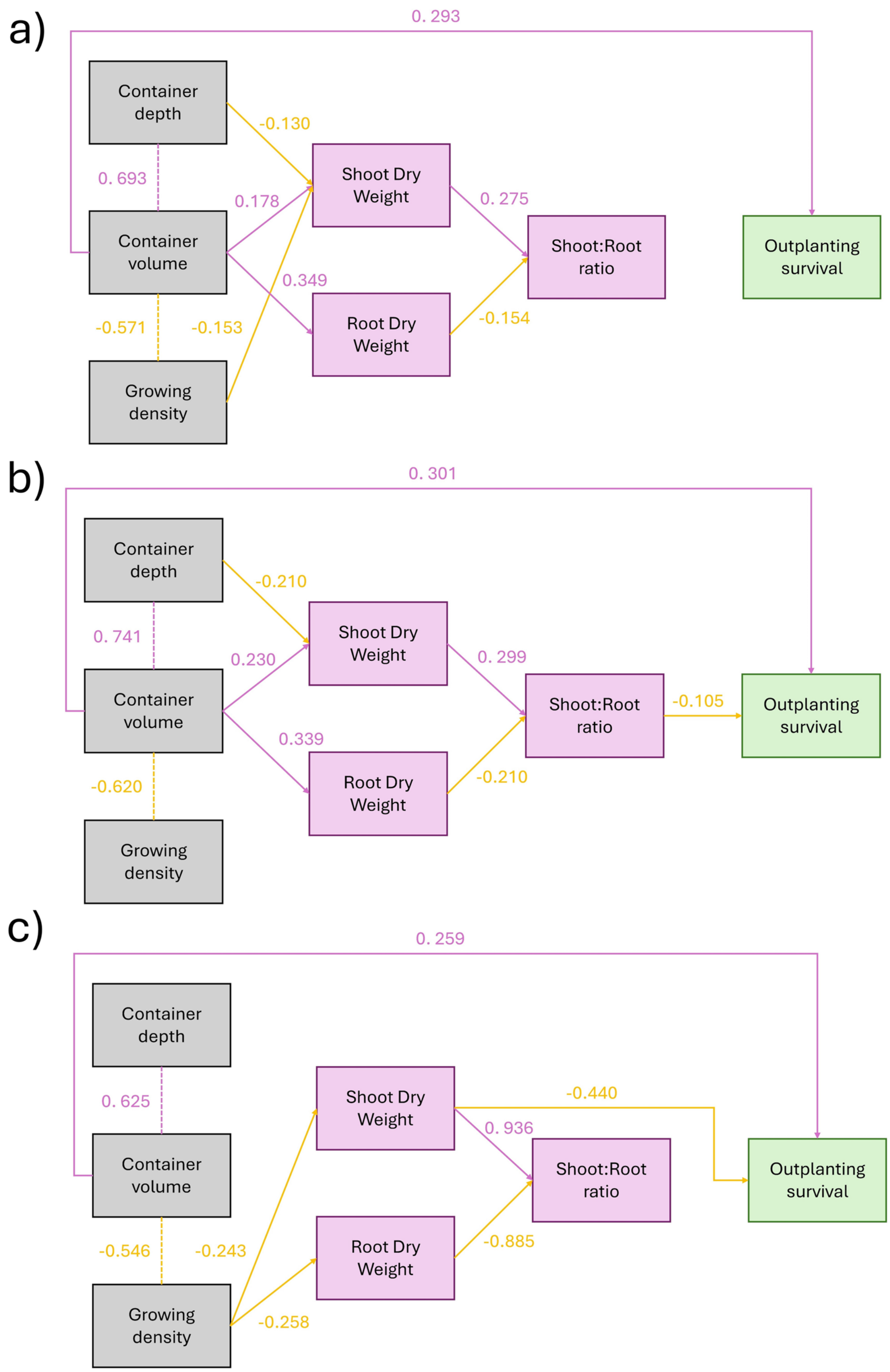

Fig. 9 Best supported structural equation models showing significant paths (p-values < 0.05) and the corresponding standardized parameters (β) for all species (**a**), angiosperms (**b**), and gymnosperms (**c**). Solid orange arrows denote negative causal effects whereas solid purple arrows depict positive effects. Dashed lines represent correlations

The positive effects of container volume on nursery growth were stronger in > 1 year-old seedlings. This indicates that extending cultivation beyond one growing season does not reduce the growth advantage of larger containers under conditions of limited rooting volume. Two reasons may explain the higher growth response to volume in older seedlings. First, the non-limiting water and nutrient supply in nurseries may sustain growth despite limited root space. Second, according to the wood density and specific leaf area of our species, which are surrogates of species relative growth rate [74], a substantial part (63.3% overall; 65.7% for angiosperms and 58.1% for gymnosperms; data not shown) of the older seedlings in our database can be classified as slow-growing species. Seedlings of slow-growing species require longer cultivation periods to reach optimal growth and plug consolidation [75]. It remains unclear how long the positive effects of container volume on growth persist, or whether root development eventually saturates and whether other issues linked to long-term cultivation such as root deformations [19, 26, 76] can arise. This question deserves further investigation in future studies.

Container width and depth influenced seedling nursery growth indirectly through their contribution to volume, but also exerted direct, dimension-specific effects (see Fig. 6, for depth). Interestingly, depth consistently emerged as a key driver for root growth, reflecting its prominent role in determining the positive effects of container volume on root growth. Conversely, width per se showed no significant effect on growth (data not reported). Greater root mass is usually associated with higher nutrient and carbohydrate storage capacity [26, 76, 77], which support new root development for exploring the soil surrounding the plug after outplanting [34, 78–80]. Additionally, deeper containers provide space for robust root development, particularly in tap-rooted species, and may also confer secondary benefits by reducing the influence of the hypoxic water layer that forms at the container bottom [30, 70, 81]. In contrast to root growth, depth alone did not significantly affect shoot growth, suggesting that, under non-limiting nutrient and water conditions in the nursery, shoot growth depends mainly on total root-explorable volume rather than depth per se. Interestingly, the influence of depth on seedling morphology varied with container type, with positive effects on root mass occurring exclusively in cell containers. Depth variation was similar across container types and therefore unlikely to have biased the results. Although the effect of container depth on root growth was evident only in angiosperms, the predominance of angiosperms in polybags in our dataset (85.7% of cases, compared with 52.8% in cavity/single containers) did not translate into a significant positive depth effect within this container type either. This indicates that differences in the proportion of angiosperms and gymnosperms across container types are unlikely to have affected the observed responses. A more plausible explanation could be related to differences in growing media. Polybags, which are widely used in developing countries, are typically filled with mineral soil rather than organic substrates [4, 19], resulting in lower substrate porosity, greater heterogeneity in soil properties across nurseries and cultivation seasons, and potentially reduced cation exchange capacity and water-holding capacity [4, 17]. These properties may constrain root proliferation and limit the capacity to exploit greater container depth, thereby reducing the relative allocation to roots compared with cell containers. Container depth reduced S:R only in ≤ 1 year-old seedlings, consistent with the promotion of root mass instead of shoot growth. This response may reflect ontogenetic patterns of root development, as early root growth is dominated by taproot elongation, which accounts for most root mass [40], and grows downwards until reaching the container bottom [39, 82]. Subsequently, first order lateral roots, which usually contribute less to total root mass, expand laterally toward the container walls [40]. In deeper containers, the transition from taproot dominance to lateral root expansion occurs later than in shallower containers [40], which may explain why the positive effect of container depth on root mass was observed only in younger seedlings.

Cultivation density showed effects opposite to those of container size, reducing both seedling root and shoot mass, regardless of container type or seedling age [27, 83, 84]. This likely reflects increased competition among seedlings for light, nutrients, and water, which is exacerbated in small, closely spaced containers where plant canopies are often in contact, limiting both light availability and the penetration of irrigation water, resulting in spindly seedlings [19, 30]. Higher cultivation density is usually associated with narrower containers, and in most marketable containers, reduced width also coincides with reduced depth, further limiting root-explorable volume and growth, as shown in our results. Therefore, although container width did not emerge as a significant predictor of seedling growth in our preliminary analysis, its link with cultivation density suggests that it may be indirectly associated with seedling morphology.

Angiosperms and gymnosperms showed distinct seedling growth responses to container properties, with SEM analysis (Fig. 9) providing further insights into these relationships and the mechanisms underlying such differences. Overall, angiosperm responses were driven by container depth and volume, while gymnosperm responses were primarily driven by cultivation density. The stronger and direct positive effect of container depth on growth, especially root growth, in angiosperms suggests that they are more responsive to variation in soil resources and may be related to the fact that taproots are more frequent in large-seeded species [85, 86]. In our database, many angiosperms, such as *Quercus*, *Juglans*, *Castanea*, *Fagus*, and *Fraxinus*, were large-seeded species. Taproot development mainly benefits from deep containers [38]. The direct effects of cultivation density observed in gymnosperms may also reflect functional differences between taxonomic groups, as many conifers — which constituted most of the gymnosperms in our dataset — are generally more shade-intolerant [59] than angiosperms, making them more sensitive to light competition [87, 88].

How Container Size and Cultivation Density Influence Outplanting Performance

Increasing container size — both volume and depth — generally promoted outplanting seedling survival, while cultivation density had a weaker, less consistent, negative effect (Fig. 8). These patterns were observed at forest planting sites but not in croplands (Fig. 8) suggesting that the effects of container properties and seedling morphology on survival mainly emerge under harsher planting sites [14]. The effect of container volume on survival appeared to be largely direct in both angiosperms and gymnosperms and only weakly mediated by container effects on seedling morphology. This suggests that other nursery and planting factors linked to larger containers exert a stronger influence on early field performance than seedling morphology. Plausible explanations for these direct effects of container volume on survival include higher seedling nutrient and assimilate production [21, 27, 89, 90], which often increase early survival independently of seedling morphology [77, 90–93]. In addition, when seedling S:R is not strongly biased toward shoot mass, larger-volume containers produce larger plugs that can proportionally retain more water and nutrients than small-volume containers, despite the higher transpiration of stock grown in them [94, 95]. This greater water storage capacity can help maintain seedling hydration during transport and early establishment [95], thereby reducing transplant shock. Pre- and post-planting factors not considered in this review, such as site preparation, weed competition, planting timing may further influence the effect of container volume on survival and should be examined in future studies. Notably, neither container size nor cultivation density significantly affected field growth. Species-specific growth capacity and site-specific environmental conditions might have outweighed the container effects on field growth [96–99]. Moreover, we analyzed multiple species, and because the data refer to absolute height increment, the results may be partly biased by the high number of species included.

Larger and deeper containers and lower cultivation density increased field survival in cell containers, but not in polybags. However, results for polybags should be interpreted with caution due to the limited number of studies available for this container type. The lack of significant effects of container volume and depth on seedling survival in polybags might be attributed to the structural and cultivation characteristics inherent to this container type. Polybags are commonly filled with field soil (see Sect. 4.1) that often has poor drainage, leading to water accumulation at the bottom that can promote root deformation [4]. Furthermore, variations in soil filling height and substrate compaction can alter effective cultivation volume and density. Similarly, container effects on survival were observed only in ≤ 1 year-old seedlings, underscoring the importance of planting seedlings as soon as they reach target sizes and hardening for optimal outplanting performance [14]. For species typically planted as ≤ 1 year-old seedlings, producing vigorous plants with well-consolidated plugs is advantageous [14]. In contrast, the less consistent results observed for seedlings older than one year likely reflect a combination of biological and management factors. Older seedlings may include slow-growing species, or represent individuals that experienced suboptimal growth during the first season and were retained in the nursery for an additional year [14]. Furthermore, increasing seedling age has been reported to diminish the positive effect of plant size on survival, especially in dry sites [14, 100, 101], suggesting that the benefits of extended cultivation may be context- and species-dependent. The low number of older seedlings in our dataset, however, precludes assessing the specific conditions under which extending the cultivation period and using larger containers may enhance outplanting survival.

Container properties, especially volume and depth, affected survival more strongly in angiosperms than in gymnosperms (Fig. 8), likely reflecting their functional differences discussed above, i.e., root development generally more pronounced [102, 103] and faster growth rates [45, 104, 105], reinforcing the importance of volume for angiosperms. SEM analysis revealed further distinct mechanisms linking nursery factors, seedling morphology, and outplanting survival for both taxonomic groups. In angiosperms, container volume had a strong positive direct effect on survival, suggesting that additional nursery (e.g., fertilization [10, 92, 106]) or site factors (e.g., site preparation [107–109]) not accounted for play a more prominent role in explaining the greater field performance of seedlings cultivated in bigger containers.

In both angiosperms and gymnosperms, SEM results revealed that container volume indirectly affected survival via seedling morphology, although the mechanism seems to differ between both taxonomic groups. In angiosperms, variations in container volume (and depth) indirectly affected survival through the S:R due to different shoot and root growth responses. Interestingly, the link between S:R and survival was negative, suggesting that pronounced imbalances — more frequent in fast-growing species and smaller containers — may reduce survival [11, 14]. A recent study [14] has highlighted that moderate S:R imbalances generally do not compromise seedling survival, and that, under standard nursery protocols, seedlings rarely develop extreme S:R that impair establishment. In gymnosperms, the indirect pathway between container properties and outplanting survival was mediated by shoot mass. Reductions in container volume, often associated with higher cultivation density, led to reduced shoot mass (Fig. 9), which in turn increased survival. These results suggest that shoot traits are particularly important in gymnosperms, likely due to harsher planting environments where initial aboveground vigor could be particularly relevant; gymnosperms are often outplanted in frost-prone locations or in sites with shallow, poor soils, or in areas with high herbivory pressure [12]. Notably, negative indirect effects of container volume on survival via seedling morphology were weaker than direct effects of volume on survival in both taxonomic groups. This indicates that direct benefits outweigh negative indirect consequences mediated by seedling morphology.

Conclusions and Recommendations

Overall, increasing container volume within the range of standard forest nursery containers (at least upward to a maximum of 1500 ml, which is the analyzed range) improves seedling morphological quality and enhances outplanting survival. We recommend this strategy when using cell containers, for stocktype commonly cultivated in not more than one year that will be planted in harsh, forest sites. Container depth can also be leveraged to produce larger seedlings, particularly by promoting root mass (and reducing S:R) in large-seeded, taproot-bearing angiosperms. In contrast, cultivation density plays a more important role in determining survival in gymnosperms than in angiosperms. In both taxonomic groups, container properties affected outplanting survival through a combination of direct effect and species-specific indirect effects mediated by seedling morphology. In angiosperms, increasing container volume, mainly through greater depth, indirectly enhances survival partly through reductions in S:R. In gymnosperms, indirect effects were instead mediated by shoot mass, which was negatively related to survival. Accordingly, container design should be adjusted to the plant taxonomic (functional) group: increasing container depth can be particularly more effective for angiosperms, whereas controlling cultivation density is more critical for gymnosperms. Most of these strategies imply higher production cost, which can be offset by increased outplanting performance. Future research should explicitly evaluate the cost effectiveness of these nursery decisions.

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Author contributions BM, EA, PVS contributed to the study conception and design. Material preparation and data collection were performed by all authors. Statistical analyses were performed by EA, PVS, AB. The first draft of the manuscript was written by BM, EA, PVS. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Barbara Mariotti[1] · Enrique Andivia[2] · Pedro Villar-Salvador[3] · Vladan Ivetić[4] · Alessandro Bizzarri[1] · Maurizio Ventura[5] · Roberto Tognetti[5] · Fabio Salbitano[6] · Claudia Cocozza[1] · Alberto Maltoni[1]

✉ Barbara Mariotti
barbara.mariotti@unifi.it

Enrique Andivia
eandivia@ucm.es

Pedro Villar-Salvador
pedro.villar@uah.es

Vladan Ivetić
vladan.ivetic@sfb.bg.ac.rs

Alessandro Bizzarri
alessandro.bizzarri@unifi.it

Maurizio Ventura
maurizio.ventura@unibz.it

Roberto Tognetti
roberto.tognetti@unibz.it

Fabio Salbitano
fsalbitano@uniss.it

Claudia Cocozza
claudia.cocozza@unifi.it

Alberto Maltoni
alberto.maltoni@unifi.it

1 Department of Agriculture, Food, Environment and Forestry (DAGRI), University of Florence, Via San Bonaventura 13, Firenze 50145, Italy

2 Department of Biodiversity, Ecology and Evolution, Faculty of Biological Sciences, Universidad Complutense de Madrid, Madrid 28040, Spain

3 Forest Ecology and Restoration Group, Departamento de Ciencias de la Vida, Universidad de Alcalá, Alcalá de Henares, Madrid 28805, Spain

4 Faculty of Forestry, University of Belgrade, Kneza Višeslava 1, Belgrade 11030, Serbia

5 Faculty of Agricultural, Environmental and Food Sciences, Piazza Università, 5, Bolzano 39100, Italy

6 Department of Agricultural Science, University of Sassari, Viale Italia 39/A, Sassari, Italy