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EDITED BY

Ivika Ostonen,
University of Tartu, Estonia

REVIEWED BY

Ziliang Zhang,
University of Illinois at Urbana-Champaign,
United States
Timo Domisch,
Natural Resources Institute Finland (Luke),
Finland

*CORRESPONDENCE

Gabriella Sferra
✉ gabriella.sferra@unimol.it

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A systematic review of studies on fine and coarse root traits measurement: towards the enhancement of urban forests monitoring and management

Daniele Fantozzi¹, Antonio Montagnoli², Dalila Trupiano¹, Paolo Di Martino¹, Gabriella Stefania Scippa¹, Gustavo Agosto², Donato Chiatante² and Gabriella Sferra^{1*}

¹Department of Bioscience and Territory, University of Molise, Pesche, Italy, ²Laboratory of Environmental and Applied Botany, Department of Biotechnology and Life Science, University of Insubria, Varese, Italy

The analysis of fine and coarse roots' functional traits has the potential to reveal the performance of the root system, which is pivotal in tree growth, development, and failure in both natural and urban forest ecosystems. Furthermore, root traits may be a powerful indicator of tree resilience mechanisms. However, due to the inherent difficulties in measuring 'the hidden half,' and despite the recent advancements, the relationships among root functional traits and biotic and abiotic drivers still suffer from a lack of information. Thus, our study aimed to evidence knowledge milestones and gaps and to categorize, discuss, and suggest future directions for effective experimental designs in fine and coarse root studies. To this end, we conducted a systematic literature review supported by backward manual referencing based on 55 root functional traits and 136 plant species potentially suitable for afforestation and reforestation of natural and urban forest ecosystems. The majority of the 168 papers on fine and coarse root studies selected in our review focused predominantly on European natural contexts for a few plant species, such as *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, and *Pinus cembra*, and root functional traits such as standing biomass, phenology production, turnover rate, and non-structural carbohydrates (NSC). Additionally, the analyzed studies frequently lack information and uniformity in experimental designs, measurements, and statistical analysis, highlighting the difficult integration and comparison of outcomes derived from different experiments and sites. Moreover, no information has been detected in selected literature about urban forest ecosystems, while most of the studies focus on natural forests. These biases observed during our literature analysis led us to give key indications for future experiment designs with fine and coarse roots involved, which may contribute to the building up of common protocols to boost the monitoring, managing, and planning of afforestation and reforestation projects.

KEYWORDS

functional traits, fine roots, coarse roots, literature metadata, experimental design, natural forest, urban forest

1 Introduction

Both natural and urban forests deliver multiple vital functions and benefits deemed as ecosystem services that rely on physical, biological, and social modifications of the environment (Mori, 2017; Win, 2019). However, specific demands drive plant management by altering forests and tree attributes (Felipe-Lucia et al., 2018), which may affect their self-organization, adaptative capacity, and resilience (Nocentini et al., 2022). Short- and long-term innovation and optimization strategies are required for the sustainable provision of these ecosystem services (Mann et al., 2022), which, to be effective, should be based not only on increasing the tree cover (Przewoźna et al., 2022), but on an integrated perspective that includes the economic, environmental, and social dynamics of the rural-to-urban gradient (Feng et al., 2021). In this scenario, restoring, increasing, and preserving forest biodiversity, including a minimum of 10% of urban areas covered by tree canopy in all cities by 2050 (European Commission, Directorate-General for Environment, 2021, 2023), as well as integrating with their sustainable strategic planning also green space networks characterizing the peri-urban areas (Verdú-Vázquez et al., 2021), represent a crucial multiple task. Thus, in the next few years, European cities are expected to accomplish a large number of tree-based projects with a priority on the maintenance/management of already established urban and non-urban ecosystems. To make these projects effective, the development of guidelines and good practices is needed.

Due to global warming, central Europe is expected to experience more frequent and long summer droughts with a higher frequency and intensity of storms, windstorms, and other impacting climate events (Pauleit et al., 2005; Solomon, 2007; IPCC, 2014). These events are currently responsible in Europe for about 50% of tree decline, which occurs both in urban and non-urban forests because of the failure interplay between the above- and below-ground tissues (Taccoen et al., 2022). An inadequate rooting response to climate change events is one of the crucial factors in tree failure (Tamasi et al., 2005; Nicoll et al., 2008; Day et al., 2010; McCarthy et al., 2010; Correa et al., 2019), even if the relationship with the potential drivers is still an open question (van Haaften et al., 2021). Evidence points to the impacts of paving and soil compaction on tree root stability and nutrient uptake and their structural collapse caused by pathogen attacks or climate extremes on poorly managed trees (Manfra et al., 2022). Consequently, the root system is a key determinant of the functioning of the forest ecosystem, and the possibility to evaluate root health, decay, and injury is crucial not only to tree stability and management but also for the safety of forests and environments in both urban and non-urban contexts (Kabir et al., 2018; van Haaften et al., 2021).

Plant species vary widely in root characteristics and lifespan and thus create formidable challenges in defining the strategic and operational plans about “where” and “how” to choose tree species for the different areas or about performing interventions on already present plants in urban or non-urban areas. In this direction, the Italian strategic plan for urban forestry built up a list of different species suitable for the afforestation and reforestation of urban areas (NRRP; Protection and enhancement of urban and extra-urban green—M2C4 3.1). This list of species is expected to be the basis for the established planting of 6.6 million trees by 2024, underscoring the issue of the heterogeneity of the new planting species and recommending planting trees according to the biogeographical and

ecological characteristics of the sites (Lenormand et al., 2018). In particular, this list includes the main species composing the flora of both Mediterranean and temperate forest ecosystems,¹ being representative of the European and pan-European biogeographical regions. Thus, these species potentially play a pivotal role at the European scale in rethinking urban and non-urban designs through successful afforestation/reforestation interventions underpinned by a thorough knowledge of vegetation distribution and their capacity to deliver ecosystem services. In this direction, specific and standardized indexes/traits quantifying the value of plant ecosystem services in urban and non-urban contexts are needed.

As reviewed by Freschét et al. (2021b), root functional traits can be analyzed to obtain knowledge about resource acquisition, protection, and element cycling of plants. Additionally, the analysis of specific root functional traits can reveal plant resilience and adaptation mechanisms to disturbance (Montagnoli et al., 2023). Some of these traits are easily measurable and often vaguely related to a single or a few functions (i.e., “soft”), or difficult to measure and more often closely related to a precise function (i.e., “hard”) (Bakker et al., 2019; Freschét et al., 2021b). Root functional roles are strictly related to some root morphological traits, such as diameter, that permit categorization into fine and coarse roots. Fine roots, representing about 2–3% of the total biomass and 33–67% of the total annual net primary production in most terrestrial ecosystems, accomplish nutrient, oxygen, and water uptake by cooperating with associate mycorrhizae (Vogt et al., 1995; Finér et al., 2011; McCormack et al., 2015). Coarse roots are responsible for the storage of reserves, the distribution of nutrients/water to the above-ground part, and providing comprehensive physical support to the plant anchorage (Zhang and Wang, 2015; Montagnoli et al., 2020). Both fine and coarse roots contribute to plant adaptation to environmental conditions through the so-called “phenotypic plasticity” modulating the root dynamics (production and turnover rate) and morphology (length, diameter, and biomass), which are essential to soil exploration and anchorage (Iversen et al., 2017; Brunner et al., 2019; Dumroese et al., 2019; Iversen and McCormack, 2021). Root traits, such as length, branching characteristics, and diameter, have been quite often related to foraging strategies, with root length being assumed to be proportional to resource acquisition (benefit) and root mass being proportional to construction and maintenance (cost). Under drier soil conditions, plants modulate the production of longer and finer roots, which results in a relatively greater length per unit mass, thereby leading to an increase in specific root length (SRL) (Ostonen et al., 2007; Montagnoli et al., 2012). Moreover, in terms of nutrient acquisition, root production has been related to lateral root branching since a reduced density is beneficial for N capture by reducing competition among root axes (Lynch, 2019; Montagnoli et al., 2022). Zadworny et al. (2016, 2017) proposed two ways of phenotypic plasticity that plants use to react to water or nutrient deficiency: quick growth of fine roots for a fast enhancement of water/nutrient acquisition, or thick root production to go in the direction of long-term ability to store resources. More generally, Cudlin et al. (2007) explained that root growth stops and death (i.e., decrease in root

1 https://www.mase.gov.it/sites/default/files/archivio/biblioteca/protezione_natura/ecoregioni_italia_eng.pdf

length and biomass and increase in root turnover) might indicate that an overall reduction in root production becomes more functional when water shortage exceeds a certain limit in terms of content and time. In addition to their important role in the exploration and exploitation of water and nutrients, from a biomechanical point of view, preferential root production and growth occur in different directions to enhance anchorage along the axis of mechanical loading (Stokes et al., 2009). In slopy soils and/or under prevailing wind conditions, several authors have demonstrated that the tree anchorage is likely attributable to the forces of the roots pushing downward, hanging upward, or standing in the wind- or lee-ward direction (Danjon et al., 2005; Ghestem et al., 2011; Yang et al., 2014, 2017; Montagnoli et al., 2022). These findings together explain that plants continuously adjust their root growth in response to environmental conditions through the modulation of new root production, longitudinal or radial growth, and the turnover of standing roots (Amendola et al., 2017; Montagnoli et al., 2021) and toward the achievement of higher functional performance. However, the main drivers and production/decomposition patterns related to the phenotypic plasticity of fine and coarse roots still need to be studied to possibly link those to the overall tree performance, especially in a global climate change scenario (Mausolf et al., 2018; Brunner et al., 2019).

In general, the studies of the root systems are limited by their below-ground existence, making them hard to view and sample (Gyssels and Poesen, 2003), especially in urban contexts where the plants experience soils with environmental inputs that are strongly far and different from rural and natural forests. From this perspective, a high magnitude of efforts should be directed toward the appropriate development of urban forest ecosystems. Additionally, even with the same study aims or in similar conditions, the lack of standardized methods and the inhomogeneity of definitions in root studies affect the accuracy and the possibility of making comparisons among experiments and replicates (Reubens et al., 2007). For example, despite the identification of fine and coarse roots through their diameters, there is a lack of a unique definition. Reubens et al. (2007) define the fine roots as having a diameter lower than 3 mm, Zhang and Wang (2015) and Zhang et al. (2020) use the threshold of 2 mm, Dybzinski et al. (2019) of 1 mm, while other scientists still divide in classes the fine roots by their diameter minor than 2 mm or ranging between 2 and 5 mm (Steele et al., 1997; Xiao et al., 2003; Børja et al., 2008). This led to the impossibility of uniformly analyzing the studies to define the relationships among root traits and functions and developmental patterns, also from a species-specific perspective.

In this scenario, we performed a systematic review of the knowledge about the functional traits of fine and coarse roots of those species for afforestation and reforestation in urban and non-urban areas, considering those present in the “Urban and extra-urban afforestation plan” (Italian Ministry of Ecological Transition, 2021a,b), which extensively include different biological forms (e.g., trees, shrubs, herbs, and grasses) used in afforestation and reforestation projects across Europe (Dimitrova et al., 2022). Indeed, there is emerging evidence that planting a diverse mix of species with characteristics representative of a reference ecosystem can facilitate the succession of functional biodiverse ecosystems over time and successfully address climate change and biodiversity loss simultaneously (Andres et al., 2022). Based on this, we critically evaluated milestones and gaps of knowledge emerging from the analysis. Additionally, we performed a

comprehensive analysis of the designs that drive the experiments on fine and coarse roots to highlight the peculiarities and general features. Such an overall assessment can lead to standardized procedures and methods applicable for experimental design in fine and coarse root research projects on tree species for afforestation and reforestation of urban and non-urban areas, boosting the development of applicative guidelines for the management of these peculiar ecosystems.

2 Methods

2.1 Searching strategy

This review is focused on the root functional traits of 136 plant species (including 79 trees and 57 shrubs) reported in the “Urban and extra-urban afforestation plan” (Italian Ministry of Ecological Transition, 2021a,b) as suitable for afforestation, reforestation, and tree planting in urban and non-urban areas. Indeed, these measures should take into consideration the high diversity of species, which also includes the different growth forms of plants. We performed a systematic literature search following the guidelines of Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA; Moher et al., 2009) using a query-based strategy and backward manual referencing of the literature. We first identified the root functional traits to be used as query terms for the automatic literature database interrogation by exploring the FRED 3.0 database that reports data related to root traits grouped in categories (Iversen and McCormack, 2021) and the paper of Freschét et al. (2021a). We considered those root traits related to architecture, chemistry, dynamics, morphology, physiology, and microbial associations together with the functional traits “root standing biomass” and “root standing necromass” crucial for the description of root dynamics in forest ecosystems. Lists derived after the exploration were crosschecked, and a comprehensive set of 55 root functional traits, categorized along with others and mapped in relation to one another, was adopted to perform the literature searches (Figure 1).

The combination of the 55 root functional traits together with the names (Latin binomials and common) of the 136 tree species were used as query terms together with the words “root” and “roots.” The common species names were chosen according to those reported in the “Taxonomy” database of the National Center for Biotechnology Information (NCBI).² In total, 7,480 queries (Supplementary File 1) were composed and used to perform searches through PubMed³ to identify articles with query terms matching their abstract, keywords, and title (last updated on 20 July 2023). The outputs were screened, edited, and tabulated by scripts in Perl (Wall et al., 2000). Additionally, the free accessible package pheatmap (v. 1.0.12; Kolde, 2019) in R (R Core Team, 2017) was used to draw a clustered heatmap based on the log scaled numbers of records identified for each species/trait combination. The clustering was done by complete hierarchical clustering based on Euclidean distances for both species and root functional traits, which were also categorized according to

² <https://www.ncbi.nlm.nih.gov/taxonomy/>

³ <https://pubmed.ncbi.nlm.nih.gov/>

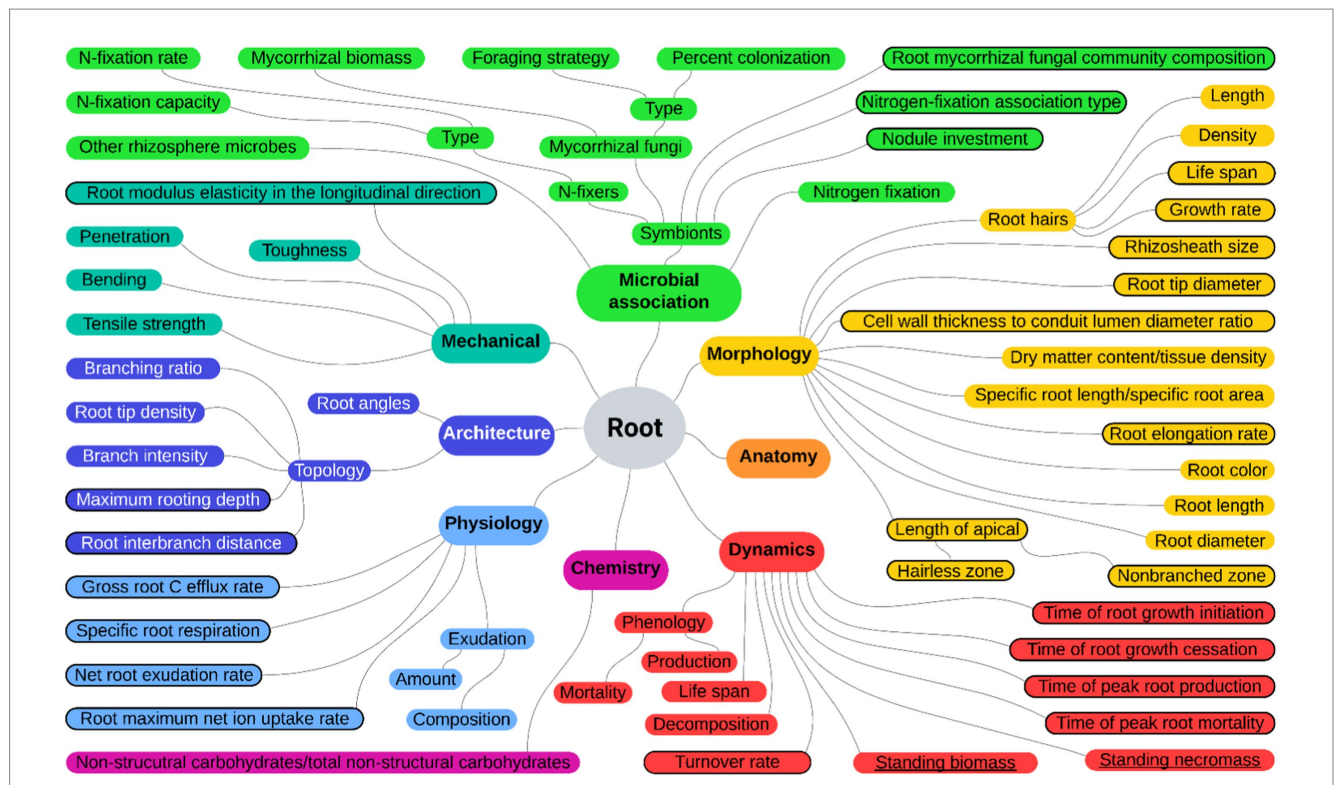


FIGURE 1
 Root functional trait categorization and mapping. Map of the 55 root functional traits used as query terms from the FRED database and from Freschét et al. (2021a; black circled) together with "root standing biomass" and "root standing necromass" (underlined) categorized according to colors: yellow for morphology, orange for anatomy, red for dynamics, purple for chemistry, light blue for physiology, blue for architecture, sea green for mechanical traits, and green for microbial association.

their recurrence in the literature search outputs. Subsequently, of all the identified records, only the scientific articles showing the terms “fine root(s)” and “coarse root(s)” in their abstract, keywords, and title and not related to the seedling stage and/or under controlled conditions were retained and considered relevant to our subsequent questions. Considering the wide range of related fields of the topic of our study, backward manual referencing based on snowballing (Wohlin et al., 2022) was also applied to identify relevant studies on the fine and coarse roots of the target species missed by query-based searches (Avenell et al., 2001; van Haafden et al., 2021). These papers, together with those identified through query-based searches, were included in the systematic literature review and underwent a full-text examination.

2.2 Data extraction and summary of selected studies

The information included in the selected original articles for the screening of their full text was categorized, considering three specific variables explained as follows: data were registered at the level of each selected original article.

The analysis of the first variable, “objective of the study,” was performed by categorizing the studies according to:

- (i) environmental constraints (e.g., drought, temperature, flooding, etc.),

- (ii) anthropogenic constraints (e.g., forest management, fertilization, irrigation, pollution, fire, etc.),
- (iii) other.

The analysis of the second variable, “root type,” was performed by categorizing the studies according to:

- (i) fine roots,
- (ii) coarse roots,
- (iii) other/not-specified types of roots as targets.

The analysis of the third variable, “experimental design,” was performed by categorizing the studies according to:

- (i) “population characteristics” (natural/afforestation/reforestation/agroforestry),
- (ii) “coordinates and localization,”
- (iii) “size of the population,”
- (iv) “plant age,”
- (v) “sampling method(s),”
- (vi) “sampling design (when, replicate, etc.),”
- (vii) “sampled organ(s),”
- (viii) “statistical method.”

Additionally, for each article, some features were reported, such as an ID (PubMed ID or EID from Scopus or DOI) and the number/type of species and root functional traits described in the article. This

procedure was performed and cross-reviewed by the authors, allowing a detailed, summarized categorization of the knowledge present in each study.

2.3 Data visualization and statistics

The categories “species,” “traits,” “objective,” “type of root,” “maximum fine root diameter,” “minimum coarse root diameter,” “site type,” “country,” “number of plants,” “plant age,” “sampling method,” “experiment duration,” “sampling number,” “months of sampling,” “sampled organ,” and “statistical analysis” were considered. Plots and statistical analysis were carried out through R (R Core Team, 2017). Specifically, the R package “wordcloud” (Fellows, 2018) was used to generate a word cloud of the keywords associated with selected articles in the database, and the package ggplot2 (Wickham, 2016) was exploited for the graphical visualization of data. The package “rworldmap” (South, 2011) was used to plot the geographical distribution of the studies. For the Whittaker biome classification of the case studies, we plotted our database through the R package “BIOMEplots” (Stefan and Levin, 2018), acquiring climate data from WorldClim (Fick and Hijmans, 2017). Additionally, the publication-per-year trend of articles related to fine and coarse roots was plotted by the “ggplot2” RStudio package (Wickham, 2016).

3 Literature resource identification: milestones and knowledge gaps of plant species and root functional traits

The query-based search in PubMed identified a total number of records equal to 25.688. These records were considered together with those identified through backward manual referencing (42 papers) and, after duplicate removal, reduced to 2.424 (Supplementary File 2). Among all the identified records, only

some were eligible for our criteria (281 papers). Records regarding experiments analyzing seedlings as plant material or plants growing under controlled conditions were also excluded (100 papers), as well as papers with no full text available (12 papers). Furthermore, a single record was excluded as not being related to an original research article. Finally, all articles with the full text available (168 papers) were included in the subsequent analysis (Figure 2). The full text of these papers was screened, and the included information was categorized according to specific variables and tabularly reported (Supplementary File 3).

Plant species were categorized according to their recurrence in the literature as “very frequent” if identified with more than 500 recurrences (13 species), “frequent” if identified by a number of recurrences ranging between 100 and 499 (28 species), “moderately frequent” if identified by a number of recurrences ranging between 99 and 10 (42 species), “lowly frequent” if identified by a number of recurrences minor than 10 (22 species), and “absent” if not identified at all (31 species) (Table 1).

From a root functional traits perspective, we also performed a categorization considering their recurrence in the literature search outputs, subdividing the root functional traits into “very frequent” if identified with more than 500 recurrences (8 traits), “frequent” if identified by a number of recurrences ranging between 100 and 499 (41 traits), “moderately frequent” if identified by a number of recurrences ranging between 99 and 10 (6 traits), “lowly frequent” if identified by a number of recurrence minor than 10 (none), and “absent” if not identified at all (none) (Table 2).

The physiological-related root functional traits are the most investigated, both for all the species and for those categorized as “very frequent” (Figure 3). In addition, root dynamics- and chemistry-related functional traits such as “phenology production” and “non-structural carbohydrates/total non-structural carbohydrates,” respectively, fall within the category of “very frequent” both for all the species and for those categorized as “very frequent” (Figure 3).

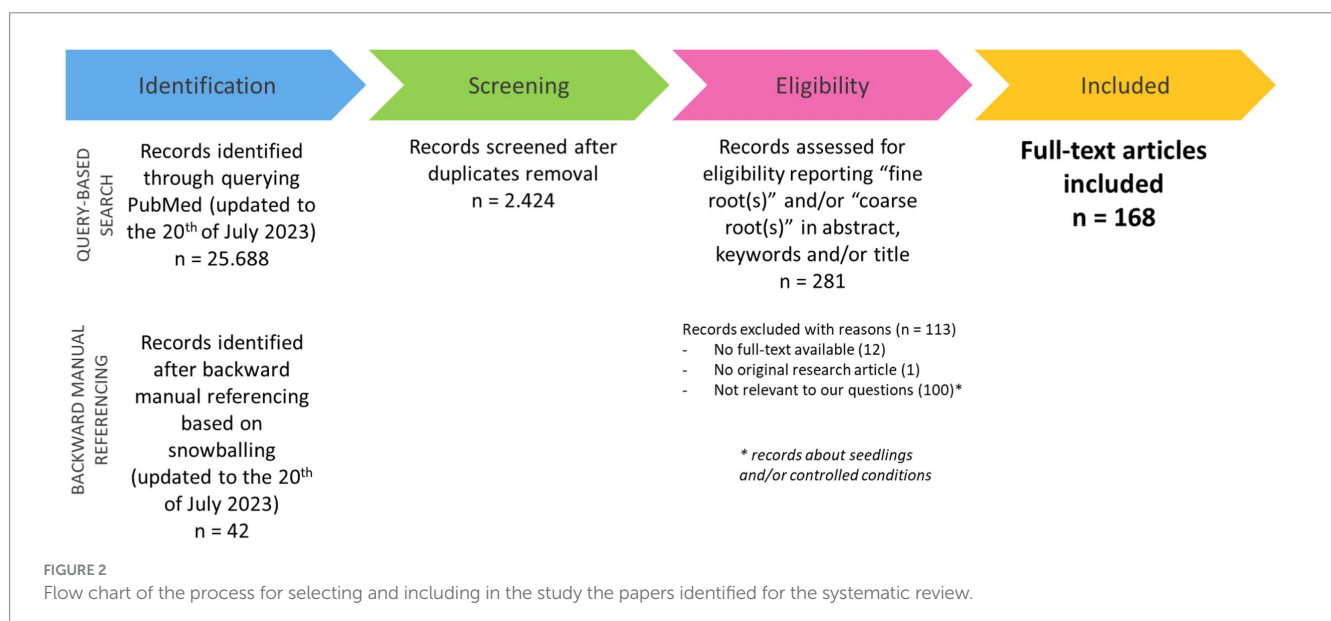


TABLE 1 Species categorization according to their recurrence in the literature search outputs.

Recurrence category (range)	Plant species (number of recurrences)
Very frequent (>500)	Trees: <i>Alnus glutinosa</i> (748), <i>Betula pendula</i> (1247), <i>Fagus sylvatica</i> (1908), <i>Olea europaea</i> (833), <i>Picea abies</i> (2994), <i>Pinus pinaster</i> (1003), <i>Pinus sylvestris</i> (3629), <i>Populus alba</i> (708), <i>Populus nigra</i> (527), <i>Populus tremula</i> (2030), <i>Quercus ilex</i> (607), <i>Quercus robur</i> (979), <i>Quercus suber</i> (544)
Frequent (100–499)	Trees: <i>Abies alba</i> (306), <i>Acer pseudoplatanus</i> (334), <i>Arbutus unedo</i> (160), <i>Carpinus betulus</i> (162), <i>Castanea sativa</i> (251), <i>Corylus avellana</i> (302), <i>Fraxinus excelsior</i> (278), <i>Larix decidua</i> (168), <i>Pinus cembra</i> (306), <i>Pinus halepensis</i> (329), <i>Pinus nigra</i> (243), <i>Prunus avium</i> (228), <i>Pyrus communis</i> (118), <i>Quercus petraea</i> (349), <i>Quercus pubescens</i> (185), <i>Taxus baccata</i> (112), <i>Tilia cordata</i> (206) Shrubs: <i>Berberis vulgaris</i> (173), <i>Hippophae rhamnoides</i> (219), <i>Ilex aquifolium</i> (136), <i>Myrtus communis</i> (138), <i>Nerium oleander</i> (164), <i>Pistacia lentiscus</i> (225), <i>Rosa canina</i> (126), <i>Rubus idaeus</i> (193), <i>Spartium junceum</i> (131), <i>Ulex europaeus</i> (301), <i>Vaccinium myrtillus</i> (377)
Moderately frequent (10–99)	Trees: <i>Acer campestre</i> (22), <i>Alnus cordata</i> (29), <i>Ceratonia siliqua</i> (56), <i>Chamaerops humilis</i> (64), <i>Frangula alnus</i> (40), <i>Fraxinus angustifolia</i> (19), <i>Juniperus macrocarpa</i> (16), <i>Juniperus oxycedrus</i> (28), <i>Laurus nobilis</i> (61), <i>Mespilus germanica</i> (12), <i>Ostrya carpinifolia</i> (18), <i>Prunus padus</i> (16), <i>Pyrus spinosa</i> (36), <i>Quercus cerris</i> (52), <i>Quercus frainetto</i> (31), <i>Salix alba</i> (96), <i>Salix atrocinerea</i> (66), <i>Salix caprea</i> (85), <i>Salix cinerea</i> (40), <i>Sorbus aucuparia</i> (29), <i>Sorbus domestica</i> (11), <i>Sorbus torminalis</i> (14), <i>Tamarix gallica</i> (29), <i>Tilia platyphyllos</i> (38), <i>Ulmus minor</i> (42) Shrubs: <i>Cistus creticus</i> (13), <i>Cistus monspeliensis</i> (44), <i>Colutea arborescens</i> (14), <i>Cytisus scoparius</i> (49), <i>Cytisus villosus</i> (36), <i>Erica arborea</i> (18), <i>Euonymus europaeus</i> (15), <i>Juniperus communis</i> (64), <i>Phillyrea latifolia</i> (39), <i>Prunus spinosa</i> (33), <i>Rhamnus alaternus</i> (24), <i>Rhododendron ferrugineum</i> (10), <i>Ruscus aculeatus</i> (20), <i>Salix purpurea</i> (70), <i>Sambucus nigra</i> (85), <i>Viburnum tinus</i> (55), <i>Vitex agnus-castus</i> (42)
Lowly frequent (<10)	Trees: <i>Acer monspessulanum</i> (6), <i>Celtis australis</i> (9), <i>Crataegus laevigata</i> (1), <i>Fraxinus ornus</i> (9), <i>Malus sylvestris</i> (1), <i>Myricaria germanica</i> (6), <i>Platanus orientalis</i> (8), <i>Quercus trojana</i> (7), <i>Rhamnus cathartica</i> (3), <i>Tamarix africana</i> (6) Shrubs: <i>Artemisia arborescens</i> (7), <i>Cistus salvifolius</i> (7), <i>Cornus mas</i> (8), <i>Cornus sanguinea</i> (7), <i>Crataegus monogyna</i> (4), <i>Cytisophyllum sessilifolium</i> (2), <i>Erica scoparia</i> (9), <i>Euphorbia dendroides</i> (5), <i>Ligustrum vulgare</i> (6), <i>Salix triandra</i> (8), <i>Viburnum lantana</i> (9), <i>Viburnum opulus</i> (2)
Absent (=0)	Trees: <i>Acer opalus</i> (0), <i>Carpinus orientalis</i> (0), <i>Cercis siliquastrum</i> (0), <i>Juniperus deltoides</i> (0), <i>Juniperus turbinata</i> (0), <i>Laburnum anagyroides</i> (0), <i>Quercus congesta</i> (0), <i>Quercus dalechampii</i> (0), <i>Quercus leptobalana</i> (0), <i>Salix eleagnos</i> (0), <i>Salix pedicellata</i> (0), <i>Sorbus aria</i> (0), <i>Sorbus graeca</i> (0), <i>Ulmus glabra</i> (0) Shrubs: <i>Anagris foetida</i> (0), <i>Celtis tournefortii</i> (0), <i>Cytisus hirsutus</i> (0), <i>Daphne laureola</i> (0), <i>Emerus major</i> (0), <i>Genista aetnensis</i> (0), <i>Genista maderensis</i> (0), <i>Genista monspessulana</i> (0), <i>Hypericum androsaemum</i> (0), <i>Paliurus spina-christi</i> (0), <i>Phillyrea angustifolia</i> (0), <i>Phlomis fruticosa</i> (0), <i>Pistacia terebinthus</i> (0), <i>Rosa sempervirens</i> (0), <i>Salix arrigonii</i> (0), <i>Salix gussonei</i> (0), <i>Teucrium fruticans</i> (0)

4 Information resulting from the screening of selected papers

A total of 168 full-text articles about fine and coarse roots were included in the database for the process of knowledge categorization based on the summary table (Supplementary File 3). The temporal analysis showed a general increase in the number of papers about fine and coarse roots published from 1992 to 2023, which is in consideration in our study (Figure 4). However, this literature production trend is characterized by alternate periods of high and low productivity. According to our results, the scientific name of the species *Fagus sylvatica* emerges as one of the most frequent keywords associated with selected papers, together with “fine root,” “*Picea abies*,” “*Pinus sylvestris*,” “non-structural carbohydrates,” and “minirhizotron” (Figure 5A). Indeed, among the 33 species present in the selected literature (Figure 5B), *Fagus sylvatica* is the most targeted species in fine and coarse root studies, as described in 55 out of 168 studies. This is followed by *Picea abies* in 50 studies, *Pinus sylvestris* in 39 studies, *Pinus cembra* in 13 studies, and *Betula pendula* in 10 studies. The rest of the species is targeted in a number of studies, including between 9 and 1 (Figure 5B).

The papers in our database regard 50 root functional traits, and the most investigated are related to root “dynamics” and, specifically, “standing biomass” in 48 out of 168 articles, “phenology production”

in 41 articles, and “turnover rate” in 38 articles (Figure 5C). Also, other functional traits are widely represented, such as “non-structural carbohydrate (NSC)/total non-structural carbohydrate (TNC)” related to “chemistry” and described in 33 articles, or “specific root respiration” related to “physiology” and described in 31 articles (Figure 5C).

The geographical distribution of the carried-out studies showed that the most represented countries are Germany (32 publications), Switzerland (20 publications), Finland (16 publications), and Italy (15 publications), with other countries represented at a lower magnitude (Supplementary Figure 1).

Among global biomes, the most represented were temperate seasonal forests, woodland/shrubland, and boreal forests (Figure 6). Both gymnosperms and angiosperms are represented in these biomes, except for the boreal forest biome, which is more represented by angiosperms than gymnosperms. Tropical seasonal forest/savanna was represented in only one publication describing a gymnosperm. Thus, data extracted from the literature showed gaps related to some biomes, which are temperate and tropical rain forests, tundra and subtropical deserts, and temperate grassland/deserts, which represent the extremes in climate space. The data spanned a gradient of annual precipitation from 42.1 to 166.3 cm and of temperature from -0.7 to 24.66°C .

The greatest part of the studies analyzed had objectives other than investigating anthropogenic or environmental constraints (Figure 7A)

TABLE 2 Root functional trait categorization according to their recurrence in the literature search outputs.

Recurrence category (range)	Root functional trait (number of recurrences)
Very frequent (>500)	Chemistry>Non-structural carbohydrates/total non-structural carbohydrates (808), Physiology>Exudation>Amount (1900), Physiology>Exudation>Composition (1874), Physiology>Gross root C efflux rate (1902), Physiology>Net root exudation rate (1902), Physiology>Root maximum net ion uptake rate (1902), Physiology>Specific root respiration (1902), Dynamics>Phenology>Production (1003)
Frequent (100–499)	Anatomy (309), Architecture>Root angles (109), Architecture>Topology>Branching intensity (110), Architecture>Topology>Branching ratio (110), Architecture>Maximum rooting depth (118), Architecture>Topology>Root interbranch distance (115), Architecture>Topology>Root tip density (115), Microbial association>Other rhizosphere microbes (327), Microbial association>Symbionts>Mycorrhizal fungi>Mycorrhizal biomass (474), Microbial association>Symbionts>Mycorrhizal fungi>Type>Foraging strategy (465), Microbial association>Symbionts>Mycorrhizal fungi>Type>Percentage colonization (465), Microbial association>Symbionts>N-fixers>Type>N-fixation capacity (184), Microbial association>Symbionts>N-fixers>Type>N-fixation rate (186), Microbial association>Symbionts>Nitrogen fixation association type (182), Microbial association>Symbionts>Nodule investment (182), Microbial association>Symbionts>Root mycorrhizal fungal community composition (201), Morphology>Cell wall thickness to conduit lumen diameter ratio (362), Morphology>Dry matter content/tissue density (358), Morphology>Length of apical hairless zone (362), Morphology>Length of apical nonbranched zone (362), Morphology>Rhizosheath size (362), Morphology>Root color (354), Morphology>Root diameter (368), Morphology>Root elongation rate (363), Morphology>Root hair>Growth rate (362), Morphology>Root hair>Life span (362), Morphology>Root hairs>Density (354), Morphology>Root hairs>Length (359), Morphology>Root length (416), Morphology>Root tip diameter (363), Morphology>Specific root length/specific root area (370), Dynamics>Decomposition (332), Dynamics>Life span (277), Dynamics>Phenology>Mortality (409), Dynamics>Standing biomass (283), Dynamics>Standing necromass (284), Dynamics>Time of peak root mortality (280), Dynamics>Time of peak root production (281), Dynamics>Time of root growth cessation (284), Dynamics>Time of root growth initiation (294), Dynamic>Turnover rate (282)
Moderately frequent (10–99)	Mechanical>Bending (86), Mechanical>Penetration (67), Mechanical>Root modulus of elasticity in the longitudinal direction (57), Mechanical>Tensile strength (57), Mechanical>Toughness (55), N-fixation/Nitrogen fixation (38)
Lowly frequent (<10)	none
Absent (=0)	none

and focused on the fine roots, a few on the coarse roots, a part targeted both fine and coarse roots, and the rest had no clear specification about this (Figure 7B). The studies were mostly carried out only in natural contexts, followed by afforestation sites, and only a few studies were carried out in agroforestry or reforestation sites or in combination of sites with diverse typologies (Figure 7C).

Notably, although the species used to search the literature are suitable for urban afforestation and reforestation, in fact, no research carried out in an urban environment emerges among the studies under analysis.

Plant age is another parameter of the experimental design considered in this analysis. A part of the selected literature (21 studies, equal to 12.5%) is based on experiments that indicated vague plant age, reporting it as a time range in years (Supplementary Figure 2A). On the contrary, about half of the studies (80 studies, equal to 47.62%) provided precise indications about this parameter (Supplementary Figure 2B). Nevertheless, most of the studies provided no information about plant age (67 studies, equal to 39.88%).

The months of sampling are clearly indicated in 71 studies (42.27%), mainly occurring in April (27 studies, 16.07%), July (28 studies, 16.67%), and October (26 studies, 15.48%), less those of the winter period (Supplementary Figure 2C). Some studies (16 studies, 9.52%) mentioned the sampling period by a season or with ambiguous indications like “before summer” and were considered as “vague.” Additionally, 81 studies (48.21%) made no description of the sampling period (Supplementary Figure 2C).

Almost half of the studies did not provide information regarding the number of plants included in the experiment (82 studies; 48.81%),

and the rest described experiments including a number of plants ranging from 2 to 606 (Supplementary Figure 2D). There is a wide range of experiment duration spanning from 1 to 156 months (91 studies, equal to 54.17%; Supplementary Figure 2E).

However, most of the studies provided no indication about the experiment duration (56 studies equal to 33.34%) or were based on a single sampling (21 studies equal to 12.5%). Most experimental designs involved only root sampling (102 studies; 60.71%), while in other 26 studies (15.48%), the roots were sampled together with one or more additional organs, and in 40 studies (23.81%), the organs targeted for sampling were not specified (Figure 8A).

Among the sampling methods used alone, the most represented was soil coring (71 studies; 42.26%), followed by excavation, described in 25 studies (14.88%), and minirhizotrons (10 studies; 5.95%) (Figure 8B). Rhizoboxes were described in five studies (2.98%), nylon meshes in three studies (1.79%), and lysimeter, 3D digitizing, and penetrating radar were described only in one study (~0.59%), respectively (Figure 8B). The rest of the studies (seven, equal to 4.17%) describe a combination of two different methods. A number of studies equal to 44 (26.19%) have no specific description of the sampling method (Figure 8B).

The maximum diameter to define a fine root is frequently set at 2 mm (83 studies, 49.40%), while only some studies apply different thresholds equal to 0.5 mm (two studies, 1.19%), 1 mm (four studies, 2.38%), 3 mm (one study, 0.60%), or 5 mm (five studies, 2.98%; Figure 8C).

It is relevant to note that in 73 studies (43.45%), there are no indications about the diameter size adopted to identify fine roots.

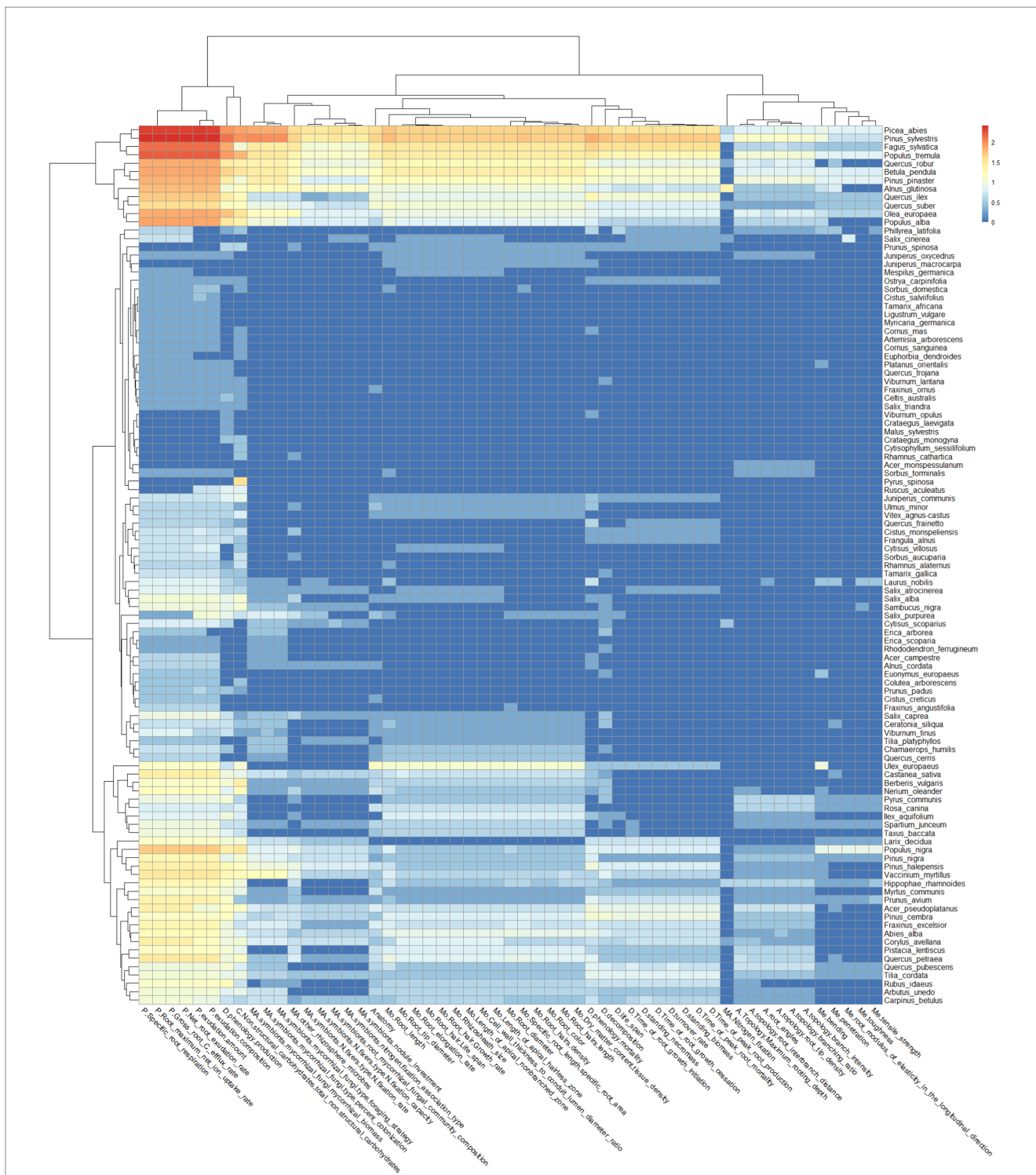


FIGURE 3
Heatmap of target species and root functional traits, which are represented in the PubMed search outputs. The x-axis shows the root functional traits, whose functional categories have been indicated as: A for architecture, C for chemistry, MA for Microbial Association, Me for mechanical, Mo for morphology, P for physiology, and D for dynamics. The y-axis shows the Latin names of target species present in the search output.

Minimum diameters to identify coarse roots are defined only in eight studies (4.76%) and are set equal to 2 mm, 5 mm, or 15 mm (Figure 8D). However, the rest of the selected studies (160, corresponding to 95.24%) report no indications about this.

Concerning the number of samplings reported in the selected literature, 93 studies (55.36%) described a number of samplings ranging from 1 to 44 (Figure 8E), and among these, 31 studies are based on a single sampling (18.45%), while others are based on two

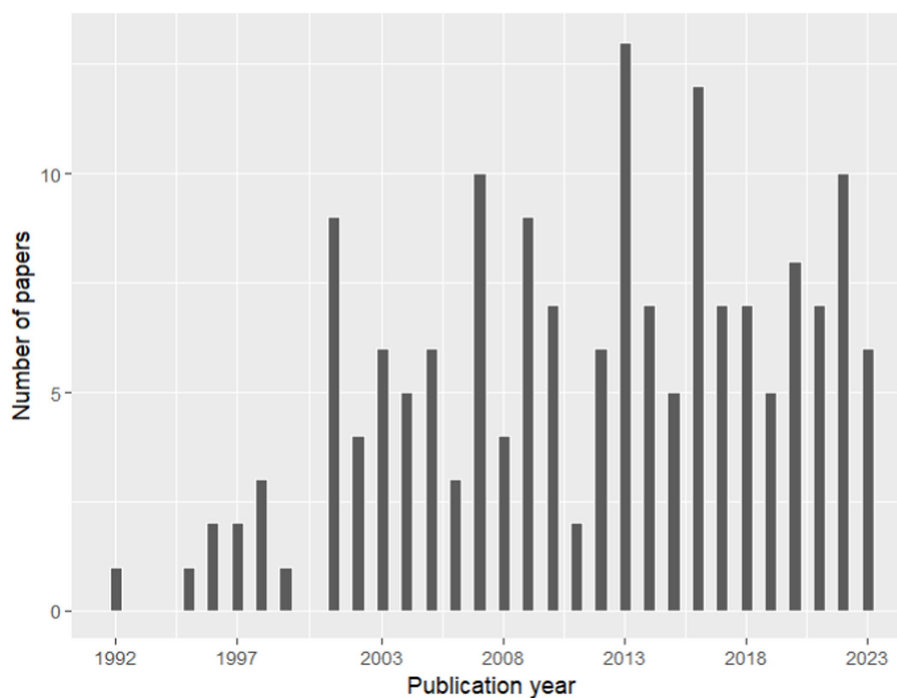


FIGURE 4
Temporal analysis per year of published papers present in our database (Source: PubMed, 1992–2023).

samplings (24 studies, 14.29%), three samplings (nine studies, 5.36%), or four samplings (10 studies, 5.95%) (Figure 8E).

Of the others, 75 out of 168 studies (44.64%) did not report precise information (Figure 8E). In Table 3, results related to the occurrence of the statistical analysis are reported. Few statistical tests were frequently used, and among these, the most commonly used was ANOVA (45.24%), followed by Student's *t*-test (13.69%), the Shapiro–Wilk test (11.31%), Pearson's correlation (10.12%), linear regression model (8.93%), Kruskal–Wallis rank sum test (7.14%), Mann–Whitney *U* test (7.14%), Tukey's HSD test (7.14%), and PCA (5.36%). Other statistical tests were applied in a number of studies ranging from 5 to 9, and the greatest part of the statistics were applied in less than four studies.

5 Discussion

We provide a general overview of the literature about root functional traits together with a revised and detailed dissection of the studies of fine and coarse roots of species targeted for afforestation and reforestation programs in urban and non-urban areas, evidencing common practices and criticisms of the applied experimental procedures.

5.1 Fine and coarse roots are mainly studied in European natural contexts for a few plant species and functional traits

Among the 136 target species, some of them, identified as “very frequent,” were well studied for their biological and economic

relevance, such as *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Olea europea*, three *Quercus* genus, and *Pinus pinaster* (Majdi, 2001; Rastogi et al., 2015; Kostelenos and Kiritsakis, 2017; Mármol et al., 2019; Rey et al., 2019; Mader et al., 2020; Smeriglio et al., 2022), and/or are model species in plant biology investigations, such as *Picea abies*, *Populus alba*, and *Populus tremula* (Brunner et al., 2001, 2004; Vasiliauskas et al., 2007; Shorohova et al., 2011; Gauthier et al., 2015).

Among the traits analyzed, all those related to root physiology were classified as “very frequent” in the literature, and among these, root exudation was a key component since it played a crucial role in both plant–soil interactions, root carbon efflux, and microbe relationship. In particular, root exudates can modify soil characteristics and locally adapt plants to abiotic/biotic stressors, giving clear hints on plant morpho-physiological plasticity in response to biotic and abiotic stressors (Canarini et al., 2019). Therefore, despite the main drivers of root exudation still need to be identified, the study of root exudation remains a key to understanding plants as holobionts, especially in natural and urban forests (Lyu and Smith, 2022).

Despite the pivotal role that fine and coarse roots play in plant development and adaptation, and despite an increasing trend in scientific production, studies on these two root categories are still lacking. Furthermore, a large part of the root studies do not focus on environmental or anthropogenic constraints, and they are mainly performed in natural sites that do not experience any urban stressors. In detail, among the 136 candidate plant species, *F. sylvatica* is a common target species in fine and coarse roots studies (Montagnoli et al., 2014; Weigt et al., 2015; Montagnoli et al., 2018; Nikolova et al., 2020) and specifically in those analyzing fine roots biomass (Braun et al., 2005; Konôpka and Lukac, 2013; Jagodzinski et al., 2016; Montagnoli et al., 2016; Geilfus et al., 2017; Konôpka et al., 2020; Montagnoli et al., 2023). In root turnover studies, species other than



F. sylvatica, such as *Picea abies* or *Pinus sylvestris*, are frequently involved (Godbold et al., 2003; Xiao et al., 2003; Vanninen and Mäkelä, 2005; Eriksson et al., 2012; Jacob et al., 2014; Mildner et al., 2014; Nacke et al., 2016; Yan et al., 2016; Zadworny et al., 2016; Grüning et al., 2017; Mariën et al., 2021). Root dynamics is frequently linked to environmental drivers such as drought, seasonality, or ozone concentration (López et al., 1998; Paoletti et al., 2007; Mainiero et al., 2009; Kuptz et al., 2011a,b; Montagnoli et al., 2014; Nickel et al., 2018; Montagnoli et al., 2019), together with traits associated with the chemistry of non-structural carbohydrate (Rosinger et al., 2020; Clausing et al., 2021). However, the greatest part of the other root functional traits is still at the beginning of the exploration of complex relationships with functions and environment, especially in the case

of coarse roots (Fresché et al., 2021a). Our results also evidenced that the studies of the fine and coarse root functional traits are limited to countries that belong mostly to Central and North-Eastern Europe and North America and only to China and Mongolia for Asia, highlighting the need to expand the exploration to other regions and biomes.

5.2 Experimental designs lack crucial information

A large part of the studies was based on a single sampling or reported as having no or vague indications of the total duration of the

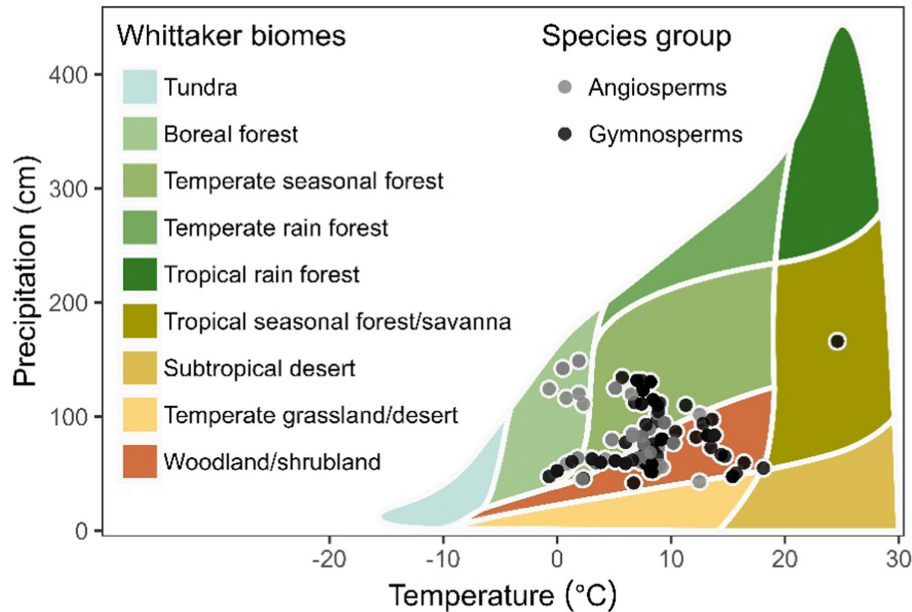


FIGURE 6 Whittaker biome plot of database locations ($n = 169$) showing mean annual temperature ($^{\circ}\text{C}$) and mean annual precipitation (cm). Each point represents a plant species: gray for angiosperms and black for gymnosperms. Climate data are from WorldClim (Fick and Hijmans, 2017).

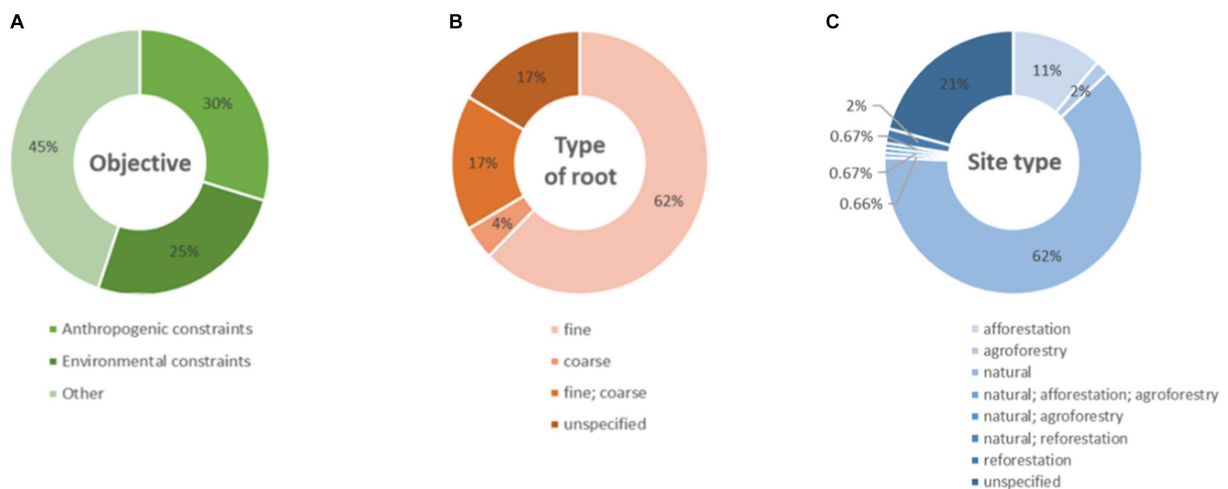


FIGURE 7 Donut charts represent (A) the percentages of objectives, (B) the type of targeted root(s), or (C) the site type(s) of the studies present in our database.

experiment or the timing of the sampling, with no clear indications of dates and months. This approximation was also observed for information concerning both the number and age of the plants analyzed. In this perspective, our findings highlight the need for protocol uniformity about the tree species sampled and analyzed as individuals or populations as they might respond differently to environmental drivers (Rytter, 2013; Dawes et al., 2015; Mausolf et al., 2018; Lak et al., 2020; Freschét et al., 2021a). The relevance of the duration of the sampling period strongly affects the outcome of the research, especially in the root context where the phenotypic plasticity is high both in the short- and long-term periods (Brunner et al., 2013; Klavina et al., 2016). For example, in fine-root turnover studies,

multiple sampling across different growing seasons is fundamental (Terzaghi et al., 2013; Kubisch et al., 2016, 2017) to avoid misestimation of production and mortality (Tingey et al., 2003).

Our findings underscored significant differences in various morphological parameters of the fine roots, except root length, when comparing different root sampling methods. Thus, increasing sampling effort (i.e., applying a combination of different sampling methods and/or considering samplings to avoid age-related bias) when designing a root experiment might lead to higher precision of the measured root characteristics (Tingey et al., 2003; Rytter, 2013; Klavina et al., 2016; Mausolf et al., 2018). In general, root studies based on samples collected from a few locations within the root zone have

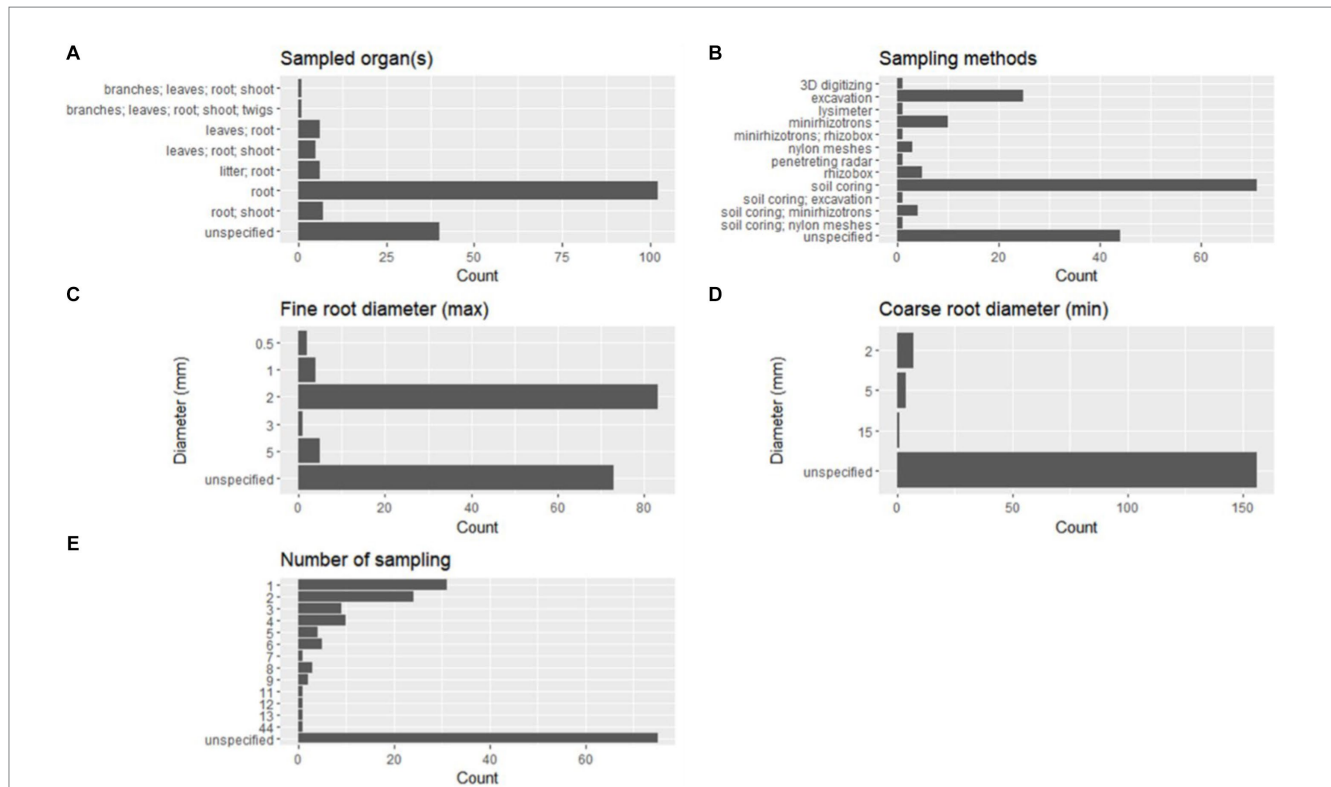


FIGURE 8 Features of the experimental designs in terms of sampled organs (A), sampling method (B), fine-root diameter (max, C), coarse root diameter (min, D), and number of samplings (E).

TABLE 3 Statistical analysis frequency according to the recurrences in the selected literature.

Recurrence frequency	Statistical analysis (number of recurrences)
>10	ANOVA (76), Student's <i>t</i> -test (23), Shapiro–Wilk test (19), Pearson's correlation (17), Linear regression (15), Kruskal–Wallis rank sum test (12), Mann–Whitney <i>U</i> test (12), Tukey's HSD test (12), PCA (9)
5–9	Kolmogorov–Smirnov test (9), Tukey's test (9), GLM (7), ANCOVA (6), Fisher's exact test (6), PERMANOVA (6), Levene test (4), Linear mixed-effects models (LMM) (5), Mixed-effects models (5)
1–4	Dunnett's test (4), Monte Carlo permutation test (4), Least significant difference (LSD) (3), Non-linear regression (3), Random forest (2), Spearman's correlation (3), Duncan test (2), Dunn's test (2), Kaplan–Meier test (2), Non-metric multidimensional scaling (2), AMOVA (1), Asymptotic decomposition (1), Bayesian models (1), Bonferroni post-hoc test (1), Bray–Curtis distances (1), Brown–Mood test (1), Canonical variate (1), Correlation analysis (1), Double exponential (1), Expected Species Accumulation (1), Gehan–Breslow test (1), Hierarchical single linkage clustering (1), <i>k</i> -mean clustering (1), Least absolute shrinkage and selection operator (LASSO) regression (1), least-square regression (1), logarithmic data transformation (1), MAESTRA (1), MANOVA (1), Mantel and Haenszel test (1), Neighbor-joining clustering (1), Network analysis (1), Power regression (1), Product-limit estimator curve (1), Random permutations (1), Redundancy analysis (1), <i>R</i> ² (1), Satterthwaite's method (1), Semivariogram (1), Sigmoid regression (1), Single exponential (1), Spatial analysis by distance (1)

lower differentiating power than whole-plant sampling (Han et al., 2014), and increasing the sample size strongly impacts the outcome of the research as the root characteristics are affected by microsite variability (Rytter, 2013).

Our findings indicate that roots are usually sampled alone in most of the studies, although coupling the analysis of other organs might help to better understand ecosystem functionality. For example, tracing non-structural carbohydrates or labeled carbon or nitrogen in different organs improves the understanding of C dynamics (Maillard et al., 2001; Dyckmans and Flessa, 2002;

Scartazza et al., 2015; Tang et al., 2022). Similarly, the analysis of the growth of both above- and below-ground organs has been linked to the presence of pollutants in the soil (Stobrawa and Lorenc-Plucińska, 2008; Dalle Fratte et al., 2022). Intriguingly, Kilpeläinen et al. (2022) identified resource competition among plant organs as a major driver of root plasticity, implicitly suggesting multiple organ studies as more complete. Therefore, we encourage root scientists to expand their collaboration, including plant scientists who might integrate analysis of the above-ground organ traits.

Another feature of the experimental design was related to the fine and coarse root definitions based on the diameter size. Fine roots are defined as short-lived, non-woody roots responsible for water and nutrient adsorption with a diameter lower than 2 mm (Rytter, 2013), which is the reference diameter we have found in the greatest part of the studies. However, from our results, diameter thresholds other than 2 mm are still used, and in the majority of studies, there is no precise indication provided about these thresholds. The coarse roots, which are woody roots crucial for soil exploration and plant stability, are frequently evaluated only as being not classified as fine roots (Rytter, 2013). Our results support this observation, as the greatest part of the authors give no threshold as a reference for the diameter of the coarse roots. Therefore, although detailed and precise information on root diameter is fundamental and can be linked to specific functional traits (Markkola et al., 1995; Menkis et al., 2004; Helmisaari et al., 2007; Børja et al., 2008; Gaul et al., 2009; Helmisaari et al., 2009; Meinen et al., 2009; Endrulat et al., 2010; Menkis et al., 2012; Terzaghi et al., 2013; Montagnoli et al., 2018; Kriiska et al., 2021; Mariën et al., 2021; Schwieger et al., 2021), our literature analysis reveals a diffuse failing in determining specific and functional diameter thresholds (Helmisaari et al., 2009; Nikolova et al., 2020).

5.3 The inadequate application of common *a priori* model-based statistics for interpreting complex dynamics of roots

Common issues related to root data collection are exacerbated by the application of complex and inappropriate statistical design (Ahrens et al., 2014; Thiese et al., 2015; Mausolf et al., 2018). Our findings are in line with this observation, which highlights the application of a large number of different statistical tests, which indicates a lack of clear and uniform statistical protocols in root studies. It is important to underline the need to build an optimal and univocal statistical approach to be applied for the study of a specific trait or set of traits that is tightly coupled with the sampling method and technique.

6 Future directions and perspectives

Our literature analysis evidenced the complete or limited root trait knowledge of the selected species for the afforestation and reforestation of urban and non-urban areas and, thus, the need to fulfill these knowledge gaps. The greatest part of the listed 136 plant species has already been reported to be widely used across Europe in afforestation and/or reforestation projects as well as in urban and non-urban areas (Dimitrova et al., 2022). For example, it has been seen that afforestation strategies in urban contexts, including *A. glutinosa* and *B. pendula*, induce a change in the soil properties, increasing acidity and nutrient contents after 45–60 years from introduction (Podwika et al., 2018). Furthermore, *Quercus* and *Populus* species have been shown to have great potential in urban afforestation and reforestation for their functionality in air quality improvement and climate regulation (Fusaro et al., 2015; Sun et al., 2017; He et al., 2018; Mariën et al.,

2021). Thus, these species may serve as possible future targets to study root systems in urban contexts.

Our study evidenced the total absence of fine and coarse root studies in urban areas and limited coverage of world regions and biomes. Despite this, urbanization forecasts suggest world regions other than Central Europe and North America as being involved with higher urban extents, like Eastern and Western Europe, South America, some regions of the northern part of Africa, and Mid, Central, and Western Asia (Seto et al., 2012). In this perspective, studies on root systems must also concern species native to or adaptable to world regions that will experience high levels of urbanization within the next few years, and this task needs to consider that the urbanization process is usually a strong driver in modeling the changes of plant species and communities (Dimitrova et al., 2022; Ruas et al., 2022). Moreover, a large effort is needed for scientists from the most studied regions to apply their knowledge to less studied countries and ecosystems through specific funding opportunities.

With the aim of sharply providing take-home messages derived from our literature review, we followed a list of crucial points summarizing the main outcomes.

- (i) *Population characteristics*: Species other than common targets for their biological and economic relevance must be included in the root studies, and a wider analysis of functional traits should also be performed for the most common target species. Additionally, sites other than natural should be taken into account, considering the large efforts toward afforestation and agroforestry programs.
- (ii) *Experimental design directions: plants of a known and uniform age and appropriate sampling (what, when, how many times, and how long)*: Plant age needs to be well-known and possibly uniform among the trees included in the experimental design. Sampling of multiple organs would give higher and more complete information about resource acquisition and utilization since organs often have complementary or competitive roles. Experiment duration must overlap and be extended beyond the period of root dynamics to fully appreciate parameter changes over time in accordance with the dynamics of the type of root category and the experiment aims. Thus, multiple samplings across spring, late summer, and/or early autumn are suggested for fine roots, while full autumn sampling with a yearly repetition is suggested for coarse roots.
- (iii) *AI may enhance statistical models to fit with biological data complexity and dynamics*: To capture the complex patterns and relationships in data derived from the intermingled and dynamic root system, complex algorithms based on machine learning, deep learning, and other artificial intelligence approaches should be considered, as they predict accurate relationships between variables without imposing any *a priori* model.

Taken together these observations, since they are coming from the analysis of the literature search outputs, may represent a solid base ground for the construction of indications for optimizing and standardizing the selection of plant species, root functional traits, and experimental design for natural and urban forest root studies.

Author contributions

DF: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. AM: Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Validation, Writing – review & editing. DT: Conceptualization, Project administration, Supervision, Writing – review & editing. PM: Data curation, Formal analysis, Writing – review & editing. GSc: Data curation, Formal analysis, Funding acquisition, Project administration, Resources, Writing – review & editing. GA: Data curation, Formal analysis, Writing – original draft. DC: Supervision, Writing – review & editing. GSf: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Writing – original draft, Writing – review & editing.

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Supplementary material

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