



Shoot growth patterns as indicators of root system recovery after transplanting in nursery-grown hackberry trees

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Abstract

Key message This study on young planted hackberry trees identifies distinct recovery stages where aboveground traits reliably predict root system regeneration, providing a basis for non-destructive assessment of post-transplant recovery.

Abstract Transplanting trees disrupts the root system, creating a root-to-shoot imbalance that challenges recovery. Post-transplant recovery is heterogeneous, with distinct growth dynamics. We hypothesized that: (1) this heterogeneity represents few growth patterns; (2) these patterns reflect specific root regeneration behaviors; and (3) aboveground traits could indicate root system recovery. To test them, we transplanted 600 young bare-root *Celtis australis* and monitored their recovery over two years. A total of 112 trees were selectively excavated at the end of each growing season to characterize root regeneration and its links with aerial growth categories. Two indicators, the Root Regeneration Score (RRS) and the Aerial Field Index (AFI), were developed to evaluate aerial growth dynamics and root regeneration. Our results showed that post-transplant heterogeneity in aboveground growth could be categorized into distinct patterns based on budbreak timing and shoot elongation dynamics. These aerial growth categories corresponded to specific root regeneration behaviors, characterized by differences in the proportion of regenerated pruned roots, new root production, and pruning wound closure rates, key traits used to construct the RRS. The AFI, integrating time to budbreak, trunk growth, and maximum shoot length, effectively distinguished growth categories and demonstrated strong predictive power for root recovery. This study provides a framework for characterizing post-transplant recovery dynamics and emphasizes the functional interplay between root and shoot recovery. The AFI offers a standardized tool for evaluating plantation success and informing urban forestry management.

Keywords Growth dynamics · Root regeneration · Root-to-shoot relationships · Transplant stress · Urban tree production · *Celtis australis*

Introduction

Urban trees play an essential role in mitigating climate change effects in cities (Roy et al. 2012; Livesley et al. 2016; Esperon-Rodriguez et al. 2022). They effectively

reduce air temperature during heat waves and provide essential ecosystem services such as flood risk reduction and biodiversity support (Armson et al. 2013; Demuzere et al. 2014; Nowak et al. 2014; Salmond et al. 2016; Berland et al. 2017; Rahman et al. 2017; Maradiaga-Marín and Cariñanos 2021; Schwaab 2021; Levinsson et al. 2024). However, these ecosystem services are primarily delivered by large, well-established trees, while newly planted trees contribute minimally until they reach sufficient size and maturity (Lindenmayer et al. 2012; Stagoll et al. 2012; Díaz-Porras et al. 2014; Riikonen et al. 2017). Furthermore, practices such as tree-topping, and more largely pruning, can significantly penalize tree services by compromising crown structure and its functioning (Muscas et al. 2024; Comin et al. 2025). Consequently, the successful establishment of urban trees represents a major challenge for urban greening objectives

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(Zürcher 2024). Currently, following transplanting, trees often exhibit reduced growth and crown deterioration, frequently leading to high mortality rates (Nowak et al. 1990; Hilbert et al. 2019; Wattenhofer and Johnson 2021), thus compromising urban canopy development and associated services.

While urban environments present inherent constraints for tree growth (Koeser et al. 2013; Watson et al. 2014; Layman et al. 2016; Hilbert et al. 2019), nursery production practices significantly contribute to these tree establishment difficulties (Gilman 1990; Gilman and Beeson 1996; Struve 2009; Levinsson 2013; Levinsson et al. 2014; Allen et al. 2017). Young trees undergo multiple transplanting during their production cycle and final urban installation (Kozłowski and Davies 1975). At each transplanting, the root system development is severely impacted through root pruning. This pruning results in substantial loss of the peripheral root system, where most of the fine roots responsible for water and nutrient absorption are located. This creates a significant imbalance between above- and belowground compartments. Additionally, structural pruned roots present open wounds vulnerable to pathogen attacks (Watson et al. 2014). These pruned roots must restore absorptive capacity through the development of new roots, regenerate to heal wounds, and replace amputated portions (Wilcox 1955; Rietveld 1959; Carlson 1974; Watson and Himelick 1982; Gilman and Yeager 1988). Furthermore, the entire root system must adapt to new soil conditions (Sands 1984). This reconstruction process is critical as water uptake remains disrupted until sufficient root regeneration occurs. Paradoxically, despite roots being the most affected plant compartment by transplanting, post-transplant root system recovery remains poorly explored. This lack of knowledge stems primarily from methodological complexity in studying root system development (Mihai et al. 2019; Comin et al. 2021). Nevertheless, it is essential to finely establish the recovering correspondences between belowground and aboveground compartments for practical purposes. Both compartments are intimately connected through resource acquisition and allocation: roots supply water from soil, while leaves capture atmospheric CO₂ and intercept light for photosynthesis (Poorter and Nagel 2000; Magnani et al. 2002; Masson et al. 2022). Consequently, the post-transplant establishment phase represents a critical period that largely determines transplanting success or failure. During this phase, high mortality rates are common, particularly within the first five years (Hilbert et al. 2019). Yet mortality represents only one facet of post-transplant response. Surviving trees display a wide range of aerial system growth dynamics, but this heterogeneity in recovery patterns remains poorly characterized. Most studies have focused on mortality rates rather than on the diversity of growth trajectories among surviving

trees. Can the variety of aboveground recovery patterns be classified? Does this variation reflect corresponding patterns in root system regeneration? If so, could observable aboveground traits serve as reliable indicators of root system recovery, avoiding the need for destructive excavations to assess root system establishment?

In nursery production and urban tree management, indicators used to assess young tree establishment rely mainly on practical observations. While these observations provide valuable insights, there remains a need for scientifically validated aboveground indicators to evaluate root system regeneration without destructive methods.

In this context, we hypothesize that post-transplant recovery patterns follow a predictable framework:

- H1: The heterogeneity in post-transplant recovery results from distinct growth dynamics ranging from successful establishment to severely impacted categories.
- H2: These aboveground growth patterns reflect corresponding patterns in root system recovery, particularly regarding the regeneration of pruned roots and their health status.
- H3: Specific aboveground traits can serve as reliable indicators of root system regeneration and health.

To test these hypotheses, we conducted a two-year study on young bare-root trees.

- (1) Following transplanting, we monitored annual shoot elongation patterns and tree growth in order to identify distinct aboveground growth patterns.
- (2) We then conducted targeted excavations from each growth category at the end of each growing season to detail both above- and belowground structures in order to assess pruned root regeneration and health status, as well as annual shoot lengths, dry masses, and leaf area.
- (3) This approach would allow us to characterize recovery patterns and identify reliable aboveground indicators of root system regeneration.

Materials and methods

Study site

The study was conducted at the BRL Espaces Naturels open-ground ornamental tree nursery in Vestric-et-Candiac, southern France (43°43'58.4"N, 4°16'18.5"E). The site is close to the Vistre River on Fluvisols and experiences a Mediterranean climate with hot, dry summers and mild winters (Météo France, 1991–2020 period). Mean monthly temperatures range from 7.1 °C in January to 24.7 °C in

July, with summer maxima frequently exceeding 30 °C. Annual precipitation averages 685 mm and follows a distinct seasonal pattern. Autumn months receive the highest rainfall with 287 mm between September and November while summer months are particularly dry with 24 mm in July and 35 mm in August. Spring and winter show intermediate precipitation levels.

Experimental design

We established a large-scale experiment ($N=600$ trees) to test the relationship between aboveground growth patterns and root system regeneration after transplanting. Post-transplant recovery was monitored over two years through phenological and growth traits. Based on identified growth patterns, we conducted targeted excavations to examine how aboveground growth patterns related to root system regeneration and health.

Plant material and nursery history

For this study, we selected Mediterranean hackberry (*Celtis australis* L., Cannabaceae), a species widely used in Mediterranean urban landscapes. Trees originated from open-ground seedlings, thus presenting genetic variability among individuals. We retrospectively reconstructed their production history by examining shoot and root architecture. Following standard nursery practices, seedlings underwent taproot pruning at 10 cm depth to promote shallow root division and facilitate bare-root harvesting. Trees were coppiced at the end of their second year at 5 cm above ground, preserving the two-year-old root system. Over the following two years, structural roots developed from the taproot pruning point, while vigorous sprouts grew from the coppicing point, benefiting from the established root system for rapid trunk growth. Trees were harvested as bare-root stock at the end of their fourth year (delivered on February 7, 2022). Upon delivery, trees were heeled-in in moist blond peat substrate behind a north-facing wall and watered daily to prevent root desiccation and maintain dormancy until planting. At study initiation, trees thus combined a four-year-old root system with two-year-old aerial parts, presenting one or two vigorous sprouts from the coppicing point.

Pre-planting structural standardization

Prior to planting, each tree was individually processed for stem and root system standardization. Trees with two main stems were reduced to a single trunk by removing the smaller or a randomly selected one when sizes were similar. Initial trunk diameter at 5 cm above the coppicing point was 14.9 ± 3.0 mm (mean $\pm$ SD, $n=600$). Tree height, estimated

from standardized photographs using image analysis (Fiji/ImageJ), was 141.4 ± 20.7 cm (mean $\pm$ SD, $n=281$). We pruned the initial root systems to an 18-cm radius using a circular template. Structural roots were cut obliquely (45°) with pruning shears to maximize the cambial perimeter available for regeneration and ensure clean cuts. These initial roots are hereafter referred to as “pruned roots”. During processing, root systems were kept immersed in water and were only air-exposed for pruning and measurements (1–3 min per tree). After standardization, root systems were dipped in clay slurry and trees were returned to heeling-in storage until planting.

Planting Protocol and irrigation

We selected two experimental plots located 500 m apart in the nursery. Each plot measured 100 $\times$ 60 m and contained two planting blocks separated by 30 m. Plots were plowed to 60 cm depth and tilled. Trees were mechanically planted on March 28–29, 2022, using a tractor-drawn planting machine that opens a linear furrow, into which an operator positions each tree before the furrow is closed behind. Spacing was 2.5 m between rows and 2 m within rows, resulting in a tree density of 2,000 trees/ha. After planting, trees received thorough watering to ensure proper root-soil contact. Given the Mediterranean summer drought conditions at the study site, drip irrigation (40 L/tree weekly, delivered overnight over 10 h via individual 4 L/h drippers) was provided during dry periods from late spring to early autumn, adjusted according to rainfall. This regime is consistent with standard post-transplant irrigation recommendations (Gilman and Beeson 1996). Trees were neither fertilized, staked, nor pruned.

Growth monitoring

Post-transplant recovery was monitored through phenological observations and growth measurements over two years. Budbreak timing was assessed by tracking the transition from dormant to swollen green buds at 7–10-day intervals, calculated as the number of days between planting and first visible bud swelling. We then monitored annual shoot elongation dynamics throughout the growing season, which extended to first frost (December 8, 2022, and November 27, 2023), marking complete leaf fall in this deciduous species. During the growing season, annual shoot elongation may consist of one or more growth flushes separated by temporary growth cessation, each flush producing a growth unit identifiable by morphological markers such as cataphyll scars (see Barthélémy and Caraglio 2007). We distinguished two types of annual shoots based on their number of growth units: monocyclic shoots, which complete their annual elongation in a single growth unit, and polycyclic shoots, which

exhibit two or more growth units (see Barthélémy and Caraglio 2007). For each tree, we recorded the date at which the first growth cycle was completed. In monocyclic trees, this date corresponded to the end of shoot elongation, while in polycyclic trees, it marked the initiation of a second growth cycle. These observations allowed us to classify trees into distinct growth categories for targeted excavations at season's end.

Tree excavation and structural characterization

We excavated trees during winter dormancy: 80 trees at the end of the first year and 32 trees at the end of the second year. Excavations were performed using a mechanized soil ball extractor (Holmac HZC30) equipped with a 70-cm diameter semi-circular blade. This method preserved all pruned roots (within the original 18-cm radius) and basal portion of newly developed roots in the root ball, allowing characterization of pruned root regeneration. After individual excavation, soil was removed using hand tools. Root systems were stored in 150-L plastic bags and kept in shade, with regular misting to prevent fine root desiccation. Before root system characterization, remaining soil was removed by gentle washing in water using a soft brush.

For each excavated tree, we characterized both aerial and root systems, distinguishing initial structures present at planting from those produced after. From the 80 first-year trees, we characterized 2,366 annual shoots, 968 pruned roots and 3,189 associated new roots. From the 32 second-year trees, we characterized 2,134 annual shoots, 395 pruned roots and 1,662 associated new roots.

Aerial system measurements

We retrospectively delimited all annual shoots constituting the aerial system of each excavated tree using cataphyll scars persisting on the bark (see Barthélémy and Caraglio 2007). Each axis, from the trunk to the smallest branches, consists of a succession of annual shoots whose limits are identifiable through these morphological markers. For each annual shoot segment, we measured its length and proximal and distal diameters. For current-year shoots, distal diameters were not measured but estimated from basal diameter thresholds established on a subset of annual shoots: distal diameter was set equal to basal diameter when basal diameter was under 1 mm, to 1 mm for basal diameters between 1 and 4 mm, and to 2 mm above 4 mm. Total aboveground volume was calculated by summing the volume of all segments, each computed using the truncated cone formula. The error introduced by estimating distal diameters on current-year shoots remains limited, as their volume represents a minor fraction of total aboveground volume.

Current-year annual shoots were further classified as monocyclic or polycyclic. For polycyclic shoots, we also recorded the presence of immediate shoots (i.e., lateral shoots developing during the same growing season as the bearer shoot) and measured their length and basal diameter. At crown level, we derived the total number of annual shoots, the numbers of monocyclic and polycyclic shoots, their mean and maximum lengths, and their cumulative basal cross-sectional area.

For each excavated tree, we measured trunk diameter at 5 cm above the coppicing point (0.01 mm precision). Trunk cross-sectional area was calculated from the mean of two orthogonal diameter measurements. Trunk growth rate ($\text{cm}^2 \cdot \text{day}^{-1}$) was calculated as:

$$\text{Growth rate} = \frac{(\text{Final} - \text{Initial Trunk Cross sectional area})}{\text{Growing season duration}}$$

For first-year trees, growing season duration was 254 days (planting to first frost). For the second-year trees, we used a cumulated duration of 482 days spanning both years, because trunk cross-sectional area integrates growth over the entire post-transplant period. We deliberately used an absolute growth rate rather than a Relative Growth Rate. This metric does not normalize growth by initial trunk cross-sectional area. Consequently, it remains independent of pre-transplant tree dimensions and can serve as a response variable for identifying factors that drive post-transplant recovery heterogeneity.

Estimation of leaf area and biomass allocation in annual shoots

To estimate leaf area and biomass allocation between annual shoot stems and leaves, we developed allometric relationships from 120 fully-leaved shoots (80 monocyclic, 40 polycyclic) collected in 2023. Each shoot was scanned with a reference scale, and total leaf area was determined through image analysis using ImageJ software. For each annual shoot, leaves were separated from the stem, and both components were oven-dried separately (60 °C, 48 h) and weighed using a precision balance (Mettler Toledo AB204-S/FACT, 0.1 mg precision). Power models ($y = a \cdot L^b$) were fitted using non-linear least-squares regression, with shoot length (L, cm) as predictor. Separate models were established for monocyclic ($n=80$) and polycyclic ($n=40$) shoots to account for morphological differences between shoot types. Shoot length was preferred over basal diameter because length measurements are subject to lower relative measurement error on thin annual shoots. Adding basal diameter as a second predictor did not improve fit given the already high R^2 values (0.918–0.988).

Leaf area (cm²):

- $Leaf\ Area_{Monocyclic\ shoot} = 5.727.Length^{1.088};$
 $R^2=0.952; p=1.4e^{-19}.$
- $Leaf\ Area_{Polycyclic\ shoot} = 2.828.Length^{1.184};$
 $R^2=0.946; p=3.1e^{-6}.$

Leaf dry mass (g):

- $Leaf\ Dry\ Mass_{Monocyclic\ shoot} = 0.067.Length^{1.157};$
 $R^2=0.949; p=2.2e^{-17}.$
- $Leaf\ Dry\ Mass_{Polycyclic\ shoot} = 0.050.Length^{1.140};$
 $R^2=0.918; p=4.3e^{-5}.$

Stem dry mass (mg):

- $Stem\ Dry\ Mass_{Monocyclic\ shoot} = 1.161.Length^{2.002};$
 $R^2=0.988; p=3.1e^{-19}.$
- $Stem\ Dry\ Mass_{Polycyclic\ shoot} = 1.730.Length^{1.847};$
 $R^2=0.933; p=7.1e^{-3}.$

We summed these individual shoot estimates to calculate total leaf area and dry mass of annual shoots, distinguishing between stems and leaves. We then derived two integrative variables. First, the axialization index, developed by Lauri and Kelner (2001), was calculated as the ratio of stem to leaf dry mass to quantify biomass allocation between axes and leaves. Second, the exposure-weighted leaf area was calculated by multiplying total leaf area by the number of days between budbreak and season end.

Root system measurements

Root system volume within the root ball was calculated by summing taproot segments and pruned roots volumes, all computed using the truncated cone formula from length and diameter measurements. Newly developed roots were excluded from this calculation because excavation preserved only their basal portions (5–15 cm), making their volumes estimates unreliable.

To characterize root regeneration after transplanting, we quantified new root production from pruned roots and assessed how effectively these new roots compensated for the loss of distal root portions caused by pruning. For each pruned root, we counted new roots and measured their basal insertion diameter. From these measurements, we derived, at the root system level, the percentage of unregenerated pruned roots, the total number of new roots, and their cumulative basal cross-sectional area. Wound closure rate of pruned roots was first calculated at the pruned root level as the ratio of the cumulative basal cross-sectional area of new roots emerging from that pruned root to its distal

cross-sectional area. At the root system level, we then averaged these individual rates across all pruned roots of each tree to obtain a mean wound closure rate per individual, expressed as a percentage. This rate was calculated both with and without roots smaller than 2 mm in diameter, as these thin roots contribute minimally to wound closure due to their poor lignification.

In addition to wound closure rate, we further characterized the health status of pruned root ends, which may directly affect regeneration potential. Because pruned root condition evolves over time, these characterizations differed between years. In first-year trees, we characterized spatial patterns of new root emergence along pruned roots on a subset of 31 trees (corresponding to 345 pruned roots and 1,296 new roots). We measured the distance between each new root insertion point and the pruned end. We then classified regeneration into three spatial distribution patterns: “exclusively distal” when all new roots emerge at the pruned end, “distal and upstream” when new roots emerge both at the pruned end and upstream, and “exclusively upstream” when all new roots emerge away from the pruned end. For cases of exclusively upstream regeneration, we measured the distance between the pruned end and the first new root insertion point, then calculated the cumulative length of non-regenerated ends per root system. In second-year trees, we assessed the health status of each pruned root across all individuals, categorizing them as “compromised” when showing distal necrosis, stub persistence, or large open dark wound, or “healthy” otherwise. This classification allowed us to calculate the percentage of compromised pruned roots per root system.

Additionally, we calculated whole-tree volume by summing aboveground and belowground volumes to integrate root and shoot traits. We also computed the ratio between the cumulative cross-sectional areas of new roots and annual shoots as an integrative trait reflecting the functional balance between absorbing and assimilating structures, as well as biomass allocation between these newly developed structures after transplanting.

Statistical analysis

We used non-parametric statistics because of the modest sample sizes for excavated trees within growth categories ($n=4-28$). Trait values were summarized using the median and interquartile range. Differences among categories were evaluated using Kruskal–Wallis tests ($\alpha=0.05$), followed by Dunn’s post-hoc tests with Benjamini–Hochberg adjustments when significant.

To explore relationships between above- and belowground compartments, we first performed an exploratory analysis using Spearman’s rank correlation matrices (*psych*

package; Revelle 2024) to identify key trait associations. Based on these results, we developed a composite Root Regeneration Score (RRS) through Principal Component Analysis (PCA, *FactoMineR* and *Factoshiny* packages; Husson et al. 2024; Vaissie et al. 2024) to synthesize root regeneration variables into a quantitative benchmark of root system recovery. We retained the most parsimonious combination of root variables that maximized total explained variance while minimizing redundancy among variables. The RRS was then computed as the weighted sum of individual tree coordinates on PC1 and PC2, with weights proportional to each component's explained variance. We then assessed relationships between this RRS and aboveground traits to identify potential non-destructive indicators of root regeneration.

Finally, to develop a practical field assessment tool capable of predicting root system recovery without excavation, we constructed the Aerial Field Index (AFI). We performed multiple regression analyses to predict the RRS from standardized aboveground traits. Candidate predictors were selected based on their practical measurability in field conditions, their individual correlation with the RRS, and their biological relevance to distinct functional dimensions of post-transplant recovery. The final model was selected based on highest adjusted R^2 and biological interpretability. Standardized regression coefficients from this model were used to weight each predictor in the AFI.

All analyses were conducted in R (version 4.3.2; R Core Team 2023) using RStudio (version 2023.12.0; RStudio Team 2023). Figures were created using Inkscape (v1.4). Statistical graphics were initially generated in RStudio, then imported and edited in Inkscape.

Results

Growth patterns of aerial systems

First-year growth patterns

Following transplanting, we identified distinct growth patterns, primarily differentiated by budbreak timing and secondarily by shoot elongation dynamics during the first growing season (Fig. 1; Table 1).

Budbreak patterns

60% of the trees exhibited budbreak within two months after transplanting (35 days $\pm$ 10; all values reported as median $\pm$ IQR; Fig. 1), and were classified as *Early-budding* trees. Conversely, 11% displayed delayed budbreak, occurring in autumn more than six months after planting (192

days $\pm$ 30), and were classified as *Late* trees. No budbreak was observed during July and August. Of the total population, 29% did not exhibit any budbreak. Among them, 7% remained alive at the end of the first growing season, as indicated by their grey-greenish trunk bark, and were classified as *Declining* trees. The remaining 22% were clearly dead, characterized by a reddish trunk bark, often accompanied by a curved trunk and signs of fungal colonization.

Fig. 1 Post-transplant growth patterns and crown architectural differentiation over two years in young Hackberry trees (*Celtis australis* L.). The initial aboveground structure at transplanting (2-year-old trees) evolved into distinct growth categories over two years, driven by two key factors: (i) timing of first budbreak (*Early* versus *Delayed*) and (ii) annual shoot elongation dynamics (polycyclic versus monocyclic growth). During the first year, trees differentiated into four categories: *Poly* (polycyclic growth, 21%), *Mono* (monocyclic growth, 39%), *Late* (delayed budbreak with progressive crown dieback, 11%), and *Declining* (no budbreak, 7%). Mortality affected 22% of the initial population. In the second year, despite synchronous spring budbreak across surviving trees, shoot elongation patterns drove further differentiation. *Poly* trees diverged into *Poly-Poly* (14%) and *Poly-Mono* (13%) categories, while *Mono* trees evolved into *Mono-Poly* (20%) and *Mono-Mono* (34%) categories. Surviving *Late* and *Declining* trees entered a crown reconstruction phase and were classified as *Restructuring* trees (10%). Mortality increased to 32%, exclusively affecting *Late* (32%) and *Declining* (75%) trees. Percentages at each bifurcation represent the proportion of the total planted population following each developmental trajectory. Black crosses indicate axes mortality

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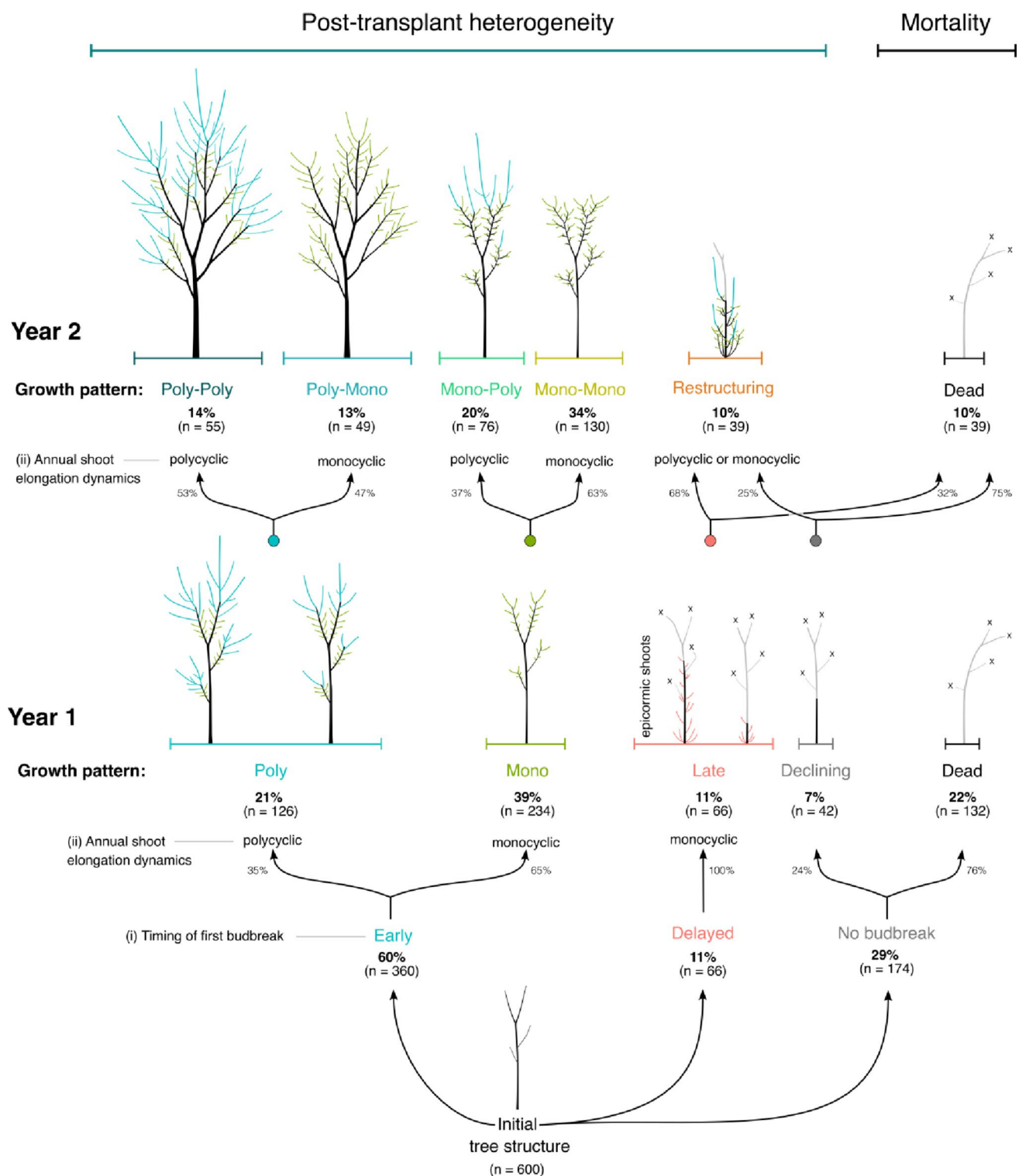
Shoot elongation patterns

In *Early-budding* trees, preformed buds from the previous year initiated their growth, maintaining sequential development at the crown periphery. Annual shoots rapidly unfolded their leaf area and completed their first elongation cycle by mid-June, ending with apical meristem cessation. Two distinct growth trajectories then emerged within this group. 35% of *Early-budding* trees initiated a second elongation cycle on some shoots, allowing sustained crown expansion throughout the growing season (*Poly* trees), whereas the remaining 65% restricted their crown expansion to the spring period (*Mono* trees).

In *Late* trees, progressive crown dieback occurred, advancing from the periphery toward the trunk base, thus creating a gradient of crown mortality within this category. Following this dieback, epicormic shoots emerged from latent buds on older living sections. These shoots completed only one elongation cycle.

Crown characteristics

Crown traits differed among the three growth pattern categories during the first year (Table 1). *Poly* trees developed the highest number of annual shoots, including polycyclic



shoots, followed by *Mono* trees with exclusively monocyclic shoots, while *Late* trees produced the fewest shoots, all epicormic (Table 1). *Poly* trees, which sustained shoot elongation throughout the growing season, formed the longest shoots. In contrast, *Mono* and *Late* trees, which completed only one growth cycle, produced shorter shoots (Table 1).

These differences resulted in contrasting leaf area development: *Poly* trees accumulated five times more leaf area than *Mono* trees, and twelve times more than *Late* trees (Table 1). The duration of the growing season further amplified these disparities: *Early-budding* trees maintained photosynthetic surfaces for 220 ± 10 days, whereas *Late*

Table 1 Shoot system, root system, and whole-tree traits characterizing growth dynamics categories at the end of the first and second year after transplanting

Year	Growth dynamics categories	Bud-break time	Total shoot number	Polycyclic shoot number	Maxi-mum shoot length	Leaf area	Exposure-weighted area	Axialisation index	Trunk growth rate	New root number	Wound closure rate >2 mm	Shoot system volume	Root system volume	Whole-tree volume	Annual shoot basal area	New root basal area	New root-to-annual shoot ratio
		<i>n</i>	<i>n</i>	<i>n</i>	<i>cm</i>	<i>m</i> ²	<i>m</i> ² ·day	<i>g g</i> ⁻¹	<i>cm</i> ² ·day ⁻¹	<i>n</i>	%	<i>cm</i> ³	<i>cm</i> ³	<i>cm</i> ³	<i>cm</i> ²	<i>cm</i> ²	
1	<i>Poly</i>	22	35 ^a ±10	23 ^a ±16	58 ^a ±21	0.50 ^a ±0.20	110 ^a ±44	0.36 ^a ±0.10	0.0102 ^a ±0.0056	52 ^a ±28	61 ^a ±12	343 ^a ±170	246 ^a ±88	595 ^a ±262	3.0 ^a ±1.3	4.9 ^a ±2.0	1.6 ^a ±0.4
	<i>Mono</i>	28	35 ^a ±10	0 ^b ±15	11 ^b ±3	0.11 ^b ±0.07	24 ^b ±14	0.09 ^b ±0.03	0.0017 ^b ±0.0019	49 ^a ±19	35 ^b ±10	97 ^b ±46	116 ^b ±47	222 ^b ±90	0.5 ^b ±0.3	1.5 ^b ±0.9	3.0 ^b ±1.1
	<i>Late</i>	22	192 ^b ±30	0 ^b ±14	8 ^b ±5	0.04 ^c ±0.05	2 ^c ±4	0.06 ^b ±0.04	0.0001 ^c ±0.0007	20 ^b ±16	1 ^c ±1	112 ^b ±46	91 ^b ±38	184 ^b ±93	0.2 ^c ±0.2	0.3 ^c ±0.2	1.7 ^a ±1.3
	<i>Declining</i>	8	NA	NA	NA	NA	NA	NA	-0.0003 ^c ±0.0005	NA	NA	100 ^b ±47	90 ^b ±20	194 ^b ±61	NA	NA	NA
2	<i>Poly-Poly</i>	4	34 ^a ±2	108 ^a ±24	36 ^a ±19	51 ^{ab} ±14	0.87 ^a ±0.15	199 ^a ±33	0.26 ^a ±0.03	0.0163 ^a ±0.0030	62 ^{NS} ±25	853 ^a ±287	415 ^a ±164	1260 ^a ±219	6.2 ^a ±1.3	10.7 ^a ±3.3	1.7 ^a ±0.2
	<i>Poly-Mono</i>	4	35 ^a ±3	90 ^a ±97	0 ^b ±9	0.52 ^{ab} ±0.45	119 ^{ab} ±102	0.16 ^{ab} ±0.03	0.0112 ^a ±0.0053	54 ^{NS} ±27	80 ^a ±22	401 ^a ±210	346 ^a ±225	734 ^{ab} ±430	2.7 ^a ±2.4	8.4 ^a ±6.9	5.1 ^b ±1.2
	<i>Mono-Poly</i>	10	34 ^a ±1	80 ^a ±25	5 ^a ±6	0.45 ^a ±0.33	102 ^a ±21	0.22 ^a ±0.12	0.0066 ^{ab} ±0.0020	53 ^{NS} ±16	59 ^{ab} ±10	389 ^{ab} ±213	292 ^{ab} ±122	704 ^{ab} ±326	2.4 ^a ±0.5	6.0 ^{ab} ±3.5	2.6 ^{bc} ±1.1
	<i>Mono-Mono</i>	6	44 ^{ab} ±24	56 ^{ab} ±30	0 ^b ±4	0.20 ^{bc} ±0.07	46 ^{abc} ±17	0.08 ^b ±0.03	0.0029 ^{abc} ±0.0018	59 ^{NS} ±13	45 ^{bc} ±25	177 ^{bc} ±123	168 ^{bc} ±93	345 ^{bc} ±192	0.8 ^b ±0.3	3.2 ^{bc} ±1.9	3.7 ^b ±0.5
	<i>Restructuring</i>	8	208 ^b ±25	26 ^b ±14	6 ^a ±4	0.18 ^c ±0.07	41 ^c ±15	0.21 ^a ±0.17	0.0009 ^c ±0.0008	30 ^{NS} ±10	28 ^c ±9	141 ^c ±72	141 ^c ±82	263 ^c ±129	0.9 ^b ±0.5	1.5 ^c ±0.6	2.0 ^{ac} ±0.4

Traits were measured or calculated from excavated trees across the growth pattern categories. Variable descriptions: "Wound closure rate >2mm": pruning wound closure rate, excluding new roots with diameters less than 2 mm (%). "Annual shoot basal area": cumulative basal cross-sectional area of annual shoots (cm²). "New root basal area": cumulative basal cross-sectional area of new roots (cm²). "New root-to-annual shoot ratio": ratio of new root basal area to annual shoot basal area

Values are presented as medians±interquartile ranges (IQR). *n* indicates the number of excavated trees per category. Shoot system volume refers to the total aboveground volume while root system volume refers to the root volume contained within the 70-cm diameter root ball. Statistical differences between categories within each year were tested using Kruskal-Wallis tests ($p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; NS=Not Significant). Different superscript letters indicate significant differences between categories based on Dunn's post-hoc test with Benjamini-Hochberg correction. NA indicates data not available

trees had only a brief growing period of 63 ± 30 days. This temporal disparity, combined with differences in total leaf area, led to large differences in exposure-weighted leaf area among categories (Table 1).

Evolution of growth pattern categories in the second year

The initial growth pattern categories evolved during the second year, mainly as differences in shoot elongation dynamics continued to drive tree development (Fig. 1). In contrast, spring budbreak was relatively synchronous across all remaining trees ($n=388$, 65% of the initial planting), occurring between March 28 and April 27, 2023.

Shoot elongation patterns

Trees from the initial *Poly* category followed two distinct trajectories in the second year: 53% maintained polycyclic growth (*Poly-Poly* trees), while 47% shifted to exclusively monocyclic growth (*Poly-Mono* trees). Similarly, trees from the initial *Mono* category diverged: 37% developed polycyclic shoots (*Mono-Poly* trees), while 63% produced exclusively monocyclic shoots (*Mono-Mono* trees). During this second year, mortality increased from 22% to 32%, affecting exclusively *Late* (32%) and *Declining* (75%) trees. The surviving *Late* (68%) and *Declining* (25%) trees entered a crown reconstruction phase and were classified as *Restructuring* trees, regardless of their annual shoot growth patterns.

Crown characteristics

Crown traits continued to vary among growth categories during the second year, following a gradient from *Poly-Poly* to *Restructuring* trees (Table 1). *Poly-Poly* trees produced the most annual shoots, including polycyclic shoots, and maintained the longest shoots, resulting in the largest leaf area. *Poly-Mono* trees developed a similar total number of shoots but exclusively monocyclic ones, with shorter shoots and a smaller leaf area. *Mono-Poly* trees began to develop a few polycyclic shoots, which resulted in longer shoots, a larger leaf area, and a more vertical crown expansion. Conversely, *Mono-Mono* trees maintained monocyclic growth, producing fewer and shorter shoots, leading to a smaller leaf area and a flattened, umbrella-like crown development. *Restructuring* trees produced the fewest annual shoots, issued from epicormic shoots, but including some polycyclic ones, contributing to longer shoot development despite the smallest leaf area.

Regeneration and health of root systems

At the end of the first year

Poly trees developed larger root systems than other categories (Fig. 2a; Table 1). All pruned roots produced new roots in *Early-budding* trees, whereas 26% (± 32) did not regenerate in *Late* trees, and no regeneration occurred in *Declining* trees. Among *Early-budding* trees, new roots were more frequently initiated at distal positions in *Poly* than in *Mono* trees (Fig. 2c). Conversely, the proportion of exclusively “upstream regeneration” increased from *Poly* (38%) to *Mono* (59%), reaching 91% in *Late* trees.

Early-budding trees produced similar numbers of new roots, while *Late* trees developed significantly fewer (Table 1). The basal portion of new roots reflected distinct developmental stages: in *Early-budding* trees, these portions showed light brown coloration, complete suberization, and an absence of fine roots near their insertion points. In contrast, in *Late* trees, 41% (± 20) of new roots displayed a white rhizodermis, lacked suberization, and had dense branching near insertion points, suggesting younger roots formed during delayed root regeneration (Fig. 2a). *Poly* trees produced a higher proportion of large-diameter roots compared to *Mono* and *Late* trees (Fig. 2b), with mean root diameter decreasing from *Poly* (2.8 ± 0.6 mm) to *Mono* (1.7 ± 0.1 mm) and *Late* trees (0.9 ± 0.3 mm). These differences in new root diameters drove the gradient in their cumulative cross-sectional area and in average pruned root wound closure rates observed across categories (Fig. 2d; Table 1).

At the end of the second year

Root system development continued to reflect divergent growth patterns, with root system volumes decreasing progressively from *Poly-Poly* to *Restructuring* trees (Fig. 2a; Table 1). By the end of the second year, all trees, including those initially classified as *Late* and *Declining*, had regenerated their pruned roots. However, pruned root health varied across categories (Fig. 2e). Trees with initial polycyclic growth (*Poly-Poly* and *Poly-Mono*) maintained mostly healthy pruned roots, whereas trees with initial monocyclic growth (*Mono-Poly* and *Mono-Mono*) exhibited a higher proportion of compromised pruned roots. *Restructuring* trees showed the poorest root health, with the majority of their pruned roots compromised (Fig. 2e).

Trees from the initial *Early-budding* categories produced similar numbers of new roots, while *Restructuring* trees developed fewer (Table 1). The mean diameter of new roots followed a consistent gradient: it was largest in trees with initial polycyclic growth (*Poly-Poly*: 3.8 ± 0.6 mm;

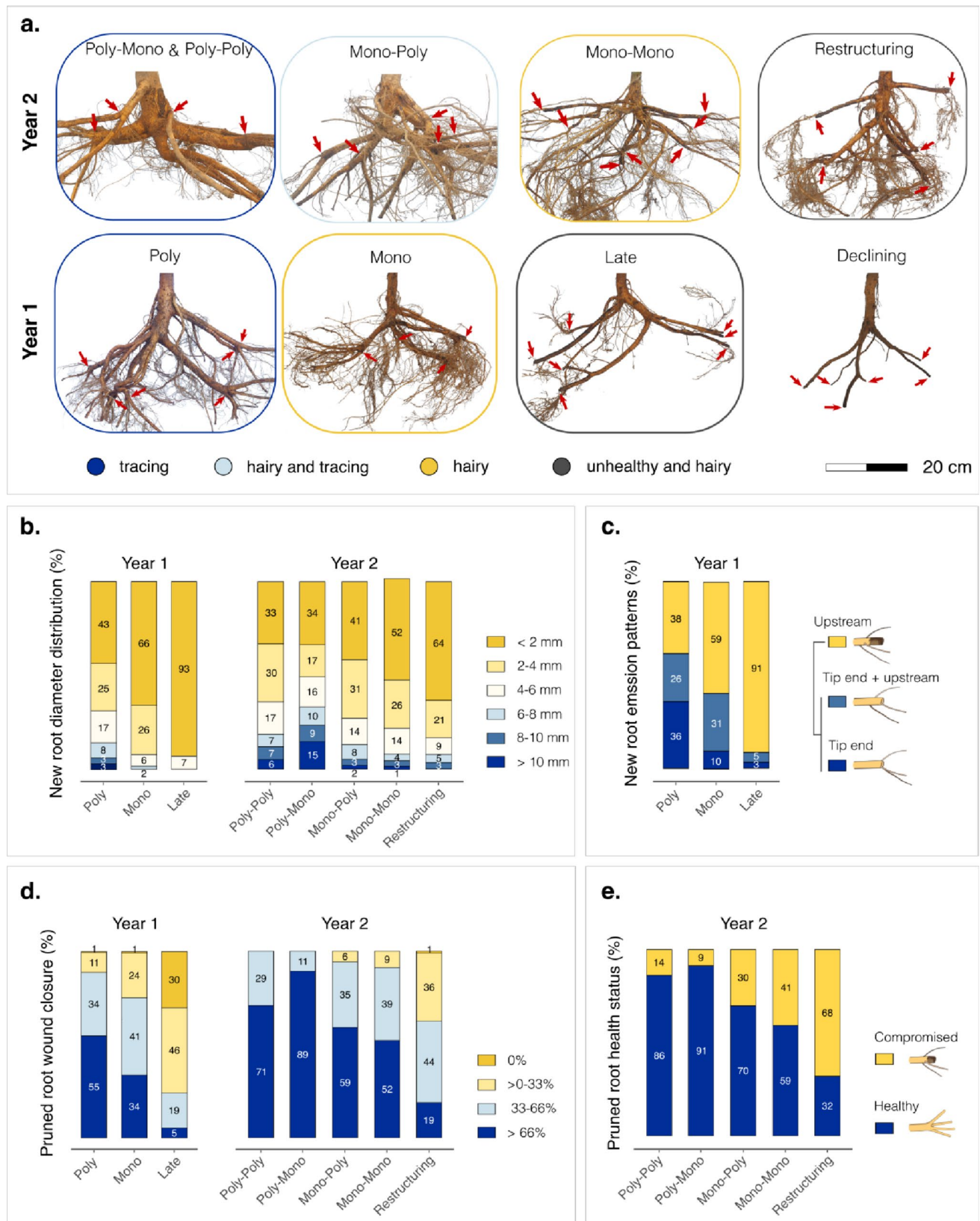


Fig. 2 Root regeneration patterns, wound closure, and health status of pruned roots across growth categories at the end of the first and second growing seasons. **(a)** Representative images of root systems illustrating differences in root volume and regeneration patterns after transplanting. In the second year, *Poly-Poly* and *Poly-Mono* categories were grouped due to their relatively similar root system characteristics. Red arrows indicate the zones where initial structural roots were pruned. Scale bar: 20 cm. **(b)** New root diameters, grouped into six diameter classes (<2 mm, 2–4 mm, 4–6 mm, 6–8 mm, 8–10 mm, >10 mm) for the first and second year. **(c)** New root emission patterns along pruned roots (reported only at the end of the first growing season), categorized as “tip-end” regeneration, “upstream” regeneration, or both. Percentages represent the proportion of these three pruned root regeneration patterns in each category. **(d)** Pruned root wound closure (%), classified into four closure categories (0%, >0–33%, 33–66%, >66%) for the first and second year. **(e)** Pruned root health (reported only at the end of the second growing season), categorized as healthy or compromised. Compromised roots included three types: (i) roots exhibiting necrosis extending from the pruned tip toward the base; (ii) pruning wounds that remained entirely open with blackened tissue; and (iii) persistent stubs following pruning. Percentages represent the proportion of pruned roots in each health category

Poly-Mono: 3.8 ± 0.9 mm), intermediate in *Mono-Poly* trees (3.1 ± 0.3 mm), and smallest in *Mono-Mono* (2.2 ± 0.7 mm) and *Restructuring* trees (2.0 ± 0.4 mm; Fig. 2b). These diameter differences drove the same gradient in cumulative cross-sectional area of new roots and in average wound closure rates across categories (Fig. 2d; Table 1).

Root-shoot relationships and allocation patterns

Crown axialization and new root-to-annual shoot ratio

Axialization index and new root-to-annual shoot ratio differed among growth categories (Table 1). The axialization index, which quantifies biomass investment in supporting stems relative to leaves within annual shoots, followed a consistent gradient across categories. In both years, polycyclic categories (*Poly*, *Poly-Poly*, *Mono-Poly*) exhibited the highest axialization indices, while monocyclic categories (*Mono*, *Late*, *Mono-Mono*, *Poly-Mono*) showed lower values. *Restructuring* trees exhibited elevated axialization indices despite their low shoot production.

The new root-to-annual shoot ratio showed an opposite gradient. Monocyclic categories consistently exhibited higher ratios than polycyclic ones. This contrast was particularly marked in the second year, where *Poly-Mono* trees reached the highest ratios in the dataset, whereas *Mono-Poly* trees showed ratios closer to consistently polycyclic categories (Table 1).

During the first year, *Poly* trees exhibited high axialization indices, reflecting biomass investment in supporting stems through successive growth flushes. Their balanced root-to-shoot ratio indicated sustained investment in both shoot and root development. In contrast, *Mono* trees completed only a single growth flush, resulting in shoots that

remained in a foliarized stage with low axialization indices. Their higher root-to-shoot ratio reflected prioritized root development over shoot expansion. *Late* trees displayed minimal structural investment in supporting stems but maintained a balanced root-to-shoot ratio.

During the second growing season, *Poly-Poly* trees maintained their high axialization index and balanced root-to-shoot ratio, while *Mono-Mono* trees continued to prioritize root development (Table 1). In contrast, transitional categories shifted toward opposite allocation strategies. *Poly-Mono* trees shifted from balanced allocation toward root prioritization, reaching the highest root-to-shoot ratios in the dataset. Conversely, *Mono-Poly* trees shifted toward higher axialization and lower root-to-shoot ratios, reflecting a progressive return to a more balanced allocation between shoots and roots. *Restructuring* trees exhibited relatively balanced root-to-shoot ratios and elevated axialization indices, reflecting crown reconstruction through a few epicormic shoots expressing polycyclic growth at the distal part of the main stem, which had been reduced by initial crown dieback.

Relationships between growth-related variables

Exposure-weighted leaf area showed a positive correlation with new root basal area ($r=0.96$, $p<0.001$). Trunk growth rate was correlated with both exposure-weighted leaf area ($r=0.91$, $p<0.001$) and new root basal area ($r=0.92$, $p<0.001$). Overall, all growth-related variables, including leaf area, new root basal area, trunk growth rate, and root system volume, were positively correlated ($r>0.82$, $p<0.001$).

Effects of budbreak timing

Budbreak timing had contrasting effects on growth-related variables during the first growing season. In *Early-bud-ding* trees, no correlations were observed between time to budbreak and new root basal area or trunk growth rate ($p>0.05$). In contrast, *Late* trees exhibited negative correlations between budbreak timing and leaf area ($r=-0.79$, $p<0.001$), new root basal area ($r=-0.84$, $p<0.001$), and wound closure rate ($r=-0.82$, $p<0.001$).

Aboveground indicators of root system recovery

Root system recovery evaluation

Using all excavated trees from both years, we developed a composite Root Regeneration Score (RRS) through principal component analysis (PCA) based on three root variables: percentage of unregenerated pruned roots, new root

basal area, and wound closure rate (Fig. 3a). This parsimonious selection from an initial set of seven root variables eliminated redundancy while increasing the total explained variance. PC1 was associated with new root production and wound closure rate, while PC2 captured the percentage of unregenerated pruned roots (Fig. 3a). The PCA showed a clear gradient of root system recovery among growth categories, from *Declining* and *Late* trees with the lowest scores to *Poly-Poly* trees with the highest (Fig. 3b).

Relationships between Root Regeneration Score and aboveground traits

The RRS was related to all aboveground traits examined, with varying strengths (Fig. 4). Time to budbreak separated trees into two groups, with delayed budbreak associated with low RRS values (Fig. 4a). Total shoot number exhibited a moderate correlation with the RRS (Fig. 4b), whereas maximum shoot length showed a stronger relationship (Fig. 4d). Exposure-weighted leaf area and trunk growth rate exhibited the strongest correlations with the RRS ($r=0.95$, $p<0.001$ and $r=0.89$, $p<0.001$, respectively; Fig. 4c, e).

Aerial Field Index development and performance

From the multiple regression analysis, three aboveground predictors of the RRS were retained: time to budbreak, trunk growth rate, and maximum shoot length. Using data

from 111 excavated trees (one outlier was excluded), the AFI was calculated as:

$$\text{Aerial Field Index} = -0.67 \times \text{Time to Budbreak}_{Std} + 0.32 \times \text{Trunk Growth}_{Std} + 0.25 \times \text{Shoot Max Length}_{Std}$$

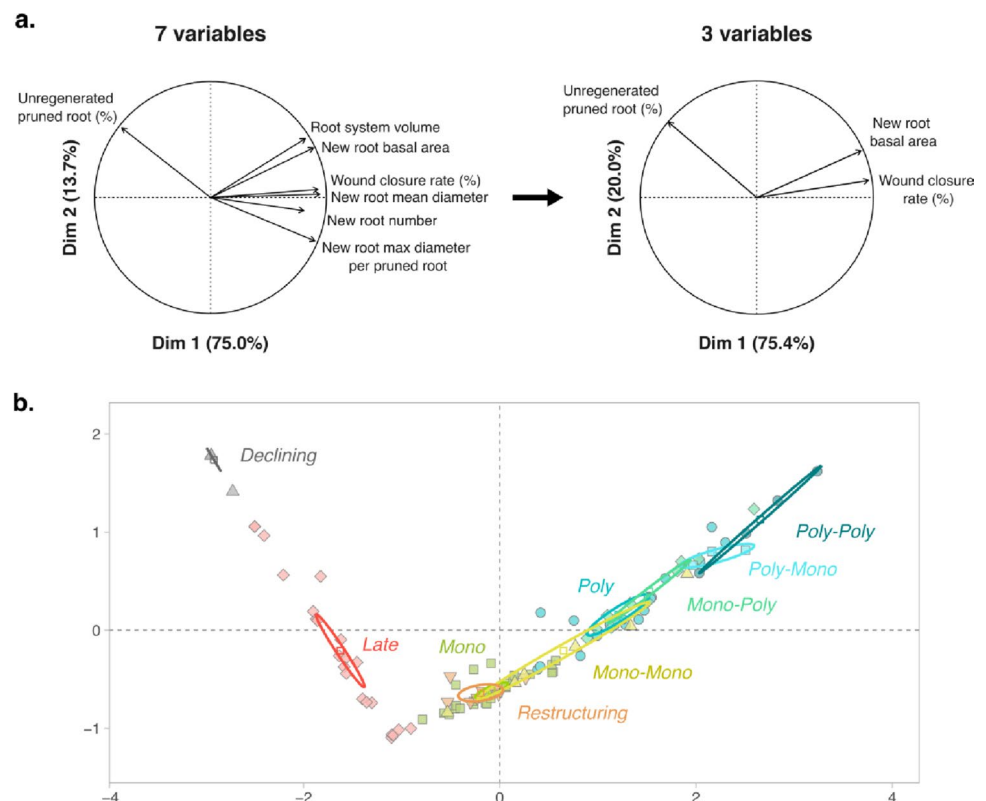
where the variables represent standardized values of days to budbreak (day), trunk growth rate ($\text{cm}^2 \cdot \text{day}^{-1}$), and maximum shoot length (cm).

The AFI showed a high correlation with the RRS ($r=0.96$, $p<0.001$). Growth categories formed distinct clusters along both axes (Fig. 4f). When applied to all surviving trees ($n=468$), the AFI correctly identified 96% of first-year growth categories (AFI ranges: *Poly* >0.65 ; *Mono* $[-0.5 : 0.65]$; *Late* $[-1.5 : -0.5]$; *Declining* $[-2 : -1.5]$). Occasional misclassifications were limited to vigorous *Mono* trees and less vigorous *Poly* trees. Validation for second-year categories was not performed due to insufficient sample sizes.

Discussion

Our two-year monitoring of 600 transplanted *Celtis australis* trees revealed that post-transplant recovery heterogeneity can be structured into a limited number of distinct growth patterns, each associated with specific root regeneration behaviors. These results support our three hypotheses.

Fig. 3 Principal Component Analysis (PCA) of root regeneration for trees excavated at the end of the first ($n=80$) and second ($n=31$) year following transplanting. **(a)** Correlation circles of seven root regeneration variables (left) and the three selected variables (right) on the first two principal components (PC1 and PC2). PC1 is associated with new root growth and pruning wound closure, while PC2 captures the percentage of unregenerated pruned roots. **(b)** Individual trees plotted according to their coordinates on PC1 and PC2. Growth categories from the first year (*Poly*, *Mono*, *Late*, and *Declining*) and second year (*Poly-Poly*, *Poly-Mono*, *Mono-Poly*, *Mono-Mono*, and *Restructuring*) are shown with confidence ellipses



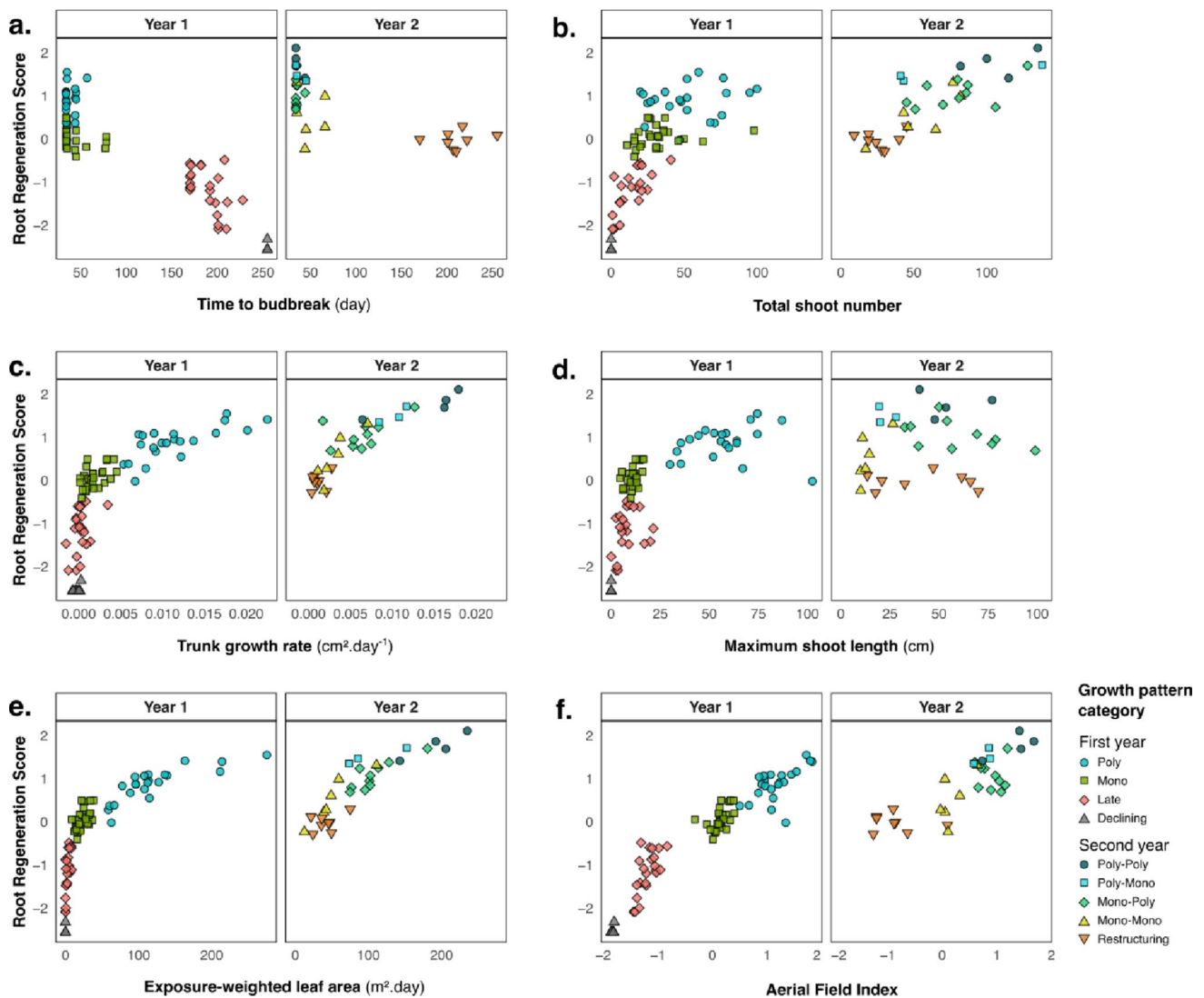


Fig. 4 Relationships between the Root Regeneration Score (RRS) and aboveground traits for trees excavated at the end of the first ($n=80$) and second ($n=31$) year. Panels show the relationships between the RRS and (a) time to budbreak (day), (b) total shoot number, (c) trunk growth rate ($\text{cm}^2 \cdot \text{day}^{-1}$), (d) maximum shoot length (cm), (e) exposure-weighted leaf area ($\text{m}^2 \cdot \text{day}$), and (f) Aerial Field Index (AFI). Data are presented separately for the first and second years in each

1. Budbreak timing and shoot elongation dynamics structure post-transplant recovery into distinct growth patterns.

Our results show that post-transplant recovery can be classified into distinct developmental trajectories, determined by two key factors. Most studies have treated recovery as a continuous gradient, primarily focusing on factors affecting growth and survival rates (Hamilton 1988; Struve 2009; Grossnickle 2012; Koeser et al. 2013; Roman et al. 2013; Watson et al. 2014; Dumins and Lazdina 2018; Wattenhofer and Johnson 2021; Collet et al. 2024; Korbik et al. 2025).

panel. Growth pattern categories are represented by different colors and symbols as follows: *Poly* (blue circles), *Mono* (green squares), *Late* (red diamonds), and *Declining* (gray upward-pointing triangles) for the first year; *Poly-Poly* (dark blue circles), *Poly-Mono* (light blue squares), *Mono-Poly* (green diamonds), *Mono-Mono* (yellow-green upward-pointing triangles), and *Restructuring* (orange downward-pointing triangles) for the second year

However, few studies have attempted to first characterize distinct post-transplant response patterns by reducing the recovery gradient into discrete categories (South and Zwolinski 1996). Our approach identified discrete categories driven by budbreak timing and shoot elongation dynamics.

The timing of budbreak after transplanting constituted the primary differentiation factor. *Early-budding* trees maintained the sequential development of their initial crown, whereas *Delayed-budding* trees experienced crown dieback requiring architectural reconstruction through epicormic shoot development. These epicormic shoots, emerging from latent buds on surviving older sections, enabled

rapid leaf area restoration after the loss of distal sequential buds (Nicolini et al. 2001; Meier et al. 2012; Moore 2021). This initial divergence in crown dynamics set the conditions for subsequent recovery trajectories.

Polycyclism then emerged as the secondary differentiation factor. While *Mono* trees restricted their development to a single spring growth flush, *Poly* trees initiated a second cycle that resulted in a five-fold increase in leaf area (Table 1). Polycyclic shoots are systematically longer than monocyclic ones and produce greater leaf area and branching (Heuret et al. 2003; Barthélémy and Caraglio 2007; Girard et al. 2011). These initial growth patterns drove further differentiation in aboveground systems during the second year (Fig. 1).

Together, budbreak timing and shoot elongation dynamics provide a robust framework for structuring the apparent continuum of post-transplant heterogeneity into discrete, biologically meaningful categories.

2. Aboveground growth patterns reflect distinct root regeneration dynamics.

Our results highlighted a tight functional coupling between above- and belowground recovery. Exposure-weighted leaf area correlated strongly with new root basal area ($r=0.96$), while trunk rate growth correlated with both new root basal area ($r=0.92$) and exposure-weighted leaf area ($r=0.91$). These results are consistent with coordination between leaf area and fine root development to support secondary growth (O'Grady et al. 2006; Jia et al. 2015; Meng et al. 2018). This coupling reflects the interdependence of three systems that transplanted trees must simultaneously re-establish: (i) new leafy shoots to maintain photosynthetic capacity, (ii) new roots to restore water and nutrient uptake, and (iii) vascular tissues to ensure hydraulic transport between them (Van den Driessche 1987; Grossnickle 2005). Despite this shared fundamental coupling, the growth categories exhibited distinct capacities for carbon acquisition and allocation to root regeneration.

First year dynamics of *Early-budding* trees

Early-budding trees followed two contrasting developmental trajectories during the first year (Fig. 5). Through their polycyclic elongation pattern, *Poly* trees developed longer annual shoots than *Mono* trees, supporting greater leaf area (Table 1). This increased transpiring surface was accompanied by crown axialization (Table 1), reflecting enhanced allocation toward stem elongation and cambial growth to sustain hydraulic conductance and mechanical support of the expanding canopy. To match this larger transpiring surface with adequate absorption capacity, we hypothesize

that carbon resources were concurrently allocated to new root elongation, branching, and cambial growth, ensuring hydraulic continuity from absorbing roots to transpiring leaves. This coordinated shoot and root development resulted in a balanced new root-to-annual shoot ratio (Table 1), consistent with theoretical predictions of convergence toward equilibrated root-to-shoot ratios (Brouwer 1963; Iwasa and Roughgarden 1984; Iwasa 2000). This functional coupling reflects the restoration of whole-tree equilibrium (Fig. 5).

In contrast, *Mono* trees terminated shoot elongation after the spring flush, fixing their leaf area for the remainder of the growing season. Their minimal axialization (Table 1) suggests an economy strategy minimizing stem investment to support foliage (Lauri and Kelner 2001; de Haldat du Lys et al. 2023). We hypothesize that this early cessation of shoot growth allowed assimilated carbon to be preferentially redirected toward root regeneration, resulting in a higher new root-to-annual shoot ratio at season end compared to *Poly* trees (Table 1). This compensatory allocation, prioritizing new root over annual shoot growth, represents a necessary step to re-establish functional balance before aerial expansion can resume (Fig. 5).

These contrasting allocation patterns between *Poly* and *Mono* trees resulted in different root regeneration characteristics. Despite producing a similar number of new roots (Table 1), *Poly* trees developed thicker roots, including a few large-diameter roots absent in *Mono* trees, marking the onset of a “tracing” root system. This selective new root development reduced the diametric gap between old pruned roots and newly developed roots, restoring hydraulic continuity more efficiently. In contrast, *Mono* trees produced thin new roots of uniformly small diameter, forming a “hairy” root system with limited wound closure and persistent diametric gaps indicating incomplete hydraulic continuity (Table 1). This absence of selective development toward larger-diameter roots did not yet allow for spatial exploration. These contrasting pruned root regeneration patterns reflect distinct recovery stages: *Poly* trees transitioned toward active soil exploration and efficient hydraulic conduction through a tracing root system, whereas *Mono* trees remained at an earlier recovery stage with limited absorption and hydraulic conductance capacity. We further hypothesize that these differences in cambial growth rate extend to xylem vessel size, with *Poly* trees developing wider vessels to sustain greater water demand (Fig. 5).

Second-year dynamics of *Early-budding* trees

Growth pattern continuity

Poly-Poly trees maintained their polycyclic shoot growth pattern, sustaining high resource acquisition capacity

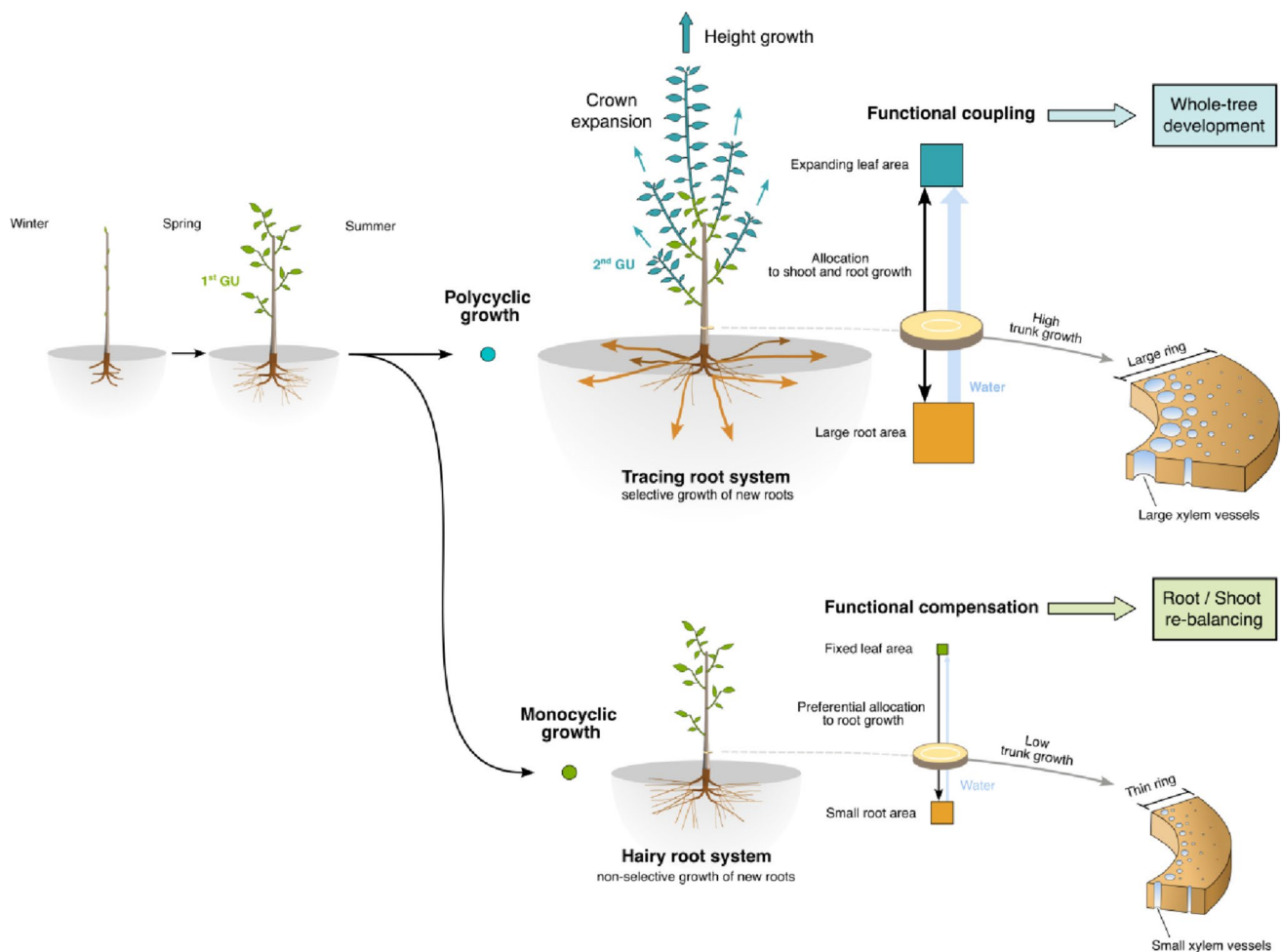


Fig. 5 Contrasting recovery dynamics in transplanted hackberry trees (*Celtis australis* L.). *Early-budding* trees initially developed monocyclic annual shoots (first growth unit, 1st GU) during spring, after which two contrasting developmental trajectories emerged. (**Top**) Trees exhibiting polycyclic shoot growth (*Poly*) initiated a second growth unit (2nd GU) in summer, resulting in expanded leaf area. This increased foliage required a concomitant enhancement of absorption capacity, leading to selective new root growth and the establishment of a tracing root system. Such coordinated above- and belowground growth reflects functional coupling, allowing rapid height growth, crown expansion, and trunk growth (whole-tree development). (**Bottom**) Trees exhibiting monocyclic shoot growth (*Mono*) ceased shoot elongation at the end of spring, limiting subsequent crown expansion

and leaf area. This limited carbon acquisition capacity did not allow for selective new root growth, resulting in the formation of a hairy root system. Nevertheless, early cessation of shoot growth permitted assimilated carbon to be preferentially allocated toward new root growth, reflecting compensatory allocation aimed at restoring root-shoot functional balance (functional compensation). Once functional balance is restored, *Mono* trees may transition toward polycyclic growth during the following growing season. Otherwise, compensatory growth continues until equilibrium is reached. Differences in trunk growth rates directly translate into contrasting annual ring widths, and we hypothesize that *Poly* trees develop wider xylem vessels to sustain the water demand of their larger leaf area, a prediction that remains to be tested through wood anatomical analysis

(Table 1). This continued aerial expansion was accompanied by effective root system development, with balanced new root-to-annual shoot ratios, high wound closure rates, and the presence of large tracing roots (Fig. 2). These characteristics indicate that *Poly-Poly* trees preserved the functional coupling established during the first year, completing their recovery process.

In contrast, *Mono-Mono* trees persisted in their monocyclic elongation pattern, with aerial development and root regeneration characteristics comparable to first-year (Table 1; Fig. 2). Their high new root-to-annual shoot

ratio confirmed continued prioritization of root over shoot growth, but root regeneration remained dominated by thin roots with limited wound closure (Table 1; Fig. 2). This stagnation prolonged functional compensation, suggesting that these trees had not yet re-established the root-to-shoot balance necessary to transition toward whole-tree development (Fig. 5).

Growth pattern shifts

Other *Early-budding* trees shifted between growth patterns during the second year. *Mono-Poly* trees transitioned from monocyclic to polycyclic shoot growth, initiating a few long, axialized shoots in their upper crown and increasing leaf area (Table 1). This shift coincided with the onset of a tracing root system, improved wound closure, and enhanced trunk growth (Table 1; Fig. 2). The resulting decrease in the new root-to-annual shoot ratio reflects a transition from compensatory allocation toward functional coupling. Conversely, *Poly-Mono* trees shifted toward monocyclic shoot growth, reducing aerial expansion. Although leaf area development was limited to spring, this transition favored increased allocation toward root regeneration, as reflected by their high new root-to-annual shoot ratio (Table 1). However, because these trees had already experienced polycyclic growth during the first year, their root systems retained the structural characteristics of *Poly-Poly* trees, including near-complete wound closure and well-developed tracing roots (Table 1). These shifts demonstrate that the balance between aerial expansion and root regeneration is modulated by the tree's shoot elongation pattern, while prior polycyclic growth confers lasting structural benefits to the root system.

Across all *Early-budding* trees, polycyclic shoot growth emerged as a consistent marker of successful recovery. Regardless of when it occurred during the two-year monitoring period, polycyclic shoot growth was systematically associated with high trunk growth rates and tracing root systems (Table 1; Fig. 2). Polycyclic shoot growth therefore represents a reliable marker of successful establishment in *Early-budding* trees after transplanting.

Delayed-budding trees: recovery challenges and outcomes

Following transplanting, *Late* and *Declining* trees first experienced pronounced crown dieback before any growth resumed. In *Late* trees, budbreak occurred only in autumn through epicormic shoot development, reducing the photosynthetically active period to 63 days compared to 220 days in *Early-budding* trees. This limited carbon assimilation window constrained root regeneration, which was delayed and at an earlier developmental stage than in *Early-budding* trees. A high proportion of pruned roots failed to regenerate entirely, and most exhibited upstream regeneration (Fig. 2c), indicating extensive distal tissue necrosis that was only halted by late-emerging new roots. Combined with minimal new root production and negligible wound closure (Table 1; Fig. 2), these conditions left *Late* trees functionally compromised, as reflected by their high mortality rate during the second year (Fig. 1). In *Declining* trees, neither

shoot emergence nor root regeneration occurred during the first year. Without absorbing roots, water uptake and carbon assimilation remained severely limited, resulting in progressive crown dieback, necrosis of pruned roots, negative trunk growth rates, and the highest mortality rate among all categories during the second year (Fig. 1).

However, surviving *Delayed-budding* trees formed the *Restructuring* category in the second year. These trees developed a few long, axialized polycyclic shoots, indicating partial crown reorganization, while otherwise exhibiting many traits typical of monocyclic trees: limited leaf area, low trunk growth rate, and a hairy root system with restricted wound closure (Table 1; Fig. 2). This coexistence of polycyclic shoots with otherwise limited growth may stem from the severe crown dieback experienced during the first year. We hypothesize that the loss of the upper crown altered the root-to-shoot balance and redirected assimilated carbon toward a reduced number of epicormic shoots located closer to the collar, where shorter hydraulic pathways may have facilitated polycyclic shoot development despite limited carbon resource availability.

The growth categories identified in this study produced distinct crown architectures that consistently reflected root system recovery (Fig. 1). This link is illustrated by two contrasting crown forms. Axialized crowns expanded in height through long polycyclic leaders, whereas foliarized crowns maintained an umbrella-like crown through exclusively short monocyclic shoots displaying a low-cost foliage (de Haldat du Lys et al. 2023). Axialized crowns were associated with tracing root systems and effective wound closure, whereas foliarized crowns corresponded to *hairy* root systems with limited regeneration (Table 1; Fig. 5). Crown architecture therefore reliably reflected root recovery status, confirming that above- and belowground development remain structurally coupled after transplanting (Laurans et al. 2024).

3. Aboveground traits as indicators of root system recovery.

The AFI developed in this study represents, to our knowledge, the first field-based index explicitly linking aboveground morphological traits to root system regeneration after transplanting. Different approaches to assess transplant recovery have relied on physiological traits (Philip et al. 2002; Ortuño et al. 2005; Martinez-Trinidad et al. 2010; Atherton et al. 2013; Uhrin and Supuka 2016; Andrianjara et al. 2024) or remote sensing methods (Song et al. 2016; Albuquerque et al. 2022; Choi and Song 2022; Morales-Gallegos et al. 2023), but these require sophisticated equipment and are often time-consuming, thus limiting their applicability for large-scale monitoring. Morphological traits such

as crown transparency (Borianne et al. 2017), shoot growth (Riikonen et al. 2011), or leaf characteristics (Levinsson et al. 2015) offer more practical alternatives through simple measurements. Although several of these traits have been proposed as indicators of tree vigor and health (Dobbertin 2005; Martinez-Trinidad et al. 2010; Grulke et al. 2020), none has been used to assess belowground recovery after tree transplant. The AFI addresses this limitation by integrating three aboveground traits into a standardized, non-destructive field tool that predicts root system recovery in operational settings.

The three traits retained in the AFI each capture a distinct and complementary dimension of post-transplant recovery. Budbreak timing carries a negative coefficient in the AFI, reflecting the detrimental effect of delayed reactivation. When budbreak is delayed, pruned roots remain without new root initiation for an extended period, allowing distal necrosis to progress from pruning wounds. This increases the proportion of unregenerated pruned roots and impairs wound closure, thereby lowering the RRS. Maximum annual shoot length integrates primary growth vigor over the growing season, with longer shoots indicating greater crown axialization sustained by water and nutrient uptake from new roots. Trunk growth rate reflects cambial activity and serves as an integrative indicator of plant performance, as it correlated positively with leaf area, annual shoot basal area, and new root basal area. Maximum shoot length and trunk growth rate thus capture meristematic performance following tree transplant. Together, these three traits integrate complementary functional dimensions of post-transplant response, namely the negative effect of reactivation delay, and the positive effect of both apical and cambial growth.

The AFI accurately predicted growth categories and root regeneration status (Fig. 4f). The few misclassifications involved vigorous *Mono* trees and less vigorous *Poly* trees, which share intermediate trait values. This overlap reflects the continuum between these two growth categories.

4. Applications, limitations, and perspectives.

The growth categories and the AFI developed in this study offer a practical framework for evaluating post-transplant recovery in operational settings, both in nursery production and in urban tree plantations, addressing the need for standardized assessment tools that go beyond survival rates (Levinsson et al. 2017). By identifying each tree's growth category and predicting its RRS, the AFI enables diagnosis of individual recovery status and supports targeted management decisions. At the plot scale, spatialization of AFI, or its predicted RRS values, can map root regeneration patterns across planting sites, revealing clusters of successful

recovery or stagnation zones where local edaphic conditions may warrant investigation and remediation. At the project scale, comparing the distribution of growth categories and mean AFI values across plantations provides a standardized basis for evaluating and benchmarking project outcomes. This multi-scale applicability makes the growth categories and the AFI a practical tool for diagnostic assessment and adaptive management of tree plantations.

Several methodological limitations should be acknowledged. First, although first-year excavations yielded adequate sample sizes, second-year samples remained modest for some categories because individual trees had grown larger, considerably increasing architectural description time. Despite these limited samples, second-year results followed a consistent gradient coherent with first-year patterns, reinforcing their biological plausibility. Second, the AFI coefficients were calibrated for young bare-root *Celtis australis*. Bare-root transplanting exposes the entire root system, whereas balled-and-burlapped or container stocks retain a growing medium avoiding desiccation, partially buffering transplant stress (Grossnickle 2012; Levinsson et al. 2014). Extending the AFI to other species, stock types, and developmental stages would require recalibrating the coefficients. However, the three underlying traits capture fundamental dimensions of post-transplant recovery, and only their relative weighting would need adjustment across contexts.

The growth categories and the AFI capture post-transplant recovery heterogeneity, but the factors driving this variability remain to be identified. Two main sets of explanatory factors can be distinguished. The first relates to individual tree structure at transplanting, shaped by cultural history during nursery production, which determines organization of both root and shoot systems, their root-to-shoot balance and the level of reserves available for recovery (Grossnickle 2005; Watson 2005; Struve 2009). The second relates to local soil conditions at the planting site. At transplanting, the quality of root-soil contact influences early root functioning, as discontinuities at the root-soil interface can restrict hydraulic conductivity and impair water uptake by pruned roots (Grossnickle 2012). Subsequently, edaphic conditions govern the seasonal availability of water and nutrients to regenerating roots. We hypothesized that post-transplant recovery depends on the interaction between these two sets of factors: trees with contrasting initial structures may respond differently under similar soil conditions, and conversely, a given tree structure may lead to different outcomes across varying edaphic environments. The RRS and AFI provide standardized response variables that make this causal framework testable through factorial analyses.

Conclusion

Our two-year monitoring of 600 transplanted *Celtis australis* trees demonstrated that post-transplant recovery heterogeneity can be reduced to a limited number of distinct, ordered growth patterns, each associated with specific root regeneration behaviors. Polycyclic trees achieved a balanced root-to-shoot ratio through coordinated above- and below-ground development, whereas monocyclic trees adopted a compensatory strategy prioritizing root regeneration over aerial expansion. These contrasting trajectories confirm that aboveground growth patterns reliably reflect belowground recovery status.

Building on this correspondence, the Aerial Field Index integrates three simple aboveground measurements into a standardized, non-destructive tool that predicts root system regeneration in operational settings. Together, the growth categories and the AFI provide a practical framework for evaluating transplant success beyond binary survival metrics, applicable to both nursery production and urban tree management. Further work is needed to extend this framework to other species, stock types, and developmental stages. More fundamentally, identifying the factors driving recovery heterogeneity represents the next step toward a predictive model of post-transplant tree establishment.

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Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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

Author Contribution Statement AdH, YC, and CA conceived the research project. AdH, EN, and YC prepared plant material prior to trans-

planting. AdH, ML, and EN collected data. AdH and ML performed data analysis. AdH and EN wrote the initial manuscript draft. EN, YC, and CA supervised the research and critically revised the manuscript.

Author Contributions All authors contributed to the study conception and design. Material preparation prior to transplanting was performed by Alexandre de Haldat, Éric Nicolini, and Yves Caraglio. Data collection was carried out by Alexandre de Haldat, Mathis Lecoq, and Éric Nicolini. Data analyses were performed by Alexandre de Haldat and Mathis Lecoq. The first draft of the manuscript was written by Alexandre de Haldat and Éric Nicolini and figures were prepared by Alexandre de Haldat. Éric Nicolini, Yves Caraglio, and Claire Atger supervised the project. All authors contributed substantially to manuscript revisions and approved the final version.

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