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**REVIEW**

# Variation Patterns of Absorptive Root Traits and Resource Acquisition Strategies of Representative Tree Species across Different Successional Stages in Subtropical Forests

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## ABSTRACT

The variation patterns of absorptive root functional traits and the differentiation of resource acquisition strategies among tree species during forest succession represent a critical scientific issue for understanding plant-soil interactions, community dynamics, and ecosystem functioning. This paper systematically reviews the multidimensional variation characteristics of absorptive root traits and their underlying ecological mechanisms in representative tree species across different successional stages in subtropical forests. Research demonstrates that functional traits of absorptive roots form a "root economics spectrum" through coordinated variation across morphological, anatomical, chemical, physiological, and symbiotic dimensions, reflecting the trade-off between resource acquisition efficiency and tissue persistence. Along the successional gradient, pioneer species exhibit an "acquisitive strategy" characterized by high specific root length (15–30 m/g), fine root diameter (0.3–0.6 mm), low tissue density (<0.30 g/cm³), high nitrogen content (15–25 mg·g$^{-1}$), and short lifespan (<1 year), whereas climax species display a "conservative strategy" featuring low specific root length, coarse root diameter, high tissue density (>0.40 g/cm³), low nitrogen content, and long lifespan. This directional differentiation is driven by environmental factors, including resource availability, competition intensity, and disturbance frequency, while simultaneously regulated by phylogenetic constraints and phenotypic plasticity. Root strategies exert

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cascading effects on ecosystem productivity, carbon sequestration, and stability through modulation of soil carbon and nitrogen cycling, nutrient availability, and resource acquisition efficiency. Under global change, the compound effects of factors such as climate warming, nitrogen deposition, and biodiversity loss may alter root strategy differentiation patterns and successional trajectories.

***Keywords:*** Absorptive Root Functional Traits; Forest Succession; Root Economics Spectrum; Resource Acquisition Strategies; Subtropical Forests; Plant-Soil Interactions

# 1. Introduction

As a critical interface for plant-soil interactions, tree root systems directly influence individual growth, interspecific competition, and community structure through water and mineral nutrient absorption, carbon allocation and storage, rhizosphere stoichiometric regulation, and interactions with microorganisms (particularly mycorrhizal fungi), thereby shaping ecosystem nutrient cycling and functional dynamics [1]. From a functional ecology perspective, root functional traits—such as specific root length (SRL), root diameter, root tissue density, cortex thickness, nitrogen/phosphorus content, lifespan and turnover rate, mycorrhizal type and hyphal abundance—collectively constitute the "root economics spectrum," reflecting the trade-off between resource acquisition efficiency and tissue persistence [2]. Generally, an "acquisitive" combination characterized by high SRL, fine diameter, and low tissue density facilitates rapid soil exploration and enhanced short-term absorption efficiency at relatively low per-unit carbon costs, but with high turnover rates and maintenance costs. Conversely, a "conservative" combination featuring coarse diameter, high tissue density, and long lifespan emphasizes structural robustness and stress tolerance, exhibiting lower absorption potential per unit length but maintaining functional stability under nutrient-scarce or stressful conditions. The spatiotemporal variations of these traits determine tree relative growth rate, survival rate, and competitive ability by regulating carbon-nutrient allocation (root-shoot trade-offs), water use, and photosynthesis-respiration balance, and feed back to soil organic matter formation and nutrient regeneration processes through rhizosphere carbon input and microbial metabolic activity, thereby driving ecosystem productivity and stability.

Along forest successional gradients, root functional traits exhibit directional stage-specific differentiation, a process tightly coupled with aboveground vegetation changes, soil environmental evolution, and resource availability dynamics. In early succession, pioneer tree species typically display an acquisitive strategy characterized by fine root diameter, high SRL, low tissue density, and rapid turnover to quickly occupy vacant ecological niches, emphasizing short-term resource acquisition and rapid growth to adapt to environmental characteristics of high light availability, pulsed nutrient supply, and intense disturbance. As succession progresses, canopy closure leads to dramatic declines in understory light availability, while soil organic matter accumulation and microbial community complexity enhance soil fertility but also intensify phosphorus fixation and interspecific resource competition [3]. Under these circumstances, late-successional species increasingly favor coarse root diameter, high tissue density, thick cortex, and long lifespan, coupled with stable and complex mycorrhizal networks to enhance resource retention and stress tolerance. This strategic shift from "rapid exploration-high turnover" to "robust maintenance-long lifespan" not only reshapes individual-scale carbon-nutrient economics but also modulates community succession rate and direction through alterations in litter quality, decomposition dynamics, and soil stoichiometry, ultimately affecting net primary productivity and soil carbon sequestration capacity. In subtropical regions, characteristics such as synchronized water-heat regimes, high species diversity, and frequent anthropogenic disturbances render forest succession multi-pathway and complex [4]. The systematic differentiation of root functional traits among representative tree species across different successional stages and their regulatory mechanisms on ecosystem functioning remain pressing scientific questions requiring in-depth investigation.

Despite significant advances in root functional ecology research in recent years, substantial knowledge gaps persist regarding definitional frameworks, functional differentiation, and turnover dynamics. First, classification criteria for absorptive roots remain inconsistent, with some researchers defining them by diameter (<2 mm), while others employ combined criteria based on anatomical structure, lifespan, and functional characteristics. This inconsistency constrains cross-species and cross-ecosystem comparative synthesis. Second, functional differentiation within absorptive roots is evident, as different branch orders (or age classes) within the same root system vary in their contributions to nutrient absorption, carbon storage, and mycorrhizal symbiosis. Younger terminal fine roots primarily undertake absorption functions, while older fine roots contribute more substantially to carbon storage and symbiotic maintenance [5]. However, systematic quantification of the relative contributions of different functional root types to ecosystem processes remains lacking. Furthermore, the dynamic regulatory mechanisms governing absorptive root lifespan and turnover rates require deeper investigation. Although existing studies indicate that environmental factors (temperature, moisture, nutrients) and biotic interactions (mycorrhizae, microbial communities, neighbor competition) jointly influence fine root lifespan and turnover, most studies remain dominated by single-factor or correlational analyses, with insufficient experimental and model-based testing of multifactor interactions and nonlinear effects. Particularly in successional gradient studies, existing work predominantly focuses on specific species or particular successional stages, lacking a systematic and comprehensive understanding of root trait differences among woody plants across successional stages, and often neglects interactions between root traits and soil environmental factors, which exert significant influences on root trait expression [6].

Based on the above understanding, systematically comparing root functional traits and nutrient acquisition strategies of representative tree species across different successional stages in subtropical regions holds substantial theoretical and practical significance for elucidating plant-soil feedback mechanisms, optimizing plantation management and close-to-nature silviculture, and enhancing the prediction reliability of forest structure and function under global change. This study focuses on the variation patterns of absorptive root functional traits across pioneer species (e.g., Pinus massoniana, Liquidambar formosana), transitional species (e.g., Schima superba, Symplocos), and climax species (e.g., Castanopsis carlesii, Cyclobalanopsis) during subtropical forest succession.

By integrating multidimensional indicators including morphology (root diameter, specific root length, tissue density), anatomy (cortex thickness, stele-root ratio), stoichiometry (C, N, P content and their ratios), and physiological and symbiotic attributes (root lifespan, mycorrhizal type and colonization rate), this study aims to address the following core scientific questions:

(1) What variation patterns do absorptive root functional traits exhibit among representative tree species at different successional stages?

(2) How do these trait variations reflect the successional differentiation between “acquisitive” and “conservative” resource strategies?

(3) What are the relative contributions of environmental drivers and phylogenetic constraints to root strategy differentiation?

(4) How do successional changes in root functional traits affect ecosystem functioning through regulation of soil carbon-nitrogen cycling and nutrient availability?

By addressing these questions, this study will enrich the application of root economics spectrum theory across successional ecology, deepen understanding of plant belowground resource utilization strategies, and provide scientific foundations for sustainable management, ecological restoration, and carbon sequestration enhancement of subtropical forests.

## 2. Framework of Absorptive Root Functional Traits and Environmental Drivers during Succession

### 2.1. Conceptual Framework and Functional Trait Architecture of Absorptive Roots

Research on functional differentiation of plant root systems has undergone a paradigm shift from coarse classification to refined categorization, a process that has profoundly transformed our understanding of belowground ecological processes. Traditional studies long relied on root diameter as the basis for classification, defining roots with diameters less than 2 mm or 0.5 mm as "fine roots," assuming that such roots possess similar properties and functions [7]. However, with deepening investigations into root structure and function, researchers gradually discovered that fine roots defined by diameter thresholds are not homogeneous units but rather heterogeneous systems composed of individuals exhibiting substantial differences in morphology, structure, and function. For example, among roots with diameters less than 2 mm, significant differences exist in carbon-nitrogen ratios across different diameter classes, with finer roots displaying markedly shorter lifespans than coarser roots. More critically, 70% of temperate tree species encompass the first five root orders within diameters less than 1 mm, including both terminal fine roots undertaking absorption functions and higher-order roots responsible for transport, which differ fundamentally in morphological characteristics, anatomical structure, and mortality processes [8]. Based on these insights, Pregitzer et al. proposed the root order classification method to recognize heterogeneity within fine roots. This method simulates river branching systems, defining the most terminal fine roots as first-order roots, with two first-order roots converging to form second-order roots, and so forth to higher orders. Research over the past decade has further confirmed that only non-woody, low-order roots (typically orders 1–2) possessing cortical cells and capable of mycorrhizal fungal colonization exhibit genuine absorptive function [9]. These absorptive roots dominate numerically, contribute disproportionately to surface area and length, exhibit high cortical proportions and mycorrhizal colonization rates, maintain elevated nutrient contents, and simultaneously display life history characteristics of short lifespan and rapid turnover, thereby constituting the core functional units for material exchange and energy flow at the plant-soil interface.

Comprehensive characterization of absorptive root functional traits requires integration of multidimensional indicators, as the diversity of nutrient and water resources, microorganisms, and other abiotic environmental factors in the soil environment where plant roots reside determines the multidimensional characteristics of absorptive root function and variation [10]. Morphological attributes represent the primary dimension for characterizing absorptive root function. Specific root length (SRL), defined as root length per unit biomass, not only correlates positively with nutrient absorption rate but also influences the total length and absorptive surface area of absorptive roots under given biomass allocation conditions, serving as a core indicator for assessing root resource acquisition efficiency [11]. Root diameter directly controls root length, root-soil contact area, and mycorrhizal colonization rate, thereby affecting a plant's capacity to acquire soil water and nutrients. Root tissue density (RTD) reflects dry matter content per unit volume of root tissue and is closely associated with root construction costs, lifespan, and decomposition resistance. Root branching intensity and topological structure determine spatial exploration patterns of root systems, with herringbone branching facilitating rapid forward exploration while dichotomous branching enhances precise localization of local nutrient patches [12]. Anatomical attributes further reveal associations between internal structure and function of absorptive roots. The ratio of cortex thickness to stele diameter (stele-root ratio) directly affects transport efficiency and storage capacity of roots, with higher stele-root ratios indicating stronger water conductance but weaker storage function. Regarding stoichiometric attributes, root C, N, and P contents and their ratios reflect plant nutrient utilization strategies and metabolic activity, with high N content typically associated with rapid growth and high metabolic activity, while high C:N ratios indicate conservative nutrient utilization strategies. Physiological and biological attributes include root lifespan, turnover rate, nutrient absorption kinetic parameters (maximum absorption rate Vmax and half-saturation constant Km), root respiration rate, and mycorrhizal type and colonization intensity, which directly reflect functional efficiency and ecological adaptability of absorptive roots [13].

These multidimensional functional traits do not exist in isolation but rather constitute the theoretical framework of the "root economics spectrum" through coordinated variation and trade-off relationships. The root economics spectrum reveals the differentiation pattern of absorptive root traits along the "acquisitive-conservative" continuum, wherein the acquisitive strategy is characterized by high SRL, fine diameter, low RTD, high N content, short lifespan, and rapid turnover, reflecting adaptations for rapid soil exploration and swift nutrient absorption at relatively low per-unit carbon costs, albeit at the expense of high maintenance costs and low stress resistance [14]. Conversely, the conservative strategy exhibits low SRL, coarse diameter, high RTD, low N content, long lifespan, and slow turnover, emphasizing tissue durability and resource retention capacity, adapted to nutrient-poor or stressful environments, but with lower short-term absorption efficiency per unit investment. This trade-off relationship demonstrates high consistency across species comparisons; for example, fine roots of fast-growing temperate tree species display smaller diameters and approximately twice the specific root length compared to slow-growing species, and angiosperm fine roots exhibit smaller average diameters than gymnosperms [15]. Mycorrhizal type, as an important dimension of the root economics spectrum, exhibits coordinated evolutionary relationships with root morphological attributes: arbuscular mycorrhizal (AM) tree species tend toward finer root diameters and higher autonomous absorption capacity, whereas ectomycorrhizal (EM) tree species typically possess coarser root diameters and stronger mycorrhizal dependence [16]. However, the universality of the root economics spectrum remains debated, with some studies finding that relationships between root tissue density and specific root length are not simply negative correlations, suggesting that root strategies may manifest as more continuous gradients rather than binary classifications [17]. This necessitates future research to validate the theoretical framework of the root economics spectrum across broader species and environmental gradients and to explore comprehensive trait spaces beyond the morphological-chemical two-dimensional plane.

Interspecific and intraspecific variation patterns in absorptive root functional traits hold critical significance for understanding species coexistence, niche differentiation, and community dynamics. Interspecific variation primarily stems from phylogenetic history and long-term evolutionary adaptation, with differences in root traits among species enabling the formation of diverse or complementary resource acquisition strategies, thereby reducing competition intensity and promoting species coexistence [18]. For example, tree species coexisting in the same community may exhibit differentiation in root vertical distribution, nutrient preferences, or mycorrhizal types, achieving spatial or resource-dimensional separation of belowground ecological niches [19]. Intraspecific variation (i.e., root plasticity) constitutes an important mechanism for plant adaptation to environmental changes, with the magnitude and direction of variation representing different species' capacity to respond to resource supply fluctuations, determining their environmental adaptability and geographic distribution ranges. Studies demonstrate that species with greater variation in root branching intensity in temperate grasslands can better cope with drought and consequently exhibit broader spatial distributions at regional scales. Plasticity levels differ significantly among root traits, with morphological traits (e.g., SRL, branching intensity) typically exhibiting high plasticity, while anatomical traits (e.g., cortical structure) and mycorrhizal types display strong phylogenetic conservatism. In successional gradient studies, distinguishing the relative contributions of interspecific differences and intraspecific plasticity is crucial for understanding the driving mechanisms of trait variation: if trait differences among successional stages are primarily driven by species replacement (interspecific variation), this reflects environmental filtering selecting for specific functional groups; if the same species exhibits significant trait adjustments across successional stages (intraspecific variation), this indicates the important role of phenotypic plasticity in adapting to environmental gradients [20].

## 2.2. Environmental Gradients and Resource Heterogeneity during Forest Succession

Forest succession, as a core process of ecosystem self-organization and recovery, is accompanied by systematic changes in aboveground vegetation structure, species composition, and environmental factors, which provide strong selective pressures for the successional differentiation of root functional traits. In subtropical regions, forest succession can typically be divided into four major stages: the pioneer stage (0–20 years) is characterized by high disturbance, open canopy, and bare soil, with abundant light but impoverished soil and severe water fluctuations; the early successional stage (20–40 years) experiences rapid canopy closure, dramatic declines in understory light availability, and intensified competition among standing trees; the mid-successional stage (40–80 years) exhibits pronounced structural differentiation, with species diversity reaching its peak and the establishment of understory regeneration layers; and the climax stage (>80 years) forms stable complex layered structures with relatively constant dominant species composition [21]. Representative tree species across different successional stages reflect the replacement patterns of functional groups: pioneer species such as Pinus massoniana and Liquidambar formosana rapidly occupy vacant ecological niches through high photosynthetic rates, rapid growth, and early reproductive maturity strategies; transitional species such as Schima superba and Symplocos spp. possess strong shade tolerance and phenotypic plasticity, enabling them to maintain competitive advantages during mid-successional stages [22]; climax species such as Castanopsis carlesii and Cyclobalanopsis glauca dominate in late succession through long lifespans, high tissue density, and conservative resource strategies. This stage-specific replacement of functional groups reflects not only the differentiation of aboveground life history strategies but is also closely associated with the coevolution of belowground root functional traits, jointly driving the successional trajectory of ecosystem functioning.

Changes in aboveground environmental gradients during succession impose multidimensional selective pressures on root functional traits, with light environment dynamics being the most prominent and far-reaching. In the pioneer stage, open canopies result in understory light intensity reaching 60–80% of full sunlight. High light availability promotes abundant photosynthetic carbon supply, enabling plants to allocate more resources to aboveground components to achieve rapid height growth, thereby gaining advantages in interspecific competition. As succession progresses to early and mid-stages, canopy closure gradually increases to 80–95%, understory light intensity plummets to 5–20% of full sunlight, and light quality undergoes significant alterations, with declining red/far-red ratios triggering shade avoidance responses in plants. These dramatic changes in light environment directly influence plant carbon allocation strategies: under high light conditions, plants tend to increase aboveground investment to maximize light capture, whereas under low light conditions, plants must balance the allocation trade-off of limited photosynthates between aboveground competition (height growth) and belowground resource acquisition (root development). Successional patterns of microclimatic factors are equally noteworthy. Canopy closure brings reduced understory temperatures (mean daily temperature decreases of 2–5 °C), increased air humidity (relative humidity increases of 10–25%), and weakened wind speeds, collectively creating a more stable microenvironment. This microclimatic buffering effect exerts dual influences on root growth and function: on one hand, reduced temperature fluctuations lower the risk of root exposure to frost or heat stress, extending the active growing period of roots; on the other hand, reduced transpirational pull may decrease water absorption pressure on roots, allowing plants to invest more metabolic resources in nutrient acquisition rather than water transport [23].

Soil environmental succession dynamics largely determine the selective direction of root functional traits, a process involving systematic restructuring of physical, chemical, and biological properties. Regarding soil physical properties, bare or semi-bare soils in early succession typically exhibit high bulk density (1.3–1.5 g/cm³), low porosity, and high root penetration resistance, limiting deep root expansion. With vegetation recovery and litter accumulation, soil organic matter content increases from 10–20 g/kg in early succession to 40–80 g/kg in mid-to-late succession, bulk density correspondingly decreases to 1.0–1.2 g/cm³, porosity increases to 50–60%, and soil water-holding capacity is significantly enhanced [24]. These improvements in physical properties provide more suitable growth media for roots, reducing mechanical resistance to root growth while enhancing soil water retention and buffering capacity. Soil chemical property succession exhibits asynchronous dynamics among nutrient elements: regarding nitrogen, soil total nitrogen content increases from 0.5–1.0 g/kg to 2.0–4.0 g/kg during succession, nitrogen mineralization rates increase, and inorganic nitrogen (ammonium + nitrate) availability is enhanced, significantly alleviating nitrogen limitation in late succession. However, phosphorus shows opposite trends. Although soil total phosphorus content changes little, under subtropical intensive weathering conditions, available phosphorus content gradually decreases from 5–15 mg $kg^{-1}$ in early succession to 2–8 mg $kg^{-1}$ in late succession due to fixation by iron and aluminum oxides, resulting in increasingly prominent phosphorus limitation in late succession [25]. Soil pH also exhibits dynamic changes across successional stages. Decomposition of acidic litter in the coniferous pioneer stage may cause pH to decline to 4.5–5.5, while with the invasion of broadleaf species and organic matter accumulation, pH may rise to 5.0–6.0. This chemical property successional gradient causes nutrient limitation types to shift from early-stage nitrogen-water co-limitation to late-stage phosphorus-nitrogen ratio imbalance, requiring plant roots to adopt corresponding nutrient acquisition strategies across different successional stages.

Successional changes in soil biological characteristics constitute the critical context for root-soil interactions, with stage-specific differentiation in microbial community structure, mycorrhizal fungal types, and soil enzyme activities profoundly influencing the expression and selection of root functional traits. Regarding microbial communities, the bacteria-to-fungi ratio exhibits a declining trend during succession, decreasing from 2–4 in the pioneer stage to 0.5–1.5 in the climax stage, reflecting enhanced fungal dominance and complexification of organic matter decomposition processes. This microbial community structural succession is both cause and effect of changes in root litter quality: high-nutrient, easily decomposable root litter in early succession promotes bacterial growth, whereas low-nutrient, high-lignin litter in late succession selects for fungal groups capable of lignocellulose degradation. Mycorrhizal fungi undergo significant type and functional transitions during succession. Early stages are dominated by arbuscular mycorrhizal (AM) fungi, whose rapid colonization and high turnover characteristics match the fast-growth strategies of pioneer species. As succession progresses, the relative abundance of ectomycorrhizal (EM) tree species (e.g., Pinus, Quercus) increases, with EM fungi enhancing acquisition of organic nitrogen and phosphorus through extramatrical hyphal networks and complex enzyme systems. Successional patterns of soil enzyme activities similarly reflect transitions in nutrient cycling strategies: phosphatase activity significantly increases in late succession to cope with declining phosphorus availability, while urease activity succession closely relates to nitrogen supply status. Spatiotemporal heterogeneity in resource availability shows an increasing trend during succession. Nutrient hotspots formed by litter decomposition, nutrient pulses released by root mortality, and water distribution differences caused by microtopography collectively constitute a complex belowground resource landscape [26]. This heterogeneity not only provides niche space for differentiation of root foraging strategies but also imposes higher demands on root plasticity and precise localization capabilities, ultimately driving the directional differentiation of root functional traits among tree species across different successional stages.

## 2.3. Selective Pressures of Environmental Gradients on Root Functional Traits

Resource availability gradients constitute the primary driving force for successional differentiation of root functional traits, with spatiotemporal patterns of soil nutrient and water dynamics at different successional stages imposing directional selective pressures on plant root strategies. In high-resource environments of early succession, relatively abundant light and pulsed nutrient supply (e.g., ash release after fire, residual fertilizer from abandoned cultivation) provide material foundations for rapid growth. Under these conditions, acquisitive strategies characterized by high specific root length (SRL) and low root tissue density (RTD) can achieve maximum soil exploration area with minimum carbon investment, rapidly capturing available nutrients. This strategy exhibits obvious growth advantages under high nutrient conditions because root biomass per unit can contact larger soil volumes, improving nutrient interception efficiency [27]. Meanwhile, lower mycorrhizal dependence enables pioneer species to directly absorb inorganic nutrients through high-density root hairs and active membrane transport systems, avoiding the carbon costs of allocating photosynthates to mycorrhizal fungi. However, as succession progresses to mid-to-late stages, although total soil nutrients increase, their availability decreases due to fixation effects, particularly the significant decline in phosphorus bioavailability. Under these circumstances, conservative strategies gradually gain dominance. Roots with coarse diameter, high RTD, and long lifespan, although exhibiting lower absorption efficiency per unit investment, can maintain positive carbon gains in low-nutrient environments by extending root longevity and improving nutrient resorption efficiency [28]. More critically, late-successional species typically establish stable symbiotic relationships with ectomycorrhizal (EM) or highly developed arbuscular mycorrhizal (AM) networks. Extramatrical hyphal extension (reaching tens of times root surface area) and organic nutrient decomposition capacity (through secretion of phosphatases, proteases, etc.) significantly enhance plant acquisition of recalcitrant nutrients. Successional gradients in water conditions similarly shape root functional trait differentiation patterns: in pioneer stages with frequent drought stress, deep root development and high root tissue density help resist water deficits, but this involves trade-offs with rapid growth strategies; whereas under microenvironmental stabilization brought by canopy closure in late succession, shallow surface roots can more effectively utilize nutrients released from litter decomposition, while higher air humidity reduces the necessity for deep root development [29].

Successional changes in interspecific competition intensity drive directional selection of root functional traits from another dimension, with competitive pressure manifesting both in belowground resource competition and in niche differentiation and coevolution. In early succession, low-density pioneer populations face the primary challenge of rapid space occupation rather than interspecific competition, with root expansion rate and soil exploration range becoming key factors determining individual fitness [30]. High SRL and well-developed shallow root systems enable pioneer species to rapidly form dense root networks, preemptively capturing surface soil nutrients and water resources—a "pre-emptive" strategy that confers significant advantages under low competition intensity. However, with community closure and increased stand density, interspecific competition in mid-to-late succession extends from aboveground light competition to belowground nutrient competition, with competition intensity increasing 3–5 fold [31]. Under high competitive pressure, the evolutionary direction of root functional traits shifts: on one hand, vertical niche differentiation becomes an important mechanism for alleviating competition, with different species achieving preferential utilization of resources in different soil layers by adjusting root depth distribution. For example, shallow-rooted species focus on nutrients released from surface organic matter decomposition, while deep-rooted species utilize a stable water supply from deep soils. On the other hand, enhanced precision foraging capacity becomes crucial. Late-successional species typically exhibit higher root branching plasticity and response sensitivity to nutrient-enriched patches, capable of rapidly increasing local root density upon detecting high-nutrient zones, achieving "precision strike" resource capture [32]. Successional adjustments in root architecture similarly reflect transitions in competitive strategies: pioneer species favor herringbone topological structures that maximize forward exploration speed, whereas late-successional species increasingly adopt dichotomous branching patterns that enhance the exploitation intensity of local resource patches [33]. Notably, belowground and aboveground competition involve trade-off relationships. In low-light late succession, plants must balance allocation of limited photosynthates between height growth (acquiring light resources) and root development (acquiring nutrients and water). This multidimensional resource competition pressure ultimately shapes comprehensive optimization patterns of root functional traits in morphology, physiology, and stoichiometry.

Disturbance frequency and intensity, as important drivers of forest succession, exert indirect but profound influences on root functional traits by altering resource pulses, selective pressures, and recovery trajectories. Frequent disturbances in high-disturbance stages (e.g., fire, typhoons, anthropogenic logging) create highly dynamic resource environments, with nutrients released in pulses and light conditions instantaneously improved. This environmental volatility selects for root trait combinations with rapid response capabilities. The short-lifespan, high-turnover root strategy of pioneer species enables them to rapidly exploit post-disturbance nutrient pulses: root rapid growth periods synchronize with nutrient release peaks, maximizing nutrient capture efficiency; simultaneously, high root turnover rates (1–3 times annually) ensure rapid regeneration even when roots are lost under unfavorable conditions. Storage root development represents another key adaptive feature. Some pioneer species accumulate carbohydrate and nutrient reserves in coarse roots or rhizomes, enabling rapid resprouting after aboveground damage through stored resources—a "pre-investment" strategy that confers obvious survival advantages in high-disturbance environments [34]. Conversely, in low-disturbance late succession, increased environmental stability reduces selective pressure for rapid recovery capacity, instead favoring long-term stable resource acquisition and stress resistance. Long-lived roots of climax species (mean lifespans of 2–3 years or longer) reduce carbon and nitrogen losses from turnover, exhibiting higher carbon use efficiency in stable environments. Successional increases in chemical defense investment similarly reflect adaptation to low-disturbance environments: high contents of phenolics, tannins, and lignin not only improve root decay resistance and disease resistance but also extend root lifespan, reducing biomass turnover required to maintain equivalent function [35].

The relative roles of phylogenetic constraints and phenotypic plasticity determine response patterns of root functional traits to successional environmental gradients, with this interaction between genetic foundation and ecological adaptation constituting a key dimension for understanding trait variation mechanisms. Phylogenetic analyses reveal that certain root traits (particularly anatomical structures and mycorrhizal types) exhibit strong phylogenetic signals, meaning closely related species are more similar in these traits, suggesting these traits are strongly constrained by evolutionary history. For example, systematic differences between angiosperms and gymnosperms in root diameter, cortex thickness, and mycorrhizal type partially stem from morphological-functional integration patterns accumulated during their divergence history [36]. This phylogenetic conservatism limits the distributional range of certain lineages along successional gradients, restricting them to successional stages matching their genetic potential. However, root morphological traits (e.g., SRL, branching intensity) exhibit high phenotypic plasticity, with the same species capable of significantly adjusting these traits under different successional stages or soil conditions to optimize resource acquisition efficiency [37]. The genetic basis of this plasticity involves complex networks of environmental perception, signal transduction, and developmental regulation. Local nutrient enrichment can trigger lateral root proliferation through hormonal signals (e.g., auxin polar transport), while drought stress promotes deep root growth through the abscisic acid pathway. The adaptive significance of phenotypic plasticity lies in expanding species' niche breadth, enabling survival and growth maintenance under resource fluctuations during succession, but this plasticity itself entails costs, including metabolic burdens of maintaining sensory systems and risks of inappropriate responses. In successional studies, distinguishing phylogenetic effects from environmental effects is crucial for understanding trait variation drivers: if species at different successional stages exhibit obvious phylogenetic differentiation (e.g., early stages dominated by Pinaceae, late stages by Fagaceae), observed trait differences partially stem from lineage replacement rather than pure environmental adaptation; conversely, if lineage composition remains relatively stable but trait expression changes significantly, this indicates environmental plasticity plays a dominant role in adapting to successional gradients.

# 3. Variation Patterns of Absorptive Root Traits among Representative Tree Species across Different Successional Stages

## 3.1. Successional Differentiation Patterns of Absorptive Root Morphological Traits

Root diameter, as the most fundamental and far-reaching trait among absorptive root morphological attributes, exhibits clear differentiation patterns among tree species at different successional stages, with this differentiation directly linked to root resource acquisition strategies and carbon investment efficiency. Absorptive roots (orders 1–2) of pioneer species such as Pinus massoniana and Liquidambar formosana typically have mean diameters concentrated in the 0.3–0.6 mm range. The fine root diameter characteristic confers geometric advantages of high surface area-to-volume ratios, enabling root systems per unit biomass to contact larger soil volumes, achieving rapid interception in early successional environments with pulsed nutrient supply. The carbon economics foundation of this fine root diameter strategy lies in lower construction costs: under equivalent biomass investment, fine root systems can produce root length and surface area several times that of coarse root systems, thereby obtaining higher absorption efficiency returns per unit carbon input [38]. Studies of temperate tree species indicate that interspecific differences in first-order fine root diameter can reach 2.5-fold, while differences further expand to 3.3-fold and 12-fold in subtropical and tropical tree species, reflecting the intensity of root morphological differentiation under different climatic zones and successional stages. In contrast, absorptive roots of climax species such as Castanopsis carlesii and Cyclobalanopsis glauca exhibit significantly increased diameter, with mean ranges of 0.6–1.2 mm. Although coarse root diameter reduces surface area per unit investment, it brings improvements in structural stability and mycorrhizal colonization potential. Research reveals that coarser roots are more readily colonized by ectomycorrhizal (EM) fungi, whereas arbuscular mycorrhizal (AM) fungi tend to colonize finer roots. This coordinated evolutionary pattern of mycorrhizal type and root diameter holds functional significance during succession: the fine root-low mycorrhizal dependence combination of pioneer species emphasizes autonomous absorption, whereas the coarse root-high mycorrhizal dependence combination of climax species enhances acquisition of organic nutrients through hyphal networks. Notably, interspecific variation in root diameter is influenced both by phylogenetic history (angiosperms have smaller mean diameters than gymnosperms) and by environmental conditions (the same tree species may reduce root diameter in infertile soils to improve exploration efficiency). Therefore, diameter differentiation observed along successional gradients results from the combined effects of genetic constraints and ecological adaptation [39].

Specific root length (SRL), defined as root length per unit root dry weight, comprehensively reflects the influences of root morphology and tissue density on resource acquisition efficiency, exhibiting trends opposite to root diameter along successional gradients. Absorptive roots of pioneer species typically possess a high SRL of 15–30 m/g, a trait combination enabling maximum soil exploration range with minimum biomass investment, conferring obvious advantages in high-light, pulsed-nutrient environments of early succession. The ecological advantage of high SRL manifests not only in the spatial exploration dimension but also in positive correlation with nutrient absorption rates: studies show that for every 10 m/g increase in SRL, nitrogen absorption rate per unit root can increase by 15–25%, a positive correlation stemming from greater absorptive surface area and higher membrane transporter protein density [40]. Additionally, the rapid turnover characteristics of high-SRL roots (mean lifespan 3–9 months) enable pioneer species to flexibly adjust belowground resource allocation, rapidly proliferating roots during nutrient-enriched periods and recovering nutrients through root senescence during nutrient-scarce periods, achieving dynamic tracking of dynamic resource environments [41]. As succession progresses to mid-to-late stages, SRL of representative tree species exhibits a gradual declining trend, with typical values of climax species decreasing to 5–15 m/g, reflecting a shift from “rapid exploration” to “long-term maintenance” strategies. Although low SRL reduces soil exploration capacity per unit investment, it enhances root structural robustness, decay resistance, and lifespan (extending to 1–3 years) by increasing root tissue density (typically from 0.2 g/cm³ to 0.4–0.6 g/cm³). In late successional environments with intense nutrient competition and relatively stable resources, this conservative strategy achieves superior long-term carbon gains through reduced maintenance costs and improved nutrient resorption efficiency. The relationship between SRL and root absorptive surface area is also modulated by root hair development. Some pioneer species further amplify the absorptive advantages of high SRL through high-density root hairs (which can increase effective absorptive area 2–10 fold), whereas late-successional species may rely more on extramatrical hyphae rather than root hairs to increase absorptive interfaces. This transition in absorption strategies has profound implications for stoichiometry and carbon allocation patterns [42].

Root tissue density (RTD), defined as dry matter content per unit root volume, serves as a key bridging trait connecting root morphology with chemical composition, lifespan, and turnover, with its successional differentiation pattern revealing fundamental transitions in carbon investment strategies. Absorptive roots of pioneer species typically maintain RTD at relatively low levels of 0.15–0.30 g/cm³. Low tissue density signifies higher cortical proportions, larger intercellular spaces, and lower degrees of cell wall thickening. This “loose” tissue structure, although reducing mechanical strength, confers advantages of rapid construction, high metabolic activity, and strong plastic responses. The rapid construction characteristics of low-RTD roots enable completion of the entire process from root primordium initiation to functional maturity within days to weeks, rapidly responding to nutrient pulses or favorable microenvironments. Simultaneously, loose tissue structure accommodates more living cells and metabolic enzymes, supporting high rates of nutrient absorption and material transport. However, the cost of low RTD is a short lifespan and low stress resistance: for every 0.1 g/cm³ decrease in tissue density, mean root lifespan may shorten by

20–40%, with resistance to pathogens and soil fauna also significantly declining [43]. RTD of late-successional species significantly increases to 0.30–0.60 g/cm³. High tissue density confers roots with stronger decay resistance, stress resistance, and longevity extension by increasing cell wall thickness, secondary metabolite deposition (e.g., lignin, tannins), and structural carbohydrate (cellulose) content [44]. This high-RTD strategy demonstrates adaptability in low-nutrient, high-competition late successional environments: although construction is slower (possibly requiring weeks to months), it ultimately achieves superior life-cycle carbon use efficiency through extended functional periods and improved nutrient resorption efficiency (recovering 50–70% of root nitrogen and phosphorus) [45]. The relationship between RTD and carbon investment efficiency is also reflected in carbon content differences per unit volume: high-RTD roots may contain 0.15–0.25 g carbon per cubic centimeter, whereas low-RTD roots contain only 0.06–0.15 g. This difference directly affects root carbon input quantity and stability to soil as a carbon source, subsequently influencing ecosystem carbon cycling through root-microbe-soil feedbacks [46].

Root branching architecture, as the spatial organizational dimension of absorptive root morphological attributes, exhibits architectural differentiation matching resource exploration strategies among tree species at different successional stages. Pioneer species typically display high branching intensity (5–15 lateral roots produced per centimeter of mother root) and dense branching networks. This "multi-branch, short lateral root" combination pattern maximizes root spatial occupancy density in surface soils, forming dense root networks to intercept nutrient leaching and rapidly deplete available resource pools [47]. Regarding branching topological structure, pioneer species favor herringbone patterns, where lateral roots extend forward from mother roots at larger angles. This architecture maximizes forward exploration speed and probability of contacting new soil, conferring obvious advantages in low-competition, high resource heterogeneity early successional environments. Conversely, late-successional species exhibit lower branching intensity (2–8 lateral roots/cm) but longer individual lateral roots, forming "few-branch, long lateral root" sparse networks. This architecture achieves resource acquisition through deep exploration and precision targeting in environments with relatively uniform resources and intense competition [48]. Topologically, climax species increasingly adopt dichotomous branching, with lateral roots bifurcating at smaller angles. Although this architecture reduces forward advancement speed, it enhances exploitation intensity and residence time in local nutrient-enriched zones, conforming to the "intensive cultivation" foraging strategy of late succession [49]. Plastic responses in branching architecture similarly reflect successional stage differences: pioneer species primarily respond to nutrient patches by increasing branch number, whereas late-successional species tend to extend existing lateral root length rather than proliferating new roots. This differentiation in response patterns stems from trade-offs in carbon allocation priorities and construction costs [50].

### 3.2. Successional Differentiation Patterns of Absorptive Root Anatomical Traits

The anatomical structure of absorptive roots, as a critical level connecting external morphology with intrinsic physiological functions, exhibits systematic differentiation in tissue composition and spatial configuration among tree species at different successional stages that matches resource transport, storage, and symbiotic strategies. The cortex, as the outermost parenchyma tissue of absorptive roots, exhibits successional changes in thickness and proportion that directly influence root storage capacity, mycorrhizal colonization space, and material exchange efficiency. Absorptive root cortex of pioneer species such as Pinus massoniana and Liquidambar formosana is relatively thin, typically comprising 40–55% of root diameter. This lower cortical proportion signifies a relatively larger stele proportion (higher stele-root ratio), enabling roots to allocate more tissue resources to transport structures such as vessels and vascular bundles to support rapid water and nutrient transport to aboveground parts [51]. The functional significance of the thin cortex strategy is also reflected in reducing radial transport resistance: nutrients traverse fewer cell layers from root epidermal cells through the cortex to reach the stele, shortening material diffusion pathways and improving overall absorption-transport efficiency [52]. Additionally, cortical cells of pioneer species are typically smaller and densely arranged, with lower intercellular space proportions (10–20%). This compact structure, although limiting gas exchange, enhances the mechanical support function of the cortex, enabling fine root systems to maintain basic morphological stability during rapid growth. Conversely, absorptive roots of late-successional species such as Castanopsis carlesii and Cyclobalanopsis glauca exhibit significantly thickened cortex, with proportions of root diameter increasing to 55–70%. Thick cortex confers multiple functional advantages: First, expanded cortical space provides containers for accumulation of storage materials such as starch granules and lipids, enabling roots to store resources during nutrient-abundant periods and mobilize reserves under unfavorable conditions to maintain basic metabolism [53]; Second, thick cortex provides more ample space for mycorrhizal fungal colonization and establishment, particularly the Hartig net of ectomycorrhizal (EM) fungi, which primarily develops in cortical intercellular spaces. Increased cortex thickness directly expands the plant-fungal interface, enhancing carbon-nutrient exchange capacity [54]. Third, cortical cells of late-successional species are typically larger with well-developed intercellular spaces (reaching 25–40%). This loose structure, although reducing tissue density, promotes rhizosphere gas exchange and root respiration efficiency, conferring adaptive significance in late successional environments with higher soil porosity [55]. A significant positive correlation exists between cortex thickness and root diameter (r = 0.65–0.85). This association is constrained both geometrically (coarse roots have greater absolute space to accommodate thick cortex) and reflects functional integration (coordinated evolution of coarse root-thick cortex-high mycorrhizal dependence).

The stele-root ratio (ratio of stele diameter to root diameter), as a key indicator quantifying internal structural allocation of root systems, exhibits successional change patterns revealing trade-off relationships between transport efficiency and storage capacity and their ecological adaptive significance. Absorptive roots of pioneer species typically maintain stele-root ratios at relatively high levels of 0.30–0.45. A high stele-root ratio signifies that roots allocate relatively more cross-sectional area to stelar tissue, particularly vascular tissues such as xylem vessels and phloem sieve tubes. This allocation pattern maximizes the axial transport capacity of roots. The hydraulic advantage of a high stele-root ratio lies in reducing resistance to water ascent: according to the Hagen-Poiseuille law, hydraulic conductivity is proportional to the fourth power of vessel radius. Pioneer species, by maintaining a larger stele diameter (even with relatively fine overall roots), can accommodate relatively large vessels, achieving efficient water transport to support rapid transpiration and photosynthesis. Regarding nutrient transport, larger vascular bundle cross-sectional area similarly increases phloem sieve tube number and material flux, enabling rapid transport of photosynthates from leaves to roots, supporting rapid root growth and turnover. However, the cost of a high stele-root ratio is a relative reduction in storage space: under constant root diameter conditions, higher stele proportion means lower cortical proportion, limiting accumulation capacity for reserve materials. This trade-off makes pioneer species more dependent on real-time absorption rather than reserve mobilization in resource-fluctuating environments. As succession progresses, the stele-root ratio of representative tree species exhibits a declining trend, with typical values of climax species decreasing to 0.20–0.35. Low stele-root ratio reflects a strategic shift from “high-flux transport” to “storage-buffering” functions. Late-successional species expand storage capacity for carbohydrates and nutrients by reducing the stele proportion and increasing the cortical proportion. This storage capacity provides important buffering in environments with decreased nutrient availability and increased competitive pressure: plants can mobilize root reserves to maintain aboveground growth during short-term nutrient supply shortages, avoiding growth stagnation due to nutrient limitation. Notably, successional changes in stele-root ratio are also associated with root lifespan: lower stele-root ratio typically accompanies longer root lifespan, possibly because physical protection and enhanced chemical defense provided by thicker cortex improve root stress resistance and durability [56].

Anatomical characteristics of water-conducting structures, particularly xylem vessel diameter, number, and spatial arrangement patterns, exhibit differentiation patterns matching water use strategies among tree species at different successional stages, profoundly influencing the trade-off between root hydraulic efficiency and safety. Xylem of absorptive roots in pioneer species typically possesses vessels with larger diameters (mean diameter 15–30 μm) but relatively fewer numbers (5–15 per square mm cross-section). This “fewer but coarser” vessel configuration pattern maximizes hydraulic conductivity per unit cross-sectional area [57]. The advantage of large-diameter vessels lies in the fact that, according to the Hagen-Poiseuille law, doubling vessel diameter increases hydraulic conductivity 16-fold (fourth-power relationship), enabling pioneer species to maintain an adequate water supply under high transpiration demand, supporting their rapid growth strategy. However, the large vessel strategy entails significant hydraulic safety risks: larger vessel diameter increases vulnerability to cavitation and embolism, particularly when encountering drought stress or freeze-thaw cycles, where air bubbles more readily form in large vessels and block water transport [58]. This hydraulic vulnerability matches the habitat characteristics of pioneer species: relatively abundant water supply in early succession reduces the frequency of severe drought, making the high-efficiency, low-safety vessel configuration still favorable in risk-benefit trade-offs. Water-conducting structures of late-successional species exhibit opposite patterns: vessel diameter significantly decreases (mean 10–20 μm), but numbers increase substantially (15–40 per mm²), forming a “many but fine” configuration. Although small-diameter vessels reduce hydraulic conductivity per individual vessel, they partially compensate for losses in total hydraulic conductivity by increasing vessel numbers. More critically, they significantly enhance hydraulic safety: small vessels have more negative cavitation critical pressures (as low as −3 to −6 MPa), enabling roots to maintain function under more severe water deficit conditions [59]. Additionally, a multi-vessel configuration provides redundancy protection mechanisms, such that even if some vessels experience embolism, remaining vessels can maintain basic water transport, avoiding catastrophic hydraulic failure. Successional increases in xylem proportion represent another important trend: xylem typically comprises 30–45% of stele area in pioneer species, increasing to 45–60% in late-successional species. Development of secondary xylem and enhanced lignification not only improve root mechanical strength and lifespan but also enhance hydraulic redundancy by increasing total vessel numbers [60].

Coupling relationships between root anatomical structure and morphological traits constitute a key dimension for understanding absorptive root functional integration and successional differentiation. Coordinated variation of these multi-level traits is constrained both by phylogeny and responsive to environmental selective pressures. Cross-species comparative studies reveal strong positive correlations between root diameter and cortex thickness (r = 0.75–0.90). This association partially stems from geometric necessity: under the premise of maintaining a certain stele-root ratio, increases in root diameter inevitably accompany increases in absolute cortex thickness. However, the strength of this correlation exceeds expectations of pure geometric effects, suggesting functional integration plays an important role: coarse roots typically undertake more storage and mycorrhizal symbiotic functions, requiring a thicker cortex to provide spatial support, whereas fine roots emphasize absorption-transport efficiency, maintaining relatively higher stele-root ratios to optimize resource flow. Constraint effects of anatomical traits on morphological traits manifest in multiple dimensions: increases in cortical proportion typically lead to decreases in root tissue density (RTD) because cortical parenchyma cell density (0.1–0.3 g/cm³) is significantly lower than xylem sclerenchyma cell density (0.4–0.8 g/cm³); increases in stele-root ratio may reduce overall tissue density by increasing proportions of cavity structures such as vessels [61]. These anatomical-morphological coupling relationships exhibit coordinated variation along successional gradients: the fine root diameter-thin cortex-high stele-root ratio-low RTD combination of pioneer species supports acquisitive strategies, whereas the coarse root diameter-thick cortex-low stele-root ratio-high RTD combination of climax species matches conservative strategies. Phylogenetic conservatism analyses show that anatomical traits exhibit stronger phylogenetic signals compared to morphological traits (Blomberg’s K values: anatomical traits 0.6–1.2, morphological traits 0.3–0.7), suggesting anatomical structures are more strongly constrained by evolutionary history with relatively weaker plastic response capacities [62]. The ecological significance of this difference lies in the fact that morphological traits, as “first responders,” can rapidly adjust to adapt to environmental fluctuations, whereas anatomical structures, as “stable frameworks,” maintain basic functional characteristics of species. The coordination and decoupling of both jointly determine plant adaptive capacity and distribution range along successional gradients [63].

### 3.3. Successional Differentiation Patterns of Absorptive Root Chemical Traits

Root nitrogen content, as a core chemical trait reflecting plant metabolic activity and growth rate, exhibits differentiation patterns tightly coupled with resource acquisition strategies among tree species at different successional stages. Absorptive root nitrogen content of pioneer species such as Pinus massoniana and Liquidambar formosana typically maintains relatively high levels of 15–25 $mg \cdot g^{-1}$. The metabolic foundation of high nitrogen investment lies in nitrogen being a key element constituting metabolically active components such as enzyme proteins, membrane transport proteins, and ribosomes. Elevated root nitrogen content directly enhances the synthetic capacity of nutrient absorption enzymes (e.g., nitrate reductase, phosphate transporters) and membrane transport system activity, thereby supporting high-rate nutrient absorption and rapid growth. Studies show that for every 5 $mg \cdot g^{-1}$ increase in absorptive root nitrogen content, maximum nutrient absorption rate (Vmax) can increase by 20–35%, with root respiration rate synchronously increasing 15–25%, reflecting the "high input-high return" characteristics of the high-nitrogen strategy [64]. However, the trade-off cost of high nitrogen content manifests in shortened root lifespan: a significant negative correlation exists between nitrogen content and root longevity ($r = -0.55$ to $-0.75$). High-nitrogen roots are more susceptible to attack by microorganisms and soil fauna due to their abundance of easily decomposable organic matter, while lower investment in defense compounds further reduces decay resistance [65]. This short-lifespan characteristic accelerates high-nitrogen root turnover rates (1–3 times annually), which, although increasing nutrient cycling rates and responsiveness to pulsed resources, also elevates carbon-nitrogen turnover losses. As succession progresses to mid-to-late stages, root nitrogen content of representative tree species exhibits a declining trend, with typical values of climax species decreasing to 8–15 $mg \cdot g^{-1}$. The low-nitrogen strategy reflects a transition from "rapid acquisition" to "nutrient conservation". Low-nitrogen roots reduce maintenance costs per unit time by lowering metabolic intensity and respiratory consumption, enabling roots to maintain longer functional periods (1–3 years or longer) in late successional environments with decreased nutrient availability. More critically, late-successional species develop efficient nitrogen resorption mechanisms, capable of recovering 50–70% of nitrogen before root senescence. This internal cycling strategy significantly reduces dependence on exogenous nitrogen, conferring obvious adaptive advantages in late succession where nitrogen supply is relatively stable but phosphorus limitation intensifies [66]. Successional changes in root nitrogen content are also coupled with soil nitrogen availability: in early succession, soil nitrogen mineralization rates are low but pulsed, with high-nitrogen root strategies enabling pioneer species to rapidly capture brief nitrogen supply peaks; in late succession, total soil nitrogen pools increase with relatively stable supply, with the low-nitrogen, long-lifespan strategy achieving adequate nitrogen acquisition through sustained absorption, reflecting dynamic trait-environment matching.

Successional differentiation in root phosphorus content and acquisition mechanisms reflects plant adaptive responses to intensifying phosphorus limitation in subtropical highly weathered soils, involving comprehensive adjustments in morphological, physiological, and symbiotic strategies. In early succession, relatively high available phosphorus content (5–15 $mg \cdot kg^{-1}$ soil) supports moderately high to high root phosphorus content in pioneer species (1.5–3.0 $mg\ g^{-1}$), enabling them to meet high growth rate demands through rapid inorganic phosphorus absorption. Phosphorus acquisition in pioneer species primarily relies on high-affinity phosphate transporters on root surfaces (e.g., PHT1 family). These transporters maintain effective absorption even under low phosphorus concentrations (micromolar levels), coupled with high specific root length strategies to achieve rapid interception of free phosphate in soil solution. However, as succession progresses, phosphorus fixation by iron and aluminum oxides gradually intensifies, with soil available phosphorus content declining to 2–8 $mg\ kg^{-1}$ while total phosphorus content changes little, resulting in significantly decreased phosphorus availability. This intensifying phosphorus limitation drives significant differentiation in phosphorus acquisition strategies of late-successional species: although root phosphorus content declines to 1.0–2.0 $mg\ g^{-1}$, insufficient inorganic phosphorus supply is partially compensated through the development of organic phosphorus utilization capacity. Rhizosphere phosphatase secretion represents a key adaptive mechanism, with rhizosphere acid phosphatase activity of late-successional species reaching 2–5 times that of pioneer species. These extracellular enzymes can hydrolyze soil organic phosphorus compounds (e.g., inositol phosphate, nucleic acids) to release inorganic phosphorus for plant absorption [67]. Organic acid secretion represents another important strategy. Climax species roots can release low molecular weight organic acids such as citrate and oxalate, promoting desorption of adsorbed phosphorus through chelation of iron and aluminum ions, or enhancing phosphorus solubility by lowering rhizosphere pH. The role of mycorrhizal fungi in phosphorus acquisition significantly strengthens with succession. Hyphal networks of ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi can expand absorptive surface area 10-100 fold, with extramatrical hyphae capable of exploring soil micropores inaccessible to roots, while phosphatases and organic acids secreted by mycorrhizal fungi further enhance the utilization efficiency of organic and recalcitrant phosphorus. Successional decline in root phosphorus content is also associated with improved phosphorus use efficiency: late-successional species maintain basic growth under lower phosphorus investment by reducing tissue phosphorus requirements (e.g., substituting lipids for phospholipids), improving phosphorus resorption efficiency (recovering 40–60% of phosphorus), and extending root lifespan (reducing turnover losses) [68].

Successional patterns of root stoichiometry (C:N:P) comprehensively reflect coordinated plant responses to multi-element limitation and fundamental shifts in growth strategies, with this stoichiometric differentiation exhibiting cascading effects at individual, population, and ecosystem scales. Absorptive root C:N ratios of pioneer species typically maintain relatively low levels of 20–35. Low C:N ratios indicate high nutrient content and rapid growth strategies, conforming to predictions of the Growth Rate Hypothesis: rapid growth requires abundant ribosomes to support protein synthesis, and ribosomes are rich in ribosomal RNA (rRNA), whose high phosphorus content and low C:N ratio characteristics cause rapidly growing tissues to exhibit low C:N:P ratios. C:P ratios of pioneer species are similarly low (150–300), reflecting high phosphorus demand and relatively adequate supply. N:P ratios (mass ratios) typically range from 8–15, approaching or slightly below the Redfield ratio (14:1), suggesting relatively balanced nitrogen-phosphorus or slight phosphorus limitation [69]. These stoichiometric characteristics enable pioneer species to achieve rapid material turnover and growth accumulation in high-resource environments, but at the cost of high sensitivity to nutrient supply fluctuations and low buffering capacity. As succession progresses, C:N ratios of representative tree species gradually increase to 40–70, with C:P ratios increasing to 400–800, reflecting transitions toward low nutrient content, conservative strategies [70]. The ecological significance of high C:N and high C:P ratios lies in reducing tissue nutrient requirements, decreasing dependence on exogenous nutrients, while simultaneously enhancing tissue durability and decomposition resistance by increasing proportions of structural carbohydrates (cellulose, lignin) and secondary metabolites. Successional changes in N:P ratios exhibit first declining then rising trends: from early to mid-succession, as soil nitrogen accumulation rates exceed phosphorus availability enhancement rates, N:P ratios may rise from 10 to 15–20, indicating intensifying phosphorus limitation; but in late succession, plants partially alleviate phosphorus limitation by developing efficient phosphorus acquisition and utilization mechanisms, with N:P ratios potentially stabilizing at 15–18. Successional differentiation in stoichiometric homeostasis also deserves attention: pioneer species exhibit lower homeostasis coefficients ($H < 3$), meaning root stoichiometry is responsive to soil nutrient ratios, capable of flexibly adjusting tissue composition according to resource supply; whereas late-successional species exhibit higher homeostasis coefficients ($H > 4$), maintaining relatively stable tissue stoichiometry. This strict regulatory capacity, although reducing plasticity, ensures stability and predictability of metabolic processes [71].

Successional accumulation patterns of secondary metabolites and defense compounds reveal dynamic adjustments in plant resource allocation trade-offs between growth and defense, profoundly influencing root lifespan, decomposition dynamics, and contributions to soil carbon-nitrogen cycling. Defense compound investment in absorptive roots of pioneer species is relatively low, with total phenolic content typically 20–50 mg $g^{-1}$, condensed tannin content 5–15 mg $g^{-1}$, and lignin content 8–15% of dry weight. This low defense investment strategy stems from rapid growth priority principles: in resource-abundant, low-competition early succession, preferentially allocating limited photosynthates to growth and reproduction rather than defense maximizes fitness gains [72]. The direct consequence of low defense compound content is enhanced root decomposability: decomposition rate constants (k values) of pioneer species root litter can reach 0.8–1.5 year$^{-1}$, with half-lives of only 6–9 months. Although rapid decomposition accelerates nutrient release and recycling, it also shortens the residence time of root-derived carbon in soil, limiting contributions to stable carbon pools. Defense investment of late-successional species increases significantly, with total phenolic content rising to 60–120 mg g$^{-1}$, condensed tannins to 20–40 mg g$^{-1}$, and lignin content reaching 20–30%. High defense compound content confers roots with stronger decay resistance and disease resistance [73]. Phenolic compounds such as tannins reduce tissue degradability by forming complexes with proteins and cell wall polysaccharides, while the highly polymerized structure of lignin represents a major obstacle to microbial decomposition. These chemical defense mechanisms significantly extend root lifespan (1–3 years) and reduce litter decomposition rates (k values 0.2–0.5 year$^{-1}$). Enhanced decomposition resistance exerts dual effects on soil carbon sequestration: on one hand, slow decomposition extends the mean residence time of organic carbon in soil, favoring formation of stable carbon pools such as humus; on the other hand, recalcitrant litter may inhibit microbial activity and nutrient mineralization, reducing nutrient availability in the short term [74]. Functional redundancy and synergistic effects exist between chemical defense and physical defense (high tissue density, thick cell walls): late-successional species typically exhibit both high RTD and high defense compound content simultaneously. This “double insurance” strategy, although increasing carbon investment costs, achieves positive net benefits in low-resource, high-stress environments by significantly extending root lifespan.

## 3.4. Successional Differentiation Patterns of Absorptive Root Physiological and Symbiotic Attributes

Root lifespan and turnover rate, as key physiological attributes connecting root structure and function, exhibit differentiation patterns highly consistent with resource acquisition strategies among tree species at different successional stages. This differentiation directly determines root carbon-nitrogen turnover fluxes and ecosystem nutrient cycling rates. Absorptive roots of pioneer species such as Pinus massoniana and Liquidambar formosana exhibit typical short lifespan-high turnover characteristics, with mean lifespans typically of 3–9 months, with some fine roots completing 2–3 turnover cycles within a growing season. The ecological advantage of the short-lifespan strategy lies in high resource allocation flexibility: roots can rapidly adjust belowground biomass allocation according to spatiotemporal changes in soil resources, rapidly proliferating roots in nutrient-enriched patches or favorable seasons to maximize absorption efficiency, while recovering nutrients through root senescence (resorbing 30–50% of nitrogen and phosphorus) under resource scarcity or unfavorable conditions, avoiding metabolic burdens of maintaining inefficient roots [75]. However, the cost of high turnover rates manifests in carbon-nitrogen turnover losses: each root death event is accompanied by 30–50% irrecoverable nutrient loss and total structural carbon input to soil. Annual turnover rates of 1.5–3 times mean that maintaining equivalent functional root biomass requires annual production inputs several times those of low-turnover species [76]. Determinants of root lifespan involve multidimensional interactions: in the morphological dimension, roots with fine diameter, high SRL, and low RTD typically exhibit shorter lifespans ($r = 0.55–0.75$), a correlation stemming both from increased tissue vulnerability and reflecting functional strategy integration; in the chemical dimension, high nitrogen content and low defense compound investment significantly shorten root lifespan because roots rich in easily decomposable organic matter are more susceptible to attack by microorganisms and soil fauna [77]; in the environmental dimension, soil temperature, moisture, and nutrient availability regulate lifespan by affecting root growth rates and senescence processes, with every 10 °C temperature increase potentially shortening root lifespan by 20–40%. Late-successional species such as Castanopsis carlesii and Cyclobalanopsis glauca exhibit opposite lifespan-turnover patterns, with mean absorptive root lifespans extending to 1–3 years or longer and annual turnover rates declining to 0.3–0.8 times. The long-lifespan strategy significantly reduces carbon-nitrogen turnover losses by lowering turnover frequency: assuming equivalent nutrient resorption efficiency (50%), reducing turnover rate from 2 times/year to 0.5 times/year can reduce turnover losses to one-quarter of the original, conferring critical adaptive significance in late successional environments with low nutrient availability [78]. Maintenance of long-lived roots depends on synergistic effects of multiple protection mechanisms: physical strength provided by high RTD, buffering effects of thick cortex, chemical resistance from high defense compound content, and protective effects of stable mycorrhizal symbiosis jointly extend functional periods [79].

Nutrient absorption kinetic parameters, as core indicators quantifying root physiological function, exhibit successional differentiation patterns revealing fine-tuned plant adaptations to soil nutrient supply patterns and fundamental differences in absorption strategies. Nutrient absorption processes typically follow Michaelis-Menten kinetics, describable by two key parameters: maximum absorption rate (Vmax) reflects root absorption potential under high-concentration nutrient conditions, while the half-saturation constant (Km) indicates root affinity for low-concentration nutrients (lower Km values indicate higher affinity) [80]. Absorptive roots of pioneer species typically exhibit high Vmax-high Km kinetic characteristics. For example, nitrate absorption Vmax in Pinus massoniana seedlings can reach 15–30 $\mu mol \cdot g^{-1} \cdot h^{-1}$, with Km values of 50–150 μM. This parameter combination enables rapid absorption under relatively high nutrient concentrations, fully exploiting pulsed nutrient supply (e.g., nitrogen mineralization peaks after rainfall, ash release after fire) [81]. The physiological foundation of high Vmax lies in high expression density and activity of membrane transport proteins (e.g., nitrate transporter NRT family, phosphate transporter PHT family). This high-investment strategy requires substantial ATP consumption and maintenance of higher root nitrogen content to support transporter synthesis, thus matching the high metabolism-rapid growth strategy of pioneer species [82]. However, high Km values mean low absorption efficiency under low-concentration conditions (e.g., nitrate nitrogen concentration in soil solution is typically below 10 μM), a trade-off reflecting specialized adaptation to high-resource environments. Late-successional species exhibit low Vmax-low Km kinetic patterns, with nitrate absorption Vmax of climax species potentially declining to 5–15 $\mu mol \cdot g^{-1} \cdot h^{-1}$, but Km values synchronously decrease to 10–50 μM. The high-affinity characteristics of low Km enable maintenance of effective absorption under low-concentration conditions, adapting to environmental characteristics of relatively stable but lower concentration nutrient supply in late succession [83]. The molecular basis of this kinetic transition involves switching of transporter types: from low-affinity, high-capacity transport systems (LATS) to high-affinity, low-capacity transport systems (HATS). Although the latter have lower maximum transport rates, their absorption efficiency is significantly higher than the former when substrate concentration approaches Km values [84]. Root respiration rate, as another key physiological indicator, similarly exhibits successional differentiation: mass-specific respiration rates of absorptive roots in pioneer species can reach 80–150 nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$, declining to 30–80 nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$ in late-successional species. Declining respiration rates reflect reduced metabolic activity and maintenance cost savings, enabling long-lived roots to maintain basic functions under lower carbon investment [85].

Mycorrhizal symbiosis, as the core form of plant-fungal mutualistic relationships, undergoes significant transitions in type, colonization rate, and functional characteristics during forest succession. This successional differentiation in symbiotic strategies profoundly influences plant nutrient acquisition capacity and carbon allocation patterns. In early succession, arbuscular mycorrhizal (AM) fungi dominate, with symbioses formed between pioneer species such as Liquidambar formosana and AM fungi characterized by rapid colonization and high turnover, with mycorrhizal colonization rates typically in the 30–60% range [86]. AM fungal hyphal structures are relatively simple (aseptate, coarser diameter), primarily establishing material exchange interfaces with root cortical cells by forming arbuscules. The advantage of this symbiotic type lies in rapid establishment (completing colonization within weeks) and relatively low demands on plant carbon allocation (10–20% of total photosynthetic carbon), matching the rapid growth and high aboveground investment strategies of pioneer species. AM fungi primarily enhance plant acquisition of phosphorus (particularly inorganic phosphorus), with extramatrical hyphal growth (reaching 5–10 times root surface area) significantly expanding the effective absorption range for phosphorus, while hyphally secreted phosphatases promote organic phosphorus mineralization [87]. However, AM fungi have relatively limited capacity for utilizing organic nitrogen and phosphorus, with functions mainly concentrated on spatial capture of inorganic nutrients rather than enzymatic decomposition of complex organic compounds. As succession progresses, the importance of ectomycorrhizal (EM) tree species gradually rises, particularly in coniferous species (e.g., late-stage Pinus massoniana, Cunninghamia) and some Fagaceae species (e.g., Quercus, Castanopsis), with EM fungi becoming the dominant symbiotic type and colonization rates reaching 60–90%. EM fungi form fungal mantles enveloping root tips and Hartig nets penetrating cortical intercellular spaces. This increased structural complexity is accompanied by expanded functional diversity: EM fungi not only substantially increase nutrient absorption interfaces through extramatrical hyphae (reaching 50–100 times root surface area), but more critically, their secreted diverse extracellular enzymes (proteases, chitinases, phenol oxidases, etc.) can decompose complex organic compounds (e.g., proteins, chitin, lignin-tannin complexes), releasing organic nitrogen and phosphorus for plant utilization. This organic nutrient utilization capacity confers critical advantages in late successional environments with low inorganic nutrient availability, enabling EM species to effectively utilize nutrient reserves in soil organic matter pools. The cost of EM symbiosis is higher carbon allocation demands (up to 20–30% of total photosynthetic carbon), but through extending stability of symbiotic relationships (mycorrhizal structures can persist for years) and enhancing nutrient acquisition efficiency, long-term carbon gains remain positive. Successional transitions in mycorrhizal types also co-evolve with root morphological attributes: AM tree species favor morphological combinations of fine root diameter and high SRL to maintain certain autonomous absorption capacity, whereas EM tree species exhibit strategies of coarse root diameter, low SRL but high mycorrhizal dependence, achieving functional optimization of carbon investment by “outsourcing” nutrient absorption functions to mycorrhizal fungi [88].

## 3.5. Integrated Variation Patterns of Absorptive Root Functional Traits

Coordinated variation patterns of absorptive root functional traits in multidimensional space constitute the core framework for understanding the root economics spectrum and successional differentiation. Multivariate statistical methods such as principal component analysis reveal the dominant axes driving trait variation and their ecological significance. Comprehensive analysis based on 96 woody tree species in subtropical regions shows that variation in root functional traits can be explained by 2–3 principal components accounting for 60–75% of total variation. The first principal component (PC1) typically represents the “acquisitive-conservative” strategy spectrum, with traits exhibiting the highest loadings including specific root length (SRL), root tissue density (RTD), root nitrogen content, root diameter, and root lifespan. These traits exhibit highly coordinated variation patterns along the PC1 axis [89]. Specifically, pioneer species positioned at the positive end of PC1 display combinations of high SRL (>20 m/g), low RTD (<0.30 g/cm³), high N content (>18 mg $g^{-1}$), fine root diameter (<0.5 mm), and short lifespan (<1 year), reflecting rapid acquisition strategies achieving maximum absorption efficiency with minimum carbon investment. Conversely, climax species at the negative end exhibit combinations of low SRL (<12 m/g), high RTD (>0.40 g/cm³), low N content (<12 mg $g^{-1}$), coarse root diameter (>0.7 mm), and long lifespan (>2 years), embodying conservative strategies of tissue durability and resource retention [90]. The second principal component (PC2) primarily reflects the mycorrhizal dependence strategy axis, with root diameter, mycorrhizal colonization rate, and cortex thickness exhibiting high loadings on this axis, revealing trade-offs between autonomous absorption and mycorrhizal assistance among different species: fine root diameter-low colonization rate combinations emphasize direct absorption, whereas coarse root diameter-high colonization rate combinations rely on extramatrical exploration by mycorrhizal hyphae. The third principal component may be associated with chemical defense strategies, with coordinated variation in phenolic, tannin, and lignin contents reflecting plant resource allocation trade-offs between growth and defense. This structured variation in multidimensional trait space suggests that although root functional traits span morphological, anatomical, chemical, and physiological levels, they do not evolve independently but rather form a few coordinated trait syndromes through functional integration. These syndromes represent adaptive optimization to different resource environments and ecological niches during long-term evolutionary processes [91].

Convergence and divergence patterns of root functional traits along successional gradients reflect the relative roles of environmental filtering and niche differentiation. This dynamic balance shapes community functional structure at different successional stages. Functional trait convergence manifests in both early and late succession but with different mechanisms: in the pioneer stage, strong environmental filtering (high light availability, pulsed nutrients, frequent disturbance) selects species with rapid acquisitive trait combinations. Even when these species are phylogenetically distant (e.g., Pinus massoniana from Pinaceae and Liquidambar formosana from Hamamelidaceae), key traits of their absorptive roots, such as SRL, RTD, and N content, still tend toward similarity, with relatively narrow trait variation ranges (coefficient of variation CV = 15–25%). This convergence pattern supports the environmental filtering hypothesis, indicating that abiotic selective pressures dominate community assembly during early successional stages [92]. In late succession, trait convergence reappears, but the driving force shifts toward biotic interactions: intense interspecific competition promotes convergence in resource acquisition strategies among coexisting species to fully exploit the limited and relatively homogeneous resource supply. For example, multiple climax species develop conservative combinations of low SRL-high RTD-long lifespan and highly developed mycorrhizal networks. In contrast, functional trait divergence is most pronounced in mid-succession, when species diversity reaches its peak, and environmental heterogeneity coexists with competitive pressure, promoting different species to occupy different positions in trait space to achieve niche differentiation [93]. For example, mid-successional stages may simultaneously harbor shallow-rooted, high-SRL surface nutrient exploiters; deep-rooted, low-SRL deep water exploiters; and coarse-rooted, high mycorrhizal-dependent organic nutrient specialists. This enhancement of trait diversity reflects resource differentiation and complementary utilization, representing an important mechanism maintaining high species coexistence [94]. Dynamic transitions between trait convergence and divergence also exhibit heterogeneity across spatial scales: at microhabitat scales (e.g., beneath individual canopies), competition-driven trait divergence may predominate; whereas at landscape scales, trait convergence driven by environmental gradients (e.g., soil texture, slope aspect) is more prominent.

Analysis of the relative contributions of interspecific and intraspecific variation reveals the weighting of genetic differentiation and phenotypic plasticity in trait successional changes. This decomposition is crucial for understanding trait variation drivers and predictive capacity. Variance partitioning analyses indicate that in total variation of absorptive root functional traits, interspecific differences typically contribute 60–85% of variation, while intraspecific variation (including among- and within-individual variation) contributes 15–40%, suggesting that phylogenetic history and species replacement are dominant factors driving trait changes along successional gradients. Variation partitioning patterns differ significantly among traits: anatomical traits (e.g., cortex thickness, stele-root ratio) and mycorrhizal types exhibit the highest proportions of interspecific variation (>80%), displaying strong phylogenetic conservatism. These traits evolve slowly and are primarily constrained genetically. Chemical traits (e.g., N, P content) show relatively balanced interspecific and intraspecific variation (50–70% vs 30–50%), reflecting moderate genetic control and environmental responsiveness. Morphological traits (e.g., SRL, branching intensity) exhibit the highest proportions of intraspecific variation (up to 40–50%), displaying strong phenotypic plasticity [95]. The ecological significance of intraspecific variation lies in expanding species niche breadth, enabling adjustment of trait expression under resource fluctuations during succession: for example, individuals of the same tree species may exhibit higher SRL and N content in high-nutrient soils while reducing these traits in infertile soils to conserve resources. However, intraspecific plasticity itself is genetically regulated, with plasticity levels differing several-fold among species. Transitional species (e.g., Schima superba) typically exhibit higher trait plasticity than specialized species (e.g., extreme pioneers or climax species), with this flexibility enabling distribution across multiple successional stages. When predicting plant responses to environmental changes, contributions of both species replacement (achieving functional adjustment through changes in species composition) and intraspecific adjustment (responding to environmental changes through phenotypic plasticity) must be considered simultaneously. Ignoring intraspecific variation may underestimate community adaptive potential by 20–40%. Future research should strengthen exploration of the genetic basis of intraspecific variation (e.g., quantitative trait locus QTL mapping) and ecological consequences (e.g., effects on fitness) to deepen understanding of multilevel drivers of trait variation mechanisms [96].

# 4. Ecological Mechanisms of Root Resource Acquisition Strategies and Ecosystem Functions

## 4.1. Differentiation Mechanisms of Root Resource Acquisition Strategies among Tree Species at Different Successional Stages

The "rapid acquisitive" resource strategy of pioneer species constitutes the functional foundation for rapid space occupation and growth in early succession. This strategy achieves optimized adaptation to high-light, pulsed-resource environments through multidimensional integration of morphological-physiological-chemical-symbiotic attributes. At the morphological level, absorptive roots of pioneer species such as Pinus massoniana and Liquidambar formosana exhibit combinations of high specific root length (15–30 m/g), fine root diameter (0.3–0.6 mm), and high branching intensity. This "multi-branched, fine root system" spatial configuration enables unit carbon investment to generate maximum soil exploration area, achieving rapid localization and interception in early successional environments with patchy nutrient distribution. Herringbone branching topology further optimizes forward exploration speed, enabling root systems to occupy extensive new soil within weeks, preemptively depleting available resource pools [97]. Predominant distribution of shallow roots (70–80% of root mass concentrated in the 0–20 cm soil layer) matches the rapid turnover characteristics of surface nutrients, particularly during the spatiotemporal window of ash deposition and initial organic matter decomposition, releasing nutrients after fire or cultivation abandonment [98]. Regarding physiological mechanisms, the rapid acquisition strategy relies on support from high nutrient absorption rates (Vmax) and high metabolic activity: nitrate Vmax of pioneer species absorptive roots can reach 15–30 $\mu mol \cdot g^{-1} \cdot h^{-1}$. This high absorption potential stems from high expression density and optimized active site configuration of membrane transport proteins (NRT, PHT families). Rapid root turnover (annual turnover rates of 1–3 times, mean lifespan 3–9 months) enables roots to dynamically track resource pulses: rapidly proliferating roots to maximize capture efficiency during nutrient-enriched periods, while recovering nutrients through root senescence (resorption rates 30–50%) and reducing maintenance costs during nutrient-scarce periods. High root respiration rates (80–150 $nmol\ CO_2 \cdot g^{-1} \cdot s^{-1}$), although increasing carbon consumption, support active material synthesis and energy conversion, enabling roots to rapidly respond to favorable conditions [99]. Regarding chemical and symbiotic characteristics, high nitrogen investment (15–25 $mg\ g^{-1}$) ensures adequate synthesis of metabolic enzymes and transport proteins, while low defense compound content (total phenolics 20–50 $mg\ g^{-1}$) preferentially allocates photosynthates to growth rather than defense, embodying "offensive" resource allocation priorities. Relatively low dependence on arbuscular mycorrhizal (AM) symbiosis (colonization rates 30–60%, carbon allocation 10–20%) maintains high autonomous absorption capacity, avoiding response lag that may result from excessive symbiont dependence. The ecological adaptive significance of this rapid acquisition strategy lies in maximizing relative growth rate (RGR) during early successional stages: through efficient capture of pulsed resources and rapid material turnover, pioneer species can complete life histories from seedling to reproductive individual within years, rapidly producing offspring and dispersing to new habitats, achieving fitness maximization under "r-selection" strategies. However, costs of this strategy manifest in low stress resistance and high maintenance costs: fine root systems are susceptible to drought and mechanical damage, high turnover rates lead to significant carbon-nitrogen turnover losses, with survival disadvantages becoming prominent under resource fluctuations or intensified competition [100].

The "conservative storage" resource strategy of climax species represents deep adaptation to low-resource, high-competition, high-stress environments in late succession. This strategy achieves long-term ecological advantages through extending tissue lifespan, improving resource use efficiency, and enhancing stress resistance. Morphologically, absorptive roots of climax species such as Castanopsis carlesii and Cyclobalanopsis glauca exhibit combinations of low specific root length (5–15 m/g), coarse root diameter (0.6–1.2 mm), high tissue density (0.30–0.60 g/cm³), and thick cortex (comprising 55–70% of root diameter). This "robust" root system, although exhibiting lower exploration efficiency per unit investment, achieves synergistic optimization of multiple functions by enhancing structural robustness, expanding storage space, and providing mycorrhizal colonization sites. Low branching intensity (2–8 lateral roots/cm) and dichotomous branching patterns enable roots to concentrate resources into deep exploration by a few major lateral roots rather than extensive surface coverage. This vertical niche expansion downward both acquires stable deep water and alleviates surface interspecific competition. Increased proportions of deep roots (30–40% of root mass distributed in the 20–60 cm soil layer) match the homogenization trend of vertical nutrient distribution in soil profiles during late succession. Regarding physiological mechanisms, the core of the conservative strategy lies in extending resource retention time rather than increasing instantaneous acquisition rates: long root lifespan (1–3 years or longer) reduces carbon-nitrogen turnover losses to one-quarter to one-fifth of rapid acquisitive types by lowering turnover frequency. Kinetic parameters of low nutrient absorption rates (Vmax 5–15 $\mu mol \cdot g^{-1} \cdot h^{-1}$) but high affinity (low Km values 10–50 μM) enable roots to maintain stable absorption under low-concentration conditions, adapting to the "trickle" mode of nutrient supply in late succession [101]. High nutrient resorption efficiency (N, P recovery rates reaching 50–70%) significantly reduces dependence on exogenous nutrients through internal cycling, maintaining positive nutrient balance in environments with declining nutrient availability. Low root respiration rates (30–80 nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$) reduce maintenance costs, enabling long-lived roots to achieve superior cumulative carbon investment returns over their life cycles compared to short-lived roots. Transitions in chemical and symbiotic characteristics further reinforce conservative strategies: low nitrogen content and high C:N ratios (40–70) reduce tissue nutrient requirements, while high defense compound investment confers roots with strong decay resistance and disease resistance, significantly extending lifespan and reducing decomposition rates. Establishment of ectomycorrhizal (EM) or highly developed AM networks (colonization rates 60–90%) "outsources" nutrient acquisition functions to mycorrhizal hyphae, with their extramatrical exploration range (reaching 50–100 times root surface area) and organic nutrient decomposition capacity (through secretion of proteases, phosphatases, etc.) greatly enhancing utilization efficiency of recalcitrant and organic nutrients [102]. Although mycorrhizal maintenance requires higher carbon allocation (20–30% of photosynthetic carbon), long-term carbon gains are significantly positive through extending the stability of symbiotic relationships (years) and enhancing absolute quantities of nutrient acquisition. The ecological adaptive significance of this conservative strategy lies in achieving fitness maximization under "K-selection" strategies: through long lifespan, low mortality, and stable resource acquisition, climax species can maintain populations in competitive, resource-limited late succession, and gradually replace pioneer species through superior shade tolerance and stress resistance, ultimately dominating communities.

Intermediate strategies of transitional species and multiple drivers of root strategy differentiation jointly reveal the complexity of trait evolution and multidimensional regulatory mechanisms during succession. Mid-successional dominant species such as Schima superba and Symplocos exhibit intermediate states in root functional traits between rapid acquisition and conservative strategies: SRL of 12–20 m/g, RTD of 0.25–0.40 g/cm³, root lifespan of 0.8–2 years. This intermediate position does not simply represent trait averaging but rather reflects adaptive optimization to the complex environments of transitional successional stages. The core advantage of transitional species lies in high phenotypic plasticity and functional flexibility: capable of tilting toward rapid acquisition strategies (increasing SRL and N content) in resource-rich microhabitats, while shifting toward conservative strategies (increasing RTD and defense investment) in infertile or highly competitive microhabitats. This "strategy switching" capacity results in niche breadths significantly larger than specialized species. Dual mycorrhizal symbiotic capacity (simultaneously establishing symbiosis with both AM and EM fungi) represents a unique advantage of some transitional species, enabling flexible utilization of functional strengths of different mycorrhizal types according to soil conditions: relying on AM for inorganic phosphorus acquisition under phosphorus limitation, while utilizing organic nitrogen through EM under nitrogen limitation. Environmental drivers of root strategy differentiation exhibit multilevel interactions: soil nutrient availability selects corresponding strategies by directly affecting cost-benefit ratios of nutrient absorption, water conditions influence water acquisition efficiency by regulating root vertical distribution and tissue density, interspecific competition drives trait divergence by promoting niche differentiation, while disturbance frequency regulates strategy selection by altering optimal lifespan-turnover combinations [103]. Phylogenetic constraints, as intrinsic factors, limit the achievable strategy ranges of certain lineages: for example, Pinaceae find it difficult to evolve extremely rapid acquisition strategies due to their anatomical structural characteristics (coarse vessels, thick cortex), while certain pioneer families (e.g., Salicaceae) are limited in transitions toward extremely conservative strategies due to a lack of EM symbiotic capacity. Phenotypic plasticity itself is also genetically regulated and involves costs. Excessive plasticity may lead to the "jack-of-all-trades, master of none" trap, preventing species from achieving the competitiveness of specialists in any environment. Therefore, root strategy differentiation observed along successional gradients results from the combined effects of genetic constraints, environmental selection, biotic interactions, and historical contingencies. Understanding this multifactor regulation is crucial for predicting community dynamics and functional responses under global change scenarios.

### 4.2. Effects of Root Functional Traits on Ecosystem Processes and Functions

Root attributes exert profound influences on soil carbon cycling by regulating the quantity, quality, and spatiotemporal distribution patterns of belowground carbon inputs. These influences exhibit significant differentiation across successional stages due to differences in root strategies. Root carbon input pathways include fine root production, root turnover mortality, root exudate release, and rhizodeposition. These processes collectively contribute 30–60% of total soil organic carbon inputs, even exceeding aboveground litter contributions in some ecosystems. The high-turnover strategy of pioneer species (annual turnover rates of 1–3 times), although increasing carbon flux from root death release (reaching 150–300 g $C \cdot m^{-2} \cdot year^{-1}$), results in relatively short carbon residence time in soil due to the easy decomposability of their root litter (decomposition rate constant $k = 0.8–1.5\ year^{-1}$, half-life 6–9 months), with most rapidly returning to the atmosphere through microbial respiration, contributing limitedly to stable carbon pools. The high flux (10–20% of net photosynthetic carbon) and easy availability (rich in simple sugars, organic acids) of pioneer species root exudates strongly stimulate microbial activity, triggering rhizosphere priming effects: fresh carbon inputs accelerate microbial decomposition of old carbon (soil organic matter), increasing rhizosphere soil carbon mineralization rates by 20–50%. This priming effect may lead to net losses of soil carbon pools in early succession. Conversely, the low-turnover strategy of climax species (annual turnover rates of 0.3–0.8 times) reduces annual root carbon input flux (80–150 g $C \cdot m^{-2} \cdot year^{-1}$), but high defense compound content (lignin 20–30%, total phenolics 60–120 mg $g^{-1}$) significantly delays decomposition ($k = 0.2–0.5\ year^{-1}$, half-life 1.5–3.5 years), allowing more root-derived carbon opportunities for microbial transformation into stable carbon pools such as humus. The low flux (5–10% of net photosynthetic carbon) and complex composition (rich in high molecular weight compounds, phenolics) of climax species root exudates reduce priming effect intensity, potentially even producing "negative priming" by inhibiting microbial activity. Mycorrhizal fungi play dual roles in carbon cycling: on one hand, mycorrhizal carbon allocation (20–30% of photosynthetic carbon) represents significant belowground carbon flow, with the low turnover and recalcitrance of ectomycorrhizal (EM) hyphae making them important sources of stable carbon pools; on the other hand, extracellular enzymes secreted by mycorrhizal fungi may accelerate organic matter decomposition, producing "mycorrhizal priming" similar to priming effects. Deep-root carbon inputs hold critical significance for subsoil carbon accumulation: 30–40% of root mass in late-successional species is distributed in the 20–60 cm soil layer. Turnover of these roots provides carbon sources to deep soils, where lower oxygen concentrations and microbial activity result in significantly lower carbon decomposition rates than surface layers, favoring long-term carbon sequestration.

Root attribute regulation of nutrient cycling involves multiple processes, including absorption, turnover, release, and rhizosphere activation, exhibiting functional differentiation matching nutrient limitation types along successional gradients. Regarding nitrogen cycling, root nitrogen absorption directly affects nitrogen availability by consuming soil inorganic nitrogen pools ($NH_4^+$, $NO_3^-$): high absorption rates (Vmax 15–30 $\mu mol \cdot g^{-1} \cdot h^{-1}$) and rapid growth of pioneer species enable them to rapidly deplete surface inorganic nitrogen during the growing season (reducing concentrations by 50–80%), limiting nitrogen leaching losses but also intensifying interspecific nitrogen competition. Nitrogen released through root turnover (via root death and decomposition) constitutes an important link in soil nitrogen cycling: high nitrogen content (15–25 mg $g^{-1}$) and rapid turnover of pioneer species result in annual nitrogen return amounts reaching 8–15 g $N \cdot m^{-2}$, rapidly mineralizing due to easy decomposability (nitrogen release half-life 3–6 months), forming rapid internal nutrient cycling. However, rapid mineralization also increases risks of nitrogen losses (e.g., gaseous losses from nitrification-denitrification, rainfall leaching). Low nitrogen content (8–15 mg $g^{-1}$) and slow turnover of late-successional species reduce annual nitrogen return amounts (3–8 g $N \cdot m^{-2}$), but enhance nitrogen retention capacity through high resorption efficiency (50–70%) and slow release (nitrogen release half-life 1–2 years), reducing losses. Rhizosphere microbially-mediated nitrogen transformation processes are similarly influenced by root traits: high carbon supply in pioneer species rhizospheres stimulates microbial nitrogen fixation (free-living nitrogen fixers) and nitrogen mineralization, whereas phenolic compounds in climax species rhizospheres may inhibit nitrification, reducing nitrate nitrogen leaching risks. Rhizosphere regulation of phosphorus cycling is particularly critical in late succession: as soil available phosphorus declines, the importance of rhizosphere phosphorus activation mechanisms (organic acid secretion, phosphatase release, mycorrhizal hyphal exploration) increases. Rhizosphere acid phosphatase activity of climax species can reach 2–5 times that of pioneer species, increasing organic phosphorus mineralization rates by 30–80%, partially compensating for insufficient inorganic phosphorus supply. Extramatrical extension of mycorrhizal hyphae (particularly EM hyphae) not only expands phosphorus absorption range but also creates microenvironments of high phosphorus activation within the hyphosphere through secreted phosphatases and organic acids, significantly enhancing the utilization efficiency of recalcitrant phosphorus. Successional adjustments in stoichiometry (C:N:P ratio changes) influence decomposer communities and nutrient mineralization patterns by altering litter quality: low C:N litter of pioneer species (20–35) promotes bacteria-dominated rapid decomposition, whereas high C:N litter of climax species (40–70) selects for fungi-dominated slow decomposition. These two decomposition pathways differ fundamentally in nutrient immobilization-release dynamics.

Root attributes exert cascading effects on ecosystem productivity and stability by influencing plant carbon allocation patterns, resource acquisition efficiency, and functional trait diversity. Successional changes in root: shoot ratios reflect carbon allocation trade-offs between above- and belowground components: low root: shoot ratios of pioneer species (0.2–0.3) invest more photosynthates into aboveground growth to maximize light capture and height competition advantages, whereas high root: shoot ratios of late-successional species (0.4–0.6) emphasize enhancement of belowground resource acquisition and storage capacity. Differences in allocation patterns directly affect whole-plant carbon balance and growth rates: under high-light, high-nutrient conditions, low root: shoot ratio strategies achieve higher relative growth rates (RGR) through optimized light energy utilization; whereas under low-light, low-nutrient conditions, high root: shoot ratio strategies maintain positive carbon gains through enhanced resource acquisition capacity. Associations between root traits and aboveground growth manifest as significant correlations in interspecific comparisons: high-SRL species typically possess higher RGR ($r = 0.45–0.65$), lower wood density, and shorter leaf lifespan, forming a “fast” whole-plant economics spectrum; whereas low-SRL species are associated with slow growth, high wood density, and long leaf lifespan in a “slow” economics spectrum. Effects of functional trait diversity on ecosystem function are most prominent in mid-succession: diversified root strategies (shallow-deep roots, fast-conservative, AM-EM) enhance total community productivity through resource differentiation and complementary utilization. This positive “diversity-productivity" effect can increase mixed forest productivity by 15–30% compared to monospecific stands. Functional redundancy plays key roles in maintaining ecosystem stability: when a functional group (e.g., rapid acquisitive species) suffers damage from stresses such as drought, other functional groups (e.g., conservative species) can partially compensate for functional losses, buffering ecosystem responses. However, excessive functional convergence may reduce redundancy, decreasing ecosystem resistance and resilience to disturbances—a concern particularly relevant during trait convergence phases in early and late succession.

### 4.3. Root Strategy Responses and Adaptations under Global Change

Climate change imposes multidimensional selective pressures on root functional traits and resource acquisition strategies by altering temperature, precipitation patterns, and atmospheric $CO_2$ concentrations. These influences exhibit differentiated response patterns among tree species at different successional stages. Warming effects on roots exhibit duality: on one hand, temperature increases directly accelerate root growth and metabolic rates, increasing root productivity by 15–40% and extending root growing seasons by 2–4 weeks. This promoting effect is more pronounced in rapidly growing pioneer species during early succession, as their high metabolic activity is more sensitive to temperature responses. On the other hand, warming synchronously increases root respiration rates ($Q_{10}$ values typically 2–3) and turnover rates, shortening mean root lifespan by 10–30%. This negative effect is relatively weaker in conservative species because their low metabolic baseline and high tissue density provide certain temperature buffering. Warming may also alter root vertical distribution: rapid surface soil temperature increases (reaching 3–5 °C) promote root migration to deeper, cooler soil layers, potentially increasing deep root proportions by 20–35%. This response manifests as significant distribution deepening in shallow-rooted pioneer species, while adjustment amplitudes are relatively smaller in deep-rooted climax species. Effects of altered precipitation patterns on root strategies are more complex: increased drought frequency selects for drought-tolerant trait combinations such as deep root systems, high root tissue density, and thick cortex. These traits are already relatively well-developed in late-successional species, conferring relative advantages under aridification scenarios. Extreme precipitation events (e.g., soil saturation from heavy rainfall) may damage shallow root systems, reducing pioneer species competitiveness, but their high root regeneration capacity (rapid turnover) provides certain recovery resilience. Elevated $CO_2$ concentrations typically promote root biomass allocation: root:shoot ratios can increase by 20–40% under doubled $CO_2$ conditions. This "root enhancement" effect is more pronounced in pioneer species because their rapid growth strategies can more fully exploit increased photosynthetic carbon supply. However, $CO_2$ effects are strongly constrained by nutrient limitation: under nitrogen-phosphorus limitation, increased photosynthates cannot be effectively converted to biomass growth. Enhanced root carbon allocation may primarily manifest as increased root C:N ratios (rising 10–30%) and increased root exudates, the latter potentially intensifying rhizosphere priming effects and accelerating soil organic matter decomposition. Comprehensive effects of climate change on different successional stages may alter successional trajectories: if drought stress intensifies while nitrogen deposition synchronously strengthens, this may favor deep-rooted, low nutrient-demanding conservative species, accelerating succession toward climax communities; conversely, if warming increases nutrient mineralization rates with ample precipitation, this may extend the dominance period of pioneer species, slowing successional processes.

Nitrogen deposition, as an important component of global change, exerts profound influences on root functional traits and resource acquisition strategies by altering soil nitrogen availability and nutrient stoichiometric ratios. These influences differ significantly across successional stages due to initial nitrogen limitation levels. In nitrogen-limited early succession, low to moderate nitrogen deposition (5–15 kg $N \cdot ha^{-1} \cdot year^{-1}$) may produce "fertilization effects": increased soil inorganic nitrogen concentrations (rising 50–150%) alleviate nitrogen limitation, promoting plant growth and aboveground biomass allocation, resulting in 15–30% declines in root:shoot ratios, with total root biomass potentially remaining unchanged or even slightly declining. Root morphological trait responses to nitrogen enrichment manifest as increased specific root length (SRL) (rising 10–25%) and decreased root tissue density (RTD) (declining 10–20%). This strategic shift toward "acquisitive" types reflects adaptive adjustments optimizing absorption efficiency in high-nutrient environments. However, root lifespan universally shortens under nitrogen deposition (decreasing 20–40%), possibly stemming from high nitrogen content reducing tissue C:N ratios, increasing root decomposability and microbial attack risks. Mycorrhizal dependence significantly declines under nitrogen deposition conditions: mycorrhizal colonization rates can decline by 20–50%, with carbon allocation proportions to mycorrhizae reducing by 30–60%, because when inorganic nitrogen is abundant, costs of direct plant absorption are lower than costs of maintaining mycorrhizal symbiosis. This "mycorrhizal suppression" effect is particularly pronounced in AM tree species. Long-term, high-intensity nitrogen deposition (>20 kg N·ha$^{-1}$·year$^{-1}$) may produce negative effects: soil acidification (pH declining 0.5–1.5 units), increased aluminum toxicity, and intensified leaching of base cations such as calcium and magnesium, which damage root health, increasing root mortality and decreasing fine root productivity. More critically, nitrogen-phosphorus ratio imbalances resulting from continuous nitrogen inputs (N:P ratios rising from 10–15 to 20–30) transform phosphorus limitation from latent to explicit, further intensifying resource imbalances in mid-to-late succession where phosphorus limitation already exists. Responses to nitrogen deposition differ significantly among tree species at different successional stages: pioneer species exhibit stronger positive responses to nitrogen addition due to their rapid growth and high nitrogen requirements, potentially gaining competitive advantages under nitrogen enrichment conditions and delaying successional processes; whereas climax species, already adapted to low-nitrogen environments, derive relatively limited benefits from nitrogen deposition and are more susceptible to negative impacts from intensified phosphorus limitation, potentially decreasing competitiveness. This differentiated response suggests nitrogen deposition may alter community succession direction, even reversing succession in extreme cases (e.g., degradation from broadleaf forests to coniferous forests or grass-shrub dominated communities).

Biodiversity loss and anthropogenic disturbances interact with factors such as climate and nitrogen deposition under global change, exerting compound influences on root resource acquisition strategies and ecosystem functions by altering functional diversity and community structure. Ecological consequences of functional diversity loss are first manifested in declining resource use efficiency: when root trait diversity decreases (e.g., species loss reduces coexistence of deep-shallow root, fast-conservative strategies), community capacity to exploit spatial and temporal heterogeneity of soil resources weakens, manifesting as 10–30% declines in total nutrient absorption and 15–25% reductions in water use efficiency. Loss of key functional groups may produce disproportionate cascading effects: for example, disappearance of deep-rooted species will significantly reduce community capacity to access deep water, decreasing whole-community drought resistance by over 50%; loss of nitrogen-fixing species or high mycorrhizal-dependent species may disrupt key pathways of nitrogen cycling and phosphorus acquisition, intensifying nutrient limitation. Loss of functional redundancy reduces ecosystem buffering capacity against disturbances: in communities with high functional diversity, when one functional group is damaged, other functional groups can compensate for functional losses, but when redundancy decreases, single disturbance events (e.g., extreme drought, pest outbreaks) may cause catastrophic declines in ecosystem function. Anthropogenic disturbances (e.g., logging, fire, land use change) indirectly affect root strategies by resetting successional processes and altering species composition: frequent moderate disturbances may maintain early successional communities, solidifying advantages of rapid acquisitive root strategies; whereas complete disturbance removal (e.g., strict protected areas) accelerates succession toward climax communities and conservative strategies. Interactive effects of multiple global change factors often exhibit non-additivity: for example, synergistic effects of warming and nitrogen deposition may increase root turnover rate amplitudes (60–100%) beyond the sum of single-factor effects (40–60%); whereas interactions between drought and biodiversity loss may produce "synergistic collapse," with declines in ecosystem drought resistance amplitudes (70–90%) far exceeding single-factor predictions (30–50%). Understanding these complex interactive effects is crucial for accurately predicting forest dynamics under global change scenarios and formulating adaptive management strategies. Future research should strengthen multifactor controlled experiments and long-term monitoring, and integrate root processes into Earth system models to enhance predictive capacity.

# 5. Conclusions and Outlook

## 5.1. Research Conclusions

This study systematically reviewed variation patterns of absorptive root traits and resource acquisition strategies among representative tree species at different successional stages in subtropical regions, obtaining the following main conclusions:

(1) Absorptive root functional traits exhibit a multi-dimensional integrated framework encompassing morphology–anatomy–chemistry–physiology–symbiosis. These traits constitute the "root economics spectrum" through coordinated variation, reflecting trade-off relationships between resource acquisition efficiency and tissue persistence, providing a theoretical foundation for understanding belowground resource utilization strategies.

(2) Along forest successional gradients, absorptive root traits of representative tree species exhibit directional differentiation from "rapid acquisitive" toward "conservative storage" types: pioneer species are characterized by combinations of high specific root length, fine root diameter, low tissue density, high nitrogen content, and short lifespan, whereas climax species display opposite trait combinations. This differentiation pattern is tightly coupled with coordinated changes in above- and below-ground environmental gradients.

(3) Environmental factors (resource availability, competition intensity, disturbance frequency) drive root strategy differentiation through multidimensional selective pressures, while the relative roles of phylogenetic constraints and phenotypic plasticity determine the balance between genetic basis and ecological adaptation of trait variation. Species replacement contributes 60–85% of trait variation, with intraspecific plasticity contributing 15–40%.

(4) Root functional traits exert cascading effects on ecosystem productivity, carbon sequestration, and stability by regulating carbon-nitrogen inputs, nutrient cycling, and resource acquisition efficiency. Maintenance of functional diversity is crucial for ecosystem resistance and resilience.

(5) Global change (climate warming, nitrogen deposition, biodiversity loss) imposes compound influences on root strategies by altering selective pressures and resource environments, potentially changing successional trajectories and ecosystem functions. This necessitates strengthening research on multifactor interactive effects and enhancing predictive capacity.

## 5.2. Future Research Outlook

Future research should deepen and expand in the following directions:

(1) Strengthen mechanistic analyses of root functional differentiation, particularly quantification of functional heterogeneity among different root orders/age classes within absorptive roots. Combine omics technologies such as transcriptomics and metabolomics to reveal the molecular genetic basis and epigenetic regulatory mechanisms of trait variation, elucidating complete pathways of environmental signal perception-transduction-response.

(2) Develop long-term dynamic monitoring systems and non-destructive observation techniques, establishing standardized successional monitoring networks. Utilize isotope tracing, continuous minirhizotron observations, and sensor technologies to precisely quantify root lifespan, turnover rates, and nutrient absorption kinetics, integrating multi-scale spatiotemporal data to reveal seasonal and interannual variation in root processes.

(3) Deepen rhizosphere micro-process research, employing high-resolution imaging techniques (e.g., neutron imaging, X-ray CT) and in situ analytical methods (e.g., nanoscale secondary ion mass spectrometry) to analyze material exchange and energy flow at the root-soil-microbe interface. Quantify the successional dynamics of rhizosphere priming effects, mycorrhizal functions, and microbial community assembly and their contributions to nutrient acquisition.

(4) Construct multifactor interactive experimental platforms, systematically evaluating individual and combined effects of global change factors such as climate change, nitrogen deposition, and drought. Integrate root processes into Earth system models and dynamic vegetation models, utilizing machine learning and other methods to enhance predictive capacity for future scenarios.

(5) Strengthen application-oriented research, guiding tree species selection and mixed-species configurations based on root functional trait databases. Develop indicator systems for root functional assessment in close-to-nature silviculture, exploring technical approaches for root management to promote carbon sequestration enhancement, ecological restoration acceleration, and forest multifunctionality improvement, providing scientific support for sustainable forest management.

## Author Contributions

Conceptualization, H.L., M.N., B.Y. and J.M.; methodology, H.L.; software, H.L.; validation, H.L., M.N., B.Y. and J.M.; formal analysis, H.L.; investigation, H.L.; resources, H.L.; data curation, H.L.; writing—original draft preparation, H.L.; writing—review and editing, H.L.; visualization, H.L.; supervision, H.L.; project administration, H.L.; funding acquisition, H.L. All authors have read and agreed to the published version of the manuscript.

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## Institutional Review Board Statement

Not applicable. This study does not involve humans or animals.

## Informed Consent Statement

Not applicable. All studies only study plants and soil. It is not related to humans; it only helps communities and governments to develop the economy.

## Data Availability Statement

Not applicable.

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## Conflicts of Interest

The authors declare no conflict of interest.

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