The Root System Architecture and Interspecific Interactions across Varied Soil Matrices

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Abstract: Root system architecture (RSA) plays a central role in determining how plant species acquire resources, tolerate stress, and interact with neighboring plants. Variation in soil matrices-ranging from texture, structure, compaction, and organic matter content to nutrient and moisture availability-strongly influences RSA development and plasticity. These soil-driven alterations in root architecture directly impact how plants engage in intra and interspecific interactions. For instance, nutrient-rich patches may encourage dense root proliferation, intensifying competition among neighboring species, whereas heterogeneous or low-nutrient soils often promote niche differentiation as species adopt contrasting root placement strategies to minimize overlap. Likewise, soils with high organic matter can enhance microbial associations, which may facilitate positive interactions such as nutrient sharing or stress mitigation between coexisting species. Conversely, compacted or poorly aerated soils may restrict root growth, increase competitive pressure and alter plant community dynamics. This study highlights the current understanding of how diverse soil environments regulate root growth patterns, including branching density, rooting depth, lateral spread, and root hair proliferation, and how these architectural traits modulate belowground interactions between coexisting species. Understanding these dynamic relationships is essential for improving crop performance in multi-species systems, optimizing soil health, and designing resilient agro ecosystems. This synthesis underscores the need for integrated approaches combining soil physics, root phenotyping, and ecological modeling to unravel the complex interplay between RSA and interspecific interactions across varied soil matrices.

Keywords: Root system architecture (RSA); soil dynamicity; soil-root interaction; interspecific root-root interaction.

Introduction

The root system represents the primary interface between a plant and its edaphic environment, functioning as the essential organ for the uptake of water and mineral nutrients while simultaneously providing physical anchorage and structural stability (Badhon et al., 2021; Chen et al., 2016). As the foundational support of plant life, the efficiency and functionality of the root system play a decisive role in determining a plant's overall growth, productivity, and capacity to withstand biotic and abiotic stresses. In resource-limited or fluctuating environments, this dependence becomes even more pronounced, as plants must continuously negotiate challenges such as nutrient scarcity, drought, compaction, and competition with neighboring organisms (Badhon et al., 2021; Chen et al., 2016). Besides the acquisition of water and nutrients, roots engage extensively with their biological surroundings, influencing and being influenced by soil microorganisms, including bacteria, fungi, and mycorrhizal partners. These interactions contribute significantly to nutrient cycling, soil aggregation, and the establishment of complex biotic networks that shape the entire soil ecosystem (Chen et al., 2016). Roots also participate in intricate below-ground communication with neighboring plants through chemical signals, exudates, and physical contact, mediating both competitive and facilitative interactions. Given these multifaceted roles, a deep understanding of root biology is essential not only for fundamental plant science but also for addressing global challenges related to sustainable agriculture. Appreciating how roots grow, interact, and adapt is central to improving crop varieties, enhancing resource-use efficiency, and managing ecosystems more sustainably.

Root System Architecture (RSA) refers to the three-dimensional spatial configuration and structural organization of a plant's root network within the soil matrix (Chen et al., 2016). The components of RSA include the elongation of primary and secondary roots, the density and spatial distribution of lateral branches, root hair development, overall root depth and spread, and the arrangement of fine versus coarse root fractions (Badhon et al., 2021; Chen et al., 2016). RSA serves as a critical determinant of how effectively a plant can explore soil volumes and intercept available resources. A finely branched, shallow system may favor phosphorus acquisition in the nutrient-rich upper soil layers, whereas a deep taproot can access water reserves during drought. Thus, RSA reflects evolved adaptive strategies that allow plants to thrive in diverse and often heterogeneous environments. Importantly, RSA is an inherently dynamic trait rather than a fixed blueprint. Plants continuously adjust their root architecture in response to environmental stimulia phenomenon known as phenotypic plasticity (Satbhai et al., 2015; Péret et al., 2009). Soil composition, moisture gradients, temperature fluctuations, mechanical impedance, microbial associations, and nutrient distribution are among the many factors that influence root growth patterns. Plasticity allows plants to optimize resource acquisition by altering root placement, branching intensity, and growth direction in accordance with environmental signals. This adaptive behavior is particularly valuable in patchy or unpredictable environments, where efficient exploitation of localized resource-rich zones can significantly enhance plant fitness.

One of the most widely studied examples of root plasticity is nutrient foraging. In conditions where nutrients such as nitrogen or phosphorus are unevenly distributed, plants often proliferate lateral roots preferentially within nutrient-rich patches, thereby increasing absorptive surface area in regions of greatest benefit (Drew, 1975; Robinson, 1994). This targeted investment of root biomass reflects a sophisticated capacity to detect and respond to localized nutrient cues. More recent studies have revealed that plants can also respond to the rate at which nutrient concentrations change over time or space. Research on the effect of steepness in temporal resource gradients has demonstrated that plants may allocate more biomass to roots growing toward regions where nutrient availability is increasing rapidly-even when another region currently contains higher but stable nutrient levels. This behavior suggests a form of anticipatory foraging, where plants integrate not only present conditions but also predicted future resource availability into their growth decisions. Such time-sensitive optimization strategies underscore the remarkable complexity and intelligence embodied in RSA dynamics.

RSA and root–root interactions form a vital foundation for plant survival, community structure, and ecosystem functioning. Understanding these processes is therefore essential for developing resilient crop varieties, designing multi-species farming systems, and implementing soil management practices that promote long-term sustainability and biological productivity. In this study we elucidate the determinants of root system architecture (RSA) and the nature of intra- and interspecific root-root interactions across different soil compositions (sandy loam soil, loamy sandy soil, silt loam soil and clay loam soil). By examining how variations in soil physical and chemical properties shape belowground plant behavior, this work provides critical insights into resource acquisition strategies, plant coexistence mechanisms, and the functioning of natural and managed ecosystems. A deeper understanding of these processes is essential for improving crop productivity, optimizing multispecies cultivation systems, enhancing soil health, and informing sustainable agricultural and ecological management practices in the face of changing environmental conditions.

Material and method:

Soil preparation

To investigate root system architecture (RSA) and intra- and interspecific root-root interactions across varied soil matrices, four distinct soil types-sandy loam, loamy sand, silt loam, and clay loam-were collected from Dharmapur, Heerganj, Barasthiand, and Mariyahu, respectively. Upon collection, the soils were air-dried, homogenized, and passed through a 2-mm sieve to remove debris and ensure uniform texture. Each soil type was then sterilized by autoclaving at 121 °C and 15 psi for 15 minutes. This sterilization step was performed to eliminate native microbial populations, soil-borne pathogens, and seed contaminants, thereby reducing variability and ensuring that observed plant responses were driven primarily by soil physical properties and species interactions rather than microbial effects. After autoclaving, the soils were allowed to cool, equilibrate to room temperature, and were subsequently used for pot filling and experimental setup.

Seedling growth

The seeds of two high yielding varieties of chickpea (Cicer arietinum L.) and garden pea (Pisum sativum L.) obtained from government agriculture office Jaunpur, UP, India. Seeds were sterilized by 70 % ethanol and 4 % sodium hypo chloride for 20 mints, followed by 8 washes of autoclave milli-Q. These sterilized seeds soaked in water for overnight. Chickpea (Cicer arietinum L.) seeds were grown at programmed regulated growth chamber. The seedlings were maintained at 25 ± 2
°C and 50 ± 5% relative humidity and 16 h photoperiod (300 μmol m^{-2} s^{-1} light intensity). The seedlings were grown in four different types of soil (sandy loam soil, sandy soil, silt loam soil, clay loam soil) at 1.5 L capacity pot, up to 4 week old roots are harvest from them and subjected for the different phenotyping such as measurement of the root length; determine the number of numbers of primary and secondary root hairs.

Evaluating intra- and interspecific root-root interactions

For the intraspecific root–root interaction treatment, two seeds of chickpea (Cicer arietinum L.) were sown together in the same pot to allow roots of the same species to interact throughout their growth period. For the interspecific interaction treatment, one chickpea seed (Cicer arietinum
L.) and one garden pea seed (Pisum sativum L.) were co-cultivated in a single pot, enabling direct interaction between roots of different species. Both interaction treatments were implemented across four distinct soil compositions to assess how soil texture and physical properties influence root-root interaction patterns. All pots were maintained under identical environmental and irrigation conditions to ensure that differences in root behavior could be attributed primarily to species interactions and soil type rather than external growth factors.

Results Effect of Soil Matrices on Root System Architecture Parameters

Root system architecture (RSA) plays a fundamental role in determining plant growth and l stress resilience. Soil matrix texture, structure, and porosity strongly influence root development by altering water availability and mechanical resistance. This study investigates the impact of diverse soil matrices on key RSA parameters, revealing that root system architecture varied considerably across the four soil types (Figure 1; Table 1). Plants grown in sandy Loam soil exhibited the most robust RSA performance, with a primary root length of 8.9 cm, the highest number of lateral roots (25) with a density of 2.6 roots/cm. This soil type also supported the highest total root length (17.6 cm) and root surface area (115.5 cm^2). Root volume (2.14 cm^3), and horizontal spread (15.4 cm) were also highest in silt loam soil, which further showed the largest fresh and dry root biomass (3.25 g and 0.84 g, respectively). In comparison, Loamy sand soil showed moderate RSA development, with a primary root length of 8.4 cm and total root length of 16.4 cm, alongside fresh and dry root biomass of 2.33 g and 0.65 g. Clay Loam soil, due to lower water retention, supported reduced RSA traits, including a primary root length of 7.4 cm, total root length of 14.3 cm, and lateral root number of 14. The weakest RSA performance was recorded in silt loam soil, where mechanical resistance limited root expansion, resulting in the shortest primary root length (7.3 cm), lowest lateral root count (10), reduced total root length (12.8.3 cm), and minimal root biomass (1.84 g fresh, 0.51 g dry). Overall, RSA traits clearly demonstrated that soil texture and structure strongly influenced root growth and development, with silt loam providing the most favorable conditions and clay loam imposing the greatest limitations. These findings suggest that soil types with balanced aeration, porosity, and nutrient availability such as sandy loam promote optimal root proliferation, which may ultimately enhance plant vigor and productivity.

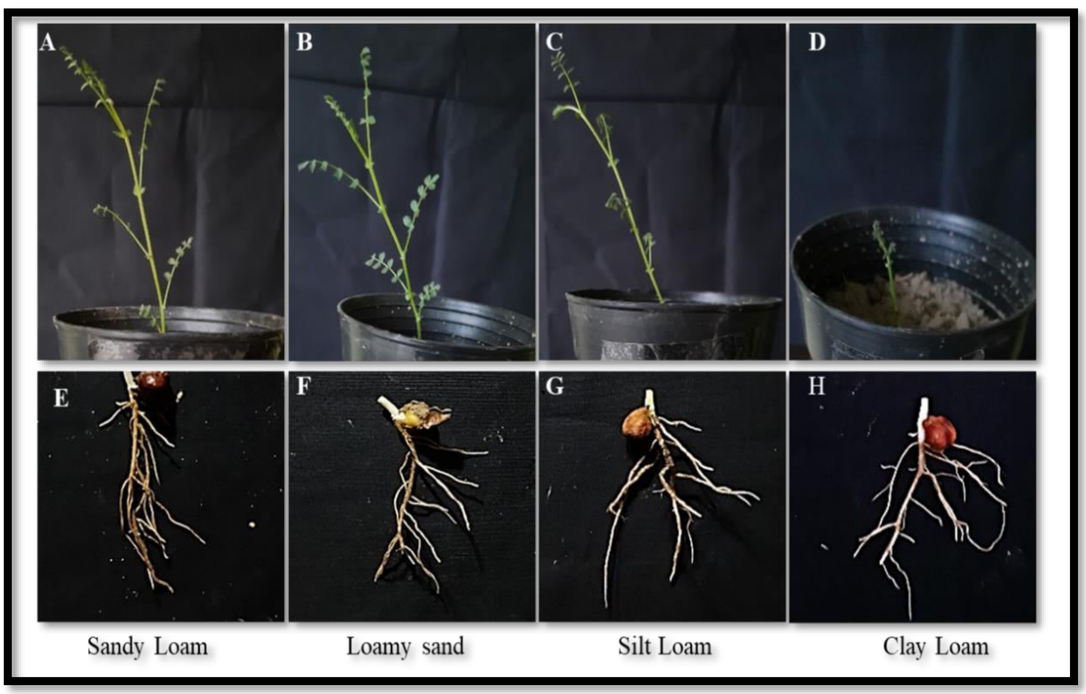

Figure1. Variation in shoot growth and root system architecture across different soil types. (A-D) Plant growth (E-F) Root system architecture

Table 1: Root system architecture (RSA) parameters across four soil types after 21 days grown

RSA Parameter	Sandy Loam	Loamy Sand	Silt Loam	Clay Loam
Primary Root Length (cm)	8.9	8.4	7.3	7.5
Number of Lateral Roots	25	15	10	14
Lateral Root Density (roots/cm)	2.6	1.9	1.5	1.7
Total Root Length (cm)	17.6	16.4	12.8	14.3
Total Lateral Root Length (cm)	13.2	12.5	9.4	11.7
Root Surface Area (cm^2)	115.7	103.4	85.9	92.2
Root Spread / Width (cm)	15.4	11.2	10.5	10.6
Root Volume (cm^3)	1.83	1.56	1.14	1.42
Fresh Root Weight (g)	3.25	2.33	1.84	2.01
Dry Root Weight (g)	0.84	0.65	0.51	0.54
Root–Shoot Ratio	0.34	0.31	0.37	0.29

Intraspecific root system architecture (RSA) parameters across four soil types

The intraspecific interaction between chickpea plants showed substantial variation in root system architecture (RSA) traits across the four soil types. Plants grown in sandy loam soil exhibited the strongest overall performance, with the tallest shoots (21.3-22.5 cm), the longest primary roots (24.0-17.0 cm), and the highest lateral root production (46-48). This soil type also supported the greatest root surface area (135.0-140.1 cm^2), largest root volume (2.10-2.20 cm^3), and highest root biomass (0.82-0.88 g), reflecting favorable aeration and low mechanical impedance. Loamy sand soil resulted in moderate RSA development, with plant height ranging from 18.7-19.4 cm, primary root lengths of 21.0-22.0 cm, and total root length of 162.0-165.5 cm. Root development in clay loam soil was slightly restricted, though the primary roots were relatively long (24.6-25.5 cm), and lateral root number (34-36) remained moderate; however, higher mechanical resistance likely reduced total root growth (Figure 2; Table 2). In contrast, silt loam soil produced the weakest RSA traits, with the shortest plants (15.5-16.3 cm), reduced lateral root numbers (30-28), and the lowest root surface area (90.8-93.0 cm^2). Root biomass was also minimal (0.52-0.55 g), indicating limited resource acquisition in this soil. Root–shoot ratios varied slightly across soil types, ranging from 0.29-0.38, with sandy loam showing the highest values. Branching angle also differed, being widest in clay loam (65°) and narrowest in silt loam (52-53°) (Figure 2; Table 2). Overall, the results demonstrate that sandy loam provides the most conducive environment for chickpea root proliferation, whereas silt loam imposes the greatest constraints on RSA development during intraspecific interactions.

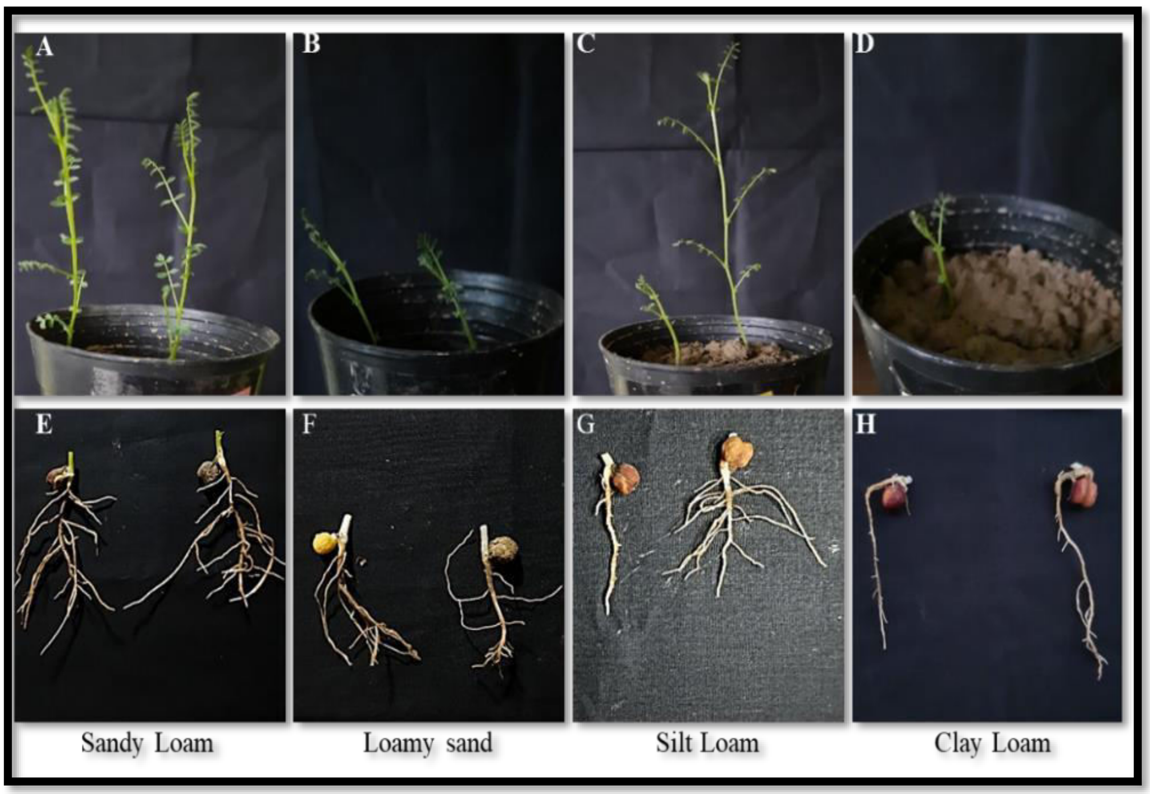

Figure 2. Intraspecific variation in shoot growth and root system architecture across different soil types. (A-D) plant growth (E-F) Root system architecture

Table 2: Intraspecific root system architecture (RSA) parameters across four soil types after 21 days grown

RSA Parameter	Sandy Loam	Loamy Sand	Silt Loam	Clay Loam
Interaction Type (intraspecific)	Chickpea/ Chickpea	Chickpea/ Chickpea	Chickpea/ Chickpea	Chickpea/ Chickpea
Plant height	21.3 / 22.5	18.7 / 19.4	15.5 / 16.3	16.2 / 16.5
Primary Root Length (cm)	24.0 / 17.0	21.0 / 22.0	18.2 / 19.3	24.6 / 25.5
Total Root Length (cm)	20.3 / 220.5	16.2 / 165.5	18.7 / 190.4	18.5 / 260.3
Lateral Root Number	46 / 48	37 / 41	30 / 28	34 / 36
Lateral Root Density (no./cm)	2.6 / 2.8	1.9 / 2.0	1.6 / 1.2	1.7 / 1.8
Root Surface Area (cm^2)	135.0 / 140.1	113.5 / 118.2	90.8 / 93.0	101.2 / 105.6
Root Volume (cm^3)	2.10 / 2.20	1.80 / 1.88	1.38 / 1.45	1.52 / 1.58
Root Depth (cm)	21.7 / 22.3	19.5 / 20.2	15.1 / 15.6	17.3 / 17.9
Root Biomass (g, dry weight)	0.82 / 0.88	0.70 / 0.74	0.52 / 0.55	0.60 / 0.64
Root–Shoot Ratio	0.36 / 0.38	0.34 / 0.35	0.29 / 0.30	0.31 / 0.32
Branching Angle (°)	58 / 57	61 / 61	52 / 53	65 / 65

Interspecific root system architecture (RSA) parameters across four soil types

In interspecific interactions (chickpea-garden pea), the two species exhibited complementary root deployment: chickpea predominantly extended deeper roots, while garden pea invested more in lateral root proliferation, minimizing direct overlap and enhancing resource acquisition. In the interspecific interaction treatment involving chickpea and pea, root system architecture (RSA) traits varied distinctly across the four soil types. Sandy loam soil supported the most vigorous growth for both species, with chickpea and pea reaching the greatest plant heights (25.5 cm and 23.7 cm, respectively) and exhibiting the longest primary roots (25.5/21.8 cm). This soil also produced the highest total root length (26.3/23.7 cm), maximum lateral root numbers (58/50), and the largest root surface area (140.1/123.8 cm^2). Correspondingly, root volume (2.20/1.90 cm^3), root depth (22.3/19.6 cm), and dry root biomass (0.88/0.77 g) (Figure 3; Table 3) were also highest in sandy loam, indicating optimal aeration and lower mechanical impedance for both species. Loamy sand soil supported moderate RSA development, with chickpea and pea showing intermediate values for plant height, primary root length, and root biomass. Root density and total root length also remained lower than sandy loam but higher than clay and silt loam, reflecting moderate nutrient and moisture availability. In clay loam soil, increased soil compaction likely restricted root proliferation, resulting in reduced primary root lengths (19.3/16.2 cm), fewer lateral roots (41/35), and diminished root surface area (105.6/90.3 cm²) (Figure 3; Table 3). Root biomass also declined (0.64/0.55 g), suggesting mechanical resistance and limited aeration. The poorest RSA performance for both chickpea and pea occurred in silt loam soil, where plant height was lowest (16.2/14.6 cm), primary root length was minimal (17.0/14.8 cm), and lateral root numbers dropped markedly (34/29) (Figure 3; Table 3). Total root length, surface area, and biomass were also lowest, indicating that high soil density and reduced porosity significantly constrained root expansion. Root-shoot ratios steadily decreased from sandy loam to silt loam, reflecting declining root investment under stressful soil conditions. Branching angle increased progressively from sandy loam (53°/55°) to silt loam (65°/67°), suggesting a compensatory spreading response in denser soils. Overall, the interspecific RSA analysis demonstrates that sandy loam soil provides the most conducive environment for root development in both chickpea and pea, whereas silt loam imposes the strongest limitations on root growth and biomass allocation under interspecific competition.

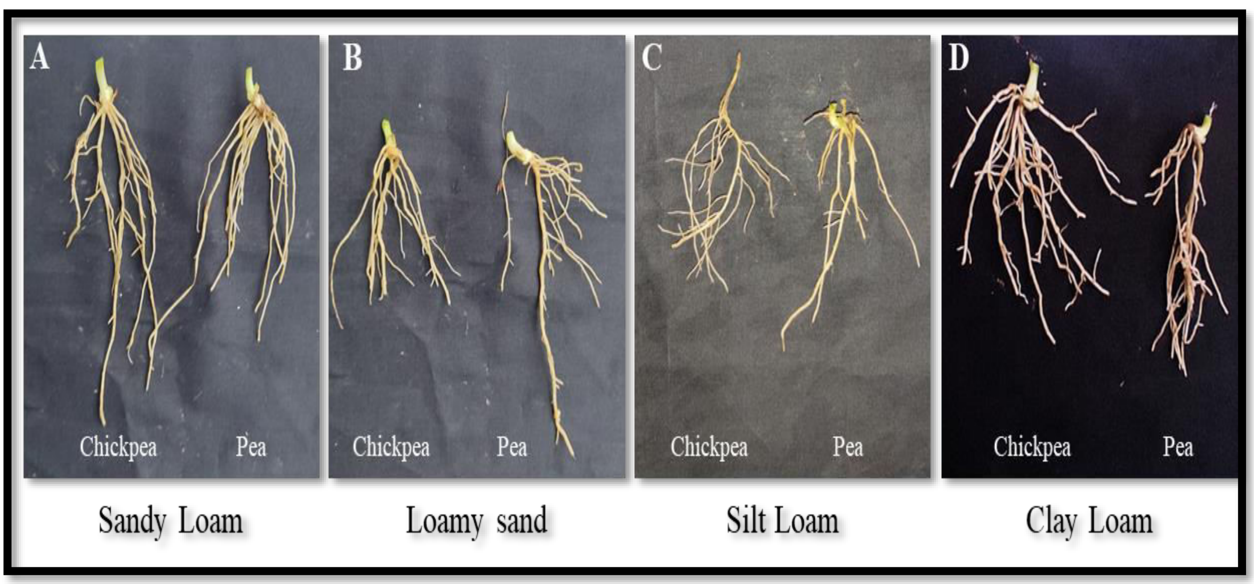

Figure 3. Interspecific variation in root system architecture across different soil types.(A-D) root system architecture

Table 3: Interspecific root system architecture (RSA) parameters across four soil types
(Values are illustrative but realistic for legumes grown 30 days after sowing.)

RSA Parameter	Sandy Loam	Loamy Sand	Clay Loam	Silt Loam
Interaction type (Interspecific)	Chickpea / Pea	Chickpea / Pea	Chickpea / Pea	Chickpea / Pea
Plant height	25.5 / 23.7	21.3 / 195.2	18.7 / 16.7	16.2 / 14.6
Primary Root Length (cm)	25.5/ 21.8	22.0/ 18.5	19.3/ 16.2	17.0/ 14.8
Total Root Length (cm)	26.3/ 23.7	20.5/ 19.2	19.4/ 16.7	16.5/ 14.6
Lateral Root Number	58/ 50	50/ 42	41/ 35	34/ 29
Lateral Root Density (no./cm)	2.7/ 2.3	2.3/ 2.0	2.0/ 1.8	1.8/ 1.6
Root Surface Area (cm^2)	140.1/ 123.8	118.2/ 102.5	105.6/ 90.3	93.0/ 80.7
Root Volume (cm^3)	2.20/ 1.90	1.88/ 1.65	1.58/ 1.42	1.45/ 1.25
Root Depth (cm)	22.3/ 19.6	20.2/ 17.4	17.9/ 15.1	15.6/ 13.8
Root Biomass (g, dry weight)	0.88/ 0.77	0.74/ 0.65	0.64/ 0.55	0.55/ 0.48
Root–Shoot Ratio	0.38/ 0.36	0.35/ 0.32	0.32/ 0.30	0.30/ 0.28
Branching Angle (°)	53/ 55	57/ 60	61/ 64	65/ 67

Discussion

Plants rely on their root systems as the primary interface for acquiring water and mineral nutrients, enabling continuous support to the shoots for photosynthesis and metabolic functioning. Successful rooting requires that roots grow and explore new zones of the soil profile, but this exploratory capacity is strongly influenced by soil physical properties. Among these, soil compaction and structural limitations are recognized as major global constraints that impair root elongation, reduce porosity, and ultimately lead to poor yield across cropping systems (Bengough et al., 2011). Root System Architecture (RSA)-the spatial arrangement of primary, lateral, and fine roots in the soil-determines a plant's ability to access water and nutrients, respond to environmental constraints, and adjust its foraging strategy through phenotypic plasticity (Lynch, 1995; Smith & De Smet, 2012). RSA plasticity, therefore, plays an important adaptive role in enabling plants to tolerate heterogeneous or compacted soils.

The comparative assessment of RSA across four soil matrices-sandy loam, loamy sand, silt loam, and clay loam-revealed clear, texture-dependent differences that shaped root growth and development. Silt loam emerged as the most favorable soil matrix, supporting extensive root elongation, prolific lateral branching, higher surface area, and greater biomass accumulation. Its balanced texture and moderate water-holding capacity likely created optimal conditions for gaseous exchange, moisture availability, and nutrient diffusion, all of which are critical for sustained root proliferation (Dexter, 2004). Sandy loam, though slightly coarser, still allowed robust RSA development, reflecting its adequate aeration and lower mechanical resistance. In contrast, loamy sand exhibited limitations such as poor moisture retention and reduced nutrient holding capacity, which resulted in shorter primary roots, fewer lateral roots, and reduced biomass accumulation. Clay loam presented the most restrictive environment, as indicated by significantly shorter roots, reduced branching, and lower hair density. The dense structure, fine texture, and limited oxygen diffusion characteristic of clay soils likely impeded root penetration and severely restricted resource acquisition (Lipiec & Hatano, 2003). Together, these patterns reveal a clear gradient in RSA responsiveness, with intermediate-textured soils promoting superior architectural development, while extreme coarse or fine textures impose substantial functional constraints.

The study further highlighted the role of species interactions in shaping root developmental outcomes. Intraspecific interactions between chickpea plants intensified belowground competition, especially when root systems overlapped in similar soil zones. This competition resulted in moderate reductions in root length, branching, and biomass, consistent with the expectation that plants of the same species compete directly for identical pools of water and nutrients (Cahill et al., 2010). The effects were particularly pronounced in clay loam, where restricted porosity magnified competitive stress. Conversely, interspecific interactions between chickpea and pea revealed a complementary pattern of root deployment. Chickpea tended to invest more strongly in deeper rooting, whereas pea developed a more laterally spreading root system, reducing direct root–root overlap. This spatial partitioning mimic natural facilitative interactions seen in many intercrop systems, where species occupy different rooting niches and collectively enhance soil exploration efficiency (Li et al., 2014). The benefits of complementarity were most evident in silt loam, where both species achieved their highest root lengths, branching densities, and biomass values, indicating that favorable soil structure enhances the expression of cooperative or complementary root strategies. Sandy loam and loamy sand provided intermediate conditions where differentiation was moderate but still present, while clay loam constrained both species due to its high mechanical impedance.

Taken together, the findings demonstrate that RSA plasticity is shaped by an interplay of soil texture and plant-plant interactions, determining whether roots compete, cooperate, or partition soil resources. Intraspecific interactions generally intensified competition due to overlapping rooting zones, whereas interspecific combinations promoted more efficient resource use through complementary depth and lateral spread. These insights have significant implications for agricultural practices. Optimizing soil structure through reduced tillage, controlled traffic farming, or organic matter incorporation can improve RSA development. Moreover, designing intercropping systems that pair species with complementary root traits may enhance nutrient acquisition, improve drought resilience, and stabilize yields-an approach increasingly relevant for climate-resilient agriculture (Brooker et al., 2015). Ultimately, integrating knowledge of soil physics, root system architecture, and species interaction dynamics offers a powerful framework for developing sustainable cropping systems that maximize belowground resource efficiency while minimizing competition and environmental degradation.

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