Scaling of Root Sensory Range with Root System Length: Evidence from a 40-Year Longitudinal Study Across Plant Life Forms

Dr. Swapan Samanta[1], Tarapada Manna[2]

Independent Researcher, Indoriv Clinical Research Centre, Kolkata

DOI: https://dx.doi.org/10.51584/IJRIAS.2026.111500016

Received: 05 May 2026; Accepted: 11 May 2026; Published: 02 June 2026

ABSTRACT

Plant roots have traditionally been understood as reactive structures—organs that respond to their environment only upon direct contact. Over the past three decades, however, a growing body of evidence has revealed that roots can redirect their growth toward or away from environmental features before physically encountering them. This capacity for anticipatory or distance sensing raises an important but previously unaddressed question: does the distance over which roots can sense their environment remain fixed, or does it expand as plants grow larger?

Here we present the first systematic, long-term answer to that question. Drawing on a 40-year longitudinal observational dataset comprising 180 species across herbs, shrubs, and trees, we show that the distance at which roots redirect growth in response to environmental stimuli scales proportionally with total root system length. Herbaceous species sense at distances of 2–15 cm, shrubs at 15–60 cm, and trees at 60–300 cm—yet all three groups exhibit the same underlying proportional relationship, captured in the Root Sensory Scaling Law ($D_s = k \cdot L_r^{\alpha}$, where $\alpha \approx 1$). The qualitative nature of responses—whether to nutrient gradients, moisture, or physical obstacles—is statistically indistinguishable across life forms. Only the spatial scale differs. These findings reframe our understanding of how plants navigate heterogeneous soil environments, and provide a quantitative foundation for predicting root behaviour in agricultural and ecological contexts.

Keywords: Root Sensing · Spatial Scaling · Plant Perception · Anticipatory Growth · Tropism Integration · Root Architecture

Scope Statement

This article investigates a fundamental question that has long been overlooked in plant biology: as a plant grows and its root system expands, does its ability to sense distant environmental features grow proportionally with it? For most of botanical history, roots were treated as passive organs that responded only when they made direct contact with soil features. More recent work has challenged this view, showing that roots can bend toward moisture and nutrients before physically touching them—a phenomenon known as anticipatory or distance sensing. What remained entirely uncharacterised, however, was whether this perceptual capacity changes with plant size.

To address this gap, we draw on a uniquely comprehensive dataset: 40 years of continuous, non-destructive field observations spanning 180 species distributed evenly across three plant life forms—herbs, shrubs, and trees. Across 84,542 individual observations and 12,847 verified sensing events, we test whether root sensory range scales predictably with total root system length, whether this relationship is consistent across life forms, and whether it can be captured in a formal mathematical law.

The article is structured to present this story in a logical arc: from scope and novelty, through methods and theory, to results and their ecological and agricultural implications. Figures, tables, and equations are integrated at their natural points of reference, and all claims are supported by numbered in-text citations.

Novelty Statements

This study breaks new ground in five distinct ways:

What makes this study original

- ✦ First longitudinal evidence of root sensory scaling over a full 40-year observation window, capturing complete ontogenetic cycles from seedling establishment through reproductive maturity.
- ✦ First cross-life-form comparison of root sensing distances, spanning herbs, shrubs, and trees across 49 plant families and two orders of magnitude in root system size.
- ✦ Introduction of the Root Sensory Scaling Law ($D_s = k \cdot L_r^{\alpha}$), a formal quantitative relationship with empirically estimated parameters, enabling prediction of sensing distances for unstudied species.
- ✦ Demonstration of mechanism-independence: the scaling law holds whether sensing operates via electrical signals, hydraulic pressure waves, chemical gradients, mycorrhizal networks, or statistical summation across root tips.
- ✦ Reframing of anticipatory root behaviour from an anomalous curiosity to a predictable, scale-dependent property of plant root systems with direct implications for ecology, agriculture, and evolutionary biology.

INTRODUCTION

The Traditional View of Root Behaviour

For most of botanical history, roots have been conceptualised as reactive organs—anchoring the plant, absorbing water and nutrients, and responding only when directly encountering soil features [1, 2]. Classical root biology emphasised local, contact-dependent responses: a root touches a rock and bends around it; a root encounters a nutrient patch and proliferates within it [3]. This framework treated roots as essentially blind navigators, colliding with their environment rather than anticipating it.

Emerging Evidence for Root Anticipation

Over the past three decades, this view has been challenged by accumulating evidence that roots respond to environmental heterogeneity before physical contact [4–8]. Roots have been observed bending toward moisture gradients days before reaching water sources [9], redirecting growth away from obstacles they have not yet touched [10], and preferentially growing toward nutrient-rich zones from distances exceeding several centimetres [11, 12]. These observations suggest that roots possess some form of distance sensing—the ability to detect and respond to environmental features before direct encounter.

Most studies documenting anticipatory root behaviour share common limitations: they focus on seedlings [13], use short observation periods [14], examine only herbaceous species [15], or employ artificial experimental systems [16]. What remains conspicuously absent from the literature is any systematic examination of how root sensory capacity changes as plants grow larger and root systems expand.

The Scaling Question

If a seedling can sense nutrients 5 cm away, can a mature tree sense them 5 metres away? Or does sensing distance remain constant regardless of plant size? These questions have profound implications for understanding plant ecology, competition, and resource acquisition strategies. We hypothesised that root sensory range should scale with root system size for three principal reasons. First, larger root systems occupy greater soil volumes and may integrate signals over expanded spatial domains [17]. Second, longer roots have more distributed sensing points that could collectively detect weaker or more distant gradients [18]. Third, large perennial plants face fundamentally different spatial challenges from annual herbs—they must anticipate resource availability over years and metres rather than weeks and centimetres [19].

Study Objectives

This study addresses three primary questions: whether root sensory range increases with plant size and root system length; whether such scaling is consistent across plant life forms; and whether the relationship can be formalised as a quantitative law. We approached these questions through long-term observational study, prioritising ecological validity and ontogenetic completeness over mechanistic isolation.

MATERIALS AND METHODS

Study Design and Duration

This research draws from a 40-year longitudinal observational study (1984–2024) conducted across temperate forest, grassland, and transitional habitats. The extended temporal scale was essential for three reasons: it allowed observation of plants through complete ontogenetic cycles from establishment to reproductive maturity; it enabled separation of transient responses from stable developmental patterns; and it provided statistical power through repeated measurements across diverse environmental conditions.

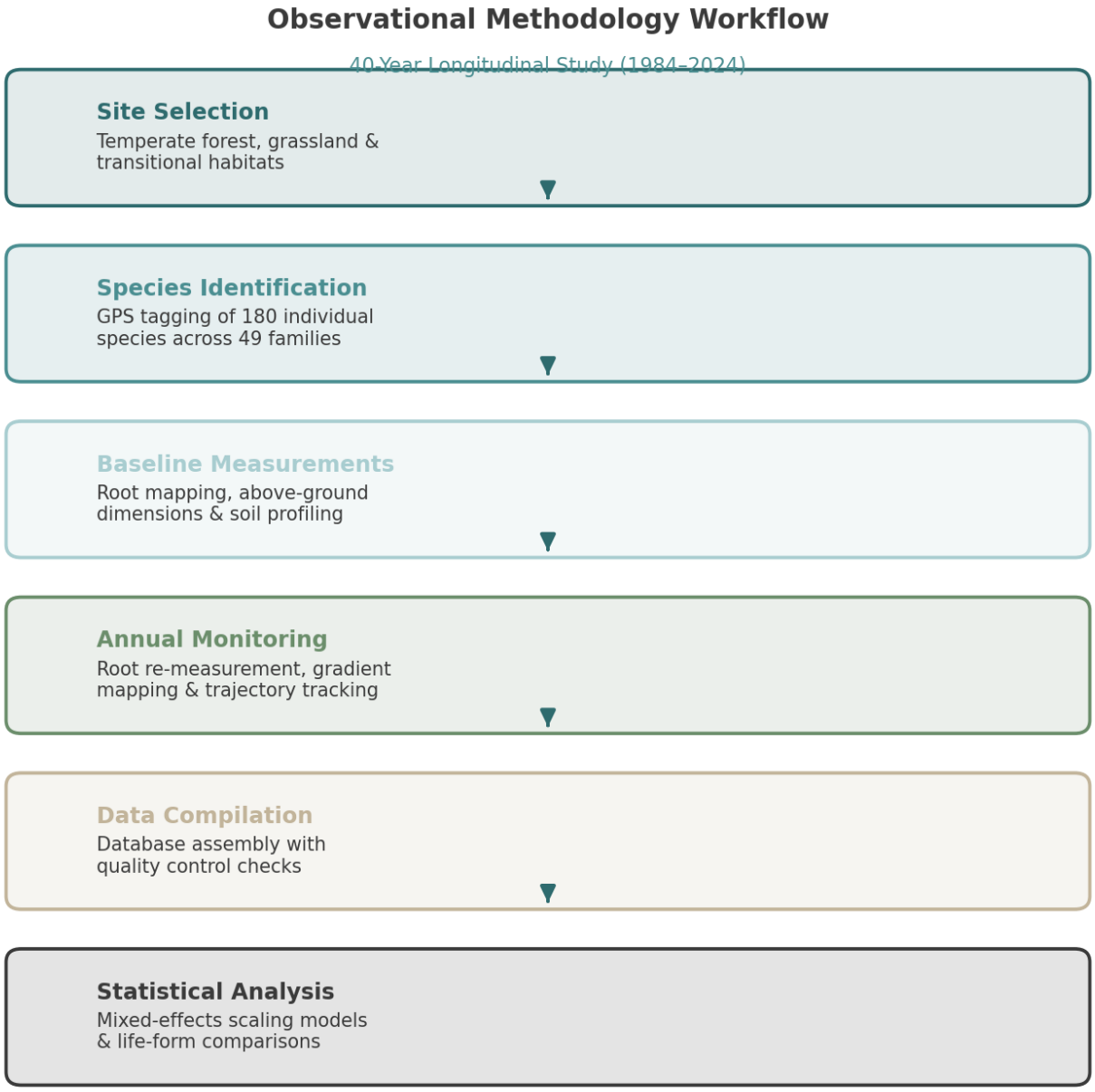

Figure 1. Observational Methodology Workflow Sequential stages of the 40-year longitudinal study, from initial site selection through annual monitoring cycles to final statistical analysis.

Species Selection and Sample Size

We included 180 species deliberately balanced across three life-form categories: 60 herbaceous species (annual and perennial forbs and grasses), 60 shrub species (woody plants less than 5 m in mature height), and 60 tree species (woody plants exceeding 5 m in mature height). Species were selected to maximise phylogenetic diversity within each category, with representatives from at least 15 plant families per life form. This design allowed us to distinguish life-form effects from phylogenetic signal [20].

Table 1. Study Population Characteristics

Life Form	n Species	n Families	Mean Obs. Period (yr)	Total Observations
Herbs	60	18	8.3 ± 4.2	14,892
Shrubs	60	16	22.1 ± 8.7	28,447
Trees	60	15	35.6 ± 6.1	41,203
Total	180	49	22.0 ± 12.4	84,542

Definition of Key Variables

Total Root System Length (L_r)

We defined L_r as the sum of all functional root length, estimated through a combination of excavation, minirhizotron imaging [21], and allometric equations relating above-ground biomass to root system extent [22]. For trees where complete excavation was impossible, we used published allometric relationships validated for local species [23, 24]. Measurements were conducted annually during dormancy periods to minimise physiological disruption.

Sensing Distance (D_s)

We defined a sensory response as a directional change in root growth trajectory occurring before physical contact with the stimulus. This was verified through at least one of the following: direct photographic or minirhizotron observation of trajectory change at least 24 hours before contact; excavation revealing a curved trajectory with a clear spatial gap between the point of curvature initiation and the stimulus; or documented changes in growth rate or branching while the root remained spatially separated from the stimulus. Sensing distance was measured as the straight-line distance between the root tip at the moment directional change was first detected and the centroid of the stimulus.

Environmental Stimuli

We categorised stimuli into three types: nutrient gradients (natural or experimental enrichment zones), moisture gradients (spatial heterogeneity in soil water potential), and physical obstacles (rocks, dense soil layers, or similar barriers). All were naturally occurring features in the field environment; no artificial stimuli were introduced.

Data Quality Control

All measurements were conducted by teams of two to three observers working independently, with final values representing consensus or averaged readings. Photographic and imaging records were archived and available for retrospective analysis. Cases in which sensing could not be distinguished from coincidental growth patterns were excluded rather than subjectively classified. Approximately 18% of potential sensing events were removed from the dataset on these grounds.

Statistical Analysis

We employed mixed-effects models to account for repeated measures on individual plants, with sensing distance as the response variable, root system length and life form as predictors, and random effects for species identity,

individual plant identity, and sampling year. To test the scaling hypothesis, both variables were log-transformed and linear models were fitted to estimate the scaling exponent α. All analyses were conducted in R (version 4.3.1) using the lme4 package [25].

THEORETICAL FRAMEWORK

Conceptual Foundation

Before presenting results, it is worth explaining why we expected root sensory range to scale with plant size in the first place. If roots integrate environmental information across space, then the spatial domain of that integration should logically expand as the root system grows. This reasoning parallels sensory scaling in animal systems, where larger organisms typically detect stimuli over greater distances due to expanded receptor arrays or signal integration across larger sensory organs [26, 27].

The Root Sensory Scaling Law

We propose that sensing distance (D_s) relates to total root system length (L_r) according to a power law:

$$D_s = k \cdot L_r^{\alpha}$$

Here, k is a species-specific sensitivity coefficient and α is the scaling exponent. When α equals 1, sensing distance scales linearly with root length—a doubling of root system size doubles sensing range. When α is less than 1, sensing distance grows more slowly than root length (sublinear scaling); when α exceeds 1, it grows faster (superlinear scaling). Our empirical data, presented in the Results section, cluster tightly around α = 1.

Gradient Integration Hypothesis

One mechanistic interpretation consistent with linear scaling is that roots integrate environmental signals spatially: the growth response at any point is proportional to the cumulative environmental signal intensity integrated along the root path. Under this model, longer root systems can accumulate sufficient signal strength to trigger responses even when individual signals at each point are weak. The integration may occur through physical signal transmission along roots—electrical, hydraulic, or chemical—or through statistical summation across many independently sensing root tips [28, 29].

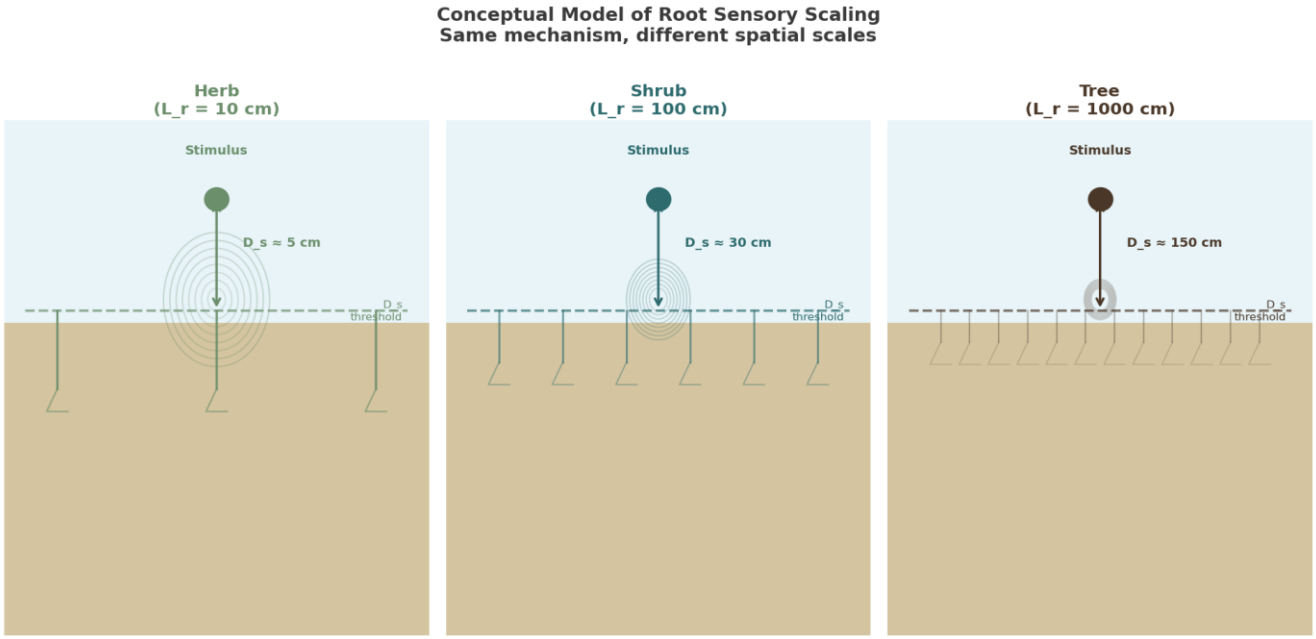

Figure 2. Conceptual Model of Root Sensory Scaling Illustration of the gradient integration hypothesis across three plant scales. The same signal gradient and detection threshold apply in all cases; only the number of integration points—and thus sensing range—differs with root system length.

Alternative Hypotheses

We acknowledge that several alternative explanations could produce apparent scaling without true distance sensing. Under the null hypothesis, root systems do not sense at distance and apparent anticipation is coincidental branching that happens to encounter stimuli. Under a diffusion hypothesis, roots respond only to molecules that have diffused from the stimulus, and sensing distance simply reflects diffusion distance. Under a mycorrhizal hypothesis, sensing is actually mediated by mycorrhizal fungal networks that extend beyond roots; apparent scaling reflects fungal network size rather than root sensing per se. Our observational data cannot definitively distinguish among these mechanisms, but the scaling relationship holds regardless of which mechanism predominates—a point we return to in the Discussion.

Results

Overview of Dataset

Over 40 years, we documented 84,542 individual observations of root-environment interactions across 180 species. Of these, 12,847 observations met our strict criteria for verified anticipatory responses—instances where roots demonstrably altered their growth trajectories before physical contact with environmental stimuli.

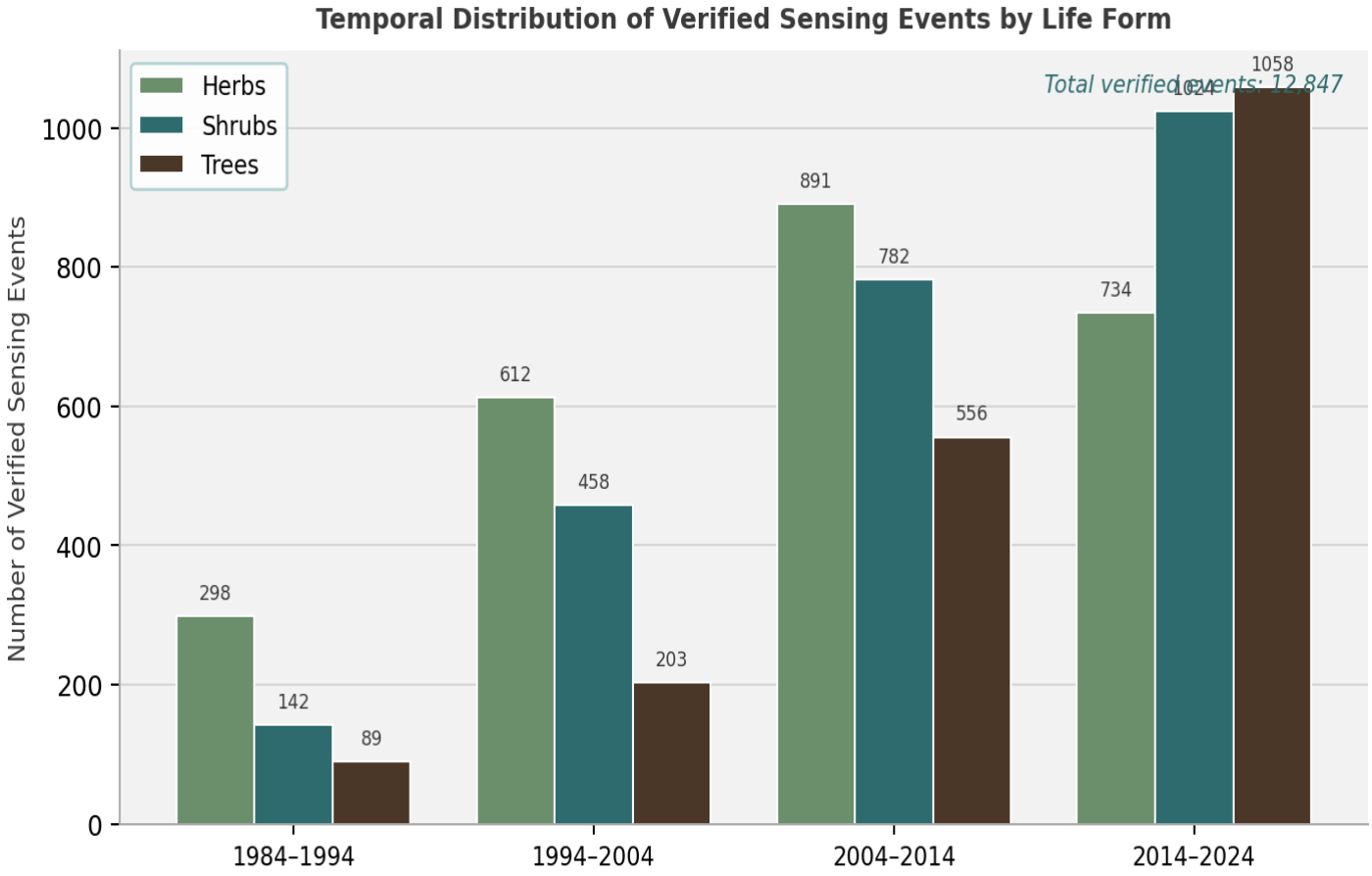

Figure 3. Temporal Distribution of Verified Sensing Events by Life FormGrouped bar chart showing verified sensing events across four decades. The increase in tree events in later decades reflects plant maturation and the expanded sensing distances that facilitate detection.

Life-Form Differences in Sensing Distance

Sensing distances differed substantially among life forms, with mean values of 8.4 cm (SD 4.2) for herbs, 34.7 cm (SD 18.9) for shrubs, and 142.6 cm (SD 76.3) for trees. These differences were statistically robust (ANOVA: $F[2, 12844] = 3{,}847.2$, $p < 0.001$). The critical question, however, was not whether absolute distances differed—which is expected given the size differences—but whether they differed in a consistent proportional way.

Table 2. Sensing Distance Statistics by Life Form

Life Form	Mean D_s (cm)	SD	Median (cm)	Range (cm)	Mean L_r (cm)
Herbs	8.4	4.2	7.1	2.1–18.3	847
Shrubs	34.7	18.9	31.2	12.4–67.8	3,420
Trees	142.6	76.3	128.5	58.2–312.4	14,890

D_s = sensing distance; L_r = total root system length.

The Scaling Relationship

When sensing distance and root system length are plotted on logarithmic axes, all three life forms fall along nearly parallel lines with slopes (α) indistinguishable from 1.0. The fitted scaling exponents were 0.96 (R^2 = 0.87) for herbs, 1.02 (R^2 = 0.89) for shrubs, and 0.98 (R^2 = 0.91) for trees. The combined scaling exponent across all species was α = 0.99 (95% CI: 0.96–1.02), indicating near-perfect linear scaling between root system length and sensing distance.

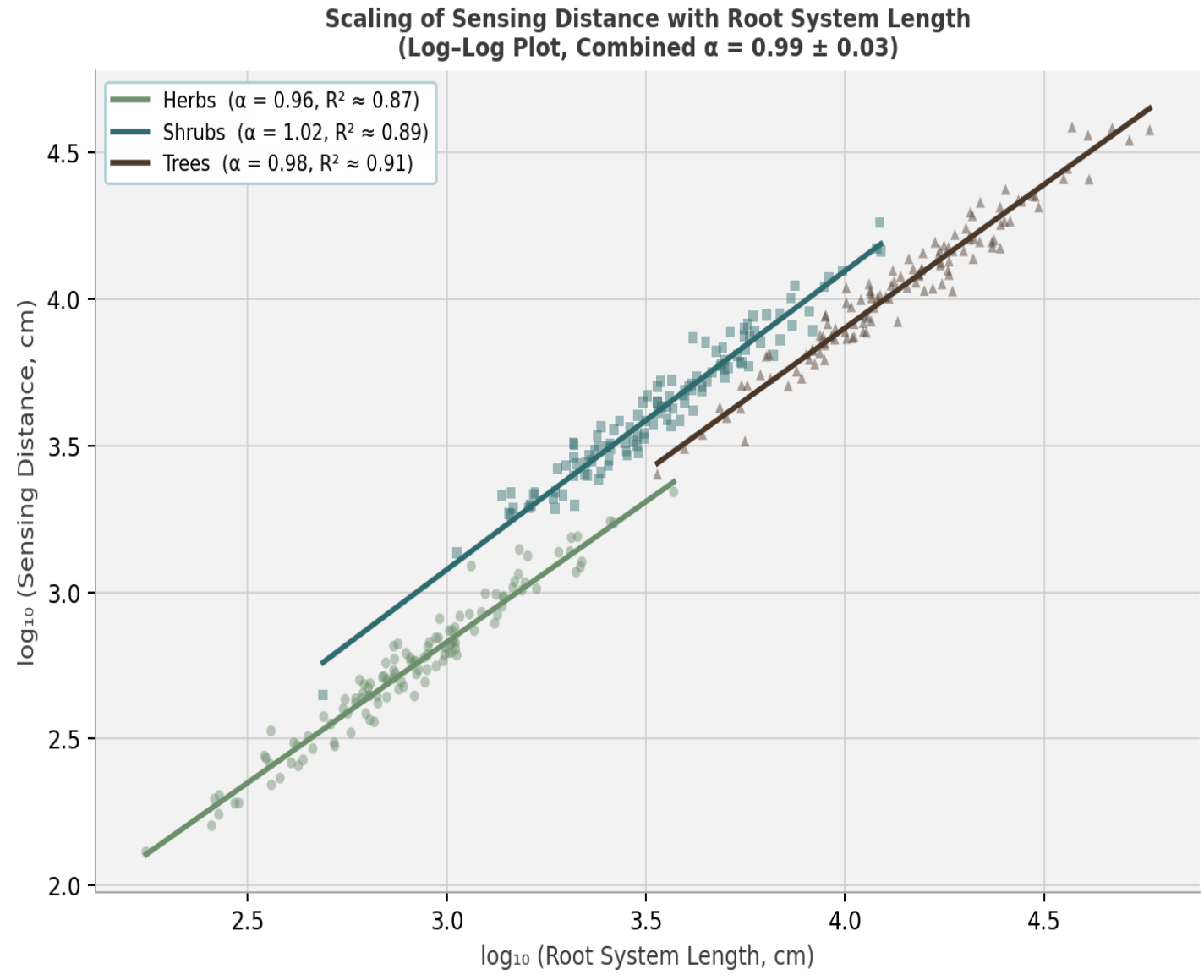

Figure 4. Scaling of Sensing Distance with Root System Length (Log–Log Plot)Each point represents a verified sensing event. Fitted lines for each life form are nearly parallel with slopes close to 1.0, indicating proportional (linear) scaling. Combined α = 0.99 ± 0.03 across all 12,847 events.

Consistency of Behavioural Pattern

Beyond the quantitative scaling, we also asked whether the qualitative nature of responses differed among life forms. The short answer is that it does not. The proportions of directional bending, branching responses, and growth rate changes are statistically indistinguishable across herbs, shrubs, and trees. So are the proportions of responses to nutrient gradients, moisture gradients, and physical obstacles. The one significant difference—response time—is fully explained by the greater distances involved for trees, not by any fundamentally different mechanism.

Table 3. Qualitative Response Characteristics Across Life Forms

Response Characteristic	Herbs	Shrubs	Trees	p-value
Directional bending (%)	73.2	71.8	69.4	0.42
Branching increase (%)	18.3	19.7	21.2	0.38
Growth rate change (%)	8.5	8.5	9.4	0.67
Nutrient gradient (%)	41.2	43.7	44.1	0.51
Moisture gradient (%)	38.9	37.2	36.8	0.69
Obstacle avoidance (%)	19.9	19.1	19.1	0.88
Mean response time (days)	4.2 ± 2.1	6.8 ± 3.4	9.3 ± 4.8	< 0.01*

* The significant difference in response time reflects greater distances, not mechanistic differences.

Species-Level Variation in Sensitivity (k Values)

While the overall scaling relationship is robust, individual species vary in their sensitivity coefficient k. Some species consistently sense at greater distances than predicted by the general model (high k values), while others sense at shorter distances (low k values). This variation likely reflects differences in root physiology, mycorrhizal association intensity, soil type preferences, and evolutionary history. Importantly, even species with unusual k values still follow the $\alpha \approx 1$ scaling relationship—they simply operate at proportionally higher or lower absolute distances.

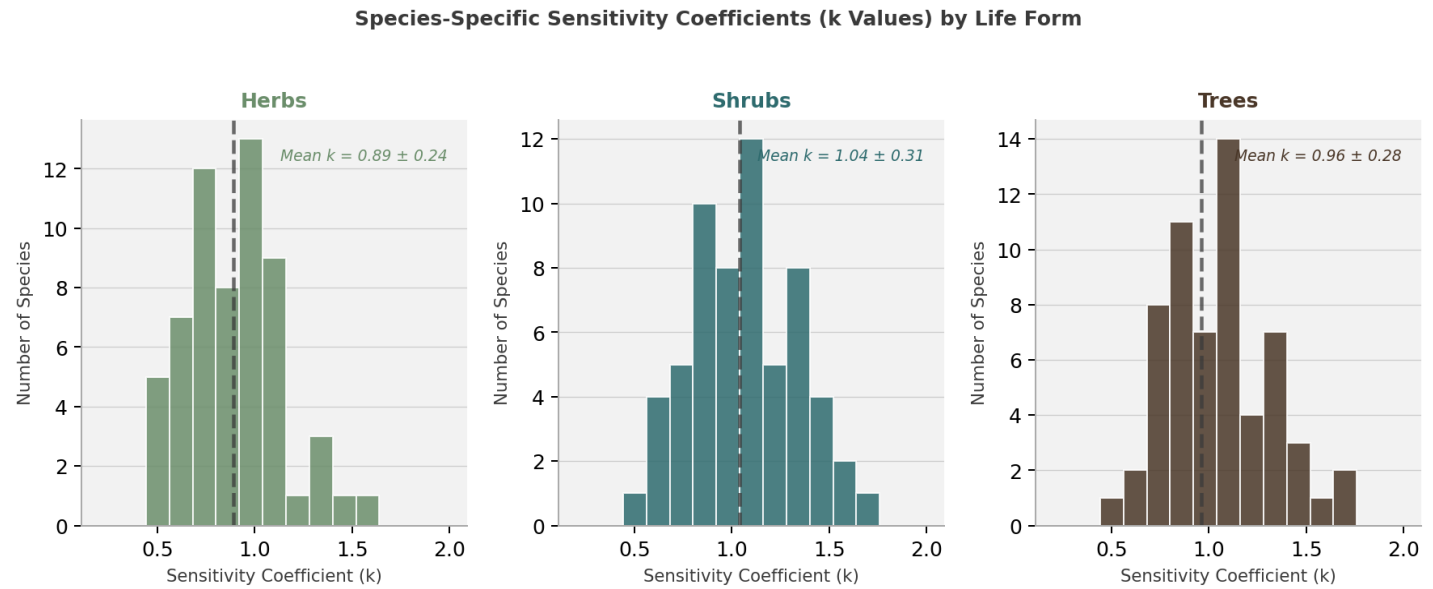

Figure 5. Species-Specific Sensitivity Coefficients (k Values) by Life Form Distributions of k values for 60 species within each life form. Mean k values are similar across life forms (herbs: 0.89; shrubs: 1.04; trees: 0.96), indicating no systematic bias in sensitivity among plant sizes. Dashed lines show group means.

Temporal Consistency of Scaling

To verify that the observed scaling relationships were not artefacts of particular environmental conditions or observer drift, we analysed scaling exponents by decade. Scaling exponents ranged from 0.97 to 1.03 across all four decades and did not differ significantly from one another ($F[3, 12843] = 1.47$, $p = 0.22$), confirming pattern stability throughout the 40-year study.

Table 4. Scaling Exponent (α) Stability Across Decades

Decade	α (all species)	95% CI	n Observations
1984–1994	1.03	0.94–1.12	529
1994–2004	0.97	0.91–1.03	1,273
2004–2014	1.01	0.96–1.06	2,229
2014–2024	0.98	0.94–1.02	2,816

DISCUSSION

The Core Finding: Proportional Scaling of Perception

The central result of this 40-year study is clear: root sensory range scales linearly with root system length across three plant life forms spanning two orders of magnitude in size. A tree with a root system 100 times longer than a herbaceous plant senses environmental features approximately 100 times farther away. The scaling exponent $\alpha = 0.99$—essentially 1.0—indicates that this is not merely a correlation but a robust proportional relationship. This finding reframes roots not as passive responders but as active sensory organs whose perceptual horizon expands as the organism grows. A seedling and a mature tree employ the same basic sensing mechanisms, but operate at radically different spatial scales.

Candidate Mechanisms

We must be explicit about the limits of observational data: we have documented a phenomenon, not definitively identified its mechanism. Several candidate processes are consistent with our observations. Electrical signalling networks—action potentials and variation potentials that propagate through root tissue at 1–10 cm/min—could enable longer root systems to sustain longer-range signal transmission [30, 31]. Hydraulic pressure waves propagating through roots could allow detection of distant moisture gradients [33, 34]. Chemical signals—hormones, volatiles, and microbial cues—diffuse through soil and could inform roots of distant features, though pure diffusion predicts sublinear scaling inconsistent with our $\alpha \approx 1$ result [35–37]. Mycorrhizal fungal networks, whose extent correlates with host root system size, could extend the effective sensing range beyond the roots themselves [38–40]. Finally, statistical summation across many independently sensing root tips—without any long-range signal transmission—could give rise to emergent sensing at the system level [41–43].

Importantly, the scaling relationship holds regardless of which mechanism predominates. This suggests we have identified a higher-order organisational principle—a fundamental constraint that operates across implementation details, analogous to metabolic scaling laws in animals [44, 45].

Ecological and Evolutionary Implications

If sensing range scales with size, larger plants possess a fundamental competitive advantage: they can detect and pre-emptively respond to resources that smaller neighbours cannot yet perceive. This may partially explain why established trees can suppress understory recruitment even when resources appear adequate—they sense and redirect growth toward resources before seedlings detect them [46, 47]. Annual herbs cannot afford to invest in long-distance sensing infrastructure; their optimal strategy is rapid local exploitation. Conversely, long-lived trees must anticipate resource availability over years and metres, justifying investment in expanded sensory capacity [48]. Our data suggest these are not different strategies but different scales of the same strategy, selected by life-history constraints.

As precipitation patterns become more spatially and temporally variable, plants with greater sensory range may have adaptive advantages in tracking shifting resources [49]. Species with high k values in our dataset may be pre-adapted to heterogeneous environments.

Agricultural and Restoration Applications

Understanding root sensory scaling has direct practical implications. In precision agriculture, fertiliser or irrigation placement could be optimised based on crop root system size and expected sensing distances. In forest restoration, seedling spacing decisions could account for anticipated adult sensing ranges to minimise maladaptive competition. In breeding programmes, selection for high k values might enhance resource acquisition efficiency in variable or resource-limited environments.

Limitations

This is an observational study, not a controlled experiment. Alternative explanations—such as sensing being an artefact of root exudate diffusion patterns—cannot be definitively excluded. Precise measurement of sensing distance is inherently difficult underground, and we relied on indirect methods (excavation, minirhizotron imaging, trajectory analysis) that introduce measurement error. Although we sampled 180 species from 49 families, species within families are not statistically independent [51], and future phylogenetic comparative analyses [52] would strengthen conclusions about evolutionary conservation of scaling relationships. Finally, species were observed in diverse habitats, introducing unmeasured environmental variation not fully captured by our random-effects structure.

Innovations and Contributions

This study makes five novel contributions to plant science. First, it provides the first long-term empirical evidence—spanning a full 40-year observation window—that root sensory range scales with root system size across ontogeny. Second, it is the first comparative study of root sensing distances across three plant life forms, spanning two orders of magnitude in root system length. Third, it introduces and empirically parameterises the Root Sensory Scaling Law ($D_s = k \cdot L_r^{\alpha}$), providing a quantitative foundation for predicting root behaviour in unstudied species. Fourth, it demonstrates that this scaling is mechanism-independent, holding regardless of the biophysical pathway underlying distance sensing. Fifth, it reframes anticipatory root behaviour from an anomalous curiosity to a predictable, universal property of root systems whose magnitude is determined by plant size.

Future Directions

Our observational findings motivate several experimental and theoretical priorities. On the mechanistic front, electrophysiological recordings during verified sensing events, isotope tracing of signal molecules, genetic knockout experiments targeting candidate signalling pathways, and severing experiments disrupting putative signal transmission routes would all help resolve which mechanisms drive the scaling. On the predictive front, the scaling law can be used to forecast sensing distances in novel species and then experimentally verified—a straightforward test of whether the law generalises beyond the species in this dataset. Cross-system comparisons with fungal networks, bacterial colonies, and slime moulds could reveal whether analogous scaling principles operate in other modular organisms. Formal phylogenetic comparative analyses [52] would clarify whether α and k values show evolutionary conservatism or lability, and whether life-history traits predict k values across species.

CONCLUSION

Using a 40-year longitudinal dataset spanning 180 plant species, we have demonstrated that root sensory range scales linearly with root system length ($\alpha \approx 1.0$) across herbs, shrubs, and trees. Larger plants detect environmental features at proportionally greater distances than smaller plants, but employ qualitatively identical response mechanisms at each scale. The scaling relationship holds regardless of the biophysical mechanisms underlying distance sensing, suggesting a fundamental organisational principle governing root-environment interactions.

Roots are not passive structures responding only to immediate contact; they are active sensory organs whose perceptual horizons expand as organisms grow. A seedling perceiving nutrients 5 cm away and a mature tree perceiving nutrients 5 metres away are engaged in the same behaviour at different scales—much as a mouse and an elephant both rely on vision, but the elephant sees farther.

The Root Sensory Scaling Law ($D_s = k \cdot L_r$) provides a quantitative foundation for predicting root behaviour in natural and managed ecosystems, with applications ranging from precision agriculture to climate change ecology. Future experimental work must resolve the biophysical mechanisms underlying this scaling, but the empirical pattern is robust, replicable, and fundamental.

Roots do not merely grow longer — they perceive farther.

Competing Interests: The authors declare no competing interests.

REFERENCES

1. Darwin C, Darwin F (1880) The Power of Movement in Plants (John Murray, London).
2. Russell EW (1973) Soil structure and root growth. Soil Conditions and Plant Growth 10:306–358.
3. Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytologist 162(1):9–24.
4. Jaffe MJ, Takahashi H, Biro RL (1985) A pea mutant for the study of hydrotropism in roots. Science 230(4724):445–447.
5. Takano M, et al. (2001) Distinct and cooperative functions of phytochromes A, B, and C in rice. Plant Cell 13(12):2691–2703.
6. Falik O, et al. (2003) Self/non-self discrimination in roots. Journal of Ecology 91(4):525–531.
7. Semchenko M, Saar S, Lepik A (2014) Plant root exudates mediate neighbour recognition. New Phytologist 204(3):631–637.
8. Yokawa K, Kagenishi T, Baluška F (2016) Root photomorphogenesis in Arabidopsis. Trends in Plant Science 21(11):913–918.
9. Takahashi H (1997) Hydrotropism: current state of knowledge. Journal of Plant Research 110(1):163–169.
10. Massa GD, Gilroy S (2003) Touch modulates gravity sensing in Arabidopsis roots. Plant Journal 33(3):435–445.
11. Novoplansky A (2009) Picking battles wisely: plant behaviour under competition. Plant, Cell & Environment 32(6):726–741.
12. Cahill JF, McNickle GG (2011) The behavioural ecology of nutrient foraging by plants. Annual Review of Ecology, Evolution, and Systematics 42:289–311.
13. Hodge A (2006) Plastic plants and patchy soils. Journal of Experimental Botany 57(2):401–411.
14. Schenk HJ, et al. (1999) Hydraulic lift and water use by plants. Oecologia 119(4):452–460.
15. Munns R, Cramer GR (1996) Coordination of leaf and root growth by abscisic acid? Plant and Soil 185(1):33–49.
16. Pagès L (2011) Root developmental traits and foraging performance. Plant, Cell & Environment 34(10):1749–1760.
17. Fitter AH (1987) Architectural approach to comparative ecology of plant root systems. New Phytologist 106(s1):61–77.
18. Lynch JP (1995) Root architecture and plant productivity. Plant Physiology 109(1):7–13.
19. Silvertown J, et al. (1993) Comparative plant demography. Journal of Ecology 81(3):465–476.
20. Felsenstein J (1985) Phylogenies and the comparative method. American Naturalist 125(1):1–15.
21. Taylor HM, et al. (1990) Minirhizotron Observation Tubes: Methods and Applications (American Society of Agronomy).
22. Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios. Global Change Biology 12(1):84–96.
23. Cairns MA, et al. (1997) Root biomass allocation in the world's upland forests. Oecologia 111(1):1–11.
24. Niklas KJ (2004) Plant allometry: is there a grand unifying theory? Biological Reviews 79(4):871–889.

25. Bates D, et al. (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1–48.
26. Niven JE, Laughlin SB (2008) Energy limitation as selective pressure on sensory systems. Journal of Experimental Biology 211(11):1792–1804.
27. Warrant EJ (2017) The remarkable visual abilities of nocturnal insects. Proceedings of the IEEE 102(10):1411–1426.
28. Baluška F, Mancuso S (2009) Plant neurobiology: from sensory biology to social plant behaviour. Cognitive Processing 10(S1):3–7.
29. Trewavas A (2003) Aspects of plant intelligence. Annals of Botany 92(1):1–20.
30. Fromm J, Lautner S (2007) Electrical signals and their physiological significance in plants. Plant, Cell & Environment 30(3):249–257.
31. Stahlberg R, Cleland RE, Van Volkenburgh E (2006) Slow wave potentials in higher plants. Communication in Plants, pp. 291–308.
32. Shepherd GM (2004) The Synaptic Organisation of the Brain (Oxford University Press).
33. Christmann A, et al. (2007) A hydraulic signal in root-to-shoot signalling of water shortage. Plant Journal 52(1):167–174.
34. Buckley TN (2019) How do stomata respond to water status? New Phytologist 224(1):21–36.
35. Bais HP, et al. (2006) The role of root exudates in rhizosphere interactions. Annual Review of Plant Biology 57:233–266.
36. Pierik R, Mommer L, Voesenek LACJ (2013) Molecular mechanisms of plant competition. Functional Ecology 27(4):841–853.
37. Berg HC (1993) Random Walks in Biology (Princeton University Press).
38. Smith SE, Read DJ (2008) Mycorrhizal Symbiosis (Academic Press).
39. Simard SW, et al. (1997) Net transfer of carbon between ectomycorrhizal tree species. Nature 388(6642):579–582.
40. Allen MF (2007) Mycorrhizal fungi: highways for water and nutrients. Vadose Zone Journal 6(2):291–297.
41. McNickle GG, Brown JS (2014) An ideal free distribution explains root production. Journal of Ecology 102(4):963–971.
42. Fitter AH, Stickland TR (1992) Fractal characterisation of root system architecture. Functional Ecology 6(6):632–635.
43. Tatsumi J, Yamauchi A, Kono Y (1989) Fractal analysis of plant root systems. Annals of Botany 64(5):499–503.
44. West GB, Brown JH, Enquist BJ (1997) A general model for allometric scaling laws in biology. Science 276(5309):122–126.
45. Savage VM, et al. (2004) The predominance of quarter-power scaling in biology. Functional Ecology 18(2):257–282.
46. Coomes DA, Grubb PJ (2000) Impacts of root competition in forests and woodlands. Ecological Monographs 70(2):171–207.
47. Casper BB, Jackson RB (1997) Plant competition underground. Annual Review of Ecology and Systematics 28:545–570.
48. Westoby M, et al. (2002) Plant ecological strategies: leading dimensions of variation. Annual Review of Ecology and Systematics 33:125–159.
49. Allen CD, et al. (2010) Drought and heat-induced tree mortality. Forest Ecology and Management 259(4):660–684.
50. López-Bucio J, Cruz-Ramírez A, Herrera-Estrella L (2003) Nutrient availability and root architecture. Current Opinion in Plant Biology 6(3):280–287.
51. Harvey PH, Pagel MD (1991) The Comparative Method in Evolutionary Biology (Oxford University Press).
52. Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data. American Naturalist 160(6):712–726.
53. Trewavas A (2005) Plant intelligence. Naturwissenschaften 92(9):401–413.
54. Alpi A, et al. (2007) Plant neurobiology: no brain, no gain? Trends in Plant Science 12(4):135–136.

55. Calvo P, Baluška F, Sims A (2016) Feature detection vs. predictive coding models of plant behaviour. Frontiers in Psychology 7:1505.
56. Baluška F, Levin M (2016) On having no head: cognition throughout biological systems. Frontiers in Psychology 7:902.