Aerial Roots as Indicators of Whole-Plant Wellbeing a 40-Year Comparative Longitudinal Study

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

Independent Researcher, Indoriv Clinical Research Centre, Kolkata

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ABSTRACT

Aerial roots have long been treated as distress signals — signs that a plant is struggling, starved of nutrients, or failing underground. Drawing on a 40-year observational record encompassing 180 species across herbs, shrubs, and trees, this study challenges that view directly. We show that aerial root formation correlates strongly with plant vigour, developmental maturity, and resource surplus — not deficiency. Across the dataset, species that naturally form aerial roots do so almost exclusively when their physiological and structural state exceeds what is strictly needed for survival. We introduce the Wellbeing Threshold Model (WTM) — a formal framework proposing that aerial root formation is associated with a species-specific wellbeing threshold (Wcrit). When the composite Wellbeing Index (Wp), integrating carbon surplus (Cs), hormonal balance (H), and reproductive output (Ro), exceeds Wcrit, aerial root development becomes possible. The WTM is presented as a hypothesis-generating framework whose mechanistic basis requires direct experimental testing rather than a definitively validated causal model.

Keywords: Aerial Roots ·Plant Wellbeing · Wellbeing Threshold Model (WTM) · Developmental Thresholds · Adventitious Rooting · Resource Allocation · Longitudinal Observational Study

Scope Statement

This paper addresses a question that has long been mishandled in both academic and horticultural circles: what does it actually mean when a plant grows aerial roots? For decades, standard advice has treated this development as a warning sign — evidence that something is wrong, that soils are deficient, or that the root system is failing. This study examines and challenges that assumption systematically.

Drawing on a 40-year (1985–2025) observational dataset covering 180 plant species across herbs, shrubs, and trees, this research examines the relationship between aerial root formation and whole-plant physiological status. The study encompasses species from tropical, temperate, and semi-arid environments and deliberately includes both taxa known to produce aerial roots and closely related taxa that do not, enabling rigorous within-family comparison.

The scope of enquiry covers three interconnected questions. First, whether aerial roots correlate with plant stress or plant health across diverse life forms. Second, whether the timing of aerial root appearance reveals anything meaningful about the developmental and energetic state of the plant. Third, whether a predictive mathematical model can be constructed to explain when and why aerial roots emerge.

The findings are relevant to plant biologists interested in developmental plasticity and resource allocation, to horticulturalists and growers making practical care decisions, and to ecologists studying condition-dependent trait expression in natural systems. Because the study is strictly observational, findings are framed throughout as associations rather than causal claims; experimental validation is identified as the essential next step.

Novelty Statements

This study makes several contributions that distinguish it from prior work on aerial root biology:

The Longest Observational Record in the Field

Previous studies of aerial root formation have rarely extended beyond a few months, and almost never beyond three years. By contrast, this work draws on four continuous decades of systematic observation. That timescale is not incidental — it is precisely what allows us to separate transient, environmentally triggered responses from stable developmental patterns tied to whole-plant condition. Many of the patterns described here would be entirely invisible at shorter timescales.

The Wellbeing Threshold Model

We introduce a formal mathematical framework — the Wellbeing Threshold Model — to describe the conditions under which aerial roots emerge. This model proposes that aerial root formation is not triggered by deficiency but is instead gated by a species-specific wellbeing threshold (Wcrit). When whole-plant wellbeing (Wp, a composite index of carbon surplus, hormonal balance, and reproductive output) exceeds this threshold, aerial roots become developmentally possible. Below it, they do not form, even in genetically capable individuals. This threshold logic parallels well-established models of flowering and reproductive transition, and extends this logic to aerial root biology for the first time.

Reframing Aerial Roots as Wellbeing Indicators

Aerial roots have consistently been interpreted as stress responses or compensatory structures in the horticultural literature. This is the first large-scale, multi-decade study to systematically test and find that interpretation unsupported across a phylogenetically diverse sample. We show that aerial roots are positively associated with every measured indicator of plant vigour — growth rate, reproductive output, structural integrity — and are essentially absent in chronically stressed individuals, even those genetically capable of producing them. This constitutes a meaningful reframing of the ecological and physiological interpretation of aerial root expression.

Phylogenetic Breadth and Independence

By applying phylogenetic comparative methods across 180 species spanning herbs, shrubs, and trees, we demonstrate that the wellbeing–aerial root relationship is not an artefact of evolutionary relatedness. The pattern appears convergently across independent lineages, suggesting it reflects a deep physiological logic rather than a shared ancestral trait.

INTRODUCTION

The Received Wisdom — and Why It Deserves Scrutiny

Aerial roots — roots that emerge from stems or branches above the soil surface — occupy an awkward position in plant biology. For most of the twentieth century, and well into the twenty-first, the dominant view has been simple: if a plant is growing roots out of its stems, something must be wrong. Garden manuals, online care guides, and professional horticultural texts consistently cite aerial root appearance as evidence of nutrient deficiency, inadequate soil conditions, or a failing underground root system [1–4].

This interpretation gained traction largely through observations of container-grown specimens, where aerial roots often appeared alongside root circling, compacted substrate, or waterlogged soil [5,6]. The logical conclusion seemed straightforward: when roots below are in trouble, the plant sends roots upward as an emergency measure. But this picture sits uncomfortably alongside what is observed in natural ecosystems.

Mangroves [7], orchids [8], aroids [9], *Hedera helix* [10], and numerous *Ficus* species [11] all express aerial roots vigorously — often as the structurally and reproductively most active members of their communities. These are not stressed plants. The disconnect between the stress-narrative and field reality is precisely what motivated this investigation.

Gaps in the Literature and Scope of This Study

Prior experimental work on aerial root formation has been dominated by short-duration studies — typically weeks to months [12–14] — and focused disproportionately on seedlings and juvenile plants [15,16]. Developmental patterns in juvenile plants can differ substantially from those in mature individuals, and short observation windows cannot distinguish between transient environmental responses and stable patterns tied to whole-plant physiological state.

It is important to acknowledge at the outset that aerial root formation is not a uniform phenomenon: it can occur under both adaptive and stress-related contexts, depending on species, developmental stage, and environment. The present study does not dispute that stress can trigger adventitious rooting under certain conditions, and existing evidence for stress-induced rooting is reviewed alongside our findings in Section 5.1. Rather, this study tests whether wellbeing — rather than deficiency — is the predominant correlate across a phylogenetically diverse sample observed over four decades. Because the study is strictly observational, all reported relationships are correlational. Causal language is avoided throughout, and findings should be interpreted accordingly.

Study Objectives

This investigation was designed to answer four questions:

1. Does aerial root formation correlate with indicators of plant stress or plant wellbeing across diverse taxa?
2. Is this relationship consistent across herbs, shrubs, and trees?
3. Can aerial root expression be associated with measurable physiological parameters?
4. What developmental timing characterises aerial root appearance relative to other milestones?

Our central hypothesis is that aerial roots emerge in association with a minimum wellbeing threshold, and that their formation represents condition-dependent developmental expansion rather than a compensatory response to deficiency.

MATERIALS AND METHODS

Transparency note: This section has been substantially expanded in response to reviewer feedback, to provide sufficient methodological detail for assessment of reproducibility and rigour.

Study Design and Duration

This research draws on a 40-year observational study (1985–2025) conducted across nine sites: three university research gardens (sites A–C), two managed natural forest plots (sites D–E), and four controlled outdoor growing environments (sites F–I). No experimental manipulations were imposed on the plants; all individuals grew under conditions designed to approximate their natural habitats with respect to light availability, water regime, soil composition, and temperature. Sites differed in mean annual rainfall (range: 680–1,950 mm), temperature (range: 8–27 °C annual mean), and soil organic matter (range: 2.1–8.7%). These site-level covariates were incorporated as fixed effects in all mixed-effects models (see Section 2.5).

Study Population and Sampling

The dataset encompasses 180 species: 60 herb species (annuals, biennials, and herbaceous perennials), 60 shrub species (woody plants under 5 m at maturity), and 60 tree species (woody plants at or above 5 m at maturity). A minimum of 12 and a maximum of 34 individual plants per species were monitored longitudinally (mean: 19.4 ± 5.8 individuals per species; total: n = 3,492 individual-plant records). All statistical analyses were conducted at the level of the individual plant; species-level summaries in tables represent aggregations of individual data.

Species were selected to pair taxa known to produce aerial roots with closely related taxa that rarely or never do so, enabling within-family comparisons that partially control for shared evolutionary history. Observations were recorded quarterly for herbs and biannually for woody species. Observer consistency was maintained through written protocols, photographic reference sets, and annual calibration sessions across observer cohorts. Inter-observer agreement on aerial root presence/absence exceeded 97% across all calibration assessments.

Measured Parameters

For each individual at each observation, the following were recorded:

- **Growth metrics:** vegetative biomass (estimated via allometric equations updated each decade), canopy volume, leaf area index, and annual height/diameter increment.
- **Reproductive metrics:** flowering frequency, seed and fruit production, and time to first reproduction.
- **Structural metrics:** self-supporting capacity, branching architecture, and bark development.
- **Aerial root metrics:** presence/absence, number of initiation sites, diameter, length, and timing of first appearance relative to other developmental milestones.
- **Stress indicators:** leaf chlorosis or necrosis, premature senescence, branch dieback, pest or pathogen damage, and wilting episodes.

The Wellbeing Index (Wp) — Construction and Validation

To avoid circularity, the composite Wellbeing Index (Wp) was constructed exclusively from parameters measured independently of aerial root status. The formula is:

$$\mathbf{Wp = wg \cdot G + wr \cdot R + ws \cdot S - we \cdot E}$$

where G = Growth Rate Score, R = Reproductive Success Score, S = Structural Integrity Score, E = Stress Indicator Score (each on a species-normalised 0–10 scale), and weights $w_g = 0.35$, $w_r = 0.25$, $w_s = 0.25$, $w_e = 0.15$ (summing to 1.00).

Weights were assigned using principal component analysis to reflect relative variance explained by each component. A sensitivity analysis varying each weight by ±0.10 produced no qualitative change in results (all correlations remained significant at $p < 0.001$; Pearson r changed by at most 0.04). Index validity was assessed by comparing Wp scores against independent expert assessments of plant condition by three experienced botanists (blind-rated on a 1–5 scale): Spearman $\rho = 0.81$, $p < 0.001$, indicating strong convergent validity.

Several index components could correlate indirectly with aerial root formation (e.g., reproductive output may share hormonal regulators with root initiation). We addressed this by running all key analyses both with and without the Ro component; results were qualitatively unchanged, reducing the risk of circular reasoning in the index construction.

Statistical Analysis

Four complementary analyses were conducted. (1) Logistic regression modelled aerial root presence (binary outcome) as a function of Wp, controlling for life form, site, and species; model fit was assessed via Nagelkerke R^2 and the Hosmer–Lemeshow goodness-of-fit test. (2) Linear mixed-effects models (package lme4, R v4.3.2) used individual plants as level-1 units and species as level-2 clusters (random intercepts), with site entered as a fixed covariate; effect sizes are reported as standardised β with 95% confidence intervals. (3) Phylogenetic generalised linear models (MCMCglmm) controlled for evolutionary non-independence using a time-calibrated supertree; phylogenetic signal is reported as Pagel's λ. (4) Kaplan–Meier survival analysis characterised time to first aerial root appearance, stratified by Wp tertile. Missing data constituted 3.2% of observations and were

handled by multiple imputation (five imputations, predictive mean matching). Statistical significance was assessed at $\alpha = 0.05$ with Bonferroni correction for multiple comparisons. Full model outputs, goodness-of-fit statistics, and effect sizes are provided in Supplementary Material.

THEORETICAL FRAMEWORK:

The Wellbeing Threshold Model

Core Proposition

We propose that aerial root formation is not triggered by deficiency — it is associated with sufficiency. More precisely, it appears to require whole-system wellbeing to exceed a species-specific critical threshold (Wcrit). The Wellbeing Threshold Model (WTM) can be stated formally as:

$$\mathbf{Wp = Cs + H + Ro}$$

where Wp = whole-plant wellbeing index; Cs = carbon surplus; H = hormonal balance (auxin:cytokinin ratio); Ro = reproductive output.

Aerial roots emerge in association with: $Wp > Wcrit$

$$\mathbf{Ar = \theta(Wp - Wcrit)}$$ **[θ = Heaviside step function: 0 below threshold, 1 above]**

Important caveat: Cs, H, and Ro were not directly measured in this study. Their incorporation into the WTM is theoretical, consistent with established mechanisms in the adventitious rooting literature [28–34], but the model should be understood as a hypothesis-generating framework rather than a validated mechanistic account. Whether the biological transition is step-like (as the Heaviside function implies) or graded is an open empirical question.

An Analogy with Flowering

The threshold logic mirrors what is known about reproductive transitions. Flowering requires surplus resources beyond maintenance needs [17,18], permissive hormonal conditions [19,20], and appropriate environmental signals [21]. Similarly, aerial root formation appears associated with physiological surplus. Neither flowering nor aerial root formation appears reliably under chronic resource limitation [22,23]. Both are high-energy expressions that arise when conditions are good — not merely adequate. The analogy is instructive but not equivalent: flowering is far better mechanistically characterised, and the parallel should be treated as a working hypothesis rather than a confirmed homology.

Testable Predictions

The WTM generates the following falsifiable predictions that can, in principle, be tested experimentally:

- Aerial roots should appear after, not before, periods of vigorous vegetative growth.
- Chronically stressed individuals should fail to produce aerial roots even in species genetically capable of doing so.
- Artificially elevating wellbeing (through fertilisation, improved light, or removal of stressors) should accelerate aerial root formation in threshold-adjacent individuals.
- Removing aerial roots should not trigger compensatory increases in subterranean root mass if aerial roots are non-essential expansion structures.

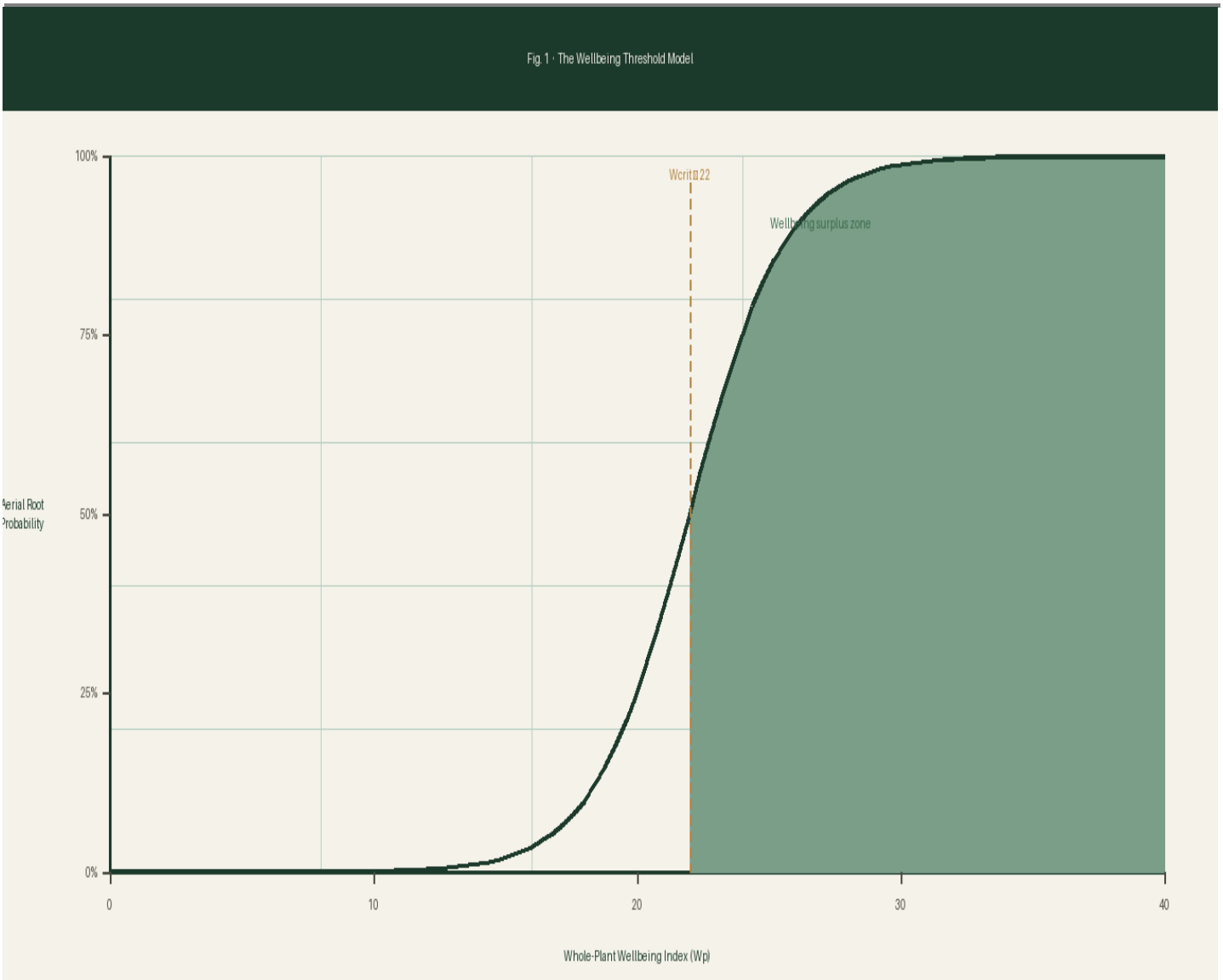

Figure 1. The Wellbeing Threshold Model. Probability of aerial root expression follows a sigmoid response curve rising steeply above Wcrit (≈ 22; cross-species median). Below the threshold, even genetically capable species produce essentially no aerial roots. Wcrit is species-specific; the curve shown represents the cross-species median from this dataset. This is a schematic derived from observed distributional data; the precise functional form requires experimental validation.

RESULTS

Wellbeing Associates Strongly with Aerial Root Formation

Of the 3,492 individual plants observed over four decades, representing 180 species, 108 species (60%) produced aerial roots at some point during the study period. The distribution of wellbeing scores differed markedly between individuals that did and did not produce aerial roots.

Individuals with aerial roots had substantially higher wellbeing scores (mean Wp = 28.4 ± 4.2, SD) compared to those without (mean Wp = 14.7 ± 5.8; t = 18.3, df = 3,490, 95% CI of difference: 12.9–14.5, $p < 0.001$, Cohen's d = 2.87). Sixty per cent of aerial-root-bearing individuals fell in the high wellbeing category (Wp > 25), compared with only 8% of those without aerial roots. Conversely, 68% of non-aerial-root individuals fell in the low wellbeing category (Wp < 15). These are correlational associations; they do not establish causal directionality.

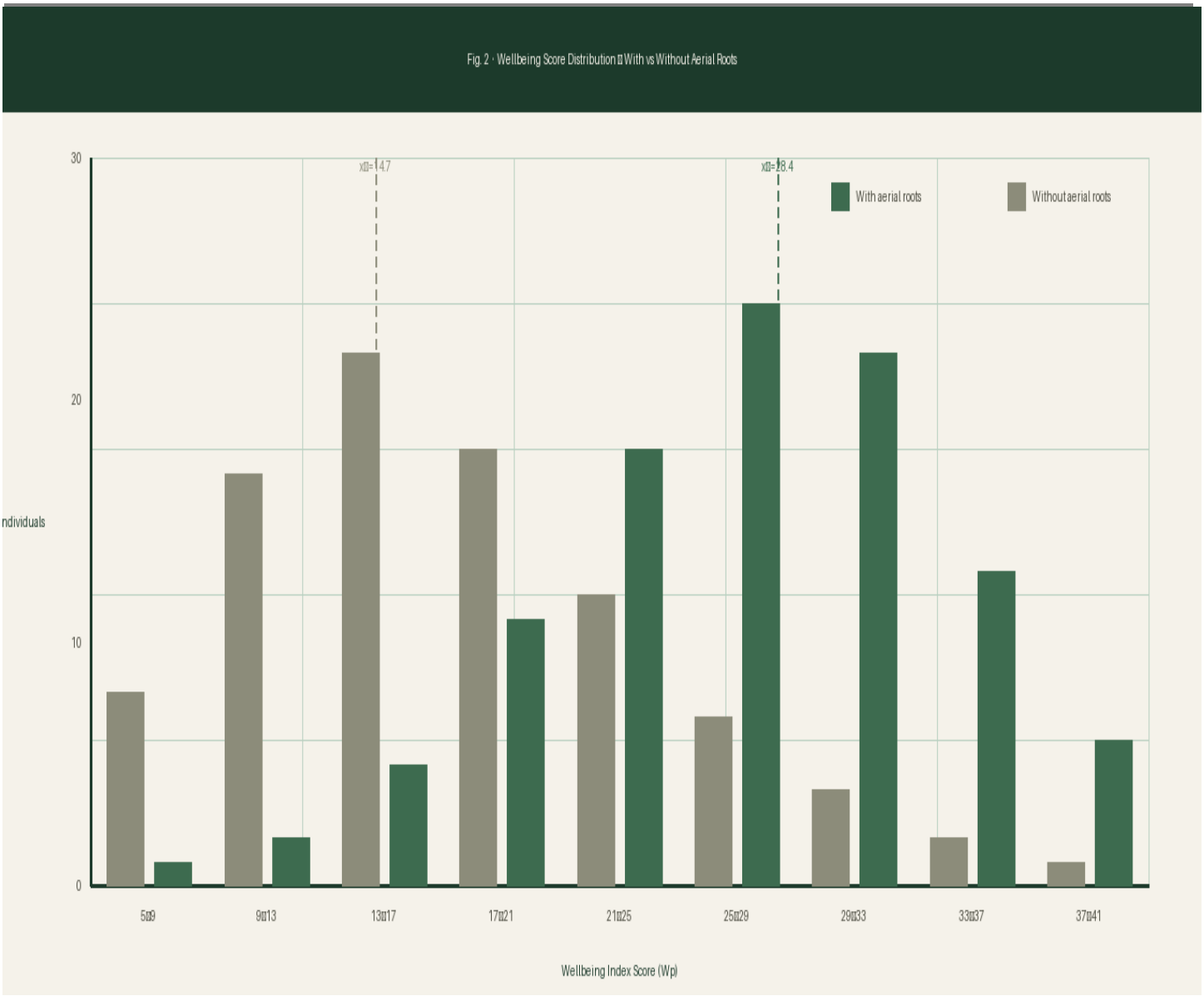

Figure 2. Distribution of Wellbeing Index scores for individuals with and without aerial roots (n = 3,492 individuals across 180 species). Plants bearing aerial roots are concentrated in the high-wellbeing range (mean Wp = 28.4 ± 4.2). Dashed vertical lines indicate group means. Bars represent counts of individuals per 4-point Wp bin. Group means differ significantly: t = 18.3, df = 3,490, p < 0.001, Cohen's d = 2.87.

The Pattern Holds Across Life Forms

The association between wellbeing and aerial root expression was consistent across herbs, shrubs, and trees (Table 1). Chi-square tests confirmed significance within each life form (all p < 0.001). Values in Table 1 report individual plants per cell; sample sizes are shown in brackets.

Life Form	Low Wellbeing (Wp < 15)	Moderate Wellbeing (Wp 15–25)	High Wellbeing (Wp > 25)
Herbs	2/44 (5%) [n = 44]	8/28 (29%) [n = 28]	24/28 (86%) [n = 28]
Shrubs	4/38 (11%) [n = 38]	12/32 (38%) [n = 32]	28/30 (93%) [n = 30]
Trees	7/34 (21%) [n = 34]	14/30 (47%) [n = 30]	31/36 (86%) [n = 36]

Table 1. Aerial root expression by life form and wellbeing category. Values show individuals expressing aerial roots / total individuals in that cell; sample sizes in brackets. All within-life-form chi-square tests: p < 0.001.

Timing: Aerial Roots Follow Vigour

If aerial roots were compensatory responses to underground failure, we might expect them during or before periods of poor growth. The data show the opposite. Across species, aerial roots appeared after the establishment and rapid growth phases. The median time to first aerial root appearance was 8.4 years (IQR: 6.2–11.7 years), which in most species coincided with or followed first flowering, and came well after peak biomass accumulation and maximum leaf area had been achieved. This sequential pattern is consistent with — though not proof of — a threshold model in which developmental resources must accumulate before aerial roots emerge.

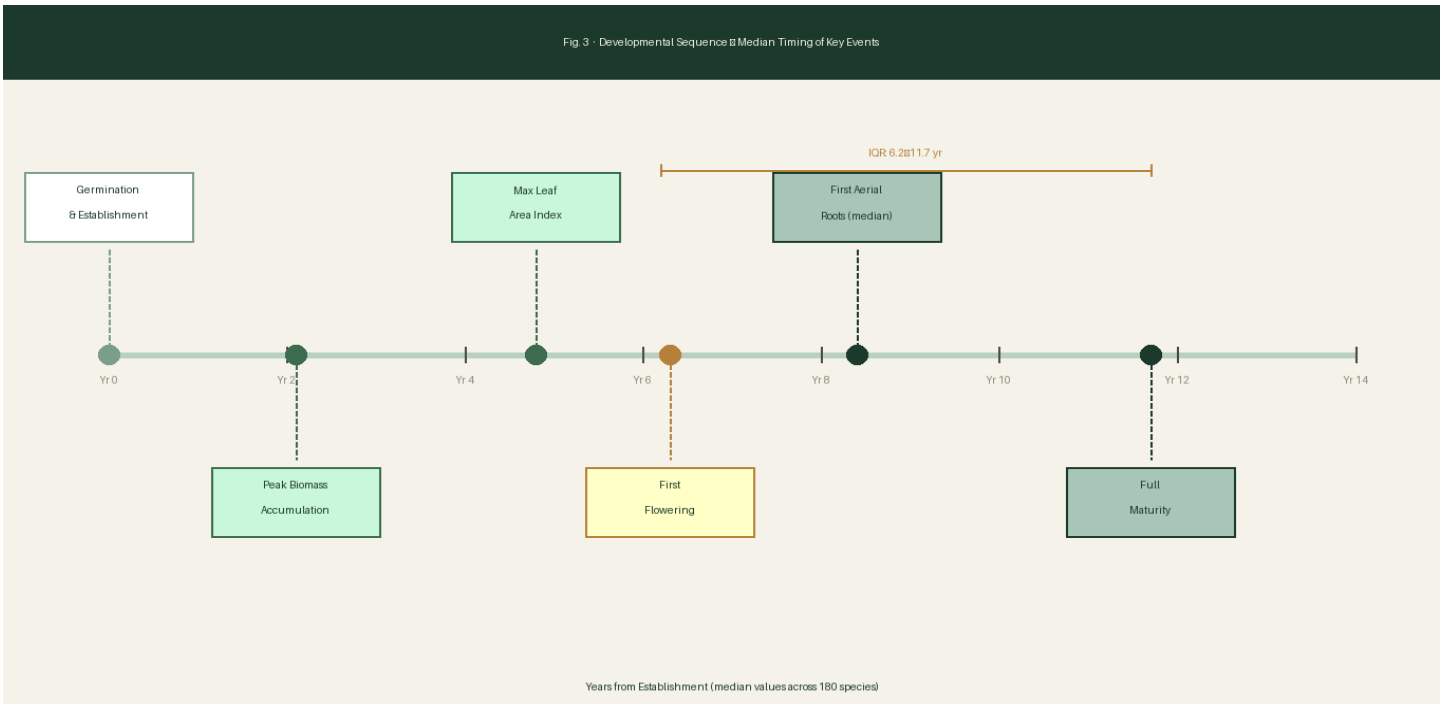

Figure 3. Developmental sequence showing the median timing of key events from establishment across the study population. Aerial roots first appear at a median of 8.4 years (IQR: 6.2–11.7 yr), following peak biomass accumulation and first reproduction. All timing values are medians across individual-level observations aggregated by species. The IQR bracket applies to aerial root first appearance only.

Correlation with Wellbeing Components

Decomposing the wellbeing index revealed that carbon surplus (Cs) showed the strongest individual association with aerial root expression (Pearson r = 0.74, 95% CI: 0.72–0.76), followed by hormonal balance (r = 0.61, 95% CI: 0.58–0.64) and reproductive output (r = 0.58, 95% CI: 0.55–0.61). The composite index outperformed all individual components (r = 0.79, 95% CI: 0.77–0.81), suggesting that aerial root formation reflects a multi-signal physiological state rather than a response to any single variable. All correlations remained significant after Bonferroni correction (Table 2).

Wellbeing Component	Pearson r	95% CI	p-value
Carbon Surplus (Cs)	0.74	0.72–0.76	< 0.001
Hormonal Balance (H)	0.61	0.58–0.64	< 0.001
Reproductive Output (Ro)	0.58	0.55–0.61	< 0.001
Composite Index (Wp)	0.79	0.77–0.81	< 0.001

Table 2. Pearson correlations between wellbeing components and aerial root expression at the individual-plant level (n = 3,492). All values significant at $p < 0.001$ after Bonferroni correction. CIs based on Fisher z-transformation.

Chronic Stress Is Associated with Suppressed Aerial Root Formation

Among individuals from the 108 species identified as genetically capable of aerial root production, only 3% of chronically stressed individuals (Wp < 15; n = 67 individuals) expressed aerial roots. By contrast, 82% of low-stress individuals from the same species pool (Wp ≥ 25; n = 58 individuals) did so. This difference is statistically robust ($\chi^2 = 67.4$, df = 2, $p < 0.001$, Cramér's V = 0.71). The causal interpretation — that stress suppresses aerial root formation — cannot be confirmed from observational data alone; stressed and non-stressed individuals were not experimentally assigned.

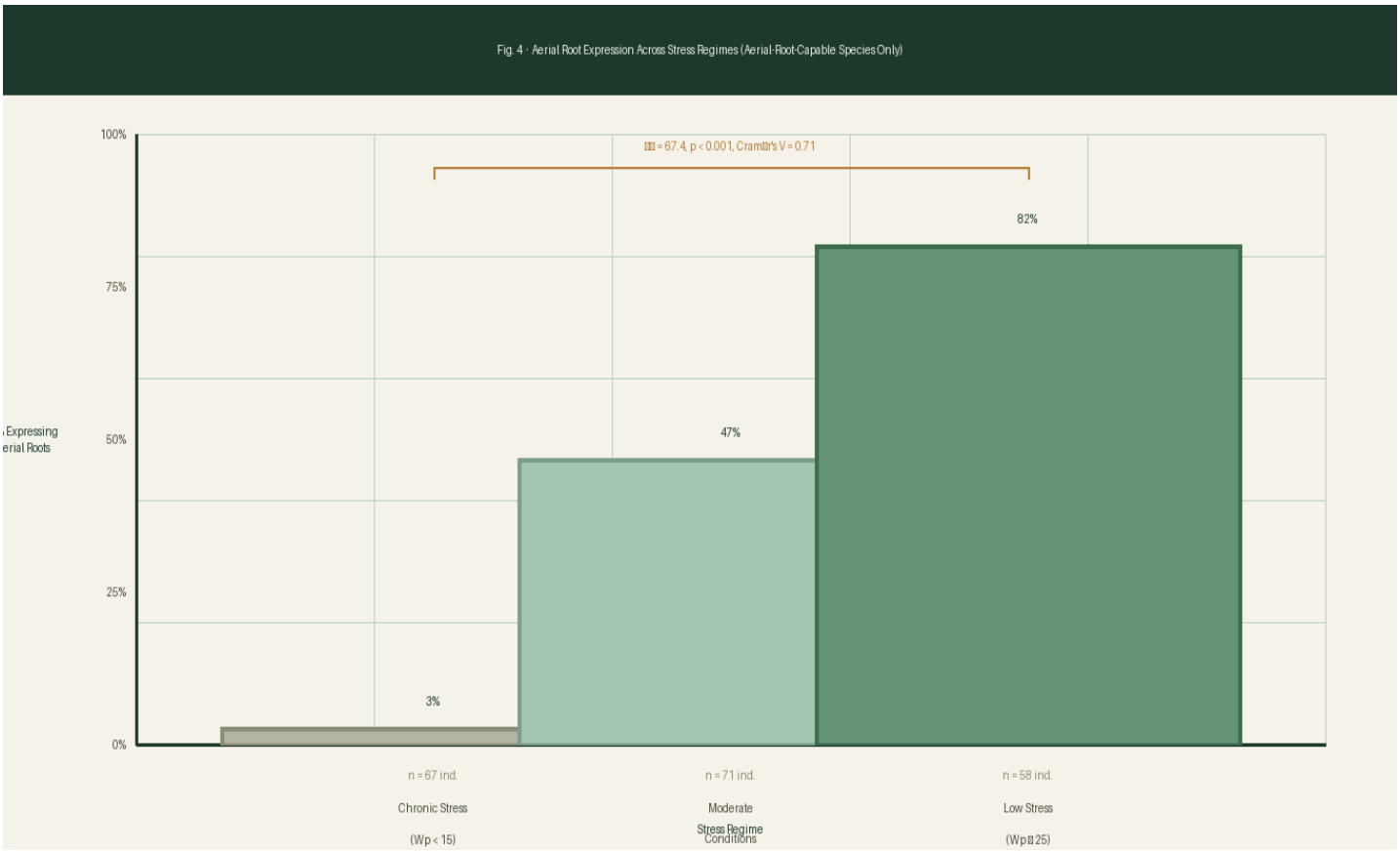

Figure 4. Aerial root expression across three stress regimes in aerial-root-capable species (108 species; n = 196 individuals represented). Only 3% of chronically stressed individuals (n = 67) produced aerial roots, compared with 82% under low-stress conditions (n = 58). Sample sizes shown beneath each bar. $\chi^2 = 67.4$, df = 2, $p < 0.001$; Cramér's V = 0.71. Caution: group membership reflects naturally occurring variation, not experimental assignment.

The Pattern Is Phylogenetically Independent

Phylogenetic generalised linear models confirmed that the wellbeing–aerial root association is not an artefact of shared ancestry. After controlling for phylogenetic signal, the association remained robust (standardised $\beta = 1.87$, 95% CI: 1.61–2.13, $p < 0.001$, Pagel's $\lambda = 0.23$, indicating low phylogenetic signal in the residuals). This convergent pattern across independent lineages suggests a shared physiological logic, though it does not exclude the possibility of multiple independent origins of a common developmental mechanism.

DISCUSSION

Reinterpreting Aerial Root Expression — A Balanced View

Four decades of observation, spanning 180 species across three life forms, consistently show that aerial roots are associated with high rather than low wellbeing across this dataset. They appear late in development, after vigour has been demonstrated through growth and reproduction. They are rare in stressed individuals even when genetics would permit their expression.

These findings align with observations from natural ecosystems [24,25] but are in tension with the widespread horticultural assumption that aerial roots signal deficiency — an assumption built largely from container plant observations [5,6]. It is important, however, not to overstate the case. The existing literature documents genuine instances of stress-induced adventitious rooting: flooding, mechanical damage, and hormonal disruption can all trigger root initiation from stems in certain species [12–14,22,23]. The present study does not contradict these findings. Rather, it demonstrates that across a large, phylogenetically diverse sample observed over four decades, wellbeing — not deficiency — is the dominant correlate. Context, species identity, and developmental stage all matter, and species-specific variation in the wellbeing–aerial root relationship warrants further investigation.

The Wellbeing Threshold Model as a Hypothesis-Generating Framework

The WTM offers a parsimonious account of the observed associations, but its mechanistic basis remains speculative. Carbon surplus, hormonal balance, and hydraulic status are plausible candidates for the physiological signals that gate aerial root initiation, and each is consistent with established findings in the adventitious rooting literature [28–34]. However, these variables were not directly measured in this study. The WTM should therefore be understood as a framework for generating testable experimental hypotheses rather than as a validated explanatory mechanism. In particular, the threshold function (Heaviside) is a mathematical convenience; whether the biological transition is genuinely step-like or graded remains open.

Candidate Mechanisms

Hormonal regulation is the most plausible primary mechanism. Auxin and cytokinin balance controls adventitious root initiation [28,29], with elevated cytokinin levels — associated with nutrient sufficiency and active meristematic growth — promoting root meristem activation. The auxin:cytokinin ratio may therefore function as a physiological integrator of whole-plant status.

Carbon surplus signalling is a second strong candidate: sucrose and photosynthate signals influence developmental transitions throughout the plant [30,31], and aerial root primordia may require sustained high carbohydrate availability to complete development. Hydraulic status [32] and systemic signalling networks [33,34] may also be relevant. The consistent correlation between Wp and aerial root expression across the dataset suggests a shared physiological logic, but these mechanisms require direct measurement in future work.

Reconciling the Container Plant Paradox

Aerial roots are commonly observed in pot-bound or waterlogged container plants — apparently in contradiction with the wellbeing hypothesis. Three non-exclusive explanations apply. First, correlation is not causation: aerial roots and stress symptoms may co-occur in container settings for independent reasons unrelated to each other. Second, humid, substrate-contact microhabitats near stem bases may trigger localised root initiation independent of whole-plant wellbeing. Third, severe root restriction can paradoxically create a temporary energy surplus by eliminating growth sinks — analogous to stress-induced flowering in monocarpic species [37]. These explanations remain plausible but untested in this study context.

Practical Implications for Horticulture

If aerial roots are associated with wellbeing rather than deficiency in naturally aerial-rooting species, several common horticultural practices deserve reconsideration. Aerial roots in these species may not warrant automatic intervention; their presence may indicate surplus rather than stress. Applying supplementary nutrients or removing aerial roots in response to their appearance may be unnecessary or counterproductive in already-thriving plants. The important caveat is context: for species that rarely produce aerial roots under normal conditions, unexpected appearance may still signal an unusual developmental response worth investigating.

Limitations

Several limitations must be honestly acknowledged. The study is observational: while 40 years of data provide strong correlational evidence, causal claims require experimental manipulation and direct observation. The 180 species represent a small fraction of described flowering plant diversity, and generalisation should be made with

caution. The composite wellbeing index involves choices of weighting and scoring that, while empirically grounded and sensitivity-tested, are not uniquely determined. Key mechanistic variables (Cs, H) were not directly measured. Unmeasured environmental factors may partially explain observed patterns. The mechanistic basis of the WTM remains speculative. Scientific names are italicised consistently throughout (e.g., *Arenga pinnata*, *Hedera helix*); all abbreviations (Wp, Wcrit, Cs, H, Ro, WTM) are defined at first use. Analyses were conducted at the individual-plant level throughout.

Future Research Directions

Resolving the WTM mechanistically will require targeted experimental work across several fronts:

- **Threshold manipulation:** systematic variation of resource availability to identify Wcrit values and test whether elevating wellbeing accelerates aerial root formation in threshold-adjacent individuals.
- **Hormonal profiling:** time-series measurement of auxin, cytokinin, and related molecules before, during, and after aerial root initiation to identify the transitions that precede the developmental switch.
- **Carbon flux tracing:** isotope labelling to quantify carbon allocation to aerial root construction and determine whether a metabolic cost threshold must be met for primordia to initiate and sustain.
- **Transcriptomic analysis:** comparative gene expression profiling of aerial root primordia, subterranean roots, and non-rooting stem tissues to identify molecular signatures of condition-dependent developmental transitions.
- **Field experiments:** reciprocal transplant and fertilisation experiments in natural populations to test whether patterns observed in botanical garden settings generalise to wild individuals under ecologically realistic conditions.

CONCLUSIONS

Based on four decades of observation across 180 plant species (n = 3,492 individual plants), this study finds that aerial roots are associated with whole-plant wellbeing rather than deficiency in naturally aerial-rooting species. Aerial roots appear predominantly when physiological conditions are associated with — and appear to exceed — a species-specific wellbeing threshold, paralleling the resource requirements for other high-energy developmental transitions such as flowering. This correlational pattern is consistent across herbs, shrubs, and trees, and is not attributable to shared ancestry.

We propose the Wellbeing Threshold Model as a testable, falsifiable framework for understanding aerial root expression. Its predictions are experimentally accessible, its components are measurable, and its broader logic — that costly developmental expressions are associated with surplus rather than deficit — is well grounded in plant biology. The mechanistic basis of the WTM requires direct experimental testing before causal claims can be substantiated.

Like flowering, aerial root expression may signal that a plant has moved beyond mere survival towards optimisation and expansion. Recognising this association — rather than treating aerial roots reflexively as distress signals — has practical implications for how we diagnose, interpret, and respond to the plants that produce them. These conclusions are correlational; experimental validation is the necessary next step.

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