

Endotherapy or Trunk Injection: Decoding Plant Signals for Sustainable Delivery in Perennial Species

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Abstract

Perennial plants form complex systems in which chemical, acoustic, and microbial communication sustains the physiological integrity of the plant holobiont. Advances in the understanding of this “language,” expressed through the phyllosphere, rhizosphere, and endosphere, have revealed how stress, defense, and cooperative signals shape both the plant microbiome and its hydraulic architecture. Within this context, vegetative endotherapy emerges as a technique capable of interacting with these internal processes, provided it is applied under appropriate physiological conditions and with formulations compatible with the vascular environment. Unlike foliar spraying and soil applications such as drenching, which may affect large volumes of soil and water and disrupt edaphic microbiota as well as surface and groundwater, endotherapy delivers compounds directly to the endosphere. Consequently, this approach can reduce product losses and environmental impacts while supporting sustainable strategies aligned with the Sustainable Development Goals and Nature-based Solutions. This short review discusses stress responses within plant compartments and the associated microbiome, examining how these dynamics relate to vegetative endotherapy in perennial plants and highlighting how precision agriculture can enhance the efficiency and sustainability of this technique.

Categories: Agricultural technology (machinery, remote sensing), Disease & pests of crops, Use of biostimulants, biofertilizers, bioinoculants in sustainable agriculture

Keywords: endotherapy, trunk injection, tree injection, sustainable development goals, nature-based solutions, precision agriculture, vocs, plant communication

Introduction And Background

Perennial plants play a central role in climate change mitigation, urban ecosystem stability, and agricultural production by accumulating biomass over decades and contributing to carbon sequestration and microclimate regulation. The reduction of green areas and the expansion of urbanization intensify heat island effects and thermal stress, reinforcing the importance of strategies aimed at the longevity and functional maintenance of these species. At broader scales, climate- and land-use-driven changes in temperature and precipitation patterns can increase stress in perennial plants, enhancing their susceptibility to pests and diseases and reinforcing the need for targeted, resource-efficient plant protection strategies [1-3].

In parallel, agricultural intensification and increased planting density, while potentially efficient, heighten competition for resources and increase vulnerability to pests and diseases [4]. In this context, conventional phytosanitary management based on foliar spraying and soil applications presents recurrent limitations, including agrochemical drift and leaching,

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impacts on soil microbiomes, environmental contamination, and the need for frequent applications [5]. Consequently, the contemporary challenge lies in increasing productivity without compromising environmental safety and the sustainability of agricultural systems.

Plants are organisms endowed with networks of chemical, mechanical, and electrical sensors, including pattern recognition receptors (PRRs), reactive oxygen species (ROS) signaling, mitogen-activated protein kinase (MAPK) cascades, and Ca^{2+} -mediated pathways, that enable them to perceive and interpret their environment, communicate with conspecifics, and adjust their metabolism to external stimuli in complex ways. This review addresses plant communication across different microbiomes, including the phyllosphere [6], with emphasis on foliar volatiles and volatilomics [7,8]; the rhizosphere, through root exudates, biotic interactions, and mycorrhizal networks known as the wood wide web [5,9,10]; and the endosphere, through electrical signals and ultrasonic emissions [11-14]. In this context, the plant holobiont, defined as the plant together with its associated microorganisms across the phyllosphere, rhizosphere, and endosphere, functions as an integrated network of exchanges and signals that supports nutrition, defense, and adaptation. These interactions can influence how stress cues are perceived and how responses are coordinated across tissues. In addition, endophytic microorganisms inhabiting stems, xylem, and phloem may act as biological filters that modulate plant defenses, internal signal transport, and molecular fate (e.g., metabolism and stabilization), with direct implications for endotherapeutic applications in perennial species [15-17].

This paper explores the “senses” of plants and examines how understanding these mechanisms can inform improvements in vegetative endotherapy for the sustainable management of perennial species. Recent progress in biological control, nanoparticles, and natural products has expanded the range of targeted formulations, which are critical for improving efficacy against pests, diseases, and nutrient deficiencies. When delivered via endotherapy, such formulations may also help mitigate biotic and abiotic stresses, particularly under conditions of rising temperatures, reduced water availability, and more frequent drought events, thereby supporting both technical performance and sustainability. However, despite these advances, the integration of plant signaling mechanisms with the optimization of vegetative endotherapy strategies remains limited, representing a critical gap in the literature. This review addresses this gap by synthesizing current evidence on plant signaling across compartments and associated microbiomes and discussing how these dynamics may shape the effectiveness, safety, and sustainability of vegetative endotherapy in perennial systems.

For this review, the literature was selected to provide a mechanistic and applied overview of vegetative endotherapy in perennial species, rather than an exhaustive systematic synthesis, with emphasis on plant physiology, vascular delivery, microbiome interactions, and injection methods. Searches were conducted using combinations of the terms “endotherapy,” “trunk injection,” “tree injection,” “pressurized injection,” “nonpressurized injection,” “passive uptake,” “gravity-based injection,” “xylem translocation,” “citrus HLB,” “coconut palm,” and “perennial crops.” Priority was given to studies that evaluated uptake, translocation, efficacy, wound response, device performance, or the delivery approach. Studies comparing pressurized, low-pressure, passive, gravity-based, or nonpressurized systems were analyzed separately to avoid overgeneralization. Conceptual reviews and engineering studies were included when relevant to device design, injection-port geometry, pressure control, or field scalability.

Review

Concepts and terminology: endotherapy versus trunk injection

To improve clarity and consistency, this review adopts “*vegetative endotherapy*” as the standard term to describe the internal therapeutic route, involving the delivery of active compounds (e.g., pesticides, antibiotics, bioformulations, and fertilizers) into the plant vascular system (e.g., xylem and phloem), enabling their systemic distribution to target tissues, regardless of the specific technique employed or the perfused organ (stem, trunk, or branches). In the English-language literature, “*trunk injection*” is widely used; however, it primarily describes the procedure (injection into the trunk) and may not encompass all applications or explicitly convey the therapeutic intent, particularly when delivery occurs through other woody organs [18-20]. The term “*tree endotherapy*,” proposed more recently, can be even more restrictive because it may exclude non-tree perennials (e.g., palms, grapevines, and shrubs), thereby narrowing the scope beyond what is

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often addressed in practice and research [21]. Overall, inconsistent terminology in vegetative endotherapy creates technical and regulatory ambiguity, reduces study comparability, and can hinder the consolidation of evidence and best practices. For this review, these terms are discussed as partially overlapping, and the chosen terminology is used for internal consistency.

Vegetative endotherapy consists of the direct application of solutions into the vascular system of plants. This technique circumvents the limitations of foliar spraying and soil applications, as the applied compounds are transported by the sap and distributed systemically. In arborescent monocotyledons, endotherapy is typically performed in the stem, whereas in woody dicotyledons they are commonly applied to the trunk. In pressurized methods, controlled pressure is used to drive calibrated volumes into the vascular tissues, promoting upward translocation along the transpiration stream driven by negative pressure within the plant. Under appropriate physiological and operational conditions, pressurized endotherapy can promote rapid distribution of applied compounds and high delivery efficiency, potentially allowing lower applied volumes or doses than some conventional nonpressurized approaches and contributing to longer reapplication intervals [22,23].

Advantages, sustainability, and scope

Compared with conventional application techniques, vegetative endotherapy offers several advantages, including reduced spray drift and environmental contamination, enhanced protection of applicators and beneficial fauna, and prolonged product activity and treatment durability, as applied substances remain longer within the vascular system [24,25]. The technique is aligned with the Nature-Based Solutions framework of the International Union for Conservation of Nature (IUCN) [26] and with the Sustainable Development Goals (SDGs) of the United Nations 2030 Agenda, contributing to efficient input use and food security (SDG 2), reduced human exposure (SDG 3), water protection (SDG 6), responsible consumption and production (SDG 12), extended longevity of perennial plants and carbon sequestration (SDG 13), and the conservation of ecosystems and non-target organisms (SDG 15) [27].

Vegetative endotherapy has the potential to help mitigate climate-related impacts by extending the longevity of trees and palms, thereby supporting continued carbon sequestration capacity, reducing heat stress, and sustaining ecosystem services. Healthy canopies exhibit higher photosynthetic performance and can contribute more effectively to mitigating urban heat islands. This technology may therefore benefit not only agricultural production, but also urban arboriculture and environmental conservation [28-30].

Delivery rate, local retention, and microbiome interactions

A less frequently discussed aspect of endotherapy is how delivery rate and residence time at the application site may influence systemic movement and local interactions with plant tissues and microorganisms. In some nonpressurized or low-pressure systems, such as drip-based infusion sets, bags, or permanent delivery systems, the application may require longer delivery periods or specific trunk positioning to accommodate the treatment volume. Under inadequate sealing or unfavorable field conditions, depressions near the injection site may accumulate rainwater or sap, potentially favoring microbial proliferation, tissue degradation, and localized vascular dysfunction. Because these approaches may not generate sufficient driving force to ensure consistent delivery, systemic movement may depend more strongly on plant physiological status and may vary across time and space. This can contribute to local retention in parenchyma or other tissues that do not directly support long-distance sap translocation, thereby reducing systemic reach [22,31,32]. In addition, the trunk microbiome is abundant and enzymatically active, comprising bacteria, fungi, and archaea, and may metabolize, transform, or inactivate molecules that remain near the application site for extended periods [15,33]. Consequently, application technique, delivery rate, sealing, and residence time are relevant determinants for minimizing local degradation and promoting systemic distribution. As a result, the microbial composition of vascular tissues should be considered as one of the factors influencing the performance of endotherapeutic formulations [15,22,34].

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Soil-Plant-Atmosphere Continuum and translocation physiology

In endotherapy, the Soil-Plant-Atmosphere Continuum (SPAC) provides the physiological basis for xylem translocation. Figure 7 summarizes how transport depends on the water potential gradient across the soil-plant-atmosphere system. In moist soils, water potential typically ranges from approximately -0.01 to -0.5 MPa, allowing water uptake with relatively low resistance. As the water column ascends through the stem, values between -0.5 and -1.5 MPa are common, reflecting the increasing tension required to maintain column continuity. In leaves, where transpiration intensifies water loss, water potential may reach -1.5 to -3.0 MPa, becoming more negative and providing the pulling force that drives upward movement of endotherapeutically injected solutions. Leaves are estimated to lose ~ 400 H_2O molecules for each CO_2 molecule assimilated during photosynthesis, a high physiological cost that demands an efficient hydraulic system to avoid desiccation. In large trees, daily water losses can reach tens to hundreds of liters, highlighting the magnitude of the pressure gradient sustaining xylem transport [35,36]. Accordingly, translocation efficiency depends directly on plant water status, underscoring the need to consider these dynamics when defining endotherapy protocols. The figure below illustrates how the plant-associated microbiome may interact with endotherapeutic applications and depicts representative water potential gradients in plants.

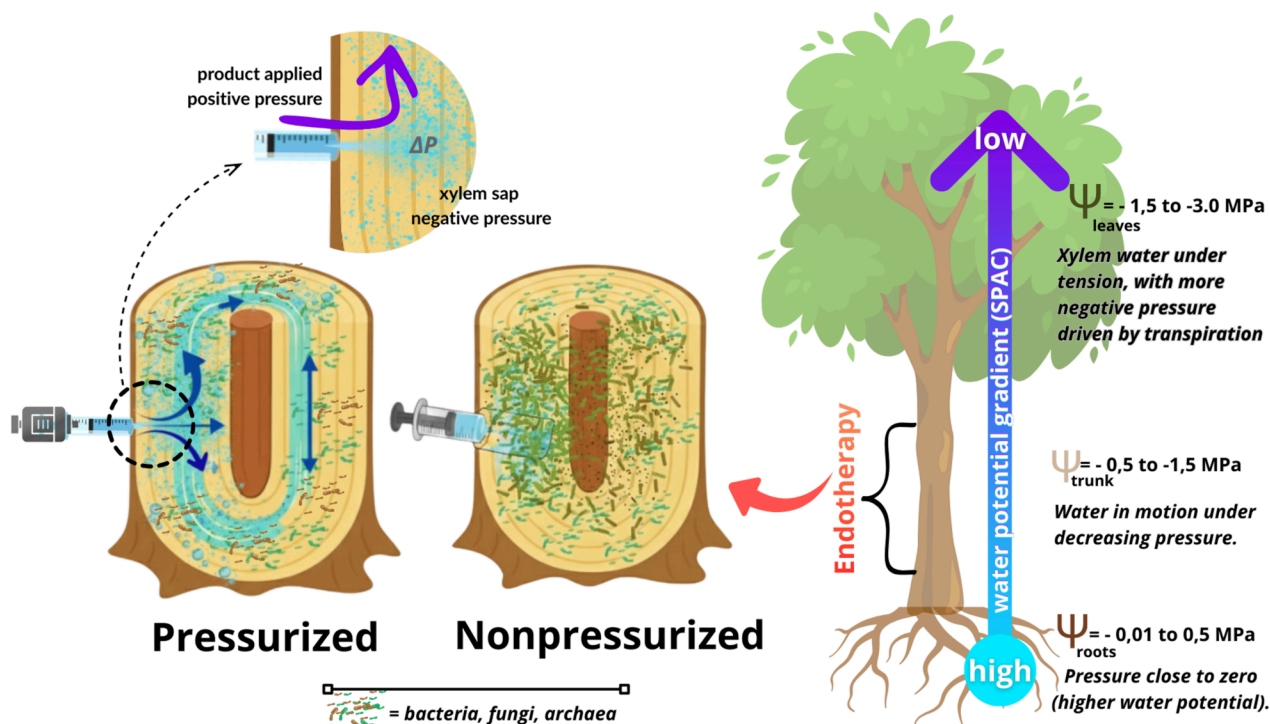


FIGURE 1: Schematic representation of pressurized and nonpressurized endotherapy and their relationship with the soil-plant-atmosphere continuum (SPAC).

Pressurized application can promote radial and vertical distribution of the applied solution, whereas nonpressurized or gravity-based delivery may result in slower or more limited xylem-driven movement, depending on plant water status, vascular functionality, formulation properties, and device design. The SPAC water potential gradient directs the upward flow of water from roots ($\Psi \approx -0.01$ to -0.5 MPa), through the trunk ($\Psi \approx -0.5$ to -1.5 MPa), to leaves ($\Psi \approx -1.5$ to -3.0 MPa), where transpiration generates the most negative pressures. ΔP = pressure differential. This gradient helps explain why endotherapy efficiency depends on plant water status and xylem functionality. Figures are conceptual representations intended to illustrate physiological mechanisms and are not drawn to scale.

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Microbiome as an internal filter and practical consequences

Vegetative endotherapy complements but does not replace pruning, irrigation, and nutrition, which sustain canopy health, SPAC gradients, and plant vigor essential for translocation efficiency. Recent studies have indicated that roots, stems, and leaves harbor distinct microbiomes, shaped by compartment-specific endophytic communities selected through biological filters unique to each niche (e.g., physicochemical conditions, tissue anatomy, and metabolic interactions) [5,9,37]. Notably, Arnold et al. [15] reported that living stem tissues can host an exceptionally dense endophytic community, on the order of trillions of microbial cells per tree, comprising metabolically active bacteria, fungi, and archaea capable of degrading and transforming organic compounds and effectively functioning as an internal biological filter. This raises an important question for vegetative endotherapy: can delivered products eliminate this internal microbiome? Available evidence suggests that complete elimination is unlikely. However, endophytes may metabolize applied compounds; their full suppression may be limited by their occupation of distinct niches within vascular tissues, chemical tolerance, and potential for rapid recovery. Consequently, endotherapeutic products that remain for prolonged periods near the injection site, as may occur with nonpressurized systems, may be more exposed to microbial transformation and to local retention within parenchyma-rich tissues that contribute less to long-distance translocation, which may help explain why some systems require longer delivery times and may show variable systemic efficiency. In contrast, under appropriate conditions, pressurized endotherapy can promote upward movement and dispersion through vascular pathways, potentially reducing prolonged local contact with the microbiome and enabling calibrated applications within a shorter time frame [11,15].

Comparative evidence on endotherapeutic delivery systems

Direct comparisons among pressurized, low-pressure, passive, and nonpressurized endotherapy systems remain relatively limited. However, the available studies show that the delivery method can affect uptake rate, systemic translocation, operational feasibility, treatment efficacy, and wound response. Importantly, these comparisons should not be interpreted as a simple binary distinction between “pressurized” and “nonpressurized” methods. Instead, each technology must be evaluated as an integrated delivery system involving the way pressure is applied, device architecture, injection-port design, formulation properties, applied volume, dose, plant anatomy, and physiological status. Table 1 summarizes selected studies that compared or contrasted different endotherapeutic delivery systems, including pressurized, low-pressure, passive, gravity-based, and nonpressurized approaches in perennial species.

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Reference	Plant matrix	Active ingredient or product class	Target or purpose	Endotherapy method evaluated
Ferracini and Alma (2008) [38]	<i>Aesculus hippocastanum</i> L.	Imidacloprid and abamectin; systemic insecticides	Control of <i>Cameraria ohridella</i>	Natural absorption, controlled pressure, and low-pressure Arbosan method
Dal Maso et al. (2019) [39]	<i>Juglans nigra</i> L.	Prochloraz plus tetraconazole, abamectin, and Carbitol; fungicides, insecticide, and adjuvant	Thousand cankers disease caused by <i>Geosmithia morbida</i> and vectored by <i>Pityophthorus juglandis</i>	Formulation screening for endotherapy under atmospheric pressure and manually applied external pressure
Stephano-Hornedo et al. (2020) [40]	<i>Citrus aurantifolia</i> Swingle	Argovit silver nanoparticles; antibacterial or antimicrobial agent	HLB associated with <i>Candidatus Liberibacter asiaticus</i>	Quikjet with manual pressure and XyllaKill with passive gravity-based uptake
Ferreira et al. (2022) [22]	<i>Cocos nucifera</i> L.	Cyproconazole plus adjuvant; systemic fungicide	Cyproconazole translocation for potential management of coconut foliar diseases	Pressurized and nonpressurized endotherapy
Archer and Albrecht (2023) [41]	<i>Citrus sinensis</i> L. Osbeck	Oxytetracycline, imidacloprid, and water; antibiotic, insecticide, and control	Systemic delivery for HLB management and Asian citrus psyllid-related treatments	High-pressure Arborjet QUIK-jet Air with Arborplug, medium-pressure Chemjet Tree Injector, and low-pressure gravity-based syringe system
Ferreira et al. (2024) [34]	<i>Cocos nucifera</i> L.	Difenoconazole, imidacloprid, thiabendazole, cyproconazole, thiamethoxam, spiroticlofen, and carbosulfan; fungicides and insecticides	Pesticide translocation in coconut stems	Pressurized and nonpressurized endotherapeutic treatments
Albrecht et al. (2025) [42]	<i>Citrus sinensis</i> L. Osbeck, Valencia and OLL-8 sweet orange	Oxytetracycline; antibiotic	Systemic OTC delivery for HLB management, productivity, fruit and juice quality, and trunk injury assessment	Drill-free Trecise/Invaio microinjection system and drill-based Chemjet Tree Injector, with different OTC doses,

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				foliar spray, and non-injected controls
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TABLE 1: Selected studies comparing endotherapeutic delivery systems in perennial species.

HLB: Huanglongbing; OTC: Oxytetracycline; AgNPs: Silver nanoparticles

In horse chestnut, Ferracini and Alma [38] compared natural absorption, controlled pressure, and the low-pressure Arbosan method for delivering imidacloprid and abamectin against *Cameraria ohridella*. Pest suppression was effective across methods, and the authors reported no significant differences among gravitational, pressure, and low-pressure treatments. However, pressure clearly improved the operational aspect of the treatment, since uptake was faster under pressure than by natural absorption, especially in physiologically compromised trees. Thus, this study does not support a universal biological superiority of pressure, but it supports the practical relevance of pressure when uptake time is a limiting factor.

In coconut palms, Ferreira et al. [22] provided one of the most direct evaluations of pressure in endotherapeutic delivery. Cyproconazole was applied to *Cocos nucifera* using pressurized and nonpressurized systems, with residue analysis and mathematical modeling used to evaluate translocation along the stem. The nonpressurized treatment used a drilled hole followed by syringe application, whereas the pressurized treatment used the Bite Infusion system, in which the solution was introduced under pressure through a hollow blade. Even with a lower applied volume in the pressurized treatment, the study showed that pressure favored faster and more efficient translocation toward the upper stem. The subsequent study by Ferreira et al. [34] expanded this comparison from a single fungicide to a mixture of commercial fungicides and insecticides, including difenoconazole, imidacloprid, thiabendazole, cyproconazole, thiamethoxam, spiroticlofen, and carbosulfan. The authors also reported an important practical limitation: the formulation used in the pressurized method had to be diluted and applied at a lower volume because of difficulty in injecting the solution with the equipment. This makes the study particularly useful for a balanced discussion, because it shows that pressure, formulation viscosity, equipment design, and applied volume interact in determining translocation efficiency.

Other studies further illustrate that delivery performance is strongly formulation- and device-dependent. Stephano-Hornedo et al. [40], working with Argovit silver nanoparticles in HLB-affected Mexican lime, compared Quikjet, applied through a silicone septum using manual pressure, and XyllaKill, in which the formulation entered the trunk passively by gravity over a few hours. The results should therefore be interpreted in relation to the AgNP suspension, concentration, device architecture, injection port, and delivery mode, rather than as evidence of a general superiority of passive over pressurized systems. Similarly, Dal Maso et al. [39] showed in black walnut that uptake rate and formulation selection are critical determinants of endotherapy performance, reinforcing that pressure effects cannot be separated from formulation behavior and injection-device characteristics.

Studies conducted in citrus by Albrecht and co-workers evaluated different endotherapeutic systems over multi-season field trials, including Arborjet, Chemjet, and Trecise/Invaio. In Archer and Albrecht [41], the results suggest that pressure is an important variable for improving delivery efficiency, but also that injection technique and wound response strongly influence the outcome. Medium- and high-pressure systems improved compound delivery compared with low-pressure injection, but this improvement involved a trade-off, since high-pressure injection with a plastic plug resulted in greater wound damage and poorer wound closure. In the subsequent study by Albrecht et al. [42], the drill-based Chemjet system, combined with a higher OTC dose, produced more favorable agronomic responses and less trunk injury than the drill-free Trecise/Invaio system. However, these studies also indicate that device performance cannot be fully explained by pressure alone, especially because detailed spatiotemporal translocation of the active ingredient was not the main focus of all trials, and treatment persistence was mainly inferred from field responses over one or two production seasons. Therefore, these results reinforce the need to evaluate endotherapeutic technologies as complete delivery systems, rather than according to the presence or absence of pressure alone.

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Overall, these studies suggest that the debate should move beyond a simple comparison between pressurized and nonpressurized endotherapy. Applied pressure is a relevant delivery variable because it can provide the driving force needed to overcome hydraulic resistance imposed by the injection port, plant vascular tissues, and formulation properties. Nevertheless, the biological and operational success of endotherapy depends on how pressure is integrated into the whole delivery system. Reviews on endotherapy and precision delivery in citrus emphasize that device architecture, injection-port design, plant anatomy, formulation properties, application timing, and wound response all influence treatment performance [43–44]. This interpretation is supported by studies showing that different injection ports heal differently [45], that oxytetracycline efficacy in citrus depends on its spatiotemporal distribution and persistence after endotherapy [46], and that both active and passive systems can enable uptake and translocation in woody plants. However, responses remain species-, pest-, and context-dependent [47]. In parallel, recent engineering studies by Ojo et al. [48,49] reinforce that pump pressure, flow rate, and injection parameters are not secondary details, but central design variables for scalable and reproducible endotherapy.

Comparative studies and conceptual analyses therefore suggest three potential advantages of controlled-pressure delivery under appropriate physiological and operational conditions. First, pressure may reduce residence time at the application site, limiting prolonged local interaction among the formulation, plant-associated microbiota, enzymes, and non-conductive tissues before systemic distribution. This remains a plausible mechanism rather than a fully demonstrated process, since direct chemical confirmation of microbial or enzymatic transformation at the injection site is still limited. Second, pressure may accelerate distribution by helping overcome anatomical and hydraulic barriers such as wood density, vessel obstruction, tyloses, embolisms, and resistance at the injection port. Third, pressure may reduce dependence on passive uptake alone, although systemic movement remains constrained by plant water status, xylem functionality, transpiration, and species-specific vascular architecture. Thus, controlled pressure can improve delivery efficiency, but it does not eliminate the need for favorable physiological conditions.

From a mechanistic perspective, drilling or perforation locally disrupts conductive tissues and creates an artificial entry point through which the applied solution should effectively reconnect with functional vascular flow. Because xylem sap is commonly under negative pressure during transpiration, upward movement depends on the water potential gradient generated along the soil-plant-atmosphere continuum. In this context, controlled positive pressure at the injection port may create a favorable pressure differential (ΔP), helping the solution re-enter functional xylem and couple with transpiration-driven sap flow. This mechanism may reduce residence time at the application site, limit prolonged contact with non-conductive tissues and plant-associated microbiota, and accelerate radial and vertical distribution. In contrast, when no external pressure is applied, some nonpressurized or gravity-fed systems may depend more strongly on passive uptake and plant water status, requiring larger volumes or longer delivery times and, in some cases, resulting in lower translocation efficiency. However, these outcomes remain dependent on species, vascular anatomy, formulation properties, device design, sealing, and physiological condition of the plant. Therefore, the central issue is not whether pressure is present or absent, but whether the device provides controlled vascular access, stable and appropriate pressure, adequate sealing, and compatibility with the formulation and plant matrix [16,22,31,32,50,51].

Despite decades of use and the availability of multiple endotherapeutic technologies, the field still relies on relatively few standardized and reproducible protocols. Although endotherapy has evolved in terms of devices and operational tools, practical outcomes often remain inconsistent across species, environments, and practitioners. This raises a fundamental question: where does the limitation lie? Is progress being constrained by the techniques themselves, by the formulations being delivered, or by the absence of physiological criteria guiding when and how applications should occur? More importantly, what is still missing to elevate endotherapy from a technical option to a reliable, robust, and reproducible practice at the grower level?

Endotherapy is effective only when guided by plant physiology and executed with technical discipline; otherwise, it risks becoming a mechanical intervention with unpredictable biological outcomes. Even well-established commercial systems can underperform when key criteria are ignored. Three technical pillars support reliable delivery. (A) Access: the injection port must be created with sharp bits and procedures that minimize overheating and unnecessary tissue disruption, ensuring true vascular access rather than a damaged cavity. (B) Pressure: delivery pressure and rate should match species-

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specific hydraulics, plant age, formulation properties, and the target tissue. Under appropriate conditions, pressurization can improve performance because it helps overcome resistance at the port, xylem tension, and opposing sap flow, thereby increasing vertical and radial distribution and the fraction of product reaching the canopy. (C) Sealing: the port must be sealed to preserve function and safety. Poor sealing may promote oxygen ingress, oxidation, stronger compartmentalization responses, leakage, and microbial colonization, which can culminate in necrosis and lasting impairment of sap conduction [18,22,31,45,52]. Endotherapy efficacy requires validated techniques integrated with species- and age-specific criteria; without both, outcomes remain unpredictable. Finally, reproducibility also depends on simple operational controls that limit procedural variability and unintended interactions during application.

Plant communication and holobiont dynamics

Plants should be understood as holobionts, functional units formed by the plant organism and its resident microbial community distributed across distinct compartments. Recent evidence confirms that these microbial assemblages influence plant growth, nutrition, defense, stress tolerance, and environmental adaptation. Among the main microbial compartments, three zones are particularly relevant: the phyllosphere (aboveground surfaces), the endosphere (internal tissues), and the rhizosphere (roots and surrounding soil). Each zone harbors distinct microbial communities shaped by compartment-specific ecological filters, including nutrient availability, the presence of exudates, microclimate, oxygenation, and exposure to the external environment. Plants actively modulate these communities through foliar secretions, root exudation, and the activation of defense pathways that can remodel the associated microbiome [16,17,33,53,54].

External plant communication, occurring through aerial and belowground pathways, represents an essential component of these dynamics. In response to biotic or abiotic stress, plants alter their profiles of volatile organic compounds (VOCs), which function as chemical signals capable of attracting natural enemies, alerting neighboring plants, or modulating the activity of associated microorganisms [55,56]. Recent reviews highlight that volatile terpenoids, one of the major classes of plant-emitted VOCs, act as central mediators of plant communication by coordinating plant-plant, plant-insect, and plant-microbe interactions, while integrating chemical signaling with defense and adaptive responses [57]. Changes in volatile emission profiles may coincide with visible leaf reddening or darkening, consistent with defensive and oxidative physiological states known to modulate VOC production [58-60]. In addition to volatiles, recent studies have demonstrated that plants experiencing water stress, mechanical injury, or infection can emit ultrasonic sounds in the 20-100 kHz range. Although inaudible to humans, these signals can be detected by sensors at distances of several meters and may be perceived by insects and other organisms, introducing an additional dimension to plant communication [13,61]. In both cases, VOCs and acoustic emissions convey information that anticipates the plant's internal physiological state, functioning as early indicators of processes occurring within the endosphere.

In the belowground domain, the rhizosphere further expands this communication system through root exudates that shape microbial communities, recruit symbionts, and activate mycorrhizal fungi. Common mycorrhizal networks (CMNs) connect neighboring plants and have been reported to enable the transfer of water, nutrients, and biochemical signals associated with defense and stress responses; however, the extent, ecological relevance, and consistency of these transfers remain under debate [62-64]. These subterranean fluxes integrate different individuals and species into a functional network, contributing to the synchronization of physiological responses among plants. Together, aerial and rhizosphere-based communication highlight that plants operate as nodes within a broader ecological network, continuously sending and receiving information that both reflects and modulates their internal physiological state.

Endosphere physiology and internal signaling

Within the plant, the endosphere is characterized by an aqueous environment composed of xylem and phloem vessels, apoplastic spaces, cell walls, and sap rich in dissolved compounds. Unlike the phyllosphere, where volatile compounds readily escape into the atmosphere, many internally produced defensive metabolites remain dissolved in the sap or associated with cell walls [49,58]. In response to stresses such as herbivory, wounding, or infection, plants activate chemical pathways leading to the production of salicylic acid (SA), jasmonates (JA), and ethylene (ET), which induce the synthesis of phytoalexins such as scopoletin, camalexin, and resveratrol, as well as soluble antimicrobial VOCs, including

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terpenoids, phenylpropanoids, and aldehydes. These metabolites play multiple roles in internal defense by disrupting microbial membranes, oxidizing cell walls, chelating essential ions, interfering with critical metabolic pathways, and activating systemic acquired resistance (SAR) [65–69].

In parallel, electrical signals and Ca^{2+} waves rapidly propagate through the vascular system. Glutamate released from wounded tissues activates glutamate receptor-like (GLR) channels, triggering Ca^{2+} waves that spread through the xylem and phloem within seconds, thereby coordinating systemic responses in distant leaves [12]. Collectively, these chemical and ionic signals can modulate the physicochemical environment of the endosphere. In particular, plant defense-related pathways, including SA and other secondary metabolites, have been reported to influence microbiome assembly, contributing to selective pressures on plant-associated microbial communities. These shifts may reduce populations of sensitive endophytes while favoring more tolerant taxa, which could, in turn, affect plant physiological functions, including hydraulic integrity, a key factor for the effectiveness of subsequent endotherapeutic applications [21,31,69].

This defense-driven rearrangement of the endophytic microbiota can either reinforce or impair essential processes such as hydraulic integrity and sap transport [21,31,69]. For this reason, understanding the endosphere is critical. It simultaneously represents the plant's internal environment, the biological target, and the transport medium for compounds delivered via endotherapy. Although they refer to distinct phenomena, the activity of endophytic microorganisms and the practice of endotherapy converge on the same principle, acting from within the plant. The endosphere corresponds to the ensemble of vascular tissues and their associated microbiome, whereas endotherapy represents the intervention that employs formulated agricultural inputs designed to be translocated through these same vascular tissues.

Physiological constraints on endotherapy effectiveness

The effectiveness of endotherapy depends on the plant's hydraulic functionality, including hydrated roots, soil with adequate conductivity, partially open stomata, and intact xylem pathways. At advanced stages of disease, when vascular obstruction, embolism formation, or collapse of the endophytic microbiome occur, sap flow is reduced, and transport of the applied compounds becomes compromised. In addition, recent studies using magnetic resonance imaging (MRI) and three-dimensional microtomography have shown that xylem transport exhibits pronounced spatial heterogeneity in pressure gradients, with portions of the flow being redirected from wider vessels to narrower ones. This behavior challenges the classical assumption of hydraulically homogeneous flow and indicates that internal transport is more complex than previously predicted. For these reasons, endotherapy tends to be more effective under prophylactic conditions or during early stages of infection, when the vascular system remains functionally responsive [31,36,55,56,69].

The rhizosphere directly influences this process, as endotherapy efficiency depends on water uptake by roots and on the integrity of the root-associated microbiota, which regulates nutrient availability, local defense responses, and overall plant physiological stability [9,70]. Another promising aspect of endotherapy is the potential use of natural compounds, such as plant hormones, botanical extracts, green leaf volatiles, microbial metabolites, or bioformulated products, which may interact more harmoniously with the plant holobiont, preserving the microbiome and reducing the risk of phytotoxicity. When applied directly into the vascular system, endotherapy also minimizes losses due to drift and leaching, thereby reducing impacts on soil microbiota as well as on surface and groundwater resources [11,21,71,72]. SAR inducers, elicitors, and priming agents, such as SA, jasmonates, and related signaling molecules, are widely discussed as preventive tools that may enhance plant defenses and reduce reliance on higher-toxicity inputs. Broader implementation will depend on standardized, reproducible protocols across species and environments [73].

Toward sustainable and precision endotherapy strategies

The practice relies on three interdependent technical requirements, as indicated by experimental observations and empirical studies reported in the literature: (1) appropriate physiological timing, such as early morning or late afternoon, when plants exhibit favorable hydraulic flow; (2) application pressure adjusted to the type of stem or stipe, plant age, and vascular architecture; and (3) formulations compatible with the vascular system, favoring high solubility, absence of insoluble particles, appropriate pH, and low viscosity to reduce resistance to injection and vascular movement [21,22,31,74,75].

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The adoption of endotherapy as a tool for the sustainable delivery of agricultural inputs becomes even more relevant in the context of precision agriculture. Chemical, biological, and physical sensors, combined with drones and satellites, along with advances in artificial intelligence (AI) and automated data collection and transmission, enable the detection of plant physiological signals such as VOC emissions, temperature changes, leaf color variation, growth patterns, and moisture status. These data streams make it possible to anticipate stress conditions and guide targeted applications. In this framework, endotherapy may shift from a primarily reactive practice toward a more preventive intervention, calibrated to the plant's actual physiological state and applied at the most appropriate moment [24,25,31].

A schematic representation of this integrated framework is shown in Figure 2, illustrating how multichannel plant communication (VOCs, acoustic signals, and mycorrhizal networks), the endophytic microbiome, and sensing technologies (sensors, drones, and satellites) converge to guide endotherapy in a precise, sustainable manner aligned with the plant's internal functioning.

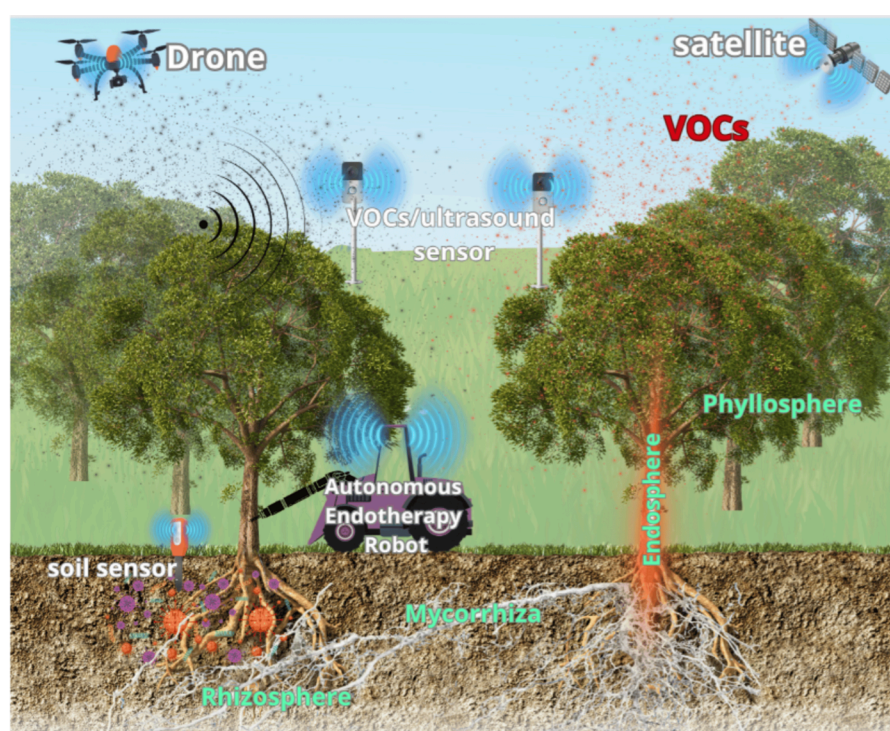


FIGURE 2: Schematic representation of plant communication and sensing technologies, including sensors, drones, and robotic platforms, that can be used as supporting tools for endotherapy.

This is a conceptual illustration intended to summarize the framework; elements are not drawn to scale.

Future advances in endotherapy will likely depend on integrating plant sensing, formulation compatibility, and delivery criteria into unified protocols. However, empirical validation and direct quantitative comparisons remain important limitations in the current literature. Studies comparing pressurized and nonpressurized systems, or endotherapy with conventional application methods, are still scarce and technically demanding, as they require controlled field trials, standardized protocols, chromatographic analyses to quantify compound distribution/translocation and residues, PCR/qPCR-based assays to monitor pathogen or microbiome responses, and physiological evaluations of plant performance. Future research should prioritize comparative assessments of translocation, efficacy, phytotoxicity, cost-effectiveness, and long-term plant responses, supporting the transition of endotherapy from a promising delivery strategy to a standardized and reproducible practice in perennial species.

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Conclusions

An integrated understanding of plant chemical, physical, and microbial signaling shows that the health of perennial species depends on a dynamic network of interactions across the phyllosphere, rhizosphere, and endosphere. Viewing plants as holobionts helps explain why endotherapy is effective only when applied in harmony with plant physiology, which requires functional hydraulic flow, a balanced microbiome, and formulations compatible with the internal vascular environment. When these conditions are met, the technique offers clear environmental advantages by reducing drift and leaching and by lowering impacts on soil and aquatic microbiota, thereby aligning perennial crop management with the Sustainable Development Goals and Nature-Based Solutions. Looking ahead, integrating plant-derived signals with precision agriculture tools such as sensors, artificial intelligence, and remote sensing can translate physiological cues into actionable data and guide treatments to the appropriate plants and application windows. To move endotherapy from a promising technique to a reproducible practice, future work should prioritize standardized protocols, species-specific criteria for timing relative to phenological stage (e.g., vegetative growth, flowering, or fruiting), pressure, improved sealing practices, and formulation guidelines that account for vascular anatomy and microbiome-mediated transformation. This shift can better align endotherapy with the functional realities of plant ecosystems while reducing reliance on repetitive interventions and indiscriminate applications.

Additional Information

Author Contributions

All authors have reviewed the final version to be published and agreed to be accountable for all aspects of the work.

Concept and design: Jordana A. Ferreira Dr., Aline de Holanda N. Maia Dr.

Acquisition, analysis, or interpretation of data: Jordana A. Ferreira Dr., Amaury A. Júnior Mr.

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Critical review of the manuscript for important intellectual content: Jordana A. Ferreira Dr., Amaury A. Júnior Mr., Aline de Holanda N. Maia Dr.

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Disclosures

Conflicts of interest: In compliance with the ICMJE uniform disclosure form, all authors declare the following:

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Data Availability Statements

Data sharing is not applicable. This work is theoretical; no datasets were generated or analyzed.

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