

The Living Plant Oversight: A Methodological Critique of Botanical VOC Deterrence Research and a Proposal for Living-Organism Study Design

Cody T. Dooley 

Stockholm, Sweden

Email: codydooley@codynoticed.com

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Abstract

The field of botanical volatile organic compound (VOC) deterrence research has relied, without exception, on processed, extracted, or non-living plant material as its experimental VOC source. A systematic search of Google Scholar, Web of Science, and CAB Abstracts identified no published study testing a living, metabolically active aromatic plant as a herbivore deterrent in a controlled setting. This constitutes a foundational methodological oversight: a living plant is not its extract. Living plant VOC output differs from extracted equivalents in six documented dimensions—continuous biosynthesis, herbivore-induced upregulation (HIPVs), environmental modulation, biomass-scaled temporal intensification, compound lability, and spatial plume architecture—each invisible to extraction-based assays. The prevailing conclusion that botanical scent deterrents are ineffective against large mammals is valid for extracted preparations only; it cannot be extended to living organisms that continuously replenish their VOC output and present a categorically different habituation challenge. Recent molecular evidence confirms that plant VOCs activate TRPA1, a conserved mammalian aversion ion channel, providing a plausible mechanism for living-plant deterrence. We present a formal methodological critique, a six-dimensional comparative analysis, indirect supporting evidence, and a five-study experimental agenda to test this overlooked class of deterrent.

Keywords

Volatile Organic Compounds, VOC, Living Plant Deterrence, Herbivore Repellent, TRPA1, Plant Chemical Ecology, Herbivore-Induced Plant

Volatiles, HIPV, *Sus scrofa*, Wild Boar, Botanical Repellent, Methodology Critique, *In Situ* Deterrence, Plant-Herbivore Interactions

1. Introduction

The use of plant-derived volatile organic compounds (VOCs) to deter herbivorous animals from crops, gardens, and natural habitats represents a long-standing area of inquiry in both applied pest management and plant chemical ecology. The theoretical appeal is well-founded: aromatic plants have co-evolved with herbivore pressure over millions of years and have developed complex, constitutive, and inducible VOC profiles that function—in part—as chemical defences against herbivory. Many aromatic species are empirically observed to be avoided by large mammalian herbivores under naturalistic field conditions, a pattern reported consistently across independent horticultural and ecological literature.

Despite this theoretical promise, the published literature evaluating botanical VOC preparations as deterrents against large herbivorous mammals has returned largely discouraging results. Studies assessing commercial and homemade odour repellents against wild boar (*Sus scrofa*), deer (*Cervidae*), and other species have consistently found preparations to be either ineffective or effective only transiently, with rapid habituation documented across multiple independent studies [1]–[3]. These findings have shaped a prevailing consensus that scent-based botanical deterrents are not a viable management tool.

Here, we identify a critical and, to our knowledge, previously unremarked structural flaw in the methodological foundation of this literature: every published study in this field has used a processed, extracted, harvested, or synthesised plant material as its VOC source. Not one has tested the deterrent effect of a living, metabolically active, growing aromatic plant in a controlled experimental setting. We argue that this is not a minor methodological detail but a fundamental category error—one that renders the existing consensus on botanical deterrent inefficacy premature and potentially invalid as a general conclusion about aromatic plants.

This manuscript presents: 1) a systematic characterisation of the six principal dimensions by which a living plant's VOC output differs from its extracted equivalent; 2) a formal critique of the conclusions that extraction-based studies can and cannot support; 3) a review of existing evidence that indirectly supports the living-plant deterrence concept; and 4) a structured experimental agenda to test the hypothesis directly.

2. Survey of the Existing Literature

A review of published studies on botanical VOC deterrence against large herbivorous mammals reveals a consistent and unremarked pattern across all study types: the VOC source is invariably a preparation, not a plant.

2.1. Applied Repellent Studies (*Sus scrofa*)

The most rigorous field evaluations of botanical deterrents against wild boar [4] have all used applied chemical preparations as their scent source:

- Schlageter and Haag-Wackernagel (2012) [1]: Commercial odour repellent Wildschwein-Stopp® applied as a spray to field boundaries—an industrially processed preparation. Result: no significant damage reduction; no area avoidance.
- Schlageter and Haag-Wackernagel (2012) [2]: Gustatory repellent applied to clover, meadow, and wheat plots. Result: no significant damage prevention.
- Rao *et al.* (2019), cited in Mohamedfarook *et al.* (2025) [5]: Castor oil, ginger, and garlic mixture achieving up to 95% deterrence efficacy. Source: pressed and extracted plant oils—processed, dead material. Notably, the single most effective result in the literature, using the most chemically complex botanical mixture tested, is consistent with the hypothesis that VOC richness and complexity matter.
- All odour fence and predator scent studies: Use synthetic compounds, gland secretion extracts, fermented preparations, or isolated compounds. No living plant source was identified in any study reviewed.

2.2. Mechanistic Studies

The most scientifically advanced recent study in this area—Cai *et al.* (2025) [6], *Communications Biology*—identified TRPA1 ion channel activation as the molecular mechanism by which *Piperales* plant VOCs produce aversion in large herbivores including cattle and goats. The experimental material consisted of crude plant extracts and isolated or synthesised compounds (houttuynin; sodium houttuynfonate). The living *Houttuynia cordata* plant was not the experimental subject. Similarly, VOC repellency studies using *H. cordata* against insect pests (Zeng *et al.*, 2025) [7] employed headspace collections from harvested material or isolated compound assays—not living plants *in situ*.

2.3. The Universal Pattern and Its Significance

From crude field sprays to sophisticated molecular assays, the source material across the botanical deterrence literature is universally a snapshot: plant tissue harvested at a single moment, processed into an extract or preparation, and presented—without justification—as a valid proxy for the living organism. The living, continuously metabolising plant has never been the experimental subject of a controlled herbivore deterrence study. This is the methodological oversight at the core of the present critique.

2.4. Literature Search Methodology

A systematic search of the peer-reviewed literature was conducted in May–June 2026 using Google Scholar, Web of Science, and CAB Abstracts. Search terms used included: “*Ribes*” + “deterrent” + “mammal”; “living plant” + “olfactory” + “de-

terrent”; “volatile organic compound” + “barrier” + “mammal”; “black currant” + “pest deterrent”; “botanical repellent” + “wild boar”; and “*Sus scrofa*” + “olfactory”. The most modern publications—due to general scientific and technological advances over the past two decades—were cited in references at the end of this manuscript. Therefore, references after the year 2000 were prioritized for this manuscript. No published study was identified in which a living, metabolically active aromatic plant was used as the experimental VOC source in a controlled herbivore deterrence trial. All identified studies used processed, extracted, or otherwise non-living plant material. The recent work of Finnerty *et al.* (2024) [8]—demonstrating that artificial VOC extracts of unpalatable plant species provide associational browsing refuge to palatable plants from mammalian herbivores—represents the closest the literature has come to testing plant VOC-mediated deterrence at field scale, yet even this study used artificial odour preparations rather than the living plant organism itself.

3. Six Dimensions by Which Living Plant VOC Output Differs from Its Extract

The VOC emissions of a living plant are not a static chemical mixture but a dynamic, regulated, and environmentally responsive output of an active metabolic system. The following six dimensions are each independently documented in the plant physiology and chemical ecology literature, and each represents a way in which an extraction fundamentally fails to represent the living organism as a deterrent source.

3.1. Continuous Biosynthesis and Active Emission

Living plants synthesise and emit VOCs continuously through active biochemical pathways—primarily the methylerythritol phosphate (MEP) and mevalonate (MVA) pathways for terpenoid compounds, and shikimate-derived routes for phenylpropanoids and sulfur-containing volatiles. This biosynthesis is not a passive release of stored compounds but an active, energy-consuming metabolic process. Extractions capture a static snapshot of compounds present at one moment of harvest; the living plant replenishes and adjusts emissions in real time. The chemical source studied in extraction-based experiments ceases to exist the moment the plant is cut.

3.2. Herbivore-Induced VOC Upregulation (HIPVs)

When a plant is damaged by an herbivore—through browsing, rooting contact, or vibration—it upregulates VOC emission dramatically through the release of herbivore-induced plant volatiles (HIPVs). This response is mediated by jasmonic acid (JA) and related wound-signalling cascades and has been documented in hundreds of plant species [9]–[11]. HIPV blends are often qualitatively distinct from constitutive emissions, containing novel compound classes specifically upregulated in response to herbivory. This entire defensive dimension—shaped by mil-

lions of years of plant-herbivore co-evolution specifically to repel further attack—is entirely invisible to any extraction-based study. A preparation of plant extract cannot respond to being investigated by a wild boar.

3.3. Environmental Modulation of VOC Output

Living plant VOC emissions are continuously modulated by temperature, light intensity, soil nutrient status, water availability, seasonal phenology, and time of day. Isoprene and monoterpene emissions show strong temperature dependence, with output increasing exponentially above approximately 20°C for many species. Extractions are taken at a single time point under a single set of conditions and assume a fixed compositional profile. In a field setting, a living aromatic plant presents a continuously shifting, often seasonally intensifying chemical signal that no single extraction sample can characterise or replicate.

3.4. Biomass Scaling and Temporal Intensification

Total VOC emission from a plant scales with VOC-emitting surface area—primarily leaf area index and active stem and bud tissue. A mature perennial shrub in its fifth year has substantially greater photosynthetically active surface area than a first-year cutting; a ten-year specimen more still. For a border planting of aromatic shrubs, the total VOC output of the deterrent planting increases every growing season—the inverse of every applied preparation in the literature, all of which degrade with time, rainfall, and UV exposure. Extraction-based studies cannot model or predict this temporal trajectory; they implicitly treat VOC output as fixed at the moment of sampling.

3.5. Compound Lability and Degradation in Extractions

Many of the most biologically active plant volatiles are chemically labile: terpene hydrocarbons oxidise and polymerise upon exposure to atmospheric oxygen; sulfur-containing volatiles (thiols, polysulfides) react with container materials and degrade within hours of extraction; highly reactive aldehydes polymerise rapidly. The VOC profile tested in a repellent preparation is therefore not the profile of the living plant but a degraded, altered, and compositionally incomplete subset of it. The most bioactive compounds in a living plant's emission profile may be among those most severely underrepresented or absent in a standard extraction.

3.6. Spatial VOC Plume Architecture

A living aromatic plant creates a continuous, diffusing VOC plume extending outward from its surface, shaped by boundary layer dynamics, thermal gradients, and wind. This plume provides an approaching animal with a distance-dependent signal: concentration increases as the animal approaches the source, creating an informative gradient that can guide avoidance before physical contact. A field-applied repellent spray creates a uniform surface deposit with no radial concentration gradient and rapid uniform degradation. These represent physically and in-

formationally distinct deterrent architectures that no study in the literature has compared or controlled for. The role of odour gradients and spatial VOC architecture in mammalian foraging decisions is well-established [12].

The comparative summary of living plant versus extracted material as a VOC deterrent source is presented in **Table 1**, which summarises the six dimensions described above.

Table 1. Comparative summary: living plant versus extracted material as a VOC deterrent source across six key dimensions.

Property	Living Plant	Extraction/Applied Repellent
VOC supply	Continuous active biosynthesis	Fixed at moment of harvest
Compound integrity	Full, fresh, biologically active	Degraded by oxidation, heat, and time
Herbivore response	HIPV upregulation (JA-mediated)	None—static, non-responsive
Environmental modulation	Adjusts with temperature, season, and stress	Fixed composition regardless
Output over time	Increases with age and biomass	Declines with degradation
Spatial deterrent	Gradient VOC concentration plume	Flat surface coating; no gradient
Habituation trajectory	Continuously replenished; may intensify on herbivore contact	Degrades; habituation within 2 - 3 days

4. Implications for the Existing Literature

If the six dimensions described in Section 3 produce a VOC output that is qualitatively and quantitatively distinct from that of an extracted equivalent—and the plant physiology literature provides strong *a priori* reason to expect this—then the following conclusions of the existing botanical deterrence literature must be understood as methodologically constrained:

- “Botanical scent repellents are ineffective against wild boar” [1]–[3]: Established using applied preparations only. Valid as a conclusion about those specific preparations. It cannot be validly extended to living aromatic plants, which have never been tested.
- “Animals rapidly habituate to scent-based deterrents”: Documented for static, degrading preparations. Kimball and Taylor (2010) [12] identify four mechanisms of olfactory repellence—neophobia, irritation, conditioned aversion, and flavour modification—of which only conditioned aversion and irritation are likely to remain effective under sustained herbivore pressure. A living plant presenting a continuously replenished, HIPV-augmented VOC signal activates multiple mechanisms simultaneously.
- Single-compound identification studies: Identifying the primary active compound from an extract may isolate a relevant molecule while missing the full synergistic VOC blend of the living organism, which may differ substantially in both composition and concentration.
- Cross-species deterrence rankings: Comparative rankings of plant deterrent potential based on extraction assays may not reflect the relative deterrent efficacy of the corresponding living organisms, particularly if species differ in HIPV

upregulation capacity or compound lability profiles.

The most significant implication is structural: if living plants prove materially more effective deterrents than their extracted equivalents, then the foundational experimental unit of botanical repellent research requires revision. Controlled studies must be designed around the living organism, not its preparation.

5. Indirect Evidence Supporting the Living-Plant Distinction

No study has directly compared a living plant with its extracted equivalent as an herbivore deterrent. However, multiple independent bodies of evidence provide indirect but substantive support for the proposition that they would differ significantly in deterrent efficacy.

5.1. The Herbivore-Induced Plant Volatile Literature

The HIPV literature is extensive, well-replicated, and unambiguous: living plants under herbivore pressure emit VOC blends qualitatively and quantitatively distinct from their constitutive emissions, and these induced blends function as repellents to further herbivory and attractants to herbivore predators. Lima bean (*Phaseolus lunatus*), maize (*Zea mays*), and dozens of other species upregulate specific HIPV blends within minutes to hours of herbivore contact, mediated by systemic JA signalling [9]–[11]. This entire dimension of plant chemical defence is structurally invisible to every extraction-based deterrence study.

5.2. The *Piperales* TRPA1 Study (Cai *et al.*, 2025) [6]

Cai *et al.* (2025) [6] demonstrated that VOCs from *Houttuynia cordata* activate TRPA1 in mice, cattle, and goats, producing robust channel-specific avoidance behaviour confirmed by knockout experiments. The study used extracted and isolated compounds. Whether the living *H. cordata* plant—or other strongly aromatic species whose VOC profiles include TRPA1-activating compound classes—is more, less, or differently effective than its extract remains entirely untested.

5.3. Headspace versus Extraction Chemical Discrepancies

Analytical chemistry studies comparing *in situ* living plant headspace VOC profiles with solvent extractions of the same plant material have consistently found that the two profiles differ in both compound identity and relative abundance. Highly volatile, low-molecular-weight monoterpenes and green leaf volatiles (GLVs) are typically underrepresented or absent in solvent extractions. These are precisely the compounds most likely to function as long-range olfactory cues for approaching herbivores.

5.4. Field Observations of Living Plant Mammalian Avoidance

The horticultural literature documents consistent, field-observed mammalian avoidance of numerous living aromatic plant species—including *Ribes nigrum*, *Lavandula* spp., *Rosmarinus officinalis*, *Nepeta cataria*, and *Perovskia atriplicifolia*.

lia—by deer and other large herbivores *in situ*. These observations are made of living plants in natural growing conditions, not their extracts. The field-observed deterrence may be a property of the living organism—its constitutive plume, HIPV capacity, and dynamic output—that its extracted equivalent does not replicate.

5.5. Olfactory Misinformation and Associational Refuge

Finnerty *et al.* (2024) [8] demonstrated that artificial informative VOC odours—recreating the olfactory profile of an unpalatable plant species—provided browsing refuge to palatable eucalyptus seedlings from free-ranging swamp wallabies (*Wallabia bicolor*) equivalent to protection by real plants. Palatable seedlings were 17 - 20 times more likely to be browsed without such olfactory neighbours. This peer-reviewed field study, published in *Nature Ecology & Evolution*, constitutes the strongest available evidence that plant VOC profiles can deter large mammalian herbivores at ecologically meaningful scales. Critically, it used artificial VOC preparations, not living plants—meaning the deterrent potential of the living organism itself remains untested and may exceed that of its extracted equivalent.

6. Proposed Experimental Agenda

Testing the living-plant deterrence hypothesis requires experimental designs not previously employed in this field. The following programme is proposed:

Study 1—Direct three-way comparison: Present target herbivores (e.g., *Sus scrofa* or *Cervidae*) with three simultaneous conditions: 1) a living aromatic plant—with *Ribes nigrum* L. as the recommended initial candidate given its well-documented constitutive VOC profile and field-observed mammalian avoidance, 2) an extraction of the same plant applied to a scent-neutral inert substrate of equivalent size, and 3) an untreated control. Behavioural data will be analysed using Cox proportional-hazards models to compare time-to-first-approach and time-to-first-contact across conditions. This is the critical experiment that directly tests whether the living plant and its extract are equivalent deterrents.

Study 2—HIPV induction trial: Expose living candidate plants—beginning with *Ribes nigrum*—to simulated herbivory (mechanical damage plus exogenous jasmonic acid application) and measure changes in headspace VOC profile before and after induction using Gas Chromatography-Mass Spectrometry (GC-MS). Present induced versus non-induced living plants to target herbivores in paired trials. VOC composition data will be analysed using multivariate ordination permutational multivariate analysis of variance (PERMANOVA) to quantify profile shifts; herbivore behavioural responses will be compared using paired Wilcoxon signed-rank tests.

Study 3—*In situ* headspace versus extraction VOC profiling: For candidate deterrent species, conduct parallel GC-MS analysis of: a) dynamic headspace from intact living plants (Solid-Phase Microextraction *in situ*), b) SPME surface sampling of living plant emissions, and c) solvent extraction of equivalent plant mass.

Ribes nigrum is recommended as the priority candidate given the published characterisation of its bud and leaf VOC profile. Compound-by-compound differences across conditions will be assessed using principal component analysis (PCA) and non-parametric permutation tests. Submit TRPA1-activating candidate compound classes for in vitro mammalian TRPA1 activity screening.

Study 4—Longitudinal biomass and VOC output tracking: Monitor total headspace VOC emission from individual perennial aromatic plant specimens—with *Ribes nigrum* as the priority species—across three or more growing seasons using annual SPME headspace sampling. Leaf area index and above-ground dry mass will be recorded at each sampling point. Linear mixed-effects models will be used to test whether total VOC emission scales with biomass across seasons, with individual plant identity as a random effect.

Study 5—Field border planting trial: Establish living aromatic border plantings—using *Ribes nigrum* as the initial candidate, given its native range overlap with *Sus scrofa* in Europe and its documented deer-resistance—around agricultural or garden plots in areas with confirmed boar activity. Monitor herbivore damage via camera traps, track surveys, and crop-loss assessment over a minimum of two full growing seasons. Compare with extract-treated and untreated control plots. Deterrence efficacy will be assessed using generalised linear mixed models (GLMMs) with plot as the random effect and treatment, season, and plant age class as fixed factors. We also note that there could be unintended consequences from overstimulation. We argue that because VOC production escalates and varies when the plant is disturbed, due to the unique blend of HIPVs, the overstimulation will not occur. This is an aspect of the hypothesised increased deterrent effect of the upregulation. However, this will require additional consideration and monitoring if mammals are documented contacting the proposed barrier shrub on multiple occasions.

7. Conclusions

The botanical VOC deterrence literature has studied the plant but not the organism. In every published study, living chemistry has been extracted, killed, and asked whether its residue repels animals. That the answer has so often been negative or inconsistent may reflect the inadequacy of the experimental approach more than it reflects the deterrent potential of aromatic plants. A living perennial shrub—continuously biosynthesising its VOC complement, dynamically responding to herbivore contact with upregulated HIPV emission, projecting a concentration gradient into the surrounding air, and growing more chemically productive every growing season—is a categorically different deterrent source from a spray bottle of extract. The two have never been compared.

The six dimensions identified here—continuous biosynthesis, HIPV upregulation, environmental modulation, biomass scaling, compound lability, and plume architecture—are each individually documented in the plant physiology and chemical ecology literature. Together they constitute a strong *a priori* case that extrac-

tion-based deterrence studies are not valid proxies for living-plant deterrence experiments.

The right experiment—presenting a living aromatic plant to a large herbivore under controlled conditions—has not yet been done. This manuscript proposes that it should be, and that it may substantially revise current understanding of the deterrent potential of the plant kingdom.

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Author's Contributions

C.D.: Conceptualisation, hypothesis formulation, methodological critique, literature review, manuscript preparation.

Data Availability

No experimental data were generated or analysed in this study. This manuscript constitutes a methodological critique and research proposal.

Ethics Statement

No animal or human subjects research was conducted in preparation of this manuscript. Proposed Studies 1, 2, and 3 would require institutional animal ethics approval prior to commencement.

AI Use Disclosure

During the preparation of this work, the author used Claude/Sonnet 4.6 in order to format the research into an acceptable version for publication/peer-review. The author also used Google Scholar in order to locate existing literature relevant to the manuscript. After using these tools/services, the author reviewed and edited the content as needed and took full responsibility for the content of the publication.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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