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REVIEW

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Sabadilla (*Schoenocaulon officinale*) as a modern green pesticide crop within a novel commercialization framework

Albert S. Radloff | **Neil O. Anderson**

Department of Horticultural Science, University of Minnesota, Saint Paul, Minnesota, USA

Correspondence
Neil O. Anderson, Department of Horticultural Science, University of Minnesota, Saint Paul, MN 55108, USA.
Email: ander044@umn.edu

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Abstract

The mounting health, environmental, and resistance challenges posed by synthetic insecticides have renewed interest in botanically derived "green pesticides." *Schoenocaulon officinale* (sabadilla), a geophytic perennial native to Mesoamerica with >2000 years of documented insecticidal use, remains undomesticated. A novel green pesticide framework for introducing new taxa is formulated. We present a narrative review of taxonomic, ethnobotanical, phytochemical, agronomic, and genetic studies of sabadilla to (i) benchmark sabadilla against the two mature green pesticide crops (pyrethrum and neem) to highlight regulatory and supply chain bottlenecks; (ii) synthesize botanical and chemical profiles, focusing on steroidal alkaloids (veratridine and cevadine) and modes of action; and (iii) identify the following four critical research gaps that must be addressed—phenology/ideotype definition, genetic diversity and population structure, modern breeding/genomic resources, and propagation/agronomy methods. Coordinated investment in these areas, coupled with streamlined biopesticide registration pathways, can transform sabadilla into a reliable, scalable source of green insecticidal alkaloids. Bridging traditional ethnobotanical knowledge with cutting-edge plant science will revive this botanical but also advance sustainable pest management and biodiversity-driven innovation.

Plain Language Summary

Overview of historical use and studies related to *Schoenocaulon officinale* (sabadilla) to position it as a candidate for domestication and development into a modern green pesticide crop. A new framework for the creation of a green pesticide is proposed.

1 | INTRODUCTION

Throughout the 20thand 21st centuries, rapid urbanization, scaling of intensive agricultural systems, and accelerating climate change reshaped global pest complexes, reducing the effective life span of conventional insecticides while heightening risks to human health, crop production

Abbreviations: EPA, Environmental Protection Agency; EU, European Union; GBS, genotyping-by-sequencing; GWAS, genome-wide association study; LD_{50}, 50% lethal dose; MOA, mode of action; R&D, research and development; SNP, single nucleotide polymorphism.

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systems, and urban and structural environments due to the ease of global insect spread (Korányi et al., 2022; Wilke et al., 2019). The synthetic chemical revolution during the World War II era precipitated development of a plethora of pest control options with a range of efficacy, for example, dichloro-diphenyl-trichloroethane [1,1′-(2,2,2-Trichloroethane-1,1-diyl)bis(4-chlorobenzene)], organophosphates, and pyrethroids to meet the global growing populations' need for effective, scalable tools (Costa, 1987; J. K. Smith, 1988). Later discoveries of nontarget toxicity, environmental persistence, and resistance evolution have progressively reduced options within this once robust tool set, resulting in increased pest control challenges. Publication of popular monographs, such as Rachel Carson's *Silent Spring* (Carson, 1962), began a movement driving research into nontarget effects, which resulted in legislative actions increasing pesticide regulatory standards in various countries around the globe (Werner & Hitzfeld, 2012), culminating in today's environment of increased pest control needs with limited tools available that meet consumer, regulator, and environmental standards.

This challenge can be overcome by reintroducing the precursor to many of today's synthetic chemistries with botanically sourced pesticides, more commonly known as "green pesticides" (Song et al., 2024). Numerous synthetic molecules can trace their origin back to plant secondary metabolites. The rapid degradation of most botanical active ingredients in soil and water lessens residue challenges and ecotoxicological burdens, increasing their appeal in modern markets (Isman, 2006). Regardless of the source and active ingredients, green pesticides require care in handling since toxicity to nontarget invertebrates (natural enemies, pollinators, and applicators) cannot be overlooked. *Schoenocaulon officinale* A. Gray (Schltdl. & Cham.), sabadilla (Melanthiaceae), a geophytic monocot native to Mesoamerica, produces the steroidal alkaloids, veratridine and cevadine, which function as green pesticidal alternatives to pyrethroids and neonicotinoids (Catterall, 1975; Chandler & McDougal, 2014). Such attributes make sabadilla an attractive alternative tool in integrated pest management programs aimed at slowing resistance development while maintaining efficacy through diversifying active ingredients.

Despite sabadilla's storied history as a green pesticide used by humans, it remains an understudied and undomesticated green pesticide with crop potential (Walle et al., 2008). Little is known beyond ethnobotanical notes and scattered chemical assays, leaving large knowledge gaps related to its phenology, production requirements, genetic diversity, or breeding potential under cultivation. All of these elements are vital to ensuring a stable raw material supply chain for green pesticide development. No morphology studies, cropping system trialing, large-scale phenotypic characterization trials, population genetic surveys, or molecular genetic work have been conducted. The current supply of sabadilla seed relies on wild harvests—leaving production to fluctuate with climate, land-use pressures, and subsequently impacting product uniformity—all of which challenge the commercialization and utility of it as a plant-based product. Likewise, habitat losses, as well as the perils of harvesting seed from species in the wild, risks reducing the gene pool as well as compromising the stability of the species in its native habitat. This knowledge gap mirrors the challenges and opportunities documented across other plant-based industries where renewed consumer and regulatory demand for natural inputs is driving investment in botanical dyes (Bechtold & Mussak, 2009), food colorants and flavors (Sigurdson et al., 2017), biofuels (Bouaid et al., 2007; Chopra et al., 2020; Sedbrook et al., 2014), and phytopharmaceuticals (Atanasov et al., 2015; Lubbe, 2013).

In this review, we (i) define green pesticides while reviewing the two most mature botanical technologies (pyrethrum and neem) and present a novel framework for green pesticide development; (ii) provide botanical context with a family-level introduction to *S. officinale* and then highlight morphology, ethnobotany, and historical uses; (iii) report the current phytochemical knowledge on its steroidal alkaloids and insecticidal potential; and (iv) identify research gaps across sabadilla horticultural production and plant genetics that must be bridged to define a crop ideotype that will ensure a successful transition from wild harvest to a domesticated, scalable crop to be used for the production of green pesticides.

2 | GREEN PESTICIDES: AN OVERVIEW

Green pesticides are defined as naturally derived pest control chemicals extracted from plants, including essential oils, alkaloids, terpenes, and phenolic compounds with insecticidal, nematicidal, fungicidal, and bactericidal properties (Song et al., 2024). Unlike their synthetic counterparts, green pesticides are typically biodegradable, less persistent in the environment, and pose lower toxicity risks to humans and beneficial fauna, such as pollinators and/or pollen and seed vectors (Mossa, 2016; Pavela & Benelli, 2016). Their chemical complexity, often comprising synergistic mixtures of multiple active compounds, slows the development of pest resistance and confers diverse modes of action, including neurotoxicity, feeding deterrence, and hormonal disruption (Koul et al., 2008; H. H. Smith et al., 2021). They are commonly marketed and certified as "organic" in the United States or "bio" (biological) in the European Union (EU) (Bayer, 2024; Grow-It-Depot, n.d.). From a botanical perspective, green pesticide sources for compound extraction are commonly woody or herbaceous perennial plant species. Harvested plant parts include most above- and/or below-ground structures. Many are still collected in the wild, due to a lack of dedicated breeding and selection efforts, in contrast with the majority of domesticated crops.

Green pesticides are efficacious on a wide range of arthropod pests, including disease vectors such as mosquitoes and agricultural pests like beetles, thrips, and aphids, with multiple modes of action and low toxicity for nontarget vertebrates (Mossa, 2016; Pavela & Benelli, 2016). It has been proposed that, as pest and pathogen resistance to conventional (synthetic) pesticides continues to develop, green pesticides have the potential to increase in market share due to their slower development of resistance, based on their complex molecular structures (O. Koul et al., 2008; Mossa, 2016; H. H. Smith et al., 2021). Despite these ecological and toxicological advantages, botanical products still represent only approximately $0.8 billion of the $79 billion global crop protection market, barely 1% of total pesticide sales (MarketandMarkets, 2024; Shirsath, 2025).

While many green pesticides have been discovered, few have been bred and commercialized as crops (Isman, 1997, 2023). Recent research in green pesticides has increased worldwide when measured in the number of publications released, with India, the United States, and China conducting the majority of research (Figure 1) (O. Koul et al., 2008; Mossa, 2016; H. H. Smith et al., 2021). Consumer support of organic or bio-certified products and increased awareness of the detrimental effects of conventional pesticides have been prominent drivers for the research (Damalas & Koutroubas, 2020). Additionally, with the increase in global production of certified organic foods and naturally derived materials for insect management tools, those that meet organic rules and regulations for certification are needed (Dayan & Duke, 2010; Dayan et al., 2009; Headrick, 2021). Despite increased research, few products have been commercialized. Existing/known green pesticides face two primary challenges: (1) varying regulatory standards across countries or unions and (2) difficulties in securing a consistent quality supply of the botanical raw materials preventing commercialization of newly researched technologies (Isman, 2006, 2023). Only a handful of green pesticides have overcome these challenges, notably *Chrysanthemum cinerariaefolium*, *Chrysanthemum coccineum* (pyrethrum; = *Tanacetum;* Asteraceae), and *Azadirachta indica* (neem; Meliaceae), and have successfully developed into commercial green pesticide crops. Both pyrethrum and neem are cultivated as crops with relatively stable supply chains and regulatory approvals, yet vary in the degree of technological adoption when compared to global fuel, fiber, or food-use crops (Isman, 2006, 2023), as delineated below.

2.1 | Pyrethrum overview

Pyrethrum is a herbaceous perennial endemic to the eastern Adriatic coast of Europe (Casida, 1980). It contains a suite of neurotoxic esters (pyrethrin I and II, cinerin I and II, and jasmolin I and II) that target insect sodium channels, inducing paralysis and insect death (Grdiša et al., 2013; Soderlund, 1995). Its rapid photodegradation limits environmental persistence, while its low mammalian toxicity and broad-spectrum efficacy have sustained its demand in organic agriculture and household pest control (Biošić et al., 2020; Lal et al., 2021).

While pyrethrum's insecticidal use encompasses >1000 years, modern production first began in 1828 in Armenia, followed by Yugoslavia in the 1840s. After World War I, production moved to Japan and later East Africa (Casida, 1980). Ecuador and Chile also produced pyrethrum during the 20th century but are no longer a major source (Anderson et al., 2021; Fist & Chung, 2015). Currently, pyrethrum is predominantly sourced from Tasmania, Australia, and Tanzania, with additional production in China, Kenya, Rwanda, and Uganda. Three product classes of pyrethrum exist on the market: (1) organic-compliant pyrethrum and (2) conventional pyrethrum, both of which are sold as pyrethrins denoting their natural origin, as well as (3) synthetic derivatives sold as pyrethroids. To the best of our knowledge, there are no published records of certified organic pyrethrum production, although Pyganic and Pyganic Specialty exist on the market as certified organic green pesticide products (Grow-It-Depot, n.d.; McLaughlin Gormley King Company, 2021).

Cultivation practices throughout Eastern Africa, the world's leading source of organic-compliant pyrethrins, remain outdated and inefficient as a result of a lack of investment by international processors in small-holder training, agronomic research and development (R&D), and plant breeding. The industry has been marred with challenges throughout Kenya and Tanzania due to processing company mismanagement, declining farmer interest from low pricing, and climate change pressures on farmers (Hortfresh Journal, 2024; Kilimokwanza, 2024, 2026; Mathias, 2024; Mwale, 2024). Modern agronomic R&D resources are lacking. However, during the 20th century substantial work was done in Kenya by industry stakeholders (Pyrethrum Board of Kenya; Kenya Agricultural Research Institute) to drive agronomic and breeding advancement (Wandahwa et al., 1996).

The majority of nonorganic-compliant pyrethrum, commonly referred to as conventional pyrethrum, is produced in Ballarat and Tasmania, Australia (Pethybridge et al., 2008). Government and private industry collaborations fostered the development of Tasmanian cropping systems and a plant breeding program starting in the 1970s, innovating up until the mid-2010s (Greenhill, 2007). Germplasm in the breeding program was derived from developed breeding lines in Kashmir, India (Bhat et al., 1985). This first pyrethrum breeding program began in the 1970s (Bhat & Pandita, 1977) from a base population in cultivation (derived from random mating)—selected for ≥1.5% PyI and PyII (pyrethrum I and II); the second population was open-pollinated seed of the base population, leading to the third recurrent selection population

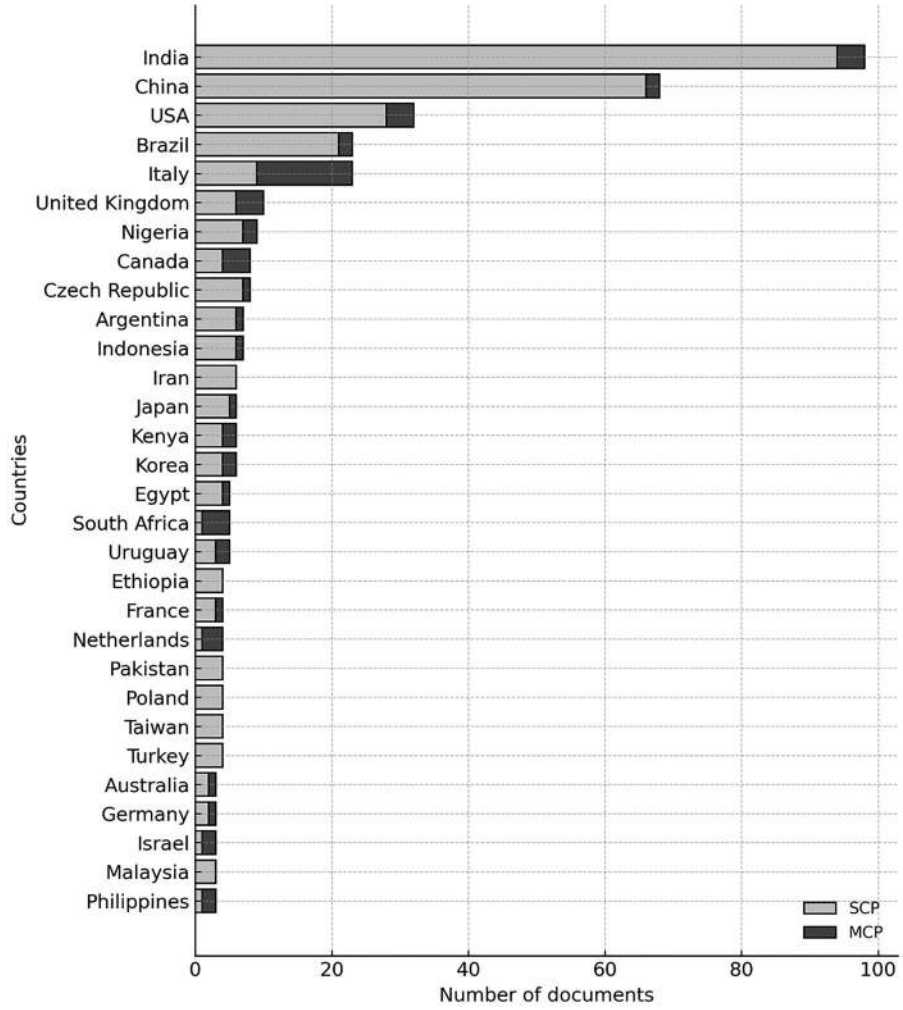


FIGURE 1 Number of published governmental, industrial, or academic documents demonstrating productivity of green pesticide research, on a per-country basis, from 1994 to 2019 (H. H. Smith et al., 2021). MCP, multiple country publications; SCP, single country publications;.

(for high pyrethrum genotypes) as the founding gene pool for the Tasmanian breeding program. More recently, however, the limited gains in breeding for increased pyrethrum content have been offset by poor stand establishment, inadequate weed control, a narrowing germplasm base, and a severe lack of disease resistance, since new pathogens continue to emerge and threaten production (Bhuiyan et al., 2019; Liu, Vaghefi, et al., 2023; Pethybridge et al., 2006, 2008; University of Tasmania, 2023). As a result, Tasmanian farmers successfully advocated for price increases in 2020 to combat the reduced profitability. The price increase per unit produced was the first since 2014, which enabled farmer investment into modern agronomic practices improving yield and efficiency (Tasmanian Farmers & Graziers Association, 2020). China maintains a modest but vertically integrated natural pyrethrum system centered in Yunnan, where public and private partnerships have driven expansion of agronomic production and research along with the adoption of advanced extraction technologies (supercritical CO_2 extraction) (Nanbao, n.d.; Zeng et al., 2024).

Due to recent increases in consumer demand, new resources for research have been developed (Table 1). For example, a 7.1 Gb draft genome was published in 2019 (Yamashiro et al., 2019). Microsatellite marker sets were developed to analyze genetic variation in breeding lines (Varga et al., 2022). Single nucleotide polymorphism (SNP) markers were used to distinguish genetic variation within and among global germplasm within the University of Minnesota Pyrethrum Breeding Program (Bower-Jernigan et al., 2025). Disease characterization and discovery studies were conducted highlighting disease management challenges (Bhuiyan et al., 2019; Liu, Vaghefi, et al., 2023). Additionally, a successful method to annualize pyrethrum flowering in 1 year was developed (Anderson et al., 2021). The raw material production challenges in pyrethrum production may be offset using these new molecular resources.

TABLE 1 Research and development resources for five plant species, categorically organized by research domains and ranked optimal to poor. Current production methods; propagule unit; genetic and genomic resources; germplasm and breeding materials; phenotyping and trialing; pathology and pest management; metabolomics and quality profiles; data management and bioinformatics; regulatory and intellectual property (IP) framework; extension, collaboration, and market intel.

	Ranking—Crop				
Research domain	**Optimal—Neem**	**Optimal—Onion**	**Good to optimal—Cannabis**	**Marginal—Pyrethrum**	**Poor—Sabadilla**
Production methods—Development and/or improvement	Seed-propagated in agroforestry or plantation systems; clonal propagation and tissue culture used experimentally	Field-grown from seed; biennial bulb vernalization required for seed production	Vegetatively propagated in greenhouses or controlled environment agriculture for uniformity; clonal cuttings standard (Adhikary et al., 2021; Talei et al., 2025)	Field-nursery seedlings transplanted to field beds under intensive monoculture or direct seeded	No documented production systems
Germplasm	Morphological characterization of 170 accessions (Rajarajan et al., 2025)	USDA-NPGS collection >1100 accessions (Ochar & Kim, 2023)	Cannabis accessions from a wide range of geographies characterized (Welling et al., 2016)	Global germplasm collection genotyped (Bower-Jernigan et al., 2025)	No documented germplasm collections
Cropping system trials	Extensive field trials & trait analysis (Rajarajan et al., 2025)	Seed yield & trait variation in germplasm (Ochar & Kim, 2023)	EU VCU field trial protocol published; flowering traits and yield components (Vonlanthen et al., 2025)	Only historical agronomic guides	No formal agronomic studies
Pathology & pest management	Azadirachtin-based IPM guidelines developed	Downy mildew resistance marker identified (Ochar & Kim, 2023)	Powdery mildew resistance locus 2 (*PM2*) mapped (Seifi et al., 2025)	No current IPM protocols outside of Tasmanian production	No pest/pathology protocols
Genetic & genomic resources	Chromosome-level assembly with Hi-C & PacBio (Du et al., 2022)	12.77 Gb chromosome-level assembly (Cho et al., 2025); *Allium* Map with RFLP, SNP & SSR maps (Ochar & Kim, 2023)	Chromosome scale reference plus new assemblies; genomes/transcriptomes (van Bakel et al., 2011)	7.1 Gb draft genome; 91.8% BUSCO or Benchmarking Universal Single-Copy Orthologs (Yamashiro et al., 2019); Microsatellite markers for population genetics (Grdiša et al., 2013)	No genomic resources available
Metabolomics & quality profiles	Tissue-specific metabolomics & transcriptomics (Du et al., 2022)	Volatile profiling via HS-SPME/GC–MS (Ochar & Kim, 2023)	Validated workflows for HPLC cannabinoid profiling (Levey et al., 2023)	GC–MS pyrethrin & terpene analysis (Yamashiro et al., 2019)	HPLC quantification of veratridine & cevadine (Hare, 1996)
Regulatory & IP framework	Registered as botanical pesticide in EU & US plus numerous regional markets	Plant variety protection (PVP) protections established; global use (Ochar & Kim, 2023)	State, Federal, and International laws; complex	Allowed as organic insecticide; limited regions	No regulatory approvals
Extension, collaboration & market intel	International Neem Network & FAO extension	Global and regional outreach association—USDA & National Onion Association (Ochar & Kim, 2023)	Regional extension networks & consortiums	Tasmania & Kenya grower groups exist. Tanzania industry fragmented	No extension networks

Abbreviations: EU, European Union; FAO, Food and Agriculture Organization; GC–MS, gas chromatography–mass spectrometry; Hi-C, chromosome conformation capture; HPLC, high-performance liquid chromatography; HS-SPME, headspace solid-phase microextraction; IPM, integrated pest management; RFLP, restriction fragment length polymorphism; SNP, single nucleotide polymorphism; SSR, simple sequence repeat; USDA-NPGS, United States Department of Agriculture-National Plant Germplasm System; VCU, Value for Cultivation and Use.

Regulatory challenges may explain the lack of innovation in product formulations. For example, the formula for PyGanic has not changed since its inception (Grow-It-Depot, n.d.). This is typical for pyrethrum products. New label expansion (using the same formulation) to add additional crops has occurred (Pate, 2020). Today, Sumitomo Chemical Company owns the vast majority of global natural pyrethrum supply through their subsidiaries: Botanical Resources of Australia and McLaughlin Gormley King Company (Clark, 2017; Costa, 1987).

2.2 | Neem overview

Neem, a woody perennial native to the Indian subcontinent, is a multipurpose tree historically used in traditional medicine and agriculture (Malakar & Mandal, 2024). Its primary bioactive compound, azadirachtin, is a tetranortriterpenoid that acts as an insect growth regulator, disrupting molting, reproduction, and feeding in a wide range of pests. Additionally, azadirachtin and additional compounds provide synergistic antifungal, antibacterial, and antiviral effects (Benelli et al., 2017). Commercial neem products include emulsifiable oils and concentrated azadirachtin extracts, which are widely adopted in organic farming. Product innovation is common across neem markets with several new formulations of neem insecticides being released over the last 5 years (Bennett, 2023; Ozone Biotech, 2024). Neem has a broad cultivation range across subtropical and tropical zones because of its drought tolerance. Production is sourced from a wide variety of cropping systems and found in more than 78 countries where it is wild-collected, found in silvopastoral systems, and/or produced in plantations (Koul & Wahab, 2004).

Genomic resources are available for neem, including a chromosome-level genome and multi-organ transcriptomes (Du et al., 2022), a >170 accession germplasm collection (Rajarajan et al., 2025), and standardized quantification assays. Continuous agronomic research supports crop advancement (Abebe, 2021; Widnyana et al., 2021). Neem R&D is supported across numerous stakeholder groups because of its utility as the "village pharmacy." However, variability in chemical content across individuals, coupled with inconsistent regulatory standards across countries, poses challenges to consistent formulation and approval (Isman, 1997, 2023).

3 | KEY CHALLENGES

3.1 | Key Challenge #1: Regulatory issues for green pesticide registration

Varying standards for regulatory approval and definitions of green pesticides lead to the time-consuming and costly rate-limiting procedures of the regulatory process that inhibit commercialization. This is exacerbated by global, regional (EU), and country-specific (United States) regulations and application systems for registration (Isman, 1997). This is best highlighted by the EU and US regulatory systems for green pesticides. Herein we will use the US system as the example of an established, tested, and rigorous registration process.

In the United States, the Environmental Protection Agency (EPA) oversees pesticide registration in a multi-step process; for the purposes of this paper we are categorizing it into three primary stages (US EPA, 2017). First, applicants file a registration package that undergoes initial content and technical screening to confirm labeling, data, and fees meet minimum standards. Second, the EPA conducts an in-depth scientific review of core toxicological, ecological, and environmental fate studies, often requiring additional long-term or higher-tier data, and integrates results into aggregate human health and ecological risk assessments under the "risk cup" framework. Third, the EPA coordinates with other agencies, solicits public comment, and issues a regulatory decision to approve, conditionally approve, or deny registration, with all products subject to periodic post-registration review (US EPA, 2017). The EPA also has a "fast track" system for biopesticides in which, if a product is selected for this program, reduced registration fees are granted and certain testing requirements may be waived requiring less data generation. This accelerates the timeline from 5 to 7 years to a minimum of 18 months (Isman, 2023). Additionally, a broad range of plant raw materials and essential oils are wholly exempted from any EPA regulation if placed on the FIFRA 25B list (Federal Insecticide, Fungicide, and Rodenticide Act) (Isman, 2023). Meanwhile, in the EU the European Food Safety Authority regulates pesticide products based on whether the primary pesticidal ingredient is exclusively used as a pesticidal ingredient or if there are alternative established uses; if the latter, fewer requirements are needed for approval. However, the rate of approval is too low to meet demand for novel pest control options (Isman, 2023).

Regulatory frameworks built to evaluate single, well-characterized synthetic molecules struggle to accommodate complex naturally derived green pesticides whose chemical profiles vary in composition and concentration. This complexity is compounded by limited regulatory experience among many botanical pesticide developers who instead employ a business model focused on existing approved products. Inconsistency in the application of organic certification standards creates further challenges; while organic food products (e.g., bread or beef) must be produced entirely from certified organic inputs (Coleman, 2012; National Organic Program, 2013), the ingredients in organic-compliant insecticides are not required to be cultivated under organic certification. Instead, these products must simply meet the National Organic Program's criteria for allowed substances in product formulation, as detailed in its program guideline specifications (National Organic Program, 2016).

Regulatory standards are updated slowly and inconsistently across regulating bodies. Data sharing and proactive engagement with regulatory bodies, lawmakers, and customer groups can promote green pesticide development and commercialization with appropriate regulation. Greater alignment between governing bodies, manufacturers, and customer groups would aid in defining data requirements. With green pesticides and their inherent natural diversity, data pertaining to molecular diversity, biosynthesis, and toxicity are of great importance.

3.2 | Key Challenge #2: Consistent quality supply of the botanical raw materials

Synthetically derived pesticides versus green pesticide development programs share data requirements such as toxicology and environmental studies. However, green pesticides are beholden to the many challenges inherent in natural production systems relating to plant-environment-pest interactions. Whether an established crop or a wild species is found to have chemical attributes qualifying it for use as a green pesticide, consistent long-term R&D is required for crop-specific production parameters to ensure consistent supply of target compound(s) and return on investment. The cost and time associated with the generation and continuous development of these plant science resources are key prohibitive elements that discourage chemical technologies from focusing efforts on green pesticides.

Continuous R&D focused on mitigating production challenges is required to ensure a consistent quality supply of the botanical raw material. Many of the challenges faced by pyrethrum, for example, limited adoption of molecular breeding, few public and private collaborations, and limited updated cropping systems research, have been overcome for the neem industry (Table 1). This corresponds with an increased number of new product registrations and the rapid global expansion of neem products. To benchmark plant science resource availability for each green pesticide crop and define targets for sabadilla, two other crops, onion (*Allium cepa* L.) and cannabis (*Cannabis sativa* L.), are included for comparative purposes (Table 1). Onion was chosen as a geophyte exemplar for sabadilla; and already boasting a chromosome-level pan-genome assembly, a >1100 accession germplasm collection, standardized phenotyping protocols, a similar geophytic structure (both with tunicate bulbs), and formal extension networks supporting global production into numerous product categories ranging from extracts to foods. Cannabis, in contrast, represents a specialty crop with medicinal-pharmaceutical secondary metabolites that add increased research costs and regulatory pressures yet still has numerous cropping systems, centers of production, genomes, comprehensive transcriptome atlas, validated biochemical assays, and SNP-based breeding pipelines, making it an ideal "Optimal" to "Good" tier crop. As presented above, neem has global support with the continuous adoption of new technologies and a persistent integration of active research (Table 1). The lack of continuity found with pyrethrum R&D is a key driver in the inconsistent quality of supply, for example, chemical content or costs per unit. Sabadilla is lacking the plant science resources to enable basic research as well as timely domestication and scaling of cropping systems (Table 1). Integrative steps in the green pesticide development process to generate plant science resources, as found in crops such as onion and cannabis, will aid in the successful commercialization of sabadilla as a green pesticide crop.

3.3 | Proposed green pesticide development process

To enable the successful development and commercialization of green pesticides, a proposed green pesticide developmental framework is developed herein (Figure 2), derived from models of distribution chains for product development in plants (Drew et al., 2010). This provides structure with the intent of reducing the negative effect of the two chronic bottlenecks to green pesticides development, that is, regulatory difficulties and consistent supply of high-quality raw materials, while clarifying how activities integrate across breeding, cropping systems development, chemistry, and regulatory work for new domesticates or established crops.

3.3.1 | Discovery and market gap analysis informing species selection

At the commencement of the green pesticide developmental framework (Figure 2), discovery and/or market gap analysis are the key drivers for candidate species selection and screening to guide subsequent complex breeding, cropping systems, toxicology, and regulatory requirements (Stages 1–3) for any new green pesticide product. Species selection decision-making would be determined either by private or public sector exploratory discovery science or evaluation of market needs and the review of the potential or existing product portfolio. Focus on compound toxicity and government regulatory pathways to accommodate toxicity is the key criteria in species selection (Figure 2), which requires testing and input from chemists and biochemists (D. Unger, personal communication, 2019). Awareness of where the chemicals of interest are most heavily concentrated in the plant, their method of reproduction, and plant life cycles are additional components of consideration at this stage. Selection of a target green pesticide species paves the way for basic/applied research on plant breeding and cropping system development to formalize sustainable supply chains that produce biomass

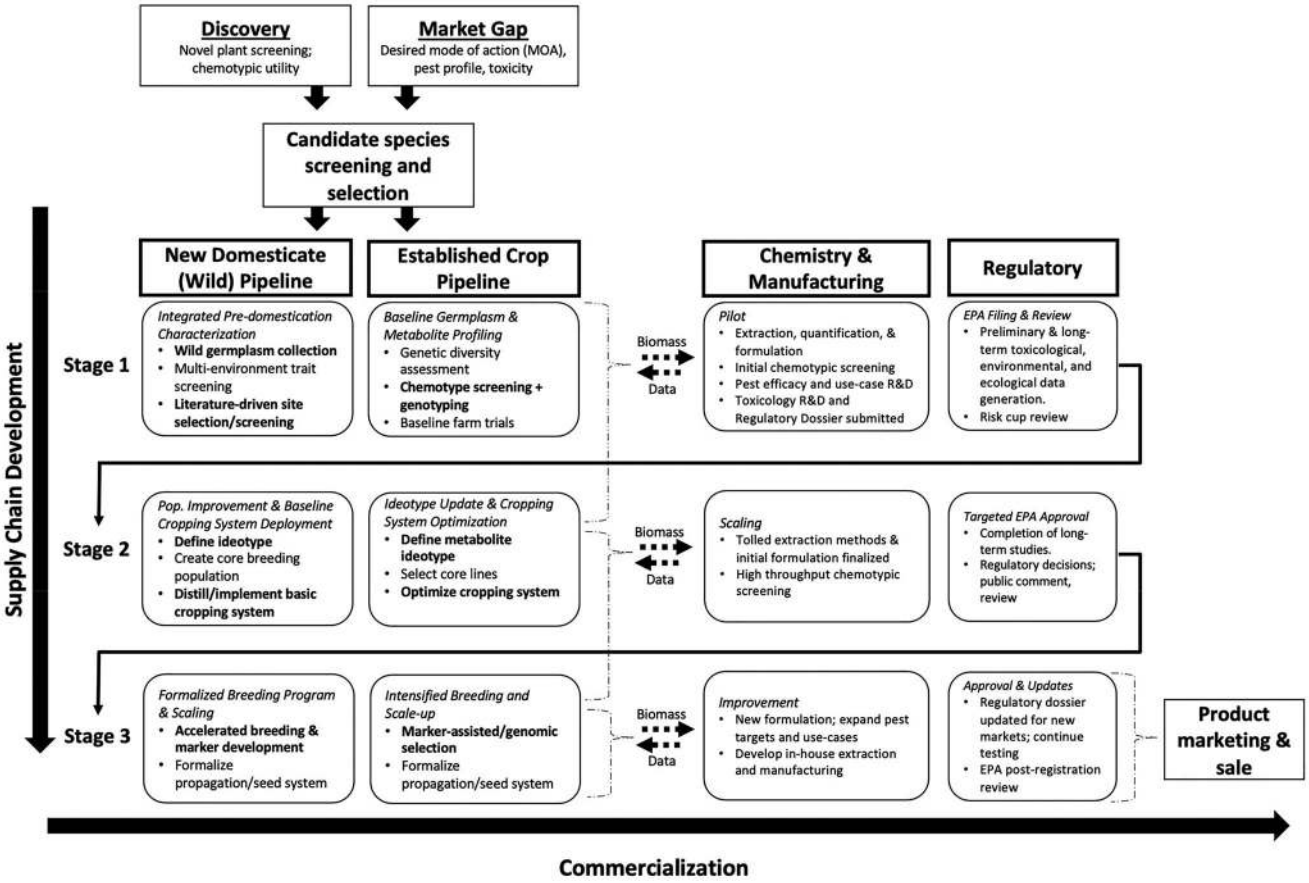


FIGURE 2 The green pesticide developmental framework with contrasting supply chain development and regulatory pipelines for commercialization, illustrating the staged progression from discovery to product marketing for botanical pesticide development. Candidate species are first identified through discovery of novel chemotypic traits and alignment with market gaps, followed by screening and selection for domestication or integration into established crop pipelines. Stage 1 emphasizes germplasm characterization, metabolite profiling, and baseline trials; Stage 2 focuses on population improvement, ideotype definition, and cropping system optimization; and Stage 3 advances to formalized breeding, scaling, and marker-assisted selection. Parallel chemistry and manufacturing pipelines progress from pilot extraction and toxicology research and development (R&D) to formulation scaling and product improvement. In tandem, regulatory milestones include Environmental Protection Agency (EPA) filing and review of core data packages, targeted approval following completion of long-term studies, and ongoing post-registration updates. The integration of biomass and data flows across these domains informs critical choices that culminate in commercialization and product sale.

for product development, toxicology and regulatory submissions, and subsequent product manufacturing and launch (Stages 1–3, Figure 2).

Plant science resources required for successful commercialization vary depending on whether the species selected is a new domesticate (wild) plant or an established crop (Figure 2). Considerable overlap occurs with metabolite profiling and genetic diversity screening. However, a wild species requires more preliminary research to describe morphology and life cycle. This knowledge can then be leveraged to create a novel ideotype (Donald, 1968). In the case of an established crop, pre-existing resources accelerate the retooling of existing breeding and production systems requiring only the addition of metabolite requirements to the crop ideotype, screening for novel genetic diversity, and awareness of pricing and costs of production.

Activities proceed in overlapping work streams of Stages 1–3 rather than in strict sequence as species selection and early cropping system work begin for both the new domesticate and established crop (Figure 2). Preplanned small lots of biomass should be routed continuously to extraction and formulation R and D; efficacy and toxicology start with pilot materials and iterate as quality improves. Data from chemistry, efficacy testing, and toxicology feed back into ideotype definition, germplasm selection, and cropping system choice, while also feeding forward into a living regulatory dossier and staged manufacturing scale-up. In practice, breeding, cropping system development, manufacturing, and regulatory all operate as coupled lanes with rolling handoffs, not as isolated endpoints. Two critical vectors in the developmental framework's magnitude and direction, that is, supply chain development and commercialization, are in continuous

evolution and development as Stages 1–3 data and assessment outputs accumulate between the crop pipelines and the chemistry and manufacturing and regulatory factors.

3.3.2 | Stage 1: Germplasm characterization, metabolite profiling, baseline trials

Stage 1 establishes baselines for the new domesticated or established crop pipelines, chemistry and manufacturing, and regulatory components within the green pesticide developmental framework (Figure 2). Integrated pre-domestication and characterization for the new domesticate (wild) pipeline commences with extensive literature reviews and wild germplasm collection. A diverse germplasm pool is required for any crop pipeline to provide genetic variation in genes, allelic diversity to allow for development or enhancement of the target chemical compound(s), or to increase or stabilize toxicity of the desired mode of action (MOA) (Anderson, 2026; Nandwani, 2019). For new crops, directed wild germplasm collection trips within the centers of origin and diversity are necessary to provide genetic, phenotypic, and chemotypic variation from which to select (Rathore et al., 2005; Vavilov, 2009). Strategic plant collection approaches will ensure a wide germplasm sampling (Anderson, 2017). Material collected during surveys of wild stands (transects of populations) across the species' native range could then utilize genotyping-by-sequencing (GBS) to assess unique genotypes, population structure, allelic richness, and adaptive gradients. These data not only inform conservation and collection strategies, but GBS would aid in preliminary genomic analysis to accelerate breeding.

Collected germplasm would require elucidation of plant reproductive barriers, ploidy levels, or other factors impacting growth for green pesticide production. Multi-site, multi-environment trait chemotype screening and genotyping capture phenotypic, chemotypic, and genotypic variability. Subsequent metabolite profiling and early toxicology screening would clarify regulatory classification and data requirements (Figure 2). Morphological and phenological data encompass vegetative growth rate, propagules, thresholds for reproductive transition, flower bud initiation and development periods, seed-set dynamics, and total target compound(s) content. A significant portion of this work will be conducted with small sample numbers and minimal replication as wild germplasm is screened and elites are selected and bulked. Preliminary screenings to quantify variability can be used to continuously provide small-lot biomass that feeds across to chemistry and manufacturing to support method development and pilot formulations (Figure 2). Early efficacy and toxicology would determine the regulatory pathway to initiate a US EPA filing (US EPA, 2017). The research required for product formulation and registration would not be delayed until the new domesticate or crop could be fully developed and established, and simultaneous data feedback from the chemistry and regulatory would continue to drive both product formulation and registration as well as breeding (Figure 2). Supply chain development would be initiated during Stage 1, leveraging multi-environment germplasm screening trials to define core cropping system needs, aiding in identifying and developing infrastructural needs and players (firms) for production of the botanical.

3.3.3 | Stage 2: Population improvement, ideotype definition, cropping system optimization

Stage 2 of the green pesticide developmental framework (Figure 2) standardizes genetics and deploys basic cropping protocols to stabilize product quality versus yield. Using preliminary data from Stage 1, the crop ideotype can be developed, that is, a conceptual model of the optimal plant phenotype (Donald, 1968), tailored to continuing green pesticides supply chain development. Indeterminate taxa may require successional seed harvest(s) to allow for optimal seed development. A crop ideotype will be developed for definition/enhancement of the crop metabolite in Stage 2. While, to the best of our knowledge, no distinct green pesticide crop ideotypes exist, other ideotype templates can be used in their creation (Tork et al., 2019; Yadav et al., 2023). A basic cropping system needs to be distilled for tie-in and implementation of the ideotype for the new domesticate crop, while an established crop would need cropping system optimization for metabolite production (Figure 2). For example, an upright, uniform plant architecture (defined in the ideotype) would facilitate development and refinement of mechanical harvesting methods and enable a high-throughput cropping system.

Propagation methods of target taxa in Stage 2 would need evaluation and development to quantify multiplication rates for both seed- (sexual) and clonal (asexual)-propagated crops. Simultaneously, field cropping system trials must define optimal plant density, soil type, irrigation, and nutrient regimes and assess the impact of environmental stress on target compound synthesis and yield. Building off supply chain development informative data from Stage 1, multi-environment trials and partner evaluations would occur while continuing to evaluate the program's current germplasm and selected numerous environments. Crucially, as in Stage 1, these experiments should integrate continuous small-lot harvests routed to pilot extraction and toxicology assays, ensuring that chemistry, manufacturing, and regulatory work evolve in tandem with crop ideotype development (Figure 2).

In Stage 2, phenotypic and chemotypic data will be leveraged for genome-wide association studies (GWASs) to link

SNP variation to phenotyped traits such as target chemical content, flowering time, and harvestable units (seed, flowers, leaves, stems, roots, or geophytic structure). Marker-assisted and genomic selection pipelines should be developed to accelerate selection cycles and recurrent breeding programs to maintain heterozygosity to safeguard against genetic bottlenecks. Integrated genomic–phenomic breeding has aided in the improvement of specialty crops, such as *Chrysanthemum cinerariifolium*, *Capsicum annuum*, and *Cocos nucifera* (Bower-Jernigan et al., 2025; da Silva et al., 2024; Liu, Anderson, et al., 2023; McCoy et al., 2023).

If targeting reproductive biomass, synchronous flowering to optimize uniform development and harvest is necessary for all crops but poses a particular challenge for taxa with indeterminate inflorescences, as noted earlier. High, uniform yields to maximize biomass throughput for chemistry and manufacturing will be needed to continue testing and enhancement of the extraction process, thereby aiding the regulatory filings to target the application for approval. Feedback between crop development pipelines and chemistry will be necessary to ensure consistently elevated target compound concentrations, simplifying regulatory and toxicology work. Defining a comprehensive green pesticide ideotype and selecting toward it will stabilize the targeted compound supply, thereby reducing risk in downstream extraction and registration while providing foundational data to advance breeding and domestication.

Stage 2 ideotype creation and refinement must consider extraction efficiency and residue profiles of target green pesticide compounds, while initial production trials should supply advanced lines or clonal genotypes for formulation optimization in ever-increasing production trials. Extraction and manufacturing need to be scaled to produce reliable pilot biomass with a first-generation formulation, positioning a scalable raw material supply chain for advancement once long-term EPA studies are completed and EPA approval is granted fully, conditionally, or denied (requiring re-filing) (Figure 2).

3.3.4 | Stage 3: Formalized breeding and scaling

Stage 3 of the green pesticide developmental framework (Figure 2) delivers improved germplasm and refined cropping systems for consistent, higher quality biomass; manufacturing and formulations are optimized at scale, and the regulatory dossier is updated to support broader claims for full commercial release. Each level should be gated by an active-ingredient cost of goods sold target minimum, with selection thresholds and unit operations chosen to meet stage-dependent cost goals.

The best propagation protocols are implemented at scale and refine cropping practices to deliver predictable biomass with consistent chemical profiles, thereby overcoming the erratic supply that has plagued other green pesticide crops. Experiences with neem and pyrethrum show that even successful green pesticides can be constrained by discontinuous raw material supply, uneven adoption of production practices, and variable regulatory acceptance that can all be tied back to inconsistent plant science resource generation and improvement (Table 1).

By Stage 3, integrating genomic selection with speed-breeding and shuttle trials across multiple environments will deliver elite cultivars faster, enabling earlier submission of regulatory data packages and updates alongside the scale-up of biomass production and dossier development (Braun et al., 1996; Jighly et al., 2019; Kumar et al., 2023). Ultimately, all of the in-depth research, product development, ideotype testing and refinement, coupled with chemistry and manufacturing, will aid in the approval of a registered green pesticide that can be moved into final product marketing and sale (Figure 2).

Overall, the green pesticide developmental framework (Figure 2) offers a scientific, pragmatic route to mitigate risks when creating a new green pesticide or refining an existing one. Accordingly, we next introduce a test "new" green pesticide, using its current state and principal gaps to orient subsequent research, crop ideotype development and close by defining next steps in relation to the development process described above.

4 | *Schoenocaulon officinale* (SABADILLA): BOTANICAL PROFILE, HISTORY, AND USES

4.1 | Crop potential

Once the botanical backbone of commercial louse powders, *Schoenocaulon officinale* A. Gray ex Benth. (Schltdl. & Cham.), has drifted into obscurity (Allen et al., 1944; Roark, 1947). While its center of origin is Mexico, it is now harvested sporadically from wild stands on Venezuelan hillsides for extraction of highly concentrated and naturally occurring sodium-channel toxins, veratridine and cevadine (Hare, 1996; Walle, 2008). Lacking domestication, its full potential as a revitalized green pesticide crop awaits. In this review, the limited literature related to taxonomic, morphological, ethnobotanical, agronomic, and chemical studies of sabadilla are aggregated to provide a unified technical baseline to identify research gaps and enable its re-emergence as a modern green pesticide crop.

4.2 | Vernacular diversity, ethnobotany, and historical trade and use

First described in 1517 by Monardes, sabadilla was reported in present day Mexico and parts of the southwestern United

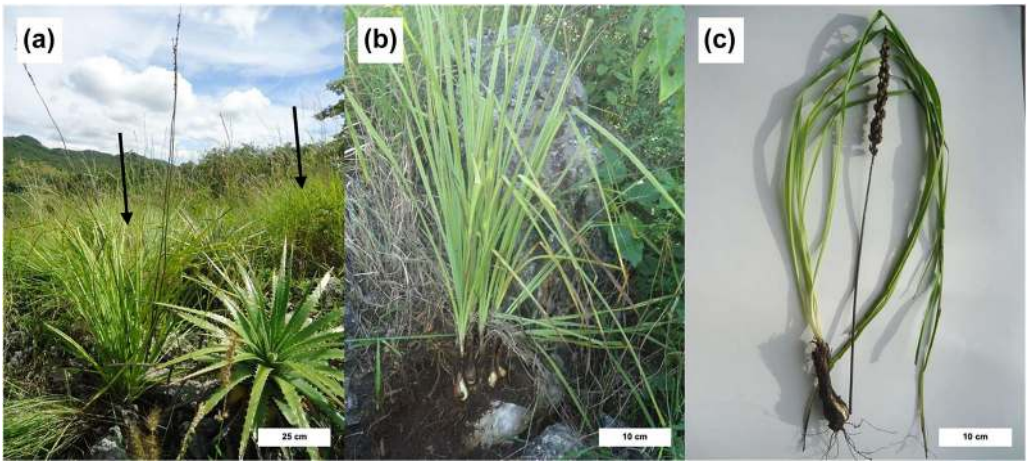


FIGURE 3 *Schoenocaulon officinale* plants in their native habitat and collected materials. (a) Individuals occurring in open grasslands between rocks (arrows). (b) Plant growing along the ecotone between grassland and forested area. (c) Collected plant showing bulb, fibrous roots, and basal leaves with attached inflorescence. All plants were observed and collected by Ejido Alfonso Moguel, Chiapas, Mexico (866 m above sea level), within a pine-oak forest grassland matrix. Scale bars = 25 cm (a), 10 cm (b and c). Photo credits: Ejido Alfonso Moguel.

States, with supporting claims made in 1640 associating it with prior taxonomic classification assigning it to the genus *Asagrea* (Allen et al., 1944; Fluckiger & Hanbury, 1879). It was found in grassy lands on eastern slopes throughout Teocelo, Huatusco, and Zacualpan, Mexico (Fluckiger & Hanbury, 1879). Populations can still be observed in these areas today as well as further south in Chiapas, Mexico (Figure 3). Wild populations have also been observed in Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Peru, and Venezuela (Zimmerman, 1958).

Several names have been used to refer to *S. officinale*. The most prominent is sabadilla, derived from the common Spanish name of "cebadilla," which was used by the Huastec people, although the Teenek used the name "sebadiya" (Alcorn, 1984; Frame, 1990). The name sabadilla is thought to be based on the plant's rough similarity with barley because of its morphologically similar seed head, called cebadilla in Spanish, which can be misleading. Numerous names in multiple languages are used to refer to sabadilla (Table 2).

Reports of sabadilla's historical use begin on the basaltic slopes of central Veracruz and Oaxaca, Mexico, where Huastec growers maintained semi-managed patches in the forest (Allen et al., 1944; Fluckiger & Hanbury, 1879). Seed powder, rich in veratridine and cevadine, served as a pediculicide and maggot suppressant and was used in open wounds (Allen et al., 1944; Fluckiger & Hanbury, 1879). Sabadilla is also recorded within the "Codex de la Cruz Badianus" by Fray Bernardino de Sahagun, a 16th-century medical and botanical text, the earliest surviving from the American continent (Alcorn, 1984).

Modern interest in the study of *Schoenocaulon* originated from the value of its alkaloids, which shared functionality with *Veratrum*, a common source of veratridine in Europe (Frame, 1990). Europeans in the 1700s and 1800s were familiar with botanical insect control methods and actively used veratrine derived from *Veratrum* rhizomes. However, challenges with sourcing and extraction of alkaloids from the rhizomes, alongside the complex mixture of cyclopentanophenanthrene and C-nor-D-homosteroidal ring structure alkaloids in *Veratrum*, drove demand toward sabadilla (Chandler & McDougal, 2014; Frame, 1990). Sabadilla's use in Europe can be traced back to the 16th century when it was brought from the Americas; the seeds were aged, heated, and then treated with alkali before being used as an insecticide (Unsworth et al., 2019). Its use as a pediculicide (compound to kill lice or scabies mites) in Europe can be found in literature dating back to 1879 as well as the use for control of intestinal worms within humans (Fluckiger & Hanbury, 1879). During World War I, sabadilla was again used as a pediculicide (Frame, 1990; C. Kim et al., 2019). Today, sabadilla can be found in the active ingredient (a.i.) listings for numerous homeopathic products throughout the world, sold as tinctures, pills, or in powder form. Even though sabadilla is cited as an a.i., it has been reported that many products commonly have no detectable levels of the botanical due to extreme dilutions (Shaw, 2011). Sabadilla products claim alleviation of flu and fever symptoms as well as allergies, such as hay fever. However, no products are approved by the US Food and Drug Administration (Walle et al., 2008). A homeopathic sabadilla product did show significant effect in improving symptoms of hay fever (Danks, 2004). Additional research testing homeopathic sabadilla products in sheep for control of internal parasites indicated no positive impact on sheep health, despite a significant decrease in parasite egg production (Benvenuti et al., 2012).

TABLE 2 Historical vernacular names of *Schoenocaulon officinale*, arranged by year of first citation, including the recorded name(s), language of use, and bibliographic reference.

Year of first citation	Recorded names	Language of use	Bibliographical source
1517	cebadilla	Spanish	(Fluckiger & Hanbury, 1879).
1640	Indian Causticke Barley	English (trade)	(Fluckiger & Hanbury, 1879)
1651	ytzcuimpatli	Nahuatl	(Frame, 1990)
1879	petite orge; cevadille; sebadille; sevadille	French	(Fluckiger & Hanbury, 1879)
1879	gebrauchliche sabadilla; g. Sabadille; lausekraut	German	(Fluckiger & Hanbury, 1879)
1879	severzaadkruid	Dutch	(Fluckiger & Hanbury, 1879)
1944	sabadilla; sebadilla; cevadilla	English (commodity)	(Allen et al., 1944)
1944	cebadilla mexicana; cebolleja; coballeta; cintul; cebadilla de Tierra Caliente; quimiophipatli; itzcuimpatli; cunicho; etzemo	Spanish, Nahuatl	(Allen et al., 1944)
1984	sebadiya	Huastec (Téenek)	(Alcorn, 1984)
2012	duá ghémel	Libyan Arabic	(De Natale & Pollio, 2012)

4.3 | Taxonomic context and evolutionary background

Sabadilla belongs to the Melanthiaceae, formerly in the Liliaceae, which is a basal, archaic family composed of flowering perennial plants. Within this family of monocots distributed across the globe (Figure 4), there are 196 species across 17 genera within five tribes containing genera of note, such as *Veratrum*, *Zigadenus*, and *Stenanthium* (C. Kim et al., 2019; S. Kim et al., 2016; Zomlefer & Judd, 2002). Species in Melanthieae are found from Arctic regions to temperate zones, whereas *Schoenocaulon* extends into Latin America. Unique within the Melanthieae, sabadilla stores its highest concentrations of steroidal alkaloids in the seed rather than in subterranean organs.

There are diverse genome sizes within the Melanthiaceae with *C*-values > 230-fold within the Parideae tribe (Pellicer et al., 2014). However, other tribes have smaller genomes with the smallest reported being that of *Schoenocaulon texanum* Scheele, within the Melanthieae, at 0.66 pg (Pellicer et al., 2014). Karyological data indicate a complex range with base chromosome numbers of $x = 5$, 8, 10, 11, 12, 15, and 17 (Pellicer et al., 2014). Sabadilla species are diploid, $2n = 2x = 16$ with their 1.5–3 μm (length) chromosomes exhibiting conspicuous kinetochores (protein structures joining chromosomes to microtubules during cell division) (Frame, 2001; Pellicer et al., 2014).

Analysis of the Internal Transcribed Spacer, a noncoding region situated between ribosomal RNA genes in the ribosomal DNA cistron, across the *Schoenocaulon* genus, confirmed 24 *Schoenocaulon* species distributed across latitude, ranging from a lone Floridian endemic (*S. dubium*) into a broad corridor from the southern United States to the southern reaches of Central America that harbors most taxa. A South American enclave restricted to *S. officinale* is believed to have been introduced (Figure 5) (Frame et al., 1999; Zomlefer et al., 2006). Phylogeographic modeling traces the ancestral genus to Central America in the early Eocene (~38 mya), followed by a southward radiation into Peru roughly 1 million years ago (C. Kim et al., 2019; Zomlefer & Judd, 2008).

4.4 | Botanical characteristics

Sabadilla is a geophytic herbaceous perennial distinguished by a single or tight cluster of fibrous-tunicate bulbs 2–6 cm long (Figures 6–8). Each bulb is wrapped in the remnants of old leaf bases that form coarse, nerve-like fibers and produces two root types: contractile roots and fine feeder roots (Eperjesi et al., 2023; Frame, 1990). This geophytic belowground storage mechanism, first recognized in Raunkiaer's (Raunkiær, 1934) life form scheme, allows sabadilla to survive prolonged, non-photosynthetic dormancy periods and resume growth when favorable conditions return (Khodorova & Boitel-Conti, 2013).

Sabadilla leaves emerge basally in a distichous to spirodistichous spiral, emerging from the fibrous tunic around the bulb (Figure 7) and can be persistent year to year (Frame, 1990). Flowers are sessile, and the perianth comprises cream-colored tepals, which exhibit radial symmetry and are arranged in two distinct whorls (Figure 7C–F). The genus is commonly distinguished by its spike-like racemes (Figure 7A,B) with inflorescences whose lowermost flowers produce capsules before the top flowers begin to produce pollen (Brinker, 1942). The reproductive morphology varies along the inflorescence. Flowers in the uppermost portion (top 1/6) are functionally staminate (Figure 7D), containing only the

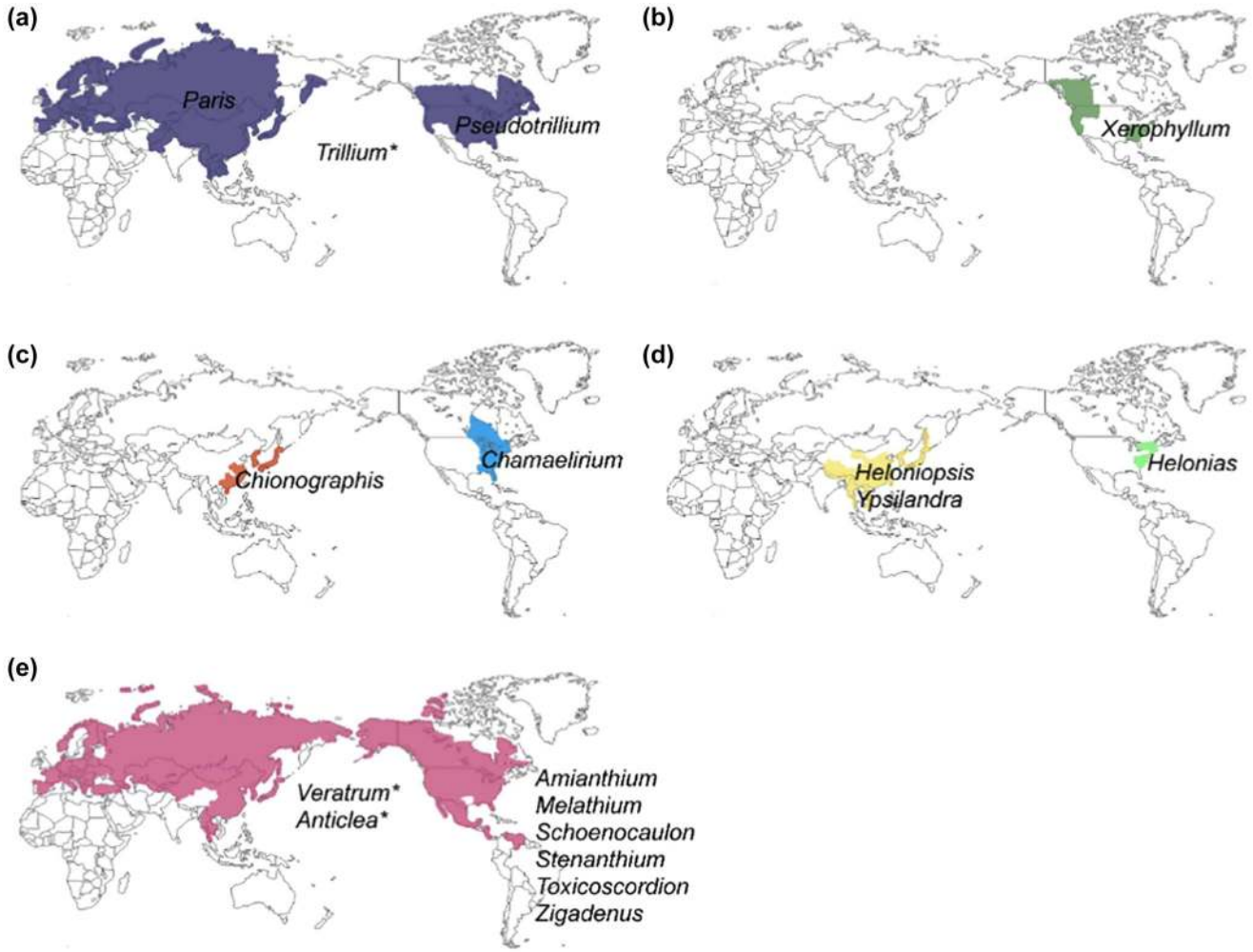


FIGURE 4 Maps highlighting the color-enhanced geographic distribution of 17 genera and five tribes of Melanthiaceae across Eurasia and North America: (a) Parideae (purple), including *Paris*, *Trillium*, and *Pseudotrillium*; (b) Xerophyllaeae (green); (c) Chionographideae (maroon) and *Chamaelirium* (light blue); (d) Heloniadeae (lime green), *Heloniopsis*, *Ypsilandra* (yellow); and (e) Melanthieae (red), *Amianthium*, *Anticlea*, *Melathium*, *Schoenocaulon*, *Stenanthium*, *Toxicoscodion*, *Veratrum*, and *Zigadenus*. Asterisks represent genera found in both Eurasia and North America (C. Kim et al., 2019).

androecium and lacking the gynoecium. In contrast, flowers below this section are perfect, possessing both the androecium and gynoecium (Figure 7C). The androecium features sagittate to reniform (arrowhead- to kidney-shaped) anthers (Figure 7C), which dehisce via extrorse mechanisms.

The gynoecium has a superior ovary (hypogynous position), with free styles and simple stigmas. The ovary is composed of three septicidal carpels, each containing 6–12 ovules per locule, which develop into one to four seeds per locule.

Pollen grains measure 20–30 μm and are monocolpate with an operculum, a feature considered an advanced adaptation for protecting pollen from environmental stressors and ensuring germination occurs under favorable conditions. A unique feature of *S. officinale* is the nectary pad, an elevated structure located near the base of each tepal. The nectariferous glands (having two on the outer tepal and one on the inner tepal) are prominent toward the base of the inner surface of the tepal, unlike other *Schoenocaulon* species whose nectar glands are inconsistent and inconspicuous (Zimmerman, 1958).

The mature raceme produces seed in the perfect flowers (Figure 7G). Septicidal capsules develop in the lowermost flowers (Figure 7H). Architecturally, a mature, established plant (≥3 years old) has multiple inflorescences at the seed development stages (Figure 7I).

Seed morphology includes a visible raphe and a minute embryo embedded in a large mass of endosperm. Seed germination in *S. officinale* is epigeal (Figure 8A,B) (Fletes, 2011; Frame, 1990). A well-established root system is quickly developed in establishing seedlings in Years 1–2 (Figure 8C). At the first flowering (∼Years 1.5–3) a single inflorescence is produced (Figure 8D). In subsequent years, multiple daughter bulbs will be produced from the original mother bulb, each of which (when reproductively competent) will produce an inflo-

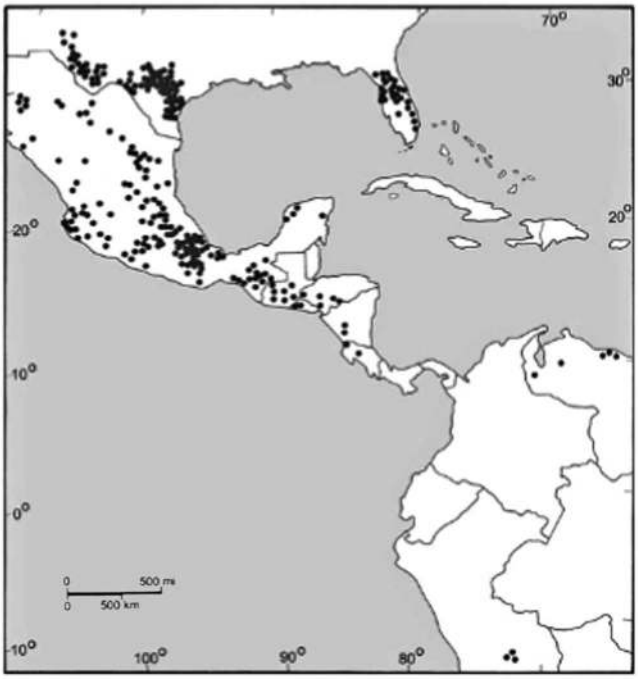


FIGURE 5 Distribution map of *Schoenocaulon* taxa (solid circles) showing documented localities across their native range in North America, Central America, and South America (Zomlefer et al., 2006).

rescence. Thus, multiple inflorescences will be generated by each established flowering plant.

Quantitative production data are scarce (Walle, 2008). Venezuelan populations surveyed and harvested for seed were found to have 97% viability in tetrazolium (triphenyl tetrazolium chloride) seed germination tests; no dormancy existed (Walle et al., 2008). In the only replicated field study to date (mixed shade agroforestry), epigeal germination ranged from 75% to 79% (Fletes, 2011; Frame, 1990). Flowering stem lengths (Figure 9) range from 70 to 200 cm in height with racemes ranging from 10 to 35 cm with as many as 100–400 flowers. Bulb sizes of 2–6 cm × 2.5–4 cm (length × diameter) with —six to eight leaves/bulb (90 cm × 4–12 mm length × width) were produced (Fletes, 2011; Frame, 1990). Waterlogged clay soils caused increased mortality (most likely due to bulb rot), underscoring sabadilla's need for well-drained soils, consistent with its native montane grassland habitats.

4.5 | *Schoenocaulon officinale* (sabadilla): Chemical constituents and insecticidal value

Interest in *S. officinale* centers on its two seedborne steroidal alkaloids, cevadine and veratridine (Figure 10), that make up ~3% of the seed by mass (Figure 11) (Frame, 1990). Together, these two alkaloids account for ~90% of the total alkaloid content found within the seeds. Outside sabadilla, these C-nor-D-

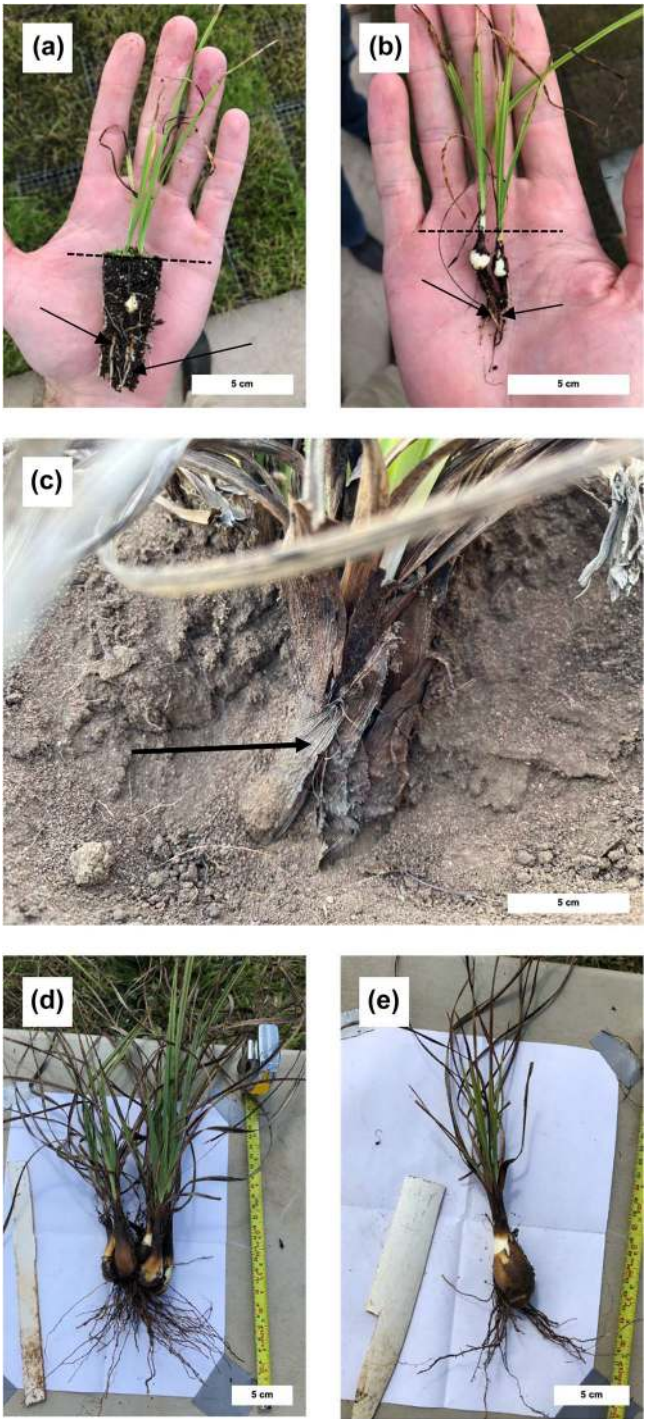


FIGURE 6 Bulb and belowground morphology of *Schoenocaulon officinale*. (a and b) Seedlings from plug trays immediately establish contractile roots (arrows), which immediately pull the newly formed small, tunicate bulbs below the soil line (dotted lines). (c) Mature bulb clusters at the soil surface wrapped in fibrous tunics (arrow). (d and e) Excavated bulbs illustrate variation in size, tunic structure, root structure, and number of bulbs. Scale bars as indicated. Photo credits: Albert S. Radloff.

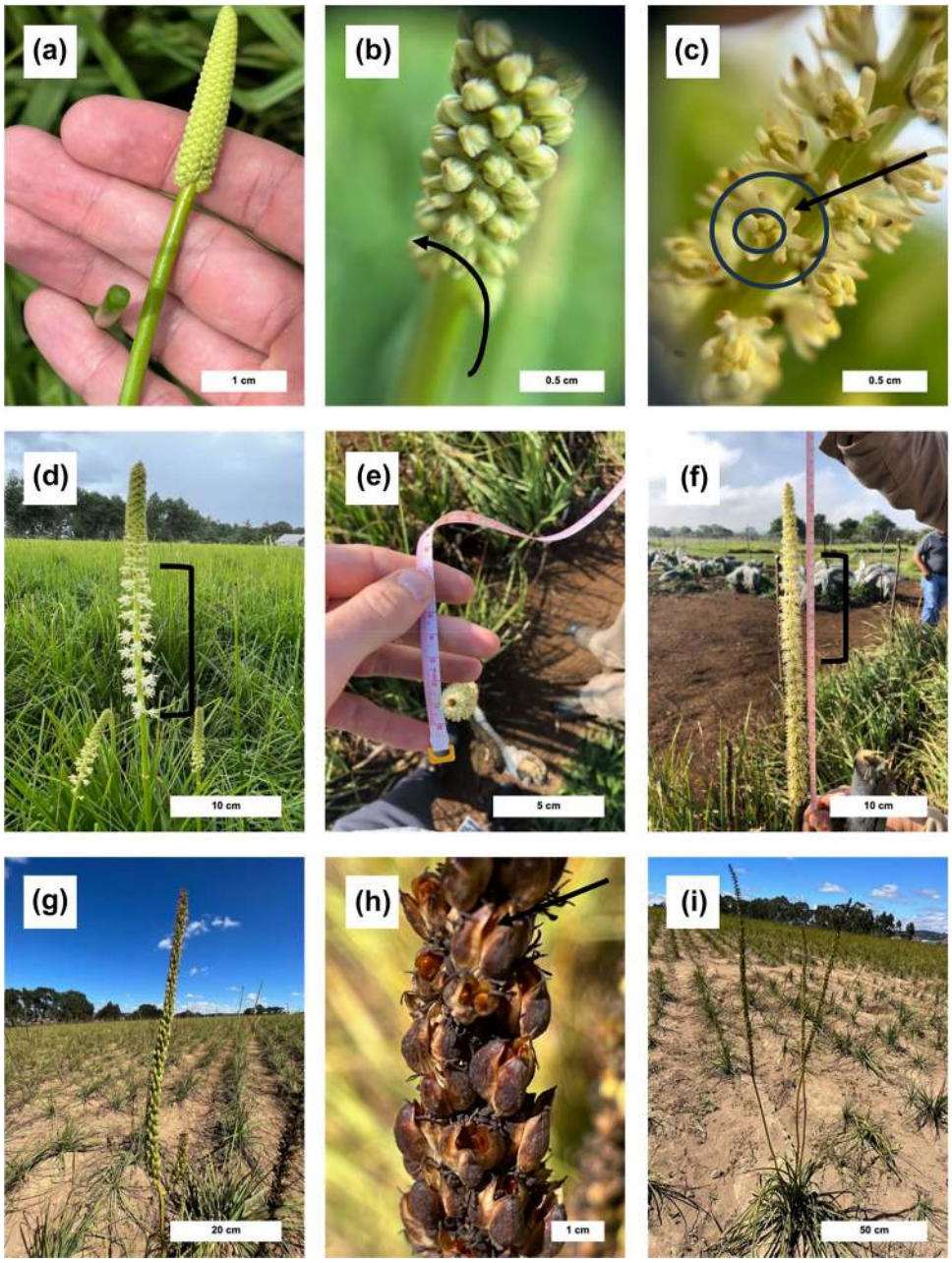


FIGURE 7 Inflorescence (raceme) development of *Schoenocaulon officinale* under cultivation. (a) Cross-sectioned inflorescence scape with early floral spike initiation of tightly compressed floret initials (top) and leafless subtending scape. (b) Close-up of immature, pre-anthesis florets (basipetal florets are ~7–12 days from anthesis). Floret anthesis proceeds acropetally in a spiral direction (arrow) with the earliest, oldest flower at the base, proceeding upward to the apex of successively younger florets and floral buds. (c) Mature inflorescence scape showing sessile arrangement of florets; sample floret (outer circle) denoting dehisced anthers (center circle) and cream-colored tepals (peripheral arrow). (d) Variation in raceme size and elongation for height and diameter with inflorescences beginning anthesis. Bracket denotes the lower florets with dehisced anthers and receptive stigmas. (e) Top (aerial) view of a mature inflorescence with lower florets (widest points) at anthesis. The central, dark ring is the apex of the inflorescence with tightly compressed immature flower buds. (f) Bracket denotes central florets on an inflorescence at the midpoint of anthesis. Florets above the bracket have yet to reach anthesis, whereas florets below the bracket are post-pollination and in seed development. (g) A mature raceme postpollination with swelling green capsules with developing seeds inside. (h) Mature, dried-down septicidal capsules dehisced for seed shattering (arrow). (i) Whole plant architecture showing three inflorescences at varying stages of post-pollination seed development. Scale bars as indicated. Photo credits: Albert S. Radloff.

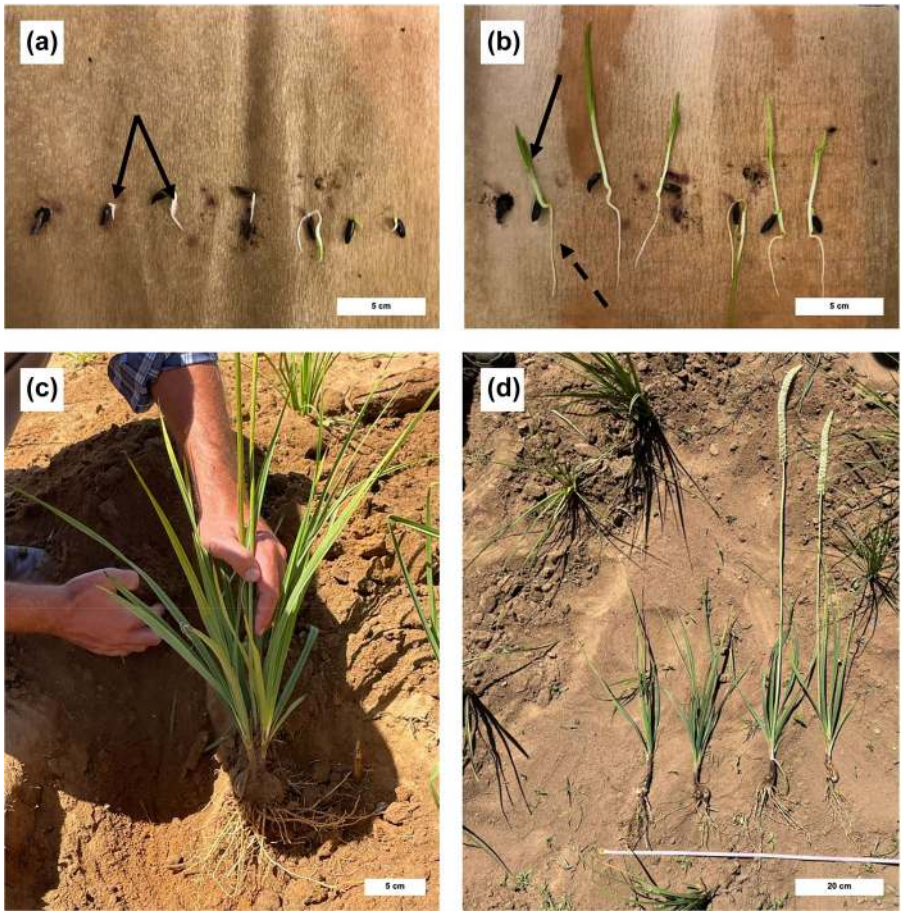


FIGURE 8 Seed germination and seedling development in *Schoenocaulon officinale*: (a) radicle emergence or germination occurring in Weeks 3–6 post-sowing (arrows) (b) green-tipped shoot (epicotyl; one cotyledon/seedling; epigeal germination; solid arrow) and root (hypocotyl; dashed arrow) differentiation and growth. (c) plant (24 months post-germination) establishing with root profile visible below soil surface. (d) Excavated seedlings (24+ months post-germination) illustrating differences in leaf number, bulb size, growth rate, and reproductive status (the left two seedlings are vegetative; the right two seedlings are reproductive). Scale bars as indicated. Photo credits: Albert S. Radloff.

homosteroidal alkaloids are confirmed in four other flowering plant families (Asclepiadaceae, Apocynaceae, Buxaceae, and Solanaceae) and in few additional Melanthiaceae taxa, with the highest levels reported in *S. officinale*, *Schoenocaulon calcicola*, and *Schoenocaulon comatum* (Frame, 1990). The principal alkaloids, veratridine and cevadine, are accompanied by smaller amounts of sabadine, sabadinine, and sabadilline/cevadilline. Historical names such as cevacine, sabine, and sabatrine refer to ester components or mixtures of these core structures rather than additional distinct alkaloids (Ikawa et al., 1945; Kupchan et al., 1962; Tomlin, 2003). Formulations historically sold in the United States under the label "sabadilla alkaloids" contained a blended extract of cevadine, veratridine, sabadilline, sabadinine, and sabadine (Tomlin, 2003).

Although seed chemistry dominates the toxicological narrative, the roots are not chemically inert. Kanchanapoom et al. (2002) isolated two new stilbene glucosides, a novel 2-aryl benzofuran, and five other previously known compounds from sabadilla root tissue, underscoring the diverse metabolic activity of the species.

4.5.1 | Structural features and MOA

Alkaloids have a high occurrence in nature and are a diverse group of molecules that are all nitrogenous secondary compounds derived from amino acids (Aniszewski, 2015). The term "alkaloid" originated when German pharmacist Wilhelm Meissner was isolating a mix of alkaloids from sabadilla (Meissner, 1819). Cevadine and veratridine are both C-nor-D-homosteroidal alkaloids, composed of a five-membered C-ring, loss of carbon atom at C-10 location (C-nor), and then the six-membered D-ring system expansion from five-membered to six-membered (D-homo) resulting in a heavily altered cholesterol (Gao et al., 2012; Xiang et al., 2022). Due to the steroidal polycyclic backbone and multiple esterified hydroxyls, these alkaloids are expected to be predominantly

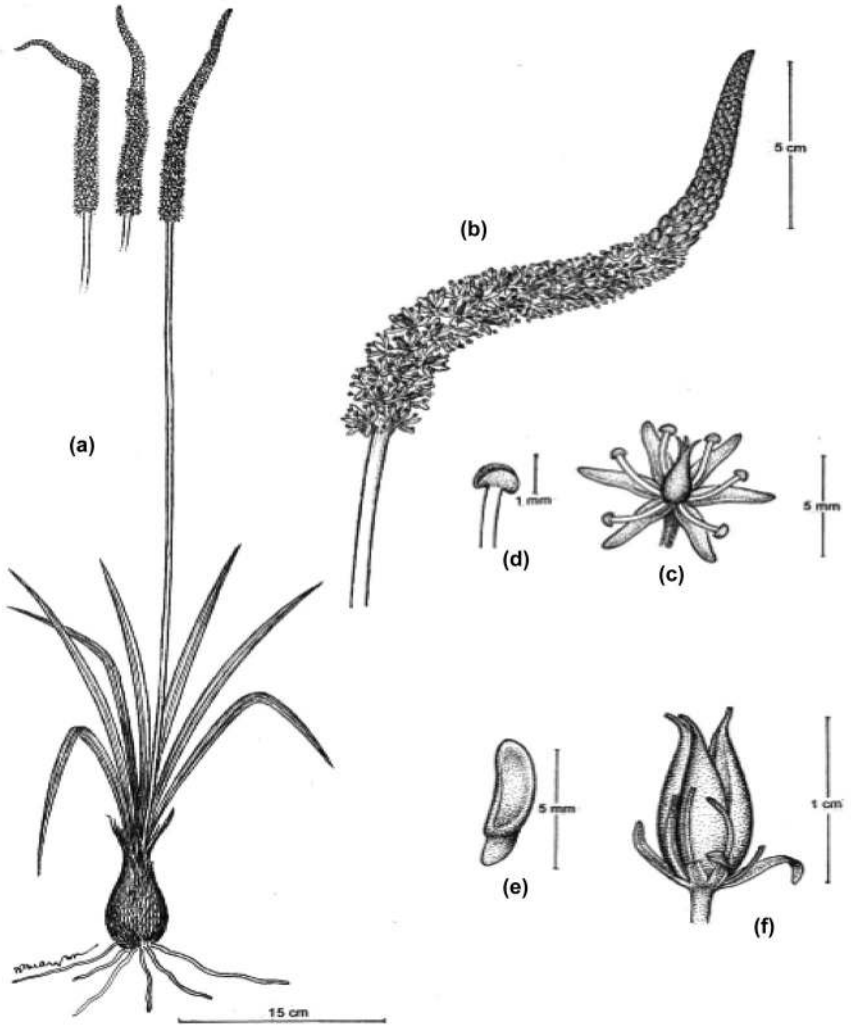


FIGURE 9 *Schoenocaulon officinale* plant morphology illustrations: (a) Whole plant habit showing the tunicate bulb, basal leaves, and floral scapes with three distinct inflorescence morphs; (b) single inflorescence (raceme), showing arrangement of individual flowers or florets; (c) flower (lateral view), with the central pistil (stigma, style, and ovaries) surrounded by six stamens and six tepals (modified sepals-petals); (d) stamen with a dehisced anther, shedding pollen (top), and subtending filament; (e) mature seed; (f) mature, septicidal capsule, partially opened (dehisced) at maturation. Scale bars: a = 15 cm; b = 5 cm; c and e = 5 mm; d = 1 mm; f = 1 cm. Based on specimen Montes 151 (VEN), illustration by Bruno Manara (Calles et al., 2019).

lipophilic, although their oxygenate substituents confer some polarity. The alkaloids function through a sodium channel effect, binding at neurotoxin receptor 2, causing nerve excitation (repetitive firing), prolonged impulse duration, and then depolarization of nerve membrane potential (Catterall, 1975). Exposure to insects results in the loss of nerve function, paralysis, and then death (Allen et al., 1944). Sabadilla seeds typically contain veratridine and cevadine in an approximately 2:1 ratio (Dayan et al., 2009). Sabadilla essential oil has been found to be one of the least toxic registered botanical insecticides with a mammalian LD_{50} (50% lethal dose) of 5000 mg/kg body weight. However, when purified down to the primary alkaloids, veratridine and cevadine, the toxicity is greater, with a rat oral LD_{50} of 13 mg/kg (Vicentini et al., 2018). Modern formulations require protective gear for use, as a dust or spray irritant, as its dust is highly irritating to the eyes and respiratory tract, as a contact poison, often causing violent sneezing; it is also a stomach poison.

4.5.2 | Historical formulations and target spectrum

Modern commercial interest in sabadilla chemistry dates to 1929, when a dust product containing trace sabadilla alkaloids was sold in the United States; by the 1970s, the EPA had registered Red Devil and Natural Guard (Dayan et al., 2009; Fisher & Bailey, 1937). Published studies have demonstrated efficacy of sabadilla formulations against a broad spectrum of pests, including lepidopteran caterpillars such as

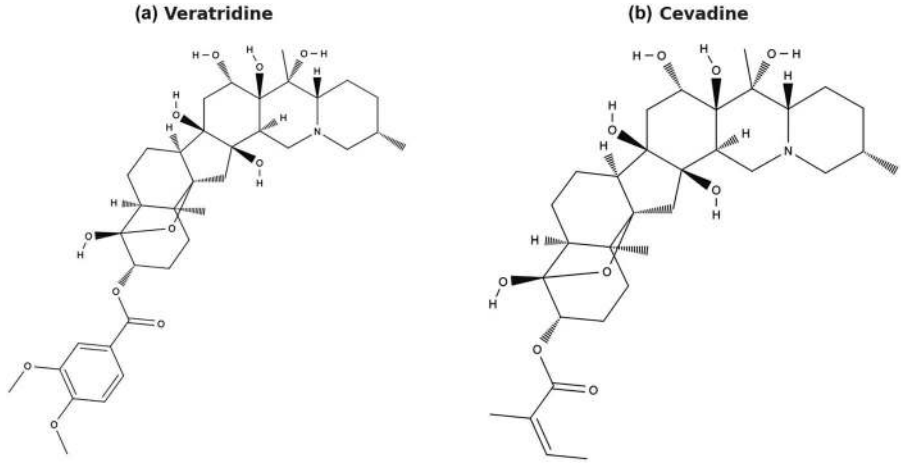


FIGURE 10 Chemical structures of the two principal alkaloids from *Schoenocaulon officinale*. (a) Veratridine; (b) Cevadine. Illustration by Bergwerf (2015).

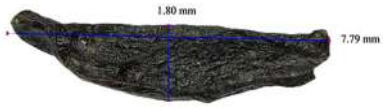


FIGURE 11 A dried *Schoenocaulon officinale* seed (30x magnification) with length and width measurements. Image captured with a Nikon Z20 lens. Photo credit: Mike Lynch, McLaughlin Gormley King Company.

the diamondback moth (*Plutella xylostella*), hemipterans such as the potato leafhopper (*Empoasca fabae*), green stink bug (*Nexara viridula*), squash bug (*Anasa tristis*), and tarnished plant bug (*Lygus lineolaris*), thysanopterans such as the western flower thrips (*Frankiniella occidentalis*), and coleopterans such as the Mexican bean beetle (*Epilachna varivestis*) and striped cucumber beetle (*Acalymma vittatum*) (Frame, 1990; Vicentini et al., 2018). When purified and turned into a functional product, the alkaloids have short residuals and degrade rapidly and can be synergized by McLaughlin Gormley King Company 264 or piperonyl butoxide. VeratranD has been used by organic farmers on citrus and avocado crops (Isman, 2006), although registration has lapsed. New products are currently under development by McLaughlin Gormley King Company, which received EPA registration for their new botanical a.i., Veratrine alkaloids extracted from sabadilla seed (McLaughlin Gormley King Company, 2025).

4.5.3 | Historical sourcing

Sourcing and collection of sabadilla seeds has been documented in Mexico, Peru, Columbia, and Venezuela (Figure 12) for export (Calles et al., 2019, 2020; Fletes, 2011; Frame, 1990, 2001; Gomero Osorio, 2001). Production



FIGURE 12 Naturalized populations of *Schoenocaulon officinale* in Venezuela, illustrating a wild-crafted system where seed is harvested from wild stands and allowed to reestablish. Population distribution and structure are visible across hillsides and disturbed slopes. Scale bar (foreground) = 1 m. Photo credit: Lukas Czerwinski, McLaughlin Gormley King Company.

occurred in Peru (pre-1950s) to support use as a pediculicide (Calles et al., 2019). Plant populations are now only found in hilly, degraded regions of Peru (Gomero Osorio, 2001). Sabadilla has also been reported in Costa Rica, and populations there appear to be native (Hammel et al., 2003). Records from 1876 indicate that 35,033 kg of seed were shipped from Caracas, Venezuela, with the majority (25,966 kg) having been delivered to Germany (Fluckiger & Hanbury, 1879). As little as 54,431 kg up to as much as 60 tonnes of sabadilla seeds were known to be exported from Venezuela into the United States (Alm, 2003; Roark, 1947). Venezuelan exports are sourced from pseudo-cultivation (wild-crafted) programs wherein wild sabadilla stands (Figure 12), broadcast across

hillsides of various regions, are collected annually with little to no interaction with the wild stands between harvest intervals (Frame, 1990). The majority of today's production is sourced from wild-collected seeds from Venezuela.

4.6 | *Schoenocaulon officinale* (sabadilla): Research gaps

Although sabadilla has a long history of ethnobotanical use and well-documented insecticidal efficacy, it remains largely undeveloped as a modern green pesticide crop. Much of the historical and contemporary research has focused on its chemical constituents and toxicological effects, leaving substantial gaps in the plant science disciplines needed for crop domestication. Figure 2 illustrates that green pesticide commercialization requires synchronous progress in germplasm characterization, ideotype definition, breeding, cropping system research, chemistry, and regulatory engagement. Generating plant science data and biomass streams that feed directly into pilot extraction and regulatory dossiers is the surest way to mitigate the twin obstacles of regulatory uncertainty and inconsistent raw material supply. Four interconnected gaps must be bridged in sequence to move sabadilla through this pipeline.

4.6.1 | Phenology and ideotype definition (Stages 1–2)

Sabadilla's basic life cycle attributes remain unquantified; there are no replicated data on plant height, seed yield, flower initiation and development, photoperiod, or thermal requirements for floral initiation. Stage 1 must, therefore, assemble diverse germplasm and conduct multi-site, multi-year trials to capture phenotypic, chemotypic, and genotypic variability. These trials should systematically record vegetative growth rate, bulb size thresholds for reproductive transition, days to flowering, seed-set dynamics, and total alkaloid content.

Stage 2 can define a sabadilla ideotype, a conceptual model of the optimal plant phenotype (Donald, 1968), tailored to green pesticides supply chains; early, synchronous flowering to synchronize harvest; high, uniform seed yields to maximize biomass throughput; consistently elevated veratridine and cevadine concentrations to simplify regulatory toxicology; and an upright, uniform architecture to enable high throughput, quality-ensuring harvest methods and minimize costs. Defining such an ideotype and selecting toward it will stabilize the alkaloid supply and, thereby, reduce risk in downstream extraction and registration while providing foundational data to advance breeding and domestication.

4.6.2 | Genetic diversity, population structure, and molecular breeding (Stages 1–3)

No sabadilla germplasm has yet been genotyped. Stage 1 should, therefore, survey wild stands across the species' range—Mexico, Venezuela, Colombia, and Peru—and employ GBS to assess population structure, allelic richness, and adaptive gradient. These data not only inform conservation and collection strategies but also allow identification of chemotypically unique accessions and provide the linkage maps that could be used in later creation of a draft sabadilla genome. In Stage 2, GWASs can link SNP variation to ideotyped traits such as alkaloid content, flowering time, and bulb uniformity. Stage 3 would aid from the development of a sabadilla genome as well as SNP array creation. Data from Stages 1 and 2 regarding genetic diversity and crop ideotype will be reutilized to initiate pre-breeding of robust new germplasm for diverse production environments to reduce supply chain risk.

4.6.3 | Propagation, agronomy, and supply chain stability (Stages 2–3)

Sabadilla's geophytic habit offers multiple avenues for propagation; sexual seed production and clonal multiplication via bulb division or tissue culture. Recent in vitro work demonstrates the feasibility of micropropagation; however, protocols must be optimized for commercial usage (Eperjesi et al., 2023). Stage 2 should compare ex vitro bulb division and micropropagation methods, quantify multiplication rates, and evaluate clonal uniformity of both morphological traits and alkaloid composition. Simultaneously, field cropping system trials must define optimal plant density, soil type, irrigation, and nutrient regimes and assess the impact of environmental stress on alkaloid synthesis and yield. These trials will be designed from preliminary data generated through Stage 1 while evaluating wild germplasm and numerous environments. Stage 3 must then deploy the best propagation protocols at scale and refine cropping practices to deliver predictable biomass with consistent chemical profiles, thereby overcoming the erratic supply that has plagued other botanicals.

4.6.4 | Integration with regulatory and commercial pipelines (all stages)

The work described above must not occur in isolation from chemistry and regulatory pathways. Stage 1 phenotyping and genotyping should include metabolite profiling and early toxicology screens to clarify regulatory classification and data

requirements and refine product formulation and target pests. Stage 2 ideotype selection must consider extraction efficiency and residue profiles, while initial agronomy trials should supply material for formulation optimization. Stage 3 breeding and production must be aligned with manufacturing scale-up and dossier preparation so that each incremental improvement in genetics or agronomy accelerates regulatory approval/expansion and market launch. By anticipating regulatory questions and generating the requisite data in concert with plant science research, sabadilla developers can avoid the costly delays that have historically hampered green pesticide commercialization.

Collectively, these efforts will generate a continuous flow of genotypic, phenotypic, and agronomic and chemical data into the regulatory and manufacturing pipelines illustrated in Figure 2. Addressing these research gaps is the linchpin for transforming sabadilla from a wild-harvested crop into a domesticated, scalable crop that meets both market demand and regulatory scrutiny.

5 | CONCLUSION

Schoenocaulon officinale stands at a crossroads: its fast-acting steroidal alkaloids, perennial geophytic habit, and centuries-long record of use position it as a promising candidate for sustainable pest management. However, a lack of basic plant science resources and coordinated development has kept it as an obscure green pesticide crop. This review highlights that Sabadilla's commercialization hinges on addressing the above-stated research gaps, completing data generation required in the green pesticide framework (Figure 2), comprehensive germplasm characterization, ideotype definition and updates, molecular breeding tools, and optimized propagation and cropping systems. Integrating these data and biomass streams directly into chemistry and regulatory work will aid the development of consistent quality alkaloids. By doing so, sabadilla research addresses the two chronic impediments facing green pesticides: regulatory uncertainty and erratic raw material supply.

The first priority is to initiate coordinated collection and phenology trials across sabadilla's native range, accompanied by high-throughput genotyping and metabolite profiling. These activities will lay the groundwork for ideotype definition, GWAS, and marker development and will supply material for pilot extraction and toxicology. In parallel with these activities, propagation protocols, both sexual and clonal, must be tested and refined to integrate into field production experiments that test plant spacing arrangements, solid, irrigation, and fertility regimes, with particular attention to alkaloid stability under variable conditions. Future research needs could expand on this pesticidal framework (Figure 2) to incorporate advanced genomic approaches enabling the elucidation of biosynthetic pathways for more targeted improvement of key traits. Such advanced genomic approaches would include whole genome sequencing and GWAS. Regulatory frameworks may shift to allow for value-added gene editing to support CRISPR-Cas9 (a genome editing technique used to change the genome by altering DNA segments using an RNA sequence to guide the Cas enzyme), which increases the value of these proposed genomic resources. Data generated from these trials should continually inform extraction optimization, formulation development, and preliminary regulatory data generation. Only by synthesizing ethnobotanical knowledge, contemporary plant science, and regulatory foresight can sabadilla emerge as a high-impact green pesticide.

AUTHOR CONTRIBUTIONS

Albert S. Radloff: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; resources; software; supervision; validation; visualization; writing—original draft; writing—review and editing. **Neil O. Anderson**: Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Albert S. Radloff https://orcid.org/0009-0002-0062-107X
Neil O. Anderson https://orcid.org/0000-0001-9794-0397

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