Botanical insecticides inspired by plant–herbivore chemical interactions

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Plants have evolved a plethora of secondary chemicals to protect themselves against herbivores and pathogens, some of which have been used historically for pest management. The extraction methods used by industry render many phytochemicals ineffective as insecticides despite their bioactivity in the natural context. In this review, we examine how plants use their secondary chemicals in nature and compare this with how they are used as insecticides to understand why the efficacy of botanical insecticides can be so variable. If the commercial production of botanical insecticides is to become a viable pest management option, factors such as production cost, resource availability, and extraction and formulation techniques need be considered alongside innovative application technologies to ensure consistent efficacy of botanical insecticides.

Phytochemicals

Although plants are sessile organisms and cannot escape danger in the way that animals do, they are not completely defenseless. Plants have different forms of defense, ranging from structural traits [1] and barriers [2] to physiological [3] and chemical defensive mechanisms [4]. For decades, researchers have been studying the defensive mechanisms that plants use against different enemies, the variety of defensive responses, and the evolution and ecological impact of those responses [5–9]. Although the evolutionary raison d'être of those traits is to protect plants from herbivores and pathogens in nature, humans have also found many uses for them. Plant secondary chemicals are of particular interest because they can be used as medicines [10], food- and beverage-flavoring agents, fragrances, textile dyes, hygiene products [11], and pest and disease management tools [12]. Plants produce a wide spectrum of chemicals in various tissues above and below ground that are used not only to defend themselves against biotic or abiotic stressors [13,14], but also to communicate with other plants [15] and organisms [16] (Box 1).

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In this review, we focus on botanical insecticides that are inspired by plant–insect chemical interactions. We briefly look at the phytochemicals that have been used for pest management and compare these with conventional (synthetic) pesticides and examine the different ways that plants use their secondary chemicals in nature in contrast to how we use them for pest management. We also discuss the practical challenges of producing commercial botanical insecticides and examine certain assumptions behind commercial botanical insecticides that are available on the market.

Botanical insecticides

All living organisms share certain chemicals and biochemical reactions that constitute their basic metabolism: for example, nucleic acids, proteins, and particular carbohydrates. In addition to the substances that participate in this primary metabolism, plants have also evolved diverse secondary metabolic pathways that produce a plethora of novel substances. Most secondary metabolites are produced from universally present precursors and, therefore, they are often classified based on their biosynthetic pathways [17]. Using a simplified classification, they can be classified as nitrogen-containing compounds, phenolics, polyacetates, and terpenoids (Box 1).

Pesticidal compounds exist within almost all classes of secondary metabolite. For example, the alkaloids nicotine [which is found in the nightshade (Solanaceae) family of plants] and strychnine (which is found in the seeds of *Strychnos* spp.) have been historically used as pesticides [18]. However, the only new botanical pesticides that have come on the North American market over the past 20 years are those based on the terpenoid azadirachtin [a limonoid found in seeds of the Indian neem tree (*Azadirachta indica; Meliaceae*)], which has been used traditionally to control pests and diseases [19], and those based on plant essential oils [20], which are used as contact toxicants, fumigants, attractants, and repellents to control agricultural pests (i.e., two-spotted spider mite, green peach aphid, and greenhouse whitefly), urban pests (i.e., housefly, bedbug, cockroaches, and ants), medical pests (i.e., mosquitoes, ticks, and lice) and veterinary pests (i.e., fleas and horseflies).

Production of botanical insecticides versus synthetic pesticides

Botanical insecticides are generally complex mixtures of several, often closely related secondary metabolites that may or may not have an important role in the toxicity of the

Box 1. Major classes of secondary metabolite used in commercial botanical pest management products

Plants have evolved diverse groups of chemicals that act as major barriers to herbivory. Some chemicals are constitutive [39], meaning that they are always present, whereas others are induced after attack [40]. Many compounds directly affect the herbivore, whereas others attract organisms from other trophic levels [44]. These chemicals can be found in, and are emitted from, all plant tissues above and below ground: toxic terpenes and volatile infochemicals are emitted from the foliage [73,74]; flowers have behavior-modifying floral scents [75]; phytotoxic root exudates are exuded from roots [76,77]; and toxic latex is exuded from the stem [78].

Plants have the capacity to convey certain information about herbivores to their natural enemies via the emission of specific chemical signals [45,47,79]. They can even respond chemically to herbivore oviposition before feeding damage occurs [80,81].

The most important botanical pesticides on the market in commercial terms are pyrethrum, neem, and essential oil-based products (Figure I). Essential oil-based products are the most diverse among the three different types. They are complex mixtures of low-molecular-weight, highly volatile secondary metabolites. Owing to their versatile nature, they have been used in variety of products, from contact toxicants to fumigants and even in behavior-modifier products, such as attractants and repellents.

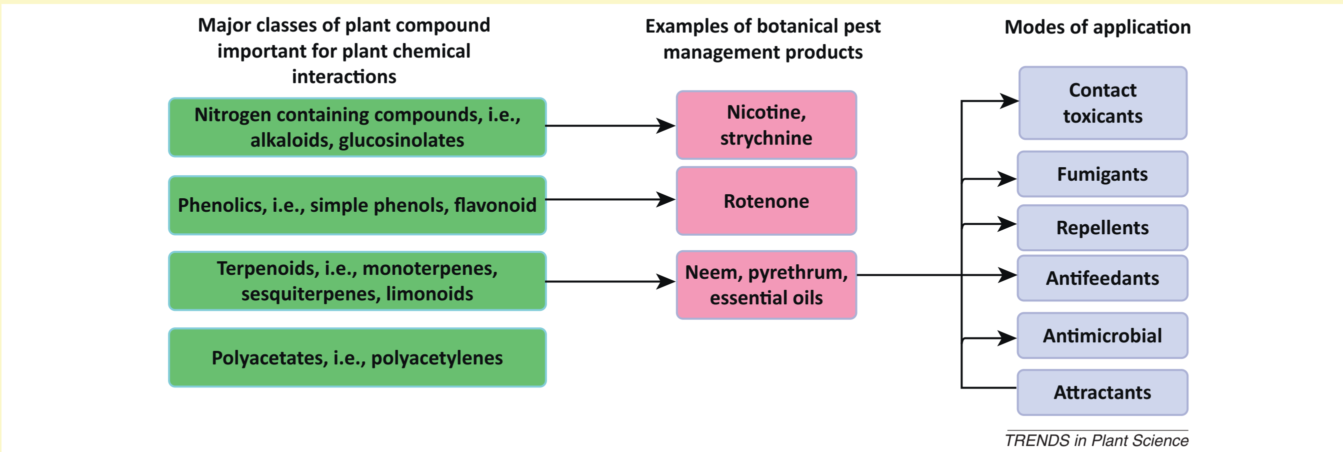

Figure I. Examples of botanical pest management products based on major classes of plant compound.

mixture. They can exhibit internal interactions in the form of synergy or antagonism, which can affect the overall toxicity of the mixture [21]. By contrast, synthetic pesticides are generally based on a single active ingredient (Table 1).

The most important difference between the production of botanical insecticides and the manufacture of synthetic pesticides is the difficulties associated with standardizing the active ingredients found in botanical pesticides: there can be great variability in the quality and composition of these toxic plant extracts. The source of this variability might be natural [22–25] or might occur as a result of using different harvest or extraction methods [26,27]. The initial biomass resource is generally outsourced and minimally monitored, in contrast to quality-control protocols that exist for synthetic pesticides. The extracts are usually specified based on the level of one or two marker compounds (putatively the active principles) even though the presence and level of other constituents in the mixture can significantly influence the overall toxicity and efficacy of the extract [21]. As a result of limited chemical standardization, the efficacy of botanical products may not be consistent [28]. However, synthetic pesticides do not have these problems owing to their simpler compositional structure compared with that of botanical insecticides, and the degree of control and standards relating to their manufacture.

Scalability limitation can also be an issue for manufacturers of botanical insecticides and depends on natural resource availability. Formulations may have to be changed to compensate for scarce and/or expensive ingredients that are not readily available to maintain the competitiveness of the product. Thus, the availability of the ingredients in the market dictates the scalability of botanical products. This is not the case for synthetic pesticides.

Botanical extracts and essential oils often comprise lipophilic and highly volatile constituents and are known to be susceptible to conversion and degradation reactions, such as oxidative and polymerization processes, which can result in loss of quality and of certain properties [29]. The stability of these substances is affected when exposed to elements such as air, light, and elevated temperatures [30]. For this reason, the residual effects of botanical insecticides can be limited and, in some cases, lacking entirely.

Despite these limitations, the use of botanical insecticides in California between 2006 and 2011 grew by almost 50% (http://www.cdpr.ca.gov/docs/pur/pur06rep/chmrpt06.pdf and http://www.cdpr.ca.gov/docs/pur/pur11rep/chmrpt11.pdf), in part because the public perceives natural products to be safer than synthetic chemicals, despite evidence to the contrary [31]. To put this in context, botanical insecticide use represents only 5.2% of biopesticides, and only 0.04% of all pesticide use in California [32]. Biopesticides represent approximately 2% of the US$60 billion global pesticide market (2012 estimate), but the segment is dominated by microbial insecticides led by products based on *Bacillus thuringiensis* [33]. The biopesticide segment is currently growing at 16% per year, compared with conventional agrochemicals that are growing at a rate of 5.5% per year [34].