

Improved Understanding of Weed Biological Control Safety and Impact with Chemical Ecology: A Review

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We review chemical ecology literature as it relates to biological control of weeds and discuss how this means of controlling invasive plants could be enhanced by the consideration of several well-established research approaches. The interface between chemical ecology and biological control of weeds presents a rich opportunity to exploit potentially coevolved relationships between agents and plants where chemical factors mediating interactions are important. Five topics seem relevant, which if implemented could improve the predictability of host range determination, agent establishment, and impact on the target weed. (1) The host secondary plant chemistry and a potential biological control agent's response to that chemistry can be exploited to improve predictability of potential agent host range. (2) Evolutionary changes may occur in secondary plant chemistry of invasive weeds that have been introduced to novel environments and exposed to a new set of biotic and abiotic stressors. Further, such a scenario facilitates rapid evolutionary changes in phenotypic traits, which in turn may help explain one mechanism of invasiveness and affect the outcome of biological control and other management options. (3) Herbivores can induce production of secondary plant compounds. (4) Variability of weed secondary chemistry which, either constitutive or inducible, can be an important factor that potentially influences the performance of some biological control agents and their impact on the target weed. (5) Finally, sequestration of secondary plant chemistry may protect herbivores against generalist predators, which might improve establishment of a biological control agent introduced to a new range and eventually impact on the target weed. Recognition of these patterns and processes can help identify the factors that impart success to a biological control program.

Key word: Biological control of weeds, chemical ecology, EICA, host range, induction, sequestration, secondary plant metabolites, variability of secondary plant metabolites.

Invasive species have become a global problem that decreases biodiversity and threatens ecosystem stability (Blackburn et al. 2004; Callaway and Ridenour 2004; Davis 2003; Mooney and Drake 1986; Sankaran and McNaughton 1999; Tilman et al. 1997; Vitousek 1990). The relationships among invasive plants, resident species, and introduced biological control agents, and ultimately the likelihood of positive (impact on target weed) or negative (nontarget effects) outcomes of classical biological control projects are largely influenced by chemically mediated interactions. Numerous hypotheses have been proposed that include chemical interactions among organisms to explain invasive species' success, including

the evolution of increased competitive ability, novel weapons, and the novel chemistry hypotheses (Blossey and Nötzold 1995; Callaway and Ridenour 2004; Cappuccino and Arnason 2006; Inderjit et al. 2006). Chemical ecology is the study of the chemical interactions between organisms and their environment. Further, it seeks to examine the production of and response to signaling molecules or semiochemicals and to decipher the information content of the mediating compounds. The discipline of classical biological control of weeds aims to regulate plant species that have become invasive in areas outside their native range by reuniting them with their host-specific herbivores from the native range. These host-specific herbivores and their host plants are potentially coevolved organisms that are linked by the secondary metabolites produced by the plant to defend against herbivores. However, many specialized herbivores have overcome these secondary metabolites and use these compounds as behavioral cues to seek out and exploit the correct host plants (Berenbaum 1990; Karban and Agrawal 2002). The

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interface between chemical ecology and weed biological control presents a rich opportunity to exploit these potentially coevolved relationships to discover effective agents for biological control of weeds. Increased vigilance and requirements for specificity require improved means of determining host specificity of potential agents prior to release. The discipline of chemical ecology offers many benefits, among them a determination of the unique mixture of chemical plant cues that elicit behavioral responses from specialized insects, some of which may serve as biological control agents. Our goal is to describe the status of the application of chemical ecology in weed biological control and to search for areas where the fields can be integrated to provide better predictions of host range, establishment, and impact on target weeds. We propose to cover five topics in this review, with some overlap among them. As they relate to weed biological control, these topics include (1) the chemistry of host specificity, (2) evolutionary changes in secondary plant chemistry in invasive species, (3) herbivore induction of secondary plant compounds, (4) variation in secondary plant compounds, and (5) herbivore sequestration of plant secondary chemistry for defense against natural enemies. The application of chemical ecology concepts and methods can also assist scientists developing biological control programs by making them aware of potential unusual environmental toxicants harbored by potential agents that could harm agricultural and native animals in regions where releases occur (e.g., Oelrichs et al. 2001).

Herbivorous insects may use a number of sensory cues, both alone and in combination, to locate and accept hosts, including visual, olfactory, gustatory, and tactile stimuli (Bernays and Chapman 1994; Heard 2000). In our review we focus on the role of plant secondary metabolites. Besides plant secondary metabolites, plant primary metabolites, such as proteins, carbohydrates, or lipids are known to affect host selection behavior of adults as well as at the larval stage (Schoonhoven et al. 1998). Other nonchemical components of host-finding by specialized herbivores may also influence host choice either alone or in combination with chemical cues. These include plant color, size, architecture, leaf toughness, and trichomes (Carmona et al. 2011). Physiological factors and other internal factors are also known to influence responsiveness of herbivores to behavioral cues (Courtney and Kibota 1989). Additionally, other aspects of chemical ecology not covered here include pheromones and allelopathy. Pheromones are indispensable tools for agricultural pest control and could assist in monitoring density and spread of released biological control agents; they have been explored for a number of agents and weeds, e.g., *Diorhabda elongata* Brulle (Coleoptera: Chrysomelidae) beetles on *Tamarix* spp. (Tamaricaceae) (Cossé et al. 2005), *Aphthona* spp. (Coleoptera: Chrysomelidae) beetles on *Euphorbia esula* L. (Euphorbiaceae) (Bartelt et al. 2001), and *Tyta luctuosa*

(Denis and Schiffermuller) (Lepidoptera: Noctuidae) moths on field bindweed *Convolvulus arvensis* L. (Convolvulaceae) (Cao et al. 2003). Moreover, allelopathy may have contributed to the success of a number of invasive weeds targeted for biological control (e.g., Callaway and Ridenour 2004; Morgan and Overholt 2005). For a recent review of the ecosystem and evolutionary contexts of allelopathy we refer to Inderjit et al. (2011).

The Chemistry Underlying Host Specificity of Biological Control Agents

Assessing the host specificity of candidate agents is one of the main tasks in prerelease studies of classical biological control projects against invasive plants. The goal is to conduct meaningful experiments with a selected list of test plant species to predict which ones in the invaded range might be colonized by the agent, and to what degree. Building on the seminal paper by Ehrlich and Raven (1964), Harris and Zwölfer (1968) and Wapshere (1974) proposed the centrifugal phylogenetic method for selecting test plant species in classical biological control projects. This method is based on the assumptions that closely related plant species are chemically and morphologically more similar than distantly related species, and that specialist herbivores can perceive and respond to the sometimes subtle differences among closely related species. The hypothesis proposes that the range of plants on which specialist herbivores can complete their development (i.e., the fundamental host range; Schaffner 2001), is restricted to a set of phylogenetically related plant species. For example, a herbivore may be able to complete its development on plant species within a plant tribe, but not on any of the plants from other tribes of the same plant family, or from any other plant family.

Concerns may arise regarding the above method, which assumes that the selection of test plant species is valid across all plant taxonomic levels. The emphasis on phylogeny to select vulnerable plant taxa may be questioned when used as a surrogate for the distribution of usually unknown phenotypic traits (e.g., secondary plant metabolites). These traits are involved in host acceptance or rejection to predict the likelihood of direct nontarget effects by biological control agents. Originally, Ehrlich and Raven (1964) proposed that many herbivores are restricted to plant taxa that share a characteristic class of plant secondary metabolites, e.g., glucosinolates or pyrrolizidine alkaloids (PAs). The fact that major classes of plant secondary metabolites are restricted to certain plant taxa is well supported by the chemotaxonomic literature (Grayer et al. 1999; Hegnauer 1962–1996). Also, over the years experimental and comparative studies have accumulated evidence that herbivores exploit many of these major classes of plant secondary metabolites during the process of host

location and acceptance (Berenbaum 1990; Macel and Vrieling 2003; Renwick et al. 2006; Zalucki et al. 1990). Hence, host associations are indeed very often conserved at higher plant taxonomic levels, such as tribes or families (Futuyma 2000).

The picture becomes, however, less clear when host affiliation is assessed at lower taxonomic levels where plant species often contain a subset of the staggering diversity of closely related structures that can be found within some of these major classes of plant secondary metabolites (e.g., Hartmann and Dierich 1998; Wink 2003). First, the distribution of some secondary metabolites in plants may only inconsistently follow taxonomic designations at lower taxonomic levels (Pelser et al. 2005; Wahlberg 2001; Wink 2003). If the herbivores can distinguish among the structurally similar metabolites within a class of secondary metabolites, then chemical similarity may be a better predictor of host use than molecular phylogenetic relationships of the host-plant species (Becerra and Venable 1999). Yet, studies assessing the evidence that host selection or performance (or both) by specialist herbivores is influenced by differences among profiles of closely related secondary metabolites revealed mixed results (e.g., pro: Adler and Kittelson 2004; Berenbaum et al. 1986; de Vos et al. 2008; Muller et al. 2010; Sun et al. 2009; against: Adler and Kittelson 2004; Lindroth et al. 1988; Moyes et al. 2000; Poelman et al. 2008; Ratzka et al. 2002). For example, in the specialist cerambycid beetle *Tetraopes tetraophthalmus* (Forster), larvae are root-feeders whose survivorship on *Asclepias* test plant species decreased with increasing phylogenetic distance from the true host, *Asclepias syriaca* L. (Apocynaceae), and total concentration of cardenolides was the only root trait that correlated with larval survival (Rasmann and Agrawal 2011). However, several of the cardenolides described from *A. syriaca* also occur in other plant genera that are not reported to be hosts of *T. tetraophthalmus*, suggesting that other plant metabolites or nonchemical factors are also involved in delimiting the host range of this beetle.

The difficulties in assigning profiles of certain classes of plant secondary metabolites to host-use patterns of specialist herbivores may be either because the herbivores cannot distinguish among closely related secondary metabolites (Macel et al. 2002), or because host selection behavior of herbivores, including specialists, is simultaneously or sequentially influenced by the presence of different attractants, including feeding stimulants as well as repellents and deterrents. For example, although the oligophagous diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is attracted by many glucosinolates, it does not attack the glucosinolate-containing plant *Barbarea vulgaris* W.T. Alton (Brassicaceae) because this plant also contains a triterpene that is a feeding deterrent to the diamondback moth (Shinoda et al. 2002).

So far, the assumptions on which Wapshere's model for test plant selection is based have been tested in a few biological control projects only. Among the best-studied weed systems is tansy ragwort, *Jacobaea vulgaris* Gaertn. (= *Senecio jacobaea* L.; Asteraceae). Ragworts are known for their potent PAs, but also for various other bioactive secondary metabolites, including chlorogenic acid, flavonoids, and benzoquinoids. PA distribution in ragweeds appears to be largely incidental within the whole clade, indicating that differences in PA profiles in *Senecio* sensu lato cannot be explained by the gain and loss of PA-specific genes (Pelser et al. 2005). The distribution of other groups of plant secondary metabolites in ragweeds is less well studied, but these chemicals all have a wider distribution in the plant kingdom than the *Senecio*-characteristic PAs (Kirk et al. 2005). Various biological control agents have been released in different parts of the world against tansy ragwort. Bioassays with the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), revealed that females exploit PAs during the host-selection process (Macel and Vrieling 2003), but that they cannot distinguish among closely related PA metabolites (Macel et al. 2002). In contrast, electrophysiological recordings from taste sensillae of *T. jacobaeae* larvae with the PA revealed the presence of PA-sensitive cells in the lateral and medial galeal sensillae; both PA cells were maximally sensitive to seneciphylline N-oxide and senecionine N-oxide, and less sensitive to other PAs (Bernays et al. 2004). Nevertheless, Bernays et al. (2004) conclude that it is likely that other compounds play a role in host selection because PAs of the type tested also occur in other genera and families. Adult feeding by the two chrysomelids *Longitarsus jacobaeae* Waterhouse and *Longitarsus flavicornis* (Stephens) (Coleoptera: Chrysomelidae), another two biological control agents of tansy ragwort, were not correlated with the PA profile of ragwort plants (Kirk et al. 2012). Because adult feeding damage in *L. jacobaeae* is correlated with larval attack rate (Rapo et al. 2010), the lack of correlations between adult feeding and PA profile suggests an absence of a significant relationship between plant PA profile and overall attack of ragwort species by *L. jacobaeae*. Leaf dry matter content as a surrogate for different life-history strategies is correlated with adult feeding patterns in *L. jacobaeae*, and to a lesser extent in *L. flavicornis*, but this trait was not correlated with phylogeny (Kirk et al. 2012). Nevertheless, female oviposition and larval performance in *L. jacobaeae* were significantly negatively correlated with phylogenetic distance (U. Schaffner, unpublished data). These findings suggest that the host range of *L. jacobaeae* is indeed restricted to a small number of closely related plant species, but that the most characteristic group of plant secondary metabolites in ragwort plants, i.e., the PAs cannot explain this pattern. Apparently, other plant traits involved in adult host selection behavior and in larval performance appear to

follow phylogeny more closely, but these traits have yet to be identified.

The host testing of the *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae) biological control agent *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) indicated that larvae would feed and complete development only on the Australian target weed and two related Australian species, *Callistemon citrinus* (Curtis) Skeels and *Callistemon viminalis* (Sol. ex Gaertn.) Cheel (all Myrtaceae) (Wheeler 2005). Examination of several plant quality factors indicated that all species shared similar terpenoid chemistry, explaining their similar feeding responses. However, third instars completed development, though poorly, on an unrelated plant, *Morella* (= *Myrica*) *cerifera* (L.) Small (Myricaceae) in quarantine if they had been fed previously on the natural host. This unrelated species was included in the testing only because it was an ecological dominant that co-occurred with the target weed in its invasive range and thus would be expected to be exposed to any released biological control agents. The poor survival and performance of larvae on this unrelated marginal host, *M. cerifera*, likely was explained by several novel, possibly toxic compounds that were not present in the other species. Follow-up common garden field host-range studies conducted 3 yr after the release of *O. vitiosa* confirmed these findings, as no adult or larval use of *M. cerifera* was found by this biological control agent (Pratt et al. 2009).

The moth *Agonopterix alstroemeriana* (Clerk) (Lepidoptera: Oecophoridae) is a specialist of poison hemlock, *Conium maculatum* L. (Apiaceae), that was accidentally introduced into North America and is now considered as a potential biological control agent of this invasive weed. Castells and Berenbaum (2008) showed that oviposition by this moth was not associated with concentration of individual piperidine alkaloids, defenses unique to *Conium* species. In contrast, the number of eggs laid by *A. alstroemeriana* was positively correlated with leaf dry weight and negatively correlated with the concentration of the widespread monoterpene (Z)-ocimene. Adding coniine to an artificial diet brought about a threefold increase in consumption by larvae of *A. alstroemeriana*, suggestive of a kairomonal activity of piperidine alkaloids and a role in host plant recognition (Castells and Berenbaum 2006).

The examples from the biological control literature illustrate that much needs to be done to better understand the relationship between plant phylogeny, host specificity of herbivores, and the phenotypic traits underlying host specificity at lower taxonomic levels. The evidence available to date indicates that there are exceptions to the assumptions on which Wapshere's approach for selecting test plant species is based (Hinz et al. 2008; Madeira et al. 2008). One way to advance this field in the contexts of both theoretical ecology and biological control is to move away from arbitrarily selecting well-known groups of

secondary metabolites toward a more holistic metabolomic approach, comparing a large set of nutritional compounds and nonnutritional secondary metabolites with results from host selection bioassays of specialist herbivores (Prince and Pohnert 2010; Sumner et al. 2003). Such an approach would be challenging, because it requires the establishment and analysis of metabolomic profiles of a relatively large number of test plant species, but it would increase the chances of identifying those plant metabolites that are most relevant in terms of host-selection behavior and host specificity of specialist herbivores. Care should be taken in studying different steps in the host location process, including habitat location, host location, and host acceptance, since the specificity of the response may vary among the steps (Heard 2000). For the time being, Wapshere's approach seems to be robust in terms of predicting host specificity of biological control candidates above the genus level, since the majority of unexpected nontarget effects are reported from congeneric plant species (Pemberton 2000).

Evolutionary Changes in Plant Chemistry and Effects on Biological Control

Plants that are introduced to a novel environment are exposed to a new set of biotic and abiotic stressors. Such a scenario may facilitate rapid evolutionary changes in phenotypic traits, which in turn may affect the outcome of biological control and other management options (Thompson 2005). Using the biological control target purple loosestrife, *Lythrum salicaria* L. (Lythraceae), as an example, Blossey and Nötzold (1995) formulated the evolution of increased competitive ability (EICA) hypothesis to explain evolution in invasive plants in the absence of natural enemies, especially specialists. This hypothesis posits that plants introduced into new areas may evolve reduced allocation to costly defenses, allowing them to increase allocation to growth, reproduction, or both. However, invasive plants still have to cope with generalist herbivores in the invaded range. Hence, the most prominent change experienced by introduced plants in terms of natural enemies is a shift in the composition toward an assemblage that is dominated by a new set of generalists. In light of the specialist–generalist dilemma (van der Meijden 1996), invasive plants experiencing some level of top-down pressure by generalist herbivores should increase their allocation to cheap defense compounds that are toxic to nonadapted generalist herbivores and reduce allocation to expensive, digestibility-reducing compounds (Joshi and Vrieling 2005; Müller-Schärer et al. 2004). This hypothesis was recently termed the shifting defense hypothesis (SDH; Doorduyn and Vrieling 2011). A meta-analysis revealed that toxic compounds increase significantly in the invaded area, supporting the predictions

of the SDH; in contrast, digestibility reducers do not show a clear trend, which might be at least partly due to the small number of studies that assessed quantitative defenses (Doorduyn and Vrieling 2011).

Theoretically, an increased allocation to cheap toxic secondary metabolites and a reduced allocation to expensive digestibility-reducing secondary metabolites, as predicted by the SDH, should benefit biological control. This is because biological control agents are specialist, potentially coevolved species that have developed a close affinity for the less-expensive qualitative defenses to find and distinguish their hosts, or to use them for their own defense, and target weeds with increased digestibility are likely to support a faster population build-up of specialist biological control agents (Müller-Schärer et al. 2004; Wheeler 2006). Yet the impact of biological control agents will depend on the type of plant defense evolved during the invasion process in the absence of specialist herbivores. If trade-offs exist between tolerance and resistance, one might expect higher per capita and overall impact of biological control agents on plant genotypes that are chemically defended by toxins and lower impact on the tolerant genotypes (Müller-Schärer et al. 2004). Resistance is a plant trait that reduces the preference or performance of herbivores whereas tolerance is the ability of a plant to withstand and survive a fixed amount of herbivore damage without a corresponding reduction in fitness (McNaughton 1983, Paige and Whitham 1987). For example, the planthopper, *Prokelisia marginata* Van Duzee (Homoptera: Delphacidae), has been released for biological control of *Spartina alterniflora* Loisel. in regions where some genotypes lack resistance to, but are tolerant of the planthopper (Garcia-Rossi et al. 2003). If these tolerant plant genotypes increase in frequency, the effectiveness of biological control would decrease.

Joshi and Vrieling (2005) provided the first experimental evidence for the SDH hypothesis. They found that invasive populations of tansy ragwort, *Jacobaea vulgaris*, demonstrated higher biomass, but that PAs, which act primarily against generalist herbivores, had higher concentrations in invasive than in native populations. The generalist herbivore *Mamestra brassicae* L. (Lepidoptera: Noctuidae) imposed lower feeding damage and had significantly lower survival on invasive than on native plants, and feeding damage was negatively correlated with total PA concentration. In contrast, the biological control agent *Tyria jacobaeae* showed a higher survival and larval and pupal biomass when reared on plants from invasive than from native populations (Joshi and Vrieling 2005). These patterns were supported by Stastny et al. (2005), who found that *L. jacobaeae*, the agent that has probably contributed most to the successful biological control of tansy ragwort in different parts of the world, imposed higher damage levels on invasive than on native ragwort populations.

Other biological control systems that have been investigated in terms of rapid evolutionary changes in plant chemistry and effects on biological control candidates or agents include Chinese tallow, *Triadica sebifera* (L.) Small (Euphorbiaceae); spotted knapweed, *Centaurea stoebe* L. (Asteraceae); purple loosestrife, *L. salicaria*; and melaleuca tree, *M. quinquenervia*. Chinese tallow, a new target for biological control, has evolved to be a faster-growing plant in its introduced range (Siemann and Rogers 2001). Huang et al. (2010) showed that a specialist herbivore grew larger on and consumed more mass of invasive plant populations than native populations, whereas a generalist showed the same performance between them. Chemical analyses showed that the invasive populations had lower tannin content, suggesting that plants from invasive populations have altered chemistry along the lines predicted by both the EICA hypothesis and the SDH. Additionally, Wang et al. (2011) examined the influence of herbivore resistance and tolerance on biological control of Chinese tallow. They found that invasive plants of Chinese tallow have lower resistance (in support of EICA) but higher herbivore tolerance toward the two biological control candidates *Heteropoderopsis bicallosicollis* Voss. (Coleoptera: Attelabidae) and *Gadirtha inexacta* Walk. (Lepidoptera: Noctuidae), suggesting that these herbivores may be able to build up high population densities in the introduced range but exert only moderate control. However, additional research is needed to determine the shape of the plant injury performance curve across a range of injury intensities, how injury intensity relates to insect density, and how much the biological control agent population densities will increase on tolerant vs. resistant plants (Pedigo et al. 1986).

Leaves of invasive populations of spotted knapweed, *C. stoebe* (= *C. maculosa* auct. non Lam.), have significantly higher levels of the defense precursor phytol and of cnicin-containing trichomes, compared to plants from native populations (Landau et al. 1994; Ridenour et al. 2008), which is in agreement with the SDH. Ridenour et al. (2008) found that generalist herbivores demonstrated significantly higher performance on plants from native European populations, whereas the biological control agents *Agapeta zoegana* L. (Lepidoptera: Tortricidae) and *Cyphocleonus achates* Fahraeus (Coleoptera: Curculionidae) showed weaker responses. Similarly, a more recent study found no differences in performance by *A. zoegana* and *C. achates* between North American and European tetraploid *C. stoebe* populations (Henery et al. unpubl.).

By retesting the plant species that was used to formulate the EICA hypothesis, Willis et al. (1999) found higher phenolic content of *L. salicaria* leaves in indigenous than in invasive genotypes. However, herbivore bioassays with the biological control agent *Galerucella californiensis* (L.) (Coleoptera: Chrysomelidae) and with a generalist herbivore revealed no significant intraspecific variation in

herbivore resistance between indigenous and nonindigenous hosts. The authors suggested that the antiherbivore defensive role of the phenolics was limited as the levels detected in the plants were lower than would explain differences in herbivore performance.

A series of studies was conducted with the invasive species *M. quinquenervia* to determine the influence of EICA on the weed and released biological control agents (Franks et al. 2008a, 2008b; 2012). Genotypes from the weed's native (Australia) and invasive (Florida) range were planted in a common garden in south Florida and the plants were subjected to herbivory by two biological control agents, *O. vitiosa* and *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae). The results do not lend support for EICA as the genotypes from the introduced and home range did not differ in resistance to insects or in competitive ability (Franks et al. 2008a). But when specific terpenoids (20 terpenoids) were monitored in invasive and native populations grown in a similar garden, most were lower in concentration in the invasive population (Franks et al. 2012). But several compounds were not different and one (*E*-nerolidol) had greater concentration in the invasive population and thus contradicted EICA. These results, which lend mixed support for EICA within the same invasive species, indicate the possible multidirectional patterns of this evolutionary response among different characters.

Comparisons in either plant chemistry or resistance to specialist herbivores between populations from the native and the introduced range have also been made with additional biological control targets, without specifically discussing the implications for biological control. For example, invasive populations of *Lepidium draba* L. (= *Cardaria draba* (L.) Desv.; Brassicaceae) express higher concentrations of *p*OHB glucosinolate in young tissue than plants from the native range (Müller and Martens 2005), but Cripps et al. (2009) found no difference in resistance to the biological control candidate *Psylliodes wrasei* Leonardi et Arnold (Coleoptera: Chrysomelidae) between native and introduced populations of this plant. In garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara & Grande (Brassicaceae), Cipollini et al. (2005) found a tendency for invasive populations to have reduced constitutive glucosinolate levels coupled with increased inducibility. Compared to European conspecifics, North American St. Johnswort, *Hypericum perforatum* L. (Clusiaceae = Hypericaceae), plants had lower levels of hypericin and pseudohypericin, compounds known to be toxic to generalist pathogens and herbivores (Maron et al. 2004); in the same experiment, a higher percentage of individuals from North American populations were infected by pathogens and died from pathogen attack compared to European genotypes.

These examples indicate that in some cases biological control systems provide support for SDH (e.g., Huang

et al. 2010; Müller and Martens 2005; Ridenour et al. 2008; Stastny et al. 2005; Wang et al. 2012), whereas in others the results do not support SDH (Cripps et al. 2009; Franks et al. 2008a; Maron et al. 2004) or are rather mixed (Cipollini et al. 2005; Franks et al. 2012; Huang et al. 2010; Joshi and Vrieling 2005; Willis et al. 1999). A lack of rapid evolution postintroduction can be explained by various factors, including a lack of genetic variation, low selection pressure, low costs of certain types of defenses, or constraints due to pleiotropic effects. It remains to be seen whether invasive plants that reveal rapid evolutionary change along the lines of SDH are indeed more amenable for biological control than those that have not evolved increased susceptibility to specialist herbivores. It is noteworthy, though, that the biological control systems that provide evidence for SDH are among the more successful biological control projects (e.g., *L. salicaria*, *J. vulgaris*).

Biological control projects offer a great opportunity to assess the effect of specialist herbivores on chemical defenses and other traits in plants. Following the same lines of argument as the SDH, plant populations from the invaded range that have been reunited with specialist herbivores through biological control measures should experience a selection pressure toward increased defenses against specialist herbivores, reduced defenses against generalist herbivores, and decreased growth rate, reproductive output, or both. In other words, traits of populations exposed to biological control should evolve away from those of invasive populations without biological control history toward those of native populations. Castells and Berenbaum (2006) found that geographic variation in plant chemistry of the invasive *Conium maculatum* (Apiaceae) in the United States was correlated with the intensity of reassociation with the moth *Agonopterix alstroemeriana* (Clerck) (Lepidoptera: Oecophoridae); regions with higher levels of *A. alstroemeriana* herbivory had also increased levels of alkaloids, compared to regions where populations were largely free from *A. alstroemeriana* herbivory. These results, however, are counter to the expected decrease in qualitative defenses resulting from reuniting the specialist herbivore and the weed (Müller-Schärer et al. 2004). Rapo et al. (2010) compared performance and resistance traits of tansy ragwort, *J. vulgaris*, populations from the introduced range (New Zealand and North America) that have either been exposed to the biological control agent *L. jacobaeae*, or that have no reported history of attack by *L. jacobaeae*. Contrary to expectation, populations with exposure to *L. jacobaeae* revealed more feeding damage by *L. jacobaeae* than populations without exposure, suggesting that *J. vulgaris* populations with biological control history evolved reduced resistance and greater tolerance levels against this biological control agent. A thorough analysis of the effect of biological control agents on phenotypic traits of invasive

populations requires a detailed recording of the biological control agent releases made, and of the variation in phenotypic traits present at the time the biological control agents are released.

The altered selection pressure in the introduced range may not only result in a change in mean levels of plant secondary metabolites, but also in a greater variance about mean levels. For example, Garcia-Rossi et al. (2003) found that genotypes of *Spartina* spp. varied more in their ability to resist and support the biological control agent *P. marginata* in a population that had been separated from the herbivore for many generations than in one that had been consistently exposed to the herbivore. Increased variation about mean defense levels may be particularly likely in cases where defenses are inducible, since a reduced frequency of expression of induced levels of defenses in the introduced range should release them from stabilizing selection. Eigenbrode et al. (2008) found that the mean constitutive and induced concentrations of PAs in houndstongue, *Cynoglossum officinale* L. (Boraginaceae), did not differ between continents, but the variability of the induced concentrations was significantly greater for plants from the introduced range. Van Dam et al. (1995) showed that the biological control agent *Mogulones crucifer* Herbst. (Coleoptera: Curculionidae) significantly consumed more of young houndstongue leaves, which have the highest PA level and the highest nitrogen percentage; it therefore remains to be shown what the consequences of a higher variability of induced concentrations of PAs in invasive houndstongue populations are in terms of biological control.

In summary, biological control projects against invasive plant species are excellent model systems in which to study the evolutionary ecology of chemical defenses in plants. It is probably no coincidence that influential hypotheses such as EICA or SDH have emerged from biological control systems. The deliberate re-exposure of plants to specialist herbivores after a long history of escape has already provided exciting insight in the chemo-ecology of herbivore–plant interactions, and is likely to continue to do so.

Herbivore Induction of Secondary Plant Chemistry and Its Effect on Biological Control

Herbivore damage to plants elicits a vast array of defensive responses that can involve proteins or secondary plant compounds (Kessler and Baldwin 2002). These responses may include direct increase in secondary metabolites, or induction, with toxic, antidigestive, or antinutritional activity (Duffey and Stout 1996). Such induction may increase production of volatile organic compounds (VOCs) that may protect plants from herbivory or pathogen attack (Shiojiri et al. 2006; Unsicker et al. 2009) or it may prime neighboring plants or adjacent

leaves with little or no vascular connection against impending herbivory by enhancing inducible chemical defense responses (Engelberth et al. 2004; Frost et al. 2007). Induction can also have indirect effects by the release of VOCs that attract natural enemies of the plant's enemies (Dicke and Van Loon 2000). Induced plant responses to herbivory reduce the preference or performance of subsequent feeding by herbivores (Agrawal 2005; Karban and Baldwin 1997; Turlings and Ton 2006). The field includes potentially novel mechanisms of pest control by stimulating chemical defenses in crop plants (Agrawal 2005; Dicke and Baldwin 2010; Karban et al. 1997). Moreover, these induced responses are major topics explaining herbivore population regulation and community structure in natural systems. These responses have the potential to influence the success of biological control projects as the agent feeding or oviposition may elicit physical or biochemical changes in the weed populations they are meant to regulate.

Inducibility of defensive compounds is important in invasive plant populations where native specialist herbivores may be absent. As defenses are expected to have fitness costs (Koricheva 2002), invasive species evolving without their adapted herbivores in their introduced range are expected to have less need and thus lower constitutive (baseline) defenses. Alternatively, invasive plants may have allocated greater resources to inducible defenses (Cipollini et al. 2003). Evidence for such a trade-off between these two types of defense was found in a number of examples (Koricheva et al. 2004), (Koricheva et al. 2004) among them weed targets for biological control.

Induced responses from prior herbivory by biological control agents were examined in *M. quinquenervia* and included herbivory by larvae of the weevil *O. vitiosa* (Wheeler and Ordung 2006). Responses were evaluated by chemical analysis of induced compounds and by bioassays of subsequent herbivory by the inducing insect (*O. vitiosa*) and *B. melaleuca*. Chemical analysis indicated that only the monoterpene α -pinene increased 1.75-fold in replacement foliage following herbivory. Despite this induced chemical change, bioassays indicated that neither biological control agent was affected by the prior herbivory. When a similar study was conducted with similar levels of damage (63% of plants vs. all plants with > 75% of tips damaged), more sustained herbivory, greater replication (30 saplings instead of four above) using insecticide-treated and untreated trees, significant increases (generally 1.5-fold) in the concentration of 10 terpenoids was found in response to herbivory by natural populations of the biological control agents *O. vitiosa* and *B. melaleuca* (Franks et al. 2012). Thus, induction occurs in response to herbivory in *M. quinquenervia* but the biological control agents appear to be unaffected by the changes.

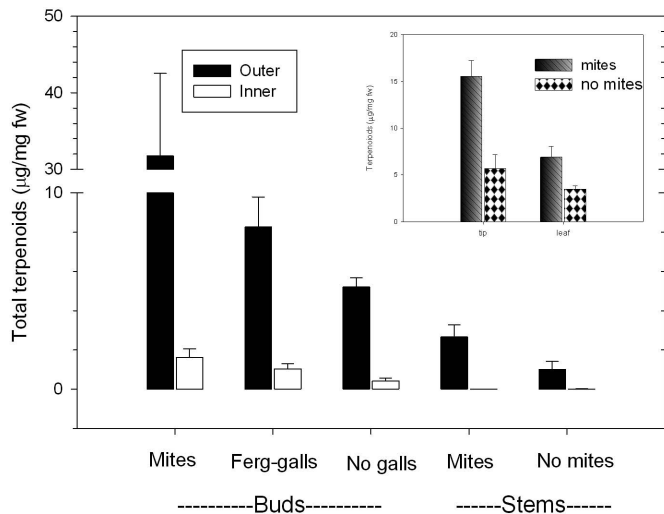


Figure 1. Changes in total terpenoid levels of *Melaleuca quinquenervia* tissues when the plant was infested with mites (*Tetranychus tumidus*) or a biological control agent, *Fergusonina turneri*. Dissections of outer or inner tissues were conducted and analyzed by gas chromatography and mass spectroscopy separately.

Additional research examined the terpenoid changes of different *M. quinquenervia* tissues when attacked by a bud gall-forming biological control agent, *Fergusonina turneri* Taylor (Diptera: Fergusoninidae), and a generalist spider mite, *Tetranychus tumidus* Banks (Acari: Tetranychidae). The experimental design included 12 plants galled by *F. turneri* and an equal number of control plants. Additionally, eight plants were infested by spider mites with six control plants. Each bud gall or ungalled bud was dissected and the outer and inner tissues were analyzed for terpenoid levels separately by gas chromatography and mass spectroscopy. Plant leaves and tips were included for comparisons that were either infested with *T. tumidus* spider mites or uninfested controls. The results were analyzed with a repeated measures ANOVA for mixed models. The tissues (outer and inner) were treated as a repeated variable as they came from the same bud or gall and thus were not independent. Analysis of *M. quinquenervia* buds and stems showed generally higher concentrations of total terpenoids in the outer tissue layers compared with the inner layers ($F_{1,48} = 25.99$; $P < 0.0001$; Figure 1). Little change in total terpenoids occurred as a result of the specialist biological control agent ($P > 0.6$). However, when the plants were damaged by the generalist spider mite, *T. tumidus*, total terpenoid levels increased in the buds and stems, especially in the outer gall tissues ($F_{1,48} = 11.03$; $P = 0.0017$). A similar total terpenoid response to mite damage was found in the undissected tips and leaves. The primary terpenoids that appeared to be inducible by the mites included a general twofold increase of α -pinene, limonene, β -caryophyllene, and viridiflorol.

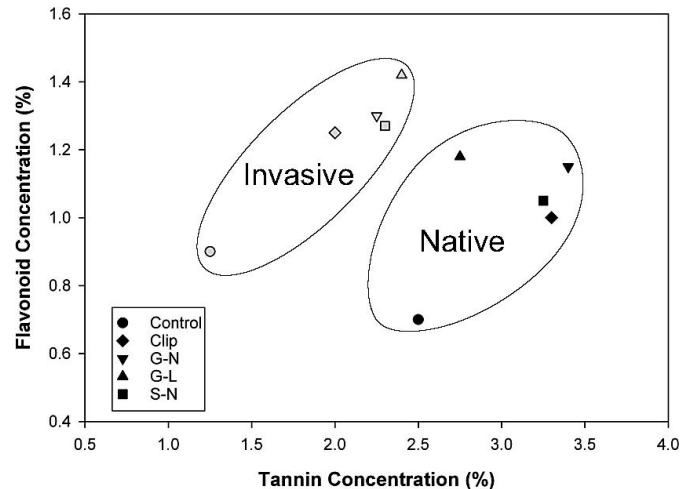


Figure 2. *Triadica sebifera* leaf total tannin and total flavonoid concentrations (% dry wt) in seedlings. Grey symbols represent the invasive populations and black symbols represent the native populations. Different shapes represent different treatments. Each point is the mean of raw data of tannin and flavonoid concentration from all populations. CLIP, damaged by clipping; G–N, damaged by generalist Noctuidae (*Grammodes geometrica*); G–L, damaged by generalist Limacodidae (*Cnidocampa flavescens*); S–N, damaged by specialist Noctuidae (*Gadirtha inexacta*). Results modified from Wang et al. (2012).

Although this plant has the capability to induce greater terpenoid levels as demonstrated by the generalist mites, host-specific gall formers with their intimate relationship with the host may be able to ameliorate the induction of these terpenoids.

Seedlings from native and invasive populations of Chinese tallow, *T. sebifera*, were damaged by leaf clipping or herbivory by three Chinese herbivore species, the generalists *Grammodes geometrica* Fabricius (Lepidoptera: Noctuidae) and *Cnidocampa flavescens* (Walker) (Lepidoptera: Limacodidae), and a specialist and potential biological control agent *Gadirtha inexacta*. Changes in the foliar concentrations of five flavonoids and four tannin compounds were determined after damage. Each treatment was replicated eight times (see Wang et al. 2012). The results indicated that increased concentrations of total flavonoids and the individual compounds (kaempferol, quercetin, quercetin glycoside, isoquercetin, and kaempferitrin) occurred in the clipping, generalist, and specialist-damaged treatments of both native and invasive plants (Figure 2; Wang et al. 2012). Similar increases were found with total tannins (Figure 2) and the individual compound tannic acid, but not for ellagic acid, catechin or gallic acid (Wang et al. 2012). Moreover, bioassays indicated that caterpillar growth generally decreased when induced treatment leaves were fed to the two generalist species, *Grammodes geometrica* and *C. flavescens*, whereas growth increased

when induced leaves were fed to the specialist potential biological control agent, *Gadirtha inexacta* (Wang et al. 2012). Moreover, induction by the specialist had the most consistent negative effect on caterpillar growth to the generalist species.

Numerous elicitors mediate plant responses to herbivore attack (Kessler and Baldwin 2002). Wound-elicited induced phytohormones include salicylic acid, jasmonic acid, and ethylene, and external application can induce plant defense responses (Diezel et al. 2009). Elicitors also come from insects, like volicitin in insect saliva (Alborn et al. 1997) and oviposition fluid of bruchid weevils (Doss et al. 2000). When methyl jasmonate was applied to invasive North American populations of garlic mustard, *A. petiolata*, higher induced levels of glucosinolates were found compared with seven native European populations (Cipollini et al. 2005). Induction by, and effect on, biological control agents has not been examined with *A. petiolata*.

Induction of hypericins and hyperforin in *H. perforatum* has been shown in response to both chemical and biotic elicitors (Sirvent and Gibson 2002). Levels of hypericin increased as much as 3.3-fold in response to methyl jasmonate. The plant pathogen *Colletotrichum gloeosporioides* (Glomerellaceae) served as a biotic elicitor where hypericins doubled compared to the control. Hypericin induction was also found from feeding elicitors in two generalist caterpillar species. However, no induced responses of hypericins were reported after the damage caused by the biological control beetles, *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) (Sirvent et al. 2003). This lack of induction by the specialist biological control agent helps to explain how this species can feed on a potential toxic species without increased mortality and decreased performance.

Intraspecific Variability in Secondary Plant Chemistry of Weeds

Despite an interest in the similarity of secondary metabolites of the target weed and the test plant species, the secondary compounds and their behavioral relevance to weed biological control agents have been little-studied. All too often little is known about the secondary plant chemistry of weeds targeted for biological control, to say nothing about their variability or biological relevance (see “The chemistry underlying host specificity of biological control agents” above). In the following section, we are primarily interested in genetic variation in the levels of secondary metabolites but acknowledge the contribution made by environmental and climatic factors.

In many plant species different chemical variants are well known and have been identified as distinct chemotypes. Examples of chemotypes or secondary compound variability in invasive weeds targeted for biological control include

J. vulgaris (Macel et al. 2002; Witte et al. 1992); *E. esula* (Holden and Mahlberg 1992); *H. perforatum* (Sirvent et al. 2002; Southwell and Bourke 2001; Walker et al. 2001); *Lantana camara* L. (Verbenaceae) (Randrianalijaona et al. 2005); and *M. quinquenervia* (Ireland et al. 2002; Wheeler et al. 2007).

The influence of variation in secondary plant chemistry on biological control agents has been studied in two weeds: tansy ragwort, *J. vulgaris*; and melaleuca, *M. quinquenervia*. For *J. vulgaris*, two distinct chemotypes are known based upon the presence of different PAs (Witte et al. 1992). However, a biological control agent, the cinnabar moth *T. jacobaeae*, did not discriminate, and larval performance did not differ between the two chemotypes of *J. vulgaris* (Vrieling and de Boer 1999). The variation in *M. quinquenervia* constituents were studied from leaves in its native range (Ireland et al. 2002) and in its adventive range including Florida (Wheeler et al. 2007). These results indicate that at least two chemotypes exist within the species in Florida, the Caribbean, Hawaii, and Australia with the possibility of a third from New Caledonia (Trilles et al. 2006). One chemotype is referred to here by its primary sesquiterpene *E*-nerolidol (chemotype I) and another is referred to by a primary sesquiterpene viridiflorol (chemotype II). Consumption by the biological control agent *O. vitiosa* of the *E*-nerolidol chemotype leaves improved growth and fecundity as female biomass and fecundity increased 2.6- to 4.5-fold over larvae fed the viridiflorol leaves (Wheeler 2006; Wheeler and Ordnung 2005). The nutritional difference helped explain the lack of reproduction during the colonization of these weevils on the incompatible viridiflorol chemotype plants in the United States (G.R. Buckingham, unpublished data) and Australia (M.F. Purcell, unpublished data).

Volatile compounds have been described from several weed species but with little information on their variability. Examples include detailed description of the foliar volatiles of yellow starthistle, *Centaurea solstitialis* L., and purple starthistle, *Centaurea calcitrapa* L. (Asteraceae), in an effort to find interspecific differences in volatile cues that might be used by biological control agents (Binder et al. 1990a, 1990b; Buttery et al. 1986). Additional analyses include continued work on this species and two other *Centaurea* species, *Centaurea cyanus* L. and *Centaurea cineraria* L., targeted for biological control (Beck et al. 2008). It would be useful to determine whether unique volatile compounds emitted by each *Centaurea* spp. are important to specialist biological control agent host attraction or if certain volatile blends are needed even if some of the volatiles in the blend occur in other species. The invasive trees *Tamarix* spp. (Tamaricaceae), produce a number of green leaf volatiles that were attractive to the biological control agent, *Diorhabda elongata* Brullé (Coleoptera: Chrysomelidae) (Cossé et al. 2006). Moreover, these compounds were more

abundant in collections from beetle-infested foliage. However, despite these examples, the behavioral and physiological relevance of volatile compounds to biological control agents is still largely unknown. Much remains to be studied about the specific mechanisms involved in host-finding by biological control agents, the importance of volatiles to host-finding and specificity, and which host volatiles may synergize with pheromones for agent host attraction.

Sequestration of Defensive Chemistry

Scientists working in the field of biological control are experiencing growing pressure to identify, prior to release, the agents that are most likely to be effective (Holt and Hochberg 1997; Morin et al. 2009; Pearson and Callaway 2003; Raghu and Van Klinken 2006). Although weeds targeted for control often contain diverse and potent doses of defensive compounds, some adapted herbivore species consume these plants with apparent impunity, even imbuing their bodies with the plant-derived substances (Duffey 1980; Opitz and Muller 2009). The impact of this sequestration of defensive compounds on the success of weed biological control agent establishment and impact is difficult to assess because of a general paucity of data. However, sequestration of these secondary metabolites is expected to improve the establishment of nascent populations of biological control agents as they protect against generalist natural enemies. Numerous examples exist identifying biotic interference of native and exotic natural enemies on the introduced biological control agents (e.g., Costello et al. 2002; Crider 2011; Dobler et al. 2000; Goeden and Louda 1976; Nimmo and Tipping 2009; Reimer 1988). Even with this interference there have been some remarkable biological control successes. Sequestration has been documented in several weed biological control projects, including in *Linaria dalmatica* (L.) Mill. (Melanthiaceae) (Jamieson and Bowers 2010), *M. quinquenervia* (Wheeler et al. 2002), and *J. vulgaris* (Dobler et al. 2000, Narberhaus et al. 2003). Three biological control agents of tansy ragwort, *L. jacobaeae*, *L. flavicornis*, and *T. jacobaeae*, sequester PAs from host plants (Dobler et al. 2000, Narberhaus et al. 2003). The invasive plant Dalmatian toadflax, *L. dalmatica*, produces at least two iridoid glycosides—antirrhinoside and linarioside—in flowers, leaves, and stems (Jamieson and Bowers 2010). Sequestration of these compounds occurred in one of the two biological control agents, the larvae of a defoliating species *Calophasia lunula* Hufnagel (Lepidoptera: Noctuidae). However, the contribution made by sequestration to the success of biological control projects is largely unknown.

The larvae of the leaf-feeding weevil *O. vitiosa*, a biological control agent of *M. quinquenervia*, are covered

with a viscous orange coating that is thought to protect against generalist predators (Montgomery and Wheeler 2000; Wheeler et al. 2003). This coating is composed of the same volatile terpenoids, 1,8-cineole, α -terpineol, and viridiflorol, found in host leaves consumed by the larvae (Wheeler et al. 2002). The composition of these larval coatings changes with the composition of the larval diet but it continues to protect from attack by predacious ants (Wheeler et al. 2003). The tremendous success of the *M. quinquenervia* biological control project has occurred despite apparent predation of *O. vitiosa* by a suite of predators, most significantly *Podisus mucronatus* Uhler (Christensen et al. 2011; Costello et al. 2002). Apparently, the protection afforded by the *M. quinquenervia* terpenoids, sequestered by *O. vitiosa* larvae, was most effective against mandibulate or chelicerate predators but was apparently less effective against predators with long haustellate mouthparts that could penetrate these defenses (Christensen et al. 2011). The weevil *O. vitiosa*, introduced against *M. quinquenervia*, has become a notable success in controlling this invasive weed (Tipping et al. 2009). The success of this biological control agent is due to many factors, among them the protection derived from sequestered plant compounds (Center et al. 2011). Certainly biological control scientists appreciate this antipredator protection provided by the sequestration of defensive compounds, but the weight given to this factor when deciding which potential agent to invest years of host testing research is difficult to assess.

Conclusion

The interface between these two disciplines, chemical ecology and biological control of weeds, offers fertile opportunities to investigate both basic and applied topics that target the chemical mechanisms behind insect–plant interactions. Scientists may be frustrated by the tedium and delays this type of research brings to the ultimate goal of delivering safe and host specific agents as alternative means of invasive species control. However, we stress in this review the importance and benefit of knowing the chemical basis of the interactions between these invasive species and the agents we develop to control them. Knowledge of the secondary plant compounds that act as behavioral cues for a potential agent can be useful to delimit its host range and when compiling a meaningful host-plant test list to determine potential risks and value of an agent. Understanding how secondary plant chemistry facilitates invasiveness and how evolutionary changes affect biological control provides a fascinating link between many interacting disciplines. Determination of the variability of secondary plant compounds and their induction to increased concentrations by herbivory can help not only explain the host range of potential agents but, after release,

explain weed population regulation and community structure. Searching for potential agents that sequester plant compounds that protect them from generalist predators can improve establishment and ultimate impact on the target weed. Fortunately research examining these interactions is being conducted by scientists from many perspectives and this review draws broadly on several adjacent and overlapping disciplines of biological control and chemical ecology.

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