

Physiological Issues in Host Range Expansion

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Abstract

Host range in a natural system is determined over evolutionary time and constrained through ecological time by behavioral, neurophysiological and physiological exaptations, by biogeographic isolation, exposure to a restricted suite of plant communities, inter- and intraspecific competition, predation, parasitism, and by influential stochastic events. When a biological control agent is transported to a novel environment, some of the evolutionary constraints and many of the behavioral constraints on host use are relaxed, encouraging host range expansion that could have occurred in its native habitat. Host-specificity tests are designed to identify plants that might serve as acceptable hosts in the new environment, but behavioral plasticity, both in host discrimination and in the physiological ability to develop on a given host, makes the task difficult at best. One particularly critical challenge lies in the choice of potential hosts to be screened. Selections are justifiably based on knowledge of the relatedness of such plants to native hosts, on the similarity of their primary allelochemicals to those found in native hosts, or both. I will argue that these criteria risk underestimating host-range (i.e., risk false negatives) because host shifts to chemically or genealogically novel plants by newly introduced agents can occur through coincidence alone. Recent evidence from lupinine chrysomelid beetles and other pharmacophagous insects suggests that evolutionary novel compounds can elicit feeding or oviposition responses when their polarity, molecular configuration and stereochemistry at binding sites meet the criteria for depolarization of stimulatory input at peripheral neuroceptors. Mechanisms for identifying plants with such compounds will be discussed.

Introduction

After more than a century of support from the lay, governmental and scientific communities, the concepts and practices of classical biological control are currently being reconsidered with respect to potential effects on non-target species (Howarth, 1983; 1991; Pimentel et al., 1984; Lockwood, 1993; Simberloff and Stiling, 1996; Louda, 1997; Strong, 1997; Thomas and Willis, 1998). A number of purported “host shifts” or “host expansions” (Marohasy, 1996), primarily by vertebrate biocontrol agents (Pimentel et al., 1984) have been cited as evidence that biological control may not be a “green” alternative to chemical control, as it has historically been touted. The timing of these criticisms is particularly ironic in view of a growing reliance on biological control

as the most viable and perhaps only remaining weapon against invasive alien plant pests. Now recognized as one of the most significant threats to North America’s native biota (Randall and Mannelli, 1996), introduced plants such as leafy spurge (*Euphorbia esula* L.; Fornasari, 1997; Jackson, 1997; Cristofaro et al., 1998), purple loosestrife (*Lythrum salicaria* L.; Blossey et al., 1994; Blossey and Hunt, 1999), and mile-a-minute weed (*Polygonum perfoliatum* L.; Okay, 1995) are just some of the invasive species that have been targeted for new biocontrol initiatives. The increasing demand for the biological control of weeds together with the current criticism of such efforts by reputable biologists has placed biocontrol practitioners and their standard protocols under the most intense scrutiny in their history.

At issue in the debate is the ability of biocontrol screening procedures to avoid false negatives (Simberloff and Stiling, 1996). That is, when prospective control agents are screened for host specificity (Blossey, 1995; Marohasy, 1998), the experimental designs involved must minimize the risk of incorrectly accepting the null hypothesis: that the agent poses no threat to non-target organisms. Advances in our knowledge of insect-plant interactions (Strong et al., 1984; Bernays and Chapman, 1994; Dobler et al., 1996), the evolution of host specificity (Mitter et al., 1991; Hopper et al., 1993; Futuyma et al., 1995; Mardulyn et al., 1997; Kopf et al., 1998), and the behavioral ecology of host switching (Futuyma, 1986; Karowe, 1990; Hawkins and Marino, 1997), however, are justifiably creating the impression that this task is extraordinarily difficult (Roitberg, 2000). Biocontrol practitioners must be concerned with a prospective agent's potential to expand its host range over both ecological and evolutionary time scales. In natural systems, host range is ecologically constrained by the behavioral, neurophysiological and physiological traits shared by members of a population, by the suite of plant species that have been and are currently within the geographic range of the population, and by the intensity of inter- and intraspecific competition, predation, and parasitism that the population must endure. Changes in host specificity are most likely to occur when one or more of these constraints is relaxed during periods of allopatric (Mayr, 1963) or allochronic (Wood and Keese, 1990) isolation. Unfortunately, a successful biological control introduction also relaxes these constraints. The agent is transported to a new environment, isolated from gene flow with the parent population, released from constraining interactions with predators, parasitoids, and interspecific competitors, and exposed to communities of novel plant species. If successful in reducing the population density of the target weed species, the agent faces diminishing host availability and, in turn, increasing intraspecific competition (Marohasy, 1996). Consequently, selection to oviposit or feed on plant species outside the normal range of acceptability becomes exceptionally intense.

Making matters worse for biocontrol practitioners seeking to identify prospective agents that might attack non-target organisms is latent behavioral plasticity triggered by stress similar to what might be encountered during an introduction. The degree to which parasitic Hymenoptera and insect herbivores

discriminate among potential hosts is highly condition-dependent (Papaj and Rausher, 1983; Bernays and Chapman, 1994; Roitberg, 2000). Host specificity has been shown to vary with photoperiod (Roitberg et al., 1992), barometric pressure (Roitberg et al., 1993), hunger (Schoonhoven, 1987; Fletcher et al., 1994), the presence of conspecifics (Visser, 1995), egg load (Minkenberg et al., 1994), and host availability (Fitt, 1986; Speirs et al., 1991; Singer et al., 1992). One can easily imagine other variables that might alter host acceptability as well. But the problem goes beyond identifying all of the factors that affect host choice, for even if this is accomplished, complex factorial screening designs are then required to identify interactions between these factors. Unfortunately, variation introduced into the analysis by each additional factor examined causes a serious loss of analytical power (Roitberg, 2000). This can be somewhat ameliorated by increasing the number of replicates in the screening design, but such solutions are almost always constrained by resources and time. Thus, at first glance it would seem that the quest to improve the accuracy of pre-release host specificity assessments has created an impossibly complex challenge for biocontrol practitioners.

For the first time, these issues have stimulated the interest of evolutionary biologists (Holt and Hochberg, 1997; Roitberg, 2000). Roitberg (2000), for example, has made a convincing case for the use of state-dependent dynamic life history models (Mangel and Clark, 1988; Mangel and Ludwig, 1992) as a first step in biocontrol screening procedures. By calculating lifetime reproductive success that results from various ecological (Heimpel et al., 1998; Roitberg, 2000) and evolutionary (Travis, 1989; Roitberg, 1990; Carrière and Roitberg, 1996; Roitberg, 1998) host-acceptance "decisions," these models can be used to determine what combination of conditions might cause a prospective biocontrol agent to expand its host range. This approach conveniently permits the analysis of several interacting factors at the theoretical level when similar empirical analyses are all but impossible (Roitberg, 2000). Thus, dynamic life history modeling designed to identify the likelihood of adaptive host switches can simplify screening protocols by identifying life history periods during which a particular candidate will be most susceptible to such switching.

Biocontrol practitioners have also recognized the logistical limitations and risks of potential false negatives that are associated with current screening protocols

(Dunn, 1978; Cullen, 1990; Marohasy, 1998). In response to these problems, Marohasy (1998) has suggested that screening procedures for the biological control of weeds can be improved by paying closer attention to behavioral mechanisms underlying host-finding and acceptance. Factors targeted as being critical to screening designs include (1) the time elapsed between the most recent period of eating (or oviposition) and testing (Papaj and Rausher, 1983), (2) pre-alighting opportunities for host discrimination (Wapshere, 1989), (3) experience-related phenomena such as short-term central nervous excitation (Menzel et al., 1993), longer-term sensitization (Marohasy, 1998), habituation to inhibiting inputs from non-hosts (Jermy et al., 1982), associative learning (Bernays and Wrubel, 1985); (4) cross contamination of non-hosts by host volatiles (Jayanth et al., 1993), and (5) loss of host-discrimination behavior due to cage effects (Cullen, 1990). If these empirical advances can be married to life history modeling as suggested by Roitberg (2000), the accuracy and efficiency of pre-release screening procedures must surely improve.

As promising as they are, however, both theoretical and empirical advances in biocontrol screening procedures have little practical value if the selection of plants to be screened is flawed. Clearly if species that could support an expansion of host range by the prospective agent are not included in the evaluation of its host specificity, the results of such evaluations will be inaccurate and false negatives may occur. In this chapter, I discuss two physiologically-based phenomena that may frequently influence host range expansion by insect herbivores and consequently may have important ramifications for the selection of plant species to be included in screening procedures for potential agents in the biological control of weeds.

Plant Selection Criteria and Their Problems

The objective of host specificity assessment in weed biocontrol is to quantify the ability of prospective biological control agents to attack non-target plant species after introduction (Schroeder, 1983; Marohasy, 1998). It has been agreed through international consensus (Greathead, 1995) that plant species should be chosen for host range screening on the basis of their taxonomic relationship to the target species (Wapshere, 1989; Harley and Forno, 1992). By sequentially exposing prospective agents to progressively less related

plant species (i.e., to different varieties of the target host, then to different species in the same genus, then to different genera in the same tribe, and so on) it is thought that all plant species that might support populations of the agent will be identified. A related approach (although one rarely done in practice) is to expose the agent to plants with similar signatures of secondary metabolic compounds, regardless of their taxonomic affiliation with the target species (Blossey, 1995). Both of these criteria for plant selection are based on the contention that "*Natura nonfacit saltum*" (nature does not make leaps), particularly when it comes to the evolution of host ranges in phytophagous insects (Futuyma, 1994). Ever since Guignard first noted in the 1890s that insect host range is mediated by the presence of common feeding stimulants (Feltwell, 1982), a great deal of evidence has been accumulated in support of the hypothesis that host shifts or expansions by phytophagous insects are often constrained to plant species sharing a common suite of phytochemicals (Ehrlich and Raven, 1964; Berenbaum, 1990; Futuyma, 1991; Farrell et al., 1992; Feeny, 1992; Becerra, 1997). Such plants typically (but not always: Berenbaum, 1981; Menken et al., 1992) are also close relatives (Mitter and Farrell, 1991).

The primary problem with this line of reasoning is that it disregards host shifts by phytophagous insects to unrelated plants with vastly different chemistries. The literature is replete with descriptions of closely related insect species that specialize on plants from different families or even different orders with widely differing secondary metabolic compounds (reviewed by Jermy, 1984). Some of these examples involve insects with haustellate mouthparts (e.g., aphids, Eastop, 1973; Müller, 1978; treehoppers, Tilmon et al., 1998), whose actual xylem and/or phloem foodstuffs may differ very little in chemical makeup among unrelated plants. However, many others involve mandibulate insects that cannot consume plant material without full exposure to the entire suite of allelochemicals present in the tissues. Table 1 provides 24 examples within the Coleoptera and Lepidoptera in which closely related species or populations within species expanded their host range not only to plants in different genera, families, or orders, but to plant species in a different subclass, or in 17 extreme cases to a different plant class. Clearly current screening procedures would have detected none of these host expansions.

Table 1. Evidence that closely related mandibulate insect species are physically capable of host shifts to genetically and chemically disparate plant taxa.

Taxon	Host Plant	Subclass (Class)	Family	Dominant Secondary Compounds ¹	Reference
Coleoptera					
Chrysomelidae <i>Diabrotica virgifera</i> complex	grasses	Commelinidae	Poaceae	ferulic acid; C-glycosylflavones	Branson & Kryan, 1981
<i>Diabrotica fuscata</i> complex	cucurbits	Dilleniidae	Cucurbitaceae	triterpenes; pyridine alkaloids; cucurbitacins	
<i>Gonioctena</i> subgenus <i>Goniomena interposita</i> Franz & Palmén	alder	Hamamelidae	Betulaceae	nontannic phenolics	Mardulyn et al., 1997
<i>Goniomena pallida</i> (L.) <i>Goniomena intermedia</i> Hell.	willow cherry	Dilleniidae Rosidae	Salicaceae Rosaceae	phenol heterosides cyanogenic compounds; triterpenoid saponins	
<i>Phratora</i> (=Phyllodecta) <i>polaris</i> (Schneider)(race1) <i>Phratora polaris</i> (race 2)	willow birch	Dilleniidae Hamamelidae	Salicaceae Betulaceae	phenol heterosides highly tanniferous with galic acid	Kopf <i>et al.</i> , 1998
<i>Lochmaea capreae</i> L. (race 1)	willow	Dilleniidae	Salicaceae	phenol heterosides	Mikheev & Kreslavsky, 1980
<i>Lochmaea capreae</i> (race 2)	birch	Hamamelidae	Betulaceae	highly tanniferous with galic acid	
<i>Syneta betulae</i> (Fabricius) (race 1) <i>Syneta betulae</i> (race 2)	birch pine	Hamamelidae (Conopsida)	Betulaceae Pinaceae	highly tanniferous with galic acid diterpene acids; phenolics (pinosylvan)	Jolivet, 1954
Lepidoptera					
Pyrilidae <i>Cactoblastis cactorum</i> (Bergroth) (cactus abundant)	cactus	Caryophyllidae	Cactaceae	isoquinoline alkaloids; triterpenoid saponins	Dodd, 1940
<i>Cactoblastis cactorum</i> (cactus depleted)	tomato melons	Asteridae Dilleniidae	Solanaceae Cucurbitaceae	tomatine (glycoalkaloid) triterpene cucurbitacins; pyridine alkaloids	
<i>Hedylepta Blackburni</i> (Butler) (ancestral)	Pritchardia palm	Arecidae	Arecaceae	polyphenols; pyridine alkaloids	Zimmerman, 1960
<i>Hedylepta</i> (5 sister spp) (derived since the introduction of banana to Hawaii 1000 y.)	banana	Zingiberidae	Musaceae	tanniferous	
Tortricidae <i>Laspeyresia</i> (Cydia) <i>pomonella</i> (L.) (race 1)	apple	Rosidae	Rosaceae	cyanogenic compounds; triterpenoid saponins	Philips & Barnes, 1975
<i>Laspeyresia</i> (Cydia) <i>pomonella</i> (race 2)	walnut	Hamamelidae	Juglandaceae	naphthaquinones	

¹Chemical signatures from Cronquist (1981)

Table 1 (continued)

Taxon	Host Plant	Subclass (Class)	Family	Dominant Secondary Compounds¹	Reference
<i>Epinora caprana</i> (Fabricius) normal host	<i>Myrica gale</i>	Hamamelidae	Myricaceae	tanniferous; triterpenes; sesquiterpenes	Winter, 1974
new host	<i>Pinus contorta</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Clepsis senecionana</i> (Hübner) normal host	<i>Myrica</i> <i>Vaccinium</i>	Hamamelidae Dilleniidae	Myricaceae Ericaceae	tanniferous; triterpenes; sesquiterpenes; phenol heterosides (arbutin); triterpene urolic acid; diterpene andromedotoxin	Winter, 1974
new hosts	<i>Picea</i> , <i>Pinus</i> , <i>Larix</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Ptycholoma lechearna</i> (L.) normal hosts	<i>Quercus</i> spp.	Hamamelidae	Fagaceae	highly tanniferous with gallic acid; triterpenes	Winter, 1974
new host	<i>Picea sitchensis</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Philedone gerningana</i> (Denis & Schiffermüller) normal hosts	<i>Vaccinium</i>	Dilleniidae	Ericaceae	phenol heterosides (arbutin); triterpene urolic acid; diterpene andromedotoxin	Winter, 1974
new hosts	<i>Potentilla</i> <i>Picea sitchensis</i>	Rosidae (Conopsida)	Rosaceae Pinaceae	cyanogenic compounds; diterpene acids; phenolics (pinosylvan)	
<i>Philedonides lunana</i> (Thunberg) normal hosts	<i>Potentilla</i>	Rosidae	Rosaceae	cyanogenic compounds; terpenoid saponins	Winter, 1974
new hosts	<i>Myrica</i> <i>Picea</i> , <i>Pinus</i> , <i>Larix</i>	Hamamelidae (Conopsida)	Myricaceae Pinaceae	tanniferous with triterpenes; sesquiterpenes diterpene acids; phenolics (pinosylvan)	
<i>Acleris caledoniana</i> (Stephens) normal hosts	<i>Myrica</i>	Hamamelidae	Myricaceae	tanniferous; triterpenes; sesquiterpenes	Winter 1974
new host	<i>Pinus contorta</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Acleris hyemana</i> (Haworth) normal hosts	<i>Calluna</i> , <i>Erica</i>	Dilleniidae	Ericaceae	phenol heterosides (arbutin); triterpene ursolic acid; diterpene andromedotoxin	Winter, 1974
new host	<i>Picea sitchensis</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	

¹Chemical signatures from Cronquist (1981)

Table 1 (continued)

Taxon	Host Plant	Subclass (Class)	Family	Dominant Secondary Compounds ¹	Reference
Cochylidae <i>Eupoecilia angustana</i> (Hübner)					
normal hosts	<i>Calluna, Erica</i>	Dilleniidae	Ericaceae	phenol heterosides (arbutin); triterpene ursolic acid; diterpene andromedotoxin	Winter, 1974
new hosts	<i>Picea sitchensis</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
Lasiocampidae <i>Lasiocampa quercus callunae</i> (Palmer)					
normal host	<i>Calluna vulgaris</i>	Dilleniidae	Ericaceae	phenol heterosides (arbutin); triterpene ursolic acid; diterpene andromedotoxin	Winter, 1974
new hosts	<i>Pinus, Picea</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Macrothylacia rubi</i> (L.)					
normal hosts	<i>Myrica</i>	Hamamelidae	Myricaceae	tanniferous, triterpenes	Winter, 1974
	<i>Calluna, Erica, Vaccinium</i>	Dilleniidae	Ericaceae	sesquiterpenes phenol heterosides (arbutin), triterpene ursolic acid; diterpene andromedotoxin	
new host	<i>Picea sitchensis</i>	(Conopsida)	Pinaceae	diterpene acids, phenolics (pinosylvan)	
Geometridae <i>Entephria caesiata</i> (Denis & Schiffermüller)					
normal hosts	<i>Vaccinium, Calluna Erica</i>	Dilleniidae	Ericaceae	phenolic heterosides (arbutin); triterpene ursolic acid; diterpene andromedotoxin	Winter, 1974
new hosts	<i>Pinus contorta</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	
<i>Hydriomena furcata</i> (Thunberg)					
normal host	<i>Vaccinium</i>	Dilleniidae	Ericaceae	phenolic heterosides (arbutin); triterpene ursolic acid; diterpene andromedotoxin	Winter, 1974
new host	<i>Pinus contorta</i>	(Conopsida)	Pinaceae	diterpene acids; phenolics (pinosylvan)	

¹Chemical signatures from Cronquist (1981)

Table 1 (concluded)

Taxon	Host Plant	Subclass (Class)	Family	Dominant Secondary Compounds ¹	Reference
Noctuidae					
<i>Blepharita</i> (= <i>Eumichtis</i>) <i>adusta</i> (Esper)					
normal hosts	<i>Myrica</i>	Hamamelidae	Myricaceae	tanniferous; triterpenes;	Winter, 1974
new hosts	<i>Salix</i> <i>Picea</i> , <i>Pinus</i>	Dilleniidae (Conopsida)	Salicaceae Pinaceae	sesquiterpenes phenol heterosides diterpene acids; phenolic (pinosylvan)	
Pieridae					
<i>Pieris rapae</i> (L.) (fed cabbage as neonates)	cabbage	Dilleniidae	Brassicaceae	glucosinolates	Renwick & Huang, 1995
<i>Pieris rapae</i> (fed nasturtium or wheat germ diet as neonates)	nasturtium	Rosidae	Tropaeolaceae	chlorogenic acid; glucosinolates	

¹Chemical signatures from Cronquist (1981)

The argument can be made that host shifts such as those that occurred in *Diabrotica* and *Goniomena* chrysomelids (Table 1) over evolutionary time are so infrequent that the risks of such events are negligible in time frames of interest to people. Possibly, but in the case of race specialization within *Phratora polaris*, *Lochmaea capreae*, and *Syneta betulae* (Table 1), host expansion happened so recently that further population divergence has not yet occurred. Moreover, it is difficult to dismiss the host switches that have occurred before our eyes among the 19 species of Lepidoptera listed in Table 1 as being too rare to worry about. In the case of *Cactoblastis cactorum* (Bergroth), host expansion occurred as a consequence of host deprivation; when normal cactus hosts were overexploited (as one would hope for in the case of a biocontrol agent), *C. cactorum* readily switched to tomatoes (Dodd, 1940). Whether *C. cactorum* is capable of permanently adapting to tomatoes remains to be seen, but the tortricid *Laspeyresia pomonella* L. clearly had the capacity to permanently adopt walnut (*Juglans regia*) as a new host without selection from host deprivation (Philips and Barnes, 1975) as did fifteen species of Lepidoptera that expanded from a variety of unrelated hosts to various conifers shortly after they were exposed to them (Winter, 1974).

Many of these taxa expanded their host ranges sometime during the course of their evolutionary histories (measured in millions of years), but others, prompted by man-induced perturbations, adopted new hosts within a single generation in recent decades. Given that host switches

without constraint from lineage or chemistry can and do occur, it is essential that we develop methods for predicting: (1) which prospective biocontrol agents have the innate capacity to adopt chemically unrelated host groups, and (2) what phytochemical signatures fall within the range of acceptability for such agents. Without this knowledge there will always be some probability that potentially acceptable plant species will be inadvertently omitted from screening designs.

Malleable Gustatory Receptors

One way to improve the chances of identifying plant species that might serve as suitable non-target hosts for biocontrol agents is to design screening procedures for maximum sensitivity. That is, screen potential hosts under conservative no-choice conditions that occur under field conditions whenever an egg is either mistakenly or purposely laid on a "non-host." This is not likely to be the rare event it was once thought to be. Gravid females may relax their efforts to discriminate among hosts if preferred species are in short supply (Wiklund, 1981; Fitt, 1986), if the period since the last oviposition has been unusually lengthened by, for example, bad weather (Papaj and Rausher, 1983, Schoonhoven, 1987; Singer et al., 1992), or during the last days of life when receptors, flight or other vital processes no longer function well. Once an egg is deposited on a novel host, the larva that emerges from that egg typically does not have enough energy reserves to leave the plant and search for another more

appropriate host. Its only real options are to attempt to eat the plant at hand or starve — a classic no-choice scenario.

Recent studies of feeding deterrents in Lepidoptera suggest that such “no choice” situations involving neonate larvae may have important implications for biocontrol screening procedures. Using the imported cabbageworm, *Pieris rapae* L., as a model, Renwick and Huang have developed good evidence that the gustatory receptors of neonate larvae are initially so malleable that the chemical signature of a novel host may not deter feeding and successful development if it is the first signature encountered (Huang and Renwick, 1995ab; Renwick and Huang, 1995, 1996; Huang and Renwick, 1997). For example, nasturtium (*Tropaeolum majus* L.) contains substantial quantities of a phenolic compound, chlorogenic acid, that deters feeding in cabbage-reared *P. rapae* larvae to the point of starvation (Huang and Renwick, 1995b). If, however, *P. rapae* hatch and feed as neonates on nasturtium without first tasting cabbage, or are fed a wheat germ diet upon hatching, larvae readily accept nasturtium as a viable host and complete development without loss of fitness (Renwick and Huang, 1995; Huang and Renwick, 1997). Induction of food preference (Szentesi and Jermy, 1989) has been ruled out as an explanation of this phenomenon since transfers from nasturtium to cabbage do not cause subsequent rejection of cabbage. Instead, Renwick and Huang believe that sensitivity to nasturtium’s chlorogenic acid develops while neonates feed on cabbage. If they are never exposed to the chemical signature of cabbage, larvae never develop sensitivity to deterrents in nasturtium or wheat germ diet.

Furthermore, cross habituation occurs readily in young *P. rapae* larvae. Early exposure to strophanthidin, cymarins, erysimoside, digitoxigenin, digitoxin, cucurbitacins E and I, and rutin (all powerful deterrents) suppressed the development of sensitivity in larvae to chlorogenic acid and thus rendered nasturtium an acceptable host (Huang and Renwick, 1995).

The mechanisms by which sensitivity is induced or suppressed in young larvae are not yet known, but available evidence suggests that, for some period after hatching, the peripheral gustatory receptors of neonate larvae can be permanently molded in ways that affect the acceptability of leaf tissue as a food source. Apparently, it is the lack of chemical suppressors in plant tissue that permits

the normal development of sensitivity in the peripheral receptors of neonates. Conversely, the presence of one or more deterrents in a novel host can permanently suppress the development of sensitivity to these and other compounds, enabling larvae to consume them without ill effects (Renwick and Huang, 1996). Obviously there are limits to the degree to which neonate peripheral receptors can be molded by the chemical signature of the first tissues consumed. The point to emphasize here, however, is that neonate larvae are far more plastic in their acceptance criteria than are older larvae, as long as they have not previously been exposed to food that lacks a particular deterrent. Thus, screening procedures will more accurately identify acceptable host species if tests are confined to hatching neonates, simulating the no choice conditions that occur every time eggs are laid on novel hosts.

One might protest that if some small percentage of eggs persistently ends up on “non-hosts” and if neonates hatching from these eggs have a greater chance of finding these plants to be suitable hosts than previously thought, why then are the host ranges of the vast majority of phytophagous insects narrowly constrained to only a few species (Bernays and Graham, 1988)? For the answer we must reconsider all of the ecological and evolutionary constraints on host range in natural systems discussed in the introduction. Oviposition mistakes and the malleability of neonate gustatory receptors might very well have played important roles in defining the current host ranges found in natural populations of phytophagous insects. But biocontrol introductions are not natural interactions. They are manipulated events that suddenly expose a phytophagous insect to an unprecedented array of novel hosts. If oviposition mistakes and neonate habituation ever influence host range expansion it should be during a biocontrol introduction.

“Loose” Gustatory Receptors

The neurophysiological basis of peripheral perception is extraordinarily complex in insect gustatory systems (Frazier, 1986; Simmonds et al., 1990; Schoonhoven et al., 1992; Städler, 1992; Mullin et al., 1994). In the simplest terms, feeding behavior is stimulated if the chemoreception of phagostimulants exceeds the chemoreception of feeding deterrents (Dethier, 1980). In caterpillars and possibly all insects, taste sensilla contain cells specialized for the production of either inhibitory or excitatory inputs to the central nervous system, upon detection of deterrent or stimulatory chemicals in foods (Frazier, 1986). Receptor sites on these cells can be highly specific (tight) or less specific (loose). Strychnine, for

example, is a compound novel to most phytophagous insects, but it readily depolarizes activation channels leading to inhibitory input in most insects; the binding requirements at these sites are sufficiently “loose” that a variety of molecular structures meet the polarity and configuration specifications for binding there. The loose characteristics of receptor sites with deterrent capabilities may be adaptive because they protect the central nervous system from exposure to damaging novel compounds (Frazier, 1992).

Of particular interest to students of host range expansion is that relatively loose binding properties of receptor sites can also enable novel and sometimes deleterious compounds to trigger feeding behavior (Tallamy et al., 1999). There are several mechanisms by which this can happen (Frazier, 1986, 1992). Some molecules bind at receptor sites leading to inhibitory inputs, but rather than depolarizing the activation channels, they simply block them. Without inhibitory inputs, even small amounts of phagostimulants, including amino acids present in the insects’ saliva, are sufficient to activate the stimulatory inputs at the sensillum and elicit feeding. Activation leading to inhibitory inputs can also be prevented when particular molecules block the stimulus removal system. Finally, loose stimulatory receptor sites themselves can encourage phagostimulation by novel compounds with the appropriate configuration and polarity at binding sites. This is apparently the mechanism by which some *Atrichopogon* flies (Ceratopogonidae) respond to terpenes in which the heptane skeleton is associated with either a 2,3-dicarboxylic anhydride or a 2,3- γ -lactone (Frenzel et al., 1992) and by which the peptide aspartame mimics the carbohydrate sucrose at vertebrate receptors, a mimicry upon which much of the sweetener industry is based. We emphasize that considerable variability in response is the rule rather than the exception in insect chemosensory systems (Frazier, 1992). If this variability is even partly genetic, a typical insect population would theoretically be fertile ground for the advent of novel feeding preferences.

There are numerous examples in insects of inappropriate feeding responses that are presumably the result of imprecision at gustatory receptors. When presented with petunia (*Petunia integrifolia* [Hooker]) plants, *Manduca sexta* L. caterpillars voraciously eat the leaves, pausing only to regurgitate everything they have just eaten. This behavior may continue until the larvae starve to death (Dethier and Crnjar, 1982). Several haustellate arthropods are stimulated to eat in the presence of toxic cucurbitacins. *Tetanychus urticae* Koch, the

two-spotted spider mite, prefers cucurbitacin-rich cucumber lines over cultivars without cucurbitacins, even though such behavior reduces mite fitness (Gould, 1978). Similarly, corn delphacids (*Peregrinus maidis* [Ashmead]), sycamore lace bugs (*Corythucha ciliata* [Say]), and pea aphids (*Acyrtosiphon pisum* [Harris]) are all stimulated to feed by exogenous coatings of cucurbitacin B, an evolutionarily novel compound to these species (Tallamy et al., 1997). Mafra-Neto and Jolivet (1994) report the eating by seven species of lace bugs (Tingidae) and plant bugs (Miridae), and one luperine chrysomelid beetle, *Diabrotica angulicollis* (Erichson), of the cantharidin-rich hemolymph oozing from the joints of disturbed *Epicauta aterrma* (Klug), a large meloid beetle from Brazil. Occasional predation is commonly exhibited by mirid plant bugs, but this is the first report of hematophagy among the phytophagous tingids and *Diabrotica* beetles. That this unusual response is triggered by cantharidin is supported by numerous studies in which traps baited with pure cantharidin attracted pyrochroid, endomychid, anthicid, and staphylinid beetles, ceratopogonid, sciarid, and anthomyiid flies, and braconid wasps (Young, 1984; Frenzel et al. 1992; Frenzel and Dettner 1994; Eisner et al. 1996).

The apparent ease with which loose gustatory receptors can lead to an association with novel compounds suggests that this mechanism may provide the missing explanation for host switches by phytophagous insects to plants with chemical signatures vastly different from those of parent hosts (Tallamy et al., 1999). If an insect with gustatory receptors that evolved in the context of meeting nutritional and pharmacological needs on one host species suddenly encounters a novel compound from a different plant, a feeding response could be elicited for one or more of the reasons discussed above. If such phagostimulation enhances the fitness of those that exhibit it, the response should rapidly move to fixation within the population. If the novel molecule (or any other compound present in the new plant) is toxic, early consumers will suffer reduced fitness. This will not, however, lead to a “tightening” of the responsible receptor’s specificity unless selection to avoid the new compound exceeds selection to maintain the loose properties of the receptor in question. Host expansion should ensue when: (1) exposure to the novel compound is sufficiently frequent to select for physiological tolerance, and (2) gene flow diluting genetic change in tolerance is reduced.

A successful biocontrol introduction could create exactly this scenario. If an agent locally reduces the

target host population to the point where most dispersing individuals have nothing on which to oviposit or feed except evolutionarily novel plant species, there will be powerful selection favoring those agents with peripheral receptors that are sufficiently loose to enable acceptance of a new host. Gene flow in the succeeding generation between agents that have successfully adopted the new host and those that were able to locate target hosts could be restricted allochronically through differences in host phenology (Wood and Keese, 1990; Wood et al., 1990) or allopatrically if, for example, the collapse of the target host population had occurred in a relatively isolated valley (Mayr, 1963). But one needs to hypothesize the restrictions of gene flow for this mechanism of host range expansion to occur. It is probable that the loose properties of the appropriate receptors are shared by all members of the population because of their selective advantage. Thus, all members of the population are physiologically predisposed to finding any novel plant bearing the appropriate components to be stimulating by coincidence alone.

Strong et al. (1984) agree that host shifts can occur even without the collapse of the parent host's population. Close proximity of abundant parent host species and novel plants creates an ecological opportunity for insects physiologically capable of interpreting the compounds in novel plants as phagostimulants rather than deterrents. For example, proximity has been evoked to explain the seven species of British Lepidoptera that expanded their host range from native moorland plants in several genera (*Myrica* – Myricaceae; *Vaccinium*, *Erica* and *Calluna* – Ericaceae) to *Pinus contorta* Douglas that were planted extensively among them (Winter, 1974). In the same vein, laboratory experiments have repeatedly demonstrated that some phytophagous insects (presumably those with loose gustatory receptors) can rapidly adapt to novel hosts when under selection from repeated exposure (Schroder, 1903; Pictet, 1911; Harrison, 1927; Kozhanchikov, 1950; Brower et al., 1967; Gould, 1979). For example, Brower et al. (1967) created a line of monarch butterflies (*Danaus plexippus* L.) that developed entirely on cabbage rather than its normal milkweed hosts.

Do loose gustatory receptors have the potential to permit a shift to any nearby plant? Certainly not; host shifts are only possible when one or more key compounds in the chemical signature of a novel plant coincidentally share the molecular configuration, polarity and solubility of

compounds in the parent host for which the insect's taste receptors originally evolved (Tallamy et al., 1999). But how can biocontrol practitioners predict which plants might produce such binding site matches? Advances in computerized molecular modeling programs have the potential to make this proposal more feasible than it sounds. The first step would be to characterize the chemical profile of the prospective agent's ancestral host species. Contributions from natural products chemists over the last three decades have been so substantial that the profile of secondary metabolic compounds in most angiosperms is readily accessible (Karrer, 1958; Hegnauer, 1962-1973; Tetenyi, 1970; Cronquist, 1981). Next, the chemical profiles of key plant species of agricultural, ornamental, environmental, and political value from the habitats of the target species should be determined. Quantitative structure-activity relationships (QSAR), a powerful technique for studying three-dimensional structure-function relationships between ligands and membrane receptors (Mullin et al., 1997; Kim and Mullin, 1998), can then be employed in conjunction with molecular modeling software to identify which compounds in these novel plants might match the binding site requirements of chemicals in the ancestral host. In essence, initial screening can be done relatively quickly and painlessly on the computer. Only plants that are found to contain compounds with similar configuration, stereochemistry, and hydrophobicity to the compounds of the ancestral host will be added to the list of plant relatives to be actually screened. Every time a new compound is modeled in this way its binding site characteristics can be stored in a cumulative data base. Eventually, the data base will be sufficiently complete that matches can be sought by quick searches rather than new modeling.

Summary

A growing awareness of environmental problems caused by the introduction of some biological control agents has created serious opposition to new biocontrol initiatives in both political and scientific circles. Despite the fact that most biocontrol mishaps have been caused by the irresponsible release of vertebrate predators, practitioners of the biological control of noxious weeds are under pressure to design infallible screening procedures to identify all non-target plants that might encourage host range expansion by prospective agents. Theoretical advances such as the use of dynamic life history modeling and empirical improvements in screening designs that incorporate behavioral mechanisms underlying host-

finding and acceptance have been proposed to address this goal, but these will increase screening accuracy very little if the proper plant species are not included in the population of non-targets to be screened. In practice, plants to be screened are selected almost exclusively on the basis of taxonomic relatedness to the target host. This approach ignores the fact that host range expansions to unrelated plants with chemical profiles that differ from the ancestral host occur over both evolutionary and ecological time frames and are well documented.

Recent studies suggest that some phytophagous insects may be physiologically capable of accepting and developing on evolutionarily novel plant species for two reasons. First, it appears that the discriminatory abilities of gustatory receptors in newly hatched larvae are shaped to an important extent by the array of chemicals those receptors encounter during the first feeding episodes of larval life. Early exposure to novel compounds that would normally deter older larvae can render such chemicals (and the plants that contain them) acceptable for life. Thus, ecological conditions that favor oviposition “mistakes” resulting in the deposition of eggs on novel plant species set the stage for the acceptance in nature of plants that would have been rejected in screening protocols using anything but unfed neonate larvae.

Second, there is growing evidence that phytophagous insects can adopt novel plants as acceptable hosts when one or more of the secondary metabolic compounds of such plants coincidentally possess the structure and polarity necessary to depolarize phagostimulatory binding sites on gustatory receptors. When this is the case, host plant acceptability is a function of the binding properties of particular compounds, not the taxonomic relatedness or class of chemical deterrents in a plant’s tissues. Computer programs that model the 3-dimensional configuration of secondary metabolic compounds can be used to identify molecules in non-target plants with binding site properties similar to those of phagostimulatory chemicals in the ancestral hosts of prospective weed control agents. Only non-targets possessing such matches need to be included in actual screens. Thus, screening procedures can be simultaneously made more conservative and more efficient by designs based solely on no choice feeding responses by unconditioned neonate larvae that are exposed to a population of non-targets prescreened by computer searches of chemical libraries.

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