11 Feeny, P., Plant apparency and chemical defense, in: Biochemical Interactions between Plants and Insects, Rec. Adv. Phytochem. 10th Edn. Eds I. M. Wallace and R. L. Mansell. Plenum, New York 1976.
12 Ferguson, J. E., and Metcalf, R. L., Cucurbitacins. Plant-derived defense compounds for Diabroticites (Coleoptera: Chrysomelidae). J. chem. Ecol. *11* (1985) 311–317.
13 Garcia, J., Hankins, W. G., and Rusiniak, K. W., Behavioral regulation of the milieu interne in man and rat. Science *185* (1974) 824–31.
14 Howard, D. F., Phillips, D. W., Jones, T. H., and Blum, M. S., Anthraquinones and anthrones: occurrence and defensive function in a chrysomelid beetle. Naturwissenschaften *69* (1982) 91–92.
15 Jolivet, P., Selection trophique chez les Clytrinae, Cryptocephalinae et Chlamisiuae (Comptosoma) et les lamprosomaticlae (Cyclica) (Coleoptera: Chrysomelidae). Acta zool. path. Antwerp. *70* (1978) 167–200.
16 Luckner, M., Secondary Metabolism in Microorganisms, Plants and Animals. Springer Verlag, Berlin 1984.
17 Noirot, C., and Quennedey, A., Fine structure of insect epidermal glands. A. rev. Ent. *19* (1974) 61–81.
18 Pasteels, J. M., and Daloze, D., Cardiac glycosides in the defensive secretion of Chrysomelid beetles: Evidence for their production by the insects. Science *197* (1977) 70–72.
19 Pasteels J. M., Breakman, J. C., Daloze, D., and Ottinger, R., Chemical defense in chrysomelid larvae and adults. Tetrahedron Lett. *38* (1982) 1891–1897.
20 Pasteels, J. M., Gregoire, J. C., and Rowell-Rahier, M., Chemical defense in arthropods. A. Rev. Ent. *28* (1983) 263–289.
21 Pasteels, J. M., Rowell-Rahier, M., Braekman, J. C., and Daloze, D., Chemical defences in leaf beetles and their larvae: The ecological, evolutionary and taxonomic significance. Biochem. Syst. Ecol. *12* (1984) 395–406.
22 Pasteels, J. M., Braekman, J. C., and Daloze, D., Chemical defense in the Chrysomelidae, in: The Biology of Chrysomelidae. Eds P. Jolivet, T. H. Hsiao and E. Petitpierre. Junk, Dordrecht 1988.
23 Pasteels, J. M., Duffey, S., and Rowell-Rahier, M., Toxins in Chrysomelid beetles: Possible evolutionary sequence from de novo synthesis to derivation from food plant chemicals. J. chem. Ecol. (1988) in press.
24 Pasteels, J. M., Rowell-Rahier, M., Randoux, T., Braekman, J. C., and Daloze, D., Pyrrolizidine alkaloids of probable host plant origin in the defensive secretion of the leaf beetle *Oreina cacaliae* (Coleoptera, Chrysomelidae) Ent. exp. appl. *49* (1988) 55–58.
25 Pasteels, J. M., Rowell-Rahier, M., and Raupp, M. J., Plant-derived defense in chrysomelid beetles, in: Novel Aspects of Insect-Plant Relationships, pp. 235–272. Ed. P. Barbosa. Wiley, New York 1988.
26 Rhoades D. F., and Cates R. G., Toward a general theory of plant antiherbivore chemistry, in: Biochemical Interactions between Plants and Insects. Rec. Adv. Phytochem. 10th Edn. Eds J. M. Wallace and R. L. Mansell. Plenum, New York 1976.
27 Rothschild, M., Secondary plant substances and warning coloration in insects, in: Insect-Plant Relationships, Symp. R. ent. Soc. London. Ed. H. F. van Emden. Blackwell, Oxford 1972.
28 Suzuki, K., Life form and its relationship to phylogeny in higher taxa of Chrysomelidae. Chrysomela *18* (1988) 9–10.
29 Tinbergen, L., The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arch. neer. zool. *13* (1960) 265–336.
30 Van Oycke, S., Braekman, J. C., Daloze, D., and Pasteels, J. M., Cardenolide biosynthesis in chrysomelid beetles. Experientia *43* (1987) 460–462.
31 Van Oycke, S., Randoux, T., Braekman, J. C., Daloze, D., and Pasteels, J. M., New cardenolide glycosides from the defense glands of chrysolinina beetles (Coleoptera: Chrysomelidae). Bull. Soc. chim. Belg. *97* (1988) 297–311.

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Insect chemical ecology. Summary and concluding remarks

M. B. Isman

Department of Plant Science, University of British Columbia, Vancouver (British Columbia V6T 2Z4, Canada)

The papers presented in this Multi-author Review provide an eclectic, rather than a comprehensive, overview of research progress within the diverse and dynamic field of insect chemical ecology. Each paper, within its subject area as defined by the author, serves as a bridge between the current state of knowledge and the next conceptual step which will be made possible by data gathered from ongoing investigations as this Review is published. In spite of the tremendous differences in subject matter between the papers, certain linkages arise from a careful examination of the collection.

Chapman and Bernays point out that direct observations of insects on plants tend to be uncommon, but are important if we are to understand the processes by which insects accept host plants. They rightly emphasize the leaf surface as the interface between the insect's battery of chemoreceptors (both olfactory and gustatory) and the plant, and suggest that the decision to accept or reject frequently occurs even before an insect takes the first bite. Renwick reaches a similar conclusion with respect to the importance of leaf surface chemistry in oviposition by insects. Both papers raise the point that acceptance/rejection is the result of a concatenation of behaviors, which can rarely be ascribed to a single, unique plant chemical. In the case of oviposition, volatile substances, in some cases acting in concert with visual stimuli, attract the insect from a distance. It is only once the insect has alighted on the plant that the surface chemicals ('arrestants') can come into play in determining the insect's ultimate decision of whether to accept or not.

The Diabroticite beetles provide a strong case in point. Metcalf and Lampman explore the evolutionary ties between this taxa and their host plants, the Cucurbitaceae. It is the unique triterpenoids, the cucurbitacins, which characterize this family of plants in the chemical sense, and these allelochemicals are powerful arrestants and feeding cues for the beetles. However, it is a blend of somewhat nonspecific floral volatiles which serve to attract the beetles to the plants. This beetle-allelochemical interaction includes two further points of interest: (1) because the cucurbitacins are such potent and specific arrestants for these insects, this knowledge has been of practical use in developing a mass trapping method for controlling pestiferous species of the beetles [1]; (2) the beetle has evolved the ability to sequester the bitter-tasting cucurbitacins from the host and utilize them in its own defense against predators [2].

Chapman and Bernays further point out the potential importance of habituation and associative learning with respect to insect feeding behavior. These phenomena, most often neglected in studies of insect-plant chemical interactions, have important consequences for the technical design of bioassays. Bioassays intended to evaluate insect feeding behavior require well-defined endpoints of short duration. Considerable evidence is accumulating to show that the internal state of the insect can have both indirect and direct effects on chemoreception, in terms of the central integration of gustatory stimuli [3], and in terms of the sensitivity of the peripheral receptors themselves [4].

The paper by Berenbaum and Isman focusses on the morphological and physiological constraints to growth and the ability to deal with putatively toxic allelochemicals. They compare two unrelated insect taxa, the Orthoptera (grasshoppers and crickets) and the Lepidoptera (butterflies and moths) with respect to their feeding habits, relative larval growth, and detoxicative potential. Both taxa include many members which have extremely broad host-plant ranges, yet, from the data available, they appear to have evolved different strategies for coping with dietary toxins. This is an example where comparisons can be tenuous – the dearth of directly comparable data (e.g. the study by Bernays [5] which was the catalyst for this review paper) can make it difficult to discern the exception from the rule.

Baker's comprehensive review of lepidopteran sex pheromones strikes the desired balance between chemistry, ecology, and the neurophysiology underlying the behavioral interface. After carefully documenting how "changing the sequence of action of relatively few enzymes accounts for most of the pheromones in Lepidoptera", he espouses a new model for antennal pheromone olfaction, wherein a high concentration (20 mM) of a low-affinity binding (carrier) protein in the sensillum liquor permits rapid migration of the pheromone molecule to the binding site on the dendritic membrane. A second player in this system is a high-affinity degradative enzyme which can clear excess pheromone within the sensillum in a matter of milliseconds, consistant with the time course of electrical events observed in electrophysiological studies of insect antennae.

Baker's paper makes several additional points which are germane to other papers in the present Review. He points out that 'attraction' – displacement through space – is really the end result of a series of behaviors. The control of upwind flight in the presence of a pheromone plume is one example of a series of behaviors contributing to what superficially appears as a single behavior (attraction). The hierarchy of behaviors associated with host acceptance and the maintenance of feeding is another example. As is the case for insect gustation, sensory adaptation (synonymous with habituation) in the olfactory reception of pheromones has been observed.

It is becoming readily apparent that natural *blends* of chemicals are important in insect chemical ecology. Again drawing data from the study of lepidopteran sex pheromones, Baker contrasts two models for the perception of blends. In the original model, it was proposed that each component of a pheromone blend elicits a specific stage in the overall behavior; the predominant component of the blend would elicit long-range attraction while the minor component(s) would elicit sequential behaviors. However, Baker points out that recent data favor a Gestalt-type model based on across-fiber neural integration. Synergism of components in insect attraction, both for pheromones and for oviposition attractants from plants [6], may be the rule with few exceptions. Finally, male moths frequently require both visual and olfactory stimuli to maintain upwind flight toward a pheromone source; combinations of sensory modalities are also important in host-finding by insects.

The emerging field of 'pheromone biochemistry' is introduced in the paper by Prestwich et al., the senior author being one of the leading investigators in this area. They describe detailed investigations of pheromone metabolism (an integral part of the model for olfaction outlined in Baker's review) in the antennae of three moth species; in the case of the diamondback moth they report that esterase enzymes capable of metabolizing this insect's pheromone occur throughout the body, unlike the male-, antennal-specific enzyme found in the polyphemus silk moth.

Prestwich et al. discuss the development of reactive analogues of insect pheromones – the acyl fluorides. These "specific enzyme-targeted pheromone mimics", which act by irreversibly modifying the binding or receptor proteins or by interfering with the pheromone degrading enzymes, provide an important example of biorational design of selective pest control agents.

In addition to reviewing and assimilating a vast literature on the chemical ecology of bark beetles (Scolytidae), Byers outlines a series of hierarchial levels for research in chemical ecology. In the case of bark beetles, the step-by-step progression (in chronological order, but exemplifying many investigations in insect chemical ecology) starts with the observation of insect behavior (attraction to host trees) followed by identification and quantitation of the relevant semiochemicals (in this case both from the host and from the insect) to determination of the mechanisms for synthesis, release and perception of the semiochemicals. Continued study of a single system can ultimately lead to a synthesis of knowledge to obtain a working theory of how the semiochemicals mediate the host-insect and insect-insect interactions.

The author provides detailed models for the regulation of attack density for several scolytid species, and also discusses interspecific interactions through which beetles avoid competition or, alternately, locate trees weakened by attack from another species. Despite the scope of his review, Byers indicates that there is much yet to investigate in this system, such as the "under the bark" interactions between beetles which are poorly understood at present.

Turning to insect chemical defense, Malcolm and Brower demonstrate how analysis of natural products in populations of insects, the cardenolides sequestered by monarch butterfly larvae from their host milkweeds and stored in the adult butterflies, can give insight into patterns of host plant utilization on a continental scale. They have found that northerly migrating monarchs exploit three key milkweed species in the southern U.S., producing offspring which are well defended chemically and thus able to continue dispersing northward where the summer host species is abundant over a broad geographical range. Even though the summer host does not contain high levels of cardenolides, sequestration of these plant-derived defenses is optomized by the insect on this host, ensuring that sufficient numbers of butterflies escape predation to reach the overwintering sites in central Mexico. Thus, a thorough examination of plant and butterfly chemistry has provided further insight into the evolution of migration in this insect.

Exocrine defensive chemistry in the leaf beetles (Chrysomelidae) is the focus for the paper by Pasteels et al. Particularly noteworthy in this group, and in contrast to the monarch-milkweed alliance, is the fact that several leaf beetle species contain cardenolides in their defensive glands, even though these compounds are not found in the beetles' host plants. The authors review their studies which demonstrate that the beetles synthesize cardenolides de novo from cholesterol, using the same biosynthetic pathway seen in plants. Most beetle species contain simpler defensive chemicals which have amino acids as precursors. However, some species also appear to sequester their defensive chemicals, e.g. pyrrolizidine alkaloids, from plants, although the authors suggest that sequestration may be a recent adaptation in evolutionary time.

The ten papers in the present Review represent a wide range of experimental approaches and an even more diverse array of insect taxa under investigation. Nonetheless, there are some common themes which serve to unite these investigations under the umbrella of insect chemical ecology.

The plasticity of insect behaviors in response to natural chemicals is an important phenomenon which underlies the ecology mediated by those chemicals. We know, for example, that sensillae have the ability to habituate or adapt to a constant stimulus in seconds or minutes. Additionally, there is evidence that environmental factors may indirectly influence the responses of insects: sensillar performance may be modified by endocrine or neural inputs reflecting the internal state of the insect. Thus there may frequently be physiological underpinnings for behaviors which are not simply the result of the stimulus-receptor interface in the peripheral sensory apparatus of the insect. These possibilities need to be recognized by those who design bioassays aimed at quantifying insect response to chemicals.

With increasing frequency, we are finding that insects respond to subtle blends of chemicals, often in cases where the behavior was previously ascribed to a single chemical or the predominating component in a mixture. Synergy in the response of insects to semiochemicals is probably widespread [7], although antagonism can certainly occur [8]. If, as McLuhan [9] states, the medium is the message, then for insects, the message may often be *multimedia*.

A further caveat to those entering the discipline of chemical ecology is to recognize that natural chemicals can have multiple interspecific roles, and therefore the labelling of a chemical as a pheromone, allomone or kairomone is *context-specific* (i.e. specific to the interacting species). A plant chemical can simultaneously be an attractant and a repellent, depending on the insect. In the extreme, substances which are clearly toxic to many organisms (e.g. the non-protein amino acid, L-canavanine) may serve as a nutrient to a highly adapted species [10].

I hope that following an examination of the papers in the present Review, the reader will be left with the impression that although significant progress has been made to date in the field of insect chemical ecology, even the best explored systems have considerable room for advancement. Although research in this field (as in many) appears to raise more questions than it answers, it remains, for investigators from several disciplines, an exciting and satisfying avenue for future study.

1 Metcalf, R. L., Ferguson, J. E., Lampman, R. L., and Anderson, J. F., Dry cucurbitacin containing baits for controlling Diabroticite beetles (Coleoptera: Chrysomelidae). J. Econ. Ent. *80* (1987) 870–875.
2 Ferguson, J. E., and Metcalf, R. L., Cucurbitacins: plant-derived defense compounds for Biabroticina (Coleoptera: Chrysomelidae). J. Chem. Ecol. *11* (1985) 311–318.
3 Blaney, W. M., Schoonhoven, L. M., and Simmonds, M. S. J., Sensitivity variations in insect chemoreceptors; a review. Experientia *42* (1986) 13–19.
4 Abisgold, J. D., and Simpson, S. J., The effect of dietary protein levels and haemolymph composition on the sensitivity of the maxillary palp chemoreceptors of locusts. J. exp. Biol. (1988) in press.
5 Bernays, E. A., Evolutionary contrasts in insects: nutritional advantages of holometabolous development. Physiol. Ent. *11* (1986) 377–382.
6 Nishida, R., Ohsugi, T., Kokubo, S., and Fukami, H., Oviposition stimulants of a *Citrus*-feeding swallowtail butterfly, *Papilio xuthus* L. Experientia *43* (1987) 342–344.
7 Berenbaum, M. R., Brementown revisited: interactions among allelochemicals in plants. Rec. Adv. Phytochem. *19* (1985) 139–169.
8 Isman, M. B., Toxicity and fate of acetylchromenes in pest insects, in: Pesticides of Plant Origin, Eds J. T. Arnason, B. J. R. Philogene and P. Morand. American Chemical Society Symposium Series (1988) in press.
9 McLuhan, M., and Fiore, Q., The Medium is the Message. An Inventory of Effects. Bantam Books, New York 1967.
10 Rosenthal, G. A., Hughes, C. G., and Janzen, D. H., L-canavanine, a dietary nitrogen source for the seed predator, *Caryedes brasiliensis* (Bruchidae). Science *217* (1982) 353–355.

0014-4754/89/030300-03\$1.50 + 0.20/0