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Insect chemical ecology

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Introduction

M. B. Isman

Department of Plant Science, University of British Columbia, Vancouver (British Columbia V6T 2A2, Canada)

Chemical ecology is the science of the inter- and intraspecific interactions between organisms that are mediated by naturally occurring chemicals. As a discipline which has emerged and stands in its own right, chemical ecology has seen an exponential growth in research activity in the past two decades, fueled largely by dramatic improvements in the capability and ease of microanalysis and structural elucidation of natural products.

It is a dozen years since Duffey[1] pointed out that 'chemical ecology' as a term is syntactically inappropriate: chemicals do not have an ecology per se. The influences which chemicals exert on organisms (e.g. attractiveness, toxicity) are extrinsic properties, rather than intrinsic ones (e.g. volatility, solubility). I raise this issue because it may be time to assess the direction that contemporary research into chemical ecology is following. Have the technological improvements in the study of natural products chemistry created an imbalance between the chemical and ecological aspects of this field? Jones[2] has recently made a plea "... for the explicit inclusion of more ecology" in chemical ecology, suggesting that the interactions (i.e. the ecology) have taken a 'back seat' to the chemistry (the mediators of the ecology). He argues that the chemical aspects may be enjoying the majority of the research effort because the chemistry "... is discrete and quantifiable, and is often manipulable". In support of his argument, he points out that of 305 papers published in the Journal of Chemical Ecology (the only journal to date solely dedicated to the discipline) in 1985 and 1986, only 12% dealt primarily with ecological aspects of the systems investigated.

Prof. J. B. Harborne avoided such criticism by entitling his widely accepted text "Introduction to Ecological Biochemistry"[3], tacitly implying that the emphasis from his perspective was on the chemistry, or more correctly, the influence (extrinisic properties) of natural products on organisms. However, he too has occasionally fallen into the trap of using the term 'chemical ecology', when the emphasis is clearly on the chemicals rather than the ecology[4]. In spite of this problem of syntax, I will hereinafter refer to 'insect chemical ecology', rather than create further confusion by erecting a novel title to describe the field.

The present Review focuses on insect chemical ecology for two reasons. Firstly, research within the domain of chemical ecology has and continues to be dominated by studies involving insects. Of the 121 papers published in the Journal of Chemical Ecology in the first half of 1988, 68% documented interactions in which chemicals eminated from or influenced insects. Similarly, at a Gordon Research Conference on the 'Chemistry of Plant Herbivore Interactions' held in 1986 at Oxnard, California, 77% of the presentations dealt with insects.

The second reason for focussing on insects in the present Review, and that which simultaneously explains the pattern of research emphasis indicated above, has to do with the nature of insects themselves. With over one million species described to date, and undoubtedly many millions more undescribed, insects are the champions of adaptive radiation in the evolutionary sense. They possess, even from the few species examined in any detail, numerous strategies for utilizing natural products as messengers (e.g. mate attractants, feeding cues) and for avoiding the potentially deleterious effects of natural toxins. The incredible diversity of insect responses to natural products has resulted in difficulty in identifying common themes or creating robustly predictive models within the discipline.

Central to the study of chemical ecology are "semiochemicals", which by definition (from the Greek semeon, a mark or signal) mediate interactions between organisms[5]. Semiochemicals can be conveniently subdivided into the pheromones, substances which function intraspecifically, and allelochemicals, which function interspecifically. This dichotomy exists not only at the level of terminology, but is also, somewhat unfortunately, evident with respect to research directions. Research into the significance of pheromones has been dominated by the study of sex attractants; the use of such chemicals as a tool for monitoring pest populations (particularly in the Lepidoptera) has been an important impetus. Nonetheless, the study of insect pheromones has had a profound impact on our understanding of neurophysiology and behavior. Much of the progress in this regard can be attributed to technical improvements in electron microscopy and neuronal recording techniques, allowing us to directly observe the minute sensory organs of insects, and in studies of single cell recording, providing a glimpse of the crucial transduction of a chemical signal into an electrical one.

Scientific literature dealing with allelochemicals has been dominated by two lines of inquiry: the influences of plant chemicals on insects, and the chemical defenses of insects. It should come as no surprise that insect-plant interactions occupy much of the foreground in the study of insect chemical ecology. Higher plants synthesize a bewildering array of 'secondary metabolites' – substances not known to have a direct role in primary metabolism. For decades these unusual chemicals were thought of as waste products of little or no significance to the plants producing them; scientific interest in such chemicals centered on their use as taxonomic markers. However, Fraenkel[6], Thorsteinson[7] and others pointed to the role (postulated by Stahl a century ago) of plant secondary metabolites as cues for the relative acceptability of plants to insects, or conversely, as defensive agents against herbivory. Over 20,000 such chemicals have been identified to date: the number awaiting structural elucidation may be two or three times that. Thus in insects and plant secondary metabolites we have two examples of extreme adaptive radiation (in the broadest sense), which serve to create a vast, richly textured interface for ecological and evolutionary relationships mediated by chemistry.

Both the pheromone and allelochemical 'camps' have charted their progress over the past two decades through various multi-authored volumes[3,5,8–11]. Particularly noteworthy is the volume edited by Rosenthal and Janzen[12], which though only a decade old, is considered somewhat of a classic in the field of insect chemical ecology. A more recent volume edited by Bell and Cardé entitled "Chemical Ecology of Insects"[13] serves as a milestone in that it synthesizes the mechanistic approaches common to the study of both pheromonal and allelochemical-based interactions.

In organizing the present Review I have not attempted to duplicate such a synthesis, but have chosen authors who could provide an indication of the current state of the art in the field of insect chemical ecology. Papers by Chapman and Bernays, Renwick, and Berenbaum and Isman underscore a theme central to the study of allelochemicals, namely the role of plant chemicals in the acceptability of plants as hosts to phytophagous insects. The influence of plant allelochemicals on feeding, oviposition and dietary utilization are reviewed, with frequent comparisons made between insect taxa. Metcalf and Lampman review the alliance of diabroticite ('cucumber') beetles with their cucurbit host plants, providing a strong case-in-point where chemistry links families of plant taxa and insect taxa.

Turning to pheromone research, Baker presents a masterful review of chemical communication in the Lepidoptera, encompassing behavioural, chemical, and physiological studies. Prestwich and co-workers give a detailed account of research on the olfactory receptors of insects – the primary physiological interface between the pheromones themselves and behaviour. Byers provides a comprehensive review of the chemical ecology of one particular insect family – the bark beetles – an example where both pheromones and allelochemicals are requisites for the successful utilization of host trees by the insects. McNeil and Delisle examine the search for the oft sought after, but rarely documented link between host plant volatiles and insect pheromones.

The final two papers deal with the evolution of insect chemical defenses. Malcolm and Brower document the case of the monarch butterfly, in which the chemicals are obtained from the host plant, and sequestered into the butterfly for protection against avian predators. Pasteels and co-workers examine the evolutionary pattern of chemical defenses in leaf beetles, a group of insects including taxa which obtain defensive chemicals from their host plants as well as those which synthesize defensive chemicals de novo.

No collection of ten papers can provide a complete overview of the field of insect chemical ecology. However I hope that the reader will benefit from the differing approaches taken by investigators – from the detailed dissection of the chemical ecology of particular taxa, to the examination and analysis of the chemical and biological processes which are common to all chemically mediated interactions between insects and other organisms.

Each of the contributions has been subjected to peer-review. I thank both the reviewers and authors for their conscientious efforts aimed at making the papers more easily understood by non-specialists. However, the field of chemical ecology, like other interdisciplinary arenas of research, is guilty of developing its own jargon which can be a barrier to the uninitiated. In particular, I hope that readers will not be deterred by the technical descriptions of the many chemicals which lack trivial names, and will see beyond them to the rich biology which follows.

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Insect behavior at the leaf surface and learning as aspects of host plant selection

R. F. Chapman and E. A. Bernays

Department of Entomological Sciences and Division of Biological Control, University of California, Berkeley (California 94 720, USA)

Summary. Direct observations on the feeding behavior of insect herbivores are uncommon, but important. The important aspects of host-plant selection by phytophagous insects that have been revealed by such observations are the role of chemicals in the leaf surface, and learning. There are few detailed reports of behavior at the leaf surface, but these indicate that many, if not all, insects exhibit behavior patterns that can be interpreted as an examination of the quality of the surface and acceptance or rejection may follow without further testing. A number of experiments show that chemicals from the leaf surface commonly contribute to the acceptability or otherwise of a plant and in most cases so far the active chemicals are of widespread occurrence, not having a specific association with the host plant. Some experiments show that the association between surface chemicals and plant palatability is learned, but in other cases there is evidence of an innate response. Habituation to deterrent chemicals has been demonstrated in the laboratory, but not in the field. Food aversion learning also occurs and may be important in dietary switching by polyphagous insects.
Key words. Behavior; learning; leaf surface; wax, insects; food selection; secondary compounds.

It is generally accepted that the food selection behavior of phytophagous insects is largely governed by the distribution of secondary chemicals in plants. Much of the evidence for this is based on experiments that record the outcome of an insect's behavior, commonly in terms of the amount eaten, but only rarely is the behavior itself described. This is probably unimportant in the development of certain evolutionary concepts, but for a proper understanding of the role of chemicals in insect ecology a fuller knowledge of the behavior is necessary. One reason for this is that the instantaneous behavior of an insect that leads it to accept or reject a particular plant may not be reflected in observations of the amount eaten after an interval. For example, on the basis of long-term feeding studies, it has become generally accepted that the range of host plants within the Solanaceae eaten by the Colorado potato beetle, *Leptinotarsa decemlineata,* is governed by the distribution of alkaloids. The tomato glycoalkaloid tomatine is one that has a deterrent effect[29]. However, infusing tomatine into potato leaves has no effect on the size of the meal taken when the beetles first encounter the leaves, even though beetles of this same strain do not eat tomato[28]. In a second example, in 6-h choice tests with larvae of the armyworm, *Pseudaletia unipuncta,* there was no evidence that nicotine had any deterrent effects, but on first encounter with nicotine-treated leaf material rejection was much more frequent than in controls[52]. It is apparent that in the field the relationship of the insects to plants containing these chemicals might not be what we would expect from the results of long term laboratory studies.

Direct observations are needed for a proper understanding of the behavior of the insects as it affects ecology, and in the past few years two areas of general interest have emerged as a result of such behavioral studies. These are: first, the importance of leaf-surface chemicals and, second, the role of learning in host-plant selection by phytophagous insects. These two topics will be briefly reviewed.

The effects of leaf-surface chemicals on behavior

The role of chemicals on the leaf surface in host-plant selection has previously been reviewed by Chapman[18]