The Chemistry of Coevolution

Herbivores. Their Interaction with Secondary Plant Metabolites. GERALD A. ROSENTHAL and DANIEL H. JANZEN, Eds. Academic Press, New York, 1979. xvi, 718 pp., illus. $59.50.

This volume is unique among collections of papers dealing with plant-herbivore coevolution in that it focuses specifically on the ecology of plant defensive chemistry. The editors have divided the book into two parts. The initial eight chapters, grouped under the heading Ecological and Evolutionary Processes, treat topics such as cost-benefit analyses of defensive chemical production, adaptive regulation of secondary metabolism, detoxification mechanisms, and host plant recognition. The second section of the book is chemically oriented. Each of its 12 chapters is devoted to the chemical and biological properties of a particular class of secondary metabolites. In terms of subject matter, this division is natural. In tenor and in spirit, however, the book is divided along different lines: the authors of four chapters attempt to synthesize the diffuse literature on herbivores and plant secondary compounds by providing evolutionary hypotheses and ecological explanations for patterns of allelochemic distribution, whereas the remaining 16 chapters are solid reviews of the chemistry and physiology of secondary compounds that do not provide much new insight into the ecological interactions between plants and herbivores.

The authors of the four synthetic chapters address, with varying degrees of success, several common themes. Rhoades, McKey, Janzen, and Chew and Rodman appear to agree, for example, that plants evolve to increase their investment in defensive compounds until the marginal increment of cost just balances the marginal increment of benefit gained. Beyond this truism, the insights provided by these authors lie in their discussions of the cost-benefit equations underlying this process. Chew and Rodman approach this topic by attempting to calculate the energetic costs associated with the production of three different classes of secondary compounds: cyanogenic glycosides, glucosinolates, and nonprotein amino acids. Their analysis, however, is not convincing. A result typical of their calculations is that 2-butylglucosinolate requires 11 more ATP and four more $NADH_2$ molecules for synthesis than does the cyanogenic glycoside lotaustralin. The validity of such a result is highly suspect. The production costs of these compounds involve so many factors left out of the analysis, including energy used for enzyme production and for compartmentalization of end products as well as the potential for recovering energy through catabolism of secondary metabolites, that the costs calculated by the authors for the two compounds may bear no relationship to the actual costs. Moreover, little can be inferred about defensive allocation from the calculations. The use of energy as a currency for measuring costs is questionable when little is known about the factors limiting the growth and survival of plants producing the compounds analyzed. As Janzen points out in his chapter, only by comparing in a herbivore-free environment the fitnesses of plants producing different quantities of a particular secondary compound can the production costs of these compounds be validly assessed.

McKey approaches the problem of costs and benefits from a different perspective, one that is both more enlightening and more firmly grounded in the biology and chemistry of secondary compounds. His discussion focuses on two factors that constrain the types of compounds plants can employ for defense. On the one hand, he demonstrates that avoidance of autotoxicity may introduce metabolic costs in addition to those involved in biosynthesis and that these added costs may render certain types of compounds prohibitively expensive under some circumstances. On the other hand, he shows that in many instances the costs associated with a particular allelochemic may be related to its effectiveness against herbivores. Secondary metabolites that are easily glycosylated for transport within a plant or are easily broken down to permit recovery of energy or nutrients are relatively susceptible to detoxification by herbivores. By contrast, the properties that make secondary compounds refractory to detoxification also render them less easily translocated by a plant and less easily catabolized to yield energy and nutrients used for plant growth.

These considerations lead quite naturally into McKey's discussion of a second common theme of these papers, the distribution of allelochemics among different parts of a plant. McKey's basic premise is that trade-offs between internal physiological constraints and protection from herbivore damage vary for different classes of secondary metabolites and for different tissues within a plant. Because of this variation, different classes of compounds are used to meet different defensive contingencies. Although somewhat speculative, his arguments admirably explain patterns such as the common occurrence of condensed tannins in bark and wood, the prevalence of toxic amino acids and lipids in seeds, and the frequent restriction of seed toxins to the seed coat.

Rhoades also discusses the allocation of chemical defenses to various plant tissues. Borrowing from a theme expressed in an earlier paper by McKey, he asserts that a plant's allocation of defensive compounds to a particular tissue or organ should be proportional to the value of that structure to the plant. Although this suggestion appears reasonable, Rhoades clouds his discussion by offering only unconvincing speculation to support it. At one point, for example, he asserts that the value of a plant part to a terrestrial macrophyte decreases in the order roots, stems, young leaves, mature leaves, and reproductive structures; yet the only justification offered for this statement is the weak contention that "each structure in this gradient is totally dependent on the function of each of the previous structures."

Other common themes addressed in these four chapters include the temporal patterning of allelochemic production, the effects of stress on plant defensive chemistry, and facultative reactions of plants to herbivore attack. McKey consistently offers the most comprehensive and incisive treatment of these topics, though he is a bit repetitive at times. Janzen quite effectively outlines many unanswered, and even unasked, questions about plant-herbivore interactions. He provides few answers, but to provide answers is not his purpose; rather, his chapter should serve as a guide for researchers entering this field of study. Apart from their unsuccessful attempt to calculate energetic costs for secondary compounds, Chew and Rodman provide a sound review of the plastic responses of plants to environmental stress, including herbivory. Rhoades's contribution is the least satisfying of the four synthetic chapters, perhaps because he relies too heavily on ad hoc hypotheses and reasoning. At the very least, however, his suggestions about optimal defense should stimulate others to examine the defense strategies of plants in more detail.

Of the remaining 16 chapters, 12 treat individual classes of secondary compounds, and the other four are devoted to mechanisms of avoidance of autoxicity by plants, perception of secondary compounds by animals, detoxification mechanisms, and the effects on herbivores of the interaction between allelochemics and host nutrients. These 16 chapters share several features. Each is an exceedingly thorough review. Each is concerned primarily with physiological processes such as the biosynthesis and degradation of secondary metabolites and the mechanisms involved in toxicity and repellency to animals. Most provide substantial introductions to the methods used in studying those processes. Though most are also about as stimulating to read as an organic chemistry text, the book succeeds in its primary goal of providing a comprehensive reference and useful source book for students and researchers in the field of plant-herbivore biology.

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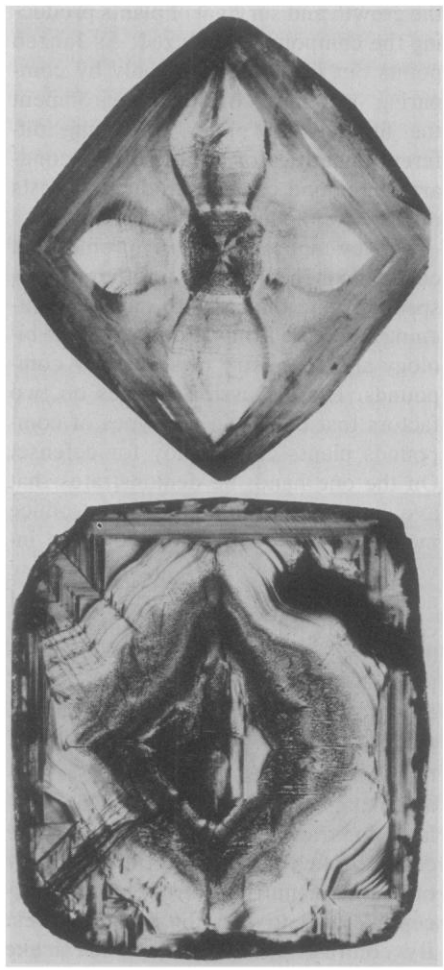
Diamonds

The Properties of Diamond. J. E. FIELD, Ed. Academic Press, New York, 1979. xvi, 674 pp., illus. $67.25.

This book is a natural and timely successor to the 1965 book *Physical Properties of Diamond* edited by R. Berman. The new book is justified by the tremendous amount of research that has been done since 1965. For example, the growth of high-quality single crystals of diamond under controlled chemical conditions has cleared up many of the questions about the elements that can go into the diamond lattice substitutionally and the spectroscopic, electrical, and mechanical effects of the foreign elements. New studies of fluorescence phenomena have brought out significant patterns of layers and domains that suggest that what appears to be an isotropic perfect crystal actually was subjected to different chemical and physical conditions during its growth. New work on strength, friction, and wear characteristics has led to a better understanding of the mechanical properties of diamond. The new book also goes beyond the coverage of the earlier one in including chapters on the geology and the synthesis of diamond and the applications of diamond in science and industry.

The authors of the 20 chapters are associated mainly with universities and research organizations in England and South Africa, and much of the work reported is a result of fruitful cooperation between the DeBeers diamond organizations and various universities in the United Kingdom. Some of the material in the book has already been published in journals.

The chapters of the book are arranged in seven groups. The first group consists of five chapters on thermal, optical, electrical, nuclear, and cathodoluminescence properties of diamond. A chapter on theory deals with attempts to understand the structure and properties of the diamond crystal lattice, both pure and with atomic-scale impurities. Two chapters on the surface properties of diamond deal with adsorbability and with surface profiles and effects. The mechanical properties of diamond are covered in chapters on strength and fracture, adhesion and friction, abrasion and wear, indentation hardness, effects of high temperature, and internal structure. Two chapters on growth cover the physics and chemistry of diamond growth and the technology of diamond synthesis. Two chapters on geology treat the geology of diamond-bearing rocks and the geologic information yielded by the inclusions within natural diamond crystals. The last two chapters of the book deal with industrial abrasive uses of diamond and with the use of diamond in, for example, optical windows, heat sinks, bearings, and electrical devices.



X-ray topographs of crystals that exhibit a center-cross etching pattern. The cross results from "epochs of mixed-habit growth in which normal growth on flat octahedral facets was accompanied by non-faceted growth on hummocky surfaces whose orientation approximated to {100} only in the mean. (The growth surfaces in the latter category are termed 'cuboid'.)" (Top) "Central section of a centre-cross diamond which well exemplifies a smooth variation in ratio of rate of growth on cuboid surfaces to that on {111} facets." The height of the specimen, apex to apex, is 5 mm. (Bottom) "A very complex centre-cross structure with discontinuities in relative rates of growth on cuboid surfaces and on {111} facets." The height of the specimen section is 3.8 mm. [Photographs by Suzuki and Lang, reproduced in *The Properties of Diamond*]

One important form of synthesized diamond, the sintered diamond compact or aggregate, is treated only briefly. Such compacts have been fabricated and marketed since the early 1970's and are used in a wide variety of industrial and scientific tools. More coverage of this kind of diamond would have been appropriate in the book. On the whole, though, the subjects treated in the book have been very well covered, and any person who works with diamond should have the book available.

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Roots

The Soil-Root Interface. Proceedings of a symposium, Oxford, England, Mar. 1978. J. L. HARLEY and R. SCOTT RUSSELL, Eds. Published for the *New Phytologist* by Academic Press, New York, 1979. xx, 448 pp., illus. $32.50.

Increasing interest in roots is not confined to genealogists and their sort. Plant and soil scientists have made plant root systems a major subject of research, as the number of recent books and conference reports on the subject attests. The papers in this volume were presented at a symposium attended by 122 participants from 13 countries. The volume contains 32 papers read in full as well as abstracts of 34 additional papers offered by participants.

The book has something for almost everyone and much too much information for any single individual to assimilate. The root-soil interface is a complex region that has a structure and function all its own but that cannot be studied independently of the soil or of the plant. It