BOOK REVIEWS

Plant Defenses

Phytochemical Induction by Herbivores. DOUGLAS W. TALLAMY and MICHAEL J. RAUPP, Eds. Wiley-Interscience, New York, 1991. xii, 481 pp., illus. $98.

Damage by herbivores can elevate levels in plants of defensive chemicals that can reduce herbivory, thereby affording protection to the plant. This type of response to the attack of herbivorous insects has fascinated entomologists, ecologists, evolutionary biologists, and plant breeders for more than 20 years, but it became a major research topic only in the 1970s. Some of the questions of immediate interest were and still are: What types of defenses are being induced? What levels of induction of defenses normally occur? How long do induced changes persist? What effect does induction have on herbivore fitness and population dynamics? Do changes in herbivore survival or fecundity in laboratory or field trials translate into changes in herbivore population sizes? Does induction increase plant fitness? *Phytochemical Induction by Herbivores* brings together a large portion of the literature on this topic and provides important reviews of the various major systems that have been studied. This volume of 17 chapters is divided into three sections that consider the chemical responses of plants to herbivore attack, the impact of induced chemicals on herbivores, and the agricultural implications of induction. Most of the chapters provide summaries of their authors' specific research systems. The book as a whole is the most comprehensive source of information on the subject of induction.

Two of the contributors to this volume have earlier provided clear definitions of induction (R. Karban and J. H. Myers, *Ann. Rev. Ecol. Syst.* **20**, 331 [1989]). An *induced response* is any change that occurs in a plant in response to a biotic or abiotic stress. *Induced resistance* is an induced response that reduces the fitness of herbivores or pathogens, and an *induced defense* is when induced resistance can be demonstrated to increase plant fitness. Acceptance of this clear set of hierarchical definitions will be beneficial to the study of induction, and although to one extent or another the contributors to this volume follow these definitions, it would have been helpful to have them stated as succinctly in this book as they originally were by Karban and Myers.

It is assumed that induction is an evolved trait of plants that reduces damage when herbivores are present and reduces the fitness costs of defense when herbivores are absent (as compared to costs of constitutive defenses, those maintained regardless of immediate circumstances). To be considered an adaptation induction should be an active response to challenges by herbivores or pathogens, not just a passive deterioration in plant quality. A distinction is often drawn between short-term induction (also known as rapidly induced responses), which occurs over a time range of minutes, hours, or days, and long-term induction (delayed induced responses), which occurs over seasons or years. A number of chapters deal primarily with short-term induction (Baldwin; Tallamy and McCloud; Raupp and Sadof; Hartley and Lawton; Edwards *et al.*; Wolfson; Raffa; Kogan and Fischer; Benedict and Chang; Karban), and generally they find evidence for induced resistance in attacked plants or plant parts (but see Hartley and Lawton). Short-term induction may have evolved as antiherbivore responses, but evolution of induction as a defense against pathogens may be even more likely (Hartley and Lawton, Kogan and Fischer). Whether long-term induction is an active, evolved response to herbivory or a passive change in plant physiology due to nutrient stress or juvenilization is debated in this volume. If numbers of chapters are any indication of the trend of opinion, then the latter hypothesis tends to have more support. Chapters by Toumi *et al.*, Bryant *et al.*, and Myers and Bazely argue that the changes in plants that are defoliated by herbivorous insects or mammals can be best explained as passive consequences of altered nutrient levels for concentrations of phytochemicals or as altered age structures of plant parts that are normally associated with higher levels of constitutive defenses. Neuvonen and Haukioja show that long-term defenses can have large effects on herbivores but that available evidence supports elements of both active and passive defense models. Even if long-term induction is best explained as a passive decrease in plant quality and not an evolved response of plants it will be important to know what effects it has on herbivore populations.

Induction of defenses is presumed to have evolved because allocation of resources to defense only when a plant is being challenged by herbivores is less costly than maintaining higher levels of constitutive defenses. Under this scenario plant genotypes able to mount induced responses would have higher fitness in herbivore-free environments but would have nearly equal fitness when herbivores are present. Thus the issue of whether defenses are costly to the plant is key to understanding the evolution of induction. Baldwin addresses the issue of whether induction of nicotine in tobacco is costly. He shows that induced plants have lower lifetime fitness than noninduced plants because of increased levels of nicotine. In one estimate of these costs, Baldwin estimates that an increase in nicotine of only 1% dry leaf mass can result in a reduction of half a million seeds. Clearly, high constitutive levels of nicotine in tobacco would be prohibitive and induction has been favored. Baldwin's work on tobacco is some of the most carefully controlled work currently being performed on induction. Though these studies indicate that defenses may be costly, they still do not address other essential evolutionary questions: Is there additive genetic variation in inducibility in natural populations? and Are inducible genotypes more fit over the range of variation in herbivore levels found in nature than are genotypes with only constitutive levels of defense? Although several chapters of this volume mention the importance of plant genotype in generating variation in inducible responses (Coleman and Jones, Karban, Benedict and Chang, Kogan and Fischer), none investigate the extent of genetic variation in induction in natural populations. Recently Zangerl (*Ecology* **71**, 1926 [1990]) and Zangerl and Berenbaum (*Ecology* **71**, 1933 [1990]) have demonstrated within- and between-population variation in induction of furanocoumarins in wild parsnip and in one population found heritable variation for induction. The ecological and evolutionary importance of genetic variation in induction will clearly become a focus of research, and this book does not deal with that issue.

Studies of induction, particularly in natural systems, have produced highly variable results. Just about every imaginable source of variation that affects plants also affects induced responses. Environmental variation (for example in light, nutrients, or water), within- and between-plant variation (population, genotype, ontogeny, phenology, leaf age, phyllotaxy), timing, extent, location, and cause of damage, and species of herbivore and the timing of its encounter with the induced tissue all gen-

erate variation in the induced response. This variation might be enough to cause one to despair that induction could ever be successfully understood. A number of chapters in this volume provide detailed accounts of how the authors either did or did not successfully traverse this obstacle course of variability. Two chapters (Coleman and Jones, Faeth) provide general reviews of major causes of variation that deal with plants and affected herbivores. Coleman and Jones found that about two-thirds of the studies they reviewed showed some evidence of induced resistance, but what they found most striking was the lack of control for a wide range of plant variables that are known to affect induced responses. In particular, plant genotype was neither manipulated nor controlled in most studies. Several chapters (Coleman and Jones, Hartley and Lawton, Faeth) stress that different herbivores can respond very differently to induced plant responses; some herbivores can even benefit from induction (Tallamy and McCloud). The message that I take away from this book is that to determine whether induced responses of plants are defensive, a combined understanding of the physiology of the host plant, of the role of genetic and various environmental variables, and of the responses of different species in the herbivore and pathogen community will be required. Together the chapters of this volume call for a new high standard of experimental control for future induction studies.

The chapters in this volume are mixed in their effectiveness. A sharper editorial pen would have improved the reasoning in a couple of chapters and would have shortened others. These faults do not take away from the importance of this book as the new starting place for researchers beginning to work on induction, however. It is a valuable reference and source of some unanswered questions.

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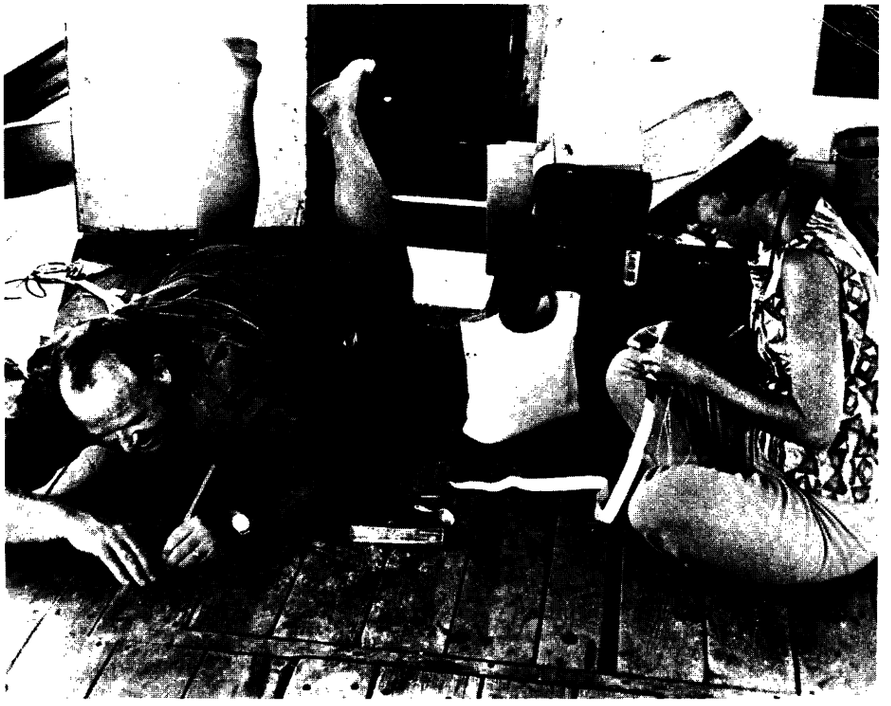
Marine Subjects

Dolphin Societies. Discoveries and Puzzles. KAREN PRYOR and KENNETH S. NORRIS, Eds. University of California Press, Berkeley, 1991. viii, 398 pp., illus. $34.95.

Cetaceans and their adaptations to an aquatic medium are unique among mammals. Furthermore, the animals are notoriously hard to observe, either directly or



"Early days of dolphin research. Editors Kenneth S. Norris and Karen Pryor on the deck of a fishing boat in Hawaii in 1966, creating an instrument belt for a trained dolphin to wear during open ocean diving tests. Odds and ends from the hardware store were used to make a belt with a rachet on it, which was supposed to measure how much the animal's chest compressed during a dive. Unfortunately, the dolphin got so much smaller in circumference, even during relatively shallow dives, that it usually came back with the belt around its tail." [From *Dolphin Societies*; photo by Harry Grodzhinsky for *Life* magazine]

with instruments. Hence compilations of work on the group are eagerly awaited, especially when they come, as this one does, from well-established workers in the field.

Rather than offering a thorough review of current work on dolphins, the editors here present a selection of what they consider to be pivotal studies woven together by informative essays on the development of this field. Their stated purposes for compiling this work are to inspire readers with the inventiveness of dolphin study methods, demonstrate the value of studying captive dolphins, and generally dispel various popular myths and misconceptions about both dolphins and dolphin research.

The book has three main sections, devoted respectively to studies of dolphins in the wild (seven chapters), analysis of teeth in the laboratory (two chapters), and studies in captivity (four chapters). Of the 13 data-oriented chapters, six present previously unpublished material and seven are new reviews of work already in the literature. Each section has one or more essays by the editors. There is no general summary in which the results are welded together into a unitary view of dolphin life.

The book clearly shows the difficulty of studying these mammals and the dedication of those who do it. Bel'kovich studied dolphins from horseback; Pryor and Schallenberger dove among dolphins captured in tuna purse seines, calmly quantifying social structure while lookouts protected them from sharks; Wells dedicated 20 years to studying a single population and concludes that it is still not possible to describe the mating system.

Three of the chapters deserve special mention because they suggest promising directions for the field in the near future. Würsig *et al.* describe a study that compares social structure of two dolphin species in both shallow- and deep-water environments in a kind of two-by-two analysis. This work shows the power of the comparative method to reveal broad-scale adaptations within a family. Wells's chapter shows that when studies do focus on single species a diversity of approaches yields the greatest in-depth information. His group links behavioral observation with selective captures to collect data on age, sex, hormone levels, and genetic markers. This approach produces more data on herd social dynamics, kinship, and survival than any other approach has. Finally, Herman's chapter on cognition and information processing shows the value to cetacean studies of applying principles developed in other disciplines, in