

Preface

Leaves are highly abundant and important biological units and are the foundation of the terrestrial limb of the global carbon cycle. But their principal function to capture and reduce carbon, coupled to their often delicate structures, makes them vulnerable to predation. Why, then, wherever there is enough water for plant growth, are leaves so abundant? In other words, how do leaves defend themselves from myriads of herbivores? This book is meant to be a broad, non-exhaustive introduction to leaf defences against leaf-eating vertebrates and invertebrates, and is written for anyone with an undergraduate training in biology. It has been my intention to avoid producing a reference work in which all the possible defence mechanisms used by leaves are listed. Moreover, with one or two exceptions, the defences of roots, flowers, seeds, and fruits are not discussed. The idea is to concentrate on leaf defences and to do this by combining two complementary outlooks: one from my professional life as an experimental molecular biologist, the other reflecting an interest in observational field biology. The writing reflects this. In a few places a more formal text gives way to anecdotes that describe leaves or leaf eaters in various parts of the globe; these are recounted in the first person. Throughout, I have tried to use an evolutionary approach without which much of nature's great beauty, both in the field and in the laboratory, is lost on me.

The book is organized so that it moves from macroscopic aspects of leaf defences towards the molecular level. That is, after a general introduction on leaves, herbivores and the extent of herbivory, the text then transitions from the impact of plant growth and form on defence through to the plant's use of specialized defence cells and, finally, to the molecular mechanisms of defence. Then, after a section on wound-inducible leaf defence mechanisms I turn to some of the partnerships between plants and the organisms that protect them. Towards the end of the book I examine anachronistic plant defences—those defence traits that show us how plants defended themselves from leaf eaters that no longer exist. Anachronistic defences have been studied in depth on several island groups, most notably on New Zealand and Hawaii. However, for some of the botanically rich islands in the Indian Ocean the story is different and we do not know whether plant-eating animals existed on certain islands prior to human arrival. In the search for these biological ghosts I use the last main chapter in an attempt to interpret putative anachronistic defences on Socotra, an island off the coast of Yemen. In making this journey to and from the laboratory and the field I have tried to place emphasis on botany, which for me is as much an appreciation of individual plant species as it is of plant families. So, as much as is possible, I mention families of plants. In most cases this is not intended to mean that the family is unique, but there are some families that seem to be more creative in their use of defences than others. Inevitably, those that I particularly like get more than their fair share of attention.

A difficulty related to this is that the field of taxonomy is, at present, moving fast. The names of genera change quickly and some family names disappear altogether. An effort has been

made to keep things up to date, although this can sometimes be awkward. This is, for example, the case when it comes to acacias, many of which have been reclassified from *Acacia* to *Vachellia*. I try to strike a balance between the new and the old here, often keeping acacia as the vernacular name (particularly when African plants are discussed).

At the outset I'd like to acknowledge several books that have been both useful and inspirational: M.J. Crawley's *Herbivory: The Dynamics of Animal-Plant Interactions*, (Blackwell, 1983); J.B. Harbourn's *Introduction to Ecological Biochemistry*, 4th edition (Academic Press, 1993); Richard Karban and Ian T. Baldwin's *Induced Responses to Herbivory* (University of Chicago Press, 1997); *Induced Resistance to Herbivory*, edited by Andreas Schaller (Springer, 2008); Schoonoven, van Loon, and Dicke's *Insect-Plant Biology*, 2nd edition (Oxford University Press, 2005); and Dale Walters' *Plant Defence: Warding off Attack by Pathogens, Herbivores, and Parasitic Plants* (Blackwell, 2011). This later book contains an up-to-date synthesis of the various theories of plant defence, a subject only briefly touched on herein. For field trips I have used and been inspired by several field guides including Jonathan Kingdon's *The Kingdon Field Guide to African Mammals* (Academic Press, 2001), R.D. Estes' *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates* (University of California Press, 1992), and John Kricher's *A Neotropical Companion* (Princeton University Press, 1997).

Now to the people who have helped me gain experience in biology. I owe, first and foremost, a great deal to the late Clarence ('Bud') Ryan to whom I was drawn in order to enter the fascinating field of plant-herbivore interaction and to search for regulatory molecules underlying inducible defence responses. Another person who both influenced and encouraged me was the late Meinhard Zenk. With Bud Ryan's support I was able to glimpse my first tropical forests in Brazil and Costa Rica, and Meinhard Zenk paved the way for an extended visit to New Caledonia where I was generously accommodated at the Institut de Recherche pour la Développement (IRD) in Noumea. For this, for some fascinating glimpses of the New Caledonian flora, and for much discussion, I'm particularly grateful to Tanguy Jaffré and Maurice Schmid. Vincent Dumontet organized a memorable field trip and I thank Yves Létocart and the staff of the 'Parc de la Rivière Bleue' for their generous help. I benefited from the company of Douglas Tallamy in Brasil and E. Durant McArthur in Utah and I owe a great deal to Brian Barlow, William (Bill) Foley and Andrew Krockenberger for nurturing my interest in the Australian flora and fauna. In New Zealand I thank Ian Payton, Mat McGlone, and David Glenney for a series of rewarding field trips, William Russell (Bill) Sykes for stimulating discussions, and Mary Korver for generous help in identifying and shipping specimens. Concerning Socotra I'm indebted to Anthony (Tony) G. Miller and Lisa Banfield, both from the Royal Botanic Garden Edinburgh (RGBE), for their help and plant identifications and for much useful discussion, to Ahmed Saeed Suleiman for his assistance in the field, and to Kay van Damme for useful advice. Follow-up work at RGBE for the Socotra trip was financed by a European Union Synthesis grant and facilitated by Alan Forrest, Sabina Knees, and John Mitchell. My thanks also go to Khaled Al-Rasheid, Ahmed H. Al Farhan, and their colleagues at King Saud University in Saudi Arabia for their support in organizing a field trip to south-western Saudi Arabia and the Farasan Islands. Tim Blackburn, also on this trip, kindly shared

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For certain more molecular aspects I have drawn on my own laboratory's research which has been supported by the Swiss National Science Foundation, The University of Lausanne, King Saud University (Riyadh), and the Leenaards Foundation. I also gratefully acknowledge support from the European Molecular Biology Organization and the European Union for financing postdoctoral fellowships in my laboratory. The section on jasmonate signalling and the origins of herbivory is condensed from the 2009 Loomis lecture that I gave at Iowa State University. Some of the other content is from lectures given at the University of Lausanne and elsewhere. I thank the members of my own laboratory at the University of Lausanne, past and present. In particular, I'm grateful to Johann ('Hans') Weber and to Philippe Reymond for their help running the laboratory while I was consumed with the task of being departmental director. It is a great pleasure to acknowledge the support of my long-serving and excellent technicians Aurore Chételat and Stéphanie Stolz. Others in Lausanne have provided useful insights. Among these people are Lionel Maumary, Alia Malfi, Roland Keller, Daniel Cherix, Laurent Keller, and Philippe Christe.

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for valuable criticism of parts of the manuscript. Inevitably, trying to bring both laboratory results and field observations together results in some sections being superficial and, of course, each and every mistake and misinterpretation is my own. For this I apologize, as I do to colleagues whose work was not cited.

Edward E. Farmer
Lausanne, Switzerland