Signaling and Communication in Plants

Jorge M. Vivanco Tiffany Weir *Editors*

Chemical Biology of the Tropics

An Interdisciplinary Approach



Signaling and Communication in Plants

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Chemical Biology of the Tropics

An Interdisciplinary Approach



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Preface

I first set foot in the Tambopata National Reserve (TNR) in Peru in June 2006. I had assembled a team of colleagues and students from Colorado State University to accompany me on an exploratory expedition to establish collaborative ties with Peruvian researchers and to familiarize ourselves with the countless opportunities to study chemical ecology in a tropical field setting. For years, I had been studying chemical interactions between organisms in a laboratory. I had published numerous papers on the interactions that occur between plants and other soil-dwelling microorganisms. Then one day a colleague criticized me for defining nature through my office window, and as stung as I was by this observation, I realized that he was right. I had yet to venture outside the safety and comfort of the laboratory to see how my expertise could be applied in the field, and I made it a goal of my sabbatical to broaden my scientific horizons. Serendipitously, an old friend from high school was working at the Field Museum in Chicago and decided to pay me a visit at the same time that I was planning my sabbatical to Peru. He had spent several years working as a free-lance guide in the Amazon, and particularly in the TNR, and shared stories and slides that inspired me to focus my sabbatical research in this incredibly biodiverse area. During the planning stages of my sabbatical, I learned of the work of Drs Eric Cosio and Waltraud Kofer from the Pontificia Universidad Catolica del Peru in Lima, who are proponents of tropical chemical ecology in Peru and who had created a successful research enterprise between their university and a private lodge in Tambopata. Collaboration was formed and my venture into tropical chemical ecology began to materialize.

That muggy June morning as I pulled on my rubber boots and drenched myself with insect repellant in preparation for my first hike in the TNR, I was not sure what I was looking for or what I expected to find. Our guide introduced us to the strangler figs, trees that germinate in the canopy of a host tree and grow downward, eventually engulfing and smothering their host with a massive tangle of fused roots. We saw the castaña, or Brazil nut trees, giants of the jungle who provide a livelihood to so many indigenous families, and the walking palms that are said to use their stilt-like root system to crawl across the jungle floor seeking open spaces where they can harvest the sunlight. Birds with brilliantly colored plumage peeked out of nest holes and flocked to pick at the clay on riverbanks, socializing and neutralizing toxins accumulated from their diet of plants, which produce these chemicals to defend themselves against the barrage of herbivores that they encounter daily. Monkeys screeched and howled overhead while insects crawled down below, but the things that truly captured my attention were the ants. Meandering trails of army and leaf cutter ants criss-crossed our paths. Lone bullet ants, as big as my thumb, crawled up trees. Ground-dwelling ants had constructed piled up mounds of dirt that were nothing less than mini-metropolises crawling with activity. However, what interested me the most were the specialized adaptations that numerous plant species had developed to accommodate these ants. On that first hike I watched ants feeding from nectaries on *Inga*, encountered heart-shaped domatia of the *Tococa* plants, and felt the bite of the *Pseudomyrmex*, the aggressive patrollers of the *Triplaris* trees. How specific were these ant-plant interactions and what was the basis of the recognition of an ant for a particular plant species? Despite the attention that has been given to studying ant chemistry and ecology, there are still many unanswered questions. I now knew what would be the focus of my sabbatical research.

My wife, a microbiology graduate student at that time, also accompanied me on this trip, and as one might expect, her attention was drawn in a completely different direction. She would impatiently flick the ants off her clothing while focusing her camera lens on the numerous fungi that we encountered on our trek. Her academic pursuits concentrated on the chemical communication between microbes and how plants can contribute or interfere in those conversations, and she was drawn to the idea of studying the incredible microbial diversity of this forest and decoding how some of the chemical signals used by microbes translate into functional microbial communities. She has since began pursuing these studies and her enthusiasm for conducting research in the rainforest matches my own, making her an integral member of my research team, as well as the co-editor of this book.

Although many people are drawn to the rainforest, the research that is done there has largely remained ecological. It is not often that those who are trained in chemistry or molecular biology and typically work in controlled laboratory environments with highly expensive and technical equipment wander out into the jungle and try to untangle the tight web of organismal interactions. We had a steep learning curve to climb if we wanted to make this opportunity successful. Some of the issues we faced were technical. For instance, it is difficult to relocate forest plots marked with fluorescent green tree ties (pink or red work much better), and you should always use rainproof sample labels. A good sense of direction (or a good GPS) is critical; stepping a few yards off the trail could leave a lab-dwelling researcher hopelessly disoriented. Of course, the most important thing we learned was an appreciation for the complexity of this ecosystem, and how important it is to reach beyond our comfort zone (and reach out to those who work outside of that zone) if we want to advance our understanding of it. It was from this lesson that the Pan-American Studies Institute (PASI) – Chemical Biology in the Tropics was born.

The PASIs are symposia funded by the National Science Foundation (NSF) designed to foster collaborations between researchers and institutes in North and

South America. Although the primary goal of these symposia is to bring together international researchers in a given discipline, I wanted to stretch that concept to bring together researchers from very different disciplines. Many of the workshop invitees had never visited or worked in the tropics, but I believed they had special knowledge and skills to contribute to a better understanding of tropical ecosystems. Our final list of participants included landscape and restoration ecologists and seasoned tropical biologists, but it also incorporated microbiologists, analytical chemists, cancer researchers, and plant physiologists. While I had hoped that the different disciplines would complement one another and that individuals would form collaborations that would result in new ways to look at old questions, the actual culmination of the PASI far exceeded my expectations.

Perhaps the success of the PASI was due to the outstanding group of participants assembled, or maybe it was the lack of electricity in individual rooms, which drove everyone to congregate in the lodge after 5 pm to discuss the day's topics over a beer and plan night hikes and collecting trips. Whatever the reason, it was a transformative experience for many of our colleagues, particularly those who had pledged themselves to a life in the laboratory; and many new collaborations and friendships were forged. This book is a product of those interactions, and our goal is to share the beauty and intricacy of tropical forests with a broader audience while introducing some of the interdisciplinary ideas that contributed to the success of the PASI. We have assembled a group of scientists to write chapters that ignited their interest in the tropical forests, and the final product is a book that includes general information on chemical ecology and biodiversity, a few first-hand accounts of the triumphs and trials of working in a tropical forest, and some informative essays detailing interesting ecological phenomena. It is our hope with this book to convey our excitement about this field of research to a broader audience and to provide incentive to a new generation of scientists to travel to the tropics and to use their ingenuity to understand species interactions. A deep understanding of this system is needed in order to preserve it. Ecologist and conservationist have done research in the tropics for decades and have helped to develop a global understanding of the functioning of this system. We now need another breed of scientists who can successfully work in interdisciplinary teams to explore how molecules and genes influence community structure and ecosystem functioning and ensure the preservation of these resources for generations to come.

Finally, I would like to thank everyone who made this book a possibility. I want to dedicate this book to all of the participants of the 2008 PASI – Chemical Biology in the Tropics; organizing this conference and participating in it has been by far the most collegial and satisfying academic experience in my career. It is because of your excitement and enthusiasm for the subjects presented here that this book was compiled. I would especially like to thank Mark W. Paschke, Margaret Lowman, Aaron Dossey, Caroline S. Chaboo, Dan Manter, Tiffany Weir, Waltraud Kofer, Art Edison, Stephan Halloy, and Eric Cosio for contributing to chapters in this book. I want to acknowledge Emily Wortman-Wunder who took care of much of the stateside planning and logistics for the PASI and also contributed to the writing of this book. Thank you to Max Gunther, the owner of Rainforest Expeditions, whose business vision included a place where research and tourism combine to advance the appreciation, understanding, and ultimately the conservation of one of our planets' greatest resources; and to the staff of the Explorer's Inn, especially the management and our numerous knowledgeable guides, for making our experiences there thoroughly educational and enjoyable. I also want to acknowledge my friend, Guillermo Knell, for igniting my passion for the Amazon rainforests. Finally, thank you to the Guggenheim and Fulbright Foundations for funding my research during my sabbatical, to the NSF for their support of the PASI and other research/educational experiences in TNR, to the Pontificia Universidad Catolica del Peru, and especially Dr. Eric Cosio for hosting my stay in Peru and providing logistic and technical assistance in initiating my tropical studies.

Fort Collins, CO, USA April 2011 Jorge M. Vivanco

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Biodiversity

Emily Wortman-Wunder, Jorge Vivanco, and Mark W. Paschke

Abstract This chapter provides a framework for the rest of the book, by defining biodiversity, describing techniques to measure biodiversity, and listing the Earth's biodiversity hotspots as identified by Norman Myer. The chapter then gives a brief discussion of theories of the causes of biodiversity, starting with the earliest theories, published in the 1960s, and ending with the most recent theories explaining various regional areas of biodiversity, several of which are controversial. Finally, the chapter concludes by exploring possible future directions of biodiversity research, and notes the importance of incorporating a more thorough knowledge of the chemistry underlying ecological interactions in areas of high biodiversity.

1 Introduction

In early August 1993, a young woman limped into a remote settlement in southwestern Ecuador (Sullivan 1993). She had hiked 5 miles through dense jungle on a broken ankle, and she was the bearer of bad news: she had survived a plane crash that killed her fiancé, the ornithologist Theodore Parker, the botanist Alwyn Gentry, and the ecologist Eduardo Aspiazu, along with two other Ecuadorians. The conservation

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world reeled in shock: Parker and Gentry were naturalists of the first order. Between the two of them they possessed over two-thirds of the unpublished knowledge of Latin American biodiversity – knowledge that had now been destroyed in a single crash. Furthermore, they died conducting critical aerial surveys of biodiversity for Conservation International's Rapid Assessment Program (RAP). This program, founded by Parker and Nobel prize-winning Dr. Murray Gell-Mann, was just a few years old and had been designed to help assess the flora and fauna of biodiversity "hotspots" to identify crucial areas for conservation. Their death was a blow to the program and an even greater blow to the world of international conservation. Furthermore, the loss of so much of the world's biodiversity knowledge in a single event made clear its vulnerability.

That the flora and fauna changes with location on Earth is one of the pillars of the ancient art of travel writing; most observers over the millennia have also noted that certain areas teem with more abundance than others. However, it took fear of this abundance being stamped out to prompt humans to coin a term for it, biodiversity, and to make a serious attempt to catalog and study it. The study of biodiversity centers on three basic questions: how do you measure biodiversity, what places on earth are most biodiverse, and why do some places have more biodiversity than others?

2 Measuring Biodiversity

How to measure biodiversity? The earliest counts of biological diversity were simply that: counts of the number of plant and animals (usually birds and mammals) divided by area. Botanist Alwyn Gentry's landmark 1988 study of tree species in the upper Amazon is a typical example: he cordoned off a hectare of Peruvian rainforest and proceeded to count all the tree species found there (Gentry 1988). Early assessments of biodiversity based on this type of species count identified tropical rainforests as the areas of highest biodiversity levels, and based those assertions on numbers of plants and vertebrate animals. Entomologists later cried foul (Stork 2007); so did biologists of marine environments, in which birds, mammals, and vascular plants tend to be underrepresented (Roberts et al. 2002; Myers et al. 2000). Microbial biologists came late to the table (Nee 2004), and to some extent are still trickling in: the first methodical study of microbial diversity across latitudinal gradients was completed only in 2006 (Fierer and Jackson 2006). Its surprise conclusion that bacterial diversity is actually far higher in temperate zones has recently been called into question. New methods for finding and counting bacteria and fungi in a sample demonstrate one of the basic problems of biodiversity counts: after a certain point, it is not possible to manually count that many species, or even, in some cases, to recognize them. Not even the most assiduous beetle collector is going to be able to recognize all 350,000 estimated beetle species, for example. The world's most compendious ornithologist, Theodore Parker, was thought to be able to recognize some 4,000 bird species, a mere fraction