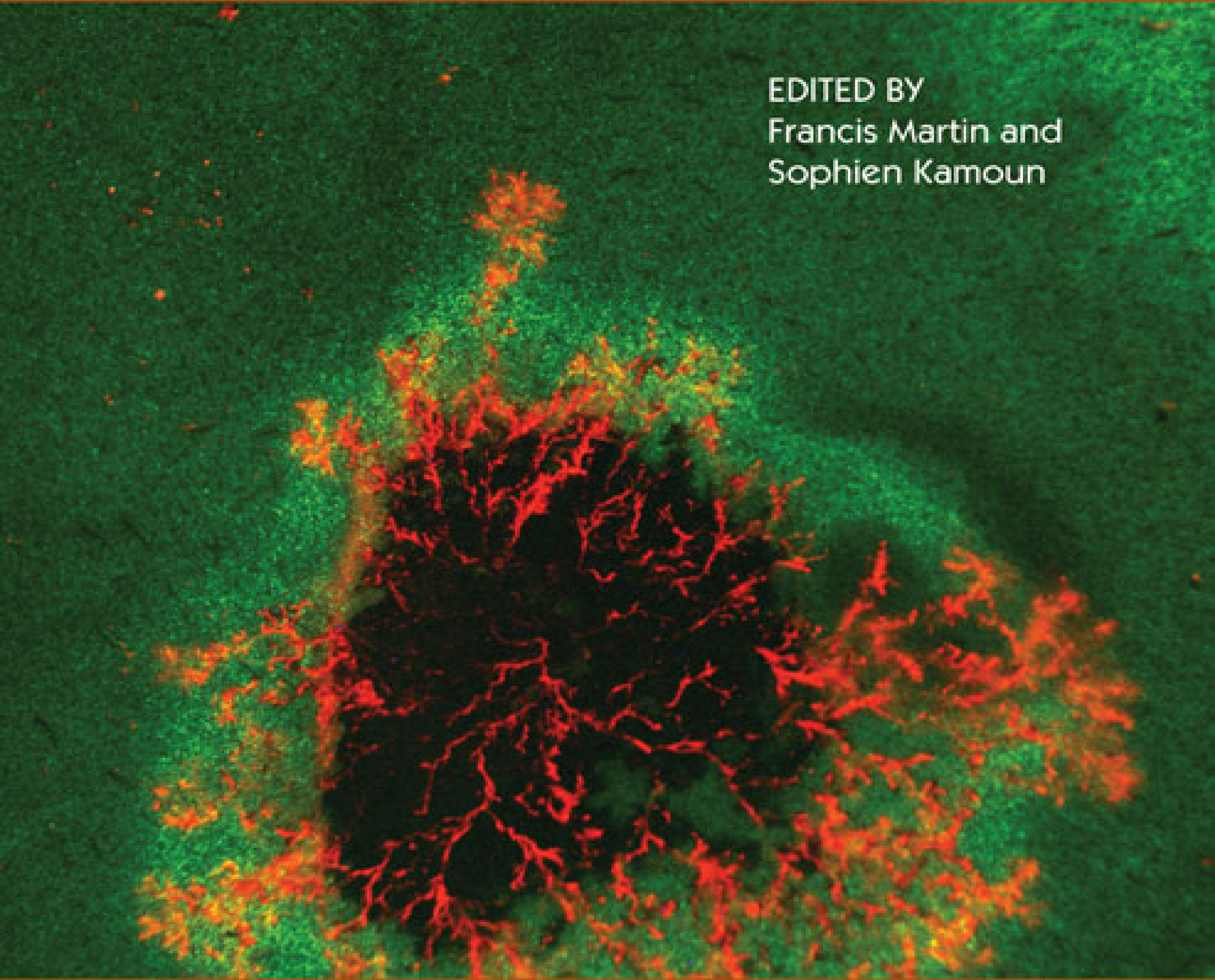
EFFECTORS IN PLANT-MICROBE INTERACTIONS



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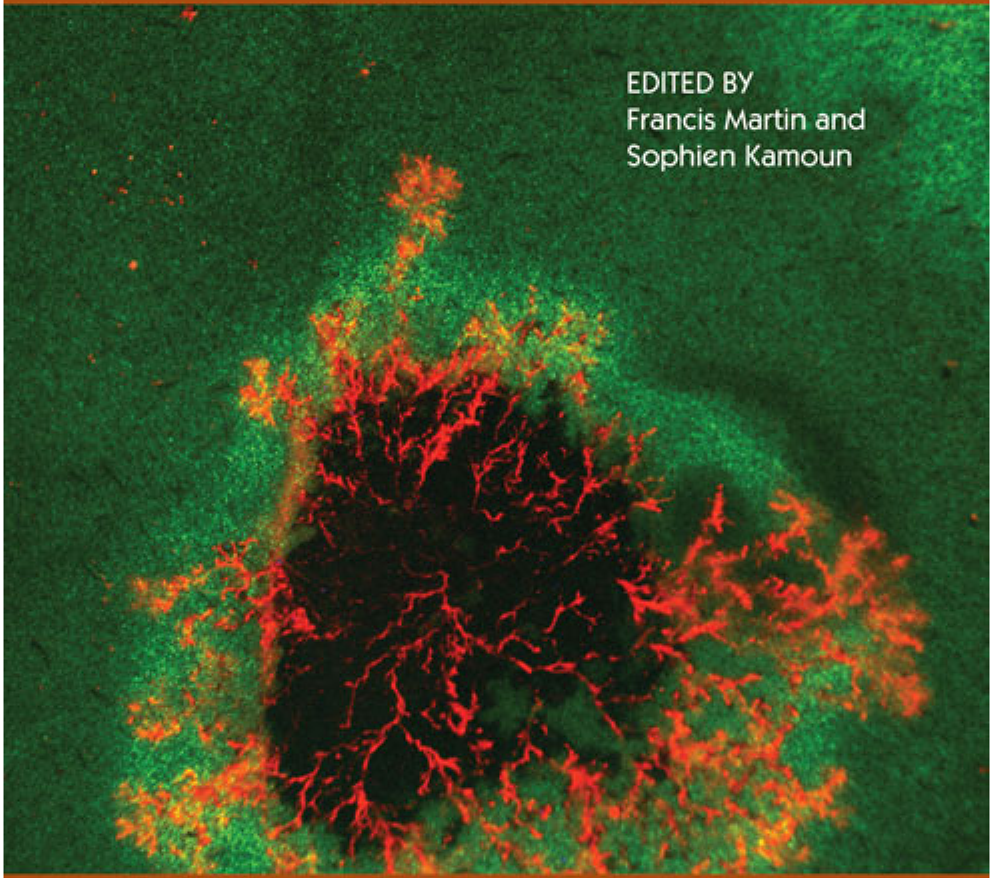

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Foreword

Effectors in Plant–Microbe Interactions: Past to Present

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The basic understanding of why a phytopathogen can cause disease on only a few species of any particular plant has long intrigued plant pathologists. In fact, if one looks at all the potential disease-causing agents of plants, the ability of a pathogen to cause disease is often the exception as most plants are able to recognize and actively defend themselves against most pathogens in nature. Early work by E.C. Stakman at the University of Minnesota in early twentieth century established the concept of the “physiological race” of a single species of rust (Stakman, 1914). He demonstrated that physiological races derived from the sexual cycle of *Puccinia graminis* gave rise to distinct strains that varied in their ability to cause disease when inoculated on various wheat varieties. This observation was critical to the concept that resistance to cereal rust pathogens was race specific and that knowledge of the genetic variation in rusts was essential to the successful breeding for disease resistance. It was then Harold Flor in the 1940s with his work on flax rust who provided a genetic explanation for Stakman's “physiological race” concept (Flor, 1942). His work established that single gene differences in both the host and pathogen controlled whether a flax rust strain caused disease on a particular cultivar of flax. Building on these prior observations and work by Al Ellingboe along with the discovery of recombinant DNA and gene cloning, I set out with Douglas Dahlbeck and Noel Keen in the early 1980s to clone a gene that defined the “physiological race” that Stakman and Flor had previously described and genetically characterized. The cloning of an “avirulence” gene from a *Pseudomonas syringae* pv. *glycinea* race established that a single gene in the pathogen controlled whether this bacterium caused disease on a particular cultivar of soybean (Staskawicz et al., 1984). In this case, the avirulence gene was recognized as a single resistance gene in soybean. However, it was not until several years later that it was established that these so-called avirulence genes also played a major role in the virulence of the pathogen. This was accomplished once methods had been established for performing site-directed gene mutations in phytopathogenic bacteria such that isogenic strains could be constructed and evaluated on hosts that did not contain the cognate resistance gene. Mutations in the *avrBs2* gene resulted in lower bacterial growth populations on pepper plants that did not contain the cognate *Bs2* gene (Kearney and Staskawicz, 1990). Once it was established that avirulence genes could be isolated in this manner, it was not long before several more examples were published. The concept that avirulence genes also had a role in virulence was further strengthened by the discovery that the “*Hrp*” gene in *Xanthomonas, Ralstonia*, and *Pseudomonas* turned out to be highly homologous to the type three secretion systems genes that had been earlier established in animal bacterial pathogens (Fenselau et al., 1992; Gough et al., 1992). Since the medical field used the term “effector protein” to describe proteins that were delivered via the bacterial type three secretion systems, phytopathologists also adopted this term to be consistent with the medical field. Since the original discovery of phytopathogenic effectors, it has become apparent that all classes of plant pathogens employ effectors to either modulate or suppress plant innate immune functions (Dodds and Rathjen, 2010). Since the field has rapidly expanded over the last 5 years, the publishing of this book is timely as it brings together a wealth of information and points of view on a wide range of pathogen effectors. There is no question that we have learned a great deal about the mode of action of pathogen effectors to date, but this field is in its infancy and surely will flourish in the years to come. The combination of molecular, cellular, genomic, and structural studies will be paramount to this effort. As for the future, the sequencing of field isolates of naturally occurring pathogens will shed new light on pathogen diversity and will provide novel insights into the evolution and function of pathogen effectors in agricultural systems. This, in turn, will greatly benefit the deployment of durable disease-resistance strategies to control disease in an environmentally sustainable manner. One can only hope that translational approaches will be employed to solve important disease problems that are currently present and for new diseases that will emerge in the future.

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Preface

Every single plant in nature is closely associated with mutualistic microbes, particularly fungi and bacteria. In addition, plants are repeatedly attacked by a multitude of pathogens and pests, including bacteria, fungi, oomycetes, nematodes, and insects. Deciphering how plants interact with both mutualistic and parasitic microbes is central to understanding their biology. One could almost argue that plant biology should be viewed as a subdiscipline of plant–microbe interactions. Identifying the plant–microbe cross talks is also crucial for a better understanding of the processes regulating the complex interactions between entangled plant and microbial communities in ecosystems.

The field of plant–microbe interactions has significantly matured in recent years. All major classes of molecular players both from plants (surface and intracellular immune receptors) and microbes (microbial pattern molecules and effectors) have now been revealed. This book focuses on effectors, secreted microbial molecules that alter plant processes and facilitate colonization. Effectors are central to our newly integrated view of plant–microbe interactions. Effectors have evolved to facilitate parasitism, for example, by suppressing host immunity in a variety of ways. However, they can also “trip on the wire” and activate plant immune receptors, a response known as effector-triggered immunity. These are complex interactions and the coevolutionary dynamics between plants and microbes have left striking marks in their genomes. Our goal was to take stock of current knowledge on effectors of plant-associated organisms and illustrate the diverse and complex ways in which effectors interact with their host plants.

The book opens with general reviews on plant immunity and how it is targeted by microbial effectors (Chapters 1 and 2). The field of effector biology has greatly benefited from genome-wide analyses, which result in complete catalogs of effector genes. Chapters 3–5 report on genome-wide analyses and evolution of effectors genes. These chapters nicely illustrate how comparative genomics greatly contributed to our understanding of effector evolution. Chapters 6–8 describe how effectors function in suppressing host immunity and how they are perceived by plant immune receptors. How effectors traffic inside plant cells is covered by Chapters 9 and 10. Finally, the closing Chapters 11–15 cover emerging topics. Effectors have been reported in a number of plant–microbe systems, including bacterial and fungal symbioses, as well as nematode and insect pests.

Effector biology is a new and fast-paced field of research. As with all emerging fields of science, consensus among researchers has not always been reached and some topics remain controversial. Readers will surely notice more than one example throughout the book. We elected to keep such “inconsistencies” rather than enforce an arbitrarily sanitized version. We hope that such differences between authors will be informative of the current dynamic state of our science.

Books may have become less fashionable in the age of tweeting and microblogging. However, we hope that there is value in a document that summarizes the current state of the field of effector biology and provides a handy complement to the literature for both novice and experienced scientists.

Francis Martin and Sophien Kamoun