The Ecology of Plant Secondary Metabolites
From Genes to Global Processes

Plant secondary metabolites (PSMs) such as terpenes and phenolic compounds are known to have numerous ecological roles, notably in defence against herbivores, pathogens and abiotic stresses, and in interactions with competitors and mutualists. This book reviews recent developments in the field to provide a synthesis of the function, ecology and evolution of PSMs, revealing our increased awareness of their integrative role in connecting natural systems. It emphasises the multiple roles of secondary metabolites in mediating the interactions between organisms and their environment at a range of scales of ecological organisation, demonstrating how genes encoding for PSM biosynthetic enzymes can have effects from the cellular scale within individual plants all the way up to global environmental processes.

A range of recent methodological advances, including molecular, transgenic and metabolomic techniques, are illustrated and promising directions for future studies are identified, making this a valuable reference for researchers and graduate students in the field.

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Although chemical interactions between plants and other organisms had been documented many years previously (e.g. Stahl, 1888; Verschaffelt, 1910), it was the seminal work of Fraenkel published in 1959 that placed the ecological function of plant secondary metabolites (PSMs) onto the agenda of modern ecology. He recognised that PSMs are not merely a repository for plants’ waste products, but rather they had a primary function: they could act as defences against enemies such as phytophagous insects. Crucially, he also realised that these enemies exert a selection pressure on the plants to defend themselves. Since then, numerous ecological roles of PSMs have been elucidated, notably as defences against a broad range of herbivores and pathogens, as mediators of interactions with competitors and mutualists, and as defence against abiotic stress. Recently, emerging developments have taken us well beyond consideration of PSMs in the context of simple interactions between pairs of species. Our view of plant secondary metabolites has shifted significantly in the past 50 years and we now understand the subtlety and scale of their effects, which cross trophic levels, spread throughout ecosystems, and even affect global processes. At the same time, methodological developments, particularly in the ‘omics’ technologies, have led to a greater understanding of the synthesis and regulation of PSMs. These methodological developments now also facilitate unique tools for the targeted manipulation of both the synthesis of PSMs and their ecological function independently of other phenotypic effects. Consequently, we are now in a position to assess the extent to which PSMs and their effects traverse natural systems from genes upwards, and, in the spirit of Fraenkel, the reciprocal effects of the biotic and abiotic environment on those genes. This is, therefore, the ideal time to take stock of our current understanding of the function, ecology and evolution of PSMs, in order to focus our future efforts to use this knowledge to best effect in science and its application.

This volume arises from a British Ecological Society Symposium entitled The integrative roles of plant secondary metabolites in natural systems which was held in 2010 at the University of Sussex, UK. It reviews recent scientific developments and provides a new synthesis of the function, ecology and evolution of PSMs that
takes account of recent advances in our awareness of their integrative roles in connecting natural systems. The roles of PSMs span from the molecular to the global: genes control their synthesis, PSMs communicate responses within plants to external conditions and damage, PSMs define interactions with other individuals of their own and other species, and their effects cascade through communities and ecosystems to global processes. Uncovering the evolution of these complex multi-functional, multi-trophic, multi-scale systems goes hand in hand with the potential to manage and exploit them. This is the new challenge for the study of the ecology of plant secondary metabolites in an era that has been facilitated, and will be further developed, by application of exciting recent methodological advances including genomics and metabolomics.

This volume, consisting primarily of invited contributions, does not try to incorporate examples of all types of PSM, cover all biomes or revisit the well-trodden path of interactions between pairs of species. Instead it focuses on areas of where new ideas are currently developing, including our greater understanding of allocation and distribution of PSMs within plants and their effects under changing environmental conditions. Some of these are drawn together in a synthesis chapter, which also identifies some cross-cutting themes and future research directions, including the costs of PSMs, evolutionary and phylogenetic considerations, methodological advances and effects on multiple components within communities or ecosystems. The authors of the individual chapters explicitly point the way for development of research required within their own domain. For the purposes of organisation and logical flow, the contributions to the symposium were grouped into themes, but, given our emerging view of PSMs as integrators, we felt it was inappropriate to include such boundaries within the published volume. Interestingly, the distribution of symposium contributions revealed a relative lack of studies spanning the full range of scales from ‘genes to communities or ecosystems’. This suggests that few research groups are able to attempt to integrate across levels of ecological organisation, and those that do attempt this difficult task have no option but to focus on one of a small set of study systems for which we have sufficient knowledge to permit this type of work. This seems one area where more ambitious approaches would be both welcome and fruitful. Increased collaboration between ecologists and researchers from other biological disciplines, such as plant physiology, cell biology, pathology and developmental biology, would also generate novel insights into the multiple roles of PSMs in all facets of plant and ecosystem biology.

We are particularly indebted to the authors of the chapters, and to all those who contributed to the symposium and to this volume. We thank the numerous anonymous reviewers of the chapters (they know who they are!), the Editorial Board of Ecological Reviews, and Cambridge University Press. We hope with
their assistance to have moved towards a greater understanding of the multiple roles of PSMs, from genes to global processes.

References

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