CHAPTER ONE

The integrative roles of plant secondary metabolites in natural systems: a synthesis

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1.1 Introduction

Since Fraenkel (1959) recognised that plant secondary metabolites (PSMs) were not simply plant waste products but served to defend them against insect herbivores, numerous ecological roles for these intriguing compounds have been established, notably as defences against a broad range of herbivores and pathogens, but also as mediators of interactions with competitors and mutualists, and as a defence against abiotic stress. A single compound can influence multiple components within an ecological system, and can have effects that act across many different scales. Add to this the huge diversity of PSMs that have now been characterised, and the possible interactive effects among them, and it is clear that PSMs either individually or as groups can no longer be considered only in the context of interactions between the plant and a single other species. They are now recognised as major contributors to the bridge between genes and ecosystems, because (context-dependent) gene expression patterns influence the phenotype of a plant. The effects of PSMs are now known to affect community dynamics and to cascade through ecosystems, driving their composition and function and acting as agents of their evolution (e.g. Whitham *et al.*, 2006). Here, we summarise the key points and emergent themes from the chapters in this book and provide a synthesis of the recent developments in the ecology and evolution of PSMs, illustrating how a range of approaches, including molecular, transgenic and metabolomic techniques, have brought us to the cusp of a new understanding of their integrative roles in ecosystems.

1.2 Distribution, allocation and evolutionary selection for PSMs

The chemical diversity of PSMs, combined with the number and complexity of potential biotic and abiotic interactions in which they are involved, has

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hitherto prevented these systems being predictable beyond the outcome of the strongest, pairwise and most well defined of these interactions. However, several recent developments are moving us towards a better understanding and predictability of the roles of PSMs in more complex systems.

The concept of costs has featured highly in our attempts to understand the temporal patterns, distribution and occurrence, and physiological limitations to the synthesis of PSMs (Rhoades, 1979, 1985; Herms & Mattson, 1992; Gershenzon, 1994; Jones & Hartley, 1999). We are now aware of the circumstances under which trade-offs among investment in PSMs and evolutionary fitness-determining characteristics apply (e.g. Siemens *et al.*, 2002; Dicke & Baldwin, 2010). The strong genetic framework for consideration of the effects of PSMs, supported by the use of natural or genetically selected or manipulated variation, paves the way for the study of their mediating roles in biotic and abiotic interactions via the fitness of plants, a currency in which both costs and benefits of PSMs can ultimately be measured (this volume: O'Reilly-Wapstra *et al.*, Chapter 2; Gershenzon *et al.*, Chapter 4; Iason *et al.*, Chapter 13; Schuman & Baldwin, Chapter 15). We are beginning to understand how PSMs and their effectiveness as defences vary across different ontogenetic, phenological and life cycle stages of plants (Iason *et al.*, 2011; O'Reilly-Wapstra *et al.*, Chapter 2; Koricheva & Barton, Chapter 3). Clear patterns emerge, with PSM concentrations increasing during the seedling stage followed by declines during leaf phenological stages. Although the underlying selective forces are often unclear (Koricheva & Barton, Chapter 3), the question is raised as to whether and to what extent selection for PSMs can act by transfer of evolutionary pressures across different life stages of plants, or between different plant tissues. We know that the complement and concentration of PSM in a particular tissue can be generated elsewhere in the plant and altered by signalling pathways (Baldwin & Ohnmeiss, 1994; van Dam, Chapter 10) and can vary markedly between different plant tissues according to their potential 'value' to the plant (Hartley *et al.*, Chapter 11). We currently require a synthesis as to how these temporal and spatial pressures interact to influence variation in PSMs over time and space within plants.

Although single secondary metabolites may act in multiple ways, the diversity of compounds present in any plant provides numerous possible permutations for them to act in combination. Cates (1996) drew attention to the potential for interactive effects of PSMs, but bio-prospecting studies that seek bioactive PSMs for human use have mainly focused on the search for 'the single active compound' (Firn & Jones, 2000). We are now increasingly considering the effects of combinations of PSMs (Gershenzon *et al.*, Chapter 4), and combinations with other traits in natural environments (Agrawal, 2011). It is clear that the use of several types of defence simultaneously by plants (Zarate *et al.*, 2007; Wei *et al.*, 2011) suggests that our older ideas of simple

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trade-offs between these different types need revision as we gain better insights into which defensive traits may evolve together.

In fact, PSMs can no longer be considered to function simply as plant defences against their enemies. Many interactions between PSMs and organisms exploiting plants are now known to be positive. For example, some soil microbes can use carbon-rich PSMs exuded from plant roots as a carbon source (Smolander *et al.*, 2006). Obviously the net effects of PSMs on some non-adapted target herbivores are negative, but for specialist herbivores, including vertebrates that have co-evolved counter-adaptations (Schoonhoven *et al.*, 2005; Forbey & Hunter, Chapter 5), they can be positive. Associated with this is the important confirmation that evolutionary selective pressure on PSMs can be exerted in opposite directions by herbivores according to their degree of specialism, specifically, positively by generalist and negatively by specialist herbivores (Lankau, 2007). As well as contrasting impacts, we now recognise the contrasting roles of many PSMs. For example, the effects of tannins and other phenolic PSMs may arise not only from their protein precipitating properties, but also from their status as pro- or antioxidants (Salminen & Karonen, 2011). A fuller understanding of the conditions under which these contrasting effects prevail is required.

This volume does not try to incorporate examples of PSM from all biomes, but focuses on areas of recent development of ideas. As our understanding of the distribution, allocation and evolutionary selection for PSMs has advanced, however, it has become clear that we have some major gaps. A review of PSMs in aquatic systems uncovered a stunning lack of knowledge of their prevalence and ecological roles (Gross & Bakker, Chapter 8). Despite seminal studies of the importance of PSMs in macrophytic plants being undertaken in the marine environment, e.g. in phytochemical induction (Cronin & Hay, 1996), there is a similar shortfall in our knowledge of the roles of PSMs, but a strong role of allelopathic interactions in shaping the planktonic community is likely (Czaran *et al.*, 2002; Suikkanen *et al.*, 2004).

1.3 Integrative roles of PSMs in connecting multiple components of ecological systems

PSMs are now recognised as having a major role in mediating interactions between different components of ecological communities, often widely separated in space and time (e.g. van der Putten *et al.*, 2001; Poelman *et al.*, 2008). They also impact on ecosystem processes and so ultimately on the structure and function of ecosystems. One such process that PSMs have long been known to influence is decomposition and hence the interactions between above- and belowground processes: the chemical composition of litter influences its decomposition rate and the recycling of nutrients through the soil–plant system (Bardgett *et al.*, 1998; Iason *et al.*, Chapter 13). But more subtly, PSMs are intimately involved in the integration of above- and belowground processes in plants via internal signalling processes, for example between roots and shoots following action on either, by herbivores, pathogens or mutualists (Kaplan *et al.*, 2008; Gange *et al.*, Chapter 9; van Dam, Chapter 10).

The recent advances beyond PSM-mediated interactions between pairs of species usher us into a new era of multi-trophic and interactive effects dissectible by experimentation involving plants with known genetic background and traits. These methods have already begun to elucidate the role of PSMs (e.g. Kessler *et al.*, 2004; Linhart *et al.*, 2005; Lankau & Strauss, 2008) and other plant traits (Johnson *et al.*, 2009) as determinants of complex interactions involving multiple species and genotypes within species. The availability of transgenic plants modified with respect to their production of PSMs has rapidly facilitated the identification of the effects of particular genes at higher ecological levels, including their mediation of multi-trophic interactions (Kessler *et al.*, 2004; Zhang *et al.*, 2009; Schuman & Baldwin, Chapter 15; Dicke *et al.*, Chapter 16). Better knowledge of genetic variation in PSMs is providing evidence of their impact at higher levels of biological organisation up to the ecosystem level (Bailey *et al.*, Chapter 14).

1.4 Ramifications of PSMs across scales from genes to global effects

Whilst the PSMs vary across global, landscape, geographical and smaller spatial scales (Moles *et al.*, 2011; Moore & DeGabriel, Chapter 12; Iason *et al.*, Chapter 13), there are relatively few studies investigating the nature and significance of this variation for the structure and function of ecosystems. Spatial variation can dominate other sources of variation, for example in structuring invertebrate communities (Tack *et al.*, 2010), and it therefore seems important to explore the role of spatial variation in PSMs further. The availability of cheaper and rapid genomic, metabolomic (Hartley *et al.*, Chapter 11) and other biochemical techniques (such as near-infrared spectroscopy, e.g. Moore *et al.*, 2010) or remote sensing techniques that can be used to process large numbers of samples or survey large areas (Moore *et al.*, 2010), is likely to facilitate a better understanding of the causes and consequences of large-scale spatial variation in PSMs for other organisms.

Large-scale impacts of PSMs are becoming clear: they both cause and respond to global-scale environmental change (Penuelas & Staudt, 2010). The release of volatile isoprenoids by trees in response to abiotic stress has a global-scale impact in that they are precursors to ozone (O_3) in the troposphere in the presence of anthropogenic nitrogen oxides (Bagnoli *et al.*, Chapter 6). Global environmental changes such as increased atmospheric O_3 and carbon dioxide are hypothesised to feed back to plants and influence their PSM concentrations (e.g. Jones & Hartley, 1999). Although some strong effects and general patterns are detectable (Bezemer & Jones, 1998), there is a surprisingly high degree of inconsistency in the responses of PSMs, and the ecology of the systems they influence, to elevated atmospheric CO_2 and atmospheric ozone (Hartley *et al.*, 2000; Lindroth, Chapter 7). The apparently idiosyncratic effects may be due to relatively few plant species having been studied at a community level, and the fact that most studies have addressed only the phenolic and terpenoid PSMs (Lindroth, Chapter 7).

1.5 Methodological developments

The developments in molecular ecology are progressing rapidly. With more and more species being fully sequenced and with development of novel techniques for global transcriptomic analyses in non-model species, new opportunities to link the PSM phenotype to molecular genetic characteristics will rapidly expand. Molecular techniques that provide new tools and specific genotypes in which to investigate the ecological aspects of PSMs can create molecular model plants to aid understanding of the biochemical and metabolic consequences of genes, such as over-expressed genes or mutant plant material in which specific genes are knocked out (Schuman & Baldwin, Chapter 15; Dicke *et al.*, Chapter 16). These techniques, along with gene silencing, provide exciting possibilities for investigating the role of PSMs in the ecology of various plants such as wild tobacco, aspen or brassicas (e.g. Kessler *et al.*, 2004, 2008; Poelman *et al.*, 2008; Broekgaarden *et al.*, 2010). The exploitation of transgenic approaches to enhance knowledge of the chemical ecology of PSMs and apply this knowledge in crop and forest protection (Degenhardt *et al.*, 2003, 2009; Aharoni *et al.*, 2005; Kos *et al.*, 2009) may offer significant research opportunities in the future.

Despite the current emphasis on the importance of ecosystem approaches, in order to solve real-world environmental problems (Millennium Ecosystem Assessment, www.maweb.org), we still have no examples of large-scale whole-ecosystem studies that allow us to integrate and quantify the multiple roles of PSMs across scales. The ecological ramifications and influences of foundation species on a community are by definition profound. Although the community genetics approach applies well to studies of the extended phenotype, including that mediated by the PSMs of foundation species (Whitham *et al.*, 2003), this approach has, as yet, not found widespread application in practical conservation management for maximising biodiversity.

The increasing availability of molecular phylogenies will facilitate hypothesis testing in terms of the evolutionary drivers of PSM diversity. For example, a phylogenetic approach to track PSM diversity and composition throughout the evolutionary history of the Burseraceae recently illustrated an increasing chemical diversity within the family across evolutionary time (Becerra *et al.*, 2009). Other possibilities include the identification of crucial stages in the

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evolution of PSMs in freshwater environments, in relation to their evolutionary history of transfer to or from aquatic to terrestrial habitats (Gross & Bakker, Chapter 8) and taxonomic associations of plants that produce tropospheric ozone-producing volatile isoprenoids (Bagnoli *et al.*, Chapter 6).

1.6 Towards further integration

Relatively few studies consider multiple groups of PSMs within a single system. We suggest that this is due to the propensity of scientists to focus on familiar groups of compounds, or taxonomic groups of organisms participating in the interactions, or indeed to study a particular type of interaction, such as plant–herbivore interactions. But it is now clear that the ecology of whole systems may be influenced by PSMs, owing to their impacts on complex multi-trophic interactions (Iason *et al.*, Chapter 13; Bailey *et al.*, Chapter 14). Even fewer studies examine the role of PSMs across the range of scales from genes to landscapes. Future truly integrative, cross-disciplinary case studies are required to fully elucidate their roles in ecological communities. We need to understand the genetic, physiological and evolutionary controls on PSM production as well as the way that impacts of PSMs feed through to the ecosystem at the landscape scale. The most useful of these case studies will involve ecological model species and the most enlightening will not be constrained by taxonomic boundaries, phytochemical groups or confined to adjacent trophic levels.

Ecological effects mediated at least in part by PSMs and that span trophic levels have indeed been identified. Examples include the correlation between herbivory and decomposition (Grime *et al.*, 1996) and the relationship between arbuscular mycorrhizal fungi on the roots and the greater preponderance of specialist herbivores on the shoots of plants (Gange *et al.*, 2002). The association between soil microbial communities and aboveground processes such as leaf herbivory invokes signalling cascades that are analogous to those involved in mediating other above/belowground interactions of plants. This analogy spans plant responses to root-herbivory, plant microbial and plant pathogenic interactions as well as responses to abiotic stressors such as drought (Pineda *et al.*, 2010; Johnson *et al.*, 2011; Gange *et al.*, Chapter 9; van Dam, Chapter 10). Generalisation of the occurrence and relative importance of these processes remains to be established.

The studies presented in this volume emphasise the multiple integrative roles of PSMs in natural systems. They demonstrate the potential we have for understanding the far-reaching ecological consequences of the genes underlying the production of PSMs, and should ultimately guide us in our choices of transgenic and other manipulations that will permit their practical application in environmental management for improved food security or other ecosystem services. The recently emerging ecological and evolutionary roles of PSMs highlighted in this volume point to the trajectories along which future studies may be launched.

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CHAPTER TWO

Natural selection for anti-herbivore plant secondary metabolites: a *Eucalyptus* system

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2.1 Introduction

Since the seminal papers of Fraenkel (1959) and Ehrlich and Raven (1964), much research has demonstrated the role of plant secondary metabolites (PSMs) as defence mechanisms against invertebrate and vertebrate herbivory. These metabolites can act directly on the herbivore as toxins (Theis & Lerdau, 2003; Gershenzon & Dudareva, 2007), digestibility reducers (Ayres *et al.*, 1997; De Gabriel *et al.*, 2009) and deterrents (Pass & Foley, 2000), and they can also act indirectly by, for example, attracting natural enemies of the herbivore (Dicke, 2009). The idea that the herbivores themselves are acting as selective agents on these PSMs has existed since it was first noted that these compounds may serve as anti-herbivore traits, and in some systems it is clear that herbivores may act as agents of natural selection on some specific PSMs (Simms & Rausher, 1989; Mauricio & Rausher, 1997; Stinchcombe & Rausher, 2001; Agrawal, 2005). However, in most systems there is still a dearth of evidence addressing this question, particularly in light of the vast number of herbivores that attack a single plant species across its entire life and the array of PSMs that are expressed in a plant species. Are all of these herbivores agents of selection and have all PSMs evolved because of the selective pressures by the herbivores, or are PSMs driven by selection from other pressures such as abiotic factors (Close & McArthur, 2002)? Knowing the answer to these questions is important when attempting to understand what is driving population divergence within species and the evolution and change in PSMs.

For selection to occur there must be additive genetic-based variability in herbivory within plant populations. This herbivory must correlate with additive genetic-based variation in plant defensive traits, and herbivory must affect plant fitness (see Box 2.1). Key papers in the late 1980s through to the late 1990s clearly demonstrated the evolutionary impact that invertebrate herbivores were having on plant chemical defences in some systems (Rausher & Simms, 1989; Simms & Rausher, 1992; Rausher, 1993; Mauricio & Rausher,

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