Plant Interactions with Arthropod Herbivores: State of the Field

Interactions between plants and their arthropod herbivores dominate the terrestrial ecology of our planet. The survival of an estimated one million or more phytophagous insect species depends on plants as a source of food. Plant-eating arthropods employ sophisticated feeding strategies to obtain nutrients from all aboveground and belowground plant parts. Rather than being passive victims in these interactions, plants cope with herbivory through the production of myriad specialized metabolites and proteins that exert toxic, repellent, or antinutritive effects on their animal attackers (see Zhu-Salzman et al., 2008). The co-evolutionary struggle between arthropod herbivores and plants to consume or not to be consumed, respectively, has shaped not only the extraordinary diversity of plant metabolism, but also the genetic diversity of plants.

The central role of plant chemicals in mediating interactions with arthropod herbivores has attracted the attention of insect physiologists and population ecologists for more than 50 years (see Berenbaum and Zangerl, 2008). Widespread interest in this field among plant biologists, however, can be traced back to 1972, when Clarence "Bud" Ryan (Fig. 1) and colleagues at Washington State University reported that insect feeding on potato and tomato plants activates local and systemic expression of proteinase inhibitors that disrupt the activity of digestive proteases in the insect gut (Green and Ryan, 1972). This seminal discovery was instrumental in establishing the paradigm that plant defense responses to herbivore attack are rapid and highly dynamic. The general theme of induced resistance runs through much, if not most, plant-insect interaction research published in *Plant Physiology*. Remarkable progress in understanding plant relations with arthropod herbivores has been achieved in the recent past; these advances were the genesis of this *Focus Issue*.

Plant-herbivore interaction research is arguably one of the most multidisciplinary endeavors in plant biology. Like all research concerned with inter-species relationships, numerous disciplines are required to accurately describe the range of chemical and ecological processes that influence the outcome of plant-herbivore interactions. A defining aspect of the field has been its focus on animals as the "other organism." The complexity of animal behavior, together with the technical difficulties associated with genetic manipulation of plant-eating animals, poses unique but not insurmountable challenges. As discussed in *Updates* by Zheng and Dicke (2008) and by Schwachtje and Baldwin (2008), an important research trend is the use of plant-insect systems to address questions of ecological relevance. The merging of molecular and ecological disciplines offers a powerful approach to understand gene function and evolution in an ecological context.

Much of contemporary plant-herbivore interaction research is focused on understanding the molecular mechanisms and ecological consequences of induced plant responses to herbivory. In their *Update*, Mithöfer and Boland (2008) discuss the early signaling events at the plant-herbivore interface. Wu et al. (2008) show that there can be significant within-species differences in these early signaling responses. Frost et al. (2008) describe molecular and ecological aspects of defense "priming," which has become an important area of research. In her *Update*, Walling (2008) describes various mechanisms by which insects evade host defense responses, thereby highlighting the co-evolutionary nature of plant-herbivore relations.

It is now clear that the jasmonate (JA) family of lipid-derived signals plays a prominent and conserved role in promoting plant resistance to herbivores. Browse and Howe (2008) discuss these roles, as well as recent progress in elucidating the mechanism of JA signaling. One notable recent discovery is that an amino acid-conjugated form of JA, JA-Ile, is a bioactive signal for defense responses and a potential ligand for the JA receptor. An article by Wang et al. (2008) indicates that JA and JA-Ile serve distinct (but overlapping) roles in defense. Chung et al. (2008) show that the levels of both JA and JA-Ile increase within 5 min of mechanical tissue damage, and provide genetic evidence that the JAZ proteins, which negatively regulate JA responses, play a role in regulating host plant resistance to herbivory. An article by Arimura et al. (2008) shows that the temporal pattern of leaf damage plays a critical role in the emission of plant volatiles that attract natural enemies of the herbivore, and that JA is likely involved in the control of this response. Lin et al. (2008) in this issue show how genome duplication allowed neofunctionalization of a terpene synthase that contributes to herbivore-induced volatile release. In an article by Jassbi et al. (2008), direct antifeedant effects of diterpenoids are demonstrated through insect bioassays involving plants that are silenced in the expression of these compounds. Koornneef and Pieterse (2008) discuss recent progress in our understanding of how JA and other signaling pathways influence the outcome of plant-pest interactions. The phenomenon of signal cross talk in plant biology has gained increased attention as scientists seek to understand how plants respond to simultaneous attack by multiple herbivores and pathogens. A novel example

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Figure 1. Clarence ''Bud'' Ryan (1931–2007). Photograph courtesy of Washington State University.

of signal cross talk is described in an article by Runyon et al. (2008), who examined how the parasitic plant *Cuscuta pentagona* affects induced defenses of tomato to insect attack.

Model plant systems, together with the increasing use of mutants that are affected in their interactions with arthropod herbivores, have contributed greatly to recent progress in the field. An article by de Vos et al. (2008) in this issue illustrates the value of *Arabidopsis thaliana* mutants for studying the role of small molecules in plant-insect interactions. In their forward-looking view of the future of plant-insect interaction research, Berenbaum and Zangerl (2008) argue convincingly that a deep understanding of chemical-mediated plant-insect interactions will require analysis of phylogenetically diverse species that extends beyond the current repertoire of model plant systems. It will also be important to learn more about the interaction of arthropod attackers with belowground plant tissues. Two *Updates*, one by Erb et al. (2008) and the other by Rasmann and Agrawal (2008), are devoted to the theme of belowground herbivory.

As is the case with all areas of plant biology, modern ''omics'' approaches have also facilitated rapid progress in research on plant-arthropod interactions. These tools have provided an unprecedented opportunity to study large-scale changes in herbivore-induced plant processes in a relatively unbiased manner. An article by Gao et al. (2008) in this issue is the first report on a plant insect-interaction where both organisms, in this case, *Acyrthosiphon pisum* (pea aphid) and *Medicago truncatula*, are the subject of ongoing genome sequencing projects. Rapid advances in DNA sequencing technology will bring research on this and other plant-herbivore model systems to a new level by making it possible to do genetic and genomic studies on both sides of the interaction.

Another important theme in research on plant-arthropod interactions is the control of herbivory on crop plants. An *Update* by Gatehouse (2008) in this issue highlights advances in transgenic approaches for creating insect-resistant crops. Enthusiasm for the use of plant proteinase inhibitors for crop protection has been tempered by the realization that insects have the capacity to synthesize, on demand, gut proteases that are insensitive to plant-derived inhibitors. A research article by Goulet et al. (2008) describes targeted engineering of plant cystatins to provide greater efficacy against insect digestive proteases. Major and Constabel (2008) describe the functional and biochemical variability of Kunitz trypsin inhibitor genes of hybrid poplar, which may provide a starting point for similar engineering efforts in tree species.

We hope that this *Focus Issue* conveys to readers the fact that plant-herbivore interaction research, while still in its infancy, is a rapidly moving multidisciplinary field with strong roots and a bright future. For that, we owe much to Bud Ryan, a founding father of this field, and we are deeply saddened by his recent passing. Bud's pioneering work on plant proteinase inhibitors (Ryan, 1990), induced resistance to herbivory (Green and Ryan, 1972), and peptide-signaled defense responses (Pearce et al., 1991) inspired several generations of biologists to pursue the study of plant-insect interactions. The impact of Bud's work is readily discernible in each of the articles contributed to this *Focus Issue*. For these reasons, we would like to dedicate this *Focus Issue* to the memory of Bud Ryan.

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