



Review

Insect-induced effects on plants and possible effectors used by galling and leaf-mining insects to manipulate their host-plant

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ABSTRACT

Gall-inducing insects are iconic examples in the manipulation and reprogramming of plant development, inducing spectacular morphological and physiological changes of host-plant tissues within which the insect feeds and grows. Despite decades of research, effectors involved in gall induction and basic mechanisms of gall formation remain unknown. Recent research suggests that some aspects of the plant manipulation shown by gall-inducers may be shared with other insect herbivorous life histories. Here, we illustrate similarities and contrasts by reviewing current knowledge of metabolic and morphological effects induced on plants by gall-inducing and leaf-mining insects, and ask whether leaf-miners can also be considered to be plant reprogrammers. We review key plant functions targeted by various plant reprogrammers, including plant-manipulating insects and nematodes, and functionally characterize insect herbivore-derived effectors to provide a broader understanding of possible mechanisms used in host-plant manipulation. Consequences of plant reprogramming in terms of ecology, coevolution and diversification of plant-manipulating insects are also discussed.

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1. Introduction

Nutrition is the cornerstone of most interactions between organisms. With more than 4 million estimated species, insects are among the most significant evolutionary successes on Earth (Novotny et al., 2002). The origin of this success can be directly linked to the diversity of their feeding strategies, of which herbivory is the most common (Schoonhoven et al., 2005; Slansky and Rodriguez, 1987). However, plant tissues are typically suboptimal nutritionally, due to unbalanced ratios and/or low levels of key nutrients and frequent requirement to detoxify plant defensive allelochemicals (Schoonhoven et al., 2005). The ability of phytophagous arthropods to exploit plant resources requires them to employ a suite of pre- and post-ingestive mechanisms to address the nutritional mismatch between what plants provide and what insects require (Behmer, 2009; Raubenheimer et al., 2009; Schoonhoven

et al., 2005). These strategies include associations with one or more symbiotic partners providing new metabolic pathways (Douglas, 2009, 2013; Moran et al., 2008), symbioses in which plants have evolved food rewards specifically for insects (e.g. Heil and McKey, 2003), and/or intricate interactions that involve insect reprogramming of host-plant development, resulting in new structures benefiting the parasitic herbivore at the expense of the plant (Giron et al., 2013; Price et al., 1987; Stone and Schönrogge, 2003).

Insect galls are structures composed of plant tissues that develop in response to stimuli produced by the gall-inducer, and present inducer-specific phenotypes and patterns of tissue differentiation (Stone and Schönrogge, 2003). The need for induction by another organism distinguished true galls from other structures that have evolved to accommodate insects but which are under plant control – such as the domatia of myrmecophytes occupied by guarding ants (e.g. Raine et al., 2002). Galls are among the most

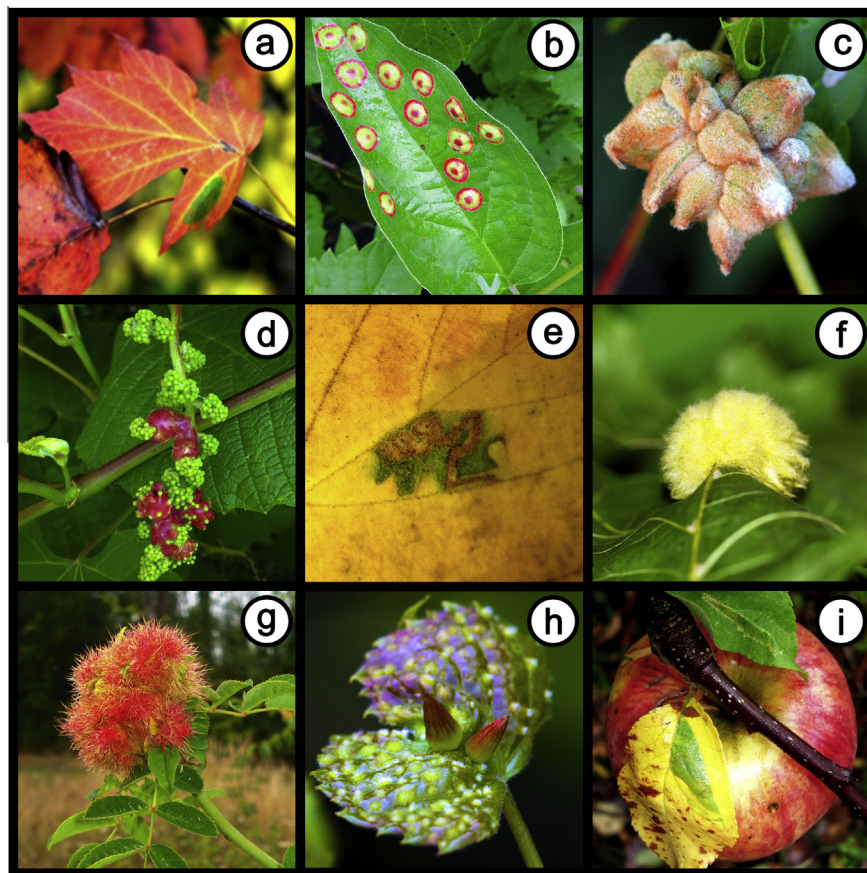


Fig. 1. Examples of plant manipulation by gall-inducing and leaf-mining insects. (a) Green-island induced by the leaf-miner *Phyllonorycter joannisi* (Lepidoptera, Gracillariidae) on maple leaf. (b) 'Blister galls' induced by a gall midge fly (unidentified species; Diptera, Cecidomyiidae) on honeysuckle leaf. (c) 'Hazelnut gall' induced by the gall midge fly *Schizomyia vitiscoryloides* (Diptera, Cecidomyiidae) on grape nodes. (d) 'Tomato galls' induced by the gall midge fly *Janetiella brevicauda* (Diptera, Cecidomyiidae) on grape flower buds. (e) Green-island (around a serpentoid mine) induced by the leaf-miner *Lyonetia clerkella* (Lepidoptera, Lyonetiidae) on a *Prunus* tree's leaf. (f) 'Woolly gall' induced by the Cynipid wasp *Callirhytis lanata* (Hymenoptera, Cynipidae) on oak leaf. (g) 'Bedeguar gall' induced by the Cynipid wasp *Diplolepis rosae* (Hymenoptera, Cynipidae) on rose leaf bud. (h) 'Tube galls' and 'pocket-like galls' respectively induced by the gall midge fly *Schizomyia viticola* (Diptera, Cecidomyiidae) and the phylloxera aphid, *Daktulosphaira vitifoliae* (Hemiptera, Phylloxeridae), on grape leaf. (i) Green-island induced by the spotted tentiform leaf-miner *Phyllonorycter blancardella* (Lepidoptera, Gracillariidae) on apple-tree leaf. Credit photo: D. Giron (a) and M. Body (b–i).

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