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Implications of bioactive solute transfer from hosts to parasitic plants

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Parasitic plants — which make their living by extracting nutrients and other resources from other plants — are important components of many natural ecosystems; and some parasitic species are also devastating agricultural pests. To date, most research on plant parasitism has focused on nutrient transfer from host to parasite and the impacts of parasites on host plants. Far less work has addressed potential effects of the translocation of bioactive non-nutrient solutes — such as phytohormones, secondary metabolites, RNAs, and proteins — on the development and physiology of parasitic plants and on their subsequent interactions with other organisms such as insect herbivores. A growing number of recent studies document the transfer of such molecules from hosts to parasites and suggest that they may have significant impacts on parasite physiology and ecology. We review this literature and discuss potential implications for management and priorities for future research.

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Introduction

Parasitic plants are important components of many terrestrial ecosystems and also have significant impacts on human agriculture. Pestiferous species, primarily from four genera of parasitic plants (*Striga*, *Orobanche*, *Phelipanche*, *and Cuscuta*), afflict farmers in many parts of the world, posing serious threats to subsistence agriculture in developing regions and causing several billions of dollars in annual economic losses to grain and vegetable production [1,2]. Reduced crop yields — and in some cases complete crop loss — result directly from parasite extraction of water and nutrients from cultivated host plants [2]. Consequently, the mechanisms of resource extraction by parasites and resulting impacts on host plants have been the subject of considerable research efforts [3,4], even though the biology and ecology of parasitic plants remains poorly studied compared to other plant groups [5]. By contrast, relatively little work to date has explored the bottom-up influence of host-derived factors on plant parasites and their subsequent interactions with other organisms.

Most previous research in this area has focused on nutrient transfer (e.g. [6]), which in addition to supporting the growth of the parasite can influence the accessibility of resources (e.g. carbon and nitrogen) to other community members — including herbivores, pollinators, decomposers and, ultimately, other plants. Thus, plant parasites can significantly influence ecosystem dynamics via effects on nutrient cycling [4,7]. However, a diverse pool of non-nutrient bioactive solutes are also likely to be translocated from host plants to parasites, including phytohormones, proteins, and RNAs that can have sweeping effects on plant development, and small molecules and proteins involved in host plant defense that might also influence subsequent interactions of the parasite with other organisms. Thus, diverse aspects of host–plant biochemistry are likely to influence the physiology and ecology of plant parasites, with implications for broader community dynamics and potentially for the management of parasitic weeds — though we currently have only a limited understanding of such influences. Here we review recent evidence regarding the transfer of host-derived extra-nutritive solutes into plant parasites and explore the known and potential implications of these exchanges for parasite biology and ecology.

Background: mechanisms of solute transfer from host to parasite

Understanding the translocation of solutes from host plants to parasites requires a basic understanding of solute transport pathways in plants. Short-range, cell-to-cell movement of solutes occurs via diffusion through spaces outside of cell membranes (i.e. the apoplast), as well as through spaces within cell membranes (i.e. the symplast) that are joined by membrane-lined transcellular tunnels called plasmodesmata [8]. Long-range movement occurs through the vascular tissues phloem and xylem. Phloem tissue comprises living sieve tube element cells with conjoined membranes that transport sugars from photosynthetically active tissues to sink tissues (e.g. roots, and new leaves). Xylem comprises dead tube-like cells (vessel elements or tracheids) that form continuous apoplastic channels for moving water and minerals from roots to the

Figure 1

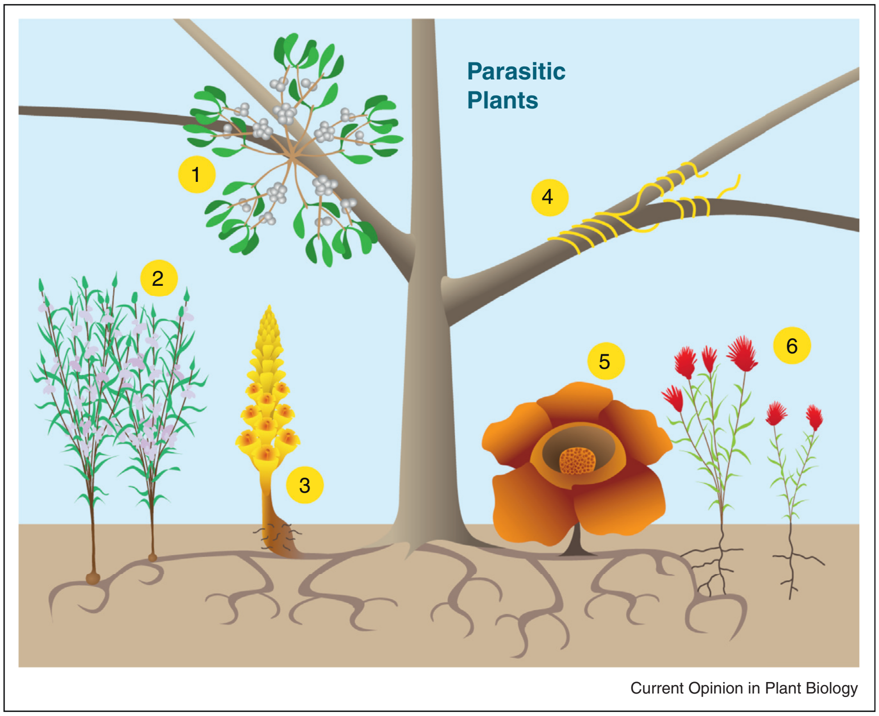

Illustration of several groups of plant parasites discussed in this review: (1) mistletoes; (2) witchweeds; (3) broomrapes; (4) dodders; (5) corpse flowers; (6) figworts. (*Note*: depicted here on a fictive generic host, these parasites utilize different and diverse hosts in nature [see Table 1]). Illustration by Nick Sloff.

upper parts of plants [8]. Phloem and xylem additionally facilitate movement of various hormones, proteins and RNAs that function in development and defense processes [9,10].

Parasitic plants (Figure 1) can potentially intercept host solutes moving via any of the above pathways by using specialized feeding organs (haustoria) that penetrate host roots or shoots and associate with host vascular tissues [3]. For example, some parasites actively recruit solutes from host apoplast via haustorial parenchymal cells, which account for the largest surface of internal host–parasite contact [11]. This appears to be a primary feeding mechanism for some parasite species [12,13], and in some cases parenchyma adjacent to host vascular tissue possess membrane invaginations that are thought to improve efficiency in solute uptake [3]. Parasites may also feed directly from the host's xylem stream by forming a conductive bridge that connects the xylem of both plants. The xylem bridge is a widespread haustorial feature among parasitic plant species; however, the nature of the xylem interface varies considerably among genera: while some parasites form cross-species perforations or pits typical of conjoined xylem elements, others penetrate host xylem with open conductive tubes called osculae, and still others do not form visibly open passageways and presumably load solutes from apoplastic spaces outside of the xylem [3] (see Table 1 for specific examples). A less common feeding strategy, documented in members of *Cuscuta*, *Striga* and *Orobanche*, is to form symplastic connections to host tissues. For example, *Cuscuta* spp. form transient plasmodesmata with adjacent host tissue during the development of their haustoria, and experiments have confirmed the ability of these structures to serve as portals for virus movement proteins [14,15]. Interspecific plasmodesmata were also seen in *Striga gesnerioides* [16]. Additionally, sieve pores connecting parasite and host phloem elements occur in *Orobanche* spp. [17]. Thus, parasites have evolved mechanisms to exploit each of the major solute transportation pathways in plants, although different species exhibit different strategies and rarely utilize all pathways (see Table 1). These contrasts raise the question of how haustorial morphology relates to feeding efficiency and selectivity — a topic with potentially important implications for parasite–host ecology as well as for the development of RNAi-based control strategies (discussed in the next section).

The degree of selectivity in solute uptake by parasites is frequently discussed in the parasitic plant literature (e.g. [6,15,18–20]). Open xylem–xylem or phloem–phloem connections might be expected to allow non-selective