

Interactions between hemiparasitic plants and their hosts

The importance of organic carbon transfer

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Key words: haustorium, heterotrophy, parasitic plant, mistletoe, *Rhinanthus*, *Striga*, $\delta^{13}\text{C}$

Abbreviations: $\Phi\text{PS}_{\text{II}}$, electron transport rate; WUE, water use efficiency

Hemiparasitic plants display a unique strategy of resource acquisition combining parasitism of other species and own photosynthetic activity. Despite the active photoassimilation and green habit, they acquire substantial amount of carbon from their hosts. The organic carbon transfer has a crucial influence on the nature of the interaction between hemiparasites and their hosts which can oscillate between parasitism and competition for light. In this minireview, we summarize methodical approaches and results of various studies dealing with carbon budget of hemiparasites and the ecological implications of carbon heterotrophy in hemiparasites.

Hemiparasitic plants withdraw resources from the vascular system of their hosts through a specialized transfer organ called haustorium.¹ Hemiparasites attack the host's xylem, in contrast to the holoparasites that infect both phloem and xylem, and as a consequence, hemiparasitic plants have access to water and mineral nutrients but little carbon.¹ Due to their reduced or non-existing root networks, hemiparasitic plants acquire virtually all mineral nutrients and water from the host while organic carbon is provided, at least in part, by their own photosynthetic activity.^{2,3} This is in contrast to holoparasitic plants which rely on the host for the supply of both organic and inorganic nutrients. The location of the attachment to the host and the degree of host dependency represent the most important characters defining the three basic functional types within hemiparasitic plants. Root hemiparasites attack host roots but their above-ground appearance is usually not substantially different from that of a non-parasitic plant. This group can be further divided in two—facultative and obligate hemiparasites consisting of plants that are able (at least sometimes) or unable to complete their life cycle without an attachment to the host respectively. Stem hemiparasites are

attached to the host stem (usually trunk or branches) and are all obligate parasites, unable to survive without a host.

Hemiparasitic plants have an ambiguous relationship with their hosts which, on the one hand, represent exclusive sources of inorganic nutrients but on the other hand, the co-occurrence of these host plants in the hemiparasite vicinity imposes competition for light. The nature and intensity of this competitive relationship varies across different groups and species of hemiparasites. The ability of hemiparasites to acquire organic carbon (largely in the form of xylem-mobile organic and amino acids) is certainly the key factor affecting this interaction since hemiparasites that are capable of efficient organic carbon abstraction should be minimally affected by shading from their host. The fact that hemiparasites can exhibit substantial carbon heterotrophy is now supported by a large number of studies, although a traditional point of view on hemiparasites that highlights the importance of inorganic resources (mainly nitrogen) acquisition is still prevailing. Therefore, we decided to summarize available information on hemiparasite heterotrophy, outline techniques for assessing the proportion of heterotrophy and estimating the overall carbon budget, and discuss possible implications of this phenomenon on hemiparasite ecology.

Mechanisms of Resource Acquisition in Different Functional Types of Hemiparasites

The anatomy of haustoria and the mechanisms of resource acquisition by root hemiparasites as well as abstraction efficiency have been shown to differ between species and are in link to their dependence on their host and life history. Annual hemiparasites such as *Striga* spp. or *Rhinanthus* spp. are capable of highly efficient abstraction of solutes from the host xylem which is underpinned by direct luminal continuity between host and parasite vessels.^{1,4-6} The transfer of solutes occurs as a passive mass flow driven by a water potential gradient between the host and the parasite. The hemiparasite maintains more negative water potential than its host, which is generated by substantially elevated transpiration rates and abnormal behaviour of stomata which do not close even in dark or under water stress conditions⁷⁻⁹ as well as the accumulation of osmotically active compounds such as

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Submitted: 05/27/10; Accepted: 05/27/10

Previously published online:

www.landesbioscience.com/journals/psb/article/12563

DOI:10.4161/psb.5.9.12563

sugar alcohols, especially mannitol.¹ In contrast, perennial species such as *Bartsia alpina*, *Olex phyllanthi* and *Santalum album* tend to display a rather conservative strategy of parasitic resource acquisition.^{8,10} Solute transfer in haustoria formed by these hemiparasites proceeds across cell walls or contact parenchyma.^{5,11,12} Although the exact mechanism is unknown, this process is probably based on an active transmembrane transport as it does not appear to require a water potential difference.¹² Transpiration rates of the perennial hemiparasites therefore tend to be similar to those of a non-parasitic plant and often do not exceed those of their host.^{11,12}

Stem hemiparasites usually parasitize tree or shrubby species. Not only do they gain nutrients and water from the host xylem, but are also provided with a favourable position in the canopy in which they can receive a large amount of photosynthetically active radiation. The solute transfer in their haustoria is usually based on a combination of all possible mechanisms (i.e., luminal continuity, across a cell wall, across parenchyma cells) relative proportion of which differs across species, individuals and individual haustoria.^{13,14} Mistletoes usually keep more negative water potential than their host; nonetheless its dynamics is usually coupled to that of the host plant and the stomata behave not as abnormally as in annual root hemiparasites.¹⁵⁻¹⁷ However, little is known about the physiology of resource acquisition in other stem hemiparasites such as species of the genus *Cassytha*.

Heterotrophic Carbon Gain

Hemiparasitic species are connected to the host xylem suggesting that water and mineral nutrients are the primary resources that are abstracted from the host. This is especially assumed in facultative root hemiparasites that are less dependent on the host resources compared to other parasitic species.¹ Many root-hemiparasitic species nonetheless display inefficient photosynthesis and high respiratory rates.⁸ Mistletoes usually exhibit photosynthetic characteristics more typical of shade plants, i.e., low mean CO₂ assimilation rates, low electron transport rate ($\Phi_{PS_{II}}$), low light saturation point and low chlorophyll a/b ratio¹⁸ despite experiencing favourable light conditions high in the canopy. In addition, seedlings of obligate root hemiparasites (e.g., *Striga* spp.) are achlorophyllous and hence completely dependent on the host. All these facts suggest that substantial transfer of organic carbon from the host must occur to support growth of many hemiparasitic species despite the lack of a connection to the phloem.⁴ The existence of a host-to-hemiparasite flux of organic carbon in a hemiparasitic relationship was demonstrated in several root-hemiparasitic associations using radioactive ¹⁴CO₂ labelling.^{19,20} Neither of these studies however presented a quantitative estimation of the carbon budget. Quantification of host-derived carbon in hemiparasites can be estimated using the stable isotopes of carbon in a hemiparasitic relationship with a host species that performs C₄ photosynthesis in contrast to the C₃ hemiparasites. Its photoassimilates are therefore significantly enriched in ¹³C compared to those of C₃ plants due to the differential isotope discrimination of RUBISCO and PEPC, primary CO₂-fixing enzymes in C₃ and

C₄ plants respectively. The proportion of host derived carbon in the hemiparasite biomass can be then calculated from the ¹³C value of biomass of a hemiparasite connected to the C₄ host using an isotope mixing model comparing it to a C₃ reference. This reference can be obtained either as measured isotopic composition of biomass of a hemiparasite attached to the C₃ host or can be calculated as an expected carbon isotope composition of the hemiparasite based on a gas exchange measurement that provide the c_i/c_a ratio (ratio between CO₂ concentration within leaf and in ambient air) using the formula of Farquhar et al.²¹:

$$\delta^{13}C_p = \delta^{13}C_{atm} - a - (b - a) c_i/c_a$$

where, $\delta^{13}C_p$ is the isotopic ratio in plant biomass, $\delta^{13}C_{atm}$ the isotopic ratio of atmospheric CO₂, *a* is the fractionation during diffusion of CO₂ in the air through stomatal pore and *b* is the net fractionation of RUBISCO. Such quantification of host-derived carbon in hemiparasites was first conducted for the hemiparasitic relationships of *Striga hermonthica* and *S. asiatica* attached to *Sorghum bicolor*. Elevated ¹³C values detected in the hemiparasites suggested that ca 28% and 35% of carbon in mature leaves of *S. hermonthica* and *S. asiatica* biomass is host-derived.²² A similar approach was then used to estimate carbon budget of numerous hemiparasitic species demonstrating that ca 20%–80% of hemiparasite biomass is derived from the host assimilates differing across species and developmental stages.²³⁻²⁵ Early developmental stages of obligatory hemiparasites (*Striga* spp.) were demonstrated to be highly dependent on host-derived carbon as expected from their belowground growth-habit (Fig. 1).^{22,23} Heterotrophic carbon acquisition appears to be particularly high in hemiparasites that display direct luminal continuity with the host vessels in haustoria such as *Striga* spp. or *Rhinanthus minor*.^{4,6} The results are however very variable across and within different studies which might be affected by different nature of individual host-hemiparasite genotype interplay.

Estimation of the carbon budget of hemiparasites parasitizing C₃ plants is also possible. Sufficient difference in water use efficiency (WUE) must however exist between the C₃ host and the hemiparasite in order to provide contrast between ¹³C values of their assimilates. This approach was used in a study dealing with root-hemiparasitic *Castilleja linariifolia*²⁶ (Fig. 1) and is the most common method for estimating the carbon budget in stem hemiparasites which rarely parasitize C₄ hosts. Numerous studies conducted in arid or semiarid conditions have thus demonstrated 50–80% proportion of host derived carbon in biomass of mistletoes (Fig. 2).²⁷⁻³⁰ This extent of heterotrophy was also confirmed by an analysis of species parasitizing CAM hosts that have a similar carbon isotope composition to C₄ plants.^{28,29} Another study dealing with New Zealand mistletoes however showed limitation of such approach for mistletoes occurring in temperate climate regions. The difference in WUE between hosts and hemiparasites was too small in this case resulting in unrealistic (sometimes more than 100% of host-derived carbon) and highly variable outputs of carbon isotope mixing models.³¹

Competitive Interactions in the Host-Hemiparasite Systems in Relation to Carbon Budget

Despite the fact that root hemiparasites are capable of abstracting substantial amounts of organic carbon from their host, their performance is limited by competition for light with the host or surrounding plants.³²⁻³⁴ In the field, this translates into the fact that root hemiparasites grow predominantly in low productive communities³⁵ in which the intensity of competition is rather restricted. A detailed mechanism of the effect of competition on hemiparasites is however not known. It is not likely that a moderate level of light deficiency would have detrimental effects on obligate hemiparasites or adult root hemiparasites given the high efficiency of heterotrophic carbon gain.^{22,23,25} In contrast, seedlings of facultative hemiparasites germinate without a host induction, start growing unattached and hence, they must be extremely sensitive to decrease of irradiance at this stage of development especially considering their low rates of photosynthesis.^{36,37} Experiments evaluating effect of shading on different life stages of hemiparasites are missing from the literature although e.g., *Striga* spp. are known to be quite independent on its own production of photoassimilates which is indicated by the existence of mature albino plants and growth of *Striga* in complete darkness.⁴

The benefits of the hemiparasitic lifestyle connected with efficient, yet low-cost nutrient acquisition, are highest in an environment where plant performance is limited by available nutrients and the primary production is relatively low.³⁸ Under such conditions, root hemiparasites can effectively decrease growth rate of their host and hence decrease its competitive ability. In particular, annual hemiparasites tend to have highly negative effect on their host performance.^{32,39,40} The decrease of the host biomass production is usually not compensated by the biomass production of the hemiparasite resulting in a general decrease of productivity of the whole community.^{32,38} The hemiparasitic systems hence do not display source-sink relationship as has been shown for holoparasitic relationships.⁴¹⁻⁴³ In addition, hemiparasites accumulate nutrients and transpire huge amounts of water preventing their effective use for biomass production by surrounding autotrophic plants. Such 'luxury use' of resources (water and mineral nutrients) further decreases site productivity. Populations of root hemiparasites are therefore not passively dependent on the occurrence of low productive stands in nature but can actively reduce productivity of communities in which they grow.^{34,38,44} However, nutrient-rich litter of hemiparasitic plants decomposes quickly, which may in some cases act in an opposite way enhancing nutrient cycling in communities.⁴⁵

Little is known on the effect of light competition on stem parasites due to methodical difficulties of studying ecological interactions of epiphytes. It is however likely that negative effects of light competition are less pronounced given the position that mistletoes occupy in the host canopy and rather high heterotrophic carbon acquisition (Fig. 2). Despite this, a case of a healthy host tree shading out a mistletoe has been reported and some mistletoes tend to perform better if their host grows under

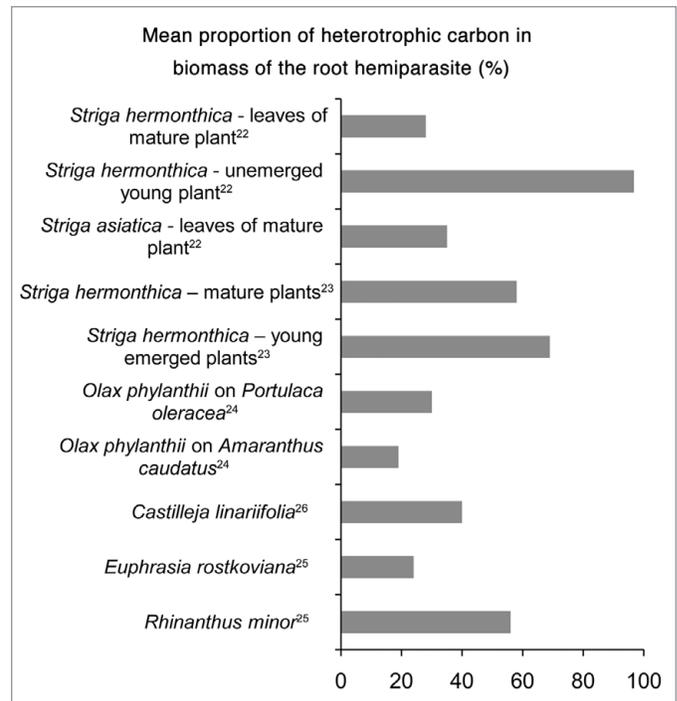


Figure 1. Mean proportion of heterotrophic carbon in biomass of various species and life stages of root-hemiparasitic plants. In some cases, only isotopic composition was reported in the original studies. Proportion of heterotrophic carbon was then calculated using an isotope mixing model as in Těšitel et al.²⁵

environmental stress such as water deficiency.⁴⁶ Dwarf-mistletoes (genus *Arceuthobium*) that are considered to be dependent on host-derived organic carbon (based on gasometric measurements;^{47,48} no detailed carbon budget studies are available) tend to perform better on vigorous host that are in a good physiological state.^{48,49} Nonetheless, even these highly heterotrophic species were demonstrated to produce more aerial shoots under high irradiance which is however not likely to be underpinned by a causal dependence of parasite performance on the light level. It is more probable that the dwarf-mistletoe is indirectly positively affected by increased photosynthetic capacity of highly irradiated branch or by elevated temperature.⁵⁰ Drawing a general conclusion on the effect of light competition on stem hemiparasites is a difficult task due to their highly variable physiology (compare e.g., rather photosynthetic mistletoe such as *Loranthus europaeus* vs. almost non-photosynthetic *Arceuthobium* spp.) and a general deficiency of studies dealing with this topic.

Conclusions and Perspectives

Carbon budget is the key parameter of biology of individual hemiparasitic species. Hitherto published studies demonstrated that many hemiparasitic species are capable of efficient organic carbon abstraction from their hosts. It is however necessary to validate how the outcomes of the growth-chamber experiments translate into the natural conditions. More field studies are therefore needed focusing especially on the role of the heterotrophic

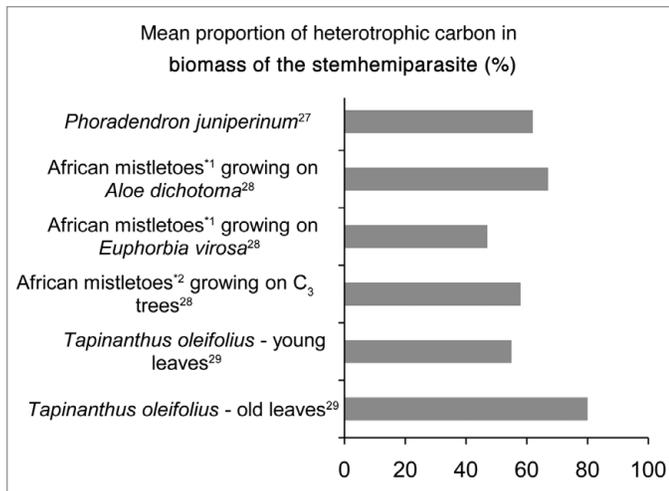


Figure 2. Mean proportion of heterotrophic carbon in different species of hemiparasitic mistletoes. In some cases, only isotopic composition was reported in the original studies. Proportion of heterotrophic carbon was then calculated using an isotope mixing model as in Těšitel et al.²⁵ African mistletoes^{*1} = *Septulina glauca*, *Tapinanthus oleifolius*, African mistletoes^{*2} = *Odonthella welwitschii*, *Plicosepalus undulatus*, *Septulina glauca*, *Tapinanthus oleifolius*, *Viscum rotundifolium*; no separate data for individual species were given in the original study.²⁸

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