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Opinion Paper

Plant-plant parasitism: Trends in the last 50 years and a call for papers for a special issue in Flora☆

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ABSTRACT

The study of plant–plant parasitism has experienced remarkable growth in the scientific literature, particularly over the past two decades. Hemi- and holoparasites, in particular, have been recognized as pivotal components within plant communities, capable of upscale effects to the ecosystem. Research on plant parasites has predominantly focused on ecological and physiological aspects of parasites and hosts, with a global distribution pattern. However, some fields remain relatively unexplored, and specific regions of Asia and the Global South (with exception of Australia and Brazil) have yet to receive comprehensive attention. Here, we introduce the theme on plant hemi- and holoparasites and explore publication trends on plant–plant parasitism over the past half-century, with a particular emphasis on papers published within the last two decades. We explore our findings to extend an invitation to researchers from diverse backgrounds and disciplines to contribute their expertise to a forthcoming Virtual Special Issue of *Flora – Morphology, Distribution, Functional Ecology of Plants* on "Plant Parasitism: Ecology, Evolution and Functional Aspects", with contributions expected from a wide range of topics related to ecology, physiology, morphology, systematics, and reproductive biology. We believe that this special issue will help in advancing our knowledge in plant-plant parasitism, fostering collaboration and facilitating the growth of this exciting area of research.

1. Introduction

Parasitism is an important ecological interaction in which organisms live inside or outside another host organism, extracting vital resources, impairing their host's development and, in some cases, leading to the host's death (Price, 1977). From an ecological perspective, the impact of parasitism extends beyond the individual species it directly affects; it also exerts a profound influence on the host population, diminishing its overall fitness (Anderson and May 1978). Therefore, parasites are able to produce cascading effects on entire communities and ecosystems' structure and functioning, given their intricate influence on trophic interactions (Marcogliese and Cone, 1997; Press and Phoenix, 2005; Watson, 2009). The dynamics of animal parasitism are well-established and extensively covered in disciplines such as Parasitology (Bush, 2001), an integral discipline for any biological undergraduate course. In general, plants are often ignored, and even when considering the realm of parasitology within the plant kingdom, for a great amount of time the focus tended to narrow down to insects, fungi, and nematodes, primarily of interest in agronomic research and crop production (Kujuit, 1969). However, parasitism has independently evolved at least 12 different times in plants (Nickrent, 2020), including about 4500 species and ushering in a fascinating array of adaptations and ecological interactions that warrant exploration and understanding (Těšitel, 2016).

The 'signature organ' and common feature to all parasitic plants is the haustorium (Yoshida et al., 2016). It consists of a specialized multicellular organ that enables parasites to establish a physical and physiological connection to their hosts, from which essential nutrients and water (and carbohydrates, for holoparasites) are extracted (Teixeira-Costa, 2021; Stewart and Press, 1990). Parasitic plants encompass a diverse range of species, which can be found among trees, shrubs, and herbs, and are often categorized into hemi- or holoparasites according to their photosynthetic ability (Press and Phoenix, 2005). Parasitic plants

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can be further classified into root or shoot parasites, depending on where the haustorium is attached to the host. Hemiparasites (such as mistletoes) have green photosynthetic leaves, but rely on their host plant for water and nutrients to survive (Fig. 1a–c). These plants belong to diverse families, including Loranthaceae, Misodendraceae, Olacaceae, Santalaceae, Scrophulariaceae, Orobanchaceae, among others. They are predominantly found within the Santalales and Lamiales orders and the haustorium attaches to the branches (Glatzel and Geils, 2009) or roots of host plants (Irving and Cameron, 2009). In contrast, holoparasites (such as parasitic vines) have evolved to be entirely or majorly dependent on their host plants for carbohydrates and do not develop photosynthetic organs (Fig. 1d). They belong to different families such as Balanophoraceae (Santalales), Lauraceae (Laurales), Convolvulaceae (Solanales), Scrophulariaceae and Orobanchaceae (Lamiales). Similar to hemiparasites, holoparasites also develop haustoria, but these structures are connected both to the xylem and to the phloem of host plants, facilitating the extraction of nutrients and carbohydrates (Birschwilks et al., 2006). These distinctions in parasitic plant adaptations, between hemiparasites with their partial photosynthetic capabilities and holoparasites relying entirely on their hosts, underscore the fascinating diversity within this group of organisms. They exhibit remarkable strategies for seed dispersion, through specialized structures or vertebrate vectors matched by their unique method of establishment via haustorium connection with a suitable host, and for survival, drawing water, nutrients and photoassimilates from another plant.

This diverse group of plants exhibits great diversity in their geographical distribution, having successfully colonized a vast array of environments, spanning from Arctic to tropical regions (Teixeira-Costa and Davis, 2021). This widespread adaptability often correlates with their ability to parasitize a wide range of hosts (Nickrent, 2020). Some can have preferences or specificities for a single host species or a limited group of species, while others possess a broad host range, such as *Dendrophthoe falcata* recorded from over 400 host species (Hawksworth et al., 1993) and *Viscum album* being documented on over 450 host species (Barney et al., 1998). Parasitic plants can also exhibit unique behaviors, including self-attachment (autoparasitism), or they may even parasitize another plant parasite (hyperparasitism or epiparasitism) (Krasylenko et al., 2021). This spectrum of interactions underscores the complexity and diversity within this group of plants.

Research on parasitic plants has a long and fascinating history that spans several centuries. For example, ancient civilizations, as well as early herbalists and botanists were captivated by the enigmatic peculiarities of mistletoes. These parasitic plants held sacred significance, symbolizing fertility and resistance for Celtic Druids as far back as the 1st century (Thomas et al., 2023). In more recent history, parasitic plants have emerged as intriguing subjects in various scientific disciplines. Their unique adaptations for dispersal and early development have intrigued countless researches and have played a pivotal role in strengthen the arguments supporting Charles Darwin's theory of evolution.

The 20th century brought significant progress in parasitic plant research, thanks to groundbreaking advances in microscopy, genetics, molecular biology, plant physiology and ecological techniques. This progress largely revolved around investigating the physiological and biochemical mechanisms that enable parasitic plants to attach to their hosts and extract nutrients. Initially, research primarily centered on the detrimental impact of these plants on their host species and the potential financial losses they could incur. Parasites were often perceived as nuisances, akin to plant pests (McRitchie, 1990) or weeds (Spears, 1960). However, notable efforts were made by ecologists worldwide to acknowledge their importance as part of the biodiversity and potential ecosystem engineers (Watson, 2009; March and Watson, 2010; Quested, 2008), but also as food resource for different guilds of animals (Watson, 2001), and a determinant component on community assemblage (Joshi

Fig. 1. Examples of plant parasites: (A) *Passovia ovata* (Loranthaceae), a shoot hemiparasite growing on the host *Byrsonima verbascifolia* (Malpighiaceae) in Brasília, Brazil; (B) *Amyema sanguinea* (Loranthaceae), a shoot hemiparasite growing on the host *Eucalyptus miniata* (Myrtaceae) in Darwin, Australia; (C) *Santalum spicatum* (Santalaceae), a root hemiparasite growing in an arboretum at Whyalla National Park, Australia and (D) *Cassytha filiformis* (Lauraceae), a shoot holoparasite growing in Brasília, Brazil. All photos by M. Scalon.

et al., 2000), specially in the context of climatic instability and a warming world (Watson et al., 2022).

2. Research on plant–plant parasitism over the last 50 years – with focus on 21st century

To get a more detailed insight on research performed on plant–plant parasitism in the last 50 years, in October 2023, we compiled data from SCOPUS (www.scopus.com) using the key-words: hemiparasite OR mistletoe OR holoparasite. Using SCOPUS tools, we refined our compilation to papers published between 1970 and 2022 (Supplementary Material). We used the data provided on SCOPUS platform to identify how many papers were published in the area of Agricultural and Biological Sciences, Environmental Science, and Earth and Planetary Sciences. We evaluated the evolution in the number of papers through time and the corresponding author's country of origin. To get a more accurate view on plant–plant parasitism research, we refined our search, compiling all papers published between 2000 and 2022 to visualize the major themes explored on Plant–Plant parasitism studies and the most studied genera and families.

In a period of 50 years, 1116 papers were published on the theme (Fig. 2a). The study of plant parasites was almost inexpressive between 1970 and 1990, with only 60 papers published within 20 years (Fig. 2a). Between 1990 and 2000 we could observe a stability at a level of ca 20 papers published per year, with a significant exponential increase after 2010 (Fig. 2a), which leads to the highest peaks of production (around 60 papers per year) occurring between the period of 2016–2021 (Fig. 2a). Thus, the 21st century has witnessed a remarkable surge in the number of publications in this field, and the trend indicates ongoing growth and expansion. This research effort spans the globe and extends back to the formal publication of research in these areas. Parasitic plants have garnered global interests, with authors hailing from over 90 countries. The majority of authors are from English speaking countries, such as the United States, Australia and the United Kingdom, with Brazil, Germany, Canada, China, Mexico and Spain behind (Fig. 2b). The realm of parasitic plant research encompasses a multidisciplinary array of fields, including taxonomy, anatomy, plant physiology, evolutionary and molecular biology, ornithology, ecology, medicine, and pharmacology. Notably, the majority of papers on parasitic plants are found in the field of Ecology, followed by Physiology and Biochemistry (Fig. 2c). This diversity of research areas underscores the multifaceted nature of parasitic plants and their importance across a spectrum of scientific disciplines (Press and Graves, 1995).

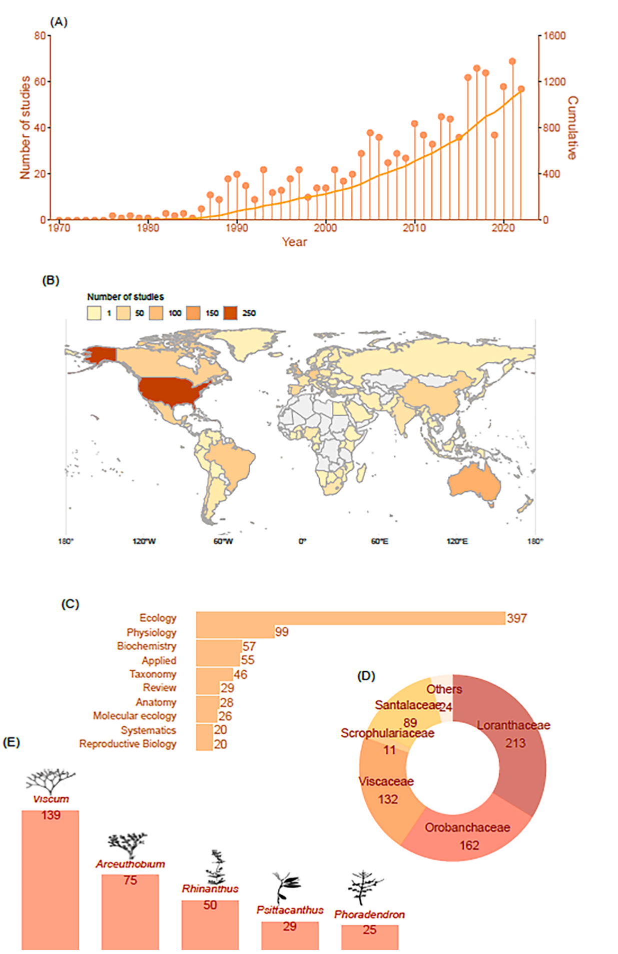

Fig. 2. Research data compiled for plant-plant parasitism studies from Scopus (www.scopus.com). (A) Evolution of number of studies per year (bars) and cumulative trend (line) between 1970 and 2022; (B) Distribution of studies per country (2000–2022); (C) Number of studies per most studied field area (2000–2022); (D) distribution for most studied families and (E) genera (2000–2022).

The most studied families are Loranthaceae (a predominant group in the tropics), Orobanchaceae (a predominant group in the temperate region) and Viscaceae (present in both temperate and tropical regions). Balanophoraceae is still a poorly known group, as well as other holoparasites, such as plants from Lauraceae (the *Cassytha* genus) and Convolvulaceae (the *Cuscuta* genus). *Viscum* is the most studied genus, followed by *Arceuthobium* (both very common in Europe and North America, respectively) and *Rhinanthus* (a common herb species of Europe). In turn, tropical most studied genera are *Psittacanthus* and *Phoradendron* (Fig. 2e), but many others such as *Loranthus* and *Struthanthus* were studied.

These data outline gaps that need to be filled, especially with studies focusing on reproductive biology of hemiparasites, molecular ecology, and even anatomy and morphology, which are the fields with less number of studies in this century (Fig. 2c). Taxonomy and systematics have been well explored, as a series of authors provided advances on taxonomy and systematics of parasitic plants (Su et al., 2015; Ortiz-Rodriguez et al., 2018; Dettke and Caires, 2021; Mathiasen and Kenaley, 2022), however the origins of some groups are still uncertain. The global south also needs more attention from researchers, especially Africa, which is still well under-studied in the theme of plant–plant parasitism (Fig. 2b). Asia, an important region for root hemiparasites (Štech and Wesselingh, 2010), also needs significant efforts (Fig. 2b).

3. Call of papers

In light of this, we are delighted to introduce our Special Issue titled "Plant Parasitism: Ecology, Evolution and Functional Aspects". We aim to explore deeper into this captivating field by inviting submissions that examine diverse aspects of both hemi- and holoparasites, affecting subterranean or aerial organs, with studies performed anywhere in the world. Our data analysis suggests that deeper approaches are needed to understand the reproductive biology, the evolution and systematics of this group, morphological aspects and even ecological studies advancing the understanding of parasitism effects on ecosystems and communities, especially in Africa, Asia and South America, the less studied regions. Potential major breakthroughs in plant-plant parasitism research that are still incipient and could have a significant impact on our understanding of plant-plant interactions might include (1) unraveling the molecular mechanisms in signaling pathways between host and parasite; (2) host recognition and nutrient transfer, which could provide insights into plant communication tools and plant defense mechanisms; (3) parasitic plant control over host survival and reproduction; (4) uncovering the evolutionary adaptations of parasitic plants and their adaptation to diverse environments and (5) developing models and tools to predict parasitic plants behavior in future climate change scenarios and their consequences both to natural environments and to forestry and agriculture. Research and opinion papers and reviews are welcomed. This endeavor promises to shed more light on the fascinating world of plant parasitism and its ecological and evolutionary implications.

CRediT authorship contribution statement

Marina C. Scalon: Conceptualization, Formal analysis, Writing – original draft. **Hermann Heilmeier:** Writing – review & editing. **Davi R. Rossatto:** Conceptualization, Data curation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Data availability

Data at supplementary material

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Supplementary materials

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