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Role of Interactions Among Host Plants, Parasitic Plants, and Plant-Parasitic Insects in Host Plant Invasion

Amanula Yimingniyazi*

Department of Plant Protection, Xinjiang Academy of Agricultural Sciences, Key Laboratory of Integrated Pest Management on Crops in Northwestern Oasis, Ministry of Agriculture, Xinjiang Key Laboratory of Agricultural Biosafety, Urumqi, China.

Review Article

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***For Correspondence**: Amanula Yimingniyazi, Department of Plant Protection, Xinjiang Academy of Agricultural Sciences, Key Laboratory of Integrated Pest Management on Crops in Northwestern Oasis, Ministry of Agriculture, Xinjiang Key Laboratory of Agricultural Biosafety, Urumqi, China.

Email: amanula.y@xjau.edu.cn or aixjau812@163.com

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ABSTRACT

During long-term evolution, host plants, parasitic plants, and plant-parasitic insects have formed complex and diverse relationships based on mutual adaptation. Studying the interactions among these three trophic levels can provide new insights into the communication mechanisms and ecological functions among them, and offer important theoretical guidance for ecological security. This paper has summarized the interactions among the three trophic levels, focusing primarily on the parasitic relationship between host plants and parasitic plants, the parasitic relationship between parasitic plants and plant parasitic insects, and the indirect relationship between host plants and plant parasitic insects. It has elaborated on the impact of these three interactions on biological invasion and summarized the theoretical hypotheses related to parasitic relationships. The shortcomings of this research have been highlighted and future research directions have been identified to provide a reference for biological control research.

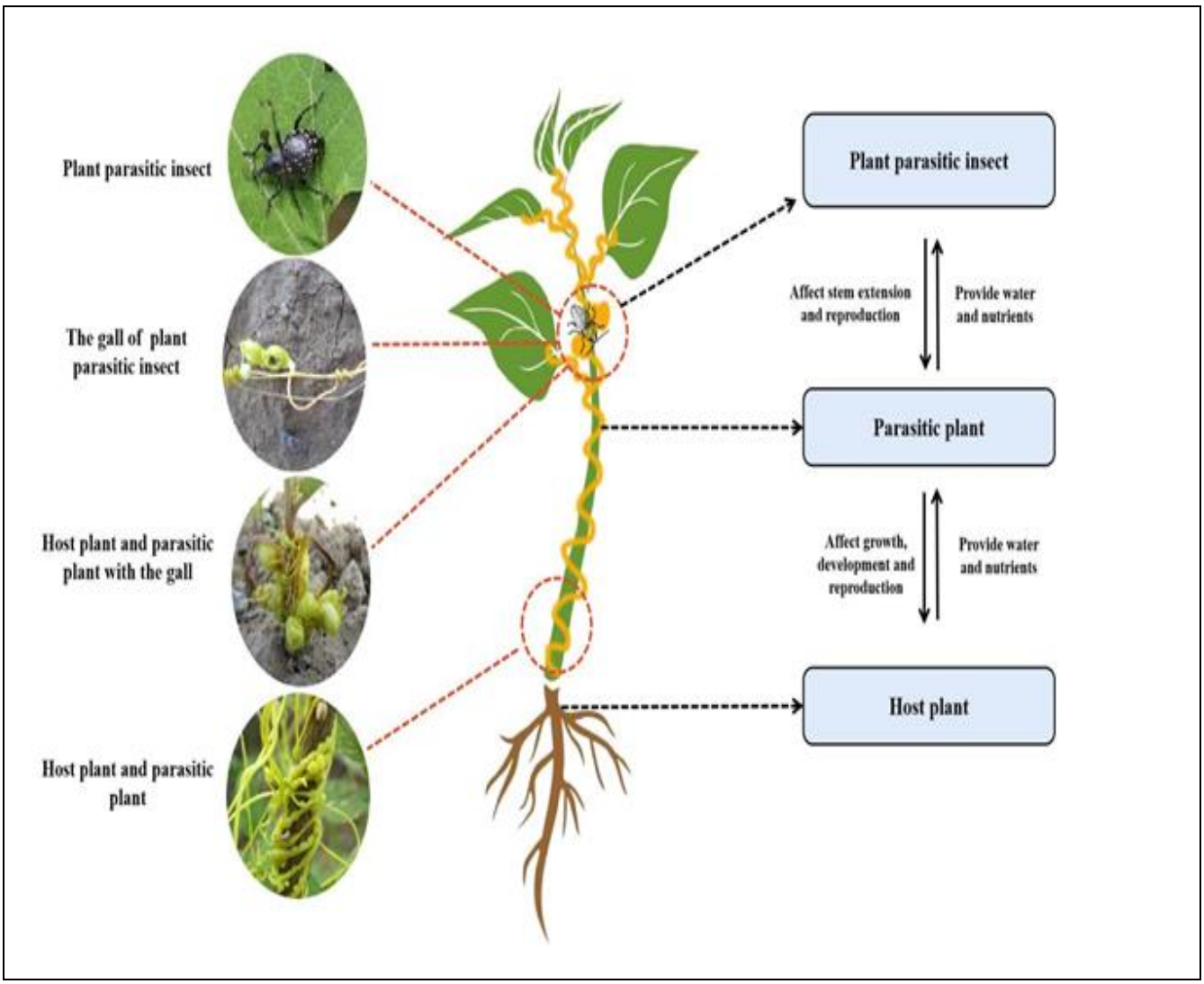
Keywords: Tertiary nutrition relationship; Parasitism; Biological invasion; Biological control

INTRODUCTION

Studying the interactions among the three trophic levels of host plants, parasitic plants, and plant parasitic insects is a key topic in theoretical and applied ecology [1-3]. Among them, the host plant, that is, the first trophic level, namely the producer, the parasitic plant, that is, the second trophic level, namely the first consumer, and the plant parasitic insect, that is, the third trophic level, namely the second consumer, adapt to each other as the prerequisite is to form an extremely complex and

diverse relationship directly or indirectly [4-6]. Parasitic plants absorb nutrients and water from host plants through haustoria to provide their own survival and development needs, thereby affecting host plants [7-9]. Plant parasitic insects affect parasitic plants by parasitizing and multiplying them as shown in figure 1.

Figure 1. Interactions among host plants, parasitic plants, and plant parasitic insects.



Host plants provide water and nutrient resources directly or indirectly to parasitic plants or plant parasitic insects.

Therefore, studying the interactions among the three trophic levels of host plants, parasitic plants, and plant parasitic insects can provide new ideas for exploring the communication mechanisms among the three, and provide important theoretical guidance for ecological security as shown in table 1 [10,11].

Table 1. Hypotheses of Parasitic Relationships.

	Hypothesis	Explanation
Common Hypotheses of Parasitic Relationships	Growth Defense Trade-Off Hypothesis	This hypothesis states that there is a balance between growth and defense for plants. Under adverse conditions, such as when plants are stressed by abiotic factors such as temperature, water, and nutrients, or damaged by biotic factors such as herbivores and insects, it will increase the investment in defense such as increasing defense substances by reducing investment in its own growth [12,13].
	Resource Availability Hypothesis	This hypothesis states that the relationship between natural enemies and resource availability will lead to changes in the balance of plant growth– defense [14,15].
	Balanced Growth Hypothesis	This hypothesis states that when plants adapt to environmental changes, they can maximize the acquisition of limited resources such as water, nutrients, and light by adjusting the distribution of biomass in various organs, thereby increasing the plant growth rate [16].
	Best Defense Hypothesis	This hypothesis states that the production of plant secondary metabolites is at the cost of reducing plant growth. Plants only produce secondary metabolites when the defense benefits obtained by secondary metabolites are greater than those obtained by plant growth [17-19].
Hypothesis of Parasitic Relationship Between Alien Species and Native Species	Enemy Release Hypothesis	The hypothesis states that the successful invasion of alien species into new habitats is due to the escape from the control of natural enemies that co-evolved in the origin, resulting in the expansion of the distribution range and the increase in number of alien species [20,21].
	Biotic Resistance from Enemies Hypothesis	This hypothesis states that in the new environment of the invasive place, local or alien natural enemies may inhibit or delay the colonization, naturalization and development of alien plants by taking the alien plants as food or host and may establish relatively strong adverse effects on the population of alien species to hinder its invasion [22].
	Evolutionary Reduced Competitive Ability Hypothesis	The hypothesis states that the attack pressure on the alien plants is reduced due to escaping from the natural enemies in native habitats such as parasites, pathogens, fungi, or animals. There tend to be fewer invasive plants in new habitats than in native habitat areas. Such life changes can weaken the competitiveness of individuals and then affect the population dynamics of invasive species. This, in turn, can become a limiting factor for the spread of invasive plants [23].
	Evolution of Increased Competitive Ability Hypothesis	The hypothesis states that the attack pressure that the alien plants suffered is reduced due to escaping from the natural enemies in native area such as parasites, pathogens, fungi, or animals. The invasive plants can distribute the resources from defense to growth and reproduction. Therefore, the invasive plants tend to be taller or produce more seeds in new habitats than in native areas. Such changes in life characteristics can enhance the competitiveness of individuals and then affect the population dynamics of invasive species, becoming the driving force for the spread of invasive plants [24,25].

LITERATURE REVIEW

To date, prior research on the relationship among the three trophic levels has mainly focused on the following aspects.

Relationship between host plants and native parasitic plants

The relationship between the host plant and the parasitic plant is a mutual relationship between two different trophic levels. This includes the host plant, which directly provides water and nutrient resources for the parasitic

plant and absorbs nutrients from the host plant through the haustorium to provide their own survival and development, thus affecting the host plant [26-28]. The relationship between the two is manifested in the following two aspects.

(1) Effect of parasitic plants on host plants. Parasitic plants do not have enough chloroplasts, lose their autotrophic ability, and rely on plundering water and nutrients from the host to maintain the nutrients needed for their own survival to varying degrees [29-31]. Therefore, parasitic plants parasitize the roots, stems, and other parts of the host. In turn, they affect the growth and development of the host plant by reducing the photosynthetic rate of the host plant, competing with the host plant for nutrients, and the competitive relationship between the host plant and the non-host plant. This further affects host plant population dynamics, community structure, function, and succession [32,33]. The influence of parasitic plants on host plant individuals is mainly manifested in the following four aspects.

First, we examined its impact on growth and development. This is mainly reflected in plant seedling growth, plant height, biomass, and leaf area. A comparative study was conducted on the effects of parasitism and non-parasitism on the morphology, quantity, and biomass of the three hosts. This showed that the parasitism of southern *Cuscuta* significantly reduced the crown width, root length, plant height, and components of the three types of cocklebur. Quantity and other indicators also affect growth and development [34]. Second, there are effects on reproductive characteristics, including the plant flowering number, fruit number, seed yield, seed-setting rate, and seed vigor. *Cuscuta campestris* is an invasive plant *Mikania micrantha*, which significantly reduces its photosynthetic capacity and inhibits the reproduction of *Mikania micrantha* by changing the distribution of the host plant biomass [35]. The third is its impact on phenology and life history. This is mainly manifested in the length and the start and end times of each stage in the life history of the host plant. After the parasitization of *Mikania micrantha* by the *Cuscuta campestris*, it can rapidly form a yellow cover on its leaves, which weakens its photosynthetic ability. Meanwhile, the *Cuscuta* absorbs the nutrients of *Mikania micrantha*, resulting in a slower growth rate [36]. Fourth, it affects competitiveness. This is mainly manifested in the acceleration or slowdown of the growth rate of plants, their biomass, and their distribution. When the exotic plant *Sapium sebiferum* enters a new environment, its resources are redistributed because they are out of the control of its natural enemies and are preferentially allocated for growth and reproduction. This leads to strong competitiveness and weak defensive capability [37].

Host plant damage caused by parasitic plants inhibits and promotes plant growth. The compensatory growth of plants depends on the net effect of promotion and inhibition. Therefore, parasitic plants may affect the host in the following three situations. First, to promote growth, parasitic plants promote the photosynthetic ability of host plants through a small degree of parasitism, compensate for the loss of host plant resources due to parasitism, and promote the growth of host plants. *Cuscuta reflexa* can increase the light saturation point of *Leguminosae* and various non-legume host plants, and *Striga* parasitic plants can promote photosynthesis in *Sorghum* [38]. Second, growth inhibition: Parasitic plants change the physiological characteristics of the host by absorbing nutrients from the host such that the host cannot grow normally or even die. *Cuscuta japonica* parasitic invasive plant *Solidago canadensis* can cause dwarf and yellow leaves, and substantially hinder its growth and development [39]. Third, parasitic plants have no influence on host plants, except for the above two types, and some parasitic plants have no obvious influence on host plant growth. In the *Orobanche cernua*-potato (Solanum tuberosum) system, parasitic plants had no pronounced effect on photosynthesis in young leaves of the host [40].

(2) Effect of host plants on parasitic plants. Host plants affect the survival, development, reproduction, and population dispersal of parasitic plants by providing them with water and nutrients. The influence of host plants on individual parasitic plants mainly manifests in the following four aspects. In terms of the impact on the distribution, the emergence of host plants increases the diversity of host plants and their environment and expands the distribution area of parasitic plants. Investigating Mistletoe and Sandalwood distribution in arid shrublands in central Australia showed that the distribution of Mistletoe in a certain area was determined by a variety of biological factors, such as host characteristics [41]. The impact on survival the emergence of host plants provides more parasitic environments for parasitic plants and improves their survival rate of parasitic plants. Parasitic plants have higher parasitism rates on adapted host plants and lower parasitism rates on non-adapted host plants or new host plants [42]. In terms of the impact on phenology and life history, the phenology and life history of parasitic plants differ among host plants. Therefore, the emergence of host plants may alter the phenology and life history characteristics of parasitic plants [43,44]. Regarding the effect on reproduction, owing to differences in the external morphology and internal structure of different host plants, the reproductive characteristics of parasitic plants vary. A comparative study on the reproductive number, that is, the fruit biomass of *Cuscuta australis* on three weeds of the genus *Xanthium* found that it was considerably lower than that of *Xanthium sibiricum* on invasive *Xanthium spinosum* and *Xanthium italicum* [34].

The relationship between parasitic plants and plant parasitic insects

The relationship between parasitic plants and plant parasitic insects is a mutual relationship between two different trophic levels. The chain-like nutritional links formed between them are known as food chains [45-47]. Among them, plant parasitic insects are insects that attach to the body or surface of host plants for a specific period or lifetime and rely on the host to obtain nutrients to maintain their own growth and development [48]. This includes *Curculio dentipes* parasitic *Quercus*, leaf gall aphid parasitic *Ulmus pumila*, and *Cnaphalocrocis medinalis* parasitic *Oryza sativa*. Plant parasitic insects feed on the host, thereby affecting the normal growth and metabolism of the host, reducing biomass, damaging tissues and organs, and limiting flowering and fruiting. In severe cases, this can lead to the death of the host [49]. The rhizomes, stems, and leaves of *Alternanthera philoxeroides* are consumed in large quantities by *Agaricales hygrophila*, inhibiting its normal growth and development of *Alternanthera philoxeroides*.

To date, research on the relationship between plant parasitic insects and their host plants has mainly focused on biological control, such as weed control using insects. *Lemascut uarils* become parasitic on *Cuscuta*, which causes *Cuscuta* insect gall formation. *Lemascut uarils'* egg–larva–pupa parasitize the gall, the larvae mainly feed on the gall tissue, and the adults mainly feed on the young stem sections of *Cuscuta*. Feeding by *Lemascut uarils* destroys the fibrous tissue in the stem segment of *Cuscuta*, thereby destroying the transport of *Cuscuta* nutrients, effectively inhibiting the extension of the stem segment of *Cuscuta* and reducing the parasitic ability of *Cuscuta* [5,49]. *Agasicles hygrophila* is a parasitic larval pupa plant that is a monophagous parasitic insect of *Alternanthera philoxeroides*. After hatching, the larvae parasitically pupate on *Alternanthera philoxeroides*. The larvae and adults feed on *Alternanthera philoxeroides* in large quantities to inhibit their growth and reproduction.

The relationship between host plants and plant parasitic insects

An indirect relationship exists between host plants and plant parasitic insects. Therefore, the formation of the relationship between the two need to rely on intermediate-media plants [50,51]. The indirect relationship between the two is mainly manifested in the following ways. Because the host plant indirectly provides water and nutrient

resources for plant parasitic insects, the host plant growth indirectly affects its growth and development. The flowers and extrafloral nectaries of plants provide nutrients for natural enemies of parasitic plants. Adults can obtain nutrients from the flowers or extrafloral nectaries, which is beneficial for prolonging adult life and improving fertility. Extrafloral nectaries high in sugar and foods high in proteins and lipids play an important role in the relationship between many plants and their natural enemies [46]. The parasitism of plant parasitic insects destroys the fibrous tissue in the stem segment of the parasitic plant, thereby destroying the transport of nutrients of the parasitic plant. This can effectively inhibit the extension of the stem segment of the parasitic plant, thereby reducing the parasitic plant parasitic ability and the effects of parasitic plants on the growth and development of host plants. The parasitism of *Lemascut uaril*s can limit the extension of the stem segment of *Cuscuta*. Gall formation can intercept the nutrients from *Cuscuta* and reduce the flowering and seed-setting rates [5]. The three trophic layers of host plants, parasitic plants, and plant parasitic insects are closely linked. Therefore, adaptive changes in plant parasitic insects may cause changes in parasitic plants, ultimately leading to changes in host plants. In their natural state, the environment in which parasitic plants and their natural enemies are located is an ecosystem in which a variety of organisms coexist. A plant is often harmed by multiple parasitic plants. Therefore, the host-searching behavior of a parasitic plant is often influenced by the parasitic behavior of other parasitic plants. Similarly, a parasitic plant often has multiple natural enemies, and the behavior of natural enemies searching for hosts will also affect each other. The natural enemies of parasitic plants may also be preyed upon or parasitized by other insects. Therefore, the study of the relationship between host plants, parasitic plants, and their natural enemies must be conducted at multiple trophic levels to fully reflect their relationships [52].

Interactions of host plant–parasitic plant–plant parasitic insects and plant invasions

After alien plants are introduced into a new environment, they escape the natural enemies and competitors in the original distribution area and leave commensal organisms that are indispensable for their survival. They then form a new interspecific relationship with local or other alien organisms in the introduced area [53-55]. Among them, positive interactions promote or increase the survival, development, and reproduction of exotic plants. Meanwhile, negative interactions inhibit or reduce plant survival, development, and reproduction [56]. By studying the interspecies relationships of alien plants, we can understand the processes of ecesis, colonization, reproduction, spread, and outbreak of alien plants after arriving in new areas. This can also provide an important theoretical basis for predicting the scope of their spread [57]. Therefore, studying interspecific relationships between alien plants and native species has become a key research focus in the field of invasive biology. The importance of the sympatric distribution of non-native host plants, parasitic plants, and plant parasitic insects is mainly manifested in the following six aspects.

First, because alien host plants are generally distributed in a concentrated manner and have a higher density than other local plants, it is easy to attract parasitic plants. This then results in parasitic plants parasitizing the non-native host plants and the indigenous plants or crops growing around the non-native plants [54]. Second, the emergence of alien host plants increases the host plant diversity. This improves the survival rate of parasitic plants and promotes their reproduction and spread, leading to a substantial decline in crop yields [58]. Parasitic plants play an important role in regulating the reproduction of alien host plants. A slightly high density of parasitic plants can limit the growth of alien plants and crop production. A reduction in the density of parasitic plants may promote the invasion of non-native host plants, which is beneficial for the growth of their populations and affects agricultural production and natural ecosystem stability [59,60]. Fourth, both parasitic plants and non-native host plants are host

plants for a variety of insects and diseases. They indirectly affect the local ecological environment and crop production by spreading insects and diseases [56]. Fifth, the parasitic plants reduce the biomass of non-native host plants by absorbing the haustorium. Meanwhile, nutrients absorbed by parasitic plants from host plants cannot be assimilated effectively, or "leakage" of resources occurs in the haustorium, thus affecting the soil nutrient cycling in ecosystem [61]. Sixth, when alien host plants, parasitic plants, and plant parasitic insects are distributed in the same domain, the plant parasitic insects inhibit the growth and development of the parasitic plants. This may promote the invasion of the alien host plants.

DISCUSSION AND DISCUSSION

Theoretical hypotheses related to the interaction of host plants–parasitic plants–natural enemies

Regarding the interaction among the above three trophic parties, international researchers have conducted extensive research and put forward various theoretical hypotheses: (1) Common hypotheses related to parasitic relationships include the growth–defense trade-off hypothesis, resource availability hypothesis, balanced growth hypothesis, and best defense hypothesis [24,62]. (2) Common hypotheses related to the parasitic relationship between alien and native species include the enemy release hypothesis, the biotic resistance from enemies hypothesis, the evolutionary reduced competitive ability hypothesis, and the evolution of increased competitive ability hypothesis [53,54,57].

Research limitations

Although considerable progress has been made in the study of host plant–parasitic plant–plant parasitic insect interactions, there are still many limitations. To date, research on parasitic relationships has mostly focused on the influence of parasitic plants on the growth, development, and invasion of host plants. Meanwhile, there have been relatively few studies on the influence of host plants on the growth, development, and reproduction of parasitic plants and the relationship between plant parasitic insects and host plants, or between parasitic plants. Second, there has been relatively little systematic research in this field. In some studies, related to parasitic relationships, experimental data can only prove the effect on one party, but there is insufficient experimental data on the other. Third, the depth of some prior research is insufficient. The interactions among alien host plants, parasitic plants, and plant parasitic insects affects the invasion of alien species and the expansion of native species. It also affects the development and reproduction of other non-native species and native species, which, in turn, increasing the impact on the invasive environment. Fourth, at present, there is no complete theoretical system to fully explain these phenomena, predation, and mutualism among the three trophic levels, such as the mutualism–enemy release hypothesis, competition–enemy release hypothesis, mutual benefit symbiosis–competitive ability hypothesis, and the natural enemy's natural enemy hypothesis. However, to date, there have been no related theories or hypotheses about the tertiary trophic relationship of host plant–parasitic. There have been some theories and hypotheses put forward on the relationship between competition plant–plant parasitic insects, that is, the parasitic–parasitic relationship. Fifth, to date, there have been relatively few studies on this topic. In the past 30 years, many studies on biological invasion mechanisms have been conducted internationally. A variety of theoretical hypotheses have been proposed, which have been verified in many invasion cases. These studies have explained the reasons why some alien species have successfully invaded. However, to date, there have been relatively few studies conducted at the national level.

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