Field Dodder: Life Cycle and Interaction with Host Plants

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Abstract

Cuscuta as a generalist type of holoparasitic plant interacts with various host plants in different manners, and all *Cuscuta* species depend (absolutely) on host plants to complete their life cycle. Field dodder is a parasitic plant that attaches to stems and leaves of broadleaf plants, including weeds, field crops, vegetables, and ornamentals, across most agricultural regions of the world. Most hosts of *Cuscuta* plants are passive, only a few hosts are known to show clear resistance (e.g., *Ipomoea* sp.). Unlike other weeds occurring in anthropogenic habitats that have been well-studied in their taxonomic, biological, and ecological aspects, as well as their anatomical and physiological properties to some extent, the parasitic flowering species of the genus *Cuscuta* have been examined very scarcely despite the great damage that they are able to cause. More extensive research is required

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in order to develop new means for parasitic weed control. A basic research should identify new targets for control within the life cycle of the parasites and among their metabolic activities.

Keywords

Field dodder · Host plant · Life cycle · Metabolic activities

Abbreviations

chl a/b	Ratio of chlorophyll a to b
DAI	Days after infestation
Fm	Maximal fluorescence
Fo	Minimum fluorescence
Fv	Variable fluorescence
Fv/Fm	Maximum quantum efficiency of photosystem II
HLR	Hypersensitive-like response
IF	Intensity of fluorescence
RCC	Relative chlorophyll content
TCC	Total chlorophyll content
Φ_{PSII}	Effective fluorescence yield of photosystem II

1   Introduction

Plants of the genus *Cuscuta* (common name: dodder) are obligate holoparasitic species. Dodders are the most important group of parasitic weeds in the world, inhabiting virtually every continent and causing sweeping damage to both crop and non-crop species [1]. Agriculturally, the most important *Cuscuta* species are *C. campestris* and *C. pentagona*, which show an almost worldwide distribution and have a wide host spectrum. Field dodder (*C. campestris*) parasitizes many different plants, inducing negative impacts on the growth and yield of infested hosts, and has significant effects on the structure and function of plant communities that are infested by these holoparasites [2, 3]. Parasitic plants fuse to host vascular systems (xylem and phloem) via a specified organ present in all parasitic plants, the haustorium. This organ serves as the structural and physiological bridge for the parasites to withdraw water, minerals and organic molecules, and solutes from host plant conductive systems, leading to severe host growth and yield reduction [4]. Parasitic plants of the genus *Cuscuta* either have no chlorophyll at all, or merely low amounts of it, or usually do not have a photosynthetic activity [5, 6]. However, all *Cuscuta* species fully depend on host plants to complete their life cycle and therefore are considered as obligate holoparasites.

Plants are sessile organisms that have evolved unique strategies for interacting with various environmental changes as well as dealing with the biological influence of other living organisms. These can roughly be divided into abiotic stress responses and biotic responses [7, 8]. Pathogenic responses are typical examples of biological interactions in plants. These include interactions with bacteria, virus, fungi, and animals (e.g., parasitic nematodes and herbivorous insects). In contrast, less is known about plant-plant

interactions. Especially, although the morphology and anatomy of *Cuscuta* spp. are well-studied, the cellular mechanisms of the interactions between parasitic plants and their susceptible hosts are not well understood.

Cuscuta can serve as a key model plant for deciphering the mechanism of parasitism as well as for examining host plant-parasite plant interactions [9]. Most studies used isotope labels and observed carbon or nitrogen flux between *Cuscuta* and the host plant [10, 11]. Some studies compared metabolites (e.g., plant hormones) in *Cuscuta* seedlings (haustorium-induced and/or non-induced seedlings) with *Cuscuta* attached to host plants [12, 13]. Documented host plant responses to attack by *Cuscuta* spp. include a hypersensitive-like response (HLR) and phytoalexin production by a non-host tropical liana in response to *C. reflexa* [14] and the expression of a PR gene by *Cuscuta*-infested alfalfa [15]. Best studied among host plant defenses against *Cuscuta* spp. are the responses of resistant tomato varieties to *C. reflexa*, in which elongation of hypodermal host cells, a subsequent HLR, and accumulation of phenolics and peroxidases at the attachment site create a mechanical barrier that can block haustorial formation [16, 17].

Effective field dodder control is extremely difficult to achieve due to the nature of attachment and close association between the host and the parasite, which requires a highly effective and selective herbicide to destroy the parasite without damaging its host. To establish strategies to control parasite growth and restrict the spread of field dodder in crop fields, it is important to learn more about this pest, studying its life cycle, development, and parasitic-host interactions.

2   Biology and Ecology Characters of Field Dodder

Autotrophic flowering plants constitute the predominant group among weed species, but weeds also include some semiparasitic and parasitic flowering plants. The parasitic plants are represented by approximately 4200 species classified in 274 genera, which makes a little more than 1% of all flowering plants. Only some 11% of all genera include species that may be considered as parasites of cultivated plants. The worst economic damage in important host crops is caused by species from only four genera: *Cuscuta*, *Arceuthobium*, *Orobanche*, and *Striga* [18]. The genus *Cuscuta* L. (dodders) is one the most diverse and challenging groups of parasitic plants with more than 200 species and over 70 varieties [19–21]. The stem of a field dodder plant is threadlike and twining, and it is either leafless or the leaves are reduced to hardly visible scales. Fully matured field dodder seeds fall off and accumulate on the ground. They may then either germinate during the following season if a suitable host plant is growing in the vicinity or may stay dormant until such conditions have occurred [22]. These stem parasites attach to the host by haustoria and depend entirely (or nearly so) on their hosts for the necessary water and nutrient supplies [2, 23]. At an appropriate moment of maturation, a field dodder plant forms inflorescences with abounding hermaphrodite and actinomorphic flowers. The flowers are hermaphroditic, tiny, mostly white, reddish, or yellow. Petals are either individual or coalescent. The corona is bell-shaped or round, mostly with four or five petals (Picture 1a, b). The flower has five stamens. The fruit is a pod containing one to four seeds. The seed is tiny,

Picture 1 Flowers of field dodder (*C. campestris* Yunck.) (Saric-Krsmanovic 2013 – org. foto)
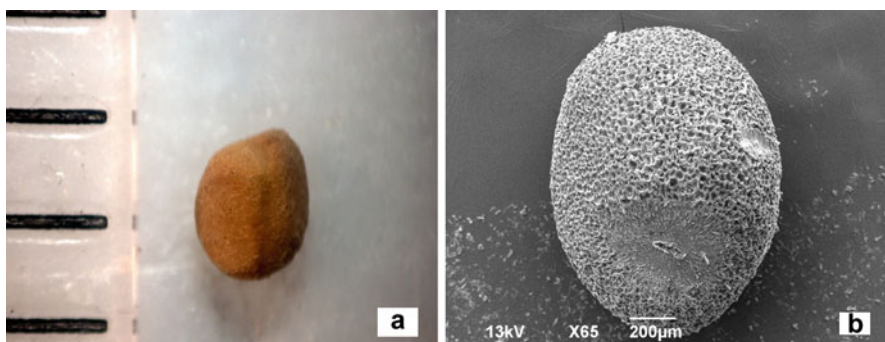
Picture 2 Seed of field dodder (*C. campestris* Yunck.) (Saric-Krsmanovic 2013 – org. foto)

spherical, rough, and light brown (Picture 2a, b). The seed of this parasitic flowering plant germinates on soil surface from May throughout June. Field dodder is a thermophilic species, and its optimal temperature for germination is 30 °C [24]. Dodder seeds retain vitality in soil over more than 10 years. A single plant is able to form up to 15,000 seeds, and their abundance constitutes the main mode of survival of that parasite in the environment [25]. Its reproduction may also be vegetative through segmentation of its threadlike stem. Such reproduction mode is frequent in alfalfa and clover crops after harvest and haying, which enables its transfer from infested plots to noninfested fields [26].

3 *Cuscuta* Life Cycle

The steps in the life cycle of parasite plants include (1) seed germination; (2) early development of the seedling; (3) search for a host plant, haustorium induction and invasion of the host, and haustorium maturation; and (4) interaction with the host plant [27, 28].

3.1   Seed Germination and Searching for a Host Plant

The life cycle of *Cuscuta,* as in other angiosperms, begins with seed germination. Germinating *Cuscuta* seedlings depends on limited seed reserves; they are unable to survive alone for a long time and must find an appropriate host plant stem within a few days [29]. *Cuscuta* seedlings normally live less than 3 weeks before becoming parasitic.

Seed dormancy is an important feature of *C. campestris* that ensures its survival as a parasite of crops [30]. There are three different types of seed dormancy (morphological, physical, and physiological), at least two of which have evolved on several separate occasions [31]. Dormancy of *C. campestris* occurs owing to its hard seed coat [32]. The percentage of hard seeds at dispersal varies among *C. campestris* [33] and *C. chinensis* plants [34]. Dormancy can be broken by the activity of soil microorganisms or by tillage, causing scarification of seed coat [35], etc. The dynamics of germination of *C. campestris* depends on a double mechanism of dormancy. After a period of primary dormancy (additional maturation caused by coat impermeability), the seed goes into an annual cycle of secondary dormancy. In *C. campestris*, secondary dormancy occurs at the end of summer, and it prevents germination during the following autumn and winter in order to avoid the season in which potential hosts of the temperate region would be scarce due to low temperatures. Secondary dormancy ends at the end of winter when temperature begins to grow and overall conditions for germination and growth of host plants improve [25]. Physical dormancy has been reported for seeds of several *Cuscuta* species: *C. campestris* [25, 30], *C. trifolii* [36], *C. monogyna* and *C. planiflora* [37], *C. chinensis* [34], *C. gronovii*, *C. umbrosa*, *C. epithymum*, and *C. epilinum* [38]. However, it is not common for *Cuscuta pedicellata* [39] because seeds of that species are readily water permeable due to a specific structure of their epidermis and endosperm.

To find and catch potential hosts, *Cuscuta* plants recognize plant volatiles as chemoattractants which guide seedling growth and increase the chances of successful establishment of a connection [29]. However, expert options vary as what is the necessary impulse for germination of field dodder seeds. Some researchers [40, 41] believe that *Cuscuta* spp. do not require host-root exudates to stimulate germination, similar to some important holoparasitic weeds of the genus *Orobanche* and some hemiparasitic weeds in the genus *Striga*. Field dodder as a stem parasite is strongly impacted by light signals, which stimulate germination of its seeds [42–44]. Field dodder seedlings tend to grow in the direction of light source, primarily red/far-red light, which help them find hosts, while far-red and blue light have a significant role in prehaustorium formation. Recognition of a host occurs through phototropic mechanisms, and some authors claim that chemotropism (movement induced by chemical stimulus) and thigmotropism (movement induced by mechanical stimulus, i.e., by touch) have equally important roles in host recognition process [45]. Mechanical stimulus, following initial contact with the host plant, induces cell differentiation and haustorium formation, and its subsequent penetration into the host stem. This is facilitated by the recruitment of stress-responsive and defense genes for host recognition and activity of cell wall-modifying enzymes [46–48]. Runyon et al. [29] found that volatile chemical substances were also important for movement of *Cuscuta*

campestris seedlings in the dark. Saric-Krsmanovic et al. [49] examined the effect of host seeds on germination and initial growth of seedlings of field dodder plants in the dark, and under white light, the seeds of four host plants were used (watermelon, red clover, alfalfa, and sugar beet). The data of host seeds showed that light was a significant initial factor (83–95%, control 95%) for stimulating seed germination of field dodder plants, apart from host presence (73–79%, control 80%). *Cuscuta* can also change from one host to another and back. If the plant needs special volatile chemicals to search for a host, it is difficult to explain why it can parasitize so many different plants except there is a strong overlap between the volatile compositions of the various plants.

3.2   Attachment and Haustorium Development

The ability to form specialized organs for absorption, i.e., haustoria (Picture 3), is the chief adaptive character of all higher parasitic plants [50]. In field dodder plants, such structures are created from the stem meristem tissue of a parasitic plant, and they are considered as modified adventive roots [22]. Haustoria may develop even when no potential host is around [43, 51, 52]. The main stimulus for developing haustorial tissue may be simply the contact with another surface, such as glass [43, 53], filter paper [54], or plastic [55].

The development of haustoria may be roughly differentiated into three stages [56]: (1) attachment (i.e., establishing of a connection with the host tissue), (2) penetration (insertion into the host tissue), and (3) conductive stage (transmission of nutrients).

Sharp pointed haustoria develop from appressoria that enable the parasite to draw organic and mineral substances from its host. Obligate parasites are unable to


Picture 3 Haustorium of *Cuscuta campestris* Sarić-Krsmanović, M. (2013). Biology of field dodder (*Cuscuta campestris* Yunk.) and options for its control. Doctoral thesis, University of Belgrade, Faculty of Agriculture. (In Serbian)
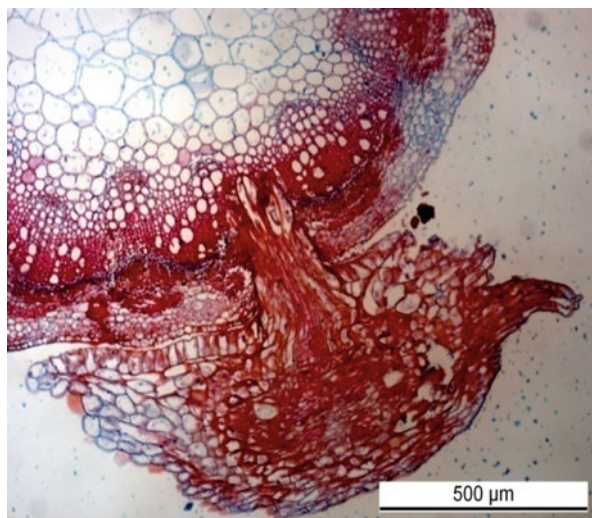
develop without assimilates drawn from their host plants because they are unable to perform photosynthesis [23, 57] or their photosynthetic capacity is very weak [50]. Even though dodder plants possess a functional photosynthetic apparatus within a ring of cells surrounding vascular tissue [50], the amount of organic matter produced there is too small to provide for the plant sufficiently, so that 99% of the required carbon is still drawn from the host [58].

After finding an appropriate host plant, the first physical contact initiates the attachment phase, in which the parasitic epidermal and parenchymal cells begin to differentiate into a secondary meristem and develop prehaustoria, also known as adhesive disk [59, 60]. Important signals initiating and controlling this pre-haustorium formation include mechanical pressure, osmotic potential, and phyto-hormones such as cytokinins and auxin [1, 61]. The prehaustorial cells start to produce and secrete adhesive substances, such as pectins and other polysaccharides, reinforcing the adhesion [47]. During the attachment phase, host cells in the prox-imity of *Cuscuta* haustoria respond with an increase in cytosolic calcium, detectable in host plants expressing aequorin as calcium reporter. Within the initial several hours of contact, *Cuscuta* also induces the host plant to produce its own sticky substances, such as arabinogalactan proteins, to promote adhesion [62]. These glycoproteins are secreted by the host plant and localized to the cell wall where they can force the adhesion together with other sticky components such as pectins.

The attachment phase is followed by penetration phase as prehaustoria develop into parasitic haustoria that penetrate the host stem through a fissure. This breach is effected by mechanical pressure [1] and is supported by biochemical degradation of host cell walls caused by secreted hydrolytic enzymes such as methylesterases [46] or complexes of lytic enzymes consisting of pectinases and cellulases [48]. Cells at the tip of the invading haustoria form "searching hyphae" which try to reach phloem or xylem cells of the host plant's vascular bundles (Picture 4). A day or two later, epidermal cells of "interior haustoria" begin to elongate and form unicellular
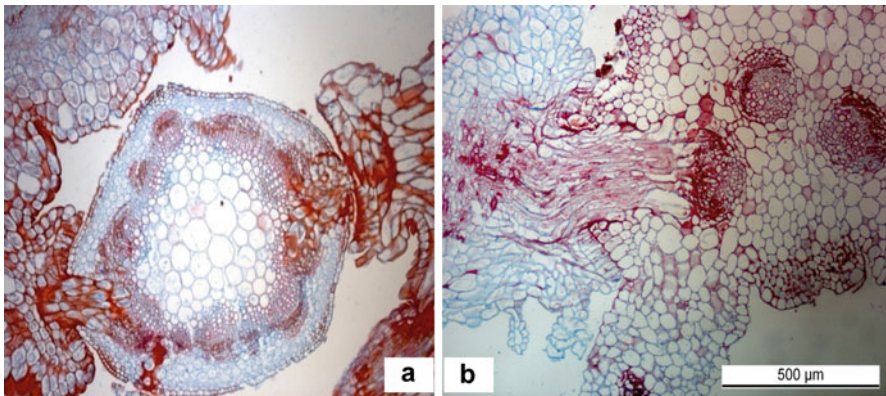
Picture 4 The haustorium searching hyphae of field dodder establishing a connection with both phloem and xylem tissues of alfalfa stem (**a**) and sugar beet petiole (**b**) (Sarić-Krsmanović 2013)

structures known as hyphae. In a compatible host, the hyphae searching for vascular tissue are able to expand from 800 to 2000 μm [1, 48], and their inter- and intracellular expansion into the host tissue depends on the mechanical as well as enzymatic processes [1]. These parasitic cells have been described as having ambivalent characters, functioning as both sieve elements and transfer cells [59, 63]. Interestingly, during this process, chimeric cell walls of host and parasite constituents are formed, and interspecific plasmodesmata build up a cytoplasmic syncytium between *Cuscuta* and its host plant [48, 64, 65]. To form a connection to the xylem, parasitic and host cells of the xylem parenchyma commence a synchronized development, fusing to build a continuous xylem tube from the host to the parasite [66]. With functional connections to the xylem and phloem of its host, the parasitic plant is supplied with water, nutrients, and carbohydrates [50, 58, 67].

4   Consequences of Field Dodder and Host Interaction

4.1   Impact on Host-Parasite Metabolites

After the establishment of a connection between host and parasite, the development of the parasite is based on the exchange of nutrients. In the process of establishing parasitic connections to its host, dodder uses a battery of hydrolytic enzymes, primarily cell wall-modifying glycosyl hydrolases [68], which have been observed directly through their activities [69] or indirectly through their structural consequences during host-tissue invasion [48]. Further, dodder appears to induce hydrolytic activities within its host [69, 70].

Transfer of fluids from the host to the parasitic plant occurs across a bridge created between the two organisms utilizing the difference in water potential of cell sap between the two plants. Parasitic flowering plants have a higher negative osmotic potential of cell sap that allows them to uptake organic nutrients from the host plant or, in other words, the phloems within vascular bundles of the parasite and the host become connected, creating a "physiological bridge" between the two plants' vascular tissues [50]. As *Cuscuta* has no roots and no effective photosynthesis system, most of the nutrients apparently come from the host phloem, but their haustoria reach into the xylem too for nutrients such as calcium. This makes *Cuscuta* a phloem feeder, and Haupt et al. [64] used fluorescent proteins to show a symplasmic connection with companion cells of phloem. A lower phloem flux here causes a reciprocal interaction between the host and the parasite. In certain cases, *Cuscuta* can be a mediator of virus infection for the host plant. Apoplasmic and symplasmic connections are found case by case. The presence of a plasmodesmata connection between *Cuscuta* and host plant was shown by Birschwilks et al. [65].

The connection between host and dodder vascular systems is continuous [65] and facilitates transport of not only water and minerals but also viruses, proteins [64], and mRNAs [71] from host to the parasite. Because plants possess hundreds of different phloem-mobile proteins and RNAs that play important roles in regulating plant development and stress responses [72], it is expected that the development and

stress tolerance of dodder could also be influenced by these host-derived mobile substances that are capable of interspecies trafficking.

The holostemparasitic plant *Cuscuta* can serve as an important system for studies on plant-plant interactions. Different responses from host plants to *Cuscuta* might be able to partially clarify some potential tendencies of plant stress response between different plant taxa and may also suggest unknown stress response mechanisms in host plants. Furuhashi et al. [73] used a unique experimental system to analyze *Cuscuta japonica* seedlings under FR light and/or with a contact signal attached to different host plants. *Cuscuta* attached to *Pueraria thunbergiana* showed a higher (>20%) mol percentage of pinitol both in the apical and middle regions (haustorium part). *Cuscuta japonica* attached to *Buxus microphylla* and *Conyza sumatrensis* contained less pinitol, and values were even lower than in *C. japonica* seedlings before parasitization. Although *C. japonica* attached to *Pueraria* did not contain large amounts of glucose and sucrose, *C. japonica* attached to *Buxus* and *Conyza* did especially in the haustorium-induced parts. Host plants without *C. japonica* parasitization clearly showed different metabolite profilings from *C. japonica* seedlings. Pinitol was dominant in *Pueraria*, and quinic acid was dominant in *Conyza* and *Buxus*. Also, glucose, myoinositol, and oxalic acid were bigger in both *Conyza* and *Buxus*, but not in *Pueraria*.

Parasite plants are clearly plants and have the same plant hormonal system and physiological response. This implies that host plants would not always be able to use the same defense strategy against parasite plants. This consideration gave rise to discussions about comparing parasite plants with herbivores [74]. Although parasite plants have been recognized as weeds that cause agricultural problems, triggering some interest [75, 76], parasitization does not always negatively influence the host plant. For example, tomatoes parasitized by *Cuscuta* altered certain plant hormones (e.g., salicylic acid) and can influence their defense system against insect herbivores [13]. Also, Runyon et al. [61] used a metabolomic profiling approach involving vapor phase extraction to measure changes in phytohormones occurring within tomato plants during parasitism by *C. pentagona*. Theirs results indicated that parasite seedlings elicit a relative paucity of host reactions when first attaching to 10-day-old tomato seedlings, whereas a second attachment by the growing parasite vine 10 days later induced large increases in several plant hormones and a strong HLR (hypersensitive-like response). Also, Runyon et al. [61] assessed the effectiveness of SA (salicylic acid)- and JA (jasmonic acid)-mediated host changes using transgenic and mutant plants. These methods give the first picture of the composition and timing of hormonal signalling induced in response to a parasitic plant. They conclude that as with herbivore and pathogen attack, plants are able to perceive invasion by parasitic plant haustoria and respond by activating induced defense pathways. Seedlings of *C. pentagona* elicited relatively few changes in the host upon first attachment to young tomato seedlings, possibly because of ontogenetic constraints in host defense or because the parasite is better able to manipulate young hosts. Older tomato plants responded to a second attachment by activating the JA and SA signalling pathways, both of which appear to mediate defenses that effectively reduce parasite growth. Parasitism also induced increases in ABA (abscisic

acid) and free fatty acids, but the roles of these compounds in defense remain uncertain. Although plant hormones play important roles for many plant interactions, including pathogenic responses, only little plant hormone research has been conducted on *Cuscuta*. Also, little is known about the influence of hormonal changes to *Cuscuta*, such as effect to haustorium induction and reciprocal interaction with host plant. Furuhashi et al. [84] firstly tested several host plant species for *Cuscuta* parasitization and also observed *Cuscuta* plant interaction in the field, in order to find interesting interactive relationship. They reported the new, unique phenomenon that a parasitic plant induced hypertrophy together with vascular tissue differentiation in the host plant stem. Plant hormone analysis clarified that cytokinin played a major role in this process. *Momordica charantia* hypertrophy response might be derived from resistance, while *Cuscuta* grow rapidly under the presence of hypertrophy response.

4.2   Impact on Host Pigment Content

Obligate parasites are not able to develop without assimilate supplies from their hosts because of their inability to perform any photosynthetic activity on their own or such photosynthetic capacity is very low [6, 50]. Their dependence on the host plant is therefore stronger, as well as their negative impact in terms of reducing chlorophyll and accessory pigments in the host plant [77]. Saric-Krsmanovic et al. [78, 79] showed a significant reduction in chlorophyll *a*, chlorophyll *b*, and carotenoids in infested alfalfa and sugar beet plants, compared to noninfested plants. Such reductions in chlorophyll *a*, chlorophyll *b*, and carotenoids were higher in infested alfalfa than infested sugar beet plants. Similarly, Fathoulla and Duhoky [80] found that different *Cuscuta* species caused not only morphological and anatomical changes in their hosts but also reduced their chlorophyll contents. Specifically, *C. campestris* and *C. chinensis* caused significant decrease in total chlorophyll contents in three tested hosts *Capsicum annuum*, *Coleus* spp., and *Helianthus annuus*, while the smallest reduction was caused by *C. monogyna*. Furthermore, these authors also revealed a significant variation in the chlorophyll content in the leaves of the same plant parasitized by different *Cuscuta* species. The differences in the infection between the different hosts by the same *Cuscuta* sp. may be related to the differences in nutrient status or sizes of the host (metabolic activities) [81].

4.3   Impact on Host Chlorophyll Fluorescence

Methods based on chlorophyll fluorescence have been used in many studies to monitor the effects of various stress factors on plants, such as water deficit, nitrogen deficit, extreme temperatures, and high salt concentrations, or to study changes in photosynthetic processes caused by herbicides or pathogen infection [82–85]. Saric-Krsmanovic et al. [78] have discovered possibilities that used chlorophyll fluorescence as an indicator of stress in host plants parasitized by field dodder. Most of the

measured parameters were affected by field dodder parasitism from the 1st day after infestation. An exception is the parameter F_v, whose lower value in infested plants was recorded on the 5th day after infestation (Table 1). The stressful influence of field dodder on alfalfa and sugar beet plants caused reductions in the parameters such as F_v, F_v/F_m, Φ_{PSII}, and IF. These findings are consistent with report from Vrbnicanin et al. [86] confirming lower values of these parameters in plants exposed to stress caused by various factors. They reported that several chlorophyll fluorescence parameters (Fv, F_v/F_m, and Φ_{PSII}) of the host *Ambrosia trifida* were influenced by the parasitism of *C. campestris*. One of the possible reasons could be that, in host plant, field dodder suppressed photosynthesis by limiting gas diffusion over stomatal and photosynthetic metabolic processes. Furuhashi et al. [87] found that photosynthetic activity in *Momordica charantia* stems parasitized by *Cuscuta* fell with time, although values in leaves were not influenced by parasitization. As F_v/F_m- and F_v'/F_m'- values decreased, the PSII is probably mainly affected by parasitization. It is necessary to consider the impacts of *Cuscuta* infection on host plant's photosynthesis in the context of environmental factors. Also, many studies [88, 89] have shown

Table 1 Chlorophyll fluorescence in noninfested (N) and infested (I) sugar beet and alfalfa plants

Days after infestation in the plant sugar beet						
Parameters		1	5	10	15	20
Fv/Fm	N	0.7752	0.7621	0.7602	0.791	0.7963
	I	0.7385	0.685	0.6505	0.753	0.7093
Φ_{PSII}	N	0.7914	0.7926	0.7892	0.7923	0.7933
	I	0.748	0.6322	0.7313	0.7777	0.7013
Fo	N	0.5446	0.5379	0.5459	0.5582	0.559
	I	0.575	0.5555	0.6769	0.5847	0.5954
Fv	N	2.0446	1.9655	2.0033	2.0297	2.0317
	I	1.4341	1.2971	1.3786	1.6165	1.4712
IF	N	1.1185	1.1009	1.1477	1.0771	1.1213
	I	0.8693	1.3835	0.9083	0.9280	1.3331
Days after infestation in the plant alfalfa						
Parameters		1	5	10	15	20
Fv/Fm	N	0.8	0.8	0.7972	0.8104	0.813
	I	0.7542	0.7322	0.6482	0.7584	0.7842
Φ_{PSII}	N	0.782	0.8098	0.7862	0.775	0.782
	I	0.7568	0.6922	0.7376	0.8002	0.7568
Fo	N	0.4908	0.4908	0.504	0.4738	0.4738
	I	0.5638	0.5832	0.5508	0.5508	0.571
Fv	N	2.0072	1.9266	2.044	2.0842	2.0378
	I	1.9942	1.8342	1.8686	1.182	1.6182
IF	N	1.1783	1.1198	1.2124	1.1697	1.0600
	I	1.1039	1.2726	0.9487	1.1209	0.9040

Fm maximal fluorescence, *Fo* minimum fluorescence, *Fv* variable fluorescence, *Fv/Fm* maximum quantum efficiency of photosystem II, *IF* intensity of fluorescence, Φ_{PSII} effective fluorescence yield of photosystem II

that chlorophyll fluorescence parameters reacted to stress at different speeds, depending on a number of factors.

4.4   Impact on Host Mineral Nutrient Content

Parasitic plants restrain the growth and reproduction of their hosts by capturing nutrients and disturbing resource balance [2]. The presence of the parasite strongly reduces the biomass by acting as a competing sink for assimilate, but more importantly, by compromising the efficiency of mineral and organic nutrient assimilation. The holoparasitic *Cuscuta* is known to constitute an overwhelming competitive sink by diverting the major portion of the current photoassimilates of the host into its own tissues [1, 3, 90]. Hibberd and Jeschke [50] observed that nitrogen uptake by a parasite depends primarily on its availability and translocation through the conducting tissue of its host plant. Also, Press et al. [91] showed that the extent of parasites competing with hosts for carbon and other nutrients depends on their relative sink strength and the degree of autotrophy of the parasite. Increasing of nitrogen and potassium contents in *Mikania micrantha* was reported by Yu et al. [92], while no impact on phosphorus content was detected in the early stages after *C. campestris* infestation. Saric-Krsmanovic et al. [79] revealed increase of some nutrient content in the infested, compared to noninfested plants. Twenty days after infestation, K_2O and organic nutrient contents in infested alfalfa plants and N and organic nutrient contents in sugar beet were higher than in noninfested plants. Final assessment (40 DAI) revealed that field dodder increased the contents of N, P_2O_5, K_2O, and organic nutrients in the infested alfalfa plants, while the infested sugar beet plants had higher contents of N and organic nutrients, compared to noninfested plants (Table 2). Different responses from host plants to *Cuscuta* might be able to partially clarify some potential tendencies of plant stress response between different plant taxa and may also suggest unknown stress response mechanisms in host plants [73]. Also, the changeable contents of nitrogen, phosphorus, potassium, and organic

Table 2 Contents (%) of nitrogen, phosphorus, potassium, and organic and mineral nutrients in alfalfa and sugar beet plants

Parameters						
Assess	Treat	N%	P_2O_5%	K_2O%	Organic nutrients %	Mineral nutrients %
Alfalfa						
40 DAI	N	2.18 ± 0.11	0.36 ± 0.03	1.40 ± 0.05	91.49 ± 0.30	8.51 ± 0.30
	I	2.33 ± 0.10	0.42 ± 0.05	1.55 ± 0.22	92.24 ± 0.62	7.76 ± 0.62
Sugar beet						
40 DAI	N	1.12 ± 0.17	0.76 ± 0.06	3.53 ± 0.21	83.09 ± 2.32	16.92 ± 2.32
	I	2.03 ± 0.16	0.48 ± 0.18	2.84 ± 0.22	85.28 ± 1.56	14.72 ± 1.56

N noninfested alfalfa and sugar beet plants, *I* infested alfalfa and sugar beet plants, *DAI* days after infestation

and mineral nutrients in noninfested and infested alfalfa and sugar beet plants may be considered as a response reaction of the host to parasitism, which mostly leads to accumulate nutrients because intensified metabolism creates a defense mechanism in the host. The changes in nutrient contents and fresh biomass have a crucial effect on the composition of plant communities and determine their invasiveness [93].

4.5   Impact on Host Anatomical Parameters

The effect of field dodder on the anatomy of cultivated host plants is still mostly an uninvestigated area. Field dodders cause changes in stalk anatomy and leaves of host plants (alfalfa and sugar beet) [79, 94, 95]. Regarding nearly all analyzed parameters of alfalfa stem (epidermis, cortex, pith, diameter), significantly lower values were recorded in infested than in noninfested plants 42 DAI (days after infestation) (Pictures 5 and 6). At the same time, our results showed that field dodder had a significant effect on most of the measured parameters (upper epidermis, palisade tissue, spongy tissue, leaf mesophyll, underside epidermis, vascular bundle cells) of alfalfa and sugar beet leaves. Furuhashi et al. [87] discovered hypertrophy and increasing number of vascular bundles in *Momordica* stems clearly induced by *Cuscuta hyphae*. This influence of the parasitic plant on its host resulted in decreasing of total photosynthetically active surface, as well as total photoassimilating tissue, which may lead to lower competitiveness of the infested plant and its weakened ability to set fruit and seed due to a major loss of nutrients assimilated by the parasite [50]. In early stages of field dodder infestation, the host plant reacts with a specific gene expression for calcium release, cell elongation, and changes in the cell wall [70, 96]. At a later stage, after hyphae have been formed, they are mostly connected to the xylem or phloem of the host, even though some of them may end up in the parenchyma. Possessing their ring-like structure, hyphae are able to connect to several sieve tubes of the host simultaneously, which increase their
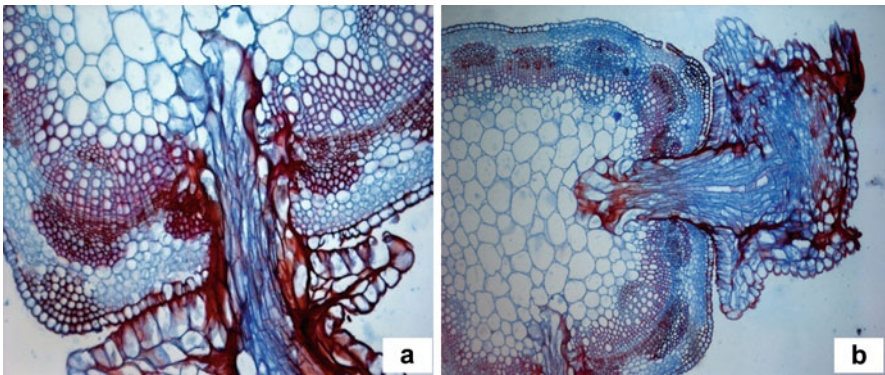
Picture 5 The haustorium searching hyphae of field dodder connecting to the central cylinder (pith) tissue of alfalfa stem (**a**, **b**) (Sarić-Krsmanović 2013)
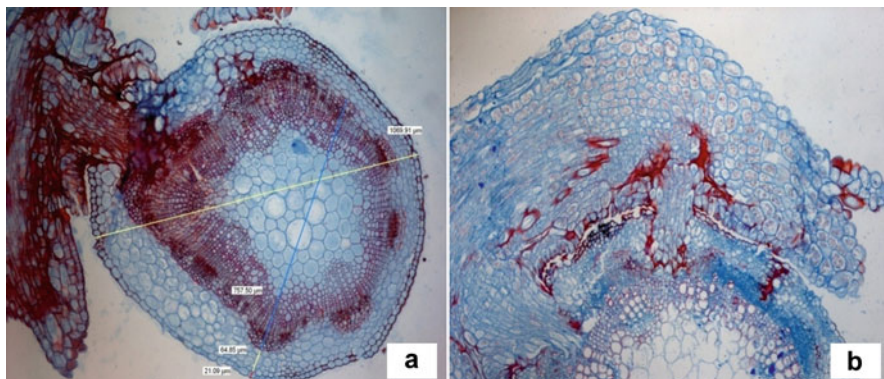
Picture 6 The haustorium searching hyphae of field dodder connecting to cortical parenchyma cells (**a**) and phloem tissue (**b**) of alfalfa stem (Sarić-Krsmanović 2013)

absorption strength, as well as their impact on the conducting tissue of the host [64]. Saric-Krsmanovic et al. [79, 95] examined the effect of field dodder on the petiole of sugar beet, and the data for the measured parameters (tracheid diameter, petiole hydraulic conductance, xylem surface, phloem cell diameter, and phloem area) indicated that this parasitic flowering plant has a significant influence on all measured parameters. In the infested sugar beet, field dodder significantly reduced the area of conducting tissues, as well as the hydraulic conductance of the petiole, compared to noninfested plants. Even though, the parasite is connected both with the host xylem and phloem, *Cuscuta* spp. mostly assimilates through the phloem [50]. In addition to the basic metabolic compounds, also some secondary products (such as alkaloids, etc.) and xenobiotics are adopted by dodder plants mostly from the phloem of the host [65]. But essential nutrients, which are deficient in the phloem, are assimilated from the host xylem [50].

In general, field dodder exhausts the host plant, so that it becomes weak, its lushness of growth declines, and fruit and seed maturation become significantly reduced [90]. Also, host plants change their habit as their axillary buds sometimes become suppressed [97], and the harm may result in total plant destruction (Picture 7).

5 Conclusions

Cuscuta, as a generalist type of holostemparasitic plants, interacts with various hosts, causing different morphological, anatomical, and physiological changes. Hosts are attacked non-specifically and sometimes even simultaneously, and one crop species may serve as a host for several dodder species. Depending on the infected plant species, *Cuscuta* infestation has more or less severe effects on the growth and reproduction of its host. Rather than causing host death, *Cuscuta* infestation seems to weaken host plants and to render them more susceptible to secondary diseases such as infection by microbes or insect and nematode infestation.

Picture 7 Field dodder
haustoria (an example of
hypersensitive reaction)
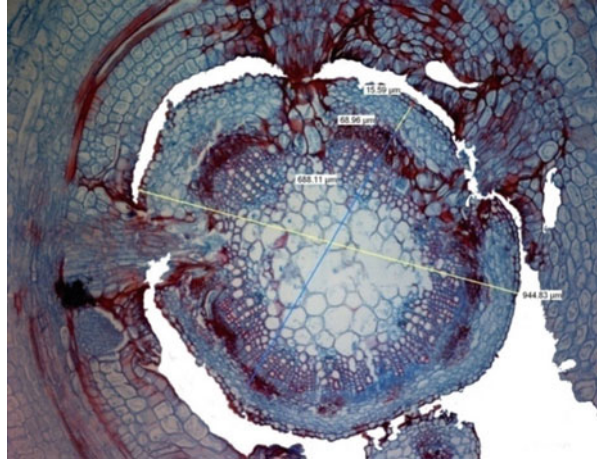
The parasitic process in *Cuscuta* begins in finding and attaching to a host plant and then developing a haustorium. The process does not always require any chemical signal but does require a light signal. A contact signal is also necessary for haustorium induction. The direct connection between *Cuscuta* and its host involves both the xylem and phloem, and mRNA and proteins can translocate. Several features indicate that *Cuscuta* is a useful model plant for parasite plant research as well as plant-plant interaction research. These include the simple anatomical structure and seedling development, no chemical requirement for haustorium induction, and the wide range of host plants. Their continuous growth and ability to successively change hosts make the occurrence of coevolution between *Cuscuta* and specific hosts unlikely. Different responses from host plants to *Cuscuta* might be able to partially clarify some potential tendencies of plant stress response between different plant taxa and may also suggest unknown stress response mechanisms in host plants. More extensive research is required in order to develop new means for parasitic weed control. It is important to learn more about this pest, studying its life cycle, development, and parasitic-host interactions.

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