



Effect of species environment on host preference of *Cuscuta campestris*

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Abstract *Cuscuta campestris* is one of the most widespread and most harmful parasitic plants in the world. It regularly infests economically important crops substantially reducing their yield. Its host preference has been frequently investigated in natural habitats, but studies have usually been performed at only one site. In this study, I tested the hypothesis that host-preference studies performed at a single site provide information only about local individuals of the host species and not about the species of hosts in general. The preferential status of host species was investigated in different geographical regions, in different species environments. Altogether 1847 relationships between parasite and plant species were examined and categorized at 171 places in Hungary. The used method took into account the frequency and intensity of infestations on the hosts, the proportion of resource use and availability, the resource distribution as well as the defence mechanisms of the hosts. The frequency and intensity of infestations greatly varied

amongst the 174 detected host species. The results confirmed that frequently parasitized hosts of *C. campestris* are not necessarily preferred. Most host species have infestations of varying intensity in different species environments. Poaceae species were found to differ from each other in the extent to which they support the parasite's growth. The study revealed also that *C. campestris* does not always develop haustoria on individuals of those species, which are unable to contribute significantly to its growth.

Keywords *Cuscuta* · Field dodder · Haustorium · Parasitic plant · Resistant species · Resource use

Introduction

Approximately 4750 parasitic plant species are known in the world, which is more than 1% of the flowering plants (Nickrent 2020). The genus *Cuscuta* (dodders) comprises nearly 200 parasitic plant species widely distributed in tropical, subtropical, and temperate regions (Nickrent 2020). *Cuscuta campestris* (field dodder) similar to all other *Cuscuta* species is a rootless obligate stem parasite that depends completely on its hosts for resources. This parasite is considered to be a dangerous agricultural pest, frequently infesting economically important cultivated plants and reducing their yield substantially

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(Lanini and Kogan 2005). *C. campestris* is the most widely distributed species of the genus and the only parasitic weed of North America that has spread throughout the Old World (Dawson et al. 1994). Human activities have played a significant role in its worldwide distribution since its propagules have been introduced into several countries and continents as contaminants of crop seeds (Dawson et al. 1994). *C. campestris* was introduced to Europe probably via France by contaminated alfalfa (*Medicago sativa*) seeds in 1840, whilst in Hungary it was first observed in 1873 (Degen 1911). Field dodder however spread beyond the agricultural fields and colonized the surrounding habitats. At present, *C. campestris* is one of the most frequent parasitic plants in Hungary mostly occurring on the edge of roads and agricultural fields (Erdős 1971; Csiky et al. 2004). This peculiar habitat type was marked as the most common habitat of this dodder also in Slovakia (Chrtek and Bertová 1988), in Czech Republic (Pyšek et al. 2012), in Croatia (Orkić et al. 2019), in Romania (Tanase et al. 2012), in Turkey (Şin et al. 2020), but also in South India (Baráth 2010) and the Andaman islands (Baráth 2009). The eco-geographical distribution and the wide host range have made this dodder one of the most damaging parasites worldwide (Dawson et al. 1994).

The host range of *C. campestris* was already systematically investigated by several authors in different geographic regions (e.g. Elarosi and Abo-Blan 1975; Jayasinghe et al. 2004; Krumbiegel 2007; Baráth and Csiky 2012; Nwokocha and Aigbokhan 2013). Some floras and taxonomic treatments (e.g. Buia 1960; Feinbrun 1972; Kojić 1973; Chrtek and Bertová 1988; Baráth and Csiky 2009) also mention a number of species or genera as frequent hosts of this parasite. Based on these studies it can be said that field dodder infest several hundreds of species, and its host ranges are similar in adjacent regions but completely different if the regions are far from each other (e.g. temperate vs. tropical regions).

Knowledge of frequent hosts can facilitate the identification of the species of *Cuscuta* itself in a given region (Lei 2001; Baráth and Csiky 2012), accordingly, they provide taxonomic information. On the other hand, the most frequently parasitized hosts are not necessarily the most preferred ones (Baráth 2012), and knowledge of the preferred hosts is more ecologically important. Besides the frequency, the intensity of infestation is an essential factor for the evaluation of

host preference. Pennings and Callaway (1996), Liao et al. (2005), and Grewell (2008) estimated the intensity of parasitism on various hosts using the number of haustoria. Although this method directly reflects the degree of investment of the parasite, in cases of some *Cuscuta* species that can coil around the host very densely, the identification and distinction of functional haustoria are extremely difficult (Baráth 2012). Additionally, there are some special cases when the number of haustoria cannot be satisfactorily used for determining the strength of parasitism (Baráth 2012). Several plant species have developed specific defence mechanisms against the parasites (Albert et al. 2008; Kaiser et al. 2015). During the localized necrosis or hypersensitive reaction, the upper haustorium (adhesive disk) can be seen and counted, but the mechanical barrier formed by dead cells around the attachment site stops the penetration of the searching hyphae, preventing the connection to the host vascular system (Capdepon et al. 1985). The intensity of infestation can also be estimated by stem density and biomass accumulation of the parasite on the hosts (e.g. Kelly et al. 1988; Kelly 1990; Lei 2001; Koch et al. 2004). Although this method reflects the reward of investment and not the degree of direct investment of the parasite, Kelly (1988, 1990) verified the correlation between them. The time of investigation and the duration of parasitism are also important, since the biomass of dodders may vary by an order of magnitude during the vegetation period (Baráth 2012; Puustinen et al. 2004).

Based on the frequency and intensity of the infestations we can get a picture of the host use by parasites, but knowledge of the host availability is also essential to evaluate host preference (Kelly et al. 1988; Baráth 2012). Liao et al. (2005) measured host availability by the relative coverage of the host species and compared that to the host use of the parasite (number of haustoria) applying Johnson's rank preference index (Johnson 1980). Although this method was able to cope with the fact that host use and availability were measured on different scales, it could not avoid the loss of information resulting from the use of ranks, instead of the measured values. Kelly et al. (1988) used proportion similarity between resource use and availability to prove that the investigated dodder does not exploit the hosts equally in the study site.

On the other hand, several factors can result in differences in host quality that are not dependent on the identity of the host species (Koch 2004). Differences amongst populations, previous selection, local adaptation, and genetic variation can significantly influence the interaction between the parasites and their hosts (Koskela et al. 2000, 2001, 2002). According to Kelly (1992), Alers-García (2005), and Sanders et al. (1993) host preference also can be affected by the height, nitrogen content, and mycorrhizal status of the hosts. Furthermore, Lei 2001, Koch et al. (2004), and Meulebrouck et al. (2009) proved that age, size, and phenology of the host plants also play an influential role in host preference. Because it is not possible to take into account the effect of all the above-mentioned factors in the fieldwork, I suppose that host-preference studies that are conducted in a single study site provide information about the interaction between parasite and host individuals rather than about the interaction between parasite and host species. Consequently, to gain a better understanding of the preference of a given parasite species to its host species, the studies need to be conducted in multiple locations, in a variety of species environments. Of course, this requires an appropriate method that can reliably synthesize the data deriving from different sites.

Materials and methods

In this study, the host preference of *C. campestris* was investigated using the method, the foundations of which were presented by Baráth in 2012. This process takes into account the frequency and intensity of infestations, the proportion of resource use and availability, and the resource distribution as well as the defence mechanisms of the hosts. With the help of this method, the preference status of the same host species can be investigated and compared in different geographical regions or/and under different species environments. With representative sampling, it is possible to determine the order of preference amongst the host species not only in a single study site but also in a large geographical territory, even in a country.

The study was carried out between 2012 and 2018, from August to October at 171 sites in Hungary (Fig. 1). Both parasitized and unparasitized plants were examined in the habitats using quadrats of 4 m² size. Relevés were taken only when *C. campestris* was

fully developed. Up to two relevés were taken at one location. The size of *Cuscuta* colonies was calculated (in square metres) from their cover value. Percent cover and the relationship type with the dodder were recorded for each plant species in the quadrats. Altogether four relationship types were distinguished between hosts and parasite:

1. There was no physical contact between parasite and individuals of the plant species;
2. There was physical contact, but the dodder did not develop a haustorium;
3. Established haustorium was found on the plant (in doubtful cases the haustorium was cut and the penetration was checked with a magnifier or using a stereo microscope);
4. Parasitism was prevented by some visible defence mechanism of the plant.

The distribution of parasite biomass was estimated on different host species using a percentage scale. Relative host use was calculated as the percentage of the total *Cuscuta* cover on the particular host species (cf. Kelly 1988). The absolute percent cover of the plant species that had physical contact with the parasite was converted into relative cover (cf. Baráth 2014; Table 1). *C. campestris* completely depends on its hosts for resources, thus the relative cover of the potential hosts reflects the relative host availability in the quadrat (cf. Liao et al. 2005). If the parasite did not show any preference for different species, it would infest the hosts in proportion to the relative host availabilities.

After the relative host use and availability were compared in the case of each infestation of all host species, they were categorized as follows: if the relative host use was bigger than the relative host availability, the infestation was considered “heavy” and received a + 1 value. When usage and availability were equal (the difference between them was 1% or less), parasitism was categorized as “medium” and got zero value. These types of infections do not reflect either positive or negative preference. If the relative host use was less than the relative host availability, it was considered “light” infestation and received a – 1 value.

Since the majority of host species were characterized by more than one type of infection, the value of preference for the different host species was determined by the proportion of their “heavy” (+ 1),

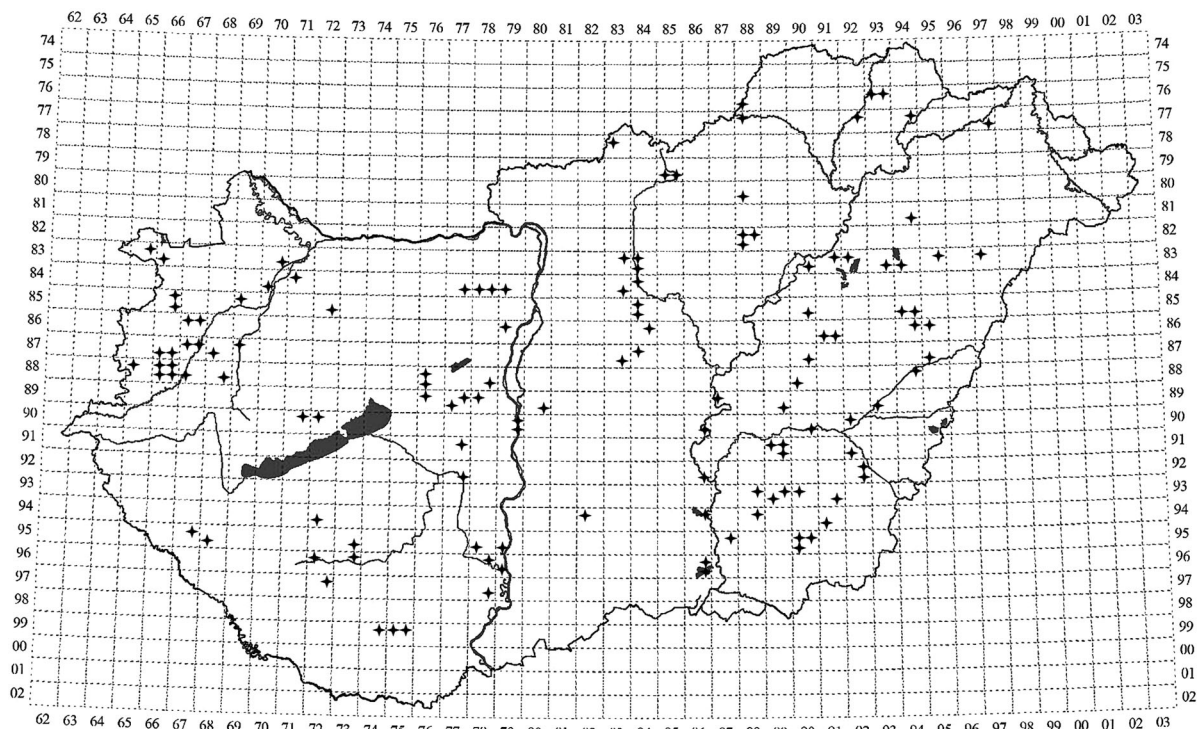


Fig. 1 Locations of the sampling quadrats in Hungary according to the grid of the central European mapping system

Table 1 The calculation of the relative host availability according to Baráth (2014)

| | Absolute percent cover | Relationship type | | Relative percent cover |
|-------------------|------------------------|-----------------------------------------|-----|------------------------|
| 1. Species | 25% | 1 (No physical contact) | – | – |
| 2. Species | 10% | 2 (Physical contact without parasitism) | 10% | → 20% |
| 3. Species | 30% | 3 (Physical contact and parasitism) | 30% | → 60% |
| 4. Species | 10% | 3 (Physical contact and parasitism) | 10% | → 20% |
| Water surface | 5% | – | – | – |
| Bare soil surface | 10% | – | – | – |
| Altogether | 100% | | 50% | → 100% |

“medium” (0), and “light” (– 1) infestations (Online Resource 1). Hosts were considered preferred, if this value was positive, in other words, they had more “heavy” than “light” infections. If the preference value was zero, species were defined as accessory hosts. Avoided host species were characterized by more “light” than “heavy” infestations, accordingly, they had a negative preference value. Those species that were parasitized only in a single study site were

categorized as occasional hosts in addition to the status of their infestation.

Kruskal–Wallis tests and Bonferroni-corrected pairwise Brunner–Munzel tests were used to verify significant differences amongst the infestation categories. The p-values of the Kruskal–Wallis tests were estimated by an unrestricted permutation test using 10,000 randomizations. The difference between the absolute cover of parasitized and unparasitized plants was also investigated using the Brunner–Munzel test.

Wilcoxon-Mann-Whitney test was used to compare the difference between the number of host species in the quadrat and the number of those plant species that have physical contact with the parasite. The homogeneity of the distributions of infestation categories amongst host species was tested by Pearson's chi-square test. The degree of correspondence between two variables was measured in every case by Kendall's τ rank correlation coefficient. Statistical analyses were performed using R software package—version 4.0.0 (R Core Team 2020).

Results

Altogether 225 plant species occurred in the investigated plots of *C. campestris* and 174 of them were found to be parasitized (Online Resource 1). Host species were distributed amongst 125 genera and 36 families. The number of species varied between 2 and 23 in the quadrats, whilst the number of hosts varied between 1 and 18. The host range of the parasite was unique in each site. During the study, altogether 1847 relationships between parasite and plant species were examined and categorized. In 567 cases, individuals of the species had no physical contact with the parasite, even though they lived in the same habitat. However, their percent cover in the quadrats was observed to be significantly lower than the percent cover of the host species of the 1280 infestations (Brunner-Munzel $BM = -15.632$ with $p < 0.001$).

There was no significant difference between the number of host species in the quadrat and the number of those plant species that have physical contact with the parasite (Wilcoxon-Mann-Whitney $U = 14,813$ with $p = 0.832$). In addition, the size of *Cuscuta* colonies showed a significant correlation with the number of host species (Kendall $\tau_b = 0.235$ with $p < 0.001$).

In the course of evaluation of the intensity of infestations, 305 “heavy”, 382 “medium”, and 593 “light” infections were noted. Altogether 88 host species (50.57%) were characterized by infections of different intensities.

It was observed that the preference ranking of the host species was different from the order of the hosts calculated by the frequency of parasitism (Kendall $\tau_b = -0.296$ with $p < 0.001$). Although the most frequently infested *Polygonum aviculare* agg. was

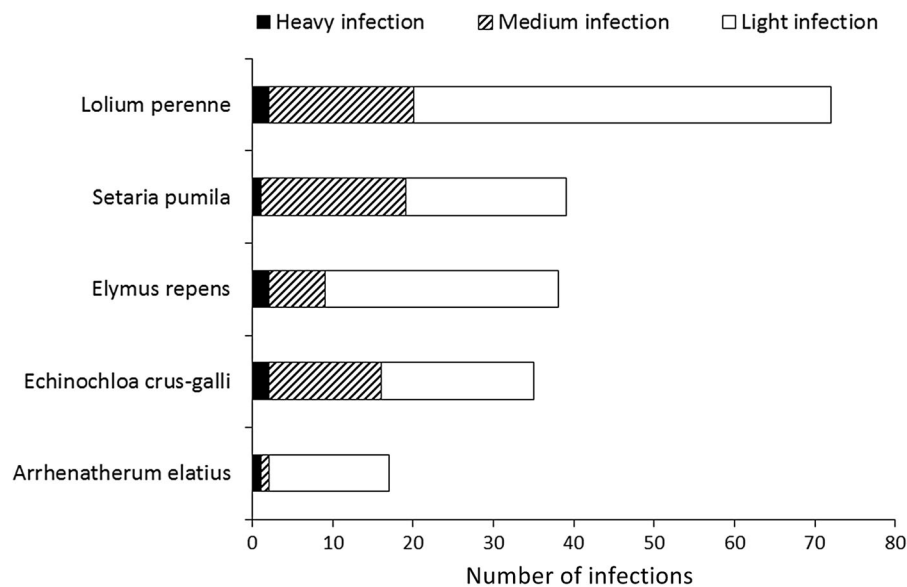
also the most preferred host, the second most frequent species, *Lolium perenne* was found to be the least preferred one (Table 2). *P. aviculare* agg. was found to be parasitized in 126 sites of the total 171 (73.68%). During the study, altogether 66 plant species were found to have “heavy” infestation but only 16 species had more “heavy” than “light” infections. Moreover, in cases of only five species were the preference values bigger than two. These five most preferred species belonged to five different families. According to the categorization system, 76 occasional hosts were recorded, which corresponds to 43.67% of the total host species. Besides, 11 of them (14.47%) were found to be “heavily” infested.

In this study, 36 different grass species were identified as hosts of *C. campestris*, but they were never found to be either preferred or accessory hosts for *C. campestris*. In addition, four of the five most avoided host species belonged to the Poaceae family. In cases of grass species, significant differences were found in the number of infections amongst the three categories (Kruskal-Wallis $H = 31.52$, $p < 0.001$). “Heavy” infections were observed to be significantly less in number than “medium” or “light” infections ($BM_{\text{heavy-medium}} = 5.253$, $p < 0.001$, $BM_{\text{heavy-light}} = 7.625$, $p < 0.001$). The difference between the number of “medium” and “light” infections was not significant ($BM_{\text{medium-light}} = 0.3276$, $p = 0.109$). On the other hand, in cases of the five most frequently parasitized grass species, significant differences were observed amongst the proportions of infestation categories ($\chi^2 = 15.7$, $p = 0.046$, Fig. 2). The proportion of “light” infections was significantly higher in the cases of *Arrhenatherum elatius* and *Elymus repens* than in the case of *Setaria pumila* ($\chi^2 = 8.6$, $p = 0.013$, $\chi^2 = 6.8$, $p = 0.033$). This difference was also significant between *Echinochloa crus-galli* and *A. elatius* ($\chi^2 = 6.6$, $p = 0.036$).

Despite the existing physical contact, *C. campestris* did not develop haustoria on some individuals of the following species: *Achillea millefolium* L. (2 individuals), *Ambrosia artemisiifolia* (3), *A. elatius* (5) *Carex hirta* (1), *Conium maculatum* (5), *Cynodon dactylon* (2), *Digitaria sanguinalis* (1), *E. crus-galli* (3), *E. repens* (4), *Festuca pratensis* (1), *Hordeum murinum* (1), *L. perenne* (5), *S. pumila* (3), *Setaria verticillata* (2), *Silene latifolia* (1), *Plantago lanceolata* (1), *Plantago major* (6), *Portulaca oleracea* (3), *Taraxacum officinale* (1), and *Zea mays* (2). However,

Table 2 Number and intensity of infections and preference values of the five most preferred and most avoided host species of *Cuscuta campestris*

| The five most preferred host species | Number of infection | Heavy infection | Medium infection | Light infection | Value of preference |
|-----------------------------------------------|---------------------|-----------------|------------------|-----------------|---------------------|
| <i>Polygonum aviculare</i> L | 126 | 101 | 6 | 19 | 82 |
| <i>Atriplex tatarica</i> L | 28 | 19 | 2 | 7 | 12 |
| <i>Convolvulus arvensis</i> L | 64 | 27 | 18 | 19 | 8 |
| <i>Tripleurospermum inodorum</i> (L.) Sch.Bip | 40 | 17 | 13 | 10 | 7 |
| <i>Robinia pseudoacacia</i> L | 4 | 3 | 1 | 0 | 3 |
| The five most avoided host species | Number of infection | Heavy infection | Medium infection | Light infection | Value of preference |
| <i>Echinochloa crus-galli</i> (L.) P.Beauv | 35 | 2 | 14 | 19 | −17 |
| <i>Setaria pumila</i> (Poir.) Roem. & Schult | 39 | 1 | 18 | 20 | −19 |
| <i>Elymus repens</i> (L.) Gould | 38 | 2 | 7 | 29 | −27 |
| <i>Ambrosia artemisiifolia</i> L | 59 | 4 | 16 | 39 | −35 |
| <i>Lolium perenne</i> L | 72 | 2 | 18 | 52 | −50 |

**Fig. 2** The five grass species most frequently parasitized by *Cuscuta campestris* and the distribution of their infestations

except for *C. maculatum* parasitized individuals of the above-mentioned species also were found in the same or another quadrat or quadrats.

During the field study, no host was found that exhibited a visible defence mechanism (such as a hypersensitivity reaction) that could prevent field

dodder infection. However, on the stem of some individuals of the species *Erodium cicutarium* (1), *Abutilon theophrasti* (1), *Lactuca serriola* (6) and *P. major* (4), a visible reaction could be observed due to the parasitism. It appeared as coloured (purple or red) spots around the attachment site of haustoria (Fig. 3a,



Fig. 3 A Red spots on the stem of *Plantago major* around the haustoria of *Cuscuta campestris*. B Transverse section of the stem of *P. major* with haustoria

b). This reaction was not visible in all individuals and never prevented parasitization.

Discussion

The results of this study confirm the previous observations (Erdős 1971; Csiky et al. 2004) that *C. campestris* can infect almost any plant species with which it comes into contact in nature. Accordingly, its host range is rather wide and taxonomically heterogeneous. According to Csiky et al. (2004) the greater the species diversity is in the habitat, the more species are parasitized by the field dodder. This observation is also in agreement with the findings of this study that the size of *Cuscuta* colony correlates with the number of host species. The great number of the occasional hosts in its host range and the fact that *C. campestris* can heavily infest these plants indicates that there is no

need to assume any coevolutionary relationship for parasitism. Probably this is one of the most important reasons why *C. campestris* is the most widely distributed species of the genus and why its host ranges are completely different in different parts of the world.

On the other hand, the intensity of infestations greatly varies amongst the host species. In 898 cases of the examined 1280 infestations (70.15%), field dodder used the hosts out of proportion to their availability. The most preferred host of the field dodder is *Polygonum aviculare* agg. in Hungary. Although the results show that frequent hosts of *C. campestris* are not necessarily preferred, *P. aviculare* agg. was also the most frequent host. This species is also mentioned as a common host from Slovakia (Chrtek and Bertová 1988), from Romania (Buia 1960), from Serbia (Kojić 1973), from Croatia (Orkić et al. 2019), from Sweden (Nilsson and Åkerberg 1939), from north-western Turkey (Şin et al. 2020), and Middle East (Chrtek and Osbornová 1991). However, even *P. aviculare* agg. can only be considered a preferred host, not a constant host of *C. campestris*. Moreover, the significance of this cosmopolitan species as a host is limited to some European and Middle East regions. *P. aviculare* agg. is not included in the host range of *C. campestris* in Sri Lanka (Jayasinke et al. 2004), in South India (Baráth 2010), in Andaman Islands (Baráth 2009), in Saudi Arabia (Elarosi and Aboblan 1975), in Sudan (Zaroug et al. 2014) in Nigeria (Nwokocha and Aigbokhan 2013), nor in North America and Hawaii (Krumbiegel 2007). Beside *P. aviculare* agg. the species *Atriplex tatarica*, *Tripleurospermum inodorum*, *Convolvulus arvensis*, and the juvenile form of *Robinia pseudoacacia* are the most preferred hosts of *C. campestris* in Hungary. All of these species are mentioned as frequent hosts for this dodder from the surrounding regions (e.g. Buia 1960; Kojić 1973; Orkić et al. 2019). The findings confirm the previous observation of Erdős (1971) who mentioned *R. pseudoacacia* as the only woody species that can be a “main” host of *C. campestris*. However, the results also show that neither *R. pseudoacacia* nor other woody species can be parasitized in their mature form. Nwokocha and Aigbokhan (2013) and Jayasinke et al. (2004) reported the same from Nigeria and Sri Lanka, respectively.

According to some previous studies (e.g. Nilsson and Åkerberg 1939; Gaertner 1950; Erdős 1971; Lei 2001; Jayasinghe et al. 2004; Nwokocha and

Aigbokhan 2013), *C. campestris* can parasitize at least 38 different Poaceae species. On the other hand, Gaertner (1950) drew attention to the fact that *Cuscuta* species cannot survive if they parasitize only grass species. The exact reason for this is not yet clear, but it may be due to the scattered vascular bundles of the stem or the fact that the life cycle of the grasses is usually shorter than required by *Cuscuta*. In this country-scale study, 36 Poaceae species were identified as hosts of *C. campestris*, though 16 of them were recognized only as occasional hosts. Field dodder was never found to infest Poaceae species alone, which confirms that *C. campestris* cannot survive only on grasses. On the other hand, the results suggest also that Poaceae species significantly differ from each other in how much they support the parasite's growth. This finding is in agreement with the previous observation of Nwokocha and Aigbokhan (2013). Although they mentioned a grass species (*Oplismenus burmanni*) amongst the most preferred hosts of *C. campestris*, according to the results of this study, species of grasses only occasionally can be heavily infested, and they are neither preferred nor accessory hosts for *C. campestris* in Hungary.

Several species that occur in the plots of *C. campestris* remain unparasitized. According to the results, the main and simple reason for this is that the parasite has no physical contact with most of them. In other words, dodder has no opportunity to infest the majority of these species. On the other hand, *C. campestris* did not always develop haustoria on individuals of some host species even when there was physical contact between them. One possible reason for this could be that the parasite had not yet developed haustoria at the time of the field study, but would have later infected these plants as well. However, the above-mentioned phenomenon has been repeatedly observed several times for certain species, which makes this explanation unlikely. For the species *Echinochloa crus-galli*, *E. repens*, *S. pumila*, *S. latifolia*, *T. officinale*, and *Z. mays*, Buia (1960) likewise reported that they appear to support the parasite rather than to feed it. It is important to highlight that all of these unparasitized individuals belonged exclusively to avoided host species or occasional hosts with a single "light" infection. Consequently, field dodder rejected parasitism on individuals of only those species, which are unable to contribute significantly to its growth. The importance

of this phenomenon is that rejection of the less valuable potential hosts occurred without the development of haustorium, prior to parasitism. Since haustorium initiation can occur host-independently also on an acrylic rod by contact stimuli (Tada et al. 1996), it can be assumed that there is an internal or external factor (or both) that prevents the formation of haustoria. A possible internal factor may be that field dodder possesses responses that may be used to effect rejection and acceptance of resources depending on the quality of the potential host. It has been already reported in cases of *Cuscuta subinclusa* and *Cuscuta europaea* by Kelly (1988, 1992). An external factor could be a substance or some substances selected by unparasitized individuals that inhibit the haustorium formation of *C. campestris*. Although such inhibitory substances have already been identified in cases of some parasitic taxa (Smith et al. 1996; Keyes et al. 2000), for dodders they are yet unknown. In this study, it is not possible to identify the factors that are responsible for the situation that some individuals of taxonomically different species remain unparasitized despite the fact that they had physical contact with *C. campestris*. Further studies are needed to answer this question. One promising target for research on resistance to field dodder could be the species *C. maculatum*. In this study, this plant is the most common unparasitized species. Despite the 10 occurrences, only 5 individuals had physical contact with dodder in 4 sites. However, *C. campestris* did not develop a single haustorium on any of the individuals, consequently, it can be said that *C. maculatum* showed 100% resistance against *C. campestris*. None of the above-mentioned studies reported this species as a host for field dodder.

Some authors (e.g. Lanini and Kogan 2005; Albert et al. 2008) have reported species that are able to prevent parasitization of *C. campestris* by a hypersensitive reaction. In this study, 12 individuals of four species showed a visual reaction against the parasite, but this never prevented the parasitism. During the observed reactions, the haustoria and the stem of *C. campestris* never died around the red or purple spots and the parasite's vitality did not appear to be reduced. The individuals that showed this reaction were found in different parts of the country, accordingly belonged to different populations. Besides, parasitized individuals of the same species without any sign of reaction were also observed in every case in the same habitat.

This phenomenon also requires further research to understand it in detail.

For 88 species, preference status was different in diverse locations in various species environments. This result suggests that these factors are independent of the identity of the host species and strongly influence the process and results of host preference, thus being able to change how much a given host species supports the growth of the parasite. In other words, these factors can result in differences in host quality. This finding confirms the hypothesis that host-preference studies performed at a single site can provide information only about local individuals of the host species and not about the species of hosts. In order to get reliable information about the preference of a given parasite species to its host species, the studies need to be conducted in multiple locations, in a variety of species environments.

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Declarations

Conflict of interest The author has no conflict of interest to declare.

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