Salinity modulates crop plants suitability as hosts for *Cuscuta campestris* parasitism

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A B S T R A C T

Cuscuta campestris Yunck. is a stem holoparasitic flowering plant, wide-spread and currently considered invasive worldwide. It has both ecological and agricultural significance. However, little is known on how the conditions of the environment, and abiotic stresses in particular, could affect the success of this parasite. A total of 22 potential host plants, belonging to 10 species and 4 families, were tested as *C. campestris* hosts under different saline regimes. The changes in survival rate (number of successful infections) and growth (as cm day^{-1}) of the parasite were studied. Salinity did significantly change the survival and growth rate of *C. campestris*, which effect was species- and cultivar-dependent. While generally the survival of the parasite decreased with increasing salinization, the opposite effect was observed on several host plants. However, survival rate did not always coincide with higher growth rate. This suggests that salinity produces different effects on the parasite depending on the host plant and these depend strongly not only on the species, but also on the cultivar. These results strongly suggest that under salt stress the suitability of various crop plants as hosts for *C. campestris* may change significantly, thus affecting the overall success of the parasite. In the light of the increased salinization of soils, this may have a significant effect on the spread of *C. campestris* and its agricultural impact.

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1. Introduction

Members of the genus *Cuscuta* include about 200 species of stem holoparasitic flowering plants (Braukmann et al., 2013) with great impact on both natural and agricultural plant communities. Overall, *Cuscuta* spp. are regarded as generalists – infecting a variety of host plant species, and a single plant simultaneously parasitizes a number of different host plants (Koch et al., 2004). The agricultural impact of several *Cuscuta* species is substantial, causing severe yield losses worldwide (Parker 2012). Yield loss due to *C. campestris* (field dodder) infestation may vary from non-significant to over 80% of the expected yield in absence of the parasite (Mishra et al., 2007). Legumes (fam. Fabaceae) are among the susceptible hosts (Farah and Al-Abdulsalam 2004), but *C. campestris* also causes severe infestation on sugar beet (*Beta vulgaris* L.) (Tóth and Tancik 2006), carrots (*Daucus carota*) (Rapparini et al., 2010), onion (*Allium cepa* L.) (Zaroug et al., 2014), eggplant (*Solanum melongena* L.) (Al-Gburi 2021), etc.

Generally, most cereals and grasses have been shown to be uncommon hosts for *Cuscuta* spp. (Dawson et al., 1994). This may be due to unfavorable anatomical structure, inability of *Cuscuta* spp. enzymes to initiate penetration through the monocotyledonous cell wall, direct defensive response, etc. (Sharma and Kapoor 2014). Some authors distinguish between primary hosts, on which *Cuscuta* spp. can establish itself since its seedling stage and further expand, and secondary hosts, that cannot serve as primary ones, but which the parasite, once installed, can successfully infect (Jayasinghe et al., 2004). Monocotyledonous plants may serve as secondary hosts.

Tomato (*Solanum lycopersicum* L.) has been shown to be resistant (or incompatible) to *Cuscuta* spp. parasitism (Amini et al., 2017; Sahm et al., 1994). The molecular basis of this resistance is

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largely unknown, although a specific host receptor responsible for the detection and response to *Cuscuta* infection was recently found in tomato (Ntoukakis and Gimenez-Ibanez 2016). The resistance may be provided also by inhibitors of cell-wall-degrading enzymes secreted by the host (Singh and Singh 1997), secretion of protease inhibitors by the host (Amini et al., 2017) and wound-like response preventing the establishment of connection to the vascular tissues of the host (Kaiser et al., 2015).

The suitability of the host may be further altered by various environmental factors, such as soil salinity. Salt stress is one of the most important restraints to agriculture worldwide, leading to a variety of physiological changes in plants (Zhu 2001). Most obviously, the reduced growth of plants under high-salinity conditions will lead to decreased biomass accumulation (Zhu 2001), which is unfavorable for parasitic plants. Abiotic stress factors would also trigger systemic defense response governed by stress hormones, which may contribute to resistance to parasites (Foyer et al., 2016; Smith et al., 2009), and lignification of the cell wall, which can interfere with haustoria formation (Jhu et al., 2020). On the other hand, high salinity may also increase susceptibility of plants to a variety of pathogens, as was shown in tomato (Triky-Dotan et al., 2005).

Relatively few studies exploring *Cuscuta* response to salinity were published. For example, *Cuscuta salina* Engelm. grows better on highly salinized *Beta vulgaris* L. hosts, but worse on such subjected to medium salinity (Frost et al., 2003). We have also reported reduced growth of *C. campestris* on Arabidopsis hosts subjected to elevated salinity (Zagorchev et al., 2018). In all cases, this seems to be a dose-dependent effect (Frost et al., 2003).

Considering the expanding abiotic stress challenge, to which both crop plants and natural plant communities are subjected (Savvides et al., 2016), the effect of such stresses on the host susceptibility to *Cuscuta* infestation is of considerable importance, because it could alter the resistance of the host, thus making it more susceptible (Zagorchev et al., 2018). This suggested alteration of the host susceptibility may further impact the success of *Cuscuta* spp. and its host preferences under a changing environment.

To the best of our knowledge, there are currently no other reports on the effects of host crop plants under different saline regimes on the growth rate of *C. campestris*. Thus, the objective of this study was to evaluate the effects on different crop plants from the Cucurbitaceae, Fabaceae, Solanaceae and Apiaceae families under different saline regimes on the successful growth rate of *C. campestris*. All plants tested served as primary hosts to the parasite.

2. Material and methods

2.1. Plant material

Cuscuta campestris Yunck. seeds were taken from the laboratory collection, gathered from a wild population (*Digitaria sanguinalis, Polygonum aviculare, Convolvulus arvensis* serving as hosts) in 2017 from the village of Telish, Cherven Briag Municipality, Pleven Province, the Danubian Plain, Bulgaria (GPS 43°19′27.3″N 24°15′15.8″E). A voucher herbarium was deposited in the Herbarium SO (Sofia University "St. Kliment Ohridski") under herbarium number SO 107784.

All host plants tested were acquired as commercially available seeds from Sortovi Semena – Sofia plc., with the exception of lentils, which were provided by Prof. Adele Muscolo. All tested host plant species are listed in Table 1.

Table 1
Host plant species and cultivars, used in the experiments.

Family Cucurbitaceae	
Cucumis sativus L. (cucumber)	cv. Cornichon de Paris
	cv. Gergana
	cv. Sandra
Cucurbita pepo L. (zucchini)	cv. Bianco di Trieste
	cv. Black Beauty
Family Fabaceae	
Lens culinaris Medik. (lentil)	cv. Eston Green
	cv. Castelluccio
Medicago sativa L. (alfalfa)	
Pisum sativum L. (pea)	cv. Ran 1
	cv. Telefono
Family Solanaceae	
Solanum melongena L. (eggplant)	cv. Rania F1
Capsicum annuum L. (pepper)	cv. Cayenne
	cv. Gold Medal
	cv. Kurtovska kapija
Solanum lycopersicum L. (tomato)	cv. Ideal
	cv. L. Milla
	cv. Oxheart
	cv. Trapezitsa
Family Apiaceae	
Daucus carota L. (carrot)	cv. Nantes
	cv. Karlena
Petroselinum crispum (Mill.) Fuss (parsley)	var. *crispum*
	var. *neapolitanum*

2.2. Growth conditions and experimental design

All host plants were grown from seeds, surface-sterilized for 10 min in 10% (v/v) commercial bleach, rinsed several times with distilled water and planted into soil:peat substrate:vermiculite mixture (2:1:1). Peat substrate was JSC "Durpeta", cat. number GP0337 (pH 5.5–6.5), N 140–190 g m^{-3}, P 160–210 g m^{-3}, K 180–230 g m^{-3}.

The host plants were set up in greenhouse conditions under natural sunlight in June, approximate photoperiod 15 h/9h (day/night), 70% relative humidity and 25 °C ± 2 ambient air temperature. These conditions were chosen because artificial light was found to alter the successful coiling of *C. campestris*. For salinity treatment experiments, all hosts were irrigated with either 0, 100, or 200 mM NaCl in tap water (1/10 of the pot volume) three times over a one-week period before the infection and twice after haustoria were macroscopically visible.

Cuscuta campestris seeds were surface-sterilized with 70% (v/v) ethanol for 3 min, followed by 10% (v/v) commercial bleach and seed coat scarification in concentrated H_2SO_4 for 15 min. After extensive wash the seeds were placed in close proximity to the respective hosts. The individual pots were placed at least 20 cm from each other to avoid attraction by neighboring plants. For every host plant species, 30 equally developed individual plants were selected and then randomly distributed into three equal groups: controls, 100 and 200 mM NaCl-treated. The following parameters of *C. campestris* growth were observed: time of the initial coiling and haustoria formation, lag phase between haustoria formation and secondary stem emergence, survival rate (e.g., number of successfully developed *C. campestris* plants), and growth rate in cm day^{-1}. All individual plants were collected and measured after 7–9 days following the secondary stem emergence. The experiment design was a randomized complete block with ten pot replications for each treatment. The trial was repeated three times and the obtained data were combined for analysis.

2.3. Statistical analysis

Two-component analysis of variance (ANOVA) was performed to assess the impact of host plant, salinity regime and the combi-

nation of them on *C. campestris* growth using JASP 0.14.1.0 (University of Amsterdam). All data were subjected to Levene's homogeneity test. All analyses were performed separately for each plant family, species and cultivar.

3. Results

The critical developmental stage of *C. campestris* is the formation of the secondary stem, which defines whether the parasite will survive or not. As expected, none of the tomato cultivars proved to be a suitable host to *C. campestris*, neither in control, nor in elevated-salinity conditions. The dying out of the parasite was accompanied by characteristic browning of the host stem (Fig. 1A). However, we recorded two cases of *C. campestris* successfully growing on cv. Ideal (control conditions) and cv. L. Milla at 100 mM NaCl (Fig. 1B), despite the defense response of the host (Fig. 1C). Out of four cultivars and three salinity regimes (a total of 360 plants), this amounts to a 0.57% survival rate of the parasite, suggesting that the resistance of this crop plant is not absolute. The growth of the surviving *C. campestris* individuals, however, was comparable to those, developing on other hosts of the Solanaceae family – approximately 2 cm day^{-1} (host – cv. Ideal, control conditions) and 1.65 cm day^{-1} (host – cv. L. Milla, 100 mM NaCl). Members of the Cucurbitaceae family also proved to be incompatible hosts in this particular case, although with no visible defense response (Fig. 1D). After haustoria formation, the parasites tended to get thinner and die out in several days. For the members of the Cucurbitaceae tested, a total of 450 plants, two individual *C. campestris* plants developed successfully, on cv. Cornichon de Paris (Fig. 1E) and cv. Sandra, both in control conditions, which amounts to a 0.43% survival rate. The growth of these *C. campestris* individuals was above the highest of all experiments: 6.57 and

4.06 cm day^{-1}, respectively. Elevated salinity did not induce susceptibility in any of the cultivars tested.

The survival rate in dependence of the host plant tended to decrease with the increase of salt concentration (Table 2), with complete prevention of development in both carrot cultivars used and lentils cv. Castelluccio, where, under 200 mM NaCl irrigation, the parasite failed to develop.

However, the time frame between haustoria formation and secondary stem emergence, or lag phase (Koch et al., 2004), showed different substantially between and within plant families. In most of the Fabaceae, the lag phase was not longer than 48 h, with the exception of pea, where it was extended to 5 ± 1 days. In the Apiaceae, the emergence of the secondary stem took 6–7 days, while, in the Solanaceae, it was extended to 10 ± 2 days. At 100 and 200 mM NaCl, however, the lag phase on eggplant was reduced to 6 ± 1 days.

The growth rates of *C. campestris* strongly depended on the host plant, including under control conditions. On the plant family level, the median growth rates were comparable when host plants were members of the Fabaceae or the Apiaceae (Fig. 2A) and decreased with salinity (Fig. 2B and C). However, at 100 mM NaCl the median growth rate within the Fabaceae was not so strongly affected as compared to the Apiaceae (Fig. 2B). In contrast, the growth rates of *C. campestris* on hosts from the Solanaceae tended to increase at 200 mM NaCl (Fig. 2C). The data, however, were not normally distributed (Fig. 2), but were mainly related to large differences in *C. campestris* growth rates depending on the species and cultivar (Fig. 3). In this respect, within the Fabaceae, the growth rates at control conditions were similar on all host plants with the exception of *Lens culinaris* cv. Castelluccio di Norcia. On this host, however, *C. campestris* growth was completely blocked at 200 mM NaCl, unlike on cv. Eston Green. Within *Pisum sativum,* at
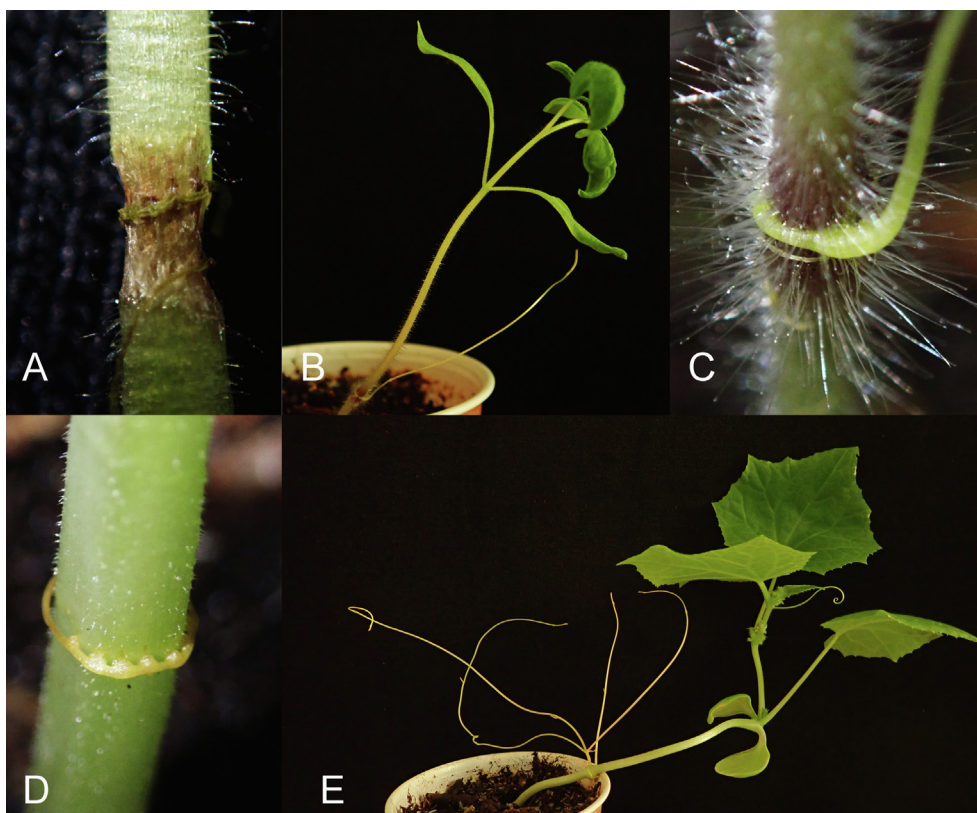

Fig. 1. *Cuscuta campestris* growth on different host plants. A – incompatible interaction with *Solanum lycopersicum*; B – successful growth on *Solanum lycopersicum*; C – overcoming of *Solanum lycopersicum* defense; D – incompatible interaction with *Cucumis sativum*; successful growth on *Cucumis sativus*.

Table 2
Survival rate in percentage of *Cuscuta campestris* on different host plants as dependent on salinity regime.

	Controls	100 mM NaCl	200 mM NaCl
Fam. Fabaceae			
Lens culinaris			
cv. Eston Green	100	100	53 ± 5
cv. Castelluccio	100	100	0
Medicago sativa	100	97 ± 6	56.7 ± 6
Pisum sativum			
cv. Ran 1	23 ± 5	26 ± 6	53 ± 5
cv. Telefono	56.7 ± 6	76 ± 11	53 ± 5
Fam. Solanaceae			
Solanum melongena	53 ± 11	70 ± 10	76 ± 11
Capsicum annuum			
cv. Cayenne	76 ± 11	50 ± 0	73 ± 6
cv. Gold Medal	100	73 ± 6	23 ± 5
cv. Kurtovska kapija	100	73 ± 6	26 ± 6
Fam. Apiaceae			
Daucus carota			
cv. Nantes	53 ± 5	56.7 ± 6	0
cv. Karlena	100	53 ± 5	0
Petroselinum crispum			
var. *crispum*	53 ± 5	26 ± 6	53 ± 5
var. *neapolitanum*	50 ± 0	53 ± 5	100

100 mM NaCl, the growth rates of the parasites were either comparable to the controls (cv. Ran 1) or to 200 mM NaCl (cv. Telefono). Within the Solanaceae, at 200 mM NaCl, *C. campestris* was nearly fully inhibited on host *Capsicum annuum* cv. Cayenne, but significantly outgrew the control plants on hosts *Capsicum annuum* cv. Kurtovska Kapiya (despite the lower survival rate, Table 2) and *Solanum melongena* (Fig. 3). Apparently, the growth rate was not related to the survival rate, as was clearly seen on *Cucumis sativus* serving as host plant. Although only single *Cuscuta* plants survived on this host, they showed comparable or even higher growth rates in comparison to the rest of the host plants (Fig. 3). On hosts *Petroselinum crispum*, it was observed that the generally higher survival rate of the parasite at higher salt concentration coincided with significantly lower growth rate.

The statistical analysis showed that the host plant family was not particularly decisive for *C. campestris* growth but had strong connection to salinity (Table 3), e.g., the effect of the abiotic stress was significantly different between members of different families. Within individual families, the effect of elevated salinity significantly affected *C. campestris* growth with little dependence on the host plant species (Table 3). However, within individual host plant species, the cultivar did also significantly affect the parasite's growth.

4. Discussion

The impact of parasitic plants on various crop plants is well documented and causes significant annual yield losses (Amini et al., 2017). The selected host plants in the present study, e.g. members of the Cucurbitaceae, Fabaceae, Solanaceae and Apiaceae families are common hosts for *Cuscuta* spp. (Lanini and Kogan 2005; Marambe et al., 2002) and are among the important crop plants in Europe, and in Bulgaria in particular. While members of the Fabaceae and Apiaceae were suitable host plants (Figs. 2 and 3), members of the Solanaceae showed varying success for the parasite. All tested Fabaceae host plants ensured very fast attachment and short lag phase of the parasite, probably due to the presumably higher nitrogen content in this family and by the large nitrogen need of members of the *Cuscuta* genus (Marambe et al., 2002). *Solanum lycopersicum* has been proved to be an incompatible/resistant host (Krause et al., 2018), although this resistance is not absolute and may vary significantly between different tomato cultivars (Kaiser et al., 2015). Only individual *Cuscuta* plants developed on this host plant, confirming the existing reports.

As previously reported, elevated salinity exhibited negative and dose-dependent effect on the parasite growth (Frost et al., 2003; Zagorchev et al., 2018). In some host plants, this effect was already significant at 100 mM NaCl and completely devastating at 200 mM NaCl, while in others, the lower salt concentration did not significantly alter the parasite's growth (Fig. 3). However, elevated salinity may also increase the susceptibility of the host (Frost et al., 2003), as shown in eggplant and in several pepper cultivars (Fig. 3). Apparently, the survival rate and the growth rate of the parasite were not directly related in all cases. While in *Petroselinum crispum*, the survival rate of the parasite increased with salinity and growth rate decreased, the opposite was observed in *Capsicum annuum* cv. Kurstovska Kapiya. The survival rate, e.g., the number
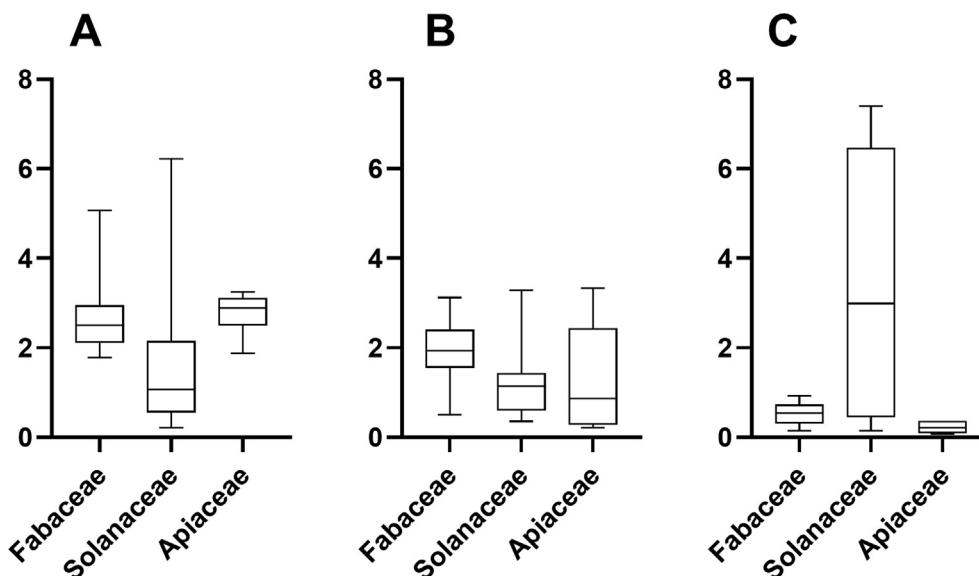

Fig. 2. Box plot of median growth of *Cuscuta campestris* and distribution of data in dependence of host plant Family at control (A), 100 mM NaCl (B) and 200 mM NaCl (C) conditions.
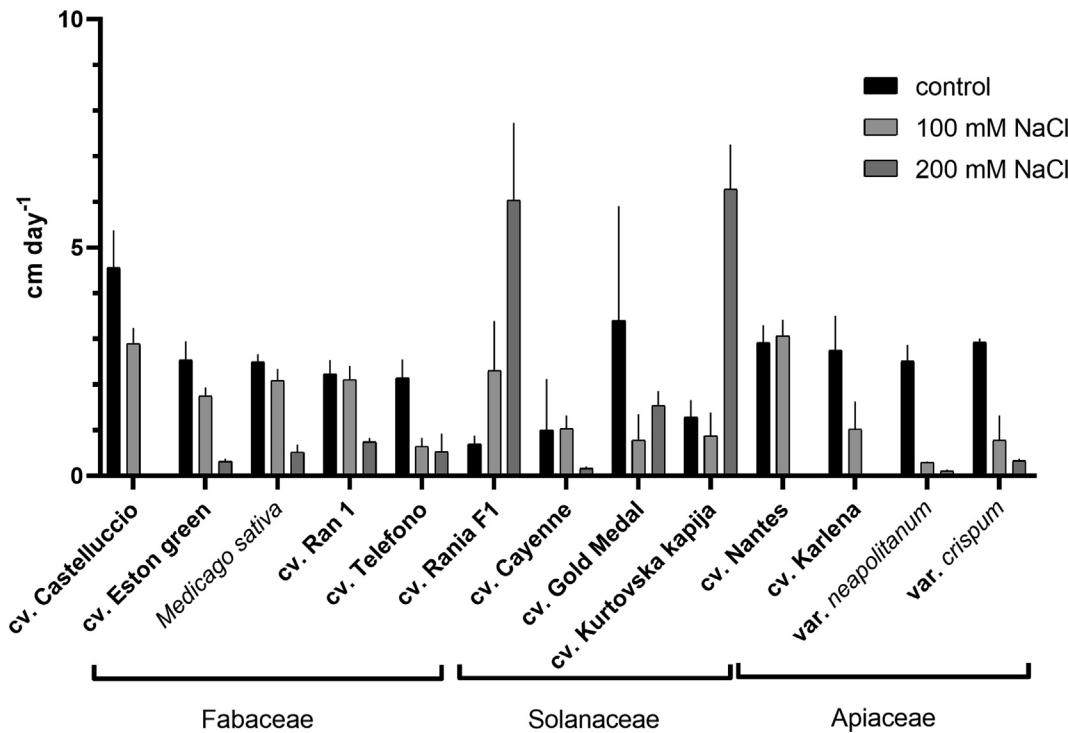
Fig. 3. Average growth in cm day^{-1} of *Cuscuta campestris* on different host plants under different salt concentration. Mean values ± SEM were shown. * - based on a single plant.

Table 3
Two-way ANOVA analysis of *Cuscuta campestris* growth rate in cm day^{-1} on different host plants under different salinity regimes.

Cases	Sum of Squares	df	Mean Square	F	p
Family	7.483	2	3.742	2.140	0.123
salinity	21.354	2	10.677	6.108	0.003
Family * salinity	79.977	4	19.994	11.437	< 0.001
On species level					
within Fabaceae					
species	3.356	2	1.678	3.773	0.033
salinity	30.877	2	15.439	34.722	< 0.001
species * salinity	4.006	4	1.002	2.253	0.085
within Solanaceae					
species	9.648	1	9.648	2.923	0.098
salinity	50.820	2	25.410	7.699	0.002
species * salinity	23.691	2	11.846	3.589	0.040
within Apiaceae					
species	3.909	1	3.909	7.640	0.012
salinity	13.265	1	13.265	25.925	< 0.001
salinity * species	2.896	1	2.896	5.661	0.027
On cultivar level					
within *Lens culinaris*					
cultivar	7.521	1	7.521	30.723	< 0.001
salinity	4.533	1	4.533	18.516	0.003
cultivar * salinity	0.574	1	0.574	2.346	0.164
within *Pisum sativum*					
cultivar	1.548	1	1.548	17.292	0.001
salinity	7.239	2	3.619	40.441	< 0.001
cultivar * salinity	1.752	2	0.876	9.786	0.003
within *Capsicum annuum*					
cultivar	19.577	2	9.788	9.403	0.002
salinity	14.020	2	7.010	6.734	0.007
cultivar * salinity	52.550	4	13.138	12.620	< 0.001
within *Daucus carota*					
cultivar	3.688	1	3.688	12.107	0.008
salinity	1.882	1	1.882	6.179	0.038
cultivar * salinity	2.644	1	2.644	8.679	0.019
within *Petroselinum crispum*					
variety	0.637	1	0.637	8.936	0.011
salinity	22.243	2	11.122	156.064	< 0.001
variety * salinity	0.055	2	0.027	0.383	0.690

of successfully attached *C. campestris*, plants is strongly dependent on the formation of haustoria, which, in turns, may be inhibited by cell wall lignification (Jhu et al., 2020), caused by elevated salinity (Neves et al., 2010). Haustoria formation may also be impeded by common defense mechanisms of the host, triggered by elevated salinity (Rejeb et al., 2014). However, abiotic stress, and elevated salinity in particular, may also increase susceptibility to pathogens in some plants (Bai et al., 2018). Next, the growth of the parasitic plant may be affected by several factors. Negative effects would be expected by reduced host biomass availability and the accumulation of toxic ions, mostly Na^+ (Wallace et al., 1978), while it has been reported that Cl^- ions do not penetrate the haustoria at significant rates (Förste et al., 2020). On the other hand, the accumulation of various compatible solutes and sugars during salt-stress response (Zhang et al., 2017) may provide a suitable nutrient source for enhanced growth of the parasite (Zagorchev et al., 2018). Thus, it is possible that under elevated salinity certain host plants express higher resistance to haustoria formation but provide more beneficial nutrient content to the parasite, and vice versa. We also recently reported that although elevated salinity has a negative effect on *C. campestris* seed germination, it did not eliminate its ability to infect hosts and grow further (Zagorchev et al., 2021). *Cuscuta campestris* is also a well-known generalist, infecting a variety of host plants (Koch et al., 2004). All this makes this parasitic plant a prominent weed species with potential to cause significant damages to various crop plants under various environmental conditions.

Cuscuta growth did not seem to be directly related to the salinity tolerance of the host plants. For example, of the lentil cultivars, Castelluccio di Norcia is naturally resistant to elevated salinity, while Eston is a salt sensitive commercial variety (Muscolo et al., 2020). Previous results have shown a relationship between imposed stress and performance of the cultivars, showing variations in salinity tolerance throughout the life cycle of each variety. Castelluccio di Norcia, showed a greater salinity tolerance with better adaptive biological and phenotypic traits in comparison with Eston (Muscolo et al., 2015). While the parasite grew better on the salt-tolerant cultivar under control and 100 mM NaCl conditions (Fig. 3), it stopped completely under 200 mM NaCl, in contrast to cv. Eston (salt-sensitive).

In short, we can assert that the initial development and growth of parasitic field dodder under elevated salinity is strongly dependent on the host plant. While predominantly inhibiting, the effect of soil salinization may also have positive effect on the parasite, as seen in some members of the Solanaceae. In the light of the increasing salinization of arable lands (Rengasamy 2006), this change in *C. campestris* growth, which was strongly dependent on the host species and cultivar, suggests a possible switch of the host preference of the parasite with possible impact on agriculture worldwide.

5. Conclusion

Although parasitic plants of the genus *Cuscuta* lack direct soil contact throughout most of their life cycle, they appeared to be influenced by soil salinity through their host plants. This impact, depending on the host species and variety, could be either positive or negative, suggesting that, under stressful conditions, the success of *Cuscuta campestris* would be altered and may lead to changes in its host preferences. However, these effects, including their agricultural impact, are difficult to predict.

Declaration of Competing Interest

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

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