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Tolerance to dodder (*Cuscuta campestris* L.) in citrus species of south of Kerman province – Iran

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ABSTRACT

Dodder is a parasitic weed that causes a lot of damage to citrus production in the south of Kerman province, Iran. Introducing cultivars which tolerant to this parasite can be considered a very effective step in controlling it. Therefore, to evaluate the tolerance of seven important citrus species to dodder, an experiment was conducted in a randomized complete block design with three replicates in greenhouse conditions for two years (2016–2017). In this experiment, the reaction of orange, local, and Kara tangerine, grapefruit, Valencia orange, local orange, and lemon seedlings to dodder infestation was investigated. The infestation was done artificially by placing 10 dodder's thallus on the seedlings of each of the mentioned species. After the successful establishment of the parasite (during 4 months), chlorophyll content, number of stems on citrus species shoots, number of capsules in infested seedlings, and seed weight on each seedling were measured and recorded. The results of this study revealed that different species of citrus showed very different reactions to the presence of dodder so that these species can be based on the success rate of its attachment to them into tolerant and sensitive species. According to the results, Valencia oranges and Bitter orange were tolerant to dodder, but lemon and tangerines (local and Kara) showed high sensitivity. A cross-sectional of plant tissues showed that concerning anatomic view, there was no difference in haustorium penetration between the different citrus species. As a result, it is recommended to use physiological, genetical, and biochemical analysis to distinguish the differences.

1. Introduction

The southern region of Kerman is one of the most important agricultural centers of Iran, especially in the production of citrus species. This region was ranked in third place, after Mazandaran and Fars provinces, with a cultivated area of 38,000 ha and production of more than 550,000 tons of different kinds of citrus species. Moreover, a great proportion of its organic citrus has been exported abroad due to the lack of chemical pesticides. Production and supply of citrus in this region started in September with the harvest of lemons and then continues with a production of Washington Novell oranges in October and ended with the harvest of sweet lemons, grapefruits, and Valencia oranges in March during the autumn and winter.

Dodder (*Cuscuta campestris*) with the common names field dodder, golden dodder, large-seeded alfalfa dodder, yellow dodder and prairie dodder, is an annual obligate stem parasite belonging to the family Cuscutaceae. The genus Cuscuta is comprised of about 175 species worldwide (García et al., 2014; Dawson et al., 1994). Among weeds, *C. campestris* is one of the most damaging species worldwide for the agricultural production of dicotyledonous crops (Goldwasser et al., 2012). This species significantly affecting the production of citrus species in this strategic region and also distributed in north, northwest, west, center as well as northeast (Jafari et al., 2016) and southeast (unpublished data) regions of Iran. The damage

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caused by dodder to its host plant varies from moderate to severe, depending on growth cause damage of the host plant and on the number of haustoria attachments (Ashigh and Marquez, 2010).

C. Campestris -infested plants gradually become weak, lush growth declines and their vegetative and generative yields decrease (Koskela et al., 2001; Fathoulla and Duhoky, 2008), spatially in south of Kerman damage (dodder) can ultimately lead to total destruction and death of the host (Citrus specious spatially Lemon). Field dodder causes most damage during massive infestation of established leguminous crops (alfalfa), also occur in vegetable crops (e.g. potato, tomato or *Ocimum basilicum*) (unpublished data).

Parasitic plants have used special absorption /adhesion various ways of attacking their hosts organ called a haustorium. This organ serves as a structural and physiological bridge for the parasites to draw minerals, water, solutes and organic molecules from the host plant's conductive systems, leading to yield reduction and host growth (Yoshida et al., 2016). Parasitic plants of the genus Cuscuta usually do not have photosynthetic activity, because neither have chlorophyll at all, or only little amounts of it (García et al., 2014; Jahanbakhshi et al., 2019).

Some species of Cuscuta are a broad host range, while others have very host-specific. in some host plant may *Cuscuta* spp. stems twine around them but not fully develop. Therefore, the stems weaken and die. some host's anatomical structure preventing the haustoria and hyphae from reaching the vascular bundles of the host may delay the growth of the parasite or even prevent it (Ghaghelestany et al., 2020; Dawson et al., 1994), but in some susceptible species plant, has significant effects on the function and structure of the communities that are infested by these holoparasites inducing negative impacts on the growth and yield of infected hosts (Albert et al., 2008; Payandeh et al., 2021).

As mentioned, the south of Kerman province is one of the main centers of citrus production in Iran. Annually, a significant part of the yield of these horticultural crops is lost due to infestation with the dodder. Therefore, this study was conducted for the first time in Iran and worldwide with the aim of evaluating the tolerance of different species of citrus species to the dodder and the introduction of tolerant citrus species.

2. Material and methods

In this study, the reaction of seven citrus species including orange, Kara mandarin, local tangerine, blood grapefruit, Valencia orange, local orange, and sour lemon to infestation with the parasitic plant during two growing seasons from 2016 to 2017 was investigated with three replicates. Seedlings of different citrus species were planted in pots (40 × 40 cm) during autumn and March in Jiroft University Research Greenhouse, with conditions of 28.6018°N, 57.8293°E, and temperatures of 25–35 °C. The pots were irrigated every four days.

With the aim of artificial infestation of each of the studied citrus species, ten thallus of dodder with the same length and diameter were collected from the nearest place to the test site and placed separately on the stems and leaves of each species. Four months after that, the number of thallus that their haustorium was attached to the stem and leaves, the number of produced capsules, the amount of chlorophyll, the fresh and dry weight of dodder were measured. To estimate the fresh and dry weight of dodder plants, they were weighted when the stems were separated accurately from the host plant and dried at 75 °C for 72 h. Chlorophyll content of control and contaminated samples to dodder in various citrus species were measured using SPAD instrument during multiple steps. This design was done in a complete randomized block design with three replications. Statistical analysis of data was performed using Macro and Genstat software and mean comparison was performed based on Fisher's Least Significant Difference Test (FLSD) at $p \leq 0.05$. The graphs were drawn using Excel software ver. 2007 (Jahanbakhshi et al., 2020; Jahanbakhshi and Kheiralipour, 2019).

3. Results and discussion

The results of the analysis of variance showed that the effect of citrus species, infestation, and their interaction during two years on chlorophyll content, number of the haustorium, and number of capsules, dry and fresh weight of dodder was significant at $p \leq 0.01$ (Table 1).

4. Chlorophyll content (SPAD Value)

According to the ANOVA table, effects of citrus species, levels of infestation, and effect of year, (year × species × infestation) on chlorophyll content of citrus species were significant ($p \leq 0.01$). Estimation of chlorophyll content in different cultivars indicated a significant difference in its content between control and treated samples. It was also found that the highest chlorophyll content was in Valencia orange with 62.7 and 62.43 (SPAD values as chlorophyll content) which was significantly higher than other species. The lowest amount was related to Kara mandarin, local mandarin, and lemon species so that during the two years of the experiment the chlorophyll content was 27.63 and 29.7, 29.69 and 30.26, 30.83 and 30.43, respectively (Fig. 1). The highest and the lowest amount of chlorophyll was achieved in control and contaminated samples, respectively (Fig. 1). It is noteworthy to mention that among citrus species including mandarins, local tangerines, and lemons, there was a significant difference between control and treatments that were artificially contaminated (Fig. 1).

Decreasing chlorophyll content leads to the reduction of photosynthesis, followed by a decline in photosynthetic assimilates as well as a decrease in growth and yield. After attaching dodder to the host, the haustorium begins to become longer and penetrate to the host tissue. The rest of haustorium growth depends on the host response (tolerance or sensitivity). With respect to anatomy, one of the most important causes of plant tolerance to parasitic plants is the formation of cambium cells or the formation of lignin cells around vascular bundles (Farah, 2007). It seems that although several methods for the management of dodder have been introduced, using resistant cultivates against dodder can be an efficient and economic method. Parasite's dependence on the host plant is, therefore, stronger, as well as their negative impact in terms of reduced chlorophyll and auxiliary pigments in the host plant (Van der Kooij et al., 2005). Similarly, Fathoulla and Duhoky, (2008) stated that *C. campestris, C. chinesis, and C. monogyna* not only caused significant decreases in anatomical and morphological changes in their hosts, but reduced also in total chlorophyll contents in their three tested hosts (*Helianthus annuus*, *Coleus* spp. and *Capsicum annum*). Similar results were obtained by Saric-Krsmanovic et al. (2019) the results have shown a significant reduction in chlorophyll *a*, chlorophyll *b*, and carotenoids in infested sugar beet and alfalfa (*Medicago sativa*) plants compared with non-infested plants.

5. Number of haustorium

Furthermore, the result of analysis of variance in Table 1 revealed that the effect of different species of dodder, the double and triple interactions have a significant effect on the number of haustorium on citrus ($p \leq 0.01$). The results of interactions of different citrus species showed that the highest number of haustorium in both years was recorded with an average of 863 in the first year and 1006 in the second year in the lemon,

Table 1
Analysis of variance (mean squares) of *Cuscuta campestris* on traits of different citrus species at two years using combined analysis.

Sources of variations	Degree of freedom	Chlorophyll amount (SPAD value)	Haustorium No.	Capsule No.	Dodder fresh weight (g)	Dodder dry weight (g)
Replication (R)	2	6.90	1236.08	5722.5	12.45	0.58
Year	1	7.36	9472.19	31050.2	40.74	25.12
R × Year	2	1.02	427.65	2611.5	3.86	2.49
Species	6	794.63**	368020.00**	567832.1**	955.48**	184.60**
Year × Species	6	3.21**	2126.40**	13109.1**	14.69*	7.36**
Infestation	1	2682.51 ns	1411810.70 ns	2217150.0 ns	6241.91*	1204.30 ns
Year × Infestation	1	12.414*	8845.70**	31050.2**	29.40**	29.60**
Species × Infestation	6	554.80**	379732.00**	567832.0**	1301.29**	232.30**
Year × Species × Infestation	6	3.80**	2224.10**	13109.0**	20.23**	7.42**
Error	52	2.28	636.50	2192.2	5.47	0.79
Total	83	132.24	72038.20	113026.0	245.54	46.9
C.V. (%)		2.99	18.90	28.80	21.70	19.10

ns,* and ** represent not significant and significant at the 5% and 1 probability levels, respectively.

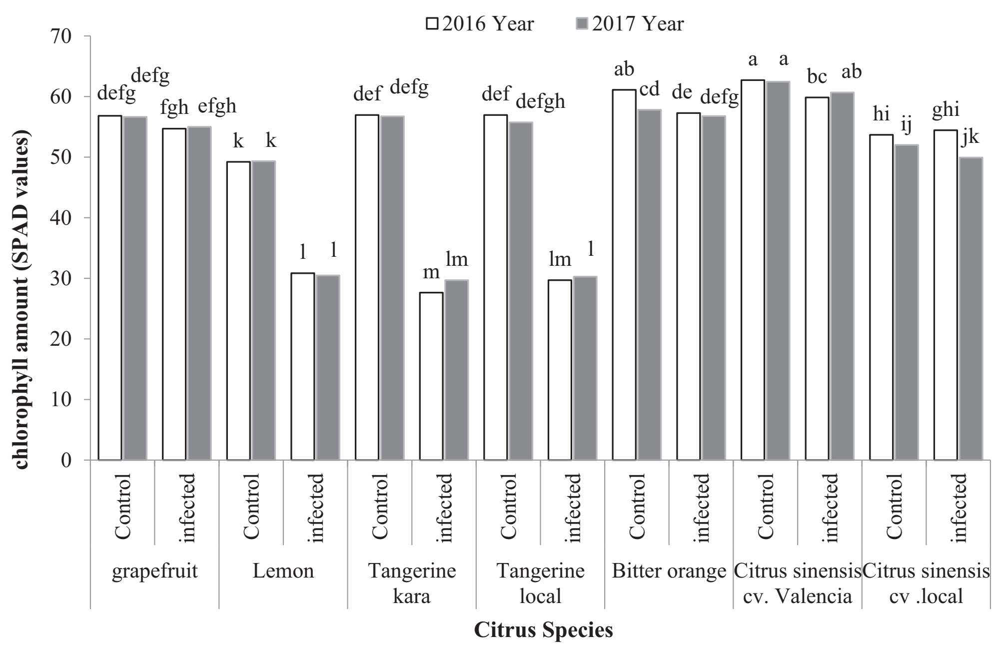

Fig. 1. Effect of *Cuscuta campestris* on chlorophyll content (SPAD values) of citrus species during two years. Means with similar letter did not show significant differences according to LSD test at $p \leq 0.05$.

respectively. The highest number of Haustorium related to Tangerine kara and local ones with averages of 436, 497, 334, and 406 in the first and second year, respectively (Fig. 2).

However, the lowest amount of haustorium, like other pre-measured traits, chlorophyll content, and dry weight belonged to Valencia orange and bitter orange species, which can be attributed to high tolerance of these two species to the parasitic plant of the dodder (Fig. 2). According to the results above, can be explained, rising air temperature lead to rise the growth trait (Number of haustorium) of the dodder plant in the second year (2017).

The tomato defense system induces genes within the early stages of haustorium development of *Cuscuta reflexa* Roxb. to stop parasitization (Werner et al., 2001). *Cuscuta* spp. growth on different hosts varies considerably (Nemli, 1987).

6. Number of capsules

It can be seen in Fig. 3 that due to the result of analysis of variance, the effect of different species of dodder, the double and triple interactions have a significant effect on the number of capsules on citrus ($p \leq 0.01$). The results of interactions of different citrus species showed that the maximum number of capsules produced during two years with an average of 906.3 and 1245, respectively, was observed in lemon. Also, Kara and local mandarin species with an average of 651.6 and 678.6 (436.6 and 611) capsules in the first and second year standing in second place (Fig. 3). According to the results above, can be explained, rising air temperature lead to rise the growth trait (Number of capsules) of the dodder plant in the second year (2017).

The minimum amount related to Bitter orange and Valencia (*Citrus sinensis* cv Valencia) during two years showed the high tolerance of these two species to the parasitic plant (Fig. 3). The result of Plant defense responses that include rapid production of reactive oxygen species (ROS-burst), increased levels of secondary metabolites (callose, phytoalexins, lignins, etc.) the elevation of the stress-related phytohormone ethylene, the induction of characteristic marker genes and signaling via networks controlled by the Phytohormone salicylic acid (SA) and jasmonic acid (Boller and Felix, 2009; Böhm et al., 2014; Wasternack et al., 2006).

7. Fresh and dry weight

As it can be seen in Table 1, the result of the analysis of variance showed that the effect of different species of citrus has a significant effect on dry and fresh weight of dodder on citrus ($p \leq 0.01$).

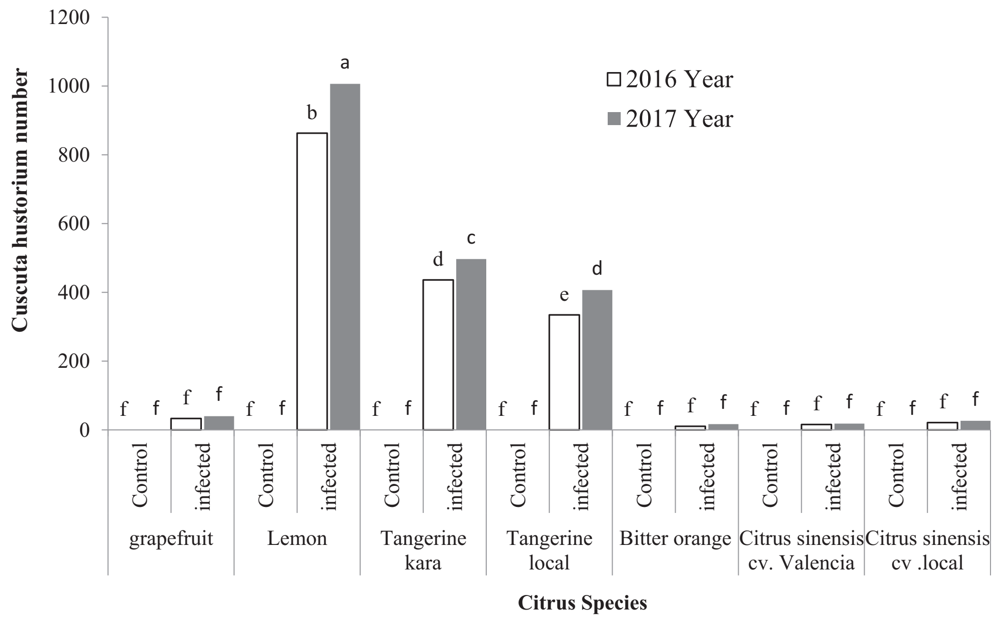

Fig. 2. Effect of *Cuscuta campestris* on haustorium number of dodder on citrus species during two years Means with similar letter did not show significant differences according to LSD test at $p \leq 0.05$.

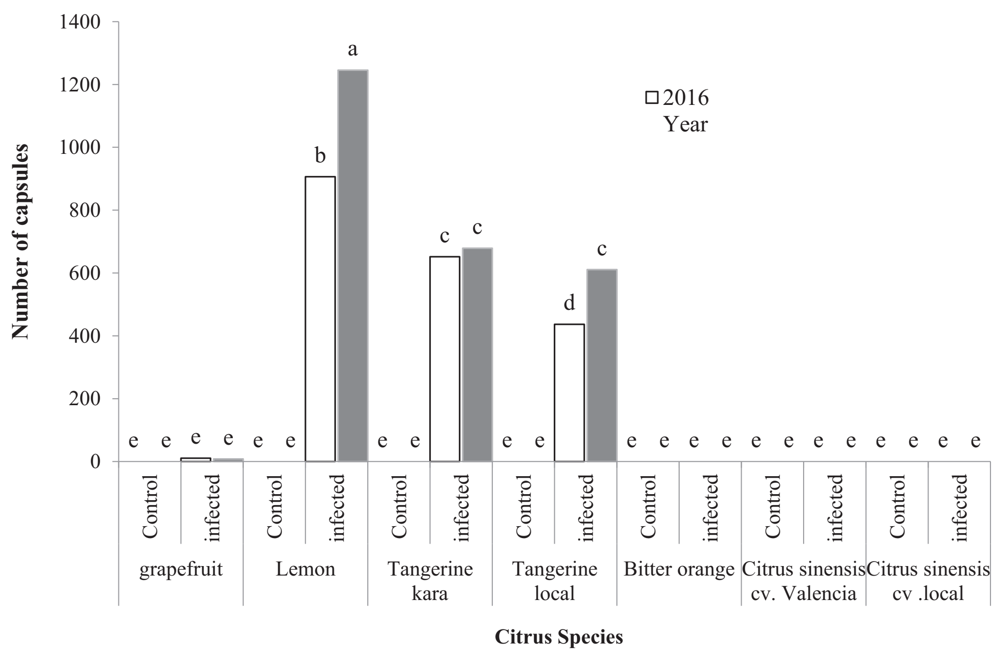

Fig. 3. Effect of *Cuscuta campestris* on capsule number of dodder on citrus species during two years. Means with similar letter did not show significant differences according to LSD test at $p \leq 0.05$.

The results of double and triple interactions on the fresh and dry weight of the dodder parasite collected in different citrus species (*Citrus* spp.) were significant in both years. Therefore, lemon species with 47.6 g and 55.07 g and Tangerine Kara with 30.7 g and 38.23 g and local Tangerine with 22.63 g and 29.26 g in the first and second year showed the highest susceptibility to dodder parasites among all species respectively (Fig. 4). While the lowest amount of fresh weight and consequently the highest tolerance was observed in Bitter orange (7.7–5.73 g) and Valencia orange (*Citrus Sinensis* cv. Valencia) (5.4–10.43 g) (Fig. 4).

The results of the dry weight of the dodder showed that lemon species with 18.05 g and 26 g and Kara Tangerine with 15.8 g and 16.60 g and local Tangerine with 12.1 g and 7.27 g in the first and second year, respectively showed the highest susceptibility to dodder parasites among the all tested species. However, the minimum dry weight and consequently the highest tolerance were observed the same as fresh weight in Bitter orange (2.73–2.64 g) and Valencia oranges. (*Citrus Sinensis* cv. Valencia) (5.4–2.9 g) (Fig. 5). According to the results above, can be explained, rising air temperature lead to rise the growth traits (Fresh and dry weight) of the dodder plant in the second year (2017).

In addition to causing severe damage to citrus species, the dodder can also transmit some severe diseases such as citrus greening (*Candidatus Liberibacter asiaticus*), phytoplasma and viral diseases.

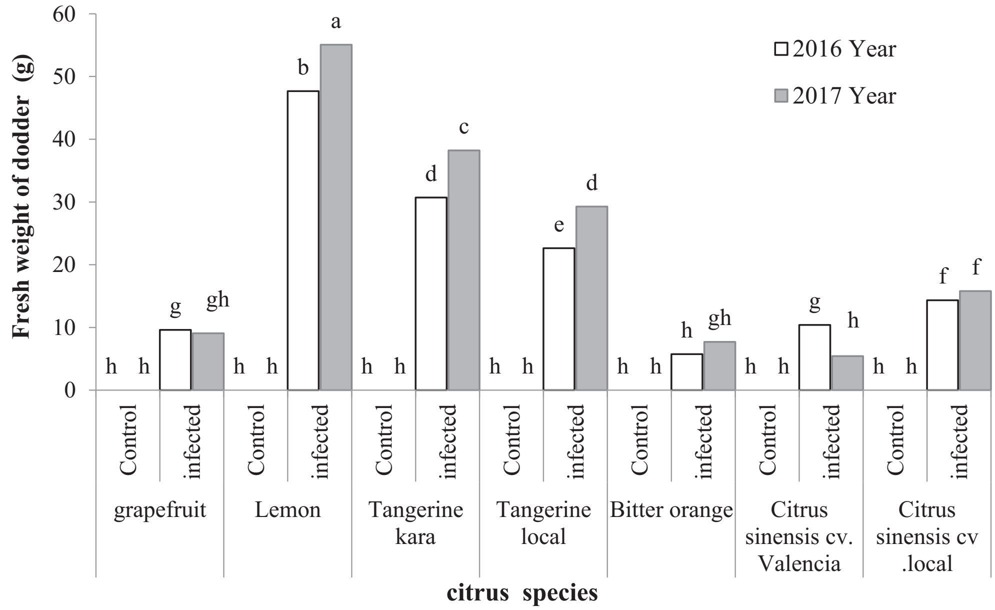

Fig. 4. Effect of *Cuscuta campestris* on fresh weight of dodder on citrus species during two years. Means with similar letter did not show significant differences according to LSD test at $p \leq 0.05$.

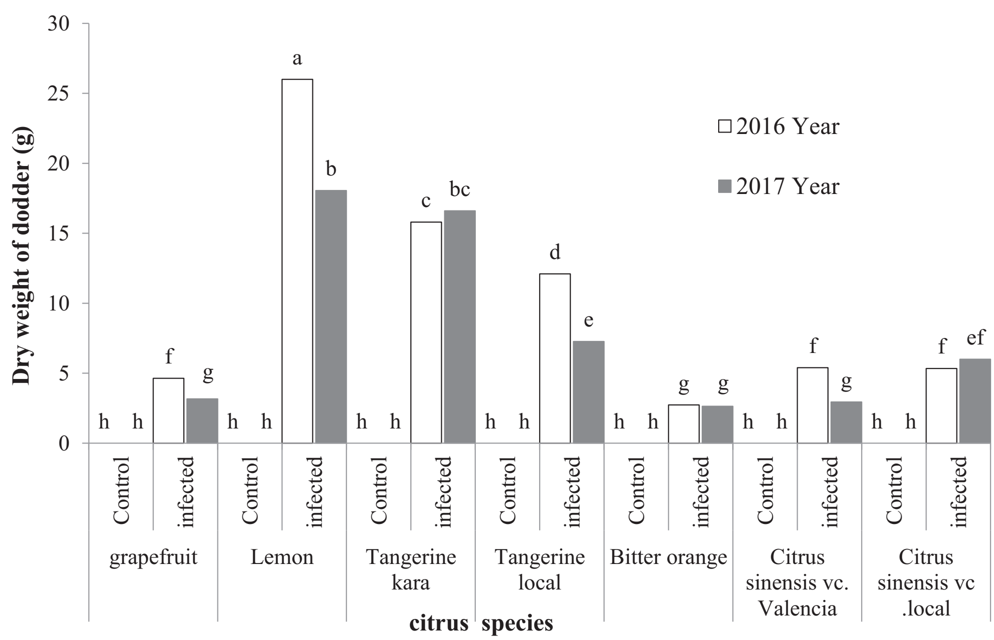

Fig. 5. Effect of *Cuscuta campestris* on fresh weight t of dodder on citrus species during two years. Means with similar letter did not show significant differences according to LSD test.

Incompatible relationships between dodder species and tomato cultivars have been reported by (Goldwasser et al., 2001). They investigated the relationships between 30 tomato (*Solanum lycopersicom*) cultivars and one species of dodder (*Cuscuta reflexa*). Development of epidermis, hypodermis and clonal cell of tomato, formation of necrotic tissues around the primary haustorium, suberization of cell walls adjacent to necrotic tissue, and inhibition of the formation of haustorium are considered as the cause of tolerance in some tomato cultivars against dodder (Goldwasser et al., 2001).

According to Goldwasser et al. (2001) towards the tolerant varieties of tomato (*S. lycopersicom*) against dodder, despite the wrapping parasite around the host, the haustorium cannot penetrate to the host tissue. Consequently, the parasite disappears. In the studies, it was found that the binding of dodder to the tolerant varieties was 75% less than the susceptible varieties, which leads to a reduction in the dodder growth up to about 70%. Although they noted that none of the tomato cultivars were fully considered as tolerant in the experiment, they showed considerable performance compared to the sensitive ones.

Fig. 6. Infestation of *Cuscuta campestris* on Lemon.

Fig. 7. Infestation of *Cuscuta campestris* on Bitter orange.

8. Haustorium penetration in plant tissue

Overall, the results of stem cross-section of the studied species in both years showed that various species of tangerine including kara and local tangerine and lemon were highly sensitive to dodder (Fig. 6). While orange species (*Poncirus trifoliata* L.) and Valencia orange (*Citrus Sinensis* cv. Valencia) exhibited high tolerance toward dodder (Figs. 7 and 11). In this study, the maximum number of haustorium formed by dodder in both years was observed on lemon and tangerine, respectively (Figs. 6, 8, 9 and 10). Moreover, the penetration of haustorium toward the vessels of limon and Tangerine cultivars including Kara and local was so that the vascular connection between the host and the vascular tissues of dodder was established desirably.

Werner et al. (2001) and Albert et al. (2008) stated that first the host plant reacts by expressing a specific gene for calcium release, cell growth and changes in the cell wall, after the formation of hyphae, they are mostly connected to the xylem or phloem of the host or even Attached to the host parenchyma. Simultaneously with their ring-like structure, hyphae can attach to several host plant sieve tubes and increase their adsorption power as well as their effect on their host conducting tissue (Haupt et al., 2001).

Fig. 8. Infestation of *Cuscuta campestris* on Tangerine Kara.

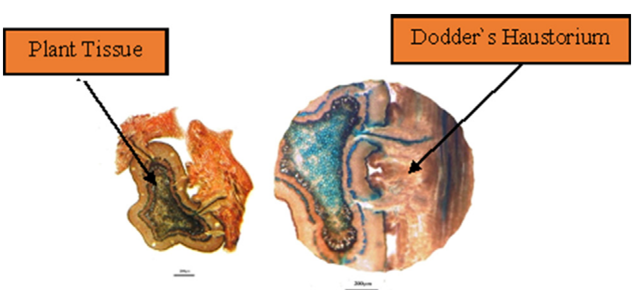

Fig. 9. Cross section of Tangerine Kara Stem and the rate of Haustorium penetration in plant tissue due to severe infestation of *Cuscuta campestris.*

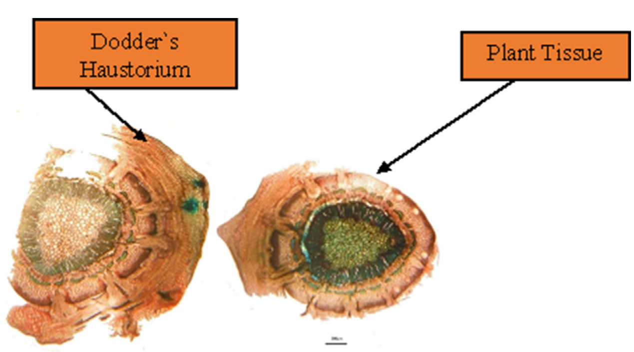

Fig. 10. Number and extent of haustorium penetration in the cross section of the attachment of the *Cuscuta campestris* to Lemon plant (*Citrus limon*).

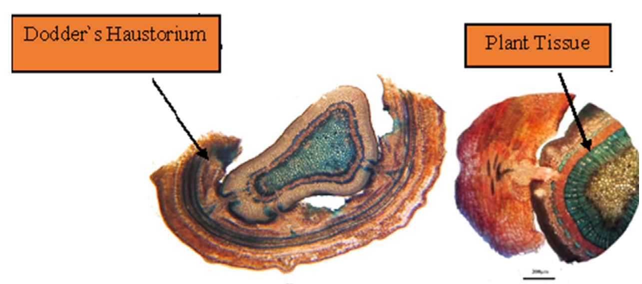

Fig. 11. Cross section of orange stem (*Poncirus trifoliata* L) and the rate of Haustoria penetration in plant tissue due to weak infestation of *Cuscuta campestris.*

9. Conclusion

The results of the experiments in both years showed a very different response of the studied species to the presence of dodder. These species can be classified into tolerant and sensitive ones based on the number of successful attachments of haustorium to them. Furthermore, the highest tolerance to dodder was related to two species of Bitter orange (*Poncirus trifoliata* L) and Valencia orange (*Citrus Sinensis* cv. Valencia). The highest susceptibility was observed in Limon and two species of kara and local tangerine. A cross-sectional of plant tissues showed that concerning anatomic view, there was no difference in haustorium penetration between the different citrus species. As a result, it is recommended to use biochemical analysis to distinguish the differences. It is suggested that further physiological, anatomical, genetical, and biochemical investigations should be performed to make clear the tolerance mechanism of different species of citrus to dodder. It can be concluded that by cultivating tolerant species in areas with a high risk of infestation, the percentage of dodder damage can be reduced.

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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