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Soil pH alters the biological parameters of cowpea aphid *Aphis craccivora* Koch (Hemiptera: Aphididae) on its host plant *Vicia faba*



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ABSTRACT

The biotic and abiotic factors including the agricultural implementation can modify soil acidification. We hypothesized that soil pH should as repercussion, alter the plant physiological and physical properties and eventually affect insect herbivores including agricultural pests. This study aimed to evaluate the impact of seven levels of soil pH on the performance of cowpea aphid *Aphis craccivora* on *Vicia faba*. Significant relationships between soil pH and growth of host bean seedlings or development and reproduction of the aphid were detected. Data demonstrated significant differences in the total longevity, the pre-reproductive, reproductive, post-reproductive and pre-viviparity periods. Within a suitable range of pH for bean growth between pH 5.3 and pH 7.2, the aphid performance was worse on seedlings growing better, however, under unfavorable extreme pH conditions, plant quality measured as height did not affect the aphids anymore and their performance was uniformly low except the case in pH 8.1 condition in which the best aphid reproduction was observed. The results confirm that soil pH affect the performance of cowpea aphid *A. craccivora* and also exhibited strong influence on the growth of broad bean plants.

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1. Introduction

Many of biotic and abiotic factors can affect the distribution and abundance of herbivorous insects (Barbosa and Schulz, 1987; Hunter et al., 1992; Dixon, 2009). However, it is not well understood how soil quality or its properties could alter the bionomics of insect herbivores. Soil properties directly or indirectly affect abiotic parameters in the habitat, *e.g.*, the availability of nutrients, water content, temperature, moisture, carbon dioxide levels and acidity in the soil (Kourtev et al., 2002; Cardoza et al., 2012). These parameters, together or separately, can alter the growth of plants

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(Robson, 1989; Passioura, 2002; Cardoza et al., 2012) and may eventually impact insects associated with the plants (Suding et al., 2005; Ehrenfeld, 2010; Vandegehuchte et al., 2010). Thus, soil quality should be an important factor determining the populations of insect herbivores because the development and reproduction of insect herbivores depend greatly on plant quality.

Among abiotic factors associated with soil quality, soil pH or acidity has been considered as a main growth-limiting factor of plants because it has a great impact on the availability and absorption of several essential nutrients such as copper (Cu), iron (Fe) calcium (Ca), manganese (Mn) and Zinc (Zn) (Foy, 1984; Robson, 1989; Bolan et al., 2003). While negative impacts on plants can be prominent at high soil pH (Tinus, 1980; Fageria and Zimmermann, 1998), low pH conditions in the soil can also cause compounding uptake of mobilized metals by plants, which are toxic to plant growth (Bolan et al., 2003; Ferguson et al., 2013). Thus, soil pH may be one of the major factors that impact insect herbivores through its indirect effects on plants. The relationship between soil pH and insect herbivores has been poorly investigated so far.

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Many plant species usually do not grow well in excessively acid soils. Legume plants, including faba bean *Vicia faba* L., use root nodules for nitrogen fixation (Bolan et al., 2003) and soil pH directly influences the activity of the root nodule bacteria, altering the plant growth indirectly (Keyser et al., 1979; Ferguson et al., 2013; Burns and Norton, 2017). Faba bean, also known as broad bean, is a vulnerable crop to infestation with various insect pests from the premature stage of growth (Capinera, 2001; Mousa et al., 2013) to the post harvest stage (Alemayehu and Getu, 2017). Thus, faba bean is a good material to examine the relationships among soil pH, plant and insect herbivore.

The cowpea aphid *Aphis craccivora* (Hemiptera: Aphididae) is one of the most serious insect pests infesting a variety of bean plants throughout the world and is often abundant in early growth stage of bean plants, negatively affecting the growth of bean plants (Karungi et al., 2000; Blackman and Eastop, 2006; Kataria and Kumar, 2016). Although the biology and management of pest aphids including *A. craccivora* have been well studied, there are very few comprehensive investigations on how soil pH could affect the performance of the pests. However, Neuvonen and Lindgren (1987) demonstrated that acid rainfall positively influenced aphid reproduction because it can decrease plant resistant to aphids. Their study suggests the potential importance of soil pH on aphid performance.

In the present study, we hypothesize that soil pH could be one of the significant factors affecting the performance of insect herbivores. Accordingly, we focus on the impacts of soil pH on the development and reproduction of an aphid species that is a serious agricultural pest and highlight the importance of physical environments such as soil quality in determining insect pest populations.

The present study was undertaken to reveal whether soil pH could affect biological parameters of the cowpea aphid developing on faba bean plants. For this purpose, we modified pH levels of a growth medium for the plants and examined the aphid performance and development on bean plants under different pH conditions. Basing on the results, we discuss the potential importance of soil pH in determining the performance and development of herbivorous insects and the process of how soil pH could affect insect populations.

2. Materials and methods

2.1. Aphid colony

Colonies of the cowpea aphid *A. craccivora* were collected from an open cowpea field in Gharbia Governorate, Egypt and were transported to the laboratory. The aphids were reared and maintained on broad bean in an incubator at a temperature of 25 ± 1 °C under a photoperiod of 12:12 h (L:D). Aphids were continuously transferred to new plants for six months until the start of the experiment.

2.2. Soil conditions

Seven pH conditions were prepared as follows: Desert sand that had been washed three times with distilled water was used as a growth medium of bean plants. After air drying, pH of the medium was justified by adding citric acid (C6H8O7) (TTCA Co., Ltd, China) and/or sodium hydroxide (NaOH) (Cambrian chemicals Ltd, U.K.); pH of the medium was accurately determined using an OMEGA PHH222 portable pH meter to prepare the medium with different pH levels, *i.e.*, pH 4.2, 5.3, 6.2, 7.2, 8.1, 9.2 and 10.1. After one week of the medium preparation, seeds of broad bean cultivar Sakha 1 obtained from Agricultural Research Center, Sakha, Kafr Elsheikh, Egypt were singly planted to the medium in polythene plastic pots. Before planting, the seeds were soaked in water for 48 h and were then allowed to germinate in the pots. The soil pH was measured several times during the experimental period to check whether any unexpected factors could change the medium pH levels during the period. Soil pH was measured by putting 10 gm of soil in 50 ml glass beaker, then 20 ml of distilled water was added to make soil water suspension with a ratio of 1:2. Thereafter, the suspension was stirred for 30 min. and the mixture was allowed to settle for two hours before using the above mentioned portable pH meter to measure the mixture's pH.

2.3. Aphid development and reproduction

Three-leaves stage broad bean seedlings were used in this experiment; *A. craccivora* is known to prefer the seedling stage (*e.g.*, Berberet et al., 2009). The experiment was conducted using glass cages (30 cm in height and 8 cm in diameter) to cover whole plant completely with a muslin cloth mesh on the top of the cage to provide air circulation and avoid aphid migration. Cages were kept in an environmental growth chamber with 25 ± 1 °C, 70 ± 5% RH and a photoperiod of 16:8h (L:D).

The experiment was launched by introducing one randomly selected viviparous apterous aphid onto a single plant in order to obtain a cohort of the first nymphal stage (=12 h). After 12 h, except one newly born nymph, the adult and the remaining off-spring were removed from the plant with a camelhair brush 0 size, therefore, a single plant set with one test aphid was prepared. Ten sets of such a plant were then arranged for each pH treatment. Thus, 70 test aphids in all were used in the experiment.

Once the nymphs were settled on the plant, they were observed on a daily basis using a 10X binocular stereomicroscope to measure the developmental (=pre-reproductive) period. After the fourth molting was observed, the observation was made to check the number of newborn nymphs on a daily basis until the adult aphid died. When newly produced nymphs were confirmed, the number of the nymphs was counted. All aphid nymphs produced by the adult aphids were removed immediately from the plant to exclude the effect of crowding or aphid density on biological parameters of the aphids.

2.4. Plant histological parameters

The anatomical samples were occupied from the base internode of broad bean stems. Specimens were fixed immediately in fixation solution, consists of formalin, alcohol and acetic acid mixture (1: 18: 1; v/v). Thereafter, they washed and dehydrated in alcohol series. Each dehydrated specimen was penetrated and embedded in paraffin wax (62-64 °C m. p.). Subsequently, each predisposition specimen was sectioned using a rotary microtome (Leica RM 2125) with 12 μ m of thickness. Each section was launched on glass slides and wax removed by dipping the whole slide in xylene. The staining process was consummated using safranine and light green (Gutmann, 1995), the sections were cleared by xylene then mounted in Canada balsam (Ruzin, 1999). The slides were examined and photographed with electric microscope (Lieca DM LS) with digital camera (Lieca DC 300). The stems histological features including diameter of xylem vessels, thickness of vascular tissues (xylem and phloem), vascular bundle dimension and stem thickness (µm) were estimated using Lieca IM 1000 image manager software. The software was calibrated using 1 cm stage micrometer scaled at 100 μ m increment at 10 \times magnifications.

2.5. Data analysis

All experiments were arranged in a complete randomized design (CRD). Developmental time and fecundity of the cowpea

aphid were evaluated using the analyses of variance (ANOVA) with the aid of SPSS statistical software.

3. Results

3.1. Soil pH and plant growth

Plant response to soil acidity was estimated by measuring the plant height among various pH degrees. The height of broad bean seedlings differed markedly among the experimental groups (Fig. 1; ANOVA; n = 70, $r^2 = 0.81$, df = 6, F = 44.91, P < 0.0001), demonstrating a strong influence of soil pH to the growth of bean plants. Plants grown in soil pH 5.3 significantly exhibited the maximum height among all pH levels as 10.58 cm (P < 0.0001), followed by pH 7.2 and 6.2 which minimized the height of plants to 9.35 and 8.00 cm respectively. There were no significant differences between plant heights in the remaining pH conditions, plants grown in these soils distinctly manifested a weak growth. Thus, for our experimental set-up with the cultivar Sakha 1, the pH conditions between 5.3 and 7.2 are suitable for bean plant growth.

3.2. Aphid development time

The development periods of the aphid *A. craccivora* immature and mature stages on the seven different soil pH degrees are presented in Table 1. Significant differences were detected for its various biological parameters according to soil acidity (ANOVA; n = 70, df = 6, F = 58.60, P < 0.0001). Mean total longevity varied significantly, in the pH 9.2 condition, the longest aphid longevity was recorded (18.90 days) which differed significantly from those of soil pH 4.2 (14.80 days), 8.1 (17.10 days), 7.2 (17.50 days), 5.3 (16.10 days), 6.2 (16.70 days) and10.1 (16.00 days). The analysis showed a significant positive relationship between development time and plant height ($r^2 = 0.32$, F = 31.40, P < 0.0001).

3.3. Aphid fecundity

The mean pre-reproductive period recorded a significant difference (P < 0.0001) between aphid reared on pH 6.2 recorded

9.00 days as the longest prereproductive period and pH 4.2 which expended only 6.10 days. However, there were no significant differences in the pre-reproductive period for aphids reared on plants grown in soils which its pH are 4.2, 5.3, 8.1 and 10.1. Contrariwise, whereas broad bean plants grown in pH 6.2 resulted in prolongation in prereproductive period to 9.00 days, it leads to reduce the reproductive period to 5.30 days, which significantly different than plants grown in pH 8.1, the females reared on these plants continue to give offspring for 9.00 days. Since the females produced the last nymph tell its death (postreproductive), it lasted 4.00 days at pH 9.2 which significantly differed with the rest of pH levels. Aphids reared on pH 10.1 recorded only 1.80 days.

The progeny production (=nymph produced per female) was compared among the different soil pH conditions. The result evidently showed that pH conditions affected progeny production or fecundity of A. craccivora (ANOVA; n = 70, df = 6, F = 11.53, P < 0.0001). As shown in Table 1 and Fig. 2, it was obvious that the females reared on plants grown in pH 8.1 reproduced the enormous number of nymphs as 44.00 nymph/lifespan, as well, females gave also the highest reproduction per day (3.70 female/day). However, aphids in pH 7.2 recorded the least reproduction level in both total progeny 11.40 nymph/lifespan, and the daily reproduction as 1.04 nymph/day. We analyzed how aphid progeny production was affected by pH and plant height; within the pH range between pH 4.2 and pH 7.2, soil pH did not have a significant impact in the progeny production (F = 1.54, P = 0.23). For this pH groups, data was combined, and a regression analysis was performed to examine a relationship between progeny production and plant height; a highly significant negative relationship was detected ($r^2 = 0.28$, F = 11.10, P = 0.0024). Thus, seedling height was a good measure as host plant quality for the aphid when soil pH conditions were suitable for host bean growth.

3.4. Broad bean anatomy

The inner structure of broad bean plant stem is quite comparable to the other dicotyledonous plants, basically, the cortex tissue, vascular cylinder which consist of pith rays, pith tissue and vascular bundles. It was realized from Table 2 and Figs. 3 and 4 that, the

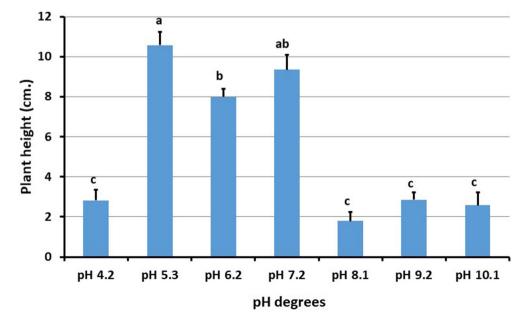


Fig. 1. Broad bean plant heights as influenced by grown in different levels of soil pH. Columns with the same letters (a, b and c) did not differ significantly when comparing pH levels.

Table 1

Developmental periods (days) and the dai	ly offspring of Aphis craccivora reared	l on broad bean at seven different	nH levels under laboratory conditions

pH levels	Biological parameters (mean ± SE)					
	Prereproductive period (d)	Previviparity period (d)	Reproductive period (d)	Postreproductive period (d)	Total longevity (d)	No. of offspring/ Female/day
pH 4.2	6.10 ± 0.10 ^d	0.84 ± 0.02 ^{de}	6.30 ± 0.45 ^{cd}	2.40 ± 0.31 ^{bc}	14.80 ± 0.44 ^d	2.27 ± 0.50 ^{bc}
рН 5.3	8.80 ± 0.13^{a}	0.93 ± 0.02^{bc}	5.10 ± 0.41^{d}	2.20 ± 0.25^{bc}	16.10 ± 0.23 ^{cd}	1.63 ± 0.59 ^{cd}
pH 6.2	9.00 ± 0.30^{a}	1.04 ± 0.01^{a}	5.30 ± 0.56^{d}	2.40 ± 0.22^{bc}	16.70 ± 0.33 ^{bc}	2.18 ± 0.46^{bc}
рН 7.2	6.40 ± 0.16^{cd}	0.78 ± 0.01^{e}	8.20 ± 0.33 ^{cd}	2.90 ± 0.31^{b}	17.50 ± 0.40^{b}	1.04 ± 0.22^{d}
pH 8.1	$6.10 \pm 0.10^{\rm d}$	0.86 ± 0.02^{cd}	9.00 ± 0.33^{a}	2.00 ± 0.21^{bc}	17.10 ± 0.46 ^{bc}	3.70 ± 0.70^{a}
рН 9.2	6.90 ± 0.10^{b}	0.98 ± 0.02^{ab}	8.00 ± 0.26^{ab}	4.00 ± 0.56^{a}	18.90 ± 0.53 ^a	1.86 ± 0.47 ^{bcd}
рН 10.1	6.80 ± 0.13 ^{bc}	0.87 ± 0.02^{cd}	7.40 ± 0.64^{bc}	$1.80 \pm 0.44^{\circ}$	16.00 ± 0.82 ^{cd}	1.91 ± 0.46^{b}

Means followed by same letters within columns do not differ significantly by the Tukey-Kramer HSD test at P < 0.05 probability level.

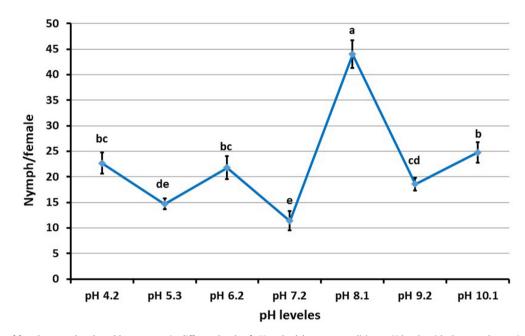


Fig. 2. Total progeny of females reared on broad bean grown in different levels of pH under laboratory conditions. pH levels with the same letters (a, b, c, d and e) did not differ significantly.

growth medium with different levels of soil acidity had adversely impact on most of stem anatomical characteristics.

The soil pH 7.2 induced the increase in all anatomical features of broad bean plant stem followed by pH 5.3 compared with other treatments. Except pH 6.2 and 9.2 which led to increase the thickness of cortex tissue and phloem tissue thickness. Generally the highest values of stem anatomical features were obtained in plants grown in pH 7.2 compared with all other growth mediums. Where, it led to an increasing of all studied characters (xylem, phloem and cortex thickness; xylem vessels diameter and vascular bundles dimension). On the other side, the lowest values of anatomical fea-

tures were recorded in pH 10.1 except the cortex thickness so recorded the lowest value of it in pH 4.2 compared with other treatments (Table 2).

4. Discussion

The present study has revealed how soil pH can affect the development and reproduction of *A. craccivora* and highlighted the importance of soil pH in determining the performance of *A. craccivora* through its indirect effects on broad bean. In Egypt, *A. crac*-

Table 2

Anatomical measurements of broad bean stem	grown in various levels of soil	pH under laboratory conditions.

pH levels	DH levels Xylem vessels diameter (μm)	Xylem thickness (μm)	Phloem thickness (μm)	Vascular bundle dimension		Cortex thickness (µm)
				thickness (µm)	width (µm)	
PH 4.2	20.00 ^{bcd}	43.33 ^c	26.67 ^{bc}	86.67 ^b	56.67 ^c	90.00 ^c
PH 5.3	33.33ª	63.33 ^b	30.00 ^{bc}	113.33 ^a	103.33 ^b	106.67 ^c
PH 6.2	23.33 ^{bc}	33.33 ^{cd}	36.66 ^{ab}	63.33 ^c	53.33 ^c	223.33 ^b
PH 7.2	46.67 ^a	106.67 ^a	46.67 ^a	120.00 ^a	143.33 ^a	450.00 ^a
PH 8.1	13.33 ^{de}	36.76 ^{cd}	26.67 ^{bc}	63.33 ^c	50.00 ^c	106.67 ^c
PH 9.2	16.67 ^{cde}	43.33 ^c	23.33°	93.33 ^b	96.67 ^b	410.67 ^a
PH 10.1	10.00 ^e	26.67 ^d	23.33°	56.67 ^c	46.67 ^c	213.33 ^b

Means followed by same letters within columns do not differ significantly by the Tukey-Kramer HSD test at P < 0.05 probability level.

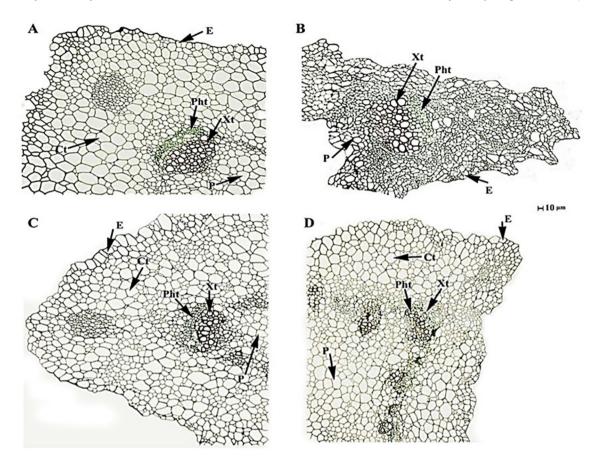


Fig. 3. Anatomical characteristics of transverse sections through the broad bean plant stem affected by different levels of pH. E: Epidermis; Xt: Xylem tissue; Pht: Phloem tissue; Ct: Cortex tissue; P: Pith. (A: pH level 7.2, B: pH level 4.2, C: pH level 5.3, D: pH level 6.2).

civora is widespread in bean fields and the management is crucial to the stable production of legumes (Salman et al., 2007; Helmi and Sharaf, 2016). To our knowledge, very few studies have addressed the effects of soil pH on aphid pests including *A. craccivora*. Because soil pH differs greatly in different localities, understanding the relationship between soil pH and pest aphids may help understanding the severity of pest aphids that commonly differs in different localities.

In this study, soil pH has a strong influence on the growth of broad bean plants. The dependence of bean plant growth on soil pH has repeatedly been documented so far (*e.g.*, Fageria and Zimmermann, 1998; Bolan et al. 2003). The growth of broad bean, measured as the height of the seedling, was greatest in the pH range between 5.3 and 7.2 (Fig. 1), which is within the pH range for normal growth of faba bean (Fageria and Zimmermann, 1998; Burns and Norton, 2017). However, below or beyond this range, seedling growth was largely suppressed (Fig. 1). Our statistical analysis indicates that 81% of variation in the seedling height is explained by the difference in soil pH. Although aphid density is known to affect the growth of host plants, this is unlikely to be involved in our study because only a single female aphid was allowed to infest the test bean seedling by excluding the progeny produced by the female.

A number of previous studies have demonstrated the importance of soil pH in determining the growth of legume plants. This is primarily because soil pH profoundly affects the activity of mutualistic root nodule symbiosis; under adverse pH conditions, nodulation is suppressed, reducing the growth rate of bean plants (Bolan et al. 2003; Burns and Norton, 2017). Therefore, the present results are in accordance with the previous studies; deleterious effects of extreme pH conditions on root nodule formation are likely to be an explanation for the low growth rates of seedlings observed below and beyond the optimal pH range.

The aphid, *A. craccivora* is known to produce 50–70 progeny during the lifetime when the host seedlings are grown with the optimal soil pH condition (*e.g.*, Soffan and Aldawood, 2014; Routray and Hari Prasad, 2016). However, in our study, *A. craccivora* was found to produce only 30–40 progeny during the lifetime in the pH conditions of 5.3, 6.2 and 7.2 (Fig. 2). Sakha 1, the variety we used in our study, may rather be resistant to the aphid, so that the aphid performance may be decreased. In fact, Salman et al. (2007) and Soffan and Aldawood (2014) showed that faba bean varieties in North Africa differed in their susceptibility to *A. craccivora* in terms of aphid development and reproduction.

An important factor affecting the aphid performance may be defense chemicals produced by bean seedlings. Plants can defend themselves physically and/or physiologically from insect attacks (Will and van Bel, 2006; Elsharkawy and Mousa, 2015; Mousa, 2020). Secondary metabolites can function as a plant defense. For example, *Aphis gossypii* suffers reduced performance on crop varieties with a high polyphenol gossypol content (Du et al., 2004). Also, an increase of peroxidase activity after aphid infestation enhances plant resistance to aphids including *A. craccivora* (Ni et al., 2001; Mai et al., 2016). Bean seedlings that grow faster may be more vigorous and have more defensive chemicals, resulting in reduced performance of the aphid. However, it is likely that such plant defense system is suppressed under stressed conditions.

Host plant quality is an important factor determining aphid performance like development and reproduction (Minks and Harrewijn, 1987; Nevo and Coll, 2001). In our study, an involve-

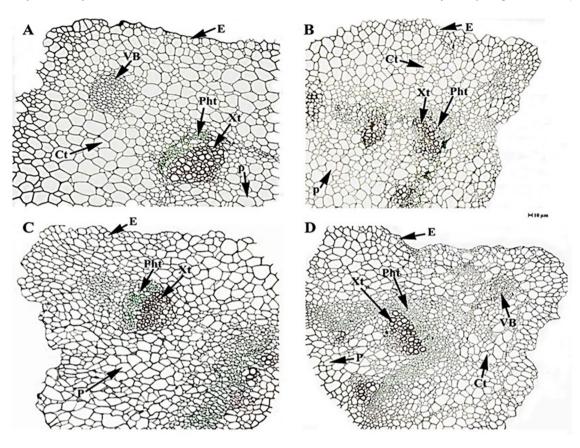


Fig. 4. Anatomical characteristics of transverse sections through the broad bean plant stem affected by different levels of PH. E: Epidermis; Xt: Xylem tissue; Pht: Phloem tissue; Ct: Cortex tissue; P: Pith; VB: Vasular bundle. (A: pH level 7.2, B: pH level 8.1, C: pH level 9.2, D: pH level 10.1.

ment of plant quality was indicated when actual and estimated numbers of lifetime progeny were compared: the data of progeny production obtained in pH 7.2 condition were significantly lower than other pH conditions. When the effect of seedling heights was taken into account, it will be clear that plant vigor would reducing aphid reproductive performance. We suspect that, in extreme pH conditions such as pH 4.2, pH 9.2 and pH 10.1, bean seedlings cannot grow normally anymore and the consequence should be a markedly lowered plant quality for the aphid, which is reflected in seedling height under these conditions. Thus, lowered host plant quality is a likely reason for the observed poor performance of A. craccivora (Fig. 2). Indeed, root nodulation of broad bean is shown to be poor in such extreme low or high pH conditions, in which plant growth and nutrition are also poor (Fageria and Zimmermann, 1998; Goenaga et al., 2013; Burns and Norton, 2017). Given plant quality is a major factor influencing the performance of many insect herbivores including aphids, the present result should be as expected.

The fecundity of *A. craccivora* was strikingly maximized in the pH 8.1 soil condition. The mean lifetime progeny production, in particular, was 1.6–2.8 times greater than the mean values in the other pH conditions. We suspect that, unlike the other unfavorable conditions, the nutritional quality of the seedlings may not be lowered in the pH 8.1 condition whereas plant defense can be weakened, which eventually results in the highest performance of the aphid. The best aphid performance has been observed in the pH 8.1 condition. Thus, we suggest that soil pH can directly affect a plant's trade-off between plant growth and defense, which lead to a somewhat complicated outcome in the herbivores' performance.

Aphids primarily exist on the deliguescent contents of the plant cells, from sieve tubes by means of piercing the epidermal and mesophyll tissues (Saheed et al., 2007). Hence, it must be able to recognize the host plant feeding cells and to direct their stylets in the right position to perforate and reach the sieve tubes at a specific site. There are several features in plant, as well in aphids which realize the specificity of the aphid/plant interaction. The length and diameter of the stylets for aphids and thickness and diameter for host plant tissues are indispensable factors for the feeding process. Consequently, the distance between the exterior surface of the plant and the phloem is a significant criterion (Will and van Bel, 2006). Hence, when aphid styles success to reach the phloem flow, it starts to produce saliva, which directly injected into the plant vascular system (Guerrieri and Digilio, 2008). This is clearly demonstrated in our findings, while the Phloem thickness, xylem vessels diameter, xylem thickness and the cortex thickness superfat to 46.67 μ m, 46.67 μ m, 106.67 μ m and 450.00 μ m at pH 7.2, total progeny of females decreased to 11.4 nymph/female. While, females laid the biggest number of nymphs 44.00 nymph/ female when the phloem thickness, xylem vessels diameter, xylem thickness and the cortex thickness reduced to 26.67 μ m, 13.33 μ m, 36.76 µm and 106.67 µm respectively (Table 2). The analysis showed that the total progeny/female negatively influenced by vascular bundle thickness ($r^2 = 0.168$, P = 0.0069) and the vascular bundle width ($r^2 = 0.141$, P = 0.014).

In the present study, we Proved that soil pH altered the plant properties and affect the performance of cowpea aphid *A. craccivora.* soil pH exhibited strong influence on the growth of broad bean plants. In extreme pH conditions, bean seedlings had abnormal growth, Thus, lowered host plant quality is a likely reason for the observed poor performance of *A. craccivora*. Aphid management can be best performed by combining different countermeasures such as chemical, physical and biological control (Capinera, 2001; Radcliffe, 2009) but understanding their ecology and factors favoring their outbreak is necessary to seek the best combination.

5. Conclusion

Our study gives an insight of how soil conditions could affect aphid pest populations. The present results are understandable only when we assume indirect effects of soil pH on plant inner structure, defense and nutritional quality. The results evidently highlight how soil conditions can affect the performance of the aboveground herbivores. We suggest that such outcome appears because soil pH conditions determine nutritional intakes of broad bean seedlings, which alters the relative resource allocation of the seedlings to plant growth versus defense, eventually impacting the aboveground aphid.

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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