

# Reproductive potential of the black bean aphid (*Aphis fabae* Scop.) on a range of faba bean (*Vicia faba* L.) accessions

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## Abstract

The black bean aphid is one of the main insect pests of faba bean, leading to yield losses in many countries. The aphid inflicts damage to faba bean through direct phloem feeding and indirectly by transmission of several viruses. Sources of genetic resistance or tolerance to the aphid have been hard to identify and to use in breeding because of the high environmental variability of the attack, the weak and partial nature of the resistance when found, and the low repeatability of experiments. A range of molecular genotyping tools is now available for identifying the genes underlying key traits in faba bean. Hence, we screened the responses of eight inbred lines (Columbo, Albus, Closed-flower, Diana, Hedin/2, Icarus, ILB938/2, and Mélodie/2) of faba bean, derived from commercial cultivars and experimental germplasm, to aphid infestation in controlled (no-choice-test) and field (preference test) conditions. In the controlled environment, aphid performance was assessed by measuring fecundity and determining the intrinsic rate of natural increase ( $r_m$ ). In the field experiment, population growth was examined on Columbo, Closed-flower, Hedin/2, and ILB938/2 during June and July. Each week, 10 plants in each plot, randomly chosen at the start, were screened for aphid colonization and number of plants attacked. For each plant, an index number was given reflecting the severity of aphid presence. Our results demonstrate a clear conformity between the results obtained from the indoor pot experiments and the field experiments. In both experiments, ILB938/2 showed partial resistance with significantly lower fecundity,  $r_m$ , and field infestation when compared with the known susceptible line Columbo. The consistently strong performance of ILB938/2 against the black bean aphid suggests that it carries a factor or factors rendering it uncondusive to aphid landing, feeding, and/or reproduction. Further investigation into the resistance mechanisms of ILB938/2 is planned.

## KEYWORDS

antibiosis, antixenosis, no-choice test, pest resistance, preference test

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## 1 | INTRODUCTION

Faba bean (*Vicia faba* L.) is a pulse crop adapted to cool-temperate conditions, produced from the sub-boreal regions of Finland and Sweden to the tropical highlands of Ecuador and Ethiopia. Its global average seed protein content and seed yield are higher than those of pea, lentil, and chickpea (FAOstat, 2022; Feedipedia, 2022), so it is widely used as a protein source for humans and livestock. Global average production for the 5 years to 2021 was 5.6 million tonnes per year (FAOstat, 2022). Its symbiotic nitrogen fixation, usually with *Rhizobium leguminosarum* biovar *viciae*, allows it to be grown with minimal input of nitrogen fertilizer. In cropping systems, it provides valuable break-crop effects, allowing soil-borne diseases of cereals to die in a grass-free growing season (Köpke & Nemecek, 2010).

The most common insect pest on faba beans in many regions, including northern Europe, is the black bean aphid (*Aphis fabae* Scop.) (Hemiptera: Aphididae). The aphid has a holocyclic life cycle and overwinters in the egg stage, primarily on the spindle tree (*Euonymus europaeus* L.), from which winged individuals migrate in May–June to faba bean crops and about 80 other host plant species (Cammel et al., 1989; Raymond et al., 2001). The severity of infestation varies from year to year, probably due to abiotic or inherent biotic factors that influence its population dynamics (Gould & Lowe, 1977; Hansen et al., 2008). Feeding by *A. fabae* damages the faba bean both directly, when the stylet penetration into the phloem results in loss of nitrogen compounds and sugars, and indirectly, when pathogenic viruses are introduced into the plant. Heavy infestations cover the leaves with carbohydrate-rich honeydew that allows the growth of sooty molds, interfering with light interception and thus photosynthesis. Yield losses of more than 50% have been attributed to severe attacks of *A. fabae* on faba bean (Banks & Macaulay, 1967; Béji et al., 2015; Hinz & Daebeler, 1981).

Integrated pest management (IPM), combining cultural, physical, chemical, and biological means of pest control, plays an important role when pest or disease problems on crops are to be maintained below their economic damage thresholds (Barzman et al., 2015). However, IPM against pest species including *A. fabae* has limited options and primarily involves broad spectrum insecticides such as the pyrethroids (Stoddard et al., 2010). Insecticide use has numerous drawbacks, as it may select for pesticide tolerance in the aphids, reduce populations of beneficial insects such as predators, parasitoids, and pollinators (Chagnon et al., 2015), and increase toxicity risks to humans (Nicolopoulou-Stamati et al., 2016). The low cost of buying and applying insecticides, and their broad effectiveness with few examples of pesticide resistance having developed in aphids, has further mitigated against significant efforts toward developing new control methods. Nevertheless, more than 30 faba bean lines have been described as resistant or partly resistant to aphid feeding, though none is currently commercially available (Béji et al., 2015; Makkouk et al., 1998; Meradsi & Laamari, 2016; Prüter & Zebitz, 1991; Stoddard et al., 2010).

One of the common mechanisms by which plants resist aphids is antibiosis, defined as an antagonistic relationship between the pest and the metabolic components produced by the plant. From the perspective of the plant, this includes either constitutive resistance or induced resistance. For constitutive resistance, morphological and/or chemical deterrents are produced that will occur consistently when the plant is attacked by herbivores. In induced resistance, the plant produces one or more chemical compounds only when needed, which will affect the plant organs attacked or protect the whole plant (Romera et al., 2019; Stenberg & Muola, 2017). From the herbivore perspective, this antagonistic effect may reduce the pest's survival, weight gain, development time, longevity, and reproduction. Therefore, antibiosis as a plant defense mechanism may result in an overall poor aphid performance, leading, in turn, to a reduction in plant damage and in yield losses (Pedigo, 1999; Walling, 2008). Furthermore, a prolongation of the aphid's development time due to antibiosis may slow the population increase by extending the time individuals in the population are exposed to the impact of natural enemies (La Rossa et al., 2013). Antixenosis as another plant defense mechanism covers factors that deter the aphids settling on plants such as trichomes on leaves and stems that curtail movement and feeding (Powell et al., 2006; Smith, 2005). Tolerance, as the third most common resistance trait of plants attacked by a pest, can be described as the capability of minimizing the loss of fitness due to the aphid feeding without affecting the aphid population growth (Koch et al., 2016; Smith, 2005). Two primary physiological mechanisms of tolerance have been described: (i) increased photosynthetic activity (Cao et al., 2015) and (ii) upregulation of detoxification mechanisms that counteract the negative effects of aphid feeding (Kerchev et al., 2012; Ramn et al., 2013).

Methods to measure the performance of aphids on plants for the purpose of evaluating resistance fall broadly into two groups, based on either growth rate (Van Emden, 1969) or reproduction rate (Birch, 1948; DeLoach, 1974; Wyatt & White, 1977). Because aphid population growth is exponential, the earliest produced nymphs contribute most, and the laborious life-table studies once used to determine the intrinsic rate of natural increase ( $r_m$ ) (Jahn et al., 2005) have been replaced by an approximation where focus is on total nymphs produced over a relative short time interval early in the female aphid reproduction period (Wyatt & White, 1977).

A range of molecular genotyping tools is now available for identifying the genes underlying key traits in faba bean (Jayakodi et al., 2022). Hence, we set out to investigate the variation in performance of *A. fabae* on a range of faba bean lines that have been used for genome sequencing or as parents in the development of genetic populations. Our aim was to identify any outliers that reduced the population growth of the aphid, where a genetic tool would be available for subsequent investigation of the underlying factors. Both controlled conditions (no-choice test) and field conditions (preference test) were included in the experimental design, in order to determine the possibilities of antibiosis and antixenosis.

## 2 | MATERIALS AND METHODS

### 2.1 | Aphid colony

The stock of *A. fabae* was obtained from viviparous apterous females collected from a faba bean field crop in 2016 at the research station, Flakkebjerg, Denmark (55°19'N, 11°23'E). The aphids were maintained in custom-made aluminum-framed net-covered cages (68 × 75 × 82 cm; length × height × depth) placed in a growth chamber (4.0 × 2.5 × 3.0 m; length × height × depth) (Juliana®, Odense, Denmark) on a potted plant of cv. "Columbo," known to be susceptible to *A. fabae* (Hansen et al., 2008). In the growth chamber, the growing conditions were set to 22 ± 1°C, relative humidity 70 ± 3%, and 12:12 h (light:dark). Plants were watered automatically by soaking a capillary mat underneath the pots for 10 min twice daily and allowing the surplus water to drain off.

**TABLE 1** Lines used in the study. Inbred lines were derived from cultivars and gene bank accessions.

Line	Region of origin	Further information
Albus	Very old landrace	White flowers and low content of condensed tannin in the seed coat
Closed-flower	Univ. Göttingen	Homozygous recessive for the closed-flower (cf) trait where petals fail to open and both scent and nectar are not produced
Columbo	Denmark	Old cultivar with white flowers and low content of condensed tannin in the seed coat. Very susceptible to aphids (Hansen et al., 2008).
Diana	Germany	Small-seeded cultivar from the 1970s, used in many studies of physiology
Hedin/2	Germany	Inbred line produced from cultivar Hedin at the University of Göttingen and used for the first genome sequence of faba bean (Jayakodi et al., 2022)
Icarus	Australia	Cultivar derived from ILB938, expressing resistance to chocolate spot disease and rust disease
ILB938/2	Ecuador/Colombia border via ICARDA	Inbred for many generations from ILB938 at Universities of Göttingen and Helsinki. A source of many valuable traits (Khazaei et al., 2018)
Mélo die/2	France	Inbred line derived from cv Mélo die, used for drought experiments and carrying the <i>vc-</i> gene for low vicine-convicine content (Khazaei et al., 2014).

### 2.2 | Host plants

Eight faba bean lines were chosen because they have been used for genome sequencing or as parents in the development of different genetic populations. Therefore, it was anticipated that if they show apparent resistance against *A. fabae*, it will be easily testable in field (Table 1). Columbo was included as the susceptible reference. Seeds were obtained as part of the project Norfab, funded by the Danish Innovation Fund. The seeds were sown into 5-L plastic pots (three seeds per pot) containing a commercial peat-based potting mix (Pindstrup Mosebrug A/S, Ryomgaard, Denmark) and after emergence thinned to one plant per pot. Each faba bean line was represented with seven potted plants and maintained in insect-proof cages as described above. The cages were placed in a growth chamber and maintained under the same environmental conditions as described above. When the plants reached plant growth stage BBCH 39-45 (flower buds visible BBCH 50 on the earliest lines), they were used for determining fecundity and  $r_m$  of the black bean aphid (see below). The study was replicated three times between April and November 2019.

### 2.3 | Fecundity and intrinsic rate of increase ( $r_m$ )—No-choice experiment

Two adult *A. fabae* females were gently moved from the rearing stock using a camel-hair brush and placed in a clip-cage. One clip-cage was placed on one fully developed leaf of each plant. Because of the weight of the clip-cage and fragility of the young plant, each clip-cage was fastened to a wooden stick in the pot that took its weight. On the following day, one recently produced nymph, F1 was kept in the clip-cage while the two adults and any other produced nymphs were removed. For each of the eight faba bean lines and in each experiment, seven plants were tagged with a clip cage containing one *A. fabae* nymph. From a previous experimental setup and based on the experimental temperature of 22–23°C, it was estimated that the developmental time from first nymph stage to a reproducing adult female would be 6–7 days. This was in agreement with the findings by Tsitsipis and Mittler (1976). The adult female was then allowed to produce offspring, F2, for a further 6 days, which were counted. At the end of the reproduction period, the leaf having the clip-cage was gently cut from the plant, placed in a plastic bag with a zip closure, and frozen at –18°C until time for counting the produced nymphs. The intrinsic rate of increase ( $r_m$ ), that relates fecundity of an individual aphid to its developmental time, was calculated using the equation by Wyatt and White (1977):

$$r_m = c \times (\ln M_d) / d,$$

where  $M_d$  is the number of F2 nymphs produced (fecundity) by the adult in the first  $d$  days of reproduction (in this case 6 days). The correction constant ( $c = 0.74$ ) for *A. fabae* is an approximation of the proportion of the total fecundity produced in the first days of reproduction (Frazer, 1972; Wyatt & White, 1977). To demonstrate

the impact of the differences in  $r_m$ , the finite growth rate,  $\lambda$ , was calculated from the  $r_m$  rates.

## 2.4 | Determination of *A. fabae* infestation—Preference test

Based on the results from the screen-house study and the availability of seed, four lines (Columbo, Hedin/2, Closed-flower, and ILB938/2) were chosen for a field study on a natural infestation by the aphid during the 2020 growing season at the Flakkebjerg research station. Columbo was the susceptible reference. The sowing time was April 21, and the target density was 45–50 plants/m<sup>2</sup> with 24 cm between rows and 8 cm between plants within rows. The plots were 1.6 × 5 m and separated by buffer plots of barley. The experiment was a randomized complete block design with four replicates. The soil was harrowed before use and considered to have a satisfactory level of phosphate (2 mg/kg) and potassium (11 mg/kg), so no fertilizers were added in the growing period. No insecticide or fungicide was used, and weeds were removed by hand throughout the study.

For each plot, 10 plants were selected at random and scouted for aphids, using the method of Banks (1954) where plants were visually examined and the number of *A. fabae* categorized in one of five arbitrary classes of infestation: (0), no aphids could be seen on the plant; (1), one aphid to a small colony confined to the very young upper leaves; (2), several aphid colonies present on the stem, though still not confined to the uppermost leaves; (3), aphids in large numbers, not in large recognizable colonies, and diffusely infesting a large proportion of the leaves and stems; (4), aphids present in large numbers, very dense, infesting all the leaves, and the stems usually black with aphids. When an observer was in doubt, it was recommended to use the higher of two possible classes as it was believed that the tendency would be to underestimate rather than overestimate the aphid numbers (Banks, 1954). The number of infested plants and the score of each infestation were recorded. Scouting started on 18 June as the previous year's observations had shown that the onset of migration of *A. fabae* from their winter host plants occurs in late spring or early summer. Scouting continued weekly until the end of July, when the aphid populations seemed to crash, possibly due to plant senescence or maturity. Furthermore, the effect of natural enemies was clearly visible and represented by different species of coccinellids, hoverfly larvae, lacewings, and parasitoids. Area under the infestation progress curve (AUIPC) was calculated for both number and score, following standard procedures for the area under a disease progress curve.

## 2.5 | Data analysis

All statistical analyses were carried out by means of SAS (SAS Institute, 2021) and SPSS (SPSS, 2021). Model selection was based on Type III Sum of Squares. *P* values less than .05 were considered statistically significant. A two-factor analysis of variance using *proc mixed*

was conducted on the no-choice data to test for a significant main effect of plant line (explanatory variable) on the dependent parameters, fecundity, and  $r_m$  of the black bean aphid with the replication in time as a random factor. Duncan's *proc hoc* multiple comparison of means test was used to separate the means.

For a better visualization, the  $r_m$  rate was expressed in terms of the finite growth rate,  $\lambda$ , which denotes how much an individual female *A. fabae* will contribute to growth of the population. The relationship between  $\lambda$  and  $r_m$  is described by the equation  $\lambda = e^{r_m}$ .

For the field study, data for score, number, and their AUIPCs were subjected to one-way analysis of variance (ANOVA) for each date of observation and a repeated measures ANOVA for all dates together. Means were separated by least significant difference ( $P < .05$ ).

## 3 | RESULTS

### 3.1 | No-choice experiment

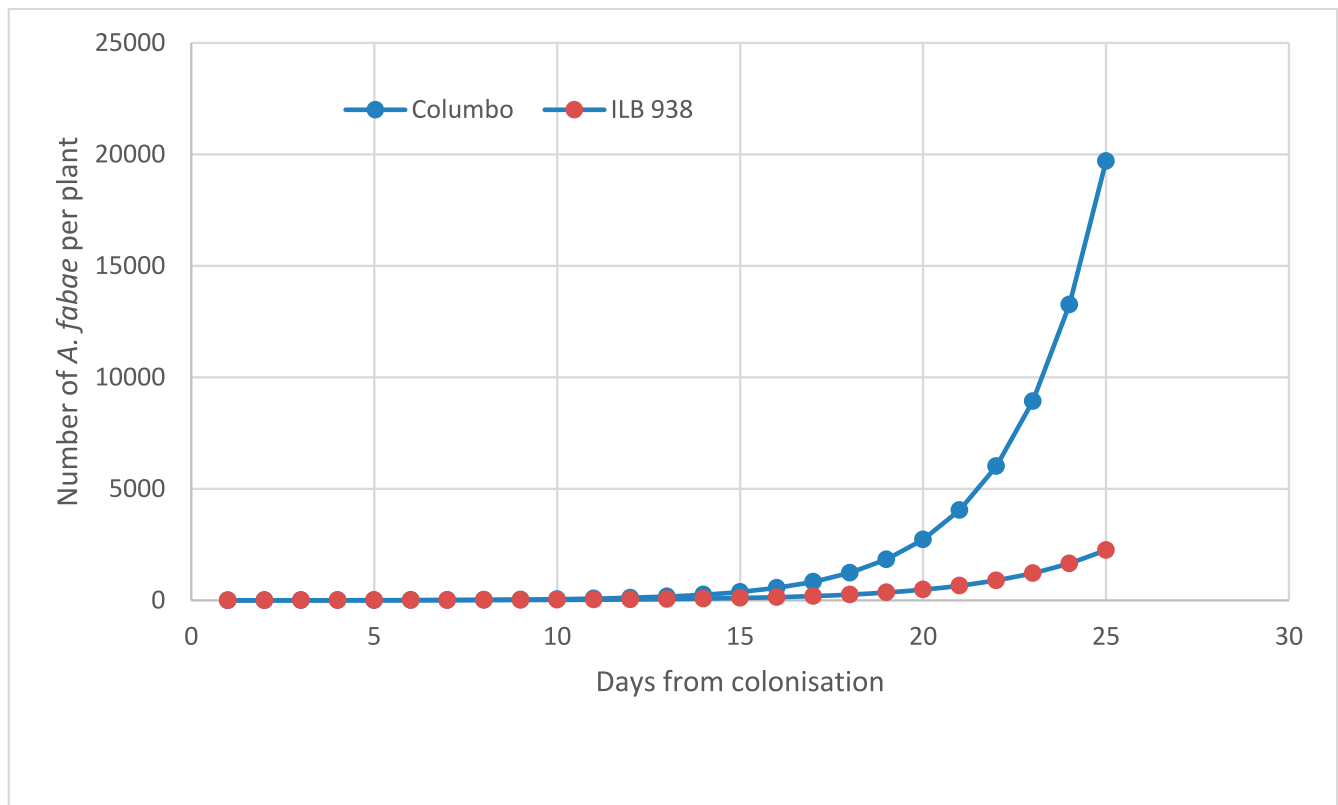
The mean fecundity and intrinsic rate of increase  $r_m$  of *A. fabae* were both highest on Columbo and lowest (over 40% lower fecundity and almost 25% lower  $r_m$ ) on ILB938/2 (Table 2). Variation among lines was significant ( $P < .0022$  for fecundity and  $P < .0002$  for  $r_m$ ). The finite growth rates  $\lambda$  were 1.49 in Columbo and 1.36 in ILB938/2. Thus, the population density of *A. fabae* will increase by 49% per day on Columbo and by 36% per day on ILB938/2, leading to a nearly ninefold difference in aphid density by 25 days (Figure 1).

### 3.2 | Field trial

The first *A. fabae* nymphs were seen on a few plants during an inspection visit at the end of May, so scouting for *A. fabae* infestation started in mid-June. Initially, the aphid infestation was sporadic, with most aphids colonizing Columbo and fewest on ILB938/2 (Figure 2). Throughout the study period, high aphid densities were rarely seen on individual plants of any of the four lines (see below). Strong winds, low daytime temperatures, and heavy rain showers in the early colonization phase (May–June) of the aphids most likely hampered their population growth. Furthermore, larvae from lacewings, coccinellids, and hover flies were seen in high numbers on plants from the end of June throughout July, which undoubtedly further slowed the population increase of the aphids. Nevertheless, by the middle of July, nearly all 10 inspected plants in a plot of Columbo carried aphids, whereas only about 3 plants of ILB938/2 did so (Figure 2a). Although counts of colonized plants were highly variable between replicates, they were significantly lower on ILB938/2 than on Columbo at all sampling date. The date × line term in the repeated measures analysis was significant, on account of the relatively variable performance of Hedin/2. The AUIPC of counts followed the same pattern of statistical differences (Table 3). ILB938/2 was separated from all three other lines by more than the least significant difference (LSD,  $P < .05$ ) only on July 8;

**TABLE 2** Mean fecundity and mean intrinsic rate of increase ( $r_m$ ) on eight faba bean lines. Mean fecundity denotes females produced per adult female in 6 days. The intrinsic rate of increase,  $r_m$ , is estimated using the equation of Wyatt and White (1977). Means followed by the same capital letters are not significantly different by the Duncan multiple range test. SE denotes standard error of the mean.

Line	Fecundity (SE)	Intrinsic rate of increase, $r_m$ (SE)	
Columbo	25.1 (1.2)	0.396 (0.021)	a
Hedin/2	22.0 (2.1)	0.376 (0.022)	ab
Albus	20.3 (2.0)	0.366 (0.021)	ab
Closed-flower	20.6 (4.5)	0.359 (0.021)	abc
Diana	19.3 (1.1)	0.358 (0.021)	abc
Icarus	19.5 (1.5)	0.340 (0.021)	bc
Melodie/2	17.5 (3.6)	0.337 (0.021)	bc
ILB 938/2	14.2 (3.2)	0.308 (0.022)	c



**FIGURE 1** Predicted numbers of black bean aphid on inbred lines of faba bean derived from cultivar Columbo and accession ILB938/2.

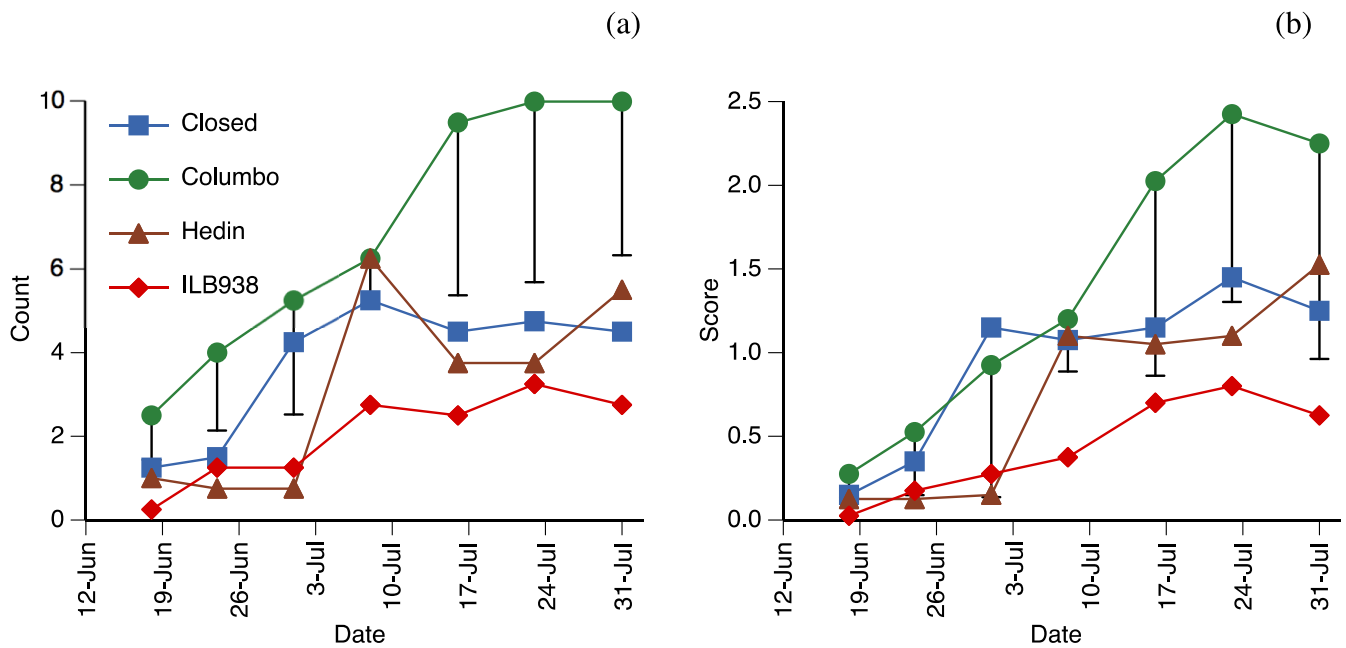
otherwise, its count was not significantly less than those of Hedin/2 and closed-flower.

The mean aphid infestation scores increased in different patterns on the four lines (Figure 2b). Columbo had the highest value except on July 1, reaching a maximum of 2.5. Closed-flower reached its maximum on July 1, briefly exceeding Columbo. Hedin/2 had fairly low scores until July 8, when it caught up with closed-flower. The scores of ILB938/2 remained low throughout, finally reaching values near 0.8. The LSD separated ILB938/2 from Columbo on three of the seven dates of observation, and the repeated-measures analysis confirmed this separation. The highly variable performance of Hedin/2 again led to a significant date  $\times$  line term in the repeated-measures analysis. The AUIPC showed more consistent differences between lines, this term being significant from July 8 onwards (Table 3).

The plants showing a high infestation early in the season ended up with stunted growth and few if any pods. ILB938/2, where few individual plants had an aphid infestation score of more than 2, compensated for the few plants that succumbed to heavy aphid attack.

## 4 | DISCUSSION

The present results show that in both controlled and field conditions, the faba bean line ILB938/2 showed partial resistance, as it was the least conducive to growth and multiplication of *A. fabae*. In the controlled (no-choice) experiment, mean fecundity was 40% lower, and the intrinsic rate of increase  $r_m$  was 25% lower on ILB938/2 than on the susceptible line Columbo, with the other six lines being



**FIGURE 2** (a) Mean number of 10 inspected plants per plot of faba bean showing aphid infestation; (b) mean infestation score of the 10 plants of Columbo, Hedin/2, closed-flower, and ILB938/2, from the onset of aphid scouting (June 18) to its end on July 31, 2020. Error bars show the least significant difference ( $P < .05$ ) from Columbo.

**TABLE 3** Areas under the disease progress curve (AUIPC) for aphid counts and scores at the end of the field experiment on July 31, 2020.

Line	AUIPC (count)		AUIPC (score)	
	Count	Letter	Score	Letter
Closed-flower	178	b	43.8	ab
Columbo	322	a	62.9	a
Hedin/2	153	b	33.1	b
ILB938/2	96	b	19.8	b
Standard error of the mean	32		8.8	

Note: Means followed by the same letter are not significantly different by LSD (.05).

intermediate (Table 2). Thus, ILB938/2 was the least conducive of the lines to aphid growth and multiplication, and this partial resistance is most compatible with an antibiosis effect. In the field experiment, where *A. fabae* had a free choice of colonizing Columbo, closed-flower, Hedin/2, and ILB938/2, more plants per plot were colonized in Columbo, and its infestation score was higher than in ILB938/2, with the other two lines again intermediate (Table 3). Due to high variability in the scores within and between plots, the statistical analyses indicated that ILB938/2 had only a moderately deterrent effect on aphid colonization and reproduction, in a manner that was compatible with both antibiosis and antixenosis.

Fecundity or the intrinsic rate of natural increase,  $r_m$ , as a reliable method for screening plants for antagonistic effects (antibiosis) against aphids, has been discussed by many due to concerns about the aphid's maternal influence (Adams & Van Emden, 1972; Bansal et al., 2021; Wojciechowicz-Zytko & Van Emden, 1995). The

reproduction of *A. fabae* on faba bean in the summer period is parthenogenetic and the asexual mothers form telescoping generations (embryos within embryos) (Dixon, 1997). Strong maternal and transgenerational effects, therefore, exist in aphids, which can affect fecundity and thereby the  $r_m$  values. However, we took the precaution to minimize potential maternal influence by rearing the aphids for one generation on each of the faba bean lines, before the mothers started producing females and scoring nymph production commenced. In these conditions, the low scores of ILB938 are most compatible with a hypothesis based on antibiosis, indicating that either their food was less nutritious food or that they fed for less time due to some phloem-specific defense mechanisms such as anti-feedants or toxins (Cao et al., 2015; Louis et al., 2010; Nalam et al., 2019; Van Emden, 1969). The clip-cages most likely excluded the possibility of antixenosis, as the aphids were prevented from moving to a possibly more palatable or nutritious line.

The field study, based on a natural infestation of *A. fabae*, produced results that were not quite as clear as those from the controlled study. Field experiments are well known by every experimenter to be influenced by many uncontrolled abiotic and biotic factors. In the present study, the early colonization phase and the following population development of the aphid were relatively slow, so the expected major attack on plants early in the summer was minimized. Spring migration from the spindle trees may have been low during the test year due to poor autumn or winter conditions (Cammel et al., 1989). Heavy showers, strong winds, and relatively low spring temperatures (Nikolova, 2019) along with the presence of natural enemies would have contributed to the slow population growth (Dixon, 1977; Ndakidemi et al., 2021; Way, 1966). Nevertheless, the large difference



between ILB938/2 and Columbo was maintained, supporting our earlier suggestion that ILB938/2 has an antagonistic effect on the performance of the black bean aphid (Morvan, 1987; Shannag & Ababneh, 2007). While the controlled study indicated antibiosis as the most likely cause for the low multiplication rate on ILB938/2, in the field study, the aphids had a choice to stay or fly away if ILB938/2 was unacceptable due to some deterrent substances released by the plant (Romera et al., 2019; Smith, 2005; Stenberg & Muola, 2017). Therefore, from the field study, we cannot be certain that antibiosis is the only factor that explains the lower performance of *A. fabae* on ILB938/2. It is clear, however, that ILB938/2 had an antagonistic effect on the performance of *A. fabae*, and this is valuable new knowledge.

The faba bean accession ILB938/2, originating from the Andean region of Columbia and Ecuador, has shown resistance to several biotic and abiotic stress factors (Khazaei et al., 2018) including water deficit (Khazaei et al., 2014) and chocolate spot disease (Gela et al., 2022), and its flavonoid composition differs from that of the lowland Swedish cultivar Aurora (Yan et al., 2019). The present results extend that list of factors to the performance of the black bean aphid, *A. fabae*. Several genetic populations are available, derived from crosses involving ILB938/2, so it should be possible to seek quantitative trait loci and candidate genes responsible for the slowed growth of aphids on this line.

The most used of those populations had Mélodie/2 as the other parent (Gela et al., 2022; Khazaei et al., 2014). Because aphid performance on Mélodie/2 was not significantly different from that on ILB938/2, we can conclude that this population is not suitable for this next study. The vicine-convicine content of Mélodie/2 is very low, so it is unlikely that these chemicals are responsible for the reduced population growth of the aphid.

Cultivar Icarus, derived from the same parent as the experimental line ILB938/2, was not significantly more conducive to aphid growth (Table 2). Similarly, two selections from the Spanish cultivar 'Baraca' differed in aphid response in a Tunisian experiment (Béji et al., 2015), showing that a minor gene, possibly at a low frequency in the population, can easily be lost, as seems to have happened in the faba bean line Icarus.

Columbo and Albus are both white-flowered genotypes that do not produce colored anthocyanin pigments in the stems and condensed tannins in the seed coats. Because both of these were associated with high aphid fecundity and  $r_m$ , the role of pigments in reduced rates of aphid population growth deserves further investigation.

An important factor for the damage aphids inflict on a plant is related to the age of plant. Aphids colonizing plants early in their life cycle will be expected to cause more damage than later when the plants typically are more vigorous (Trotta et al., 2021). The ninefold difference in potential population size between Columbo and ILB938/2 (Figure 1) was based on an ideal world with no food or space limitations and no natural enemies to inflict on their numbers. Such an ideal world does not exist for aphids. Aphids interact with their surroundings, which contributes to controlling their numbers. Biotic factors such as predation and both intra- and interspecific

competition, along with mortality caused by abiotic factors such as temperature, humidity, and heavy rainfall, all reduce the reproductive capacity of the aphids and hence the speed at which the population will increase (Dixon, 1997, 2003). Thus, the de facto impact on the aphid population including damage on the faba bean plants, based on the 13% (absolute; 26% relative) difference in the finite growth rate between Columbo and ILB938/2, remains speculative.

## 5 | CONCLUSIONS

The present screen-house and field studies showed that the faba bean accession ILB938/2 has an antagonistic effect on the performance of the black bean aphid, *A. fabae*, consistent with antibiosis and possibly antixenosis. It needs to be established whether these effects are sufficiently large to lead to higher grain yields. Nevertheless, this new knowledge contributes to the value of ILB938/2 as a carrier of interesting traits for faba bean breeding programs. The genetic, physiological, and biochemical basis of this antagonism remains to be identified, and the existence of genetic populations resulting from crosses involving this line will help in this future work. Identification of chromosome regions through quantitative-trait locus (QTL) analysis of a segregating population derived from ILB938/2 and another parent or through genome-wide association analysis of a diversity population would provide valuable indicators of candidate genes for testing in a pre-breeding program.

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## CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available in <https://datadryad.org>.

## ORCID

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