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On the virulence of two *Beauveria bassiana* strains against the fall webworm, *Hyphantria cunea* (Durry) (Lepidoptera: Erebidae), larvae and their biological properties in relation to different abiotic factors

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Abstract

Background: The genus *Beauveria* is frequently used as a mycoinsecticides in many countries to control insect pests in agriculture, it is being very effective against the fall webworm, *Hyphantria cunea* (Durry) (Lepidoptera: Erebidae), which is a pest of trees in forests and orchards. Multiple abiotic factors during fungal growth are well known to influence mycelial growth and several physiological adaptations in the conidia produced.

Results: In this study, the pathogenicity of the *Beauveria bassiana* strains Bb10331 and Bb7725 against *H. cunea* was evaluated. Peptone potato dextrose agar (PPDA) was used as the medium and colony diameter, conidiation capacity, conidial germination rate were directly affected by relative humidity (RH), illumination, and the ambient pH. The LC_{50} values of Bb10331 and Bb7725 to *H. cunea* were 4.72×10^6 and 3.28×10^6 conidia·ml^{-1}, respectively, after 120 h post treatments, while their corresponding LT_{50} values were 71.13 and 74.54 h at the concentration of 1×10^8 conidia/ml. The Bb7725 had a conidial germination rate than did Bb10331 at the same RH. The two strains grew faster under a dark:light (D:L) photoperiod of 12:12 h, and this particular light condition was also most suitable for their conidia production. The optimum pH for the growth and conidiation of the two strains was approximately 7.0.

Conclusions: Both strains are promising for pest control, possessing effective virulence against *H. cunea*, but this is slightly stronger in Bb7725 than Bb10331. The values of abiotic factors apt to promote the biological properties of each *B. bassiana* were different.

Keywords: *Beauveria bassiana*, Virulence, Abiotic factors, *Hyphantria cunea*

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Background

The fall webworm *Hyphantria cunea* (Durry) (Lepidoptera: Erebidae) has spread widely in China since 1979, when it invaded Liaoning Province, and is now distributed across the provinces of Beijing, Tianjin, Hebei, Shandong, Shanxi, Jiangsu, and Anhui provinces in China (Bai et al. 2020). This caterpillar feeds on leaves of its host plants and overwinters in soil around the damaged trees (Zibaee et al. 2013). Currently, chemical insecticides are still the most commonly used method for controlling *H. cunea* populations and outbreaks (Bi et al. 2018). However, many pesticides have long-term residual effects and also adversely affect natural enemies, as well causing significant environmental pollution (Kim et al. 2020). Therefore, the use of entomopathogens, namely, viruses, fungi, bacteria, protozoa, and nematodes for the biological inhibition of insect pests has become an important tool for pest control (Humber 2016).

Beauveria bassiana is an aerobic pathogenic fungus that parasitizes insect hosts. It has been extensively studied and widely applied in the biological control of agricultural crop and forestry pests as an alternative environment-friendly pest management approach (Kim et al. 2020). This fungus not only infects insects at different life-cycle phases but also exerts lasting sustained effects on the next generation (Bi et al. 2018). Host infection by *B. bassiana* occurs via germinating conidia that penetrate the insect's cuticle and reach the hemocoel (Wilson et al. 2017). Environmental factors, including temperature, relative humidity (RH), light, and nutrient composition, can influence the fungal pathogenicity (Padmini and Padmaja 2010). In particular, both temperature and humidity significantly affect the growth, germination, survival, and virulence of such pathogens (Bugeme et al. 2008). Ambient pH influences the activity of some enzymes associated with acidification or alkalization of host tissues in the infection course of plant pathogenic fungi (Prusky and Yacoby 2003). Therefore, biocontrol strategies based on *B. bassiana* do not just depend upon the interaction between host and pathogen but also on the local environmental conditions to which they are exposed (Mishra et al. 2013).

In a previous study, from among 13 strains of *B. bassiana*, two of *B. bassiana* (Bb10331 and Bb7725) were found capable of high virulence against *H. cunea* larvae (Bai et al. 2015). In addition, PPDA medium was deemed as the most suitable medium for the growth of Bb10331 and Bb7725. The effect of temperature on both strains was similar. Their optimum temperature for mycelial growth was 29 °C, and that for conidiation capacity was 26 °C, while that for conidial germination was 26–29°C.

The present study aimed to evaluate the virulence of those two strains of *B. bassiana* against *H. cunea* larvae, as well the effects of some environmental factors on the biological properties of two strains.

Methods

Insect culture

Pupae of *H. cunea* were obtained from a laboratory-housed population of *H. cunea* (collected wild moths) at the Chinese Academy of Forestry, Qinghuangdao, in Hebei Province, China. The pupae were maintained in a climate chamber at 25 ± 1 °C and an RH 50–60% under a light:dark (L:D) photoperiod of 16:8 h. Plant leaves from *Morus alba* were provided as a food for the larvae.

Microbial strains and media

The Bb10331 strain was obtained from the overwintering pupae of *H. cunea* infected with *B. bassiana* in the laboratory. The Bb7725 strain came from the Strain Preservation Center of the Chinese Academy of Forestry.

Virulence of the two strains against *Hyphantria cunea*

Fourteen-day-old conidia were used to assay the virulence of the two strains against *H. cunea* larvae infected via feeding. Leaves were separately smeared with 0.35 ml of 1×10^8, 1×10^7, 1×10^6, 1×10^5, and 1×10^4 conidia/ml suspension (treatment) or 0.05% Tween-80 (control), and then dried indoors. For each treatment, the Petri dish was first moisturized by adding to it four layers of sterilized filter paper, and the treated leaves were placed inside each dish. A larvicidal bioassay was performed using 20 *H. cunea* larvae (3rd or 4th instars) per treatment. After inoculation with either strain, each batch of the treated larvae was maintained in a large Petri dish for 5 days at 25 °C and an RH of 80–90%, and monitored daily to record mortality. The fungal virulence to the larvae of each strain was analyzed in terms of a corrected mortality rate. The median lethal concentration (LC_{50}) after 120 h of treatments was calculated. The median lethal time, LT_{50}, was estimated using leaves that were smeared with 0.35 ml of the 1×10^8 conidia/ml suspension. The bioassay of each type was repeated 3 times.

$$\text{Corrected mortality rate}\,(\%) = \left(\frac{\text{mortality in treatment} - \text{mortality in control}}{1 - \text{mortality in control}}\right) \times 100$$

Effects of abiotic factors on the biological properties of the two fungal strains

Colony disks were placed on PPDA medium and cultured in an incubator at different HR (75, 85, 90, 95, and 100%), different light conditions: full dark (0 L:24 D), 12 h light (12 L:12 D), and full light (24 L:0 D), and

different pH levels (5.0–9.0), respectively. Each temperature was replicated three times. The biological performance of each of the two strains was evaluated. For the full dark treatments, the Petri dishes were maintained in the same incubator those for the white light treatments, but inside a plastic box with ventilation holes that was covered with a thick black cloth sleeve.

Assays for biological properties

A medium (2% sucrose and 0.5% peptone) was used to quantify the conidial germination rate of each treatment at 6, 12, and 24 h. Their conidia were observed three times per replicate, with approximately 100 conidiation events observed in total. Colony growth rates were evaluated by measuring the diameters of different treatments on day 3, 6, and 10, respectively. Each treatment was repeated 5 times. After 14 days of incubation at 25 °C and 12 L:12 D, three colony disks (ϕ = 5 mm) at the same position from the center of the Petri plates were bored with a cork borer. Conidia on each disk were then gently brushed off into 20 ml of 0.05% Tween-80 via vortex. The conidial concentration in the suspension was determined using a hemocytometer and converted to the number of conidia per square centimeter culture. Each treatment was repeated thrice (Zhu et al. 2016).

Data analysis

Mortality data were corrected using the control group mortality, using Excel. The LC_{50} and LT_{50}, correlation coefficient (R), and 95% confidence interval values of virulence regression equations were calculated by SPSS (v22.0)

Results

Virulence of the two strains to *Hyphantria cunea*

The virulence of Bb10331 and Bb7725 strains against *H. cunea* was evinced by their corresponding LC_{50} and LT_{50} values of the 2 strains. The relative difference in the LC_{50} and LT_{50} values between the two strains were 1.44×10^6 conidia·ml^{-1} and 3.41 h, respectively (Table 1).

Effect of relative humidity on biological properties of the two fungal strains

The conidial germination rate of the two strains under differing RH was fitted by a curve. As illustrated in Fig. 1, the conidia germination rate of Bb7725 exceeds that of Bb10331, and both germinations' rate increased with an increasing RH. The curve equations of Bb7725 and Bb10331 strains were $y = -0.040\ x^2 + 7.487\ x - 258.8$ (R^2 = 0.984) and $y = -0.036\ x^2 + 6.880\ x - 238.9$ (R^2 = 0.982), respectively (Fig. 1).

Effect of illumination on biological properties of the two fungal strains

The Bb10331 strain always maintained high values for colony diameter and conidiation capacity than Bb7725, except on the 3rd day (Fig. 2). The colony diameter of either strain was maximal at D:L = 12:12 h. After 24 h of culturing, the conidial germination rates of both strains were the highest in the dark, but after 48 h, they had generally increased significantly. The conidial germination rate of Bb7725 strain reached 100% at three illumination conditions (Figs. 2 and 3).

Table 2 shows that mycelium produced more conidiation under a full light regime. In general, Bb7725 had lower values for the conidial germination rate than Bb10331. The conidiation capacity of the two strains at D:L= 12:12 h and full light was significantly higher ($P < 0.05$) than that in full dark (Table 3).

Effect of pH on biological properties of two strains

As Fig. 3 shows, the colony diameter of either strain increased at first and then decreased as the pH increased. The colony diameter of Bb7725 (48.94 mm) peaked at pH = 6.0, while of Bb10331, it was the largest (43.77 mm) at pH = 6.5. The curve equations of Bb7725 and Bb10331 strains were $y = -2.903x^2 + 40.65x - 93.53$ (R^2 = 0.639) and $y = -2.293x^2 + 32.52x - 71.79$ (R^2 = 0.860), respectively (Fig. 4). The maximum conidiation capacity was observed at pH = 7.0. The conidiation capacity at pH = 9 was significantly lower than that at other pH values. As the pH value increased, the conidia germination rate evidently decreased. The conidial germination rate was greatest at pH 5.5~6.0, reaching 90.14~91.27%, and they were significantly higher than the conidial germination at other pH values.

Discussion

The genus *Beauveria* is often used as a mycoinsecticides in many countries to control insect pests in agriculture. The conidia of entomopathogenic fungi (EPF) must retain high viability and virulence for effective biological

Table 1 Virulence of Bb10331 and Bb7725 to *Hyphantria cunea*

Strain	Median lethal concentration after 120 h		Median lethal time at 1×10^8 conidia·ml^{-1}	
	LC_{50} (95% CI)/$\times 10^6$ conidia·ml^{-1}	Correlation coefficient	LT_{50} (95% CI)/h	Correlation coefficient
Bb-10331	4.72 (2.46~10.67)	0.9884	74.54 (69.11~80.61)	0.9732
Bb-7725	3.28 (1.76~6.88)	0.9749	71.13 (65.96~76.66)	0.9749

LC_{50} and LT_{50} refer to median lethal concentration and median lethal time, respectively
The 95% confidence intervals (CI) were calculated by delta method that accounts for asymptotic relationships

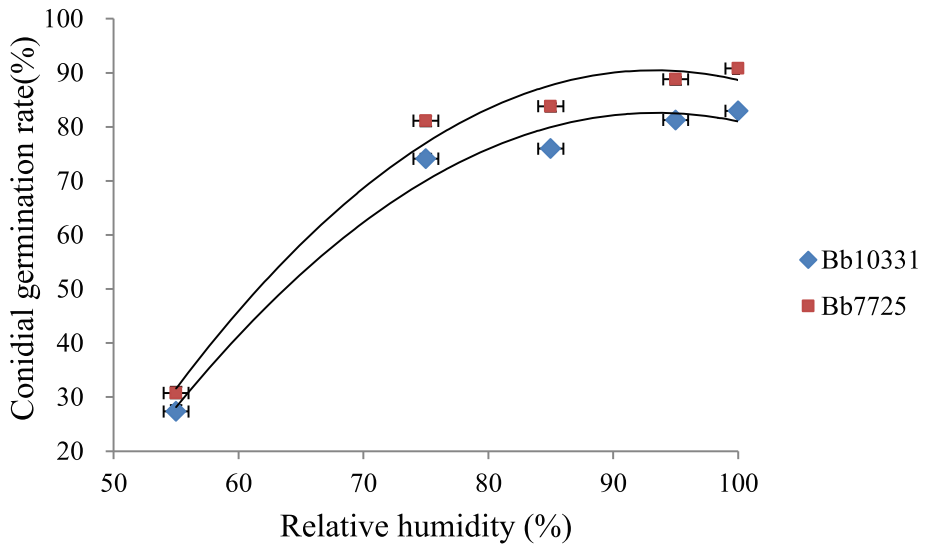

Fig. 1 Conidial germination rate at different relative humidity

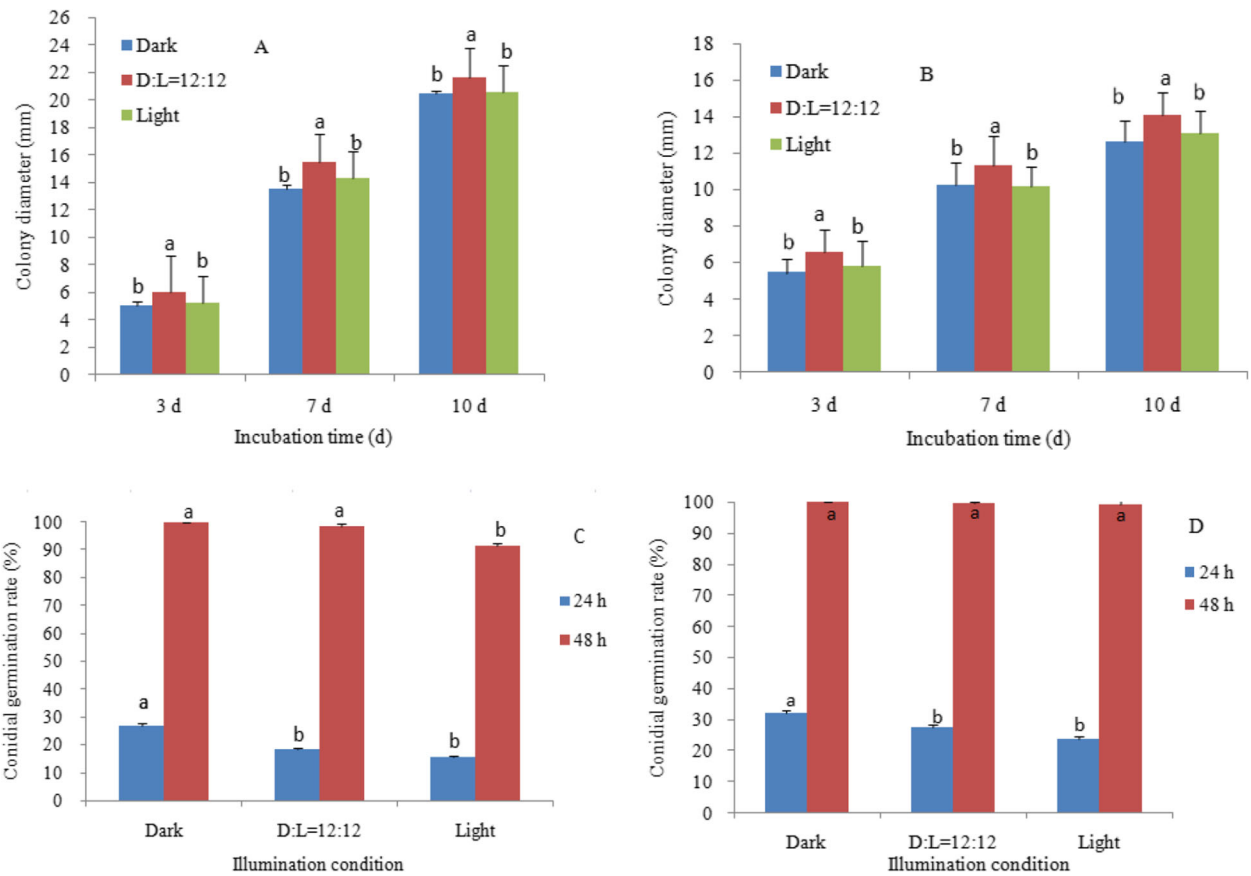

Fig. 2 Colony diameter and conidial germination rate at different illumination. **A**~**B** respectively showed the colony diameters of Bb 10331 and Bb 7725 under different light treatments. **C**~**D** respectively showed the conidial germination rate of Bb 10331 and Bb 7725 under different light treatments. Means followed by similar letters on columns of the same color are not significantly different at 5%

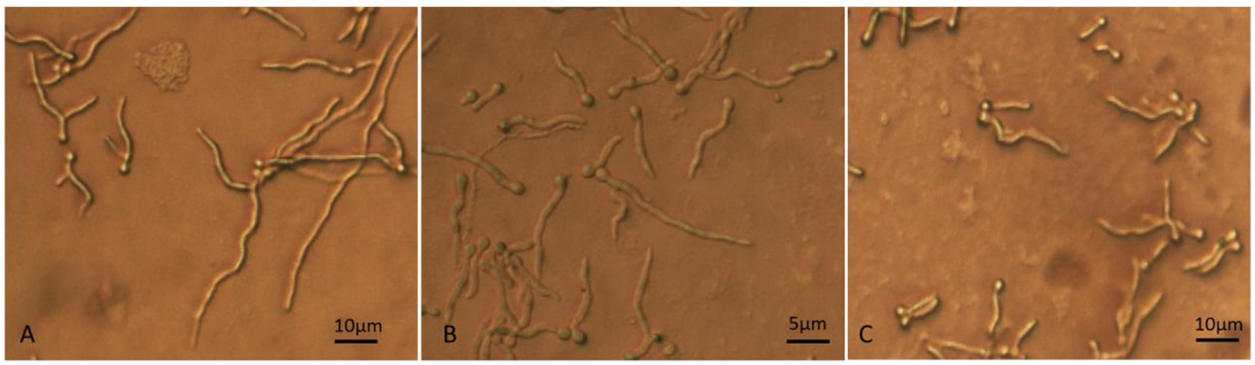

Fig. 3 Conidial germination rate of the Bb7725 strain under different light conditions at 48 h **A** full light (20×); **B** dark: light photoperiod of 12:12 h (40×), and **C** full dark (20×)

control to ensue (Hong et al. 2002). Biocontrol strategies based on entomopathogenic fungi are not only dependent upon the interaction between host and pathogen but also on the environment to which they are exposed (Mishra et al. 2013). In this study, two *B. bassiana* strains differed somewhat in their virulence against *H. cunea*, which might be related to their biological properties. Multiple abiotic factors were shown capable of influencing conidiation in Bb10331 and Bb7725, including the medium type, carbon to nitrogen ratio, and the temperature. The two strains' colony diameter, conidiation capacity, and their conidia germination rate were directly impacted by RH, illumination regime, and ambient pH.

Humidity is one of the most important environmental factors affecting the survival and activity of entomopathogenic fungi (Bugti et al. 2020). Not only concentration it affect fungal germination, it is also essential for EPF infection and subsequent sporulation on insect cadavers (Mishra et al. 2013). Early work by Ferron (1977) demonstrated that 92% RH is required for *B. bassiana* to get conidial germination in the absence of the host. However, in this study, when RH is 70%, the conidial germination rate of both strains could surpass 70%. That is to say, the relative humidity required for conidial germination of different fungal strains varies among them. In addition, the infection potential of EPF also depends upon the exposure time to favorable humidity conditions, given the positive correlation between them (Fargues and Luz 2000). Our results indicated that the optimum RH for the Bb10331 and Bb7725 strains was 95–100%. However, it is necessary to further compare the infection of these two strains against *H. cunea* at different RH levels in subsequent studies.

Table 2 The conidiation capacity of Bb10331 and Bb7725 at different illumination

Isolate	Conidiation capacity/×10^6 conidia·ml^{-1}		
	Dark	D:L=12:12	Full light
Bb10331	0.35 ± 0.06 b	0.67 ± 0.06 a	0.73 ± 0.05 a
Bb7725	0.06 ± 0.01b	0.23 ± 0.03 a	0.24 ± 0.03 a

The number after ± is standard deviation. Means followed by similar letters in a column are not significantly different at 5%

Illumination is one of the many signals that fungi use to perceive and to interact with their environment, providing them with critical information about their habitat (Corrochano 2007). Many studies have shown that illumination regimes have conspicuous effects on mycelial growth, conidial germination, and conidiation capacity (Fanelli et al. 2012; Dias et al. 2019). Fungal species can exhibit differential responses to light; for example, fungi sense light to protect themselves against DNA damage caused by certain color or solar ultraviolet wavelengths, by timing the release of spores or by inducing enhanced tolerance to stress for better physiological adaptation (Chelico and Khachatourians 2008; Braga et al. 2015). In the present study, the mycelium produced more conidia under light than dark conditions. This result is consistent with that of Dias et al. (2019). Although Bb10331's colony diameter and conidiation capacity surpassed Bb7725's, it had a lower conidial germination rate. This result suggests that Bb7725 has a higher effective conidia capacity. The phytochrome gene deletion in a strain of the insect pathogen *B. bassiana* generated higher osmosensitivity, an increased antioxidant capability, and weakened conidial thermotolerance (Qiu et al. 2014). Accordingly, the mycelial growth, conidiation capacity, and conidial germination rate of the two strains studied here differed under the same light treatment, likely due to their differential expression of phytochrome genes. Crucially, the lethal ability of either strain against *H. cunea* depends on their number of germinated conidia. Finally, the colors and types of light can also play an important role in the biological characteristics of *B. bassiana* strains (Yu et al. 2013; Qiu et al. 2014).

Ambient pH is an environmental stimulus capable of inducing a series of physiological and cellular events in

Table 3 The conidiation capacity and conidia germination rate of 2 strains

pH value	Conidiation capacity ($\times 10^8$ conidia·ml^{-1})		Conidia germination rate (%)	
	Bb10331	Bb7725	Bb10331	Bb7725
5.0	2.17 ± 0.23 d	0.47 ± 0.11 d	79.71 ± 1.34 b	81.60 ± 1.57 b
5.5	2.28 ± 0.33 bcd	1.23 ± 0.20 bc	89.45 ± 2.87 a	91.27 ± 2.60 a
6.0	2.40 ± 0.23 bcd	1.75 ± 0.22 bc	88.28 ± 1.83 a	90.14 ± 1.81 a
6.5	3.14 ± 0.32 ab	2.47 ± 0.29 a	83.14 ± 1.06 b	83.98 ± 1.56 b
7.0	3.69 ± 0.33 a	2.37 ± 0.25 a	80.23 ± 1.2 0 b	81.27 ± 1.55 b
7.5	2.79 ± 0.27 bc	1.84 ± 0.09 b	73.14 ± 1.72 c	75.11 ± 1.32 c
8.0	2.70 ± 0.29 bcd	1.50 ± 0.22 bc	53.04 ± 1.18 d	63.34 ± 1.76 d
9.0	1.45 ± 0.12 e	1.23 ± 0.27 c	3.84 ± 0.23 e	6.61 ± 0.69 e

The number after ± is standard deviation. Means followed by similar letters in a column are not significantly different at 5%

microorganisms. Fungal adaptation to ambient pH relies on homeostasis of intracellular pH and the proper expression of permeases, secreted proteases, toxins, and antibiotics (Zhu et al. 2016). Work by Zhu et al. (2016) also confirmed that PacC and Pal partners regulate the growth and conidiation of *B. bassiana* in a pH-dependent manner and highlighted their importance for this fungal response to pH. Furthermore, pH variously affects different species of fungi; for example, the ambient pH has a major regulatory influence on conidiation in these species of *Trichoderma atroviride* and *T. hamatum*, whose conidiation and growth are favored by low pH (Steyaert et al. 2010). By contrast, in our study, the colony diameter and conidiation of both strains tended to increase initially but then diminished with a higher pH; this proves that their conidiation as well as growth are favored by a neutral pH. It has been speculated that the strong alkaline conditions may foster the production of fragmented vacuoles in hyphal cells, inducing high osmosensitivity in these cells (Antonio et al. 2010). Moreover, the responsive genes involved in various cellular events, such as growth, ion tolerance, cell differentiation, cell wall remodeling, secondary metabolism, and host infection are expressed under suitable pH conditions (Merhej et al. 2011; Cornet and Gaillardin 2014; O'Meara et al. 2014).

Conclusion

It is important to identify abiotic factors conferring optimal biological properties of different strains, as they directly affect their virulence against target pests. Although both Bb10331 and Bb7725 exhibit robust virulence against *H. cunea*, the virulence of Bb 7725 is slightly stronger than that of Bb10331. Furthermore, the values of abiotic factors for attaining the most suitable biological properties of each *B. bassiana* were different. These two promising strains should now be tested under field conditions to confirm their virulence against *H. cunea*.

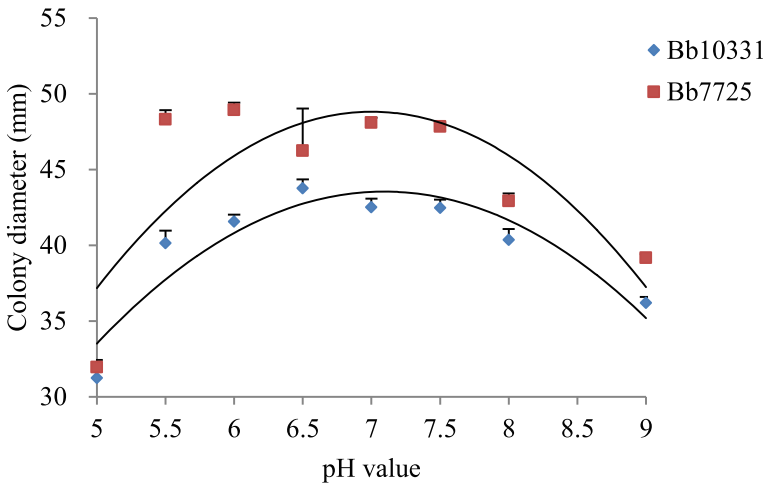

Fig. 4 Colony diameter at different pH values

Abbreviations
Bb: *Beauveria bassiana*; PPDA: Peptone potato dextrose agar; CI: Confidence intervals; LC: Lethal concentration; LT: Lethal time

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Authors' contributions
BSL conceived and designed the experiments; RRH and PHB performed the experiments and conducted the data analyses; JPY conducted the data analyses. All authors have read and approved the manuscript.

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Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
There is no conflict of interest.

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