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Survival of *Plodia interpunctella* (Hübner) larvae treated with 98% N_2 and the life history of their next generation

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Research Paper

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Abstract

Understanding the development and reproduction of insects surviving controlled atmosphere treatment may help in developing sound pest management strategies. The developmental duration, survival percentage, and oviposition of *Plodia interpunctella* and its F_1 generation were determined after the fifth instar larvae (the last-stage larvae) were exposed to 98% N_2 for different exposure times. The survival percentage of the last-stage larvae treated with 98% N_2 for 6, 4, 1.5, and 0 day was 70, 80, 91, and 100%, respectively when measured 24 h after treatment. The survival percentage of the last-stage larvae that developed to pupae was 37, 55, 73, and 96%, corresponding to the different exposure times. The developmental time needed to pass from pupa to adult emergence of specimens treated as the last-stage larvae were 8, 7, 6, and 6 days corresponding respectively to high N_2 treatment after 6, 4, 1.5, and 0 day of exposure. The mean number of eggs laid by the subsequent females developed from the treated last-stage larvae was 35, 66, 81, and 123, respectively. The oviposition inhibition ratio of the F_1 generation decreased by more than 33% compared with that of the parental generation. When the last-stage larvae were exposed to 98% N_2 for longer than 4 days, the immature developmental time of surviving individuals in the F_1 generation was delayed more than 6 days due to slower egg hatching and longer development of the first and second instar larvae stages. The population trend index of the F_1 generation was lower when raised from the treated last-stage larvae than those from untreated controls.

Introduction

The Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), is a pest that can infest approximately 200 varieties of stored commodities, and which has attracted increasing attention in recent years (Sauer and Shelton, 2002; Arbogast and Chini, 2005; Mohandass *et al.*, 2007; Ndomo-Moualeu *et al.*, 2014; Han *et al.*, 2016; Predojević *et al.*, 2017). Numerous researches on the biology of *P. interpunctella* have been conducted, and it has even been used as a biological model. The development of the Indian meal moth under natural environmental conditions (Pourbehi *et al.*, 2013; Razazzian *et al.*, 2015) and the effect of different diets, temperatures, and humidity conditions on their development and survivorship (Arbogast, 2007; Noureddin *et al.*, 2008) has been reported.

Management of stored product insect pests is transforming from insecticide-based methods into nonchemical approaches (Arthur and Phillips, 2003) because more attention is being given to insecticide pollution and food safety (Navarro, 2012). The application of controlled atmosphere to kill insects as an effective alternative to chemical pesticides is increasing and is suitable for a wide variety of agricultural and food products (Jayas and Jeyamkondan, 2002; Navarro, 2012). Research on controlling insect pests by using high concentrations of nitrogen (N_2) during commodity storage has been reported (Sen *et al.*, 2010; Lorenzo *et al.*, 2020; Moncini *et al.*, 2020). Nitrogen is not generally a toxin to pests, as it comprises 78% of the earth's atmosphere. However, according to Navarro (2012), a low concentration of oxygen (O_2), is toxic to insects. One of the means creating low-oxygen atmosphere is by adding nitrogen. Using high concentrations of N_2 to replace air and produce low O_2 concentrations is the most commonly used controlled atmosphere method for controlling postharvest insects in China (Zhang *et al.*, 2007; Yang *et al.*, 2011).

The efficacy of high concentrations of N_2 is influenced by the insect species, developmental stage, and physical environmental factors such as temperature, humidity, and gas concentration (Ofuya and Reichmuth, 2002; Hashem *et al.*, 2012; Huang *et al.*, 2020). The population inhibition rate of rice weevil was 99.94% after 90 days of treatment with 2% O_2 at 28°C (Lao *et al.*, 2012). Survivors had altered developmental time and fitness, which affected the efficacy of future treatment with a controlled atmosphere. Studying insect population dynamics after exposure to high N_2 concentrations is the basis of controlled atmosphere application.

Tribolium castaneum (Herbst), *Cryptolestes pusillus* (Schnherr), and *Cryptolestes ferrugineus* (Stephens) specimens surviving exposure to 7.5 and 8.6% CO_2 for 1 or 3 weeks had lower oviposition ratios and longer immature development times (White *et al.*, 1995). Short exposure time (1–3 days) to 8% O_2 could result in significant developmental delays in the immature stages of *T. castaneum* (Kharel *et al.*, 2019). There are few reports on the development of insects surviving high concentrations of N_2. Studying the development and reproduction of insects surviving exposure to high N_2 concentrations could strengthen our understanding of insect population dynamics and help develop an integrated insect management strategy.

The development and reproduction of *P. interpunctella* larvae that survived exposure to 98% N_2 at different exposure times were evaluated in this study. Our aim was to answer the following questions: What is the effect and efficiency of N_2 treatment on the developmental duration, survival percentage, and oviposition of *P. interpunctella* larvae and its F_1 generation? What is the population trend index of the F_1 generation of the surviving larvae?

Materials and methods

Insects and treatments

The Indian meal moth used in this study was collected from a grain depot located in Zhengzhou, China, and cultured for more than three years in the laboratory at 75 ± 5% relative humidity (RH) and 28 ± 1°C. The diet was a mixture of oatmeal, whole wheat flour, and yeast powder at a weight ratio of 30:19:1. One hundred fifth instar larvae (5 days old) of both sexes were gently transferred using a fine-hair brush into a plastic cage (7 cm diameter × 6 cm height). The reason for choosing the fifth instar larvae (last-stage larvae) was that this insect stage most tolerant to 98% N_2 (Huang *et al.*, 2020). Before transferring the larvae, 10 g of diet was introduced into the plastic cage, and the cage was covered by polyamide fiber gauze (0.18 mm opening) after the 100 larvae were introduced. The larvae were fed a sufficient diet before selection and introduction to prevent cannibalism (Fox, 1975). The number of dead larvae and their bodies were carefully examined under a stereomicroscope to check if the body was intact in this study. Although the inner cage volume was small and crowded for 100 larvae, and the larvae always wandered, the total number of larvae (including both dead and live larvae) did not change.

The cages with the larvae and diet were placed in chambers (60 × 35 × 40 cm), which were made of armor plates with 2 mm thick. The procedure and method used to maintain the N_2 concentration and environmental conditions (28 ± 1°C, 75 ± 5% RH) inside the chamber were reported by Huang *et al.* (2020); therefore, the parameters related to the N_2 treatment are summarized here. The half time from 500 to 250 Pa of pressure drop for airtightness in the chambers was approximately 180 s. The atmosphere of 98% N_2 mixed with 2% air in the chamber was maintained by supplying 99.999% N_2 from a liquid N_2 cylinder (23.2 cm diameter × 123 cm high and the pressure inside the cylinder was 14 MPa), and it was recirculated by a pump (DC24 V, Hailin Technology Co., Ltd., Chengdu, China). The N_2 concentration in the chamber was monitored by an N_2 meter (MOT500—LM(N_2), Kenuoer Co., Shenzhen, China). The concentration of N_2 was maintained in the range of 97.88–98.02%. The flow rate of 99.999% N_2 was 80 l h^{-1} at the very beginning, and the 98% concentration of N_2 in the chamber was maintained by monitoring the N_2 and O_2 concentrations and adjusting the flow rate every 24 h during the experiments. The relative humidity (75 ± 5%) inside the chamber was maintained by saturated sodium chloride solution kept in a 250 ml beaker. During the test, the chambers were placed in a room controlled by an air-conditioner (KFR-72LW/(72566) Ab-3, Gree Electric Appliances Inc. Zhuhai, China). The room temperature was maintained at 28 ± 1°C. Therefore, the experiment was conducted at 28 ± 1°C, 75 ± 5% RH, and a light: dark photoperiod of 16:8 h.

There were three replicates for each treatment and control. The cages containing 10 g diet and 100 larvae used as the control were kept in the same chamber but without introducing N_2. After the 1.5, 4, and 6 days of exposure to the 98% N_2, the treated larvae were individually transferred into plastic containers (5 cm diameter × 4 cm containing 2 g diet) covered by polyamide mesh (0.18 mm opening), which were kept in an incubator at 28 ± 1°C and 75 ± 5% RH until adult emergence. The reason for choosing these treatment times was that treatment with 98% N_2 for 1.5, 4, and 6 days could achieve less than 100% mortality. The larvae were able to pupate and emerge to adults in the controls in less than 6 days, but some of them did not pupate during the treatment period because their development was inhibited by the 98% N_2.

The number of surviving and dead larvae was counted 24 h after treatment. The resulting data were used to calculate the survival percentage of the tested larvae at 24 h. The larval instars stage was determined by measuring their head capsule width and molting times (Perez-Mendoza and Aguilera-Pen, 2004; Vukajlović *et al.*, 2019) every 24 h until all larvae pupated. Larvae were sexed by examining the dorsal integument of the last instar larvae. The male larvae were identified by observing the dark patch formed by the testis, which is visible in the medium plane of the mid-dorsal abdomen, while the female larvae have no visible patch (Allotey and Goswami, 1990; Ndomo-Moualeu *et al.*, 2014). The numbers of males and females were used to calculate the sex ratio.

The incubation conditions of pupae were the same as those of larvae, and the pupae were observed every 24 h until adult emergence. Ten pairs of newly emerged moths developed from the treated larvae were reared in a plastic container (10 cm diameter × 8 cm height) covered by polyamide mesh (0.18 mm opening). To make sure a pair of adults had enough time to mate without being disturbed, small plastic cages (3 cm diameter × 3 cm height) were used to separate each pair of adults. After a pair of adults was positioned in the opposite direction, the pair was quickly covered by the cage (without touching them). After the pair moved into the cage, the cage was quickly covered by a layer of polyamide mesh. The mesh was fixed on the cage by double-side tapes. This procedure was performed carefully with minimal disturbance. The pair was kept inside the cage until they completed egg-laying. Eggs were collected from the mated pair inside each cage. The number of eggs laid by each female was counted every day until the death of the female. The dead females were dissected to determine whether they laid all their eggs. If their abdomens and genitalia were full of eggs and secretions, it indicated that they did not complete the egg-laying. The eggs retained in the ovaries were not counted.

The survival percentage of pupae and adults was also measured during the incubation period, and these percentages were calculated as follows:

$$S_P = \frac{N_A}{N_P} \times 100\% \quad (1)$$

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$$S_A = \left(1 - \frac{N_{NE} + N_{PE}}{N_F}\right) \times 100\% \quad (2)$$

where, N_A is the number of treated larvae that developed to the adult stage, N_P is the total number of treated larvae that developed to pupae, S_P is the survival percentage of the pupae (%), N_F is the number of females that emerged from the treated larvae, N_{NE} is the number of females that did not lay eggs at all and died N_{PE} is the number of females that did not lay all their eggs and died, and S_A is the survival percentage of adults that emerged from the treated larvae (%).

One hundred of the laid eggs by the moths (developed from the larvae that survived after the treatment) were gently introduced into a cage (6.5 cm diameter × 4 cm height) with a fine hairbrush. During the introduction, eggs were selected at random and observed carefully under a stereomicroscope to eliminate damaged eggs. The developmental duration and hatching ratio of the eggs were checked and recorded. The newly hatched larvae were individually transferred into cylindrical plastic containers (5 cm diameter × 4 cm height) covered by polyamide mesh (0.18 mm opening). Two grams of diet was placed into each container before the larvae were introduced. The development and mortality of every larval instar were observed daily until all surviving larvae developed to the adult stage, and the adults laid eggs under the incubation conditions. There were three replicates for each treatment (parental and F_1 generation at the three N_2 treatments) and the control.

Statistical analysis

Based on the survival percentage of each developmental stage, female ratio, and oviposition, the population trend index of F_1 generation was calculated as (Xu *et al.*, 2003; Tao *et al.*, 2008):

$$I = SeS_1S_2S_3S_4S_5S_pS_A\mathrm{FP}_f P_{♀} \quad (3)$$

where, I is the population trend index, S is the survival percentage, $\mathrm{FP_f}$ is the average number of eggs laid by each female, and $P_{♀}$ is the female ratio. The subscripts of e, 1, 2, 3, 4, 5, P, and A represent egg, larvae from the first to the fifth instar, pupa, and adult, respectively.

Data on the developmental duration, survival percentage, oviposition, and population trend index (I) are presented as the mean ± SD ($n = 3$) and were subjected to the general linear model (GLM) for univariate analysis of variance using IBM SPSS Statistics 20. After the GLM was conducted, Tukey's test at the 0.05 level was used to compare the treatment means of developmental duration, survival percentage, and oviposition of surviving larvae treated with 98% N_2 at the three exposure times.

Results

Biology of the parental generation

Survival percentage

Although some treated larvae survived exposure to the N_2 treatment, not all of them could pupate as some died before pupation, some surviving pupae did not develop to adults, and some emerged females did not lay eggs or could only lay few eggs before they died. For example, the larvae under the 6-days treatment showed 69.7% survival percentage measured at 24 h after exposure, and 37.2% survival percentage when it was measured before pupation (Table 1). Both pupae and adults that developed from the surviving larvae had a significantly lower survival percentage than the control (Table 1).

Developmental time and oviposition

The developmental time of surviving larvae was significantly longer than that of the control, as were those of the pupae and adults that emerged from the treated larvae (Table 1). The developmental duration of treated larvae after being exposed to 98% N_2 for 6, 4, and 1.5 days was delayed by 11.0, 7.8, and 3.2 days, respectively. These results indicated that the development of larvae treated with 98% N_2 was significantly delayed (Table 1). Even after 1.5 days of exposure to 98% N_2, larvae had a 3-d delay in their development to pupation. The longer the larval exposure time to N_2 was, the longer the resulting developmental duration of the surviving larvae, pupae, and adults that developed from treated last-stage larvae. The mean number of eggs laid by females that developed from the larvae surviving exposure to 98% N_2 for 6, 4, and 1.5 days was 35, 66, and 81; respectively, and these were significantly lower than those of untreated larvae (Table 1). Therefore, the oviposition of the adult female moths that emerged from the surviving larvae was strongly inhibited by the 98% N_2 treatment.

Biology of the F_1 generation

Developmental duration

The developmental duration of the F_1 generation resulting from the eggs laid by the adults that developed from the larvae exposed to 98% N_2 for 6 and 4 days was significantly different from that of the untreated controls, but not for the 1.5 days treatment after the F_1 eggs hatched (Table 2). The developmental time of the F_1 generation after the 3rd instar was not significantly influenced. This indicated that the 98% N_2 treatment could affect not only the developmental duration of the parental generation, but also the early developing stages of the F_1 generation. If the treatment time was less than 1.5 days, the developmental time of the F_1 generation was not significantly affected (Table 2).

Survival percentage and population trend index value of the F_1 generation

Generally, the survival percentage of the F_1 generation that hatched from eggs laid by the adults developed from the larvae exposed to 98% N_2 was significantly reduced compared to that of the control. The survival percentage was lower in N_2 treatments with longer exposure time, and the more stages of the F_1 generation were affected (Table 3). The population trend index (I) of the F_1 generation developed from the larvae treated with 98% N_2 for 6, 4, and 1.5 days was approximately 15.7, 18.0, and 25.4, respectively, while the I value was 28.1 under the control condition (Table 3). Therefore, the longer the N_2 exposure time, the lower was the value of the population trend index.

Discussion

The fifth instar (last stage) larvae of *P. interpunctella* have very different biology from other instar larvae in that they wander away from food in search of pupation sites (Mohandass *et al.*, 2007); therefore, the infestations are often undetected until the fifth instar larvae disperse from infestation locations and wander in search of pupation sites (Arthur, 1997). The wandering larvae of *P. interpunctella* are usually difficult to control by conventional

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Table 1. Development duration, survival rate, and oviposition inhibition of *P. interpunctella* larvae surviving exposure to 98% N_2 in different treatment times

Exposure time (d)[A]	Survival rate (%)[B]	Development duration (d)[C]			Survival rate (%)[D]			FP[E]	IR[F]
		Larvae	Pupae	Adults	Larvae (S_{LP})	Pupae (Sp)	Adults (S_A)		
6	69.7 ± 2.1a	14.1 ± 1.0a	8.4 ± 0.5a	5.4 ± 1.0a	37.2 ± 2.5a	76.0 ± 3.2a	64.8 ± 3.4a	35.3 ± 5.0a	71.2
4	80.3 ± 1.5b	10.9 ± 1.2b	7.2 ± 1.0b	4.3 ± 0.3b	54.7 ± 3.4b	78.9 ± 1.8a	75.7 ± 1.5b	65.5 ± 7.5b	46.7
1.5	90.7 ± 2.5c	6.3 ± 1.2c	6.1 ± 1.0c	3.6 ± 0.6c	72.8 ± 1.0c	90.1 ± 1.3b	84.8 ± 2.3c	81.2 ± 5.4c	33.9
Control	100.0 ± 0.0d	3.1 ± 0.3d	5.9 ± 0.2c	3.1 ± 0.5c	95.6 ± 2.0d	95.3 ± 1.1c	94.5 ± 1.8d	122.8 ± 8.3d	0.0
F[G]	158.1	73.2	18.0	22.9	333.1	62.1	86.018	88.9	-
P[G]	< 0.01	< 0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	-

[A]Exposure time (days) and statistic. The fifth instar larvae were exposed to 98% N_2 and the column provides the treatment time.
[B]The survival rate of the larvae determined in 24 h after removed from 98% N_2.
[C]The developmental duration of the larvae surviving exposure to 98% N_2 = days of the fifth instar (5 days after exuviation) in 98% N_2 + days of the survived larvae (removed from 98% N_2) to pupation. The development duration of the adults was the days of the adults before oviposition.
[D]S_{LP} is the survival rate of larvae which could develop to pupa stage, S_P is the survival rate of pupa which could develop to adult stage (equation 1), and S_A is the survival rate of the female adults which could lay all their eggs (equation 2).
[E]Average number of eggs laid (±SD) by each female emerged from the larvae surviving the N_2 treatment.
[F]Inhibition ratio of oviposition (%) = [(number of eggs laid by each female at control condition − egg number laid by each female under treated condition)/(egg number laid by each female at control condition) × 100%].
[G]Statistics of General Linear Model (GLM) of univariate analysis, and degree of freedom for each test was 3.
[B] to [E]Different letters after the number (means ± SD) in the same column indicated significantly different at $\alpha = 0.05$ level (Tukey test). There were three replicates for each treatment, $N = 3$.

neurotoxic insecticides compared to adult stored-product beetles in some researches (Arthur, 1995, 1997). The fifth instar larva of *P. interpunctella* is also the most tolerant stage to 98% N_2 (Huang *et al.*, 2020). Therefore, it is more beneficial to understand the development of surviving fifth instar larvae of *P. interpunctella* after exposure to 98% N_2, and the reproduction of adults resulting from exposed larvae.

Life span and oviposition of insects could be affected by the food type, food quality and quantity, prior treatment, presence of other insects, insect density, disturbances due to experimental operation, and environmental factors such as temperature, relative humidity, and light-dark cycles (Sambaraju, 2007). Unfavorable conditions of these factors could result in stress on their development and oviposition. During the entire experiment, enough high quality feed was provided, and temperature and RH were controlled at their optimum developmental conditions. One source of stress might have been the transferring of insects from one container to another. We transferred insects five times in this study: (1–2) the last-stage larvae were transferred before and after N_2 treatment; (3) moths moved into the plastic cage by themselves; (4) 100 eggs of the F_1 generation of the last-stage larvae were introduced into a cage; and (5) the newly hatched larvae were individually transferred into cylindrical plastic containers. The stress caused by transferring the moths might be negligible because the moths moved into the cage by themselves. Larvae and eggs were transferred by using a fine-hair brush. Using a fine-hair brush to transfer insects is a common method and the stress due to this transfer might be also minimal. Insects might have been disturbed during these transfers, even though these transfers were required for this study.

Different combinations of exposure time and gas concentration of controlled atmosphere can result in different mortality due to different effects on the development and reproduction of the treated insects (White *et al.*, 1995; Wang *et al.*, 2001). The most tolerant stage (larvae) of *P. interpunctella* can be fully killed in 98% N_2 for 12 days at 28°C (Huang *et al.*, 2020). The survival ratio of *P. interpunctella* in jujube (*Zizyphus jujuba* Miller) decreased with increasing exposure time and reached 0% when the jujubes were exposed to low-pressure (1.3 kPa) for 41.6 h at 25°C (Hou *et al.*, 2018). In a similar study on eggs, larvae, and pupae of *P. interpunctella* (Mbata and Phillips, 2001), mortality of the insects increased with increasing exposure time (from 30 min to 144.0 h) at a low pressure (32.5 mm Hg). Even though survivors can continue their development and reproduction after a sublethal exposure, our study found that they performed poorly as a function of either delayed development, increased mortality, or reduced oviposition. The average life cycle of *P. interpunctella* (from egg to adult emergence) at 25°C and 40% RH was 7 days under hermetic condition (Quellhorst *et al.*, 2018). The pupation rate and emergence rate of the *P. interpunctella* larvae (20 days after egg hatching) in 5% O_2 were 85 and 11%, respectively, while they were 100% in the control. The pupal period was delayed by about 33 days compared with that in the control (Tian *et al.*, 2016). Our data demonstrated the same trend for the developmental duration of surviving pupae and adults, after the last-stage larvae were exposed to 98% N_2 for different periods of time. The biology of the treated larvae, such as the developmental time and oviposition of the treated larvae and the biology of its F_1 generation, was changed. These delay and change will retard population growth, thereby helping the hermetic system and modified atmosphere treatment more effective in controlling insect numbers (Kharel *et al.*, 2019). Hence, storing grain and

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Table 2. Development duration of F_1 generation of *P. interpunctella* emerged from the larvae surviving exposure to 98% N_2 in different exposure times

Exposure time (d)[A]	Eggs[B]	1st instar	2nd instar	3rd instar	4th instar	5th instar	Pupae	Total[C]
6	4.8 ± 0.9a	5.9 ± 0.4a	6.3 ± 1.2a	6.8 ± 3.0	7.3 ± 1.2	9.0 ± 1.2	6.1 ± 10.1	48.9 ± 2.1a
4	4.4 ± 0.7ab	4.6 ± 1.6b	5.6 ± 2.8a	6.5 ± 01.5	7.4 ± 0.9	9.1 ± 1.1	6.0 ± 1.0	45.9 ± 1.4ab
1.5	3.8 ± 0.7ab	4.1 ± 1.3bc	5.0 ± 0.5ab	6.6 ± 1.5	7.4 ± 1.7	8.9 ± 1.3	6.1 ± 0.5	43.1 ± 1.4bc
control	3.25 ± 1.1b	3.9 ± 0.3c	4.9 ± 1.0b	6.2 ± 1.2	7.3 ± 0.7	8.8 ± 1.2	5.6 ± 1.4	40.2 ± 1.3c
F[D]	4.2	35.5	7.6	0.935	0.006	0.036	0.5	17.0
P[D]	0.048	< 0.01	0.01	0.137	0.999	0.990	0.694	< 0.01

[A]Exposure time (days) and statistic. The fifth instar larvae were exposed to 98% N_2 and the column provides the treatment time. The development duration presented in the table was the duration of the F_1 generation emerged from the larvae surviving exposure to 98% N_2.
[B to C]Different letters after the number (means ± SD) in the same column indicated significantly different at $\alpha = 0.05$ level (Tukey's test).
[C]The total development duration of the F_1 generation from egg to adult.
[D]Statistics of General Linear Model (GLM) of univariate analysis, and degree of freedom for each test was 3.

processed food commodities in 98% N_2 for different periods of time (even a short period such as 1.5 h) could partially or fully control population development of the insect.

Compared with that of the controls, egg production was reduced to 37% when mated females of *P. interpunctella* were exposed to 96% CO_2 for 1 hour. Low O_2 might inhibit egg development or block ovipositional response (Lum and Phillips, 1972). In our study, the number of eggs laid by females that developed from the larvae exposed to 98% N_2 for different times was significantly lower than that of the control.

The population trend index (I) is widely used for evaluating the influence of environmental factors and developing pest management guidelines (Bellows *et al.*, 1992; Carey, 2001). Hypoxia has been shown to reduce oviposition, progeny development, body mass, and longevity of the insects (Cheng *et al.*, 2012; Yan *et al.*, 2016); all of which slow overall population growth. We found that the population trend index of the F_1 generation of *P. interpunctella* that developed from the larvae that survived after being exposed to 98% N_2 for 6, 4, and 1.5 days was clearly lower than that of the control. These results indicate that a short exposure time to low O_2 can result in insect survival, but the population trend index of progeny is decreased.

Exposure to 98% N_2 for a period clearly affected the development and oviposition of *P. interpunctella*, which was likely due to changes in insect physiology caused by low oxygen under the controlled atmosphere (Greenlee and Harrison, 2005; Harrison *et al.*, 2006). The present work suggests that such effects can last beyond the treatment period, and might gradually recede during further development. In our study, the inhibition effect of high concentration N_2 on the F_1 generation decreased compared to that on the treated parental generation. These changes might be related to the tolerance of different developmental stages to adverse

Table 3. Mean (± SD) percent survival and biological parameters of F_1 generation of *P. interpunctella* emerged from the larvae surviving exposure to 98% N_2 as last instar larvae in different exposure times

		Treatment time (d)				*Statistic*	
Life stage surviving		6	4	1.5	Control	F[E]	P[E]
Life stage surviving	Eggs	57.7 ± 1.5a	65.3 ± 1.2b	72.7 ± 1.5c	81.3 ± 1.5d	147.5	< 0.01
	1st-instar	78.6 ± 1.6a	86.7 ± 1.0b	87.2 ± 0.6b	86.5 ± 1.0b	42.1	< 0.01
	2nd-instar	82.6 ± 2.0a	87.7 ± 1.4b	87.9 ± 1.0b	87.7 ± 0.8b	10.2	0.004
	3rd-instar	84.9 ± 1.8a	85.9 ± 2.0a	88.6 ± 3.1a	89.7 ± 0.8a	3.5	0.072
	4th-instar	89.6 ± 1.6a	91.4 ± 1.2ab	90.6 ± 0.7ab	93.4 ± 1.0b	5.7	0.022
	5th-instar	90.7 ± 2.2a	91.4 ± 1.7a	93.3 ± 0.4ab	95.5 ± 1.1b	6.2	0.018
	Pupa	94.9 ± 2.0a	93.5 ± 1.4a	94.7 ± 1.4a	95.9 ± 2.1a	1.0	0.427
	Pre-oviposition[A]	95.9 ± 0.3a	96.0 ± 1.6a	96.7 ± 1.2a	97.2 ± 1.1 a	0.8	0.542
	Oviposition[B]	94.4 ± 2.1a	94.8 ± 1.7a	96.5 ± 1.7a	94.2 ± 1.4a	1.0	0.434
	Overall[C]	22.3 ± 1.2a	30.3 ± 0.6b	36.7 ± 2.5c	43.3 ± 1.5d	93.3	< 0.01
FP_f[D]		112.4 ± 5.6a	105.8 ± 5.3ab	120.8 ± 6.8b	122.2 ± 4.2b	6.0	0.019
I[D]		15.7 ± 0.5a	18.0 ± 1.3a	25.4 ± 1.4b	28.1 ± 1.2c	80.7	< 0.01

Different letters after the number (means ± SD) in the same row indicated significantly different at $\alpha = 0.05$ level (Tukey's test).
[A]The survival rate of the females before laying eggs.
[B]The survival rate of the females during egg laying.
[C]Overall = the overall survival rate from egg to adult.
[D]FP_f = Average number of eggs laid by females, and I is the population trend index.
[E]Statistics of General Linear Model (GLM) of univariate analysis, and degree of freedom for each test was 3.

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conditions (Margus *et al.*, 2019). Exposure to high pesticide doses is generally lethal and exerts a strong selection pressure, while exposure to mild or sublethal doses may lead to within and transgenerational stress effects on survival and fitness-related traits. These effects, in turn, may contribute to the persistence of populations (Räsänen and Kruuk, 2007). Similarly, exposure to controlled atmosphere for short and sublethal periods could lead to life history differences between the parental and F_1 generation of *P. interpunctella*. Adaptation may be one mechanism for developing tolerance or resistance to controlled atmospheres. To prevent the survival of insects and the development of resistance, the exposure time of controlled atmosphere should be arranged based on insect species and stages, environmental conditions, and concentration of the modified or controlled atmosphere.

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