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ORIGINAL PAPER

Diapause incidence and critical day length of Asian corn borer (*Ostrinia furnacalis*) populations exhibit a latitudinal cline in both pure and hybrid strains

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Abstract
The Asian corn borer, *Ostrinia furnacalis*, is a serious pest and is widely distributed in corn-producing regions throughout China. This insect enters facultative diapause as fully grown larvae in response to short day lengths. Here, we evaluate the changes in diapause incidence and critical day length (CDL) by crossing a tropical strain with five subtropical and temperate strains from a 2897-km latitudinal gradient to investigate the latitudinal variations in diapause induction and CDL and their heredity. Photoperiodic responses of diapause induction in the different geographical strains at different temperatures showed that diapause incidence and CDL increased with increasing latitude and decreased with increasing temperature. Similarly, diapause incidence and CDL for the hybrid strains also showed an increase with increasing latitude or decreasing temperature. Conversely, the diapause incidences were significantly lower and the CDLs were significantly shorter in hybrid strains than their parents with high diapause incidence. Furthermore, the males had significantly more influence than the females on the incidence of diapause in subsequent progeny. Diapause incidence and CDL in *O. furnacalis* are strikingly different among pure strains and hybrid strains. The photoperiodic response controlling diapause is strongly heritable, with diapause being a partial dominant character over nondiapause, with the incidence of diapause mainly determined by the male parent. These results can help us to predict the time course of diapause induction in nature and may provide a genetic means for pest management by providing information on the overwintering capabilities of the hybrids.

Keywords *Ostrinia furnacalis* · Diapause · Critical day length · Photoperiod · Temperature · Intraspecific hybridization

Key message

- The Asian corn borer, *Ostrinia furnacalis*, is a serious pest of corn.
- We evaluated changes in diapause incidence and critical day length (CDL) by crossing a tropical strain with five subtropical and temperate strains.
- We demonstrated that diapause incidence and CDL for both pure strains and their hybrid strains exhibit a latitudinal cline.
- These findings can help us to predict the time course of diapause induction and may provide a genetic means for pest management through intraspecific hybridization.

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Introduction

The Asian corn borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), is a serious economic pest of corn production in China. The estimated average annual losses in China due to this insect range from 6 to 9 million tons per year and can be much greater in an outbreak year (Zhou and He 1995). The moth is widely distributed in corn-producing regions throughout China and enters facultative diapause as fully grown larvae in response to short day lengths (Du and Cai 1964; Gong et al. 1984; Dai et al. 2000; Guo et al. 2013; Yang et al. 2014). It has now become very clear that the most important cue influencing diapause induction in *O. furnacalis* is the photoperiod in subtropical and temperate regions (Xia et al. 2012; Guo et al. 2013; Huang et al. 2013; Xiao et al. 2015; Fu et al. 2015).

The most important feature of the photoperiodic response is the so-called critical day length (CDL), which is defined as the day length at which 50% of the individuals in a population enter diapause and 50% can continue development (Beck 1980; Saunders 2002). Changes in day length are caused directly by the movements of the Earth itself, resulting in the increase or decrease in photoperiod being entirely predictable at each latitude, with the initiation of diapause occurring at an appropriate photoperiod (Taylor 1980). Strains from high latitudes, where winter begins earlier in the year than at lower latitudes, are likely to show diapause onset at longer photoperiods than strains from lower latitudes (Tauber et al. 1986). Therefore, many widely distributed insects show clinal geographical variation in CDL, with higher latitudes corresponding to a longer CDL (Tauber et al. 1986; Danilevskii 1965; Danks 1987; Tyukmaeva et al. 2011; Bean et al. 2012; Wang et al. 2012; Chen et al. 2013). Such variability in CDL indicates ecological plasticity and reflects adaptation to a wide array of climatic conditions. Understanding the geographical variation in CDL can help us to predict the timing of diapause induction in a strain in nature. In addition, similarity between CDL estimates derived from laboratory studies using different photoperiods and CDLs observed under field conditions has been reported in the zygaenid moth *Pseudopidorus fasciata* (*Pidorus euchromioides*), the leaf beetle *Diorhabda elongata*, the rice stem borer *Chilo suppressalis* and *O. furnacalis* (Xue and Kallenborn 1998; Bean et al. 2007; Xiao et al. 2010; Yang et al. 2014).

Cross-mating strains from different geographical areas have been generated in many insects and have revealed that there are various modes of inheritance of diapause in different species (Beck 1980; Tauber et al. 1986; Danilevskii 1965; Danks 1987; Saunders 2002). However, only a few hybridization studies have tested the change in CDL when insects are subjected to different temperatures. Crosses made between geographical strains under different photoperiods for the knot grass moth *Acronycta rumicis* (Danilevskii 1965), the fly *Sarcophaga peregrina* (Kurahashi and Ohtaki 1977), the flesh fly *Sarcophaga similes* (Goto 2009), the spider mite *Tetranychus urticae* (Vaz Neues et al. 1990) and the cotton bollworm *Helicoverpa armigera* (Chen et al. 2012) have shown that the incidence of diapause and the CDL of their hybrid strains was intermediate between those of their parents, suggesting that the CDL is heritable.

The incidence of diapause in reciprocal crosses has been largely determined by the maternal line in such species as the anise swallowtail *Papilio zelicaon* (Sims 1983), the blow fly *Calliphora vicinia* (McWatters and Saunders 1997) and the cabbage beetle *Collaphellus bowringi* (Kuang et al. 2011; Chen et al. 2014) in reciprocal crosses. Interestingly, most of the lepidopteran species typically exhibited paternal effects rather than maternal effects, such as: the moth *Pionea forficalis* (King 1974), the pink bollworm *Pectinophora gossypiella* (Raina et al. 1981), the European corn borer *Ostrinia nubilalis* (Ikten et al. 2011), the comma butterfly *Polygonia c-album* (Söderlind and Nylin 2011), the Asian corn borer *O. furnacalis* (Xia et al. 2012; Huang et al. 2013; Xiao et al. 2015; Fu et al. 2015) and the cotton bollworm *H. armigera* (Chen et al. 2012), in which reciprocal crosses of high-diapause-strain fathers produced a higher incidence of diapause among their offspring than did low-diapause-strain fathers. Understanding the inheritance of diapause has important and direct implications for both theoretical and applied biology. As a component of pest management, the seasonal asynchrony caused by crossing a nondiapause or a low-diapause tropical strain with a temperate strain could be applied to pest populations (Showers 1981; Showers et al. 1990). That is, an introduction of low-diapause genes into a temperate population would result in the incidence of nondiapause, thus seriously affecting the overwintering capabilities of the population. Moreover, more recent study has demonstrated that intraspecific hybridization between a subtropical strain and a temperate strain of *O. furnacalis* reduced fitness of hybrids in term of larval development time, body weight, growth rate and sex ratio (He et al. 2019).

In previous studies, we investigated the incidence of diapause and the CDL in *O. furnacalis* by crossing two geographically isolated populations (Xia et al. 2012; Huang et al. 2013; Xiao et al. 2015; Fu et al. 2015). All reciprocal cross and backcross experiments in the moth revealed that: (1) The CDL of F1 progeny is intermediate between the CDLs of their parents and that there is a sex linkage in the inheritance of diapause induction, with the male parent having a greater influence on the following F1 progeny; (2) the photoperiodic response controlling diapause in the moth is heritable; (3) the inheritance of diapause in the moth does not fit a purely additive hypothesis; rather, the capacity for diapause is transmitted genetically in the manner of incomplete dominance. However, latitudinal variation in diapause incidence and CDL in *O. furnacalis* has not been systematically investigated along a latitudinal gradient in China. In addition, whether the CDLs of hybrid strains show a latitudinal clinal variation needs to be examined. In the present study, we measured the changes in diapause incidence and the CDL in *O. furnacalis* by crossing a tropical strain with five subtropical and temperate strains along a 2897-km latitudinal gradient in China (18.8°–44.9° N) under a range of photoperiods and temperature regimes. The purpose of this study was to evaluate the relationship between CDL and latitude for diapause incidence along a latitudinal gradient. Such studies may eventually lead to a better understanding of the genetic architecture of diapause and help determine whether intergeographic hybridization in *O. furnacalis* can serve as a means of pest management by resulting in asynchrony in breeding seasons.

Materials and methods

Insect material and culture

Six geographically isolated strains of *O. furnacalis* were used in this study, including (1) the temperate Harbin strain (HB) from Harbin city (44.9° N, 127.2° E), Heilongjiang Province, (2) the temperate Langfang strain (LF) from Langfang city (39.5° N, 116.7° E), Hebei Province, (3) the temperate Taian strain (TA) from Taian city (36.2° N, 117.1° E), Shandong Province, (4) the subtropical Nanchang strain (NC) from Nanchang city (28.8° N, 115.9° E), Jiangxi Province, (5) the subtropical Guangzhou strain (GZ) from Guangzhou city (23.1° N, 113.2° E), Guangdong Province, and (6) the tropical Ledong strain (LD) from Ledong city (18.8° N, 109.2° E), Hainan Province (Fig. 1). Approximately 50 female moths were collected from corn fields in late June and August 2013 in each of the six regions. Adults were placed into plastic bags with cotton balls moistened with a sugar solution (10% of honey added to 90% water by volume) to produce egg masses. The egg masses were collected in Petri dishes every day. After hatching, the larvae were transferred to plastic boxes (diameter 12 cm, height 15 cm) and reared on an artificial diet (Qiao et al. 2008) under a diapause-averting photoperiod of LD 18:6 h at 25 °C until pupation. The pupae were placed individually in one of 24 wells in a plastic plate with each well measuring 1.5 × 2 cm (diameter × height) until adult eclosion. Adults were sexed on the day of eclosion, and females were allowed to mate with males from either the same strain or a different strain.

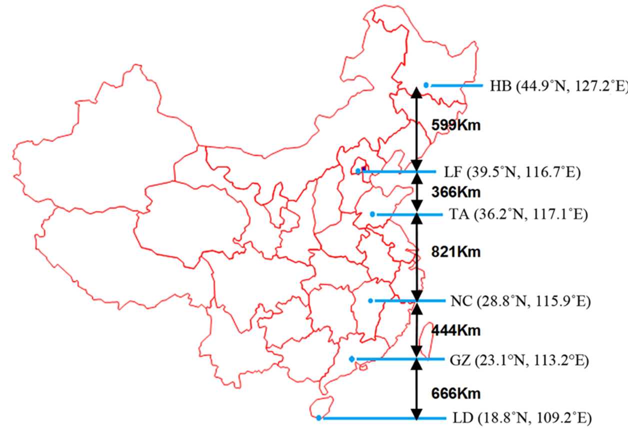


Fig. 1 Geographical locations of the six strains of *O. furnacalis* used in the study

Crosses

Pure strains and reciprocal parental crosses were made as follows (females shown on the left, males on the right): LD × LD, LD × GZ, GZ × LD, GZ × GZ; LD × LD, LD × NC, NC × LD, NC × NC; LD × LD, LD × TA, TA × LD, TA × TA; LD × LD, LD × LF, LF × LD, LF × LF; LD × LD, LD × HB, HB × LD, HB × HB. At least 80 pairs were used in each cross. The progeny of these crosses were reared under a range of constant photoperiods from LD 11:13 to LD 18:6 at constant temperatures of 22, 25 and 28 °C. Unless otherwise stated, each experimental regime was tested by rearing in three to five replicates of at least 50 newly hatched larvae per replicate. For all experiments, we observed the incidence of diapause, determined by the proportion of mature larvae that failed to pupate within 2 weeks after comparable control cultures had completed pupation.

Experiments were performed in illuminated incubators (LRH-250-GS, Guangdong Medical Appliances Plant, Guangdong, China). The light intensity during the photophase was approximately 1.97 W m^{-2}, and the variation in temperature was ± 1 °C.

Statistical analysis

Statistical analyses were conducted using the SPSS 17.0 statistical software package (IBM, www.ibm.com). Logistic regression analyses were used to estimate the CDL for each group, i.e., the day length inducing 50% probability of diapause, including 95% confidence intervals, by calculating the predicted 50% value for each strain under each temperature treatment. Linear regression was used to analyze the relationship between latitude and critical photoperiod. One-way analysis of variance (ANOVA) and Tukey's test were used to compare the differences in critical day length among different groups and to determine whether differences in the incidence of diapause in the different groups under each day length at different temperatures were significantly different.

Results

The incidence of diapause and CDL among geographically pure strains

The incidence of diapause reflects the proportion of a strain that enters diapause under the short day length conditions. The tropical LD strain exhibited a very low incidence of diapause (6.3–6.6%) under the short day lengths of 11 and 12 h at the lower temperature of 22 °C (Fig. 2). All larvae developed without diapause in the LD strain under the other treatments. The incidences of diapause in the other five subtropical and temperate strains showed an increase with increasing latitude and a decrease with increasing temperature (Fig. 2, S1 Table). For example, the incidences of diapause in the subtropical GZ strain under the day length of 14 h significantly increased from 12.7 to 99.6% at 22 °C, from 8.7 to 94.8% at 25 °C and from 0 to 92.4% at 28 °C with increasing latitude (at 22 °C: $F_{5,24}=5144.9$, $P=0.000$; at 25 °C: $F_{5,24}=3964.3$, $P=0.000$; at 28 °C: $F_{5,24}=911.1$, $P=0.000$). The incidence of diapause in the subtropical NC strain under the day length of 14 h significantly decreased with increasing temperature, with 95.2% diapause at 22 °C, 25.2% diapause at 25 °C and 18.2% diapause at 28 °C ($F_{2,6}=341.5$, $P=0.000$).

Almost all individuals (> 93%) from the temperate TA, LF, HB and subtropical NC strains entered diapause under the short day length of 13 h at the high temperature of 28 °C, whereas only 14.3% of the individuals from the subtropical GZ strain entered diapause under the same rearing conditions (Fig. 2, S1 Table).

Due to the low diapause incidence in the LD strain under all temperature conditions, no CDL could be determined. The CDLs of the other five geographical strains were highly affected by latitude and temperature. The CDLs had a strong and positive correlation with the latitudinal origin of the strains at 22, 25 and 28 °C (S1 Fig. and Table 1; at 22 °C, $y=0.123x+10.682$, $R^2=0.980$, $P<0.05$; at 25 °C, $y=0.146x+9.477$, $R^2=0.991$, $P<0.05$; at 28 °C, $y=0.130x+9.430$, $R^2=0.927$, $P<0.05$), showing a significant increase in CDL with increasing latitude ($P<0$ 05). The CDLs also significantly shortened with increasing temperature in all strains (Table 2, $P<0.05$).

The incidence of diapause and the CDL when the tropical LD strain was crosses with different subtropical and temperate strains

Figure 3 presents the photoperiodic response curves for the induction of diapause at 22, 25 and 28 °C when the tropical LD strain with a very-low-diapause response was crossed with the subtropical (GZ, NC) and temperate strains (TA, LF, HB) from a latitudinal gradient. All reciprocal crosses indicated that the hybrid strains exhibited a clear long-day response, irrespective of the direction of the crosses, suggesting that the photoperiodic response controlling diapause in this moth is strongly heritable, with diapause being a partially dominant character over nondiapause.

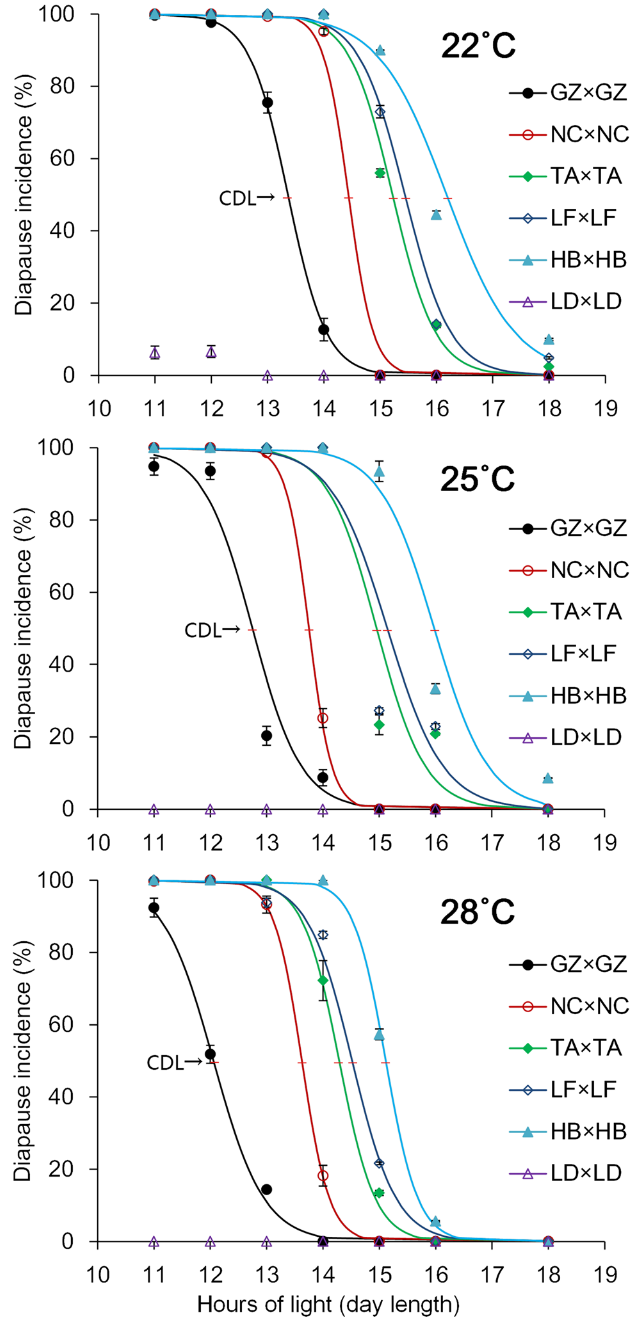


Fig. 2 Photoperiodic response curves for the induction of larval diapause in six pure geographical strains of *O. furnacalis* at 22, 25 and 28 °C. $N=111$–491 for each point

Table 1 Geographic variation in critical day length (CDL) for diapause induction in *O. furnacalis* at different temperatures

Temperature	Strain	CDL (h)	± 95% CI
22 °C	GZ (23.1° N, 113.2° E)	13.36	13.29–13.43[a]
	NC (28.8° N, 115.9° E)	14.44	14.33–14.56[b]
	TA (36.2° N, 117.1° E)	15.22	14.99–15.51[c]
	LF (39.5° N, 116.7° E)	15.44	15.12–15.82[c]
	HB (44.9° N, 127.2° E)	16.18	16.00–16.39[d]
25 °C	GZ	12.75	12.54–12.95[a]
	NC	13.75	13.70–13.80[b]
	TA	14.95	14.70–15.22[c]
	LF	15.14	14.89–15.38[c]
	HB	15.98	15.74–16.31[d]
28 °C	GZ	12.06	11.96–12.15[a]
	NC	13.63	13.21–13.96[b]
	TA	14.29	14.22–14.36[c]
	LF	14.52	14.40–14.64[c]
	HB	15.11	15.05–15.17[d]

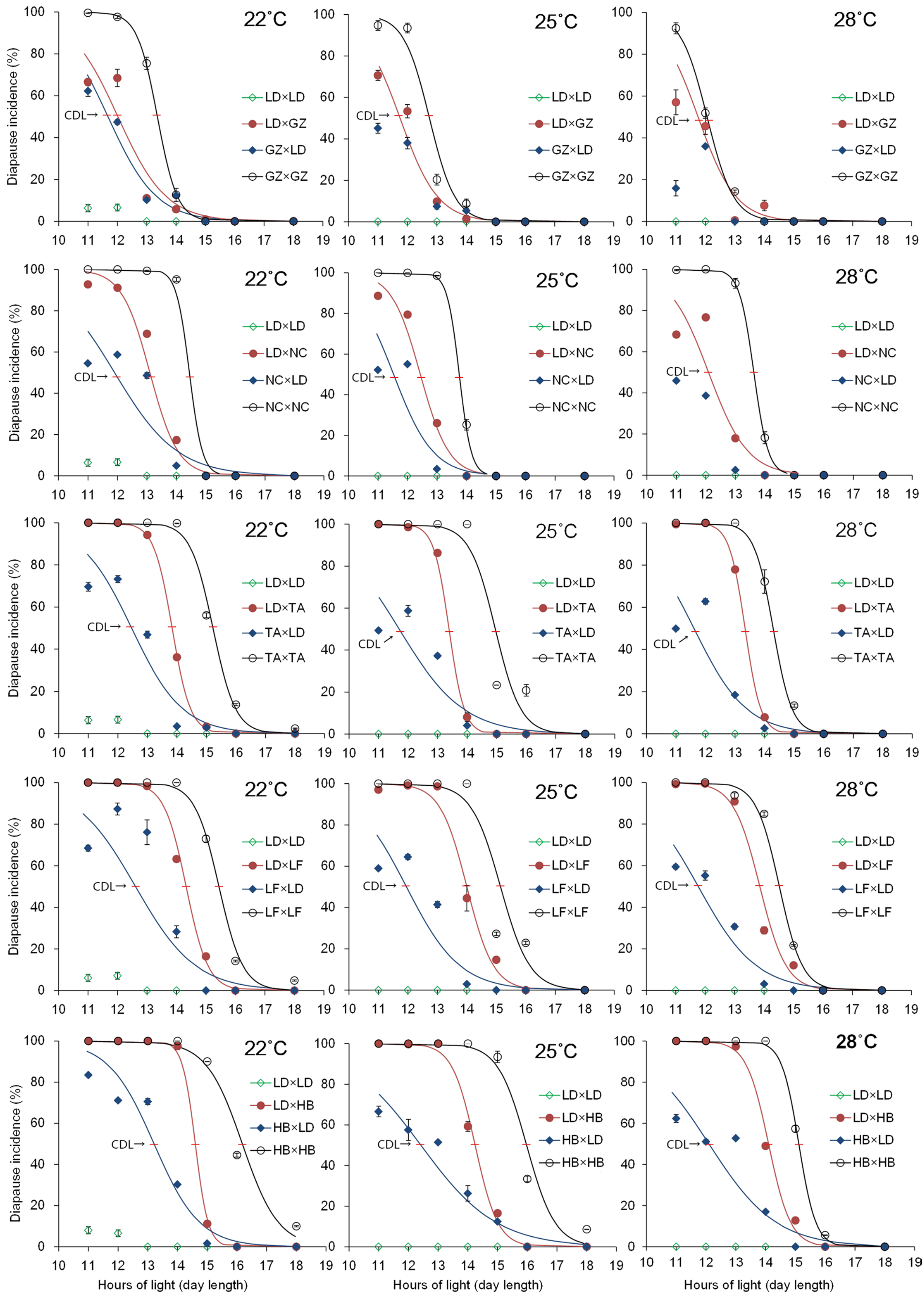
Data are means and 95% confidence intervals; values followed by the same superscript lowercase letter within a column do not differ significantly at the 5% level according to Tukey's test after one-way analysis of variance

The incidences of diapause for all hybrid strains were between those of their parents, with a significantly higher diapause incidence in the hybrid strains derived from a LD-strain mother in comparison with the hybrid strains with the LD-strain father. For example, the incidences of diapause in the LD × GZ hybrid strain under the day length of 12 h at 22, 25 and 28 °C were 68.5%, 53.4% and 45.5%, respectively (S2 Table), whereas the incidence of diapause in the GZ × LD was 47.4%, 38.0% and 35.9% under the same rearing conditions (S3 Table), with significant differences between the two hybrid strains (at 22 °C: $t = 4.94$, $df = 4$, $P < 0.05$; at 25 °C: $t = 3.59$, $df = 4$, $P < 0.05$; at 28 °C: $t = 3.52$, $df = 4$, $P < 0.05$). Similarly, the incidences of diapause between the LD × HB and HB × LD strain were also significantly different under the day length of 14 h at 22, 25 and 28 °C with 97.6% diapause vs. 30.2% diapause at 22 °C: ($t = 37.19$, $df = 4$, $P < 0.05$), 59.2% diapause vs. 26.3% diapause at 25 °C ($t = 7.29$, $df = 4$, $P < 0.05$) and 49.2% diapause vs. 17.0% diapause at 28 °C ($t = 26.54$, $df = 4$, $P < 0.05$). Similar to the pure strains, the hybrid strains also showed a gradual increase in diapause incidence with increasing latitude. For example, when the LD mothers crossed with other latitudinal strains under the day length of 13 h at 22, 25 and 28 °C, the incidence of diapause for their hybrid strains significantly increased with increasing latitude, with the percentages of diapause of 11.0%, 86.3%, 98.7%, 98.3% and 100% at 22 °C, 9.8%, 26.0.8%, 86.0%, 98.7% and 100% at 25 °C and 0.5%, 17.9%, 77.9%, 90.8% and 97.3% at 28 °C, with all showing significant differences ($P < 0.05$; S2 Table). Similar results also were also found when the LD-strain fathers were crossed with the different latitudinal strains under the day length of 13 h at 25 and 28 °C; the incidence of diapause in their hybrid strains significantly increased with increasing latitude. In all reciprocal crosses, the incidences of diapause in hybrids with LD fathers were significantly lower than those in hybrids with LD mothers, showing a strong paternal effect ($P < 0.05$; S3 Table).

Table 2 Changes in critical day length (CDL) for hybrid strains of *O. furnacalis* when the tropical LD strain was crossed with subtropical (GZ, NC) and temperate (TA, LF, HB) strains (females on the left, males on the right)

	Hybrid strain	CDL (h)	± 95% CI	Hybrid strain	CDL (h)	± 95% CI
22 °C	LD × GZ	12.02	11.68–12.31[a]	GZ × LD	11.68	11.39–11.91[a]
	LD × NC	13.10	12.88–13.33[b]	NC × LD	11.90	11.42–12.29[a]
	LD × TA	13.84	13.76–13.91[c]	TA × LD	12.47	12.15–12.75[ab]
	LD × LF	14.33	14.24–14.41[cd]	LF × LD	12.61	12.15–13.05[ab]
	LD × HB	14.60	14.52–14.68[d]	HB × LD	13.21	12.88–13.55[b]
25 °C	LD × GZ	11.75	11.60–11.89[a]	GZ × LD		
	LD × NC	12.43	12.28–12.58[b]	NC × LD	11.53	11.13–11.81[a]
	LD × TA	13.39	13.30–13.47[c]	TA × LD	11.70	11.12–12.11[a]
	LD × LF	14.00	13.74–14.28[d]	LF × LD	11.95	11.52–12.3[a]
	LD × HB	14.24	14.16–14.33[d]	HB × LD	12.42	12.08–12.71[a]
28 °C	LD × GZ	11.75	11.60–11.89[a]	GZ × LD		
	LD × NC	12.09	11.77–12.38[a]	NC × LD		
	LD × TA	13.34	13.15–13.56[b]	TA × LD	11.61	11.17–11.94[a]
	LD × LF	13.85	13.71–14.00[bc]	LF × LD	11.76	11.46–12.02[a]
	LD × HB	14.10	14.01–14.19[c]	HB × LD	12.10	11.69–12.44[a]

Data are means and 95% confidence intervals; values followed by the same superscript lowercase letter within a column do not differ significantly at the 5% level according to Tukey's test after one-way analysis of variance


22˚C
25˚C
28˚C
Diapause incidence (%)
Hours of light (day length)
CDL→
LD×LD
LD×GZ
GZ×LD
GZ×GZ
LD×NC
NC×LD
NC×NC
LD×TA
TA×LD
TA×TA
LD×LF
LF×LD
LF×LF
LD×HB
HB×LD
HB×HB

◂**Fig. 3** Photoperiodic response curves for the induction of larval diapause in *O. furnacalis* at 22, 25 and 28 °C when the tropical LD strain reciprocally crossed with the subtropical GZ and NC strains, and temperate TA, LF and HB strains (females on the left, males on the right). $N = 111–463$ for each point

The CDLs of the hybrid strains with the LD mothers were longer than those of the hybrid strains with LD fathers at all temperatures (Table 2), with a difference of 0.34–1.72 h for the five hybrid strains at 22 °C, 0.9–2.05 h for the four hybrid strains at 25 °C and 1.73–2.09 h for the three hybrid strains at 28 °C, showing a strong paternal influence on the CDL. The CDLs significantly differed between the hybrid strains with the LD fathers and their pure strains at all temperatures (Table 1 vs. Table 2, $P < 0.05$) (at 22 °C, 11.6 h for GZ × LD vs. 13.36 h for GZ; 11.9 h for NC × LD vs. 14.4 h for NC; 12.47 h for TA × LD vs. 15.22 h for TA; 12.61 h for LF × LD vs. 15.44 h for LF; 13.21 h for HB × LD vs. 16.18 h for HB; at 25 °C, 11.53 h for NC × LD vs. 13.75 h for NC; 11.7 h for TA × LD vs. 14.95 h for TA; 11.95 h for LF × LD vs. 15.14 h for LF; 12.42 h for HB × LD vs. 15.98 h for HB; at 28 °C 11.61 h for TA × LD vs. 14.29 h for TA; 11.76 h for LF × LD vs. 14.52 h for LF; 12.1 h for HB × LD vs. 15.11 h for HB).

The CDLs for the hybrid strains also showed a strong and positive correlation with the latitudinal origin of the strains at 22, 25 and 28 °C (S2 Fig. A and B, Table 2 for the hybrid strain with an LD mother: at 22 °C, $y = 0.118x + 9.496$, $R^2 = 0.964$, $P < 0.05$; at 25 °C, $y = 0.121x + 8.995$, $R^2 = 0.980$, $P < 0.05$; at 28 °C, $y = 0.120x + 8.899$, $R^2 = 0.963$, $P < 0.05$; for the hybrid strain with an LD father: at 22 °C, $y = 0079x + 9.5931$, $R^2 = 0.9806$, $P < 0.05$; at 25 °C, $y = 0.0546x + 9.8611$, $R^2 = 0.9014$, $P < 0.05$; at 28 °C, $y = 0.057x + 9.533$, $R^2 = 0.9533$, $P < 0.05$). The CDLs for the hybrid strains with LD mothers significantly increased with increasing latitude ($P < 0.05$, S2 Fig. A, Table 2). The CDLs for the hybrid strains with LD fathers gradually increased with increasing latitude at 22, 25 and 28 °C, with a significant difference at 22 °C ($P < 0.05$, S2 Fig. B, Table 2). The CDLs for the hybrid strains significantly differed among temperatures ($P < 0.05$).

Discussion

The photoperiodic responses for diapause induction in the present study revealed that the diapause response to photoperiod and temperature in *O. furnacalis* strikingly differed among strains (Fig. 2). The temperate strains (from 36.2° N to 44.9° N) and the subtropical NC strain (from 28.8° N) reacted strongly to the photoperiod, with a much weaker effect of temperature; almost all individuals entered diapause under the short day length of 13 h, even at the high temperature of 28 °C. The subtropical GZ strain (from 23.1° N) seemed to be significantly influenced by temperature; only 14.3% of the individuals entered diapause under the same rearing conditions. The tropical LD strain (from 18.8° N) almost lost photoperiodic sensitivity, and only 6.3–6.6% of the individuals entered diapause under the short day lengths of 11 and 12 h at the lower temperature of 22 °C. The latitudinal difference in diapause induction reflects adaptation to different local environmental conditions, with important ecological effects.

In nature, the response pattern of photoperiodic control of diapause induction in temperate strains and the subtropical NC strain ensures that their larvae that hatch under the high-temperature conditions occurring between July and early September will enter diapause, thus preventing the production of a subsequent generation due to the ensuing low temperatures and the ripening and senescence of corn plants. According to our field investigations, nearly all larvae in the first generation of the temperate HB strain entered diapause during July, the warmest time of the year (with a mean temperature of approximately 23.5 °C and a gradually shortening day length of < 16 h), thus mainly producing one generation per year (Lu et al. 1995). Nearly all larvae of the temperate LF strain that hatched during mid-August entered diapause (with a mean temperature of approximately 25 °C and a gradually shortening day length of < 14.8 h), thus producing two to three generations per year (Yu and Yu 2013). Nearly all larvae of the temperate TA strain that hatched during late August entered diapause (with a mean temperature of about 25 °C and a gradually shortening day length of < 14.6 h), thus mainly producing three generations per year. Nearly all larvae of the subtropical NC strain that hatched during early September entered diapause (with a mean temperature of slightly higher than 25 °C and a gradually shortening day length of < 13.2 h), thus mainly producing four generations per year (Yang et al. 2014).

In nature, the response pattern of temperature dependence of diapause induction in the subtropical GZ strain enables the moth to better utilize locally available environmental resources and a longer time for growth and breeding. In fact, field investigations showed that almost all larvae of the subtropical GZ strain that hatched in November entered diapause in response to lower temperatures (approximately 20 °C) and short day lengths (< 12 h); thus, there are five to six generations per year (Wang et al. 2000). However, only a very small proportion of larvae of the tropical LD strain that hatched in early December enter diapause in response to lower temperatures (slightly higher than 20 °C) and short day lengths; thus, there are seven generations per year (Xia et al. 2012). It is clear that the seasonal timing of diapause induction in different geographical strains in nature not only is associated with larval overwintering mechanisms, but also determines their voltinism. Awareness of the important phenological events is important for the development of effective pest management strategies.

Many widely distributed insects with a long-day response show clinal geographical variation in CDL, with a gradually increase in CDL toward the north, but the degree of variation varies among different insect species (Tauber et al. 1986). A number of species for which CDL changes by 1–1.5 h per 5° of latitude have been found (Danilevskii 1965; Tauber et al. 1986; Danks 1987). Of the traits we studied, the CDLs for diapause induction in *O. furnacalis* are strongly and positively correlated with the latitudinal origin of the strain at different temperatures (Table 1, Fig. 3). Interestingly, we found a different change in CDL between the subtropical and the temperate regions. In the subtropical regions, the CDLs of the GZ strain (from 23.1° N) for each 5° of latitude were 1–1.5 h shorter than those of the NC strain (from 28.8° N) at 22, 25 and 28 °C (Table 1), which is in consistent with the general rule. In the temperate regions, the CDLs of the LF strain (from 39.5° N) and HB strain (from 44.9° N) increased by only 0.59–0.84 h per five-degree increase in latitude at 22, 25 and 28 °C (Table 1). This result indicates that the patterns of geographical variation in CDL are based on complex interactions among latitude, local conditions and the genetic flexibility among strains.

In the present study, we first tested the changes in diapause incidence and the CDL of hybrid strains by crossing a tropical strain with subtropical and temperate strains along a latitudinal gradient. All reciprocal crosses indicated that the hybrid strains exhibited a clear long-day response, irrespective of the direction of the crosses, suggesting that the photoperiodic response controlling diapause in this moth is strongly heritable, with diapause being a partially dominant character over nondiapause. Thus, the incidence of diapause in the hybrid strains tended toward that of their diapause parents. In the present five cross-mating experiments, we further confirmed that the temperate strains more strongly reacted to photoperiod than the subtropical strains. As shown in the LD × TA, LD × LF and LD × HB crosses (with temperate-strain fathers), the incidences of diapause (99.1–100%) were nearly the same as those in the TA × TA, LF × LF and HB × HB crosses (100%) under the short day lengths of 11, 12 and 13 h at all temperatures, whereas the incidences of diapause in the LD × GZ (0.55–68.5%) and LD × NC (17.9–92.7%) crosses (with subtropical strain fathers) were significantly lower than those in the GZ × GZ (14.3–99.6%) and NC × NC (93.3–100%) crosses under the same rearing conditions (S1 and S2 Tables). The differences in the diapause capability among the five cross-mating experiments indicate that the diapause gene (or genes) is more powerful in the temperate strains than it is in the subtropical strains.

The present five cross-mating experiments in *O. furnacalis* further reveal that paternal effects on diapause incidence are stronger than maternal effects. As shown in the LD × GZ, LD × NC, LD × TA, LD × LF and LD × HB crosses, the high-diapause-strain fathers resulted in a significantly higher incidence of diapause in comparison with the GZ × LD, NC × LD, TA × LD, LF × LD and HB × LD crosses with the low-diapause-strain fathers (Fig. 3, S1 and S2 Tables), suggesting that diapause responses in this moth may be sex-linked to the parental male. However, the precise mechanism and relevance of the paternal effect are still unknown. Because lepidopteran females are the heterogametic sex (XY or ZW) and males are the homogametic sex (XX or ZZ) (Robinson 1971), sex linkage cannot easily explain such patterns (Nylin 2013). More interestingly, when we compared the incidences of diapause in the different hybrid strains along a latitudinal gradient, we found, like in the pure strains, that the frequency of diapause incidence in the hybrid strains also exhibited a latitudinal cline, i.e., an increase in diapause incidence with increasing latitude (S1 Fig., S1 and S2 Tables). Accordingly, the CDLs of the hybrid strains at all temperatures also exhibited a latitudinal cline, with an increase with increasing latitude and a decrease with increasing rearing temperature (Table 2, S2 Fig.). Moreover, the CDLs of the hybrid strains with tropical LD-strain fathers were significantly shorter than those of the hybrid strains with tropical LD-strain mothers. Our results further suggest that the CDL for diapause induction in this moth is a quantitative life history trait shown to be under polygenic control (Tauber et al. 1986), and genetic and molecular tests have demonstrated that the CDL has a complex underlying mechanism (Emerson et al. 2009). To the best of our knowledge, this is the first report showing that incidence of diapause and the CDL of the different geographical hybrid strains also exhibits a latitudinal cline.

As agricultural entomologists, we are particularly interested in how our studies may help us design appropriate management strategies to reduce the damage caused by the Asian corn borer. The present results regarding the use of intraspecific hybridization for diapause induction may provide a genetic means to suppress pest populations. As shown in Tables 1 and 2, the CDLs for the subtropical NC strain and the temperate TA, LF and HB strains are 13.75, 14.95, 15.14 and 15.98 h, respectively, at 25 °C, whereas the CDLs of the NC × LD, TA × LD, LF × LD and HB × LD strains are 11.53, 11.7, 11.95 and 12.42 h, respectively, which are more than 2–3 h shorter than those of their parents. Therefore, if a large number of the tropical LD-strain males are released in a cornfield in the Harbin region during late June to early-July and in the TA, LF and NC regions during early August to late August, and allowed to mate with the females of the HB, TA, LF and NC strains, the larval progeny that are produced by these crosses would be forced to pupate and to emerge as adults between the end of August and early September in the HB region and during October in the TA, LF and NC regions.

Consequently, the newly emerged adults would die with the onset of winter, thus reducing the number of adults available for mating and egg laying the following year.

Conclusions

The photoperiodic responses for diapause induction in *O. furnacalis* revealed that diapause response to photoperiod and temperature in this insect varied dramatically among the different geographical strains. Both the temperate strains and northward subtropical NC strain reacted strongly to photoperiod but with a much weaker effect of temperature, whereas the southward subtropical GZ strain showed temperature dependence in diapause induction. Conversely, only a very small proportion of the tropical LD strain entered diapause in response to short day lengths and lower temperatures. In nature, the response pattern of photoperiodic control of diapause induction in the temperate and subtropical NC strains ensures that larvae that hatch under higher-temperature conditions will enter diapause. The response pattern of temperature dependence of diapause induction in the subtropical GZ strain and the pattern of nondiapause in the tropical LD strain enable the moth to more efficiently utilize available environmental resources and ensure a longer time for growth and breeding. All reciprocal crosses revealed that diapause incidence and CDL are potentially polygenic and under autosomal control and strongly heritable with paternal dominance. However, the genetic properties underlying the diversity in this important trait remain unclear. The CDLs of the hybrid strains derived from mating with tropical strain males were significantly shorter in comparison with those of the associated pure strains with high diapause incidence. These findings can help us to predict the time course of diapause induction in nature and may provide a genetic means for pest management by providing information on the overwintering capabilities of the hybrids.

Authors' contributions

FX and HL conceived and designed the study. HL, CC and HH conducted the experiments. TJ analyzed the data. FX and GY wrote the manuscript. All authors read and approved the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animals rights This article does not contain any studies with human participants or animals (vertebrates) performed by any of the authors.

Informed consent Informed consent was obtained from all individual participants included in the study.

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