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Photoperiodism and Seasonality in Neotropical Population of *Plutella xylostella* L. (Lepidoptera: Yponomeutidae)

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Fotoperiodismo e Sazonalidade em População Neotropical de *Plutella xylostella* L. (Lepidoptera: Yponomeutidae)

RESUMO - Populações neotropicais de *Plutella xylostella* L. possuem ciclos sazonais de crescimento e declíneo e a migração é um fator-chave na geração da dinâmica populacional. Devido à previsibilidade sazonal das oscilações populacionais, o fotoperíodo poderia agir como o sinal que desencadea o comportamento migratório do inseto. Migrações de insetos são geralmente precedidas por diapausa reprodutiva, uma típica resposta fotoperiódica caracterizada por alterações morfológicas, fisiológicas e comportamentais que possibilitam discriminar as formas migratórias das não-migratórias. Neste estudo, foi testado se o desenvolvimento pré-imaginal e reprodutivo de *P. xylostella*, proveniente de Minas Gerais, é inibido por fotoperíodos equivalentes aos comprimentos de dias em que ocorrem as fases de crescimento ou de declínio das populações naturais. Nenhuma evidencia de resposta fotoperiódica foi encontrada para os insetos criados em laboratório sob cinco regimes constantes de fotoperíodos, variando de oito a dezesseis horas-luz-dia. Não houve variação significativa na sobrevivência e na duração dos estágios de ovo, larva e pupa. O peso das pupas também não foi afetado, assim como o tamanho, a fecundidade e a longevidade dos adultos. Embora algumas espécies de insetos possuam respostas fotoperiódicas geograficamente diferenciadas, a sugestão de alguns autores de que a cosmopolita *P. xylostella* responde ao fotoperíodo em regiões de clima temperado foi questionada. Os dados experimentais não suportaram a hipótese de que a sazonalidade migratória e populacional de *P. xylostella* dependem do fotoperíodo como sinal de anúncio de mudanças temporais na qualidade do habitat.

PALAVRAS-CHAVE: Diapausa, dinâmica populacional, fotoperíodo, migração

ABSTRACT - Neotropical populations of the diamondback moth *Plutella xylostella* L. have seasonal cycles of growth and decrease, and moth migration plays a fundamental role in generating such population dynamics. Since the oscillation of these populations is predictable, photoperiod might operate as a signal that triggers the migratory behaviour of the insect. Migration in insects is usually preceded by reproductive diapause, a photoperiodic response that can be characterised by morphological, physiological and behavioural alterations that permit to discriminate between migratory and non-migratory forms. In this study, I tested whether the pre-imaginal and reproductive development of *P. xylostella* from Minas Gerais (Brazil) is affected by artificial day-lengths that are equivalent to the periods of natural population growth or decrease. No evidence of photoperiodic response was found for the insect reared in laboratory on five different constant photoperiods, from 8h to 16h of light per day. There was no significant variation in survival and duration of egg, larva, and pupa stages or in pupal weight, adult size (forewing length), fecundity, and longevity. Although some species have geographically distinct photoperiodic responses, previous assumptions that cosmopolitan *P. xylostella* responds to photoperiod in temperate regions was questioned. Migratory and population seasonality among neotropical populations of *P. xylostella* certainly occurs independently of the photoperiodic announcement of seasonal changes in habitat quality.

KEY WORDS: Day-length, diapause, migration, photoperiod, population dynamics

Changes in day-length operate as token stimuli for many animals, announcing the approach of predictable seasonal events. The photoperiod stimulates, in the individual, a series of preparatory physiological arrangements for an imminent deterioration of habitat. The most known photoperiodic response in insects is the diapause (Beck 1980, Leather *et al*. 1993, Bell 1994), which usually implies the total interruption in the development of specific stages of the insect life cycle. In some cases, however, individuals can simply be stimulated to decelerate their development or moults. Insects entering diapause often also undergo morphological changes (Saunders 1976, Beck 1980, Nechols *et al*. 1999). Diapause in adult insects is characterised by total or partial suppression of the reproductive development (Hodek 1983).

The development of migratory forms can also be stimulated by photoperiod (Rankin & Singer 1984). There is a connection between diapause and migration, because both are parts of the same physiological syndrome (Kennedy 1961). This close relationship is observed among species that migrate to enter diapause in a different habitat, or species that enter reproductive diapause before starting the migratory flight (Saunders 1976, Nechols *et al*. 1999). In the last case, migration is a pre-reproductive event related to suppression of the sexual development or oocyte maturation (Dingle 1972). Therefore, migratory and non-migratory forms or generations usually differ because the former live longer, retard their reproductive activities, lay fewer eggs, and probably have smaller body sizes (Campos *et al*. 2004).

Change in day-length might be a fundamental process governing predictable population dynamics in unstable environments, where individual photoperiodic responses would be translated into changes in the rate of population growth. For example, when migration is the adaptive response to escape from temporary and inhospitable conditions, the population become extinct in the source habitat; however, at the same time a more favourable place is being colonized. In this situation, predictable and desynchronised population cycles of extinction and colonisation happen in different regions. The insect migratory behaviour and the consequent population oscillations would be commanded by the photoperiod.

The cosmopolitan diamondback moth (DBM), *Plutella xylostella* L. has become the most destructive insect of the Brassicaceae (Talekar & Shelton 1993). Neotropical populations of DBM have seasonal cycles of growth and decrease. These cycles have higher densities between late August and early November and predictable influxes of migrants are the proximate cause of the population growth (Campos *et al*. 2006). The environmental stimuli potentially triggering the migratory behaviour of DBM have received little attention (Shirai 1993, Begun *et al*. 1997, Campos *et al*. 2004), althougth seasonal change in the day-length was believed to stimulate lower fecundity in this species (Harcourt & Cass 1966, Babushkina 1990, Leather 1995). Because migration and consequent population oscillation of *P. xylostella* are predictable (Campos *et al*. 2006), the photoperiod may act as a stimulatory signal to the insect takes off. To check this hypothesis, I verified whether the pre-imaginal and reproductive development of DBM is inhibited by artificial day-lengths that are equivalent to the periods of natural population growth and decrease.

Material and Methods

The sampling procedure and descriptive statistical models for seasonal cycles among neotropical populations of DBM were reported elsewhere (Campos *et al*. 2006). Brassicas are ephemeral plants cultivated during the whole year in the tropics. In southeast Brazil, they are always available in regional scale, but not necessarily within a small area. Therefore, a local system with continuous crops of cabbage (*Brassica oleracea* var. *capitata* cv. Matsukase) and other irrigated brassicas was installed in Viçosa, Minas Gerais State, Brazil. During three years, larvae from second to fourth instar and pupae of DBM were sampled throughout the development of 25 cabbage crops. The samples were taken from the middle of each crop, limited to the central eight rows. Six plants were taken at random in each row, with a total of 48 plants sampled weekly in each crop. The average number of immatures (larvae + pupae) per plant per crop (two or three crops of different ages were weekly present) was used in the calculation of general densities. The average population density was monthly calculated during the three years, each year being a replicate. The monthly densities were analysed by linear regression as function of the photoperiod on the 15th day of each month, at 20^0: 45' S, 42^0: 50' W, in Minas Gerais.

The laboratory experiment was conducted in environmental chambers placed into a constant temperature room (25 ± 0.5°C) and 65 ± 5% relative humidity. The environmental chambers were illuminated with four fluorescent (20 W) light bulbs each. *P. xylostella* was obtained from greenhouse rearing, where larvae were fed cabbage grown in plastic pots. Paper towel envelopes containing macerated cabbage leaves were inserted in cages containing approximately 150 moth couples. The envelopes were offered to oviposition in the afternoon, removed from the greenhouse early in the morning, and taken to the acclimatized room. In this room, paper tower pieces containing individualized groups (cohorts) of 100 eggs were deposited on potted 60 day-old cabbages, and then placed into the environmental chambers. Third instar larvae were transferred with a fine hairbrush to a new plant, where they stayed until pupation.

Thirty egg cohorts were reared, with six replicates (n = 6) in each of the following five photoperiodic regimes: 8:16, 10:14, 12:12, 14:10, and 16:8 hours-light/hours-dark per day at 25°C. The entire cohort was used to estimate survival and duration of the different developmental stages, including adult longevity. Eighteen pupae couples from each cohort were sampled, and they were weighed using an analytical scale. The pupae couples were handled with a brush and isolated in transparent plastic boxes (10 cm x 10 cm x 5 cm). A fragment of median leaf (from 80 day-old cabbage) was inserted in the box as soon as the adults emerged. Leaf fragments were changed daily, and the eggs laid on them were quantified with a stereomicroscope. Eggs laid on the box walls also were counted daily, and eliminated. Forewing length was measured under a stereomicroscope with ocular micrometer, after the couples' death. The eighteen couples from each cohort were used to estimate pupal weight, fecundity, and adult body size (forewing length). We assumed that different body parts of the insects vary isometrically, that is, that the variation in wing length correlates with variation in body size (Honek 1993). The phenotypic variables of *P. xylostella* were submitted to analysis of variance (ANOVA) as function of the photoperiodic regime.

Results

In Southwest Brazil, *P. xylostella* is more abundant in October (Campos *et al*. 2006) within a narrow range of photoperiods (11-13h of light per day). On the other hand, *P. xylostella* has been seldom found in the same day-lengths during the first half a year. Therefore, the population cycles do not coincide with the seasonal photoperiodic variation (Fig.1). No significant correlation was observed between natural day-length and population density during the first ($R^2 = 0.01$; F = 0.05 and P = 0.84) and the second ($R^2 = 0.09$; F = 0.40 and P = 0,56) half the year. Nevertheless, from July to October, one may draw attention to the coincidence between day-length increase and the population growth phase ($R^2 = 0.96$; F = 45.46 and P = 0.02). Population decrease also started when days were longer than 12h of light (Fig. 1). However, the laboratory experiment did not support a causal relation between photoperiod and population oscillation (Tables 1, 2).

Photoperiods experienced did not affect the pre-imaginal and reproductive development of DBM. In none of the photoperiodic regimes, either the development of immature forms was interrupted or survival levels were altered. Duration of the each developmental stages, including adult longevity, was not significantly modified (Table 1). Pupal weight, fecundity, and adult body size (wing length) did not vary significantly either, and males and females showed similar trends (Table 2).

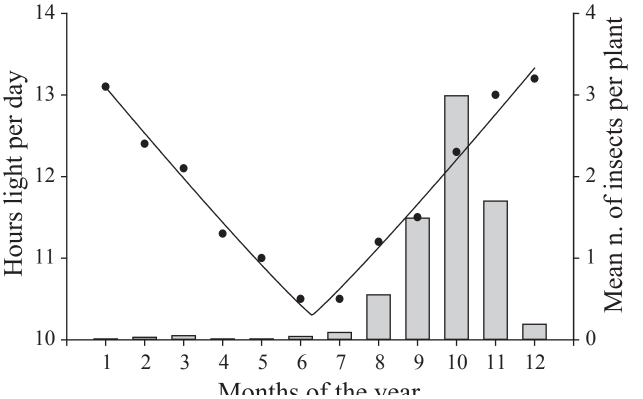

Fig. 1. Oscillation pattern of Neotropical populations of *P. xylostella* and seasonal photoperiod variation. Bars are means (larvae + pupae) for three years; dots are photophases on the 15th day of each month, at 20^0: 45' S, 42^0: 50' W (MG, Brazil).

Discussion

Even though *P. xylostella* is sensitive to artificial light (Sakanoshita and Yanagita 1976), the laboratory data did not support the hypothesis that, in neotropical areas, this insect responds to change in day-length (Tables 1, 2). Insect migration is usually associated with decrease in fecundity, delay in reproductive activity (reproductive diapause), increase in longevity, and morphological alterations such as reduction of adult body size and weight (Kennedy 1961; Dingle 1972). Reduced body size and fecundity, and increased longevity and pre-ovipositional period have been also associated to unfavorable environments and migration in *P. xylostella* (Hillyer & Thorsteinson 1971, Pivnick *et al*. 1990, Branco & Gatehouse 1999, Campos *et al*. 2004). Although the relationship between intraspecific body size variation and migration is controversial (Rankin & Burchsted 1992), some authors have inferred that the smaller the individuals of *P. xylostella*, the more active migrants they are (Pittendrigh & Pivnick 1993; Muhamad *et al*. 1994; Begun *et al*. 1996, 1997; Campos *et al*. 2004). None of these phenotypic variables responded to experimentally manipulated photoperiod (Tables 1, 2), and females started laying eggs a day after emergence. Therefore, *P. xylostella* does not seem to use photoperiod to modulate its seasonal migratory activity in tropical areas. Photoperiod had no effect on flight ability and other traits associated with migration among populations of *P. xylostella* from temperate regions of Japan (Shirai 1993). Crema & Castelo-Branco (2004) also show that the ovarian development and oviposition of DBM from Brazil were not affected by artificial photoperiods.

The coincidence between day-length increase and population growth (Fig. 1) induces spurious inferences. If these variables were dependent, photoperiod would be acting on the source habitat of immigrants. Because population stopped increasing after day-length reached 12h (Fig. 1), hypotheses about photoperiod-related immigration inhibition in the source habitat or emigration stimulation at

Table 1. Survival and duration of each developmental phase of *P. xylostella* reared under different light-dark cycles of artificial illumination. Mean ± SE of n = 6 initial cohorts of 100-120 eggs each.

Photoperiodic regime (light/dark)		Survival (%)			Duration (days)			
		Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Adults
8L/16E		94.0 ± 0.98	85.3 ± 1.49	99.7 ± 0.25	3.0 ± 0.00	8.8 ± 0.10	4.3 ± 0.16	4.4 ± 0.19
10L/14E		94.1 ± 0.37	83.7 ± 1.17	98.2 ± 1.08	3.0 ± 0.00	8.9 ± 0.15	4.4 ± 0.16	4.5 ± 0.17
12L/12E		94.7 ± 0.93	81.9 ± 3.87	98.8 ± 0.46	3.0 ± 0.00	8.7 ± 0.18	4.3 ± 0.10	4.5 ± 0.16
14L/10E		95.3 ± 0.87	83.2 ± 1.93	98.5 ± 0.64	3.0 ± 0.00	8.8 ± 0.24	4.4 ± 0.16	4.6 ± 0.19
16L/8E		93.3 ± 1.14	83.5 ± 2.86	98.8 ± 0.48	3.0 ± 0.00	8.8 ± 0.23	4.4 ± 0.16	4.4 ± 0.19
ANOVA	F	0.791	0.267	0.896		0.282	0.800	0.929
	P	> 0.40	> 0.40	> 0.40		> 0.40	> 0.40	> 0.40

Table 2. Weight, size and fecundity of *P. xylostella* reared under different light-dark cycles of artificial illumination. Total mean ± SE of n = 6 groups with 18 couples each.

Photoperiodic regime (light/dark)		Pupal weight (mg)		Forewing length (mm)		Total of eggs laid by female
		Females	Males	Females	Males	
8L/16E		61.4 ± 1.73	50.8 ± 0.96	6.0 ± 0.08	5.5 ± 0.03	78.2 ± 6.41
10L/14E		62.0 ± 0.93	51.6 ± 0.55	6.1 ± 0.05	5.5 ± 0.05	72.3 ± 2.82
12L/12E		61.1 ± 0.71	52.3 ± 0.85	6.0 ± 0.03	5.5 ± 0.04	73.9 ± 4.60
14L/10E		61.8 ± 1.05	51.4 ± 0.84	6.1 ± 0.05	5.5 ± 0.04	79.6 ± 4.88
16L/8E		60.5 ± 1.15	50.3 ± 1.78	6.0 ± 0.09	5.4 ± 0.06	70.2 ± 3.84
ANOVA	F	0.248	0.870	1.842	2.203	0.684
	P	> 0.40	> 0.40	> 0.15	> 0.09	> 0.40

the local habitat may also be raised. However, if individuals do not respond to changes in day-length, the direct causal relationship between photoperiod and population dynamics does not exist because changes in population size are due to physiological and behavioural responses of individuals (Kingsolver 1989). The influxes of immigrants in August-September (Campos *et al*. 2006) and a supposedly migratory efflux in November-December are not caused by photoperiod among neotropical populations of DBM.

The absence of photoperiod response among individuals of Neotropical populations of DBM does not necessarily exclude responses among populations of temperate regions. Intraspecific geographic variation in photoperiodic responses can occur due to genetic divergences among populations that are well adapted to regional conditions (Ando 1983). Penetration of Neartic species in tropical areas can also be followed by the genetic lost of diapause (Shapiro 1978). Therefore, populations of cosmopolitan insects such as *P. xylostella* may respond differently to environmental signals of seasonal change, especially along the latitudinal gradient. In Canada, Harcourt & Cass (1966) noted that fecundity of *P. xylostella* is gradually reduced between summer and autumn, correlating with day-length. The same correlation between day-length and fecundity was recorded by Babushkina (1990) in field populations of Russia. The observed correlations led those authors and Leather (1995) to propose a direct causal relation between photoperiod and fecundity.

Except for short periods of quiescence in very low temperatures, DBM does not enter developmental diapause and no stage of its life cycle resists rigorous winters (Smith & Sears 1982, Honda 1992, Talekar & Shelton 1993, Saito 1994). Therefore, if reproductive diapause occurs in populations of temperate regions, as Harcourt & Cass (1966) and Babushkina (1990) suggested, the phenomenon should be associated with seasonal emigrations to regions with more appropriate temperatures and food resources. However, the more probable photoperiodic response in this case would be a delay in oocyte maturation and oviposition, better than the strong reduction of the realised fecundity (eggs laid). Additionally, photoperiodic responses usually occur in a more abrupt manner, with a clear cut photoperiodic threshold (Saunders 1976, Beck 1980). Therefore, the fecundity of *P. xylostella* should not be gradually reduced along the successive generations subjected to decreasing photoperiods. The hypothesis that individuals and populations of DBM are directly affected by photoperiod in temperate regions seems implausible. It is more probable that the correlation between fecundity and photoperiod indicates an indirect relationship of cause and effect. For example, seasonal changes in host plant quality may establish a link between climatic changes and the insect reproductive performance. In temperate (Talekar & Shelton 1993, Chapman *et al*. 2002) and tropical (Campos *et al*. 2006) areas, seasonal migrations and consequent predictable oscillations of *P. xylostella* populations certainly occur independently of photoperiod taking part as announcement of changes in habitat quality. The DBM uses high altitude aerial currents to cross over long distances in a very short time (Chapman *et al* 2002, Coulson *et al*. 2002), but photoperiod does not seem to be an environmental stimulus to the insect takeoff at the beginning of the migratory flight.

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