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Seasonality in neotropical populations of *Plutella xylostella* (Lepidoptera): resource availability and migration

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Abstract The present study aimed to verify (1) whether seasonal increases in neotropical populations of *Plutella xylostella* are directly provoked by regular influxes of migrants, and (2) whether temporal variation in food availability is the ecological process behind such predictable events. Over 3 years, plants that *P. xylostella* prefers were cultivated and irrigated in order to provide a continuous and abundant supply of food. Nevertheless, seasonal oscillations in the population of the herbivore still occurred. The hypothesis of seasonal availability of host plants could not explain the population pattern. In April, when the insect was practically extinct from the area, an artificial infestation (immigration) with 10,000 pupae established a precocious population. Therefore, the start of the natural cycles of population growth, during July–August, seems to be due to external factors, rather than an improvement in local conditions for resident individuals. In the beginning of the natural cycles, the increase in the density of adults significantly preceded the increase in immatures. *Plutella xylostella* does not diapause, and therefore immigration is the proximate cause of the seasonal population increases. Hypotheses about local factors are suggested to explain the decreasing phase of the predictable population cycles.

Keywords Brassicaceae · Diamondback moth · Dispersal · Herbivore · Insect · Population dynamics · Seasonal

Introduction

Population seasonality refers to a regular ecological event that always occurs at the same time of the year. A priori, the phenomenon is not necessarily connected with conventional climatic seasons. Nevertheless, in tropical populations and communities of insects, seasonal cycles have been frequently attributed to variations in plant availability caused by alternating dry and rainy seasons (Wolda 1978a, b, 1988; Janzen 1987; Pinheiro et al. 2002; Hopkins and Memmott 2003). In fact, some herbivore insects have their life histories adjusted to the cycles of availability of new leaves (Jones 1987; Braby 1995). If food availability in the rainy season is the only explanation for seasonal increases in tropical populations of herbivores, then ephemeral plants, cultivated and irrigated throughout the whole year, would be under continuous and intense attack.

The diamondback moth *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) is distributed in all parts of the world where plants of the family Brassicaceae occur (Talekar and Shelton 1993), and *Brassica* is the preferred genus (Araiza et al. 1990; Idris and Grafius 1996). The insect does not survive rigorous winters (Honda 1992), although it can develop from about 10–35°C (Hardy 1938). *Plutella xylostella* possesses high genetic flexibility. It was the first insect to develop resistance to DDT (Ankersmit 1954) and, more recently, to *Bacillus thuringiensis* (McGaughey 1994). It has acquired near-immediate resistance to all categories of insecticides employed at large scales (Shelton et al. 1993). Individuals also have enough phenotypic plasticity to modulate traits of their life histories according to environmental conditions during larval development (Campos et al. 2004). Such an opportunistic and flexible life history of *P. xylostella* makes it possible to consider that, in the absence of other ecological and evolutionary pressures, the insect should occur throughout the whole year in sites where pleasant temperatures and lush brassicas are always available. However, this study shows that,

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despite a continuous and abundant supply of food, neotropical populations of *P. xylostella* can still exhibit seasonal oscillations. Other processes than plant availability should be involved in the generation of such a population pattern. Because the population dynamics are predictable, one should also consider that an adaptive component may be involved. The evolutionary component of the population dynamics depends on the extent to which the insect behaviour has been shaped by the seasonality of the habitat. Adaptive behaviours associated with reproduction and/or migration may be more important processes for generating population cycles than local mortality.

Empirical studies of insect populations have historically emphasised local and proximate causes of mortality (Cornell et al. 1998), although reproductive behaviour and birth rates have also been considered (Price et al. 1990). Migration may also evolve as a mechanism that allows individuals to avoid predictable collapses in births or survival (Southwood 1962). In fact, habitat deterioration, both in temperate and tropical climates, can be overcome by migration (Janzen 1987; Jones 1987; Wolda 1988; Braby 1995; Nechols et al. 1999). *Plutella xylostella* possesses high migratory ability, even over long distances (Shirai 1995; Coulson et al. 2002). Therefore, it is reasonable to suppose that migration is the most important proximate cause of seasonality in neotropical populations of *P. xylostella*, even when the ecological and evolutionary mechanisms are ignored. The present study aimed to verify (1) whether seasonal increases in neotropical populations of *P. xylostella* are directly provoked by regular influxes of migrants, and (2) whether temporal variation in food availability is the ecological process behind such predictable events.

Methods

The local system

Brassicas are ephemeral plants cultivated yearlong in the tropics. In southeast Brazil, they are always available at a 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 (20°45'S, 42°52'W and altitude 648 m). The local climate is relatively stable and it can be characterised by two main seasons: hot and wet (monthly averages of about 21°C and 175 mm) from October to March versus cool and dry (monthly averages of about 17°C and 32 mm) from April to September. During the years of the study, monthly minimum and maximum average temperatures stayed between 13 and 27°C.

For 3 years, a continuous population sampling of *P. xylostella* was carried out in the crops of cabbage. The crops were also used in an experiment of population

manipulation. The crops contained about 1,000 plants cultivated in 12 parallel rows, each 45 m long. The plants lasted 10–11 weeks, from the time the seedlings were transplanted until harvest, and a new crop was established before the previous crop was harvested. The ages of the crops were overlapped because *P. xylostella* performs better on younger plants (Campos et al. 2003). Therefore, two or three crops of different ages, 20–30 m apart from each other, were available for sampling. During the sampling period there were also adjoining crops of other Brassicaceae (broccoli, cauliflower, Chinese cabbage, collard or mustard), although outside the local system there were no other cultivated brassicas within a radius of at least 15 km. No insecticide or herbicide was used on the brassicas, and invader plants were mechanically removed. The soil, rich in organic matter, did not receive chemical fertiliser, and plants were irrigated whenever needed.

Population sampling and description of the temporal pattern of variation

Larvae from second to fourth instar and pupae of *P. xylostella* 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 from each row, with a total of 48 plants sampled weekly in each crop. The average number of immatures (larvae + pupae) per plant per crop (crops of different ages were present) was used in the calculation of general weekly and biweekly average densities.

Adult individuals were also sampled. Four traps with sexual pheromones (delta model) were distributed in each sampling crop. The males caught by the adhesive cartons were quantified weekly. Sexual pheromone traps have generally been indicated to estimate populations of *P. xylostella* (Baker et al. 1982; Shirai and Nakamura 1995; Reddy and Urs 1997). The average number of adults (males) per trap per crop was used in the calculation of general weekly and biweekly average densities.

Immigration as proximate cause of the seasonal population growth

Immigration could be accepted as a cause of the population growth if the density of adults increased significantly before the increase of immatures. On the other hand, if immatures increased before adults, variation in mortality or fecundity of local residents would better explain the population growth. Therefore, the weekly densities of immatures (averages of the 3 years) were analysed, through linear regressions as a function of the density of adults sampled: (a) in the same week, (b) in the previous week, (c) 2 weeks before, (d) 3 weeks before, (e) 4 weeks before, and (f) 5 weeks before. A smaller variance would indicate the time lag between

cause and consequence. The density of adults was similarly analysed as a function of the density of immatures.

The seasonal population growth could also be understood as dependent on immigration (external factors) if an artificial infestation (immigration) were to result in the establishment of a precocious population. The natural population cycles, hence, would be independent of an improvement in the local ecological conditions for resident individuals. An artificial infestation of the area was carried out in April of the third year, when the local population was nearly extinct. About 10,000 pupae were obtained from a greenhouse rearing.

They were put in trays suspended at the mean height of the plants, placed in the centre of two crops aged 4 and 8 weeks. Adults emerged 4–5 days after placement in the field.

Results

The general biweekly average densities of immatures and adults were plotted, and the annual variation exhibited a similar trend for 3 years (Fig. 1). Therefore, each year was considered as a replication for fitting descriptive

Fig. 1 Seasonal variation of the population densities of immature and adult *P. xylostella*. Host plants were always available during 3 consecutive years. In April of the third year, the local population was precociously increased by an artificial infestation with pupae

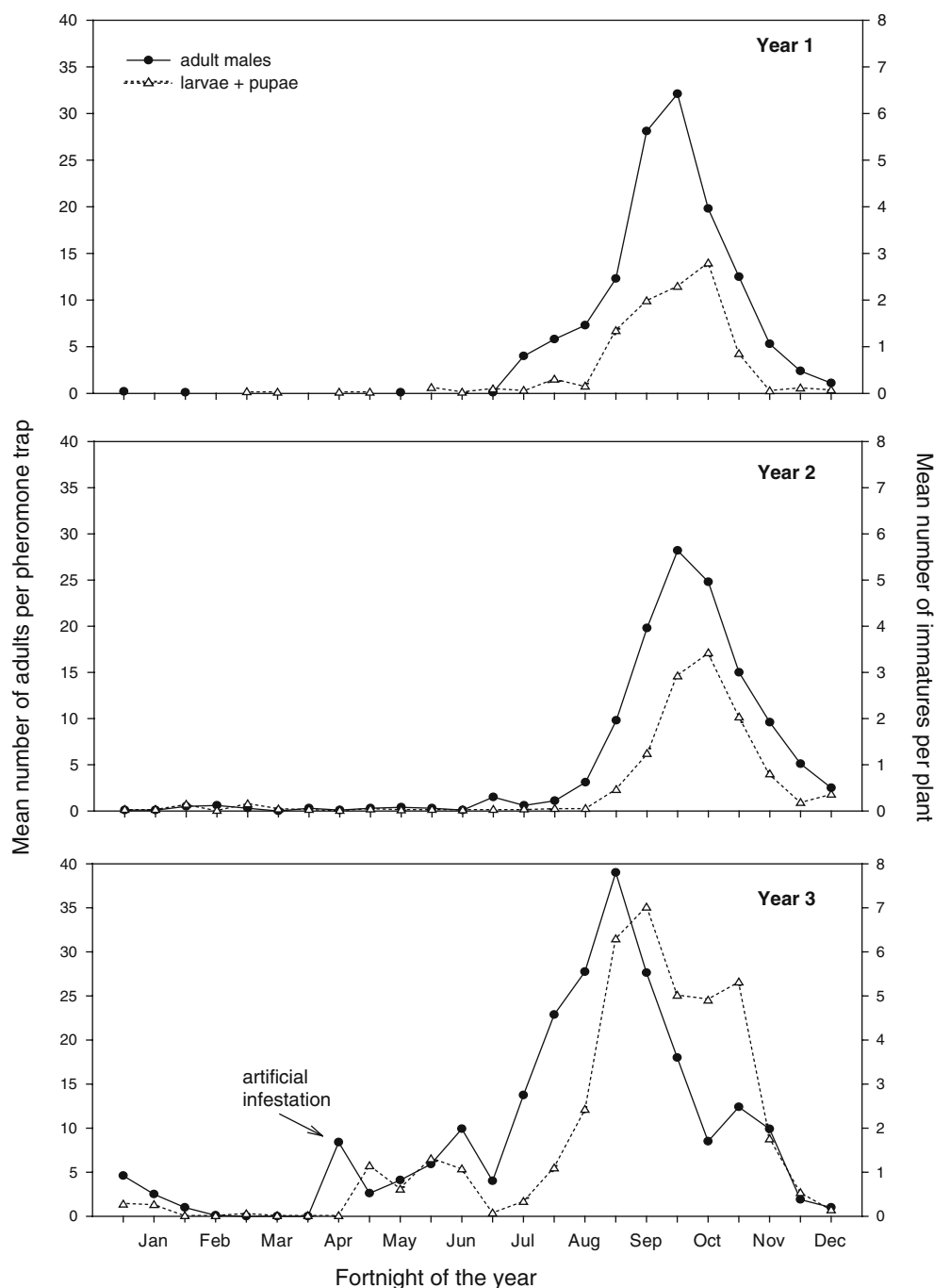
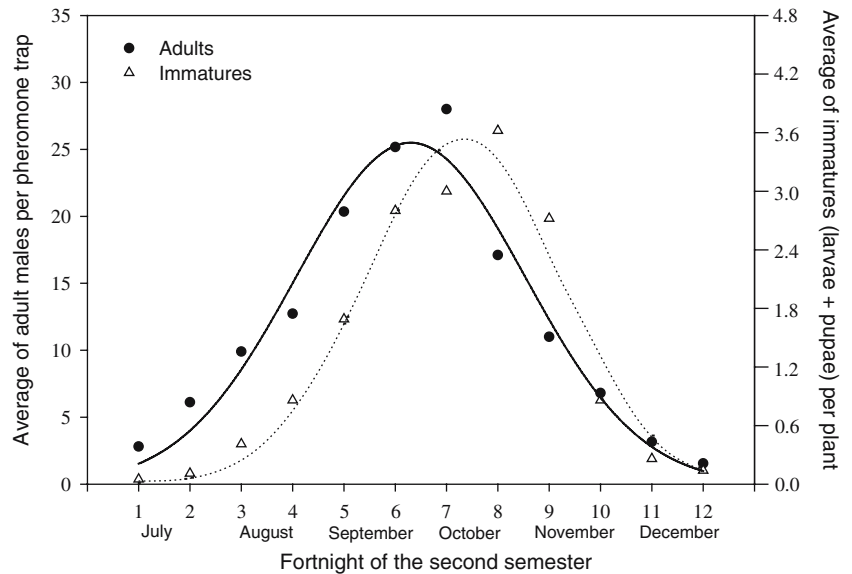


Fig. 2 Seasonal pattern of growth and decrease in neotropical population of *P. xylostella*. The population stayed extinct during the first semester, and the estimated peak of adults occurred 2 weeks before the population peak of immatures (6.3 and 7.3 fortnights, respectively). Dots in the graph represent the average density for 3 years (see Fig. 1). Curves fitted are: $y = 25.5 \exp(-0.5[(x-6.3)/2.2]^2)$ for adults ($R^2 = 0.96$, $F = 117.3$, $P < 0.0001$), and $y = 3.5 \exp(-0.5[(x-7.3)/1.9]^2)$ for immatures ($R^2 = 0.96$, $F = 113.1$, $P < 0.0001$)



models of the temporal patterns of growth and decline in the densities of immatures and adults (Fig. 2).

Despite the continuous and abundant supply of food, *P. xylostella* was rare during the whole first semester, except in the third year, and occurred regularly from July to December (Fig. 1). The population increase in April of the third year was due to the artificial infestation. Most of the 10,000 pupae released in the field may have left the site as adults because the next average number of recaptures was only 8.4 males per trap. Nevertheless, the number of remaining adults was enough to establish a precocious population until the beginning of the natural population cycle in the second semester (Fig. 1).

On average for 3 years, the natural population cycles had higher densities between late August and early November, but the estimated peak of adults preceded the peak of immatures. In the equation $y = a \exp(-0.5[(x-b)/c]^2)$, b is an estimate of the fortnight in which the maximum population density, a , occurred. Adults peaked in the sixth fortnight of the second semester, and immatures peaked 15 days later (parameter b estimated as 6.3 and 7.3, respectively) (Fig. 2).

The biweekly densities of immatures on the plants correlated significantly with the males caught by the traps (linear regression with $R^2 = 0.57$, $F = 76.9$ and $P < 0.0001$), but the relationship of cause and effect between variables was not clear over the whole year (Fig. 1). On the other hand, a simple graphical analysis of the rising phase of the cycles (Figs. 1, 2) suggests that the abundance of adults increased before that of immatures. The number of moths flying in the site at the beginning of each cycle was also disproportionately larger than the very small number of immatures sampled in the previous weeks. In fact, the weekly densities of immatures correlated best and most significantly with adults caught 2 or 3 weeks before (Fig. 3c, d). There was

no significant relationship of adults as a function of immatures sampled in previous weeks (Fig. 4b-f).

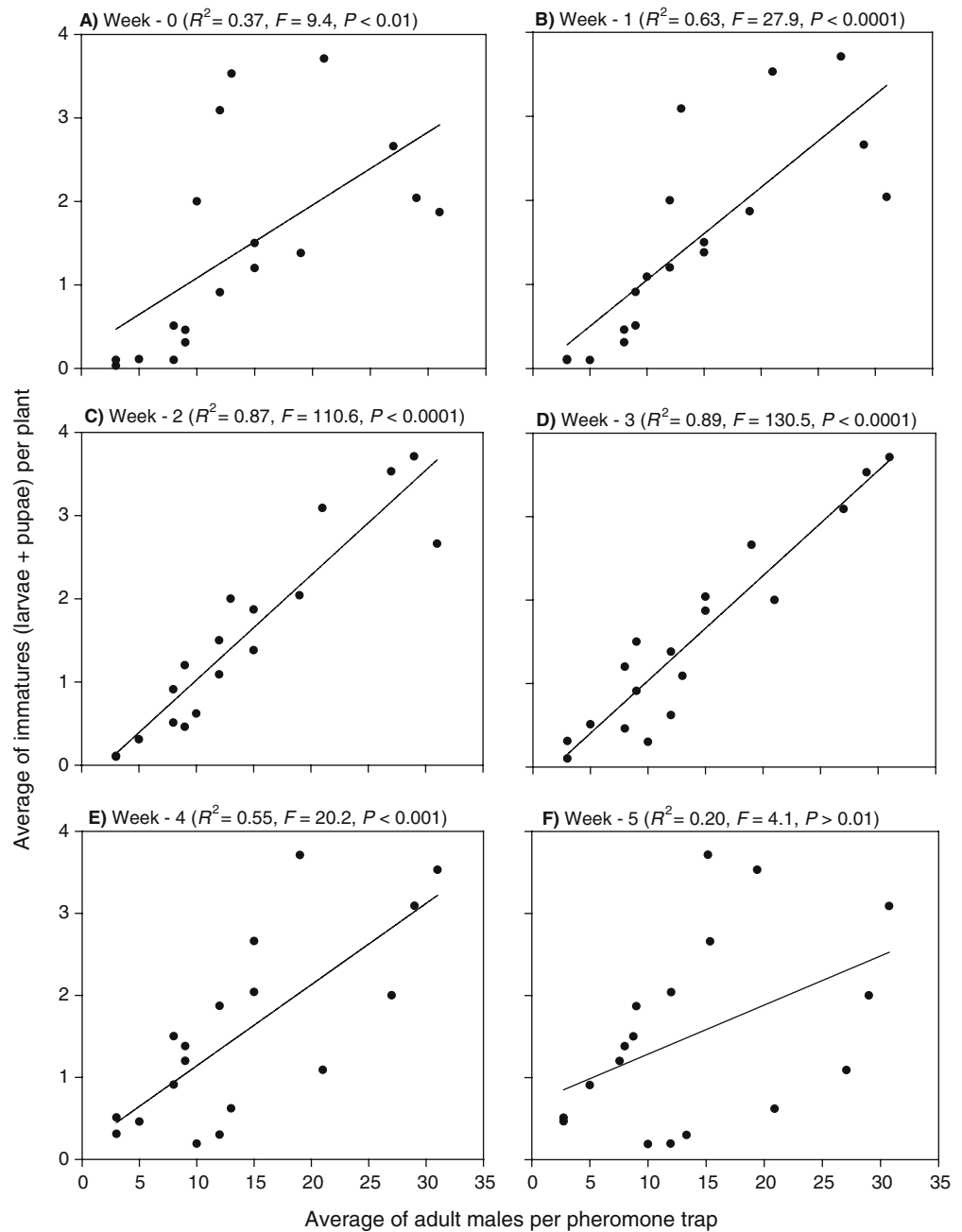
Discussion

In this study, the pattern of continuous resource availability that occurs at a regional scale in southeast Brazil was artificially set in a small area. Adaptive behaviours or mechanistic ecological responses of *P. xylostella* should occur as functions of this pattern of availability of host plants. In spite of the abundant and continuous supply of food, which was arranged locally, the herbivore exhibited a strong seasonal variation in abundance (Figs. 1, 2). The hypothesis of seasonal availability of resources could not explain the seasonality in neotropical populations of *P. xylostella*. Alternative hypotheses may be divided into two categories: those that explain the increasing phase of the annual population cycle and those related to the decreasing phase.

Seasonal influx of migrants, population growth, and the role of local and external factors

The generation time of *P. xylostella* is about 3 weeks at 25°C (Campos et al. 2003), and each seasonal peak (Figs. 1, 2) may consist of overlapped generations. The duration of the entire life cycle of *P. xylostella* is about 22 days at 25°C, and the phases of larva and pupa take no more than 9 and 5 days, respectively (Campos et al. 2003), or about 2 weeks total. Therefore, the increase in the density of adults caused the increase in the density of immatures, and the time lag between cause and result was 2–3 weeks (Figs. 3, 4). Influxes of migrants were the proximate cause of the predictable population growth because (1) the local density of adults suddenly increased when immatures were almost extinct, and (2) the density

Fig. 3A–F Density of immatures of *P. xylostella* as a function of adults sampled: **A** in the same week; **B** in the previous week; **C** 2 weeks before; **D** 3 weeks before; **E** 4 weeks before; and **F** 5 weeks before. Dots in the graph correspond to the average density of 3 years, during the 18 initial weeks of the second semester (see Figs. 1, 2)

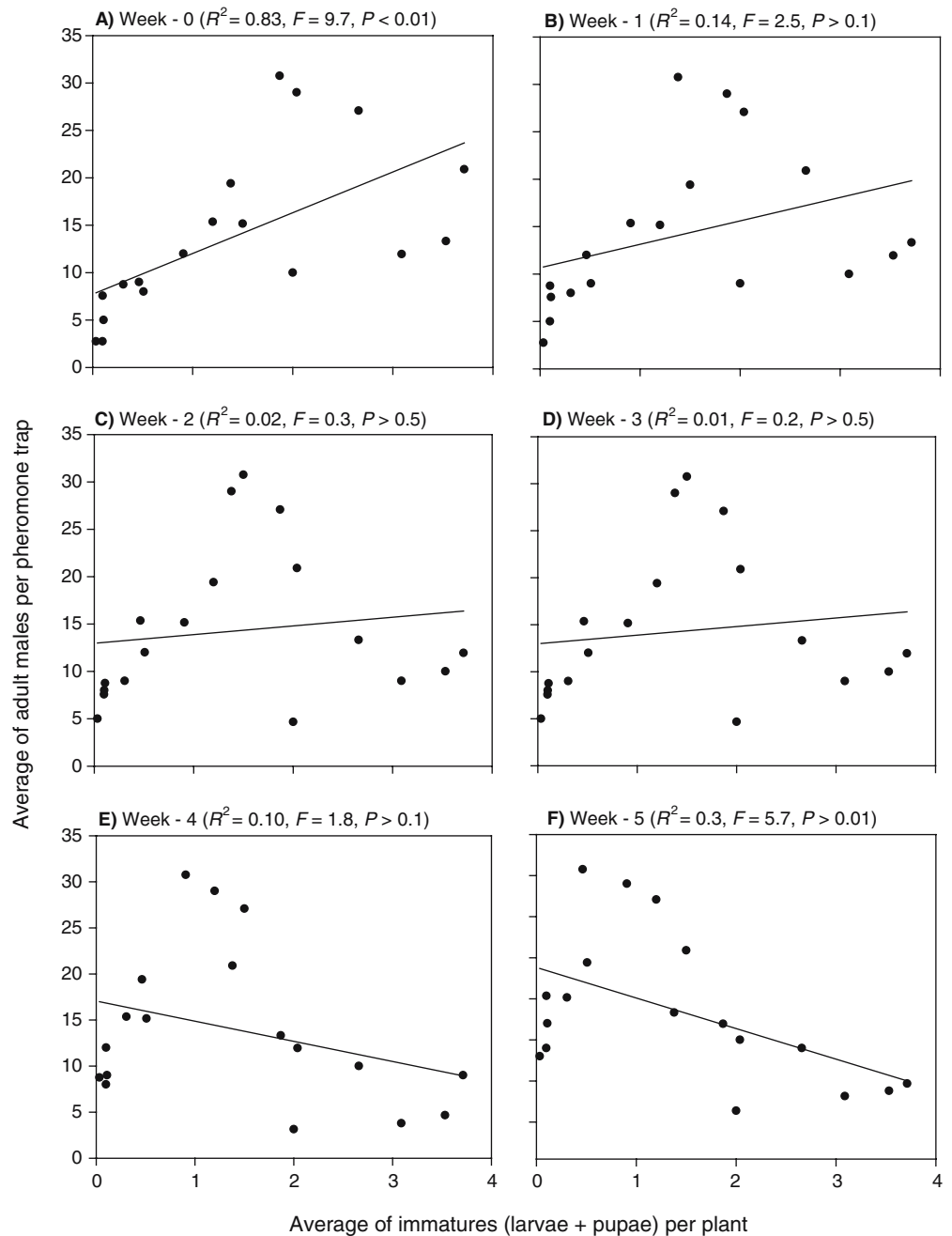


of larvae and pupae increased 2–3 weeks after the increase in adults (Figs. 2, 3, 4). Increases in birth and survival rates or interruption of emigration of local residents could not explain why adults occurred before immatures. Additionally, pupae or adults did not diapause locally from December to July. Except for short periods of lethargy at very low temperatures, there is no evidence for diapause in *P. xylostella* (Honda 1992; Talekar and Shelton 1993; Saito 1994). In temperate regions, annual occurrences and outbreaks of this insect have also resulted from migratory influxes (Chapman et al. 2002).

From the ecological point of view, migration triggers sudden population changes, both in source and

destination (Gilpin and Hanski 1991). However, migration may also be viewed as an adaptive strategy that allows individuals to increase their chances of survival and reproduction (Dingle 1978). Insects emigrate when their habitat deteriorates or gives signs that it is about to deteriorate. By searching for better conditions or resources, the chances for reproductive success increase (Southwood 1962). The concept assumes that migration is a non-accidental process whose causes may be mainly found in the source habitat. The influxes of *P. xylostella* were not accidental because they occurred predictably at the same time of the year. However, migratory influxes do not necessarily imply successful colonisation, because the population estab-

Fig. 4A–F Density of adult males of *P. xylostella* as a function of immatures sampled: **A** in the same week; **B** in the previous week; **C** 2 weeks before; **D** 3 weeks before; **E** 4 weeks before; and **F** 5 weeks before. *Dots* in the graph correspond to the average density of 3 years, during the 18 initial weeks of the second semester (see Figs. 1, 2)



lishment also depends on favourable conditions in the destination. Was the season of immigration and population growth determined by external factors, or did migrants land and get established in the area when local conditions improved?

The artificial infestation and the establishment of a precocious population (Fig. 1) supported the hypothesis that local conditions had been good since April. The migratory influxes occurred mainly during the cooler period of the year (June–August) (Fig. 2), so local low temperatures did not hinder an earlier colonisation. High rainfall mechanically decreases survival and reproduction of *P. xylostella*, and populations can be consequently limited (Harcourt 1963; Tabashnik and

Mau 1986). However, precipitation in southeast Brazil is lower from March to September, and it could not have delayed the population growth until September. It is unlikely that the time of immigration was determined by an improvement in local conditions.

The seasonal influxes of *P. xylostella* seem to be due to external factors affecting the source populations and/or aerial movements of the insect. The seasonal population growth cannot be satisfactorily explained without proper answers to the following questions: Where do migratory moths come from? Which cues stimulate the migratory takeoff in the source habitat? What is the role of seasonal air currents on insect movement and destination?

Plutella xylostella uses high altitude aerial currents to cross over long distances in a very short time (Chapman et al. 2002; Coulson et al. 2002). Long-distance flights via wind currents are a fundamental process in causing population outbreaks (Drake and Farrow 1988), and places of wind convergence are particularly suitable for receiving higher insect densities (Reynolds et al. 1997). Therefore, seasonal growth in tropical populations of *P. xylostella* may be largely dependent on annual patterns of atmospheric circulation. Environmental stimulus (e.g. Shirai 1995; Campos et al. 2004) in the source habitat may be also important to the insect takeoff at the beginning of the migratory flight.

The predictable phase of population decrease

The decreasing phase of the annual cycles always started in October and the population was nearly extinct at the end of December (Figs. 1, 2). Why did the population suddenly decrease, and why was it unable to persist until the next year? Whereas population growth seems to depend on external factors, local processes may explain subsequent population decline and extinction.

The decrease in the adult population was followed, 2 weeks later, by a corresponding reduction in the density of immatures (Figs. 2, 3); the interruption of the influx of adults certainly reduced the rate of population increase. Nevertheless, in the absence of local ecological pressures, the population would continue to grow due to the local births. Therefore, local factors negatively affected the survival and reproduction of individuals and caused the collapse of the population. The following explanatory mechanisms are suggested: (1) lower quality of the host plants, (2) higher temperatures, (3) more rainfall, and (4) greater numbers of attacks by parasitoids. Partial data from observation and experimentation (W.G. Campos, unpublished) have shown that a combination of suppressive factors seems to prompt the population collapse. Host brassicas that are cultivated in the hotter season have shown to reduce the fecundity of *P. xylostella* in relation to plants of the cooler season. In the laboratory, the intrinsic rate of population growth (r) decreases at temperatures higher than 25°C, which are recorded in the field from October to February. Higher levels of rainfall also occur during this period. Finally, the level of parasitoidism is about 50% during the peak of the host population, but it reaches more than 95% in December, when *P. xylostella* practically disappears from the region. To avoid this series of unfavourable factors, the moths might also be adapted to abandon the habitat as soon as they emerge from the pupae. To stay in the habitat would be counter-adaptive.

The spatio-temporal scale of the population pattern

The seasonal population fluctuation of *P. xylostella* replicated locally for 3 years; however, more confident

generalisations could be made if several small local populations showed synchronised oscillations at a regional scale. The population pattern that was locally identified probably represents an isolated sample of a larger scale event. Actually, a similar population trend has been reported for another place in Brazil (Guilloux et al. 2003). The causal processes of the population decrease and extinction should be examined at a regional scale. If this hypothesis is correct, the scale of population equilibrium (no extinction and no outbreaks) of the cosmopolitan *P. xylostella* is continental or global. Localised outbreaks would be isolated statistical points of dynamics occurring at a much larger spatio-temporal scale.

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