# CROP PROTECTION

# Performance of an Oligophagous Insect in Relation to the Age of the Host Plant

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## Performance de um Inseto Oligófago em Relação à Idade da Planta Hospedeira

RESUMO - A performance de insetos folívoros monófagos e oligófagos deveria ser afetada negativamente pelo envelhecimento das suas plantas hospedeiras. *Plutella xylostella* L. (Lepidoptera: Yponomeutidae), uma especialista em Cruciferae, foi criada em laboratório com folhas destacadas de repolho (*Brassica oleraceae* var. *capitata)*. Foram utilizadas a quarta folha expandida de plantas de diferentes idades mais as folhas dos três estratos da planta madura. O envelhecimento da planta aumentou a mortalidade pre-imaginal e reduziu a taxa de desenvolvimento das larvas, o peso das pupas e a fecundidade dos adultos. A taxa reprodutiva líquida (*Ro*) e a taxa intrínseca de crescimento populacional (*r*) diminuíram com o envelhecimento da planta. Nenhuma das categorias de folhas da planta madura mostrou-se qualitativamente superior às folhas de plantas mais jovens. Se em condições de campo existir uma correlação positiva entre preferencia de oviposição e performance da prole, espera-se uma tendência temporal decrescente na intensidade de ataque de larvas ao longo do desenvolvimento da planta.

PALAVRAS-CHAVE: Desenvolvimento larval, sucesso reprodutivo, fenologia da planta, *Plutella xylostella,* Lepidoptera

ABSTRACT - The performance of monophagous and oligophagous herbivore insects should be negatively influenced by the ageing of their host plants. *Plutella xylostella* L. (Lepidoptera: Yponomeutidae), a specialist in Cruciferae, was reared in the laboratory on detached cabbage leaves (*Brassica oleraceae* var. *capitata)*. We used fourth expanded leaves from differently aged plants, and leaves from three strata of the mature plant. Plant ageing increased pre-imaginal mortality and reduced larval developing rate, pupae weight, and fecundity. The insect net reproductive rate (*Ro*) and intrinsic rate of population growth (*r*) decreased as plant aged. No leaf category of mature plants was qualitatively superior to leaves from younger plants. If there exist a positive correlation between oviposition preference and offspring performance, in field conditions, a decreasing temporal trend in the intensity of attack along the host plant development can be expected.

KEY WORDS: Larval development, reproductive sucess, plant phenology, *Plutella xylostella,* Lepidoptera

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Herbivore insects may be more common in some developmental phases of their host plants (Spiegel & Price 1996, Waltz & Whitham 1997). The processes of physiological ageing of individualised leaves (Raupp & Denno 1983) and plants (Wilde *et al.* 1969, van Emden & Bashford 1971) are important for herbivore life history. Therefore, insect attack should be influenced by the ontogenetic changes in the host plant quality.

Plant quality may be understood as a wide and relative concept that encompasses all chemical and physical plant features, which interact and affect Darwinian fitness of one specific herbivore. Plant quality directly affects food consumption, survival and development of larvae. The effects also extend to several treats of the adults, such as weight, size, reproductive ability, longevity and morphology (Leather 1990, Albert & Bauce 1994, Dodds *et al.* 1996, Tammaru 1998). Even though the effects of plant quality may usually be sub-lethal, the several treats of the insect life history can be synthesised by the net reproductive rate (*Ro*) or by the intrinsic rate of increase (*r*). They can be used as unified measures of plant quality, herbivore performance, or even approximations of the insect Darwinian fitness.

Rhoades & Cates (1976) and Feeny (1976) suggested that insects with a narrow range of host plants should prefer newer and more nutritive tissues, even though they usually have a higher concentration of toxic compounds. If this hypothesis is correct and also applies to the physiological ageing of the plant as a whole, and not only to individualised leaves, then specialised insects should perform worse on mature than on young plants of the same species. In this paper we tested if host plant ageing, even though it produces new leaves after mature, negatively affects the performance of the oligophagous *Plutella xylostella* L. (Lepidoptera: Yponomeutidae).

## Material and Methods

The host plants (*Brassica oleraceae* var. *capitata* cv. Matsukase) were grown in field conditions and no chemicals were used. Thirty-day old seedlings were transplanted to a 0.5 x 1.0 m spacing plots. The upper foliage started forming the cabbage head seven weeks later. These new leaves of the mature plant were harder than leaves of younger plants, and the expanded leaves surrounding the head became fibrous. The oldest and senescent leaves of the lower stratum also became yellowish.

The larvae of *P. xylostella* used in the experiment were obtained from a greenhouse rearing. The laboratory experiment was carried out with constant temperature (25 ± 0.5ºC), photoperiod (14D/10L) and relative air humidity (65 ± 5%). Cohorts of 100-120 eggs were deposited on detached fresh leaves. Larvae were reared in the fourth expanded leaves (middle stratum) from differently aged cabbage: 3-4 weeks, 5-6 weeks, 7-8 weeks, and 9-10 weeks after transplantation. The insect was also reared on leaves from the upper and the lower strata of mature plants (9-10 weeks). Nine egg cohorts were reared in each one of the six different leaf categories.

Soon after reaching the second instar, the larvae were transferred to fresh leaves; the leaves were renewed every day, until all larvae pupated. After sex determination, the pupae were weighted. Eighteen couples of pupae from each initial egg cohort were isolated in transparent plastic boxes (10 x 10 x 5 cm). A fragment of median cabbage leaf was inserted in the box as soon as adults emerged. Solution of honey was not offered to adults, to avoid interference on fecundity and longevity determined by plant nutrients acquired in the larval stage. The leaf fragments were changed everyday, and the eggs quantified.

The eighteen couples from each cohort were used to determine the pupae weight and adult fecundity. However, we used the entire cohort to estimate survival and duration of different developmental stages, including adult longevity. We used the percentage of eggs of the initial cohort that did not develop to adult and the fecundity of the surviving adults to calculate the net reproductive rate (*Ro*). Sexual ratio in *P. xylostella* is 1:1, therefore *Ro* = (fecundity – pre-imaginal mortality)/2. The simple formula $r = lnRo/Gt$ was used to calculate the intrinsic rate of increase ($r$). $Gt$ is the generation time, obtained by the sum of the pre-imaginal period and half of the adult lifetime.

The results were analysed by Generalised Linear Modelling - GLIM, using plant age and strata as explanatory variables and insect phenotypic traits (larval stage duration, larval survival, female pupae weight, male pupae weight, fecundity, life cycle duration, *Ro*, and *r*) as response variables.

## Results and Discussion

Plant development affected all phenotypic traits of *P. xylostella*, and the response intensity depended on plant strata (Table 1, Figs. 1 and 2). Although the mature and stratified plant continued to produce new leaves, there was a general trend of increase in larval stage duration (Fig. 1B) and in life cycle duration (Fig. 1F). Conversely, there was a decreasing trend in larval survival (Fig. 1A), pupae weight (Figs. 1C and 1D), and fecundity (Fig. 1E).

Net reproductive rate (*Ro*), which is the balance between fecundity and pre-imaginal mortality, showed a trend to decrease with plant development (Fig. 2A). Leaves from middle and upper strata allowed a higher reproductive success than senescent leaves from the lower stratum. However, no category of leaf from mature plants was qualitatively superior to leaves from younger plants (Fig. 2A).

Intrinsic rate of population growth (*r*), which is the balance between fecundity, pre-imaginal mortality and generation time, also showed a trend to decrease with plant development (Fig. 2B). Leaves from middle stratum allowed a higher potential of population growth than leaves from other strata. However, no leaf from mature plant produced a higher *r* than leaves from younger plants (Fig. 2B).

Coleman *et al*. (1996) found no evidence for phenotypic induced responses in cabbage. Therefore, we assumed that the nature of nutritional and defensive changes occurring along plant ageing is ontogenetic or constitutive.

Some authors suggest that herbivore insects can compensate for lowered nutrient availability by increasing their food intake rate or by prolonging their feeding periods (Slansky & Feeny 1977, Augner 1995). Larval stage duration was prolonged with plant ageing (Fig.1B). However, if *P. xylostella* compensated for lower nutrient availability in mature cabbage, then this physiological ability do not seem adequate, because accumulated reserves did not assure a constant weight of pupae (Figs. 1C and 1D) neither the subsequent adult fecundity (Fig. 1E).

Larval mortality was not estimated for each instar, but it may have specially increased in the fragile and endophytic first instar. First-instar larvae should have more difficulty to penetrate the mesophyle, chew and digest the tough and fibrous leaves of mature plants. Atwal (1955) noticed that first-instar larvae of *P. xylostella* failed to mine and died in mature and senescent cabbage leaves. New leaves of mature cabbage may also be 10 times tougher than leaves from young plants (Broadway & Missurelli 1990). Therefore, prolongation of larval stage with plant ageing may be due more to mechanical obstacles to the small larvae than to an evolutionary and physiological strategy to compensate for lower nutrient availability. Plant physical traits may be as important as their chemicals to determine insect feeding performance.

Pupae weight is usually positively correlated with fecundity (Gilbert 1984) and both covariated with plant maturation (Figs. 1C and 1E). However, the pupae had the same weight when fed on lower and upper leaves from mature plants, but they presented higher fecundity when fed on lower leaves. Pupa weight seems an unsuitable parameter to estimate feeding performance or reproductive success. Insect

Table 1. Analysis of covariance (ANCOVA) for life history traits of *P. xylostella* in relation to host plant age and leaf strata.

| Larval stage duration | Source | d.f. | SSA | SE | F | Probability |
|---|---|---|---|---|---|---|
| | Regression | 3 | 180.9 | 60.3 | 163.3 | < 0.0001 |
| | Age | 1 | 101.5 | 101.5 | 274.8 | < 0.0001 |
| | Strata | 2 | 79.4 | 39.7 | 107.5 | < 0.0001 |
| | Error | 49 | 18.1 | 0.3693 | | |
| | Total | 52 | 199.1 | | | |
| Larvae survival | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 2218.7 | 739.6 | 21.9 | < 0.0001 |
| | Age | 1 | 1220 | 1220 | 36.2 | < 0.0001 |
| | Strata | 2 | 998.7 | 499.4 | 14.8 | < 0.0001 |
| | Error | 49 | 1652.1 | 33.72 | | |
| | Total | 52 | 3870.5 | | | |
| Female pupae weight | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 2590 | 863.3 | 248.8 | < 0.0001 |
| | Age | 1 | 1348 | 1348 | 388.5 | < 0.0001 |
| | Strata | 2 | 1242 | 621 | 178.9 | < 0.0001 |
| | Error | 49 | 169.8 | 3.47 | | |
| | Total | 52 | 2759.3 | | | |
| Male pupae weight | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 493.5 | 164.5 | 60.1 | < 0.0001 |
| | Age | 1 | 201.7 | 201.7 | 73.7 | < 0.0001 |
| | Strata | 2 | 291.8 | 145.9 | 53.3 | < 0.0001 |
| | Error | 49 | 134.12 | 2.737 | | |
| | Total | 52 | 627.63 | | | |
| Fecundity | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 27495 | 9165 | 36.5 | < 0.0001 |
| | Age | 1 | 11886 | 11886 | 47.3 | < 0.0001 |
| | Strata | 2 | 15609 | 7804.5 | 31.1 | < 0.0001 |
| | Error | 49 | 12312 | 251.3 | | |
| | Total | 52 | 39808 | | | |
| Life cycle duration | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 480.3 | 160.1 | 285.1 | < 0.0001 |
| | Age | 1 | 234.8 | 234.8 | 418.2 | < 0.0001 |
| | Strata | 2 | 245.5 | 122.8 | 218.7 | < 0.0001 |
| | Error | 49 | 27.5 | 0.5615 | | |
| | Total | 52 | 507.8 | | | |
| Net reproductive rate (Ro) | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 7652 | 2550.7 | 70.4 | < 0.0001 |
| | Age | 1 | 4098 | 4098 | 113.1 | < 0.0001 |
| | Strata | 2 | 3554 | 1777 | 49.0 | < 0.0001 |
| | Error | 49 | 1775.2 | 36.23 | | |
| | Total | 52 | 9427.7 | | | |
| Intrinsic rate of population growth | Source | d.f. | SSA | SE | F | Probability |
| | Regression | 3 | 0.05467 | 0.018223 | 327.8 | < 0.0001 |
| | Age | 1 | 0.03487 | 0.03487 | 627.2 | < 0.0001 |
| | Strata | 2 | 0.01980 | 0.0099 | 178.1 | < 0.0001 |
| | Error | 49 | 0.002726 | 0.00005565 | | |
| | Total | 52 | 0.057393 | | | |

weight or size should be used to estimate fecundity only when the whole population is exposed to the same conditions (Leather 1988, Honek 1993).

During plant ageing, the reproductive success of *P. xylostella* decreased (Fig. 2A) due to lower fecundity (Fig. 1E) and higher larval mortality (Fig. 1A), caused by reduced leaf quality. However, the time spent in larval development may also be important to the insect Darwinian fitness. For example, prolonged pre-imaginal stage may indirectly increase mortality, because individuals are exposed to weather and

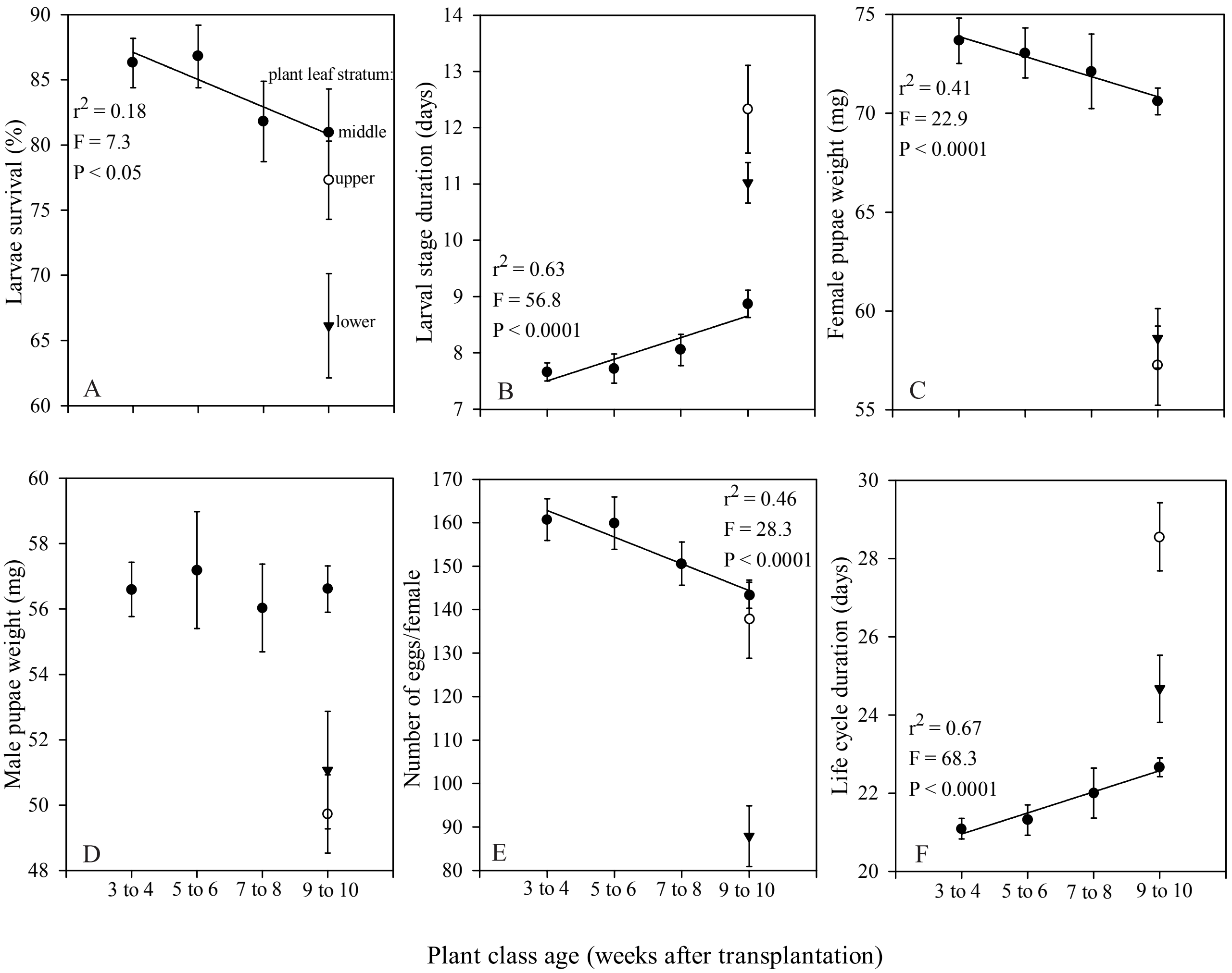

Figure 1. Phenotype of *P. xylostella* in relation to host plant age. Cabbage ageing affected all life history traits, but response intensity depended on leaf stratum in mature plant (see Table 1). Points and bars indicate average ± confidence interval at 5% (n = 9).

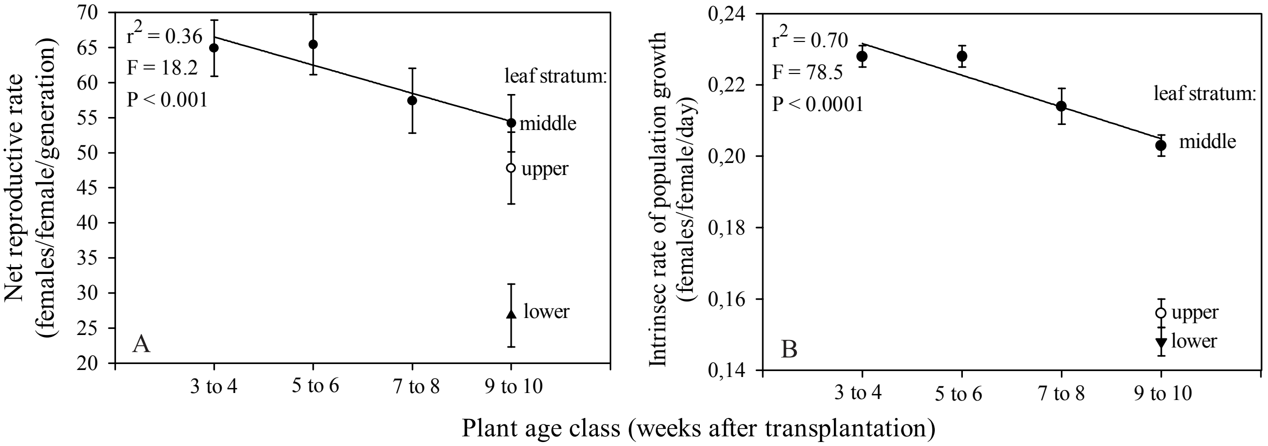

Figure 2. Net reproductive rate (*Ro*) (A) and intrinsic rate of population growth (*r*) (B) of *P. xylostella* in relation to host plant age. Response intensity depended on leaf stratum in mature cabbage (see Table 1). Points and bars indicate average ± confidence interval at 5% (n = 9)

natural enemies for additional time (but see Leather & Walsh 1993). If larval stage prolongation (Fig. 1B) indirectly increases mortality, the rate *r* is a more realistic measure of the Darwinian fitness than rate *Ro*. In this case, the negative effect of the plant maturation on herbivore insect was even more significant (Table 1, Fig. 2B).

New tissues are usually protected against herbivores attack by toxins, but the concentration of toxic compounds is reduced during their maturation (McKey 1974). However, the reduction of toxic defences may be compensated by: (i) increasing digestibility reducers, (ii) increasing components with low or no nutritional value, (iii) decreasing water content, and (iv) decreasing nutrient availability, mainly nitrogen and minerals (Rhoades & Cates 1976, Mattson 1980, Clancy *et al.* 1988). Glucosinolates, toxic compounds to non specialist insects, decrease in concentration during *Brassica* tissue maturation (Hopkins *et al*. 1998), as well as soluble nitrogen (van Emden & Bashford 1969). Conversely, protease inhibitors, substances known by their ability to reduce the digestive activity and the development of *P. xylostella* and of other caterpillars, increase their activity with plant maturation, except in senescent leaves (Broadway & Colvin 1992, Broadway 1995). As a Brassica specialist, *P. xylostella* was not negatively affected by higher glucosinolate concentrations in young plants. On the other hand, ontogenetic changes in protease inhibitors, nutrients available, water and fibbers, associated to the increase in plant quantitative defences (*sensu* Feeny 1976), may have negatively affected the insect in old cabbage. Leaf maturation reduced insect performance and the senescence accentuated the trend (Figs. 1 and 2).

Maturation and senescence are distinct processes of plant ageing (Kearsley & Whitham 1989) and the senescent yellowish leaves from the lower stratum were qualitatively inferior than mature and actively photosynthesising leaves from the middle stratum. Senescence involves an intense nutrient transport to stocking sites or to new tissues in the plant (Hill 1980). Senescent tissues have, for instance, the lowest nitrogen concentration in the plant (Mattson 1980). Nitrogen content decrease in old tissues correlates with a decrease in performance of several insects (Leather 1990), including some that feed on *Brassicae* (van Emden & Bashford 1969, 1971). Poor nutritional quality of senescent leaves may explain the lowest insect performance in the plant.

During plant development, toxic defences may also be relocated from senescent to young and more important tissues (McKey 1974, Iwasa & Kubo 1996). Therefore, young leaves from mature plants should have a higher toxin concentration than old and senescent leaves. In addition, it is possible that insects find difficult to extract nutrients from young leaves of mature plants. Protease inhibitors attain their peak in these latter leaves, which are tougher and more fibrous than leaves from young plants (Broadway & Missurelli 1990). Even though herbivores that regularly feed on Cruciferae tolerate glucosinolates, this ability may have physiological costs because the responses to the toxins are usually curvilinear and concentration-dependent (Siemens & Mitchell-Olds 1996). Therefore, nutritional benefit from young leaves of old plants should not compensate metabolic costs of succeeding the summation of their qualitative and quantitative defences.

Although mature plants continue to produce new leaves, the quality of the whole individual decreases in relation to their younger stages. Further studies are necessary, using other ephemeral plant species, in order to reinforce the hypothesis that plant development negatively affects insect performance and fitness. It is also possible that insects poorly efficient in wining glucosinolates barriers refuse young plants as well new leaves from mature plants, but they may be able to use preferencialy leaves from the middle and lower strata, less defended by toxins. Polyphagous caterpillars of *Trichoplusia ni* Hübner seem to choose these kind of cabbage leaves (Broadway & Colvin 1992). Therefore, it is also necessary to verify if the decreasing performance of the oligophagous *P. xyllostella* along plant ontogenesis extends to polyphagous species or if they present an inverse trend. If so, we could expect opposing oviposition patterns, and non-parallel temporal trends in attack intensity along short-lived plant development. Monophagous and oligophagous herbivore insects would be found more frequently in young plants, and polyphagous would be more common in mature ones.

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