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Larval food plants can regulate the cabbage moth, *Mamestra brassicae* population

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Abstract

The effect of different food plants on various parameters of development and hibernation in the cabbage moth, *Mamestra brassicae* L. (Lepidoptera Noctuidae), a serious polyphagous pest, was tested. *Brassica oleracea*, *Brassica napus*, *Beta vulgaris*, *Allium cepa* and *Pisum sativum*, differed in their influence on larval development rate, on body mass, mass loss and mortality and on the intensity of pupal diapause. When the larvae were fed on *A. cepa*, *B. vulgaris* and particularly on *P. sativum*, larval development was longer, mortality was higher and pupae had a smaller body mass with diapause not deeply engaged, leading to death during hibernation. Therefore, *P. sativum* may be used to exhaust the resources of *M. brassicae* until local outbreaks perish. This study provides strategic information for establishing integrated pest management for cropping systems and for predicting the population dynamics of the cabbage moth.

Key words: *Mamestra brassicae*, food plants, development rate, body mass, pupal diapause, metabolic rate.

Introduction

The cabbage moth, *Mamestra brassicae* L. (Lepidoptera Noctuidae) is a serious pest throughout the world. In the past, it was only a sporadic pest in the Baltic countries, but it has gradually become more widespread and damaging, probably due to climate warming (Bale *et al.*, 2002). In northern areas, it usually has one full generation, although, in more favourable years, a second generation may occur (Finch and Thompson, 1982). The cabbage moth is a polyphagous pest on over 70 host plant species in 22 families (Rojas *et al.*, 2000). In addition to feeding on wild plants and one of the main host cabbage, *Brassica oleracea* (L.), the larvae may also cause substantial economic losses to a wide range of other vegetable crops (Turnock and Carl, 1995).

Protection of vegetables from the cabbage moth is primarily based on the use of chemical insecticides. Chemical control has several unwanted side effects, such as pesticide residues in consumer products and a decrease of biodiversity in the cropping system. Therefore, more environmentally-friendly methods should be developed for the control of this pest. For this purpose, it is essential to clarify which factors influence its population dynamics.

For polyphagous insects, the availability of different host plants plays an important role in triggering population outbreaks (Singh and Parihar, 1988) and studying the effects of food quality on the insect's biology is important for understanding host plant suitability in infesting pest species (Xue *et al.*, 2010). Plant quality is a broad term that encompasses any physical, chemical or biological traits of plants (Zehnder, 2006). For normal growth and development of larvae the proportions of nutritional elements in the food plant are of primary importance (Awmack and Leather, 2002; Syed and Abro, 2003). Variation in host plant quality influences insect herbivore survival and development time (Zehnder, 2006). Studies by Liu *et al.* (2007; 2009; 2010) on the cotton bollworm, *Helicoverpa armigera* (Hubner), established a direct correlation between larval food quality and the duration of development, pupal mass as well as the number of progeny. Furthermore, food quality may interact with photoperiodic and temperature responses to influence diapause induction, as demonstrated for pupal diapause in *Hyphantria cunea* (Drury) (Morris, 1967), *H. armigera* (Liu *et al.*, 2009; 2010) and larval diapause in *Choristoneura rosaceana* (Harris) (Hunter and McNeil, 1997).

According to Harvey (1962), diapause is a state of developmental arrest in insects, characterized by minima in both endergonic biosynthetic activities such as protein synthesis and exergonic energy trapping activities such as metabolic rate and gas exchange patterns. Diapause is induced by various environmental cues and represents a complex dynamic process characterized by several specific physiological and behavioural features (Tauber *et al.*, 1986; Danks, 1987; Denlinger, 1991). The best known cues associated with diapause are photoperiod and temperature (Tauber *et al.*, 1986); other factors, such as food quality of larvae (Hunter and McNeil, 1997; Liu *et al.*, 2009; 2010), humidity (Lenga *et al.*, 1993), pathogens (Metspalu, 1976) and predation (Kroon *et al.*, 2008) have been found to influence the intensity of diapause of various insect and mite species. Liu *et al.* (2009) showed that high quality larval food plants provide a better preparation for diapause, which appears to be a prerequisite for successful overwintering and increased survival of *H. armigera*.

Various parameters can be indicative of the intensity of diapause: greatly decreased metabolic rate (Withers, 1992), reduced respiration, frequency of gas exchange cycles (Kestler, 1991), transpiration (Jõgar *et al.*, 2004), heartbeats and circulation (Tartes *et al.*, 2002) as well as cold hardiness (Denlinger, 1991).

A facultative pupal diapause in *M. brassicae* is induced in northern regions by the short photoperiod (critical photoperiodic threshold LD13:11) accompanying the low temperature of autumn. Pupae survive the winter in the soil at a depth to 10 cm. Adult development can be initiated only after exposure for several weeks at circa 5 °C (Goto and Hukushima, 1995). Some information is available on induction and development of *M. brassicae* diapause, showing the major role of day length and temperature (Goto and Hukushima, 1995; Hodek, 1996). In spite of its economic importance, little information exists on the nutritional value of different food plants for *M. brassicae*. This information is essential for developing a theoretical foundation for managing overwintering populations and forecasting their population dynamics. In order to examine the interactions between the food plant and the cabbage moth, five annual crop plants commonly cultivated in Northern vegetable gardens were chosen, the effect of which on the population dynamics of *M. brassica* is unclear.

The aim of this work was: 1) to study the influence of food plants on certain biological parameters of *M. brassicae*: the duration of the larval development, larval and pupal mortality, the pupal body mass and, sex ratio; 2) to investigate the possible effects of larval food plants on the intensity of pupal diapause. The following indicators were assessed: pupal mass loss, standard metabolic rate (SMR), discontinuous gas exchange (DGE) and supercooling points (SCP).

Materials and methods

Experimental design

Egg clutches of *M. brassicae* were collected from white cabbage on an experimental field of the Estonian University of Life Sciences near Tartu in 2009. To avoid the systematic error by the time factor affecting the food plant quality, the clutches were all collected within one week. Only egg clutches containing at least 100 eggs were included in the experiment. Larvae hatched from each egg clutch were divided into 5 groups, each fed on one of the following food plants: white cabbage (*Brassica oleracea* L. var. *capitata* L., variety ‘Krautman’), pea (*Pisum sativum* L., variety ‘Aamisepp’), red beet (*Beta vulgaris* L., variety ‘Bordoo’), onion (*Allium cepa* L., variety ‘Peipsiäärne’) and swede (*Brassica napus* L. var. *napobrassica* (L.) Rchb, variety ‘Kõpu’). Each food plant treatment consisted of at least 100 larvae (five treatments, each with five replications, each of them with at least 20 larvae, i.e. in all no fewer than 500 larvae). The food plants were selected according to their importance as cash crops as well as their known associations with *M. brassicae*. All food plants were grown on the same experimental field under uniform agronomic conditions. Newly hatched larvae were reared in Petri dishes (15 cm diameter and 2 cm deep), at 20 larvae (representing one replicate) per dish, until the 3rd instar. The larvae were then placed in groups of five in 1 l breeding vessels covered with net and layered with sheets of filter paper to absorb excessive moisture. Larvae were reared on cut leaves of the food plant in environmental test chambers “Sanyo”. The leaves were replaced daily. The duration of the experiment with the larvae is indicated in figure 1. Larval mortality was recorded at 24 h intervals. Before pupation, a 10 cm deep layer of peat was placed on the bottom of the vessels to allow the larvae to dig in and pupate. To obtain winter diapausing pupae, larvae were

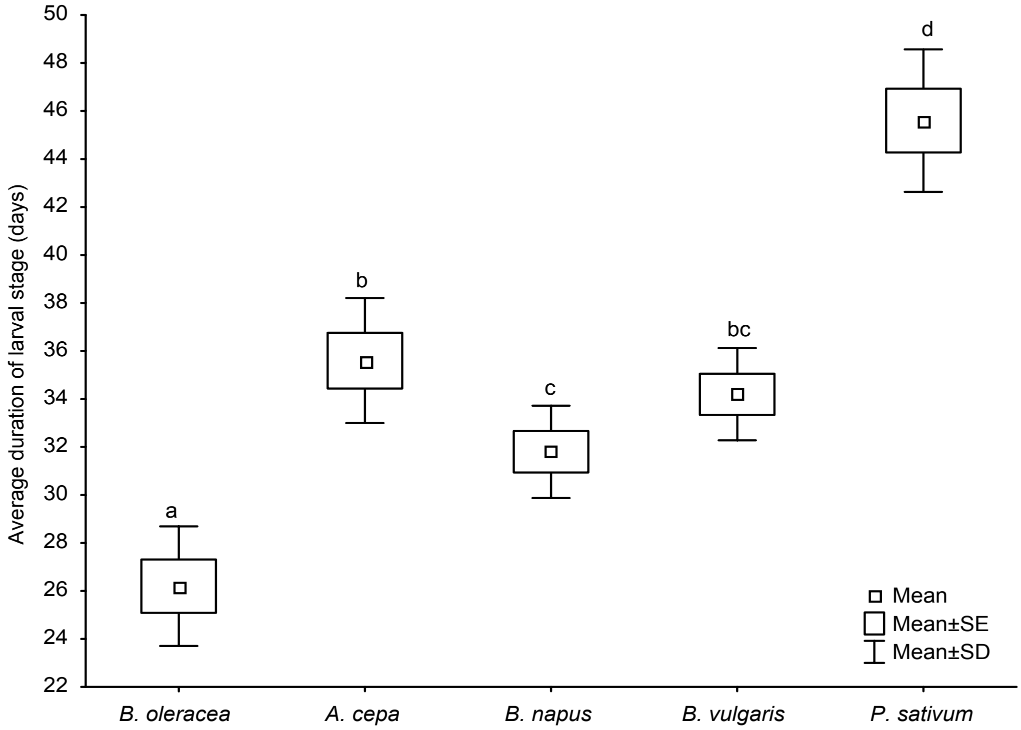

Figure 1. Average duration of larval stage of *M. brassicae* reared different food plants. Different letters indicate significant differences ($P < 0.05$, ANOVA, LSD-test).

reared at 21 °C with a short photoperiod 12:12 DL and 75% RH. To ensure that the pupae reached a stable diapause state, they were then kept in the peat for one month, before collection by hand-sorting. Under these conditions, 100% of the obtained pupae were in diapause. Each pupa was classified as alive or dead according to the presence or absence, respectively, of abdominal movement in response to touch. Pupal gender was determined according to external sexual characters on the ventral side of the last abdominal segments (Sannino and Espinosa, 1999). Diapausing pupae were stored in the dark, at 21 ± 2 °C and 75 ± 10% RH in a state of 'permanent' diapause in standard plastic Eppendorf tubes (volume 1.5 ml, the cover of the tube was pierced with a needle). According to Jõgar (2006) such insect chambers have an extremely low water loss rate at room temperature and ambient humidity. At room temperature (20-22 °C) non-chilled pupae can stay in the state of "permanent" diapause for several months.

Weighing

One month old pupae taken out from the peat were weighed at the same time to avoid mistakes in the comparisons of means (initial weight). After that, the pupae were weighed weekly for three months. Each pupa was weighed on an analytical balance to 0.1 mg (Explorer Balances, Ohaus Corporation, Pine Brook, New Jersey). To minimize manipulation stress, the handling was carried out with the Eppendorf tube. Mass loss of each pupa was calculated as the difference between its initial body weight at one month and its final body weight.

Respirometry

The physiological state of an insect is usually estimated by standard metabolic rate (SMR) (Keister and Buck, 1964), commonly by flow-through CO_2 respirometry (Lighton, 1996; Chown and Nicolson, 2004). SMR is defined as a value measured at a particular temperature, when the insect is quiet, inactive, is not digesting a meal, nor exposed to any stress (Withers, 1992). In long cycle insects, when only about one burst is released during a day, the SMR is difficult to measure via the CO_2 flow-through analyser, so we measured it in diapausing *M. brassicae* pupae by oxygen consumption (Slama, 2010). O_2 consumption provides a good indicator of diapause depth (Tauber *et al.*, 1986). Respirometry was conducted on 3 month-old pupae in deep diapause (Metspalu, 1976; Jõgar, 2006). Metabolic rate (O_2 g^{-1} h^{-1}) was measured using an electrolytic volumetric manometric system characterised by a continuous (uninterrupted) O_2 compensating system (for design see Kuusik *et al.*, 1996; Tartes *et al.*, 1999; 2002; Lighton, 2008). Each test pupa was placed in the respiratory chamber and left undisturbed for 30 min. The respiration of the pupae was measured for at least 3 hours.

Calorimetry

The pattern of discontinuous gas exchange (DGE) cycles has often been used to characterize the physiological state of an insect (Kestler, 1991). We recorded the frequency of DGE in diapausing pupae by means of a custom made calorimetric system (Harak *et al.*, 1999) with six channels which enabled recording of the heat flow simultaneously in six individuals. Each measurement lasted 72 hours. The duration of DGE cyles was determined in ten pupae (five male and five female) from each treatment. Since the sexes produced identical results, the readings were combined for analysis. Calorimetry is the method for continuous recording of DGE for weeks in individuals without evoking stress by handling and adjusting the apparatus. A simple twin differential calorimeter was constructed of vessels made from copper foil (0.1 mm) connected with copper-constantan thermocouples, while a micro-nano-voltmeter and recorder were used (Kuusik *et al.*, 1994; Harak *et al.*, 1999; Jõgar *et al.*, 2005). The volume of both the insects and reference vessels was 0.5 ml and the sensitivity of the calorimeter was 50 μV m W^{-1} with a detection limit of 4 μW. The calorimeter was calibrated electrically by the Joule effect (Hemminger and Höhe, 1984). The calorimeter was sufficiently sensitive to record CO_2 releases by bursts and abrupt air intakes into the tracheae of the pupae.

Supercooling points

The supercooling point (SCP) of diapausing pupae was measured using a copper-constantan thermocouples-thermometer (RS-232, Data logger Thermometer; TES Electrical Electronic, Taipei, Taiwan). Low temperatures were attained by deep-freeze Haier HF-103 (−30 °C). The thoracic tergite of the pupa were fixed to the thermocouple, placed in a Styrofoam box and then transferred to a freezer chamber. The temperature of the insect box was lowered at a rate of 0.5 °C min^{-1}, starting at 20 °C and ending at −30 °C. The temperature at which freezing produced a release of latent heat was taken as the SCP of the individual. The number of pupae is presented in table 3.

Statistical analysis

Data were analysed using STATISTICA 9.1 (StatSoft, Inc/USA). Differences of means of replications in developmental time, larval and pupal mortality and SCP of the larvae reared on the different food plant were analyzed with one-way ANOVA. Replications' means of different food plant treatments were compared with Fisher's LSD *post-hoc* tests ($P \leq 0.05$). A two-way ANOVA was used to determine the effects of the food plant, gender and their interaction effects on pupal body mass and mass loss as well as on supercooling points of hibernating pupae. Computerised data acquisition from the respirometer and calorimeter and the analysis of these data were performed using the DAS 1401 A/D (analogue-digital) hardware and the Test-Point software (Keithley, Metrabyte, Cleveland, OH, USA) with a sampling rate of 10 HZ. Four bipolar channels allowed simultaneous recording of four events and standard metabolic rate (Mean ± SD) was calculated automatically using a statistical program (StatSoft ver. 8 Inc/USA). A one-way ANOVA and a Fisher's LSD-test were used to determine the differences between standard metabolic rate (SMR) and duration of DGE cycles in diapausing pupae of different food plant treatments.

Results

Larval parameters

Developmental time

The development of *M. brassicae* larvae was significantly affected by the food plant ($F_{4,20} = 42.9$, $P < 0.0001$, figure 1). The development time of larvae reared on *P. sativum* was significantly longer (mean larval duration 45.6 ± 2.6 days) than of those reared on *A. cepa* (35.6 ± 2.3 days), *B. vulgaris* (34.2 ± 1.7 days), *B. napus* (31.8 ± 1.72 days), and on *B. oleracea* (26.2 ± 2.2 days). The larval period on *B. oleracea* was significantly shorter than on all other host plants ($P < 0.05$, LSD-test). The development of larvae reared on *A. cepa*, *B. napus* and *B. vulgaris* significantly differed from those reared on *B. oleracea* and *P. sativum* but did not differ between *A. cepa* and *B. vulgaris* ($P = 0.37$, LSD-test) or between *B. napus* and *B. vulgaris* ($P = 0.13$, LSD-test).

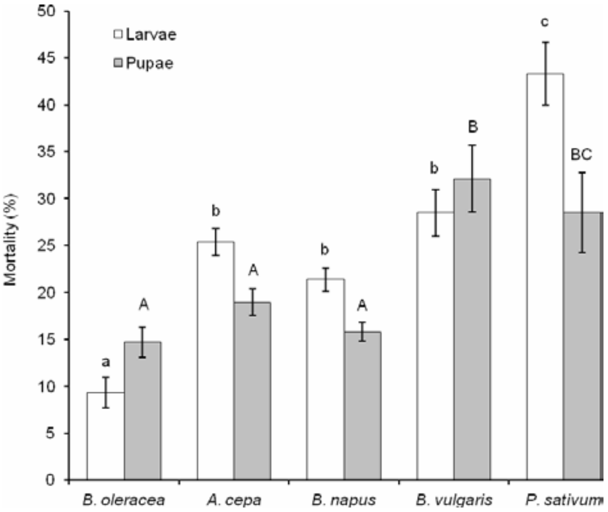

Figure 2. Larval and pupal mortality of *M. brassicae* reared different food plants. Different lowercase letters show significant differences between larvae and capital letters significant differences between pupae at $P < 0.05$, LSD-test.

Mortality

The mortality of *M. brassicae* larvae was affected by the food plant ($F_{4,20} = 32.1$, $P \leq 0.0001$, figure 2) and was significantly the lowest on *B. oleracea*, compared to all the other plant species tested (all values $P < 0.05$). *P. sativum* appeared to be the least suitable food plant for larval development as it induced a significantly higher mortality than all the other food plants (all values $P < 0.05$).

Pupal parameters

Sex ratio

The sex-ratio of the pupae from larvae fed on *B. oleracea* was female-biased (table 1), whereas pupae from larvae fed on *A. cepa*, *B. napus*, *P. sativum* and on *B. vulgaris* had a male-biased sex ratio.

Mortality

The mortality of *M. brassicae* pupae was also significantly affected by the food plant ($F_{4,20} = 8.4$, $P \leq 0.0001$, figure 2). The highest average pupal mortality occurred in insects fed on *B. vulgaris* and *P. sativum* with 32% and 28%, respectively, of the pupae dying during the experimental period. The pupal mortality on *A. cepa* reached 19% whereas only 15-16% of pupae died on *B. oleracea* and *B. napus.* Hence, the host plants can be categorized into two groups by pupal mortality: 1) *B. oleracea-B. napus-A. cepa*; 2) *P. sativum-B. vulgaris*, with no significant differences between plants within the groups (LSD-test, $P > 0.05$).

Mass and mass loss in diapausing pupae

The pupal mass (initial weight) (table 1) of *M. brassicae* was significantly affected by the food plant (Two-way ANOVA: $F_{4,60} = 3.2$, $P = 0.017$), and by the gender per food plant interaction (Two-way ANOVA: $F_{4,60} = 2.97$, $P = 0.026$) whereas gender alone had no significant effect (Two-way ANOVA: $F_{1,60} = 3.073$, $P = 0.08$). Pupal mass loss on overall was not significantly affected by the food plant or gender, but the interaction between gender and the food plant was significant (table 2).

In male pupae, food plant was a significant factor ($F_{4,30} = 9.37$, $P < 0.0001$). The highest pupal mass loss

Table 1. Pupal mass (Mean ± SE, mg) and sex ratio of *M. brassicae* larvae reared on five different food plants.

Food plants	Pupal mass (mg) ♀♀	Pupal mass (mg) ♂♂	Pupal sex ratio ♀ : ♂
Allium cepa	417.0 ± 13.9 ab	424.8 ± 11.58 a	1 : 1.23
Brassica oleracea	461.0 ± 10.85 b	415.9 ± 13.0 ab	1 : 0.52
Beta vulgaris	399.3 ± 34.2 ab	465.0 ± 9.95 ad	1 : 1.4
Pisum sativum	346.3 ± 47.0 a	367.0 ± 42.3 b	1 : 1.32
Brassica napus	403.9 ± 16.19 a	474.5 ± 18.4 d	1 : 1.31
F	2.84	3.77	
d.f.	4	4	
P	0.04	0.01	

Pupal mass data are shown as mean ± standard error.
Means within columns followed by different letters are significantly different at $P \leq 0.05$ (LSD-test).

Table 2. Pupal mass loss of *M. brassicae*, effect of sex and treatment (two-way ANOVA).

Effect	*d.f.*	*MS*	*F*	*P*
Food plant	4	121.10	2.30	0.069
Gender	1	33.62	0.63	0.427
Interaction	4	264.70	5.02	0.001
Error	60	52.68		

Table 3. Means ± SE of supercooling point (SCP) °C of *M. brassicae* pupae from larvae reared on different food plants.

Food plants	SCP (°C) ♀♀ (Mean ± SE)	n	SCP (°C) ♂♂ (Mean ± SE)	n
Brassica oleracea	−21.4 ± 0.32	25	−21.3 ± 0.35	13
Allium cepa	−20.6 ± 0.25	21	−20.8 ± 0.23	25
Brassica napus	−21.1 ± 0.44	16	−21.6 ± 0.31	21
Beta vulgaris	−20.7 ± 0.38	10	−21.1 ±0.42	14
Pisum sativum	−21.1 ± 0.41	10	−20.7 ±0.42	15

(26.1% of the initial weight) occurred on *B. napus.* It was significantly higher (all-values $P < 0.05$) than on all the other plants (6.4% on *P. sativum*, 4.8% on *B. oleracea,* 4.5% on *A. cepa*, and 4.4% on *B. vulgaris*).

The food plant had no significant effect on mass loss of female pupae ($F_{4,30} = 1.362$, $P = 0.27$); the highest mass loss appeared on *A. cepa* (12.2 %), followed by *P. sativum* (7.5 %), *B. vulgaris* (4.8 %), *B. oleracea* (4.6%) and *B. napus* (4.4%).

Diapause parameters

Respiration

The standard metabolic rate (SMR) of diapausing pupae, measured as the rate of O_2 consumption, was significantly affected by the food plant ($F_{4,37} = 8.50$, $P < 0.0001$). The SMR, was the lowest on *B. oleracea* (mean 0.038 ± 0.006 ml O_2 g^{-1} h^{-1}; n = 12) and the highest on *P. sativum* (mean 0.067 ± 0.01 ml O_2 g^{-1} h^{-1}; n = 7) with a significant difference between the two (LSD-test, $P < 0.05$). The SMR of pupae from larvae fed on *B. oleracea* significantly differed from those fed on *B. vulgaris* (mean 0.048 ± 0.01 ml O_2 g^{-1} h^{-1}; n = 8) and *A. cepa* (mean 0.054 ± 0.01 ml O_2 g^{-1} h^{-1}; n = 8) but did not differ from *B. napus* (mean 0.043 ± 0.0035 ml O_2 g^{-1} h^{-1}; n=8). Gender had no significant effect on the rate of O_2 consumption.

Calorimetry

The time lapse between DGE bursts of *M. brassicae* pupae was significantly affected by the food plant of the larvae ($F_{4,45} = 17.58$, $P < 0.0001$). The time lapse between bursts lasted significantly longer ($P < 0.0001$, LSD-test) in pupae from larvae reared on *B. oleracea* (mean 18.8 ± 2.2 h, n = 10) and shorter ($P < 0.0001$, LSD- test) on *P. sativum* (mean 9 ± 2.3 h, n = 10) respectively, than in pupae from larvae reared on all other food plants. The periods between the DGE bursts of pupae from larvae fed on *B. napus* (mean 15.1 ± 2.9 h, n = 10), *B. vulgaris* (mean 15.2 ± 2.5 h, n = 10) and *A. cepa* (mean 14.2 ± 2.5 h, n = 10) were not significantly ($P > 0.05$, LSD-test) different from each other, but were significantly different from those of pupae from larvae reared on *B. oleracea* ($P < 0.03$, LSD-test) and *P. sativum* ($P < 0{,}0001$, LSD-test).

Supercooling points

The SCP (table 3) was not significantly affected by the food plant ($F_{4,161} = 1.55$, $P = 0.19$), the gender ($F_{1,161} = 0.33$, $P = 0.56$) or gender per food plant interaction ($F_{4,161} = 0.40$, $P = 0.8$).

Discussion

Knowledge of the effects of food on phytophages is essential for understanding the population dynamics of insect pests and how variation in plant quality can influence both current and future generations. In the case of *M. brassicae* only a few studies have examined the effect of food plants on the developmental stages (Sengonca *et al.*, 2000; Gols, 2008) or on the overall performance of this species (Poelman *et al.*, 2008; Harvey and Gols, 2011). The direct comparison of data can be problematic because different host plants, environmental conditions and populations were used in these studies.

Our study demonstrated that food plants have an impact on various life history traits of *M. brassicae.* The development time of larvae varied considerably with the food plant. This occurrence is supported by studies with *M. brassicae* by Sengonca *et al.* (2000), Gols (2008) and Harvey and Gols (2011). In the present study, it was found that larval development of *M. brassicae* was significantly slower on *P. sativum* than on *B. oleracea*, *B. napus*, *B. vulgaris* or *A. cepa*, (figure 1). Generally, slower development or digestion and lower fertility rate in herbivorous insects are caused by lower food quality (Chen *et al*., 2004). To compensate for deficiency of essential nutrients, insects may alter the efficiency with which they acquire or process the food by behavioural (increased consumption) or physiological (increased digestion, adsorption or conversion) response or a combination thereof (Slansky and Scriber, 1985; Simpson and Simpson, 1990). Moreover, in the field conditions, poor host plant quality may have an indirect effect on population density by increasing the exposure time of insects to their natural enemies as a result of prolonged developmental times (Sarfraz *et al.*, 2006). By contrast, faster development may result in a shorter life cycle, higher reproductivity, and more rapid population growth (Singh and Parihar, 1988; Liu *et al.*, 2004) whereas suitable food plants may give rise to the second full generation of *M. brassicae*, therefore increasing crop damage in northern regions.

There are many factors that can affect food suitability, including nutrient content. The production of chemicals, such as toxins and digestibility reducers, may interfere with the physiology of the insects and decrease survival (Schoonhoven *et al.*, 2005). Our results showed that host plant affected survival of *M. brassicae* larvae and pupae. Larval mortality was higher on *P. sativum* than on the other plants tested (figure 2). Due to the high mortality in younger larval stages (our unpublished data) we may predict that crop damage will remain at a lower level in *P. sativum* than in the other test plant species. Early instars are more susceptible to plant allelochemicals and other plant quality characteristics than later instars (Zalucki *et al*., 2002). High larval mortality reduced the number of pupae from larvae fed on *B. vulgaris*, *A. cepa* and *P. sativum* than *B. oleracea* or *B. napus*. These differences could be due to variation in nutritional and phago-stimulant factors such as carbon and nitrogen as well as defensive metabolites that directly affect potential and achieved herbivore development (Amwack and Leather, 2002).

Body mass is an important fitness indicator in insect population dynamics (Liu *et al.*, 2004) as females emerging from heavier pupae lay more eggs (Haukioja and Neuvonen, 1985) consequently affecting potential growth rate of the population. Pupal body mass depends directly on reserves stored at the larval stage, and pupae with small body mass appear when growing conditions, including food quality in the larval stage are unfavourable (Harvey and Gols, 2011). Pupal body mass of *M. brassicae* varied with food plant. The lowest mean pupal body mass was found for pupae from larvae fed on *P. sativum* compared with other larval food plants tested. This suggests that those insects cannot clear the hurdle of food quality and the nutritional features could be directly reflected in the abundance of progeny (Ruohomäki *et al.*, 2000). Pupal body mass in *M. brassicae* differed between sexes: female pupae were lighter on all food plants than on *B. oleracea*, suggesting they were nutritionally suboptimal. Poor food quality normally results in smaller females producing fewer eggs (Ohsaki and Yoshibumi, 1994). In many insect species, females are larger than males as higher body mass is biologically more important for females being a key precondition for the abundance of the progeny (Armbruster and Hutchinson, 2002). Moreover, nutritional requirements of female and male larvae are somewhat different. Male larvae tend to consume more lipids, possibly because of their greater energy need (to enable longer mating flights), whereas females need more protein for egg production. Male mating success is less dependent on size (Gotthard, 2008) and their reproductive fitness is usually most closely correlated with the number of mates inseminated. Such differences may explain why females are often more sensitive than males to variation in plant quality, resulting in differential survival and fecundity on hosts of different quality (Johns *et al.*, 2009).

The sex ratio of the pupae could also determine whether the population can adapt to a certain food plant. Merzeevskaja (1971) suggested that female-bias in noctuid moths implies high quality food and higher fecundity than other sex ratios. Similarly, Awmack and Leather (2002) showed that a slight prevalence of females in a population results from good quality larval food plants. Morrill *et al.* (2000) found that host quality affects the sex ratio of both phytophagous and entomophagous Hymenoptera with more females produced on plants of higher quality. Sex ratio indicating optimal food plant quality was exhibited only on *B. oleracea* in our experiment, as other food plants produced a male-biased population.

Liu *et al.* (2007) found that the higher quality of the larval host plants, the better the insect's preparedness for overwintering and the higher its chances for survival. In our case, the larval food plants affected potential overwintering success of *M. brassicae* pupae. Diapause intensity (Belozerov, 2009; Kostal, 2006) is characterised by SMR, which in deep diapausing lepidopteran pupae may decrease to very low levels –0.01-0.04 ml O_2 g^{-1} h^{-1} (Keister and Buck, 1964; Jõgar *et al.*, 2007). On the contrary, at the initiation of pupal diapauses of *Pieris brassicae* (L.), a considerably higher SMR (0.07-1.2 ml O_2 g^{-1} h^{-1}) may be observed (Jõgar *et al.*, 2011). We found a similar SMR in *M. brassicae* pupae which suggests that the diapause was not very intense, when the larvae were reared on less suitable food plants. On *P. sativum*, the significantly higher SMR in the pupae was a sign of an abnormally decreased intensity of diapause, which may lead to overconsumption of the resources during the winter. Our results indicate the most suitable food plant was *B. oleracea*, as shown by the lowest level of SMR in diapausing pupae. Such a low level of SMR points to a deep diapause which favours overwintering of the pupae (Fourche, 1977).

In addition to the SMR, patterns of discontinuous exchange (DGE) cycles are used to characterise the physiological state of an insect (Kestler, 1985; 1991). Many diapausing insects exchange respiratory gases discontinuously in a three-phase discontinuous gas exchange cycle with constriction (C) fluttering (F) and open (O) phase. During these, CO_2 is expelled in bursts. To avoid losing water through respiration, they open their tracheae periodically, a phenomenon known as discontinuous ventilation. Diapausing pupae of *P. brassicae* and *M. brassicae* expel CO_2 by only 1-2 bursts per day (Metspalu and Hiiesaar, 1984; Jõgar *et al.*, 2007). Deep diapause of *M. brassicae* pupae in our experiment on *B. oleracea* was characterized by DGEs with large outbursts of CO_2 (15-20 minutes), and time lapses between outbursts, that occurred only once or twice per 24 hours, were long. However, on *P. sativum*, the outbursts were shorter (4-5 minutes), they occurred more frequently (3-4 times per 24 h) and were coupled with relatively high metabolic rates. Resulting pupae were characterized by frequent gas emission cycles, higher respiration rate and body mass loss. This suggests that pupal diapause had not developed normally and such a physiological state is probably unfit for the overwintering period.

Although cold hardiness and diapause are both essential for the survival of most overwintering insects, the relationship between them is less clear (Denlinger, 1991). Supercooling points have been considered an index of cold hardiness in many, but not all, insects (Worland, 2005). Tsutsui *et al.* (1988) and Goto *et al.* (2001) found that diapause and non-diapause pupae of *M. brassicae* did not differ significantly in their SCPs, and SCPs can therefore not be used to assess the depth of diapause in *M. brassicae*. Probably the pupae of

M. brassicae have a supercooling ability as a specific physiological property independent of diapause. However, SCP can be affected by other factors. For example, it was shown that SCP of diapausing pupae of *H. armigera* is affected by the quality of the larval food plant. Low water content can elevate the concentration of cryo-protective substances and decrease supercooling point. The SCPs have been shown to be significantly related to the concentration of glycerol, which depends on food plant quality (Liu *et al*., 2007; 2009). In our experiment, such results were not confirmed as there was no significant difference between the SCP of the pupae from larvae reared on different food plants. Nevertheless, female pupae of *M. brassicae* exhibited somewhat lower SCPs on *B. oleracea*, while SCPs tended to be lower in male pupae from *B. napus* fed larvae, even though these differences were not significant.

Our results indicate that larval food plants have the potential to influence the population dynamics of the cabbage moth. Considering all determined factors, the five food plants tested can be arranged in decreasing order of host suitability, with *B. oleracea* being the most suitable food plant followed by *B. napus*, *A. cepa*, *B. vulgaris* and *P. sativum*. The mortality rate of the larvae fed on suboptimal food plants was high, the pupae were underweight and diapause was not as deep as expected. This confirms that different food plants can play an important role in triggering or suppressing outbreaks. On several occasions, we have observed a sudden decrease in the abundance of *M. brassicae* the year following mass reproductions which have not been explained by an increase in predator or pathogen populations. We conclude that one of the reasons for this phenomenon is the reduced viability of larvae growing on lower quality food plants. The results of this study could be of help for integrated crop management strategies that aim to minimise the damage and economic losses caused by *M. brassicae* by maximising the control of the pest in a more environmentally friendly way. This may be achieved by substituting *Brassica* crops and onion with pea (or other suboptimal food plants) that assist in exhausting the resources of the pest in the outbreak site. Greater consideration should be given to the availability and quality of the host plants of the pest when planning both crop layouts within a field and subsequent cropping/rotational practices from year to year to minimise the success and survival of cabbage moth. Future studies focussed on assessment of the chemical components of the food plants would help us better understand the mechanisms of host suitability.

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