Development, survival, body weight and oviposition rates of *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae) when reared on seven cabbage cultivars

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Plant cultivars that negatively influence fitness of target phytophagous insects can be an important component of integrated pest management when they substantially restrict population growth of the target pest. In this study, the effects of seven cabbage (*Brassica oleracea* var. *capitata* L.) cultivars on survival and development of immature stages, pupal weights, moth longevity and oviposition rates of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), were evaluated in the laboratory. Under the no choice test, overall survival of *P. xylostella* immature stages was highest on Karabo (67.26 %) and lowest on Megaton (44.92 %). The larval and pupal developmental period, and thus generation time took longer on Empowa (18.48 d), Karabo (14.64 d) and Beverly Hills (17.48 d), while development on Hollywood F1 (13.79 d) was the fastest. Male and female *P. xylostella* pupal weights were lower in larvae that fed on Megaton (4.13 and 4.65 mg), Menzania (4.53 and 4.91 mg), and Hollywood F1 (4.11 and 5.08 mg), whereas pupal weights from Karabo (6.0 and 6.82 mg) were the heaviest. Unfed female moths reared on Beverly Hills lived the longest (5.05 d), whereas those reared on Leano (3.54 d) and Megaton (3.89 d) lived for a shortest period. Under the choice-test, *P. xylostella* laid significantly more eggs on Empowa (48.8 %) and Hollywood F1 (45.6 %) and least on Menzania (11.8 %) and Leano (10.6 %). Although these results show differential impact of the cultivars on the fitness parameters studied, low survival rate of offspring on a crop is the primary target for using plant resistance as a pest management tactic. As survival rates of immature *P. xylostella* were lower on Megaton together with lower pupal weights and moth longevity, which together negatively impacts fecundity, and thus overall fitness of the pest was lower when developing on it. Megaton was more resistant to *P. xylostella*. The results of this study show that Megaton can play a major role in restricting population growth of this pest and generational number of eggs deposited on it.

Key words: diamondback moth, oviposition preference, offspring performance, plant resistance, integrated pest management

INTRODUCTION

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is an oligophagous pest of plants in the family Brassicaceae (Furlong *et al.* 2013). Since the larvae are forced to feed, and develop if possible, on plants on which they hatch (Löhr & Gathu 2002; Zalucki *et al.* 2002; Sarfraz *et al.* 2010), *P. xylostella* is a perfect target for investigating the impact of different *Brassica* species and/or cultivars on offspring fitness. Although Brassicaceae are well known for their glucosinolate-myrosinase defensive system which is largely efficient against generalist insect herbivores and microorganisms (Müller & Sieling 2006), specialist herbivores like *P. xylostella* use glucosinolates as oviposition and feeding stimulants, and their volatile breakdown products for host location (Renwick 2006). However, the composition of glucosinolates and/or quantity varies between species, cultivars and organs of the same plant (Harvey *et al.* 2007; Martin & Müller 2007; van Leur *et al*. 2008). High content of glucosinolates (>0.6 μmol/g of fresh weight) and associated myrosinase has been found to be detrimental to *P. xylostella* offspring fitness, which suggests that the counter-adaptation to glucosinolate hydrolysis by the pest may be dose-dependent (Siemens & Mitchell-Olds 1996; Li *et al.* 2000; Agerbirk *et al.* 2003). Other studies have shown that the presence of saponin, a feeding deterrent, is a major reason

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for the low survival of *P. xylostella* on *Barbarea vulgaris* (Shinoda *et al*. 2002; Agerbirk *et al*. 2003). The high attraction to gravid moths and low survival of larvae is observed on several species of wild host plants. As a consequence, several studies have investigated the potential of using wild host plants as trap crops (Charleston & Kfir 2000; Badenes-Perez *et al*. 2004; Lu *et al*. 2004), but *P. xylostella* can survive fairly well on some species (Kahuthia-Gathu *et al.* 2008). Where the bottom-up effect of a trap crop is sufficiently strong, the cost of controlling the target pest can be substantially reduced (Badenes-Perez *et al*. 2005). However, adoption of trap cropping is often hampered by: 1) unwillingness of growers to cultivate, in limited farmland space, plants they do not have a market for (Khan *et al*. 2007); 2) trap crop harbouring other pests of the main crop (Nofemela 2008); 3) variable success of the strategy (Shelton & Badenes-Perez 2006).

Although high or induced glucosinolate and myrosinase content can reduce herbivory and increase plant fitness (Agrawal 1999), breeding crops for high expression has so far led to reduced crop yield (Stowe & Marquis 2011). As growers prefer to cultivate crops with better agronomic traits, it is important to investigate among the currently available crops the ones possessing resistance against *P. xylostella* (Hamilton *et al.* 2005). Several studies have shown that *P. xylostella* fitness differs among *Brassica* crops (Golizadeh *et al*. 2009; Niu *et al*. 2013) and even among cultivars (Ebrahimi *et al.* 2008; Soufbaf *et al*. 2010; Fathi *et al.* 2011). The resistance mechanisms range from antibiosis resistance as reflected by lower survival and longer developmental rates of larvae (Golizadeh *et al.* 2009; Soufbaf *et al*. 2010; Fathi *et al.* 2011), antixenosis as reflected by variable oviposition preference (Ebrahimi *et al*. 2008) to plant tolerance (Sarfraz *et al*. 2007). Thus, these studies emphasize the need to further investigate the influence of intrinsic factors already present in the various *Brassica* crops that make them resistant to *P. xylostella.* Although reduced oviposition can be considered the first line of reducing infestations by a target pest (Hamilton *et al*. 2005), it is unlikely to work in mono-cropping as gravid moths will lay eggs regardless, and thus selection of cultivar with reduced survival of larvae becomes a critical factor to the cost of controlling the pest. This aspect is very important in South Africa where *P. xylostella* enters a population outbreak phase in spring (Nofemela 2010).

Over 132 600 t of cabbage (*Brassica oleracea* var. *capitata* L.) and other *Brassica* crops are estimated to have been harvested from 2314 ha during 2013 in South Africa (FAO STAT 2015), the bulk of which is consumed mainly by rural and peri-urban communities to supplement the largely maize-based diet. As of November 2014, 51 cabbage cultivars were registered for commercial production in South Africa, excluding red cabbage hybrids (DAFF 2014). But to our knowledge, no attempt has ever been made to investigate the fitness of *P. xylostella* on the different cabbage cultivars in South Africa. In an attempt to provide baseline data on fitness of *P. xylostella* on different cabbage cultivars, the study presented here investigated several life history parameters (developmental time, survival rates of immature stages, pupal weight, and longevity of the moths without food) of the offspring on seven cultivars. The ovipositional preference for either of the seven cultivars by the moths was also investigated. The results of this study are particularly useful in identifying cultivars on which *P. xylostella* performs badly with the view of recommending those cultivars for integrated pest management.

MATERIAL AND METHODS

Insect culture

The larvae and pupae of *P. xylostella* were originally collected from cabbage fields at Brits Agricultural Research Station (23 °25′33″S 27 °76′67″E, altitude 1102 m), North West Province, South Africa (Nofemela 2004), and at Baviaanspoort Correctional Services Centre (25°38′S 28°30′E, alt. 1164 m) in Pretoria, Gauteng Province, South Africa. The moth culture was reared on week-old *Brassica napus* L. seedlings following the method described in Nofemela (2004) in rearing cages (43 (L) × 30 (B) × 33 (H) cm) made of wood, glass and gauze. At monthly intervals, the culture was bolstered with field-collected individuals.

Host plants

Seven cabbage cultivars: Empowa, Beverly Hills, Karabo, Leano, Hollywood Fl, Megaton and Menzania, were used in this study. Each cultivar was raised from seeds in a greenhouse, and the seedlings were transplanted into 12.5 cm plastic pots filled with a mixture of compost, soil and vermiculite at 2:1:1 ratio at the four-leaf stage. The plants were then taken to the laboratory at six- to eight-leaf stage to conduct experiments. The plants were taken care of by irrigating, removing weeds and physical control of insect pests when necessary.

Experiments

All experiments were conducted in climate-controlled rooms maintained at 22 ± 1 °C (mean ± S.D.), 60 ± 5 % RH and 16L:8D photoperiod at Agricultural Research Council – Plant Protection Research Institute, Rietondale Research station, Pretoria, South Africa.

No-choice test

One plant from each cultivar was placed singly in a cage made from a 3.7-l transparent rectangular plastic container with large holes cut on opposite sides and replaced with gauze for ventilation. The lids of the containers were cut to fit the mouth of the 12.5 cm plastic pot with a cabbage plant, and the container was then inverted over the plant. Each of the seven cabbage cultivars had five replicates. Two pairs of newly emerged (<16 h old) male and female moths from the culture that were mating were placed in each cage with a plant. The female moths were allowed to oviposit on the plants for 48 h.

Thereafter, the moths were removed and the numbers of eggs laid on each plant were recorded with the aid of a magnifying glass. Hatching of the eggs was monitored every day at 09:00 and 15:00. As neonate larvae mine the leaves on hatching (Ullyett 1947), the number of first instar larvae was recorded as they leave the mines to feed on the leaf surface. Thus, the duration of the first instar stadium was determined as the difference between larval appearance on the leaf surface and the day of egg hatching. The durations of development in each of the subsequent larval instars was also monitored every day on each plant.

The survival rates of all larval instars were recorded. The number of pupae that were formed on each plant was recorded, as well as duration of the pupal stage. Survival of pupae, as determined by proportion of *P. xylostella* moths that emerged out of the total number of pupae, was also recorded. Pupal weights were measured using a Sartorius GMBH® scale (Sartorius GMBH, Göttingen, Germany). On emergence, the moths were separated based on sex and placed individually in Petri dishes. The days lived by each moth were recorded at 09:00 and 15:00 to determine longevity without food.

Choice test

The ovipositional preference of the moths was tested by placing all seven cabbage cultivars in a large (27 (L) × 27 (B) × 40 (H) cm) gauze-covered cage. This experiment also enables one to establish if female moths choose to oviposit mainly on cabbage cultivars that provide the highest fitness gain for the progeny as determined from the no-choice test. Four pairs of mating moths from the culture were introduced into the cage and the females were allowed to oviposit on the plants for 48 h. Thereafter, the plants were removed from the cage and the numbers of eggs laid on each plant were recorded with the aid of a magnifying glass. The cages were cleaned with soap and water after each trial, and thereafter left in the sun to dry. The position of each cultivar in the cage was randomized in each of the five replicates.

Data analysis

The data on duration of development, survival rates, generation time, pupal weights, longevity, and oviposition rates were subjected to a one-way analysis of variance (ANOVA). Prior to ANOVA, Shapiro-Wilk test was performed on the standardized residuals to test for deviations from normality. In cases where there was significant deviation from normality, the outliers were removed until the data set was normally distributed. Where significant differences were detected with ANOVA, the means were separated using Student's *t*-least significant difference (LSD) test. All data analyses were performed at 5 % level of significance (SAS 1999).

RESULTS

Duration of development

There was a significant difference ($F_{6,441} = 3.33$, $P = 0.0157$) in the durations of development of first instars (Table 1) as they fed on the different host plant cultivars. The duration of the first instar was shortest on Hollywood F1 and longest on Beverly Hills (Table 1). There were no significant differences in the durations of development among second instar ($F_{6,434} = 1.13$, $P = 0.377$) and third instar ($F_{6,415} = 1.33$, $P = 0.2839$) larvae on the different cabbage cultivars (Table 1). The duration of the fourth instar was significantly different ($F_{6,348} = 2.56$, $P = 0.0461$) among the cultivars. The shortest period was observed on Karabo, Megaton, Hollywood F1, Menzania and the longest devel-

Table 1. The duration of development (days) of *Plutella xylostella* life stages (mean ± S.D.) when reared on seven cabbage cultivars in the laboratory.

Cultivar	First instar	Second instar	Third instar	Fourth instar	Pupa	Generational time
Beverly Hills	4.27 ± 1.23 a	2.0 ± 0.77 a	1.91 ± 0.78 a	3.18 ± 1.19 ab	5.90 ± 1.27 a	17.48 ± 1.36 ab
Empowa	3.99 ± 1.00 ab	1.49 ± 0.42 a	1.47 ± 0.43 a	3.62 ± 1.22 a	5.80 ± 0.96 a	18.48 ± 1.38 a
Karabo	3.52 ± 0.38 ab	1.54 ± 0.33 a	1.47 ± 0.40 a	2.60 ± 0.84 b	5.43 ± 0.58 a	17.64 ± 0.81 ab
Megaton	3.24 ± 1.06 abc	1.53 ± 0.62 a	2.11 ± 0.40 a	2.87 ± 1.17 b	3.81 ± 0.81 bc	16.78 ± 0.66 bc
Menzania	3.22 ± 0.79 abc	1.52 ± 0.52 a	1.93 ± 0.71 a	2.72 ± 1.26 b	5.17 ± 1.44 a	16.81 ± 2.16 bc
Leano	3.06 ± 0.75 bc	1.84 ± 0.75 a	1.78 ± 0.78 a	3.27 ± 1.24 ab	3.33 ± 0.50 c	15.43 ± 0.72 c
Hollywood F1	2.17 ± 0.53 c	1.29 ± 0.31 a	1.47 ± 0.34 a	2.63 ± 0.63 b	4.25 ± 0.91 b	13.80 ± 1.03 d

Means with the same letters are not significantly different at $P = 0.05$ according to Student's *t*-LSD test.

opmental time was on Empowa (Table 1). The developmental rates of pupae were significantly different ($F_{6,248} = 12.46$, $P < 0.001$) among the seven cabbage cultivars (Table 1). The shortest development was observed on Leano and the longest on Beverly Hills, Empowa, Karabo and Menzania (Table 1). The generational times (*i.e.* duration of egg–adult development) of *P. xylostella* were significantly different ($F_{6,248} = 11.81$, $P < 0.001$) among the cabbage cultivars (Table 1). The generation time was shortest on Hollywood F1 and longest on Empowa (Table 1).

Pupal weights

There was a significant difference ($F_{1,523} = 59.18$, $P < 0.001$) in body weights of male (5.13 ± 1.12 mg) (mean ± S.D.) and female (5.71 ± 1.2 mg) pupae that developed on the various cultivars. The male pupal weights were also significantly different ($F_{6,253} = 30.29$, $P < 0.001$) among the cultivars (Table 2). The pupae that developed from Karabo and Beverly Hills were heaviest and those from Hollywood F1, Megaton and Menzania were the lightest.

The female pupal weights also differed significantly ($F_{6,269} = 24.92$, $P < 0.001$) among the seven cabbage cultivars (Table 2). Females that developed on Karabo were the heaviest and those that developed on Hollywood F1, Menzania and Megaton were the lightest (Table 2). Pupal weights from Beverly Hills, Empowa and Leano were intermediate (Table 2).

Table 2. Pupal weights (mg) (mean ± S.D.) of *Plutella xylostella* reared on different cabbage cultivars.

Cultivar	Male	Female
Karabo	6.0 ± 0.88 a	6.82 ± 0.98 a
Beverly Hills	5.88 ± 1.01 ab	6.09 ± 1.22 b
Empowa	5.46 ± 0.81 b	6.07 ± 0.88 b
Leano	4.87 ± 0.76 c	6.0 ± 0.88 b
Hollywood F1	4.11 ± 0.7 d	5.08 ± 1.06 c
Menzania	4.53 ± 0.61 cd	4.91 ± 0.79 c
Megaton	4.13 ± 1.29 d	4.65 ± 0.99 c

Means with the same letters are not significantly different at $P = 0.05$ according to Student's *t*-LSD test.

Longevity without food

The longevity of unfed male *P. xylostella* was significantly different ($F_{6,139} = 10.76$, $P < 0.001$) among the cabbage cultivars (Table 3). Male moths reared on Beverly Hills had the longest lifespan and those that developed on Leano had the shortest lifespan (Table 3).

The longevity of female moths was significantly different ($F_{6,139} = 15.47$, $P < 0.001$) from the different cabbage cultivars (Table 3). Females that developed on Beverly Hills had a longer lifespan without food whereas those that developed on Leano had the shortest life span (Table 3).

Oviposition preference

The numbers of eggs deposited on the cabbage cultivars was significantly different ($F_{6,34} = 2.68$, $P = 0.0391$) (Fig. 1). The moths laid most eggs on Empowa and the least on Menzania and Leano (Fig. 1).

Survival rates

As first instar larvae leave the mines in order to moult to second instar (Ullyett 1947), for practical purposes, the starting point for investigating survival rates of larvae on the different cabbage cultivars is the first instar larvae that had left the mines. There was no significant difference ($F_{6,34} = 0.80$, $P = 0.5795$) in the survival rates of second instar larvae among the cabbage cultivars (Table 4).

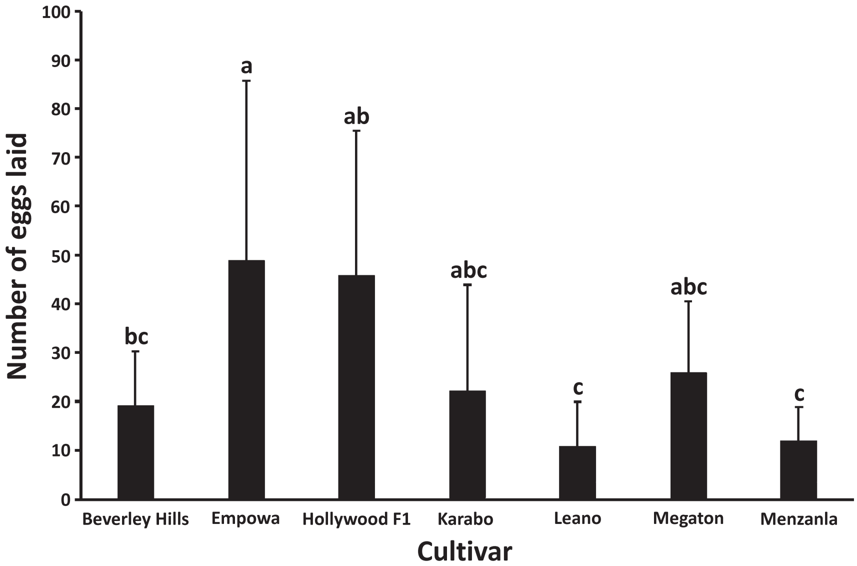

Fig. 1. Oviposition preference of *Plutella xylostella* among seven cabbage cultivars. Means with the same letter are not significantly different at $P = 0.05$ according to Student's *t*-LSD test.

Table 3. Longevity (days) of unfed adult *Plutella xylostella* when reared on seven cabbage cultivars.

Cultivar	Male	Female
Beverly Hills	4.56 ± 0.89 a	5.05 ± 0.69 a
Empowa	4.36 ± 0.61 ab	4.55 ± 0.71 bc
Menzania	3.96 ± 0.52 bc	4.65 ± 0.54 b
Karabo	3.93 ± 0.78 c	4.2 ± 0.70 cd
Megaton	3.74 ± 0.72 c	3.89 ± 0.45 de
Hollywood F1	3.61 ± 0.59 c	3.99 ± 0.624 d
Leano	3.11 ± 0.34 d	3.54 ± 0.22 e

Means with the same letters are not significantly different at $P = 0.05$ according to Student's *t*-LSD test.

There was 100 % survival rate through the second instar for larvae that developed on Beverly Hills, Megaton, Hollywood F1, Karabo and Leano, whereas 98.88 % were still alive on Empowa and Menzania at the end of the second instar (Table 4). The survival rates of the larvae through the third instar were significantly different ($F_{6,34} = 4.21$, $P = 0.005$) among the cabbage cultivars (Table 4). The highest survival rate of third instars was observed on Beverly Hills, Empowa, Hollywood F1, Karabo and Leano, and survival was lowest on Megaton (Table 4). The survival rates of the fourth instar larvae on the different cabbage cultivars was significantly different ($F_{6,34} = 2.64$, $P = 0.0414$). The highest survival rate was observed on *P. xylostella* that developed on Empowa, Hollywood F1, Karabo and Leano and the least on Megaton (Table 4). There was no significant difference ($F_{6,24} = 1.98$, $P = 0.1079$) in survival rates of *P. xylostella* pupae on the different cabbage cultivars. Overall survival of *P. xylostella* immature stages

Table 4. Survival rates (%) of *Plutella xylostella* immature stages on the different cabbage cultivars.

Cultivar	Second instar	Third instar	Fourth instar	Pupa
Beverly Hills	100 ± 0.00 a	100 ± 0.00 a	81.46 ± 16.38 ab	50.48 ± 35.97 a
Empowa	98.88 ± 2.5 a	98.88 ± 2.5 a	93.88 ± 10.83 a	83.22 ± 16.01 a
Hollywood F1	100 ± 0.00 a	96.66 ± 7.47 a	90 ± 14.9 a	88.66 ± 14.05 a
Karabo	100 ± 0.00 a	95.52 ± 8.74 a	95.04 ± 8.67 a	95.04 ± 8.66 a
Leano	100 ± 0.00 a	100 ± 0.00 a	96 ± 8.94 a	80.84 ± 34.69 a
Megaton	100 ± 0.00 a	66.30 ± 32.7 b	60.96 ± 29.65 b	60.96 ± 29.66 a
Menzania	98.88 ± 2.5 a	98.88 ± 2.5 a	85.82 ± 18.84 a	85.82 ± 18.84 a

Means with the same letters are not significantly different at $P = 0.05$ according to Student's *t*-LSD test.

was highest on Karabo (67.26 %) and lowest on Megaton (44.92 %).

DISCUSSION

In terms of the preference-performance hypothesis, females are expected to preferentially choose hosts on which the fitness of their offspring will be better (Mayhew 1997). When given a choice among the seven cultivars, *P. xylostella* laid the most eggs on Empowa and oviposited the least on Leano and Menzania in the present study. Furthermore, the fitness of *P. xylostella* offspring as measured by survival rates of immature stages, their developmental rates, pupal weights and longevity of moths without food differed significantly among cabbage cultivars. Survival rates of offspring are an important parameter in pest management, as they determine expected pest load on the crop. Overall survival of *P. xylostella* immature stages was lowest on Megaton, while survival rates on Empowa, Leano and Menzania were similar. This result is interesting in that *P. xylostella* oviposited the least number of eggs on Leano and Menzania even though survival rates of offspring were as high on Empowa. In contrast, the survival rates of the offspring were lowest on Megaton overall, despite this cultivar having received the intermediate number of eggs from the female moths. Thus, it is expected that Megaton will have lower infestations in the field due to its lower suitability for development of *P. xylostella.* The inability of *P. xylostella* to accurately choose to oviposit on host plants that support the highest survival of its offspring is widely reported (Lu *et al*. 2004; Sarfraz *et al*. 2006, 2007; Ebrahimi *et al*. 2008; Marchioro & Foerster 2014). However, Zhang *et al*. (2012) found a positive relationship between oviposition preference and host suitability for offspring development.

As *P. xylostella* is dependent entirely on resources acquired during larval development for egg production, its realized fecundity is correlated with lifespan (Kahuthia-Gathu *et al*. 2008). In the field, moths may not have access to adequate carbohydrate resource which in turn may influence their longevity and the number of eggs laid in a lifetime (Winkler *et al*. 2009). If adults do not have access to carbohydrates, they utilize nutrients derived from larval reserves for maintenance (Strand & Casas 2007). Thus, the amount and quality of nutrients obtained during the larval stage influences longevity in cases where moths do not have access to supplemental food. In the present study, longevity of unfed female moths was longer on Beverly Hills and shortest on Leano and Megaton. Although longevity of unfed male moths on Empowa was similar to Beverly Hills, female longevity was significantly shorter on Empowa. Reduced adult longevity is known to have an additional effect on population density (Asaro & Berisford 2001) in addition to survival rates of immature stages (Nofemela 2010). As far as results on female longevity show, lower incidence of *P. xylostella* on Megaton is expected, as survival of immature stages was also lower.

For many insects, positive relationships between adult longevity, fecundity and body size has been established (Tammaru *et al.* 2002), including *P. xylostella* (Sarfraz *et al*. 2007; Kahuthia-Gathu *et al*. 2008). In many instances, the weight of pupae is used as a proxy for adult body size (Tammaru *et al.* 2002). In this study, the pupae from larvae that fed on Megaton, Menzania and Hollywood F1 were the smallest, whereas pupae from Karabo were the heaviest. Thus, the low lifespan of the moths from Megaton is positively related to the low weight of pupae.

As smaller individuals are more prone to faster depletion of nutrient reserves in periods of starvation than larger individuals (Gotthard 2001; Stoks *et al*. 2006), there is benefit for being large. However, it may require a longer period of development to achieve a large body size (Heisswolf *et al*. 2005). This can be a fitness cost for species that suffer heavy mortality from natural enemies during the immature stages (Williams 1999). Parasitoids are an important natural mortality factor of *P. xylostella* larvae and pupae during November–May in South Africa, and longer developmental time will extend exposure of hosts to these natural enemies (Kfir 1997; Nofemela 2010). The durations of larval and pupal periods, and thus generation time, took longer on Empowa, Karabo and Beverly Hills. The shortest duration of development was observed on Hollywood F1. The clear linear relationship between duration of development and pupal weight of *P. xylostella* was observed on Hollywood F1 and Karabo.

In conclusion, the results of this study add to the existing body of knowledge that different host plants or cultivars have a differential impact on fitness of *P. xylostella* (see Verkerk & Wright 1994; Sarfraz *et al*. 2007). Although the fitness parameters measured for *P. xylostella* in this study are all useful for evaluating cultivar effects on phytophagous insects (Moreau *et al.* 2006), low survival rate of offspring on a crop is the primary target for using plant resistance as a pest management tactic. While plant resistance to *P. xylostella* remains relatively underexplored as a pest control tactic in South Africa, the results of this study shows that Megaton can play a major role in restricting population growth of this pest and generational number of eggs deposited on it. This is especially important for the spring period when *P. xylostella* density is high due to lower efficacy of parasitoids (Nofemela 2010). The additional fitness costs in terms of reduced body weight of females and their longevity (and fecundity) make Megaton an attractive option for integrated pest management for *P. xylostella*.

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