

# Development and Survival of *Spodoptera exigua* (Lepidoptera: Noctuidae) on Alternate Crops in Cotton Cropping Pattern, With Implications to Integrated Pest Management

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## Abstract

*Spodoptera exigua* (Hübner) is a polyphagous pest that shifts its population to different hosts during its life cycle to receive nutritive advantages. Therefore, demographic evaluation of alternate hosts is important for effective pest management. Here, we have evaluated castor (*Ricinus communis* L.), cauliflower (*Brassica oleracea* L.), cotton (*Gossypium hirsutum* L.), okra (*Abelmoschus esculentus* L.), and spinach (*Spinacia oleracea* L.) for growth, survival, and population development of *S. exigua*. Development of early populations of *S. exigua* is best supported on castor where earlier instars had least mortalities (10%) compared with spinach (36%), although later instars and pupae had significantly higher mortalities (20.8%) on it. Spinach and okra, on the other hand, promote larval survivals in later instars. Little or no differences in stadia lengths were observed during early development of larvae and, interestingly, the longevity of female moths increased significantly when reared on castor, cauliflower, and spinach (12.3, 11.3, and 11.7 d, respectively), resulting into significantly higher fecundity. The survival curves of all five populations have clearly demonstrated a steep early decline in larval numbers when reared on okra and only 60% larvae could survive. These findings conclude that *S. exigua* when fed on spinach was greatly disadvantaged in terms of growth and development; hence, the pest's field population can be opportunistically controlled by spraying adjacent spinach fields. In addition, the results highlight the vulnerable stages in pest's life cycle in the field where we can apply integrated control strategies for its effective management.

**Key words:** host suitability, host switching, polyphagy, survival

Cotton (*Gossypium hirsutum* L.) is an important nonfood cash crop and a major export commodity for agricultural-based economies worldwide (Pan et al. 2007, Hatab 2009). It is being extensively cultivated for its high commercial values and, hence, many new varieties have been developed (Satybalidin et al. 2013). Since the introduction of transgenic Bt varieties, some of the minor pests have resurged to be devastating pests of the cotton crop (Whitehouse et al. 2005, Lu et al. 2010). *Spodoptera exigua* (Hübner) is one of such pest species, which has recently become a serious pest of not only cotton but also other crops grown in the same cropping pattern, including okra (*Abelmoschus esculentus* L.) and castor (*Ricinus communis* L.). However, after the harvest of these crops, the pest moves to vegetables such as cauliflower (*Brassica oleracea* L.) and spinach (*Spinacia oleracea* L.). These alternative crops offer a continual availability of hosts where the *S. exigua* can maintain its population, round the year.

Population growth and success of an insect herbivore are contingent to host plant traits, the nutritional value of the plant tissue (Awmack and Leather 2002), and defensive plant metabolites (Stam et al. 2014), they feed upon. Hence, suitability of host plant species on which an herbivore develops significantly affects the vigor and immunity in various life stages and ultimately the success of pest control strategies (Sarfaraz et al. 2006, 2007). Therefore, we suggest that due consideration be given to the biological relationship of the herbivore to its available host plants in devising integrated pest management strategies.

Beet armyworm (*S. exigua*) is a typical example of a polyphagous pest that damages valuable crops including cotton, corn, tobacco, several vegetables, fruits, and commercial crops (Anonymous 2014). It is a serious pest of vegetables, flower crops, and economically important field crops including cotton in Pakistan (Ahmad and

Mehmood 2015). Here, its population not only thrives on the crops of interest but also utilizes common weeds, such as horse purslane (*Trianthema portuclacstrum* L.) and pigweed (*Amaranthus retroflexus* L.), as a nutritional supplement for larval development (Anonymous 2014). Being cosmopolitan and an economically devastating pest, it is well known to the farming community and is being chemically controlled by indiscriminate use of broad-spectrum insecticides. This has led to the development of pesticide resistance in beet armyworm, even against novel compounds (Adamski et al. 2005, Ahmad et al. 2007, Abbas et al. 2012, Ahmad and Mehmood 2015). One way of tackling this issue, in the long run, would be ecological management strategies through behavioral manipulation (Midega et al. 2015).

During its life cycle in the field, female moths of *S. exigua* are known to have selective oviposition preferences for various hosts, with nutritional advantages to young larvae (Berdegué et al. 1998, Saeed et al. 2010, Johns et al. 2015). Therefore, understanding the herbivore–plant system influencing the fitness cost of chemical-resistant populations (Janmaat et al. 2007, Jafary et al. 2016) can lead toward the long-term ecological management of polyphagous pests.

By understanding the host relationships of polyphagous insects in terms of the nutritive values of alternate hosts, we may also exploit the pest population on unfavorable hosts to augment pest management strategy. But to understand when and where the treatment would be most effective, we should have a good idea of the life history traits of *S. exigua* population on alternate host plants available in the cropping pattern. Hence, in this study, we evaluated alternate crops in cotton cropping pattern which are used as hosts by the natural population of *S. exigua* to identify the most vulnerable stage in pest life cycle on the most unfavorable host plant.

## Materials and Methods

### Selection of Host Plants

Five of the common host plants of *S. exigua* from the cotton production area were selected. These included castor (*Ricinus communis* L., var. wild type), cotton (*Gossypium hirsutum* L., var. Neelam-121, Neelam Seeds Pvt. Limited, Pakistan), cauliflower (*Brassica oleracea* L., var. Snow Crown, Asgreen Seeds (Pvt.) Limited, Pakistan), okra (*Abelmoschus esculentus* L., var. Dilpasand, Farm Seeds Pakistan Limited, Pakistan), and spinach (*Spinacia oleracea* L., var. Green Queen, 4Brother Seeds Corporation, Pakistan). These species were selected based on our hypothesis that the population of *S. exigua* shifts to one of them during their life cycle in the field, to gain physiological benefits either in terms of better nutritive value or to avoid natural pressures being exerted. The selected host plants were planted in pots (0.3 m  $\phi$  by 0.3 m H) and maintained at  $27 \pm 3^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity (RH), and a photoperiod of 16:8 (L:D) h in a glasshouse to ensure a continuous supply of food resources for each population during bioassays. The plants were fertilized using compound NPK fertilizer blend (Zerkhez Green by Engro Fertilizers Limited, Pakistan) and the applied doses were fixed based on the recommended field rates of NPK for each crop (i.e., castor: 40:40:20 kg/ha, cauliflower: 100:50:200 kg/ha, cotton: 60:60:20 kg/ha, okra: 300:300:150 kg/ha, and spinach: 90:90:90 kg/ha).

### Insect Rearing and Data Collection

Field-collected egg batches from all five host plants were brought back to the laboratory to start the experiment. Ten eggs were placed in a petri dish (90 mm  $\phi$  by 15 mm), and there were 20 replications for each host type. The complete studies were conducted at

$26 \pm 2^\circ\text{C}$ ,  $60 \pm 10\%$  RH, and a photoperiod of 14:10 (L:D) h. Once hatched, the larvae were fed on freshly collected, washed, and air-dried leaves from the fifth node from the top of each natal host. The leaves were replaced daily until pupation. The daily data for larval emergence, mortality, and longevity were recorded until the completion of their life cycle. Once the larvae pupated, the pupal weight and pupal periods were recorded after sex-sorting the pupae by observing the sternum for the position of gonophores (Chen and Chang 1989). The adults were paired and kept in plastic jars provided with 10% honey solution diet to harvest eggs. Strips of finely meshed lining sheets (5 by 15 cm) were suspended in the jars as the oviposition substrate. Average female fecundity on each host plant was calculated from total egg count laid by females under observation until they died.

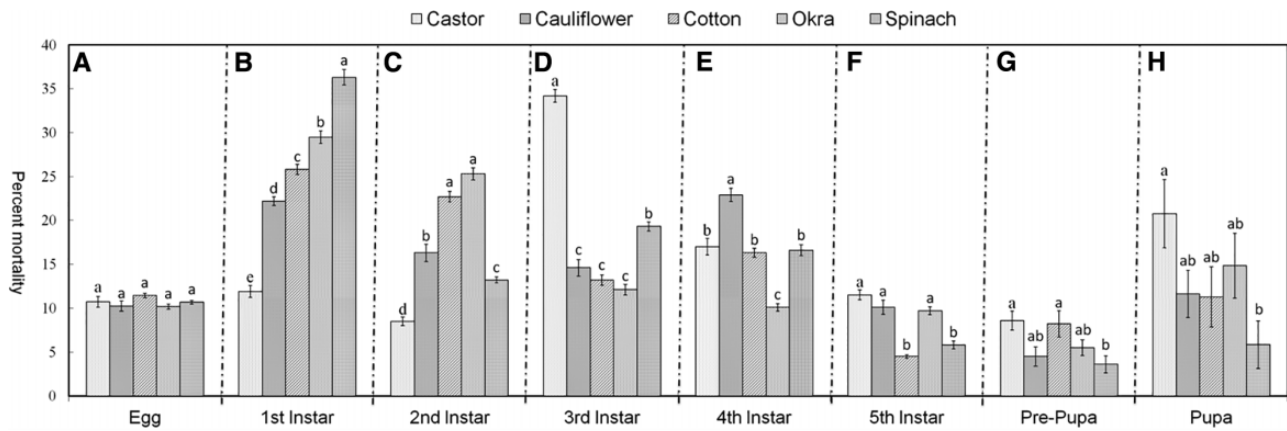
### Statistical Analysis

The experiment was conducted in a randomized complete block design and was replicated 20 times. The data collected for percent mortality and longevity of different life stages and various physiological parameters, including pupal weight, fecundity, and sex ratios, were tested for homoscedasticity using Levene's test to conform to ANOVA assumptions (Levene 1960). The analyses were conducted using the type of host as the independent factor and the developmental and growth parameters as dependent factors. Where significant, the means were subjected to post hoc multiple pairwise comparisons across hosts ( $P \leq 0.05$ ; Tukey's HSD). The cumulative survivals, mean, and median survival times for each population were calculated using Kaplan–Meier's survival analysis and were subjected to log-rank (Mantel–Cox) co-efficient (Mantel 1966). The data were analyzed using SPSS version 17.0 software (SPSS 2008).

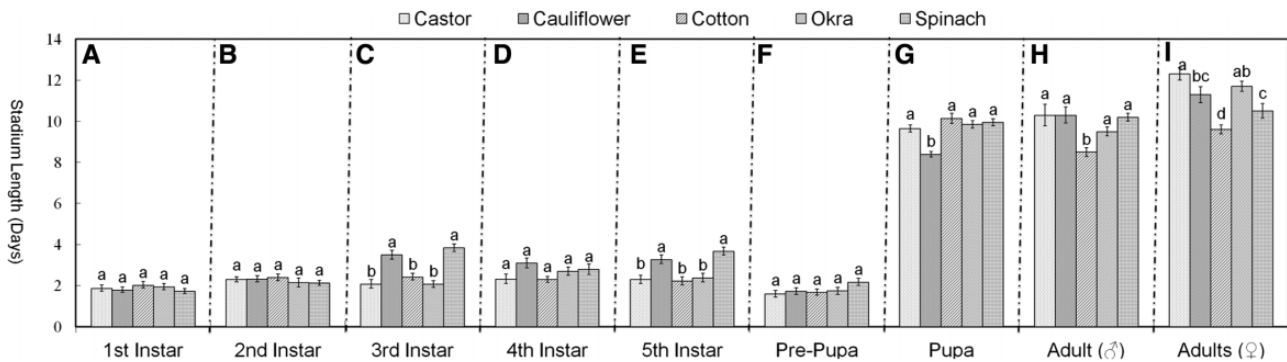
## Results

### Effect of Host Plants on Mortality

The results have indicated that different hosts have no significant effect on egg mortality ( $F_{4, 99} = 1.454$ ;  $P = 0.223$ ; Fig. 1A). In terms of mortality of larvae when reared on different hosts, an obvious trend of decrease in mortality was observed from early instars to the later instars (Fig. 1B–F). There had been a significant difference in mortality of the first-instar larvae ( $F_{4, 99} = 176.32$ ;  $P < 0.001$ ; Fig. 1B). Highest mortality of the first instar had been observed when the larvae were reared on spinach, followed by those reared on okra (Fig. 1B). Castor, on the other hand, had supported the early instars better than all other resources (Fig. 1B). The similar trend was observed in mortality of second-instar larvae ( $F_{4, 99} = 1.107.43$ ;  $P < 0.001$ ), except in the case of spinach where significant decrease in larval mortality was observed, and it was significantly less than that on okra, cotton, and cauliflower (Fig. 1C). Percent mortality of the third instar was also significantly affected by different host plants ( $F_{4, 99} = 172.29$ ;  $P < 0.001$ ). Highest mortality of second-instar larvae was observed on castor followed by that on spinach, whereas all other hosts had shown significantly similar but lower mortality compared with castor and spinach (Fig. 1D). Percent mortality of fourth-instar larvae was also significantly affected by different host plants ( $F_{4, 99} = 44.84$ ;  $P < 0.001$ ), where highest mortality was observed when the larvae were reared on cauliflower and the lowest mortality was observed on okra (Fig. 1E). This trend of percent mortality was consistent in the fifth instar of the larvae ( $F_{4, 99} = 1.454$ ;  $P = 0.001$ ), with an exception that a significant decrease in larval mortality was observed when reared on cotton (Fig. 1F).



**Fig. 1.** Stage-specific mortality of *S. exigua* reared on different hosts. Percent mortality of eggs (A), first- to fifth-instar larvae (B–F), prepupa (G), and pupa (H). Bars represent means and the error bars are 95% CI. The lowercase letters above bars indicate the outcomes of post hoc pairwise comparisons across hosts, where the bars with same letters for each of the comparisons outlined above, were not statistically different from one another.



**Fig. 2.** Longevity of *S. exigua* reared on different hosts. Stadia lengths of first- to fifth-instar larvae (A–E), prepupa (F), pupa (G), male and female adults (H–I). Bars represent means and the error bars are 95% CI. The lowercase letters above bars indicate the outcomes of post hoc pairwise comparisons across hosts, where the bars with same letters for each of the comparisons outlined above, were not statistically different from one another.

Significantly different ( $F_{4, 99} = 3.89$ ;  $P = 0.006$ ) and lowest mortality in prepupal stage was observed in larvae that were fed on spinach as compared with those that were fed on all other host plants (Fig. 1G). Pupal mortality had also been significantly affected by different hosts ( $F_{4, 99} = 2.70$ ;  $P = 0.035$ ), where significantly highest mortality was observed on castor and the lowest mortality was observed on spinach (Fig. 1H).

### Effect of Host Plants on Longevity

No significant effect of different host plants on the first and second stadia of larvae reared had been observed ( $F_{4, 99} = 0.651$ ;  $P = 0.628$  and  $F_{4, 99} = 0.574$ ;  $P = 0.682$ ), respectively (Fig. 2A and B). However, the stadium length of the third instar had been significantly affected by feeding on different host plants ( $F_{4, 99} = 19.58$ ;  $P < 0.001$ ; Fig. 2C). The longest and statistically similar stadia were observed in the larvae fed on cauliflower and spinach, whereas those reared on all other hosts had significantly lower but similar length of stadia (Fig. 2C). The longevity of fourth instar was also nonsignificantly affected by different hosts ( $F_{4, 99} = 2.38$ ;  $P = 0.057$ ; Fig. 2D). The fifth instar, however, again had significantly different stadia length owing to feeding on different host plants ( $F_{4, 99} = 10.68$ ;  $P < 0.001$ ; Fig. 2D), and the trend was observed very similar to that of the third-instar longevity (Fig. 2C and E). No significant difference ( $F_{4, 99} = 1.97$ ;  $P = 0.106$ ) was observed in the longevity of prepupal stadium (Fig. 2F), whereas pupal duration was

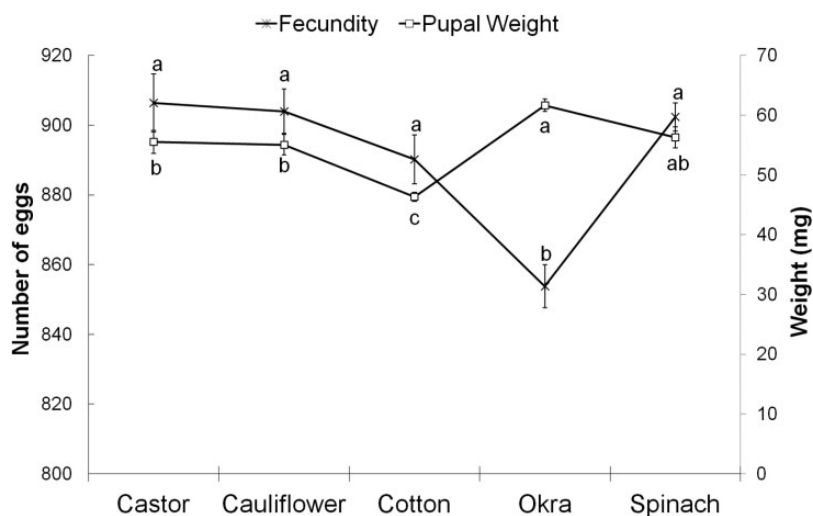
significantly lower on cauliflower compared with all other resources ( $F_{4, 99} = 14.02$ ;  $P < 0.001$ ; Fig. 2G).

Longevity of both male and female moths have been significantly different on different hosts ( $F_{4, 99} = 10.94$ ;  $P < 0.001$  and  $F_{4, 99} = 23.37$ ;  $P < 0.001$ ), respectively (Fig. 2H and I). The longest duration the male moths survived was on castor, cauliflower, okra, and spinach, whereas those reared on cotton had significantly lower longevity compared with those reared on other resources (Fig. 2H). The longevity of female adults on castor and okra were statistically similar but highest followed by the longevity of female moths that were reared on cauliflower and spinach (Fig. 2I). The shortest span of female adults was observed when reared on cotton (Fig. 2I).

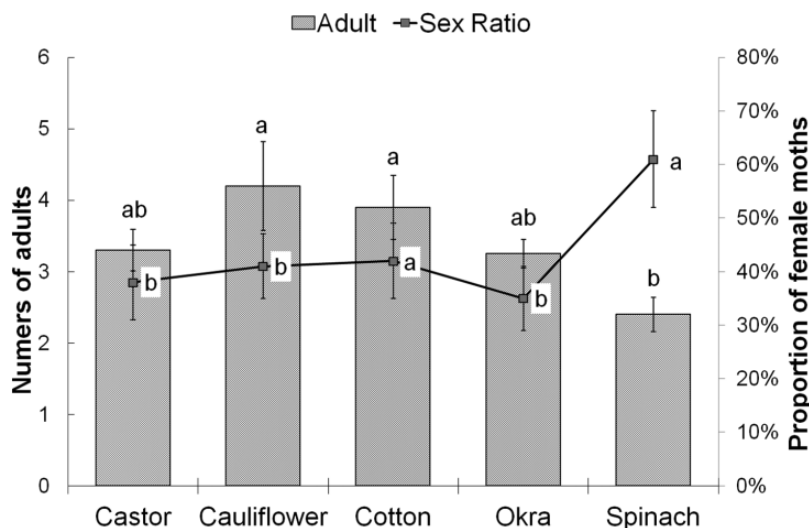
### Effect of Host Plants on Physiological Development

The data on various physiological parameters during the development of *S. exigua* including pupal weight, fecundity, and sex ratio of adult moths have revealed that host plants can significantly affect these parameters ( $F_{4, 99} = 13.05$ ;  $P < 0.001$ ,  $F_{4, 99} = 11.19$ ;  $P < 0.001$ , and  $F_{4, 99} = 4.27$ ;  $P = 0.003$ ), respectively (Figs. 3 and 4).

The highest pupal weight accumulation was observed when the larvae were reared on okra followed by those reared on spinach, castor, and cauliflower, which was statistically similar to each other (Fig. 3). The lightest pupae were produced by the larvae fed on cotton (Fig. 3). In terms of fecundity, however, surprisingly the lowest numbers of eggs laid per female were observed on okra in spite of



**Fig. 3.** Fecundity (---) and pupal weights (—□—) of *S. exigua* reared on different hosts. The data presented as means and the error bars are 95% CI. The lowercase letters above each point indicate the outcomes of post hoc pairwise comparisons across hosts, where the same letters for each of the comparisons outlined above, were not statistically different from one another.



**Fig. 4.** Numbers of adults (shaded bars) and sex ratio (—■—) of *S. exigua* populations reared on different hosts. The data presented as means and the error bars as 95% CI. The lowercase letters above each bars and line indicate the outcomes of post hoc pairwise comparisons across hosts, where the same letters for each of the comparisons outlined above, were not statistically different from one another.

having highest pupal weights (Fig. 3). The results have indicated that fecundity of female is not significantly correlated with pupal weights (Supp. Fig. 1 [online only]). Moreover, total number of adult eclosed was minimum in the population that was reared on spinach ( $F_{4, 99} = 6.264$ ;  $P < 0.001$ ), but their sex ratio has revealed that eclosed adults have the highest proportion of female moth compared with those that eclosed on other resources, hence had statistically similar sex ratios (Fig. 4).

#### Survival Analysis of *S. exigua* Reared on Different Hosts

Kaplan–Meier’s survival analysis of all five populations reared on different hosts has revealed a significant difference in mean survival times of population (Log Rank [Mantel–Cox]:  $\chi^2 = 124.696$ ;  $df = 4$ ;  $P < 0.001$ ; Fig. 5). Maximum survival time was recorded when the populations were maintained on cauliflower, followed by that on

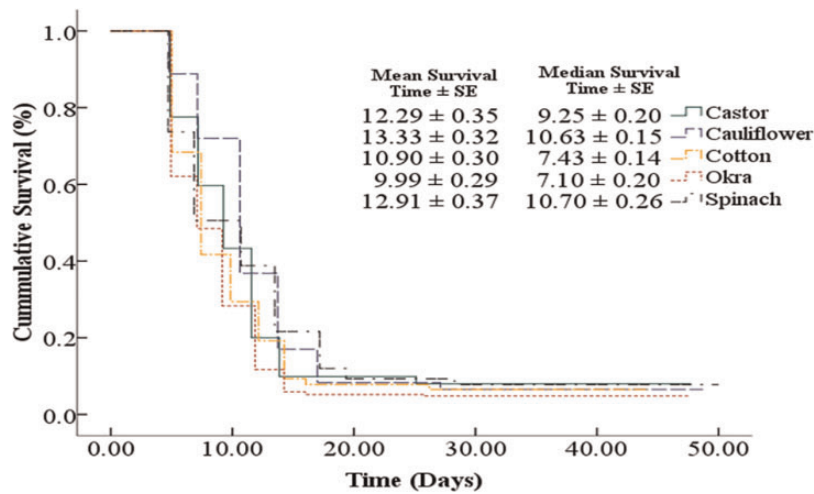
castor and spinach, whereas when reared on okra, the minimum survival time was observed (Fig. 5).

The survival curve denotes that the population reared on cauliflower had been advanced throughout the developmental periods compared with other populations. There has been least decline in numbers at early stages of life cycle and prolonged duration during each stadia, whereas this population has relatively higher decline as it reached pupation (Fig. 5). In contrast to that, population that was reared on okra observed more decline in numbers at the early stages of its life cycle (Fig. 5). At the end of the life cycle, the populations that were cultured on castor and spinach had higher numbers of surviving individuals compared with all other populations (Fig. 5).

#### Discussion

As we have reared *S. exigua* populations on excised leaves within laboratory conditions, it may raise questions about the authenticity of





**Fig. 5.** Survival analysis of *S. exigua* reared on different hosts. Kaplan–Meier’s survival curve for insects reared on castor (green-solid line), cauliflower (blue-dash line), cotton (yellow-dash/dot line), okra (red-dot line), and spinach (black-dash/dot line) presenting cumulative survivals.

the findings because host-utilization behavior and suitability of host plant may be different in the field on whole plants. But earlier studies on parallel evaluation of population development and growth on excised leaves and whole plants have reported no difference among both types of studies (Greenberg et al. 2002). Hence, we are confident that our results report true differences among host-utilization patterns of *S. exigua*.

In general, the results have demonstrated that populations of *S. exigua* were able to survive on all different hosts; however, quite significant variations in terms of host suitability have been identified. These findings support our hypothesis that different hosts may alter the vigor and vitality of pest populations. In support of our findings, it has been established earlier that even the leaves from different cultivars or different parts of plants have different nutritive value for insect pests (Kashyap and Verma 1984, Sison and Shanower 1994, Kumar et al. 2012); hence, variations in development and insect vigor are inevitable when fed on different hosts. We know that apart from the nutritive constituents in a plant, other biochemical compounds (secondary metabolites) may affect the digestibility of insects, hence altering the developmental parameters of an herbivore (Kranthi et al. 2002, Sethi et al. 2006, Rosenthal and Berenbaum 2012). Conforming to the hypothesis discussed above, we observed that physiological traits of *S. exigua* have been significantly affected by different hosts. Having a sigmoid growth pattern of *S. exigua* population (Calcagno et al. 2002), we have observed exponential fecundities on all hosts and this was not affected by host types. These findings are in conformity to those reporting no effect of host plants on normal hatching percentage of eggs (Sivapragasam and Syed 2001, Azidah and Sofian-Azirun 2006). But as the time passes, higher mortalities of earlier instars were recorded which decreased as the larvae aged, with a few exceptions as for when they were reared on spinach. These findings strengthen the earlier reports mentioning higher mortalities in earlier stages of larval development (Casimero et al. 2000, Naseri et al. 2009).

Regarding the mortality of earlier instar larvae, we observed that castor supported the earlier instars much better than all other resources. This gives the gist of the suitability of castor leaves for young larvae. Hence, it suggests that the tender nature of castor leaves support newly hatched larvae providing them with a suitable medium. However, later in their life cycle, the same resource becomes unsuitable for the development and survival of aged larvae

might be because of producing “ricin,” a potent protein synthesis inhibitor found in castor beans (Freeman and Beattie 2008). Furthermore, highest mortality of pupae observed on castor demonstrates the poor nutritive value of castor leaves (Rossi et al. 2012). Based on these findings, we may suggest the use of insecticides on castor when the larvae are at least in their fourth instar. This will give better kill compared with when applied as soon as population starts to develop on castor.

Cauliflower and spinach have similar effects on population development in terms of supporting larval development. The most vulnerable stage of insect on these resources had been inferred to be when the larvae are in their first instar. If the chemical control is applied timely as soon as the eggs are spotted on cauliflower and spinach crop, the best control can be obtained. Okra, on the other hand, has provided better survival and more weight accumulations to pupae, which have suggested an excellent nutritive value of its leaves for the development of *S. exigua* population. However, despite accumulation of highest pupal weights when fed on okra, the females had laid least eggs. In contrast to this, when fed on cotton leaves, the larvae accumulated least pupal weights but female laid relatively more eggs compared with okra fed populations. Hence, it can be inferred that oviposition potential is not related to pupal weight. This finding is in contrast to other established literature (Tisdale and Sappington 2001, Montezano et al. 2013) reporting a significant correlation between fecundity and pupal weight for *S. exigua* reared on artificial diet. This warrants further explanation after understanding the nutritive constituents of both resources because the availability of vital nutrients is directly related to the reproductive potentials of the insects (Awmack and Leather 2002).

In terms of sex ratio expressed as proportion of females that eclosed, we observed that spinach although least supported the population and resulted in the least number of adults that could eclose, the proportion of females was highest in population reared on spinach compared with all other resources. Responding to a natural phenomenon of survival of the fittest and to ensure the continuity of the population on poor host, i.e., spinach, more females could have been produced as suggested by earlier developmental studies (Papaj 2000, Awmack and Leather 2002). Hence, despite having significantly lower number of adults produced, the fecundity on spinach had not been significantly different on spinach as compared with all other resources. These findings also suggest that spinach

leaves might have interacted chemically to influence egg laying and enhancing oviposition, and the same is reported earlier that the host plant influences the preference for oviposition (Berdegué et al. 1998, Poveda et al. 2012, Foster 2013, Gamberale-Stille et al. 2014).

In conclusion, all these variations in developmental patterns of *S. exigua* on test resources could be owing to different nutritive constituents of each resource and at the same time owing to the presence of various metabolites affecting the physiology of the insects. If we can establish a clear understanding of these nutritive relationships of crops with insect pest, we can better project the risks and crop losses due to insect pests. But above all, utilizing this information we can apply chemical control against the insect pests at the point when they are naturally disadvantaged by their hosts. As in this study, we have suggested the most vulnerable time to apply pesticides on different crops.

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