

Differential Response of Potato Tuber Moth and its Parasitoids to Different Solanaceous Hosts: Implication to PTM Management in Tomatoes

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Abstract

Potato tuber moth is an oligophagous pest of different solanaceous crops. The present study evaluated the potential of intercropping tomato with other solanaceous species as trap crops in safeguarding tomato from PTM damage. Paired potato, wild solanum, eggplant, tobacco, and tomato were caged open in the field as sole and mixed species and also planted in the open as sole and mixed crops. The paired plants were artificially inoculated with four mated females. The open field grown plants were left for natural infestation. The leaves of the different solanaceous species were inspected once a week for PTM larvae presence and level of parasitism was also determined in the lab. In the cage experiment, unlike for same species paired; there was a significant difference in PTM larva density for each paired species and the lowest larval density was in tomato. Whereas in the open field, the number of recovered larvae on eggplant and tomato was significantly lower than on the other species. In the field cages, *Diadegma mollipla* (Holmgren) release in the field cage parasitized larvae only on the leaves that were present potato, wild solanum, and eggplant. Similar results were obtained in the open field. Unidentified parasitoid was recorded on tobacco leaves of tobacco in the open field. The results illustrate that presence of potato, tobacco, eggplant or wild solanum present in the proximity of tomato field would serve as trap plant for PTM and its parasitoids and help reduce damage to tomatoes fruits.

Keywords: *Diadegma mollipla*, infestation, parasitism, PTM, solanaceous

Introduction

Proper spatiotemporal implementation of on-farm biodiversity with intercropping can create an agroecosystem which per se prevent/reduce pest attack, maintain soil fertility and guarantee sustainable productivity (Cook *et al.*, 2007; Mousavi

and Eskandari, 2011; Daud *et al.*, 2014; Mishra, 2014). Intercropping, also called polyculture or mixed cropping, is a practice of cultivating two or more crops at same space and time (Ouma and Jeruto, 2010; Lithourgidis *et al.*, 2011). One of the important aspects of intercropping is the ability to reduce pest and disease

incidence (Lithourgidis *et al.*, 2011). Intercropping is also known to have a major impact on trophic interactions and biological control (Andow, 1991). Thus, increasing diversity in the field through intercropping enhances biological control and reduces the damage by insect pest. Pimentel (1961) and Root (1973) developed the "Enemy Hypothesis". The hypothesis stated that number of herbivores in intercropped system is less abundant than in monocropped due to the abundance of predators and parasitoids.

Three species of Lepidoptera (Gelechiidae) are known as potato tuber moth (PTM) because the larva bore into potato tubers in the field and in potato stores (Rondon, 2010). PTM, *Phthorimaea operculella* (Zeller), is by far the most widespread and important oligophagous pest of a range of solanaceous species like tomato, potato, eggplant, tobacco and other non-tuberous solanaceous crops, weeds, and wild plants (Fenemore, 1988; Kroschel *et al.*, 1996; Rondon, 2010). In potato, significant economic loss is attributed to tuber damage both in field and storage; foliar damage doesn't often cause significant economic loss (Rondon, 2010). The pest is mainly distributed in warm temperate and tropical regions where the host plants are grown (Golizadeh and Esmaeili, 2012).

PTM is a major pest of tomato grown in an open field in Ethiopia and causes significant fruit damage (Tsedeke and Gashawbeza, 1994) and the most important damage occurs in maturing and matured fruits (Bayeh *et al.*, 2006). However, PTM inflicted lower leaf damage on tomato planted in proximity to potato (Bayeh *et al.*, 2007). Bayeh *et al.* (2004 and 2007) reported that tomato at the vegetative stage is a suboptimal host to PTM and provide natural enemy free

space (EFS), a host plant that provides a refuge against natural enemies. The EFS provided might allow PTM to sustain itself at a suboptimal level on leaves and peak during fruiting period. The presence of EFS to the PTM in tomatoes prompted us to test whether other solanaceous hosts, other than potato, also provide PTM with similar development niches.

A number of natural enemies attack PTM in all growing regions where it occurs. The predominant ones are larval and egg-larval parasitoids in the hymenopteran families, Braconidae and Ichneumonidae. In addition coccinellids, chrysopids larvae, predatory Heteroptera, carabid and staphylinid beetles, and earwigs prey on PTM eggs and larvae. Nonetheless, the rate of parasitism varies from location to location (Kfir, 2003). In Ethiopia *D. mollipla* and *Chelonus* spp. are the only identified larval parasitoids on PTM and one more unidentified larval parasitoid has been reported (Adhanom *et al.*, 1985; Tewodros *et al.*, 2019). *D. mollipla* was known to parasitize PTM on potato and accounted for about 66% of the parasitoids recovered from potato plants (Bayeh *et al.*, 2004). This was also found to be the case in major potato growing areas in the central highlands of Ethiopia where 15-40% PTM larval parasitism were recorded under farmer's condition (Bayeh unpublished data). Therefore the study reported herein was undertaken to determine the preference of PTM amongst potato, tomato, eggplant, tobacco, and wild solanum in an open field and field cage while they are planted as sole, paired, and intercropped. Furthermore, the level of parasitism in the respective host plants was determined from the recovered larvae. The study was carried out in the central highlands of Ethiopia at Holetta Agricultural Research Center (HARC)

located 44 km west of Addis Ababa and positioned at 38° 32' N 9° 3' E at an altitude of about 2,400 meters.

Materials and Methods

PTM and *D. mollipla* rearing

A starting stock of PTM used to establish colony was collected from potato fields and diffused light stores at HARC. Five adults of each sex were introduced into a plastic box kept in laboratory at room temperature and provided with surface wounded potato tuber for oviposition and food for larvae. Honey and water in a piece of cotton was provided through the mesh on the perforated lid food source for the introduced adult. As the larvae pupated they were transferred into a Petri dish for adult emergence. The source of *D. mollipla* for the field cage experiment was field collected PTM larvae which has been reared in the laboratory at room temperature by providing potato leaves and the emerging adult parasitoids were used to establish a parasitoid colony. In establishing the colony, second and third instar larvae were exposed to mated females of *D. mollipla* while feeding in the leaves of potato in a plastic box. *D. mollipla* pupae were then transferred into a cup and provided with water and honey on a cotton twig for adult food source.

Field cage experiment

Seedlings of tomato (*Solanum lycopersicum*), eggplant (*Solanum melongena*), tobacco (*Nicotiana tabacum*), and wild solanum (*Solanum nigrum/indicum*) rose in a greenhouse were transplanted into a plot of 168m² at HARC. Potato (*Solanum tuberosum*) was planted in the field prior to transplanting the other plant species. Di-ammonium phosphate (DAP) and Urea were applied

during planting at a rate of 195 kg/ha and 165 kg/ha, respectively. The plants were furrow-irrigated twice a week. All possible pairing of the five plant species was done. A total of 18 plants per species were used in the pairing. The paired plants were caged in field cages of 0.6m (L)*0.6m (B)*1m (H) immediately after transplanting or potato emergence. The plants were placed 0.15m away from the sides of the cages. The distance between paired plants was fixed at 0.3m, the cages and replicates were spaced at 1.3m. The field cages were covered with nylon mesh to exclude other herbivores and natural enemies. The mesh cover was extended 0.25m below the soil surface in order to prevent access of soil-borne predators, such as spiders and ants, to the cages. After a month, two pairs of female adult PTM were released into each cage. Ten days later, a newly emerged pair of the parasitoids, *D. mollipla*, was released into each cage and provided with drops of honey as food source. Ten days after the introduction of the parasitoids, the plants were carefully cut at the stem-root crown and all the PTM larvae present were recorded and transferred to leaves of the respective host plants, which were replaced every other day until all the developing larvae had pupated. Level of parasitism was also determined.

Open Field experiment

Pure stand

Tomato, wild solanum, tobacco, and eggplant seedlings were grown from seeds in a greenhouse. Seedlings, free of PTM infestation, were transplanted into separate plots each sized 1.8m*2.25m in three replicates with distances of 0.3m, 0.75m, and 1m between plants, rows, and plots, respectively. Potato tubers were planted in the field three weeks prior to transplanting of the other species. A total

of 18 seedlings were used per plot per species with three rows per plot. Diammonium phosphate (DAP) and Urea were applied during planting at the rate of 195 kg/ha and 165 kg/ha, respectively. All necessary agronomic practices were made including weekly irrigation. Fifteen days after transplanting, assessment of foliage for PTM infestation was started and continued for eight consecutive weeks. Larvae were recorded, collected and reared in a laboratory on the respective host plants from which they were recovered and percentage parasitism was determined.

Mixed stand

In mixed stands, 24 seedlings of each of the above five species were planted in plots each sized 3m*3m with three replications and each plot had four rows planted with 40 seedlings, eight from each species. All the seedlings were planted randomly in the four rows of each plot with 1:1:1:1 ratio in every plot. The distance between plants, rows and plots and data collection and all other procedures were same as described above in the pure stands.

Data analysis

The data analysis was done using the program JMP IN version 4.0. All the field data were checked for normality and all data except the field cage were log

transformed. A one-way ANOVA was used on the data number of PTM larvae recovered and the rates of parasitism from the open field in the pure and mixed stands. Percentage parasitism and number of larvae in the field cage was analyzed using paired sample T-test. The significance level was set to $\alpha = 0.05$.

Results and Discussion

Field cage experiment

Number of larvae

In the field cages, the number of larvae recorded were similar between pairs of the same plant species ($p > 0.05$) (Fig 1).

Potato, tobacco, wild solanum and eggplant each paired separately with tomato, had more larvae than that of the accompanied tomato. No larvae were found on tomato paired with eggplant or wild solanum. More larvae were detected on tobacco than that of the paired eggplant, potato or wild solanum. There was also a significant interaction in potato vs eggplant and wild solanum vs eggplant pairs ($p < 0.05$). No such effect was observed between wild solanum and potato pairs ($t = 4$ and $p > 0.05$) (Fig 2) and the highest number of larvae was recorded on tobacco.

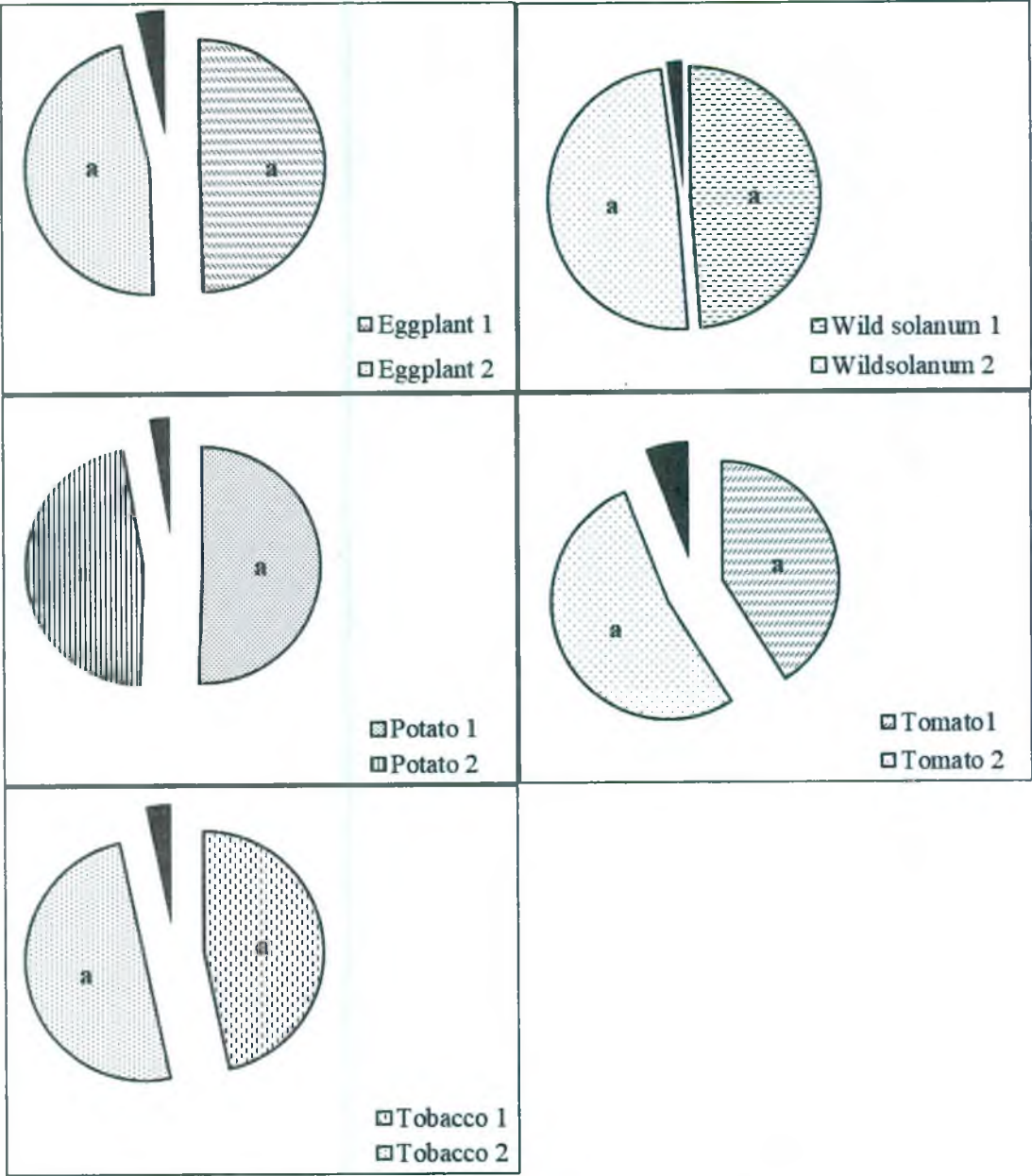
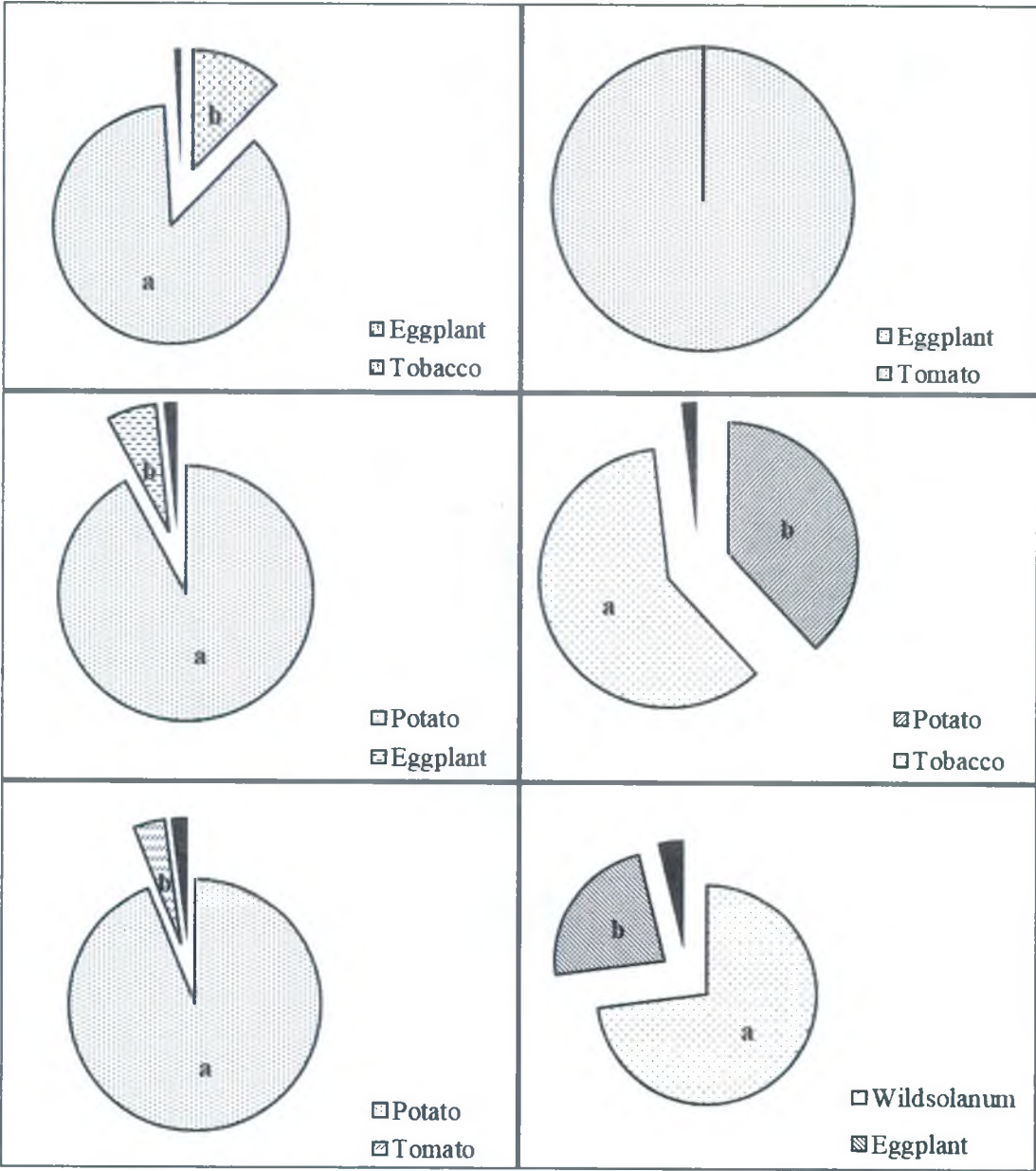


Figure 1. Mean number of PTM larvae collected between the same plants species paired in a cage. Black: standard error. Same letter (s) is not significantly different from each other (Paired T-test, $p < 0.05$).



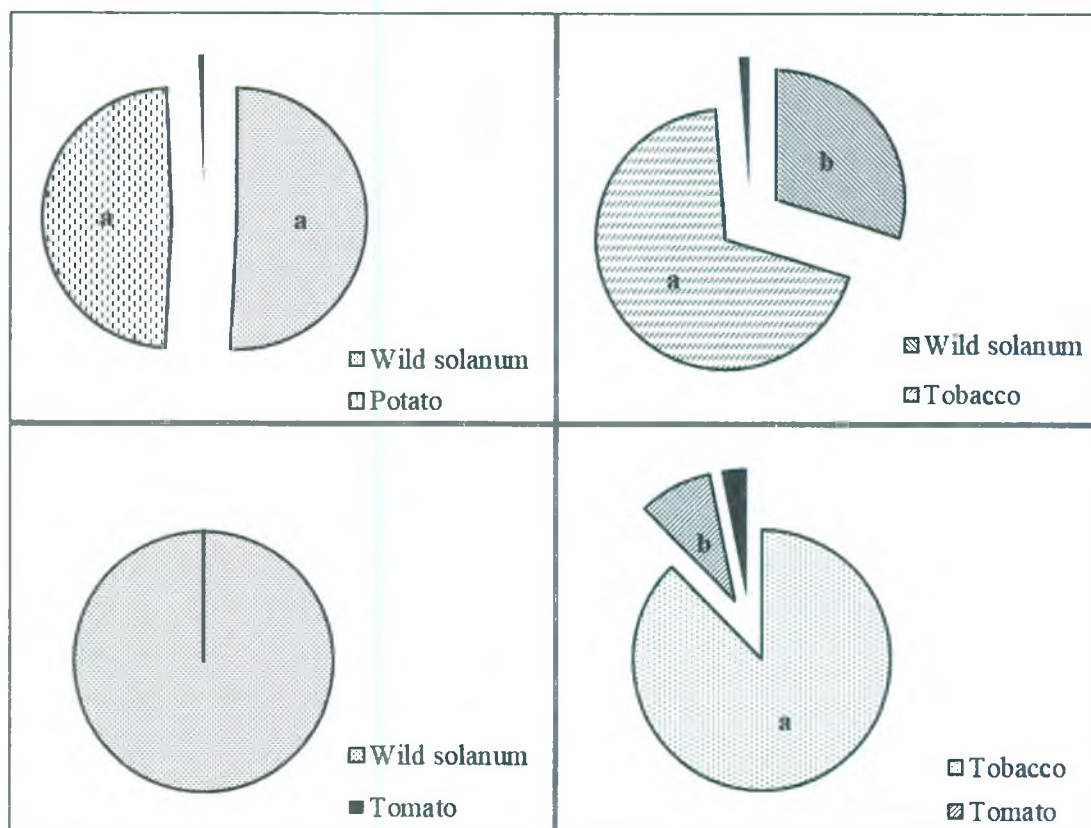


Figure 2. Mean number of PTM larvae collected in different plants species paired in a cage. Black, standard error. Lower case lettering represents significant difference between slices within a chart (Paired sample T-test, $p < 0.05$).

Percent parasitism

There were significantly higher percent parasitism in eggplant, potato, and wild solanum as each paired independently in a cage with tobacco or tomato, while percent parasitism in tobacco and tomato was almost zero (Fig 3). No parasitism was detected on eggplant when paired

with potato or wild solanum. However, more than 50 and 19 % parasitism was detected on potato and wild solanum, respectively (Fig 3). Same plant pairs showed no difference in level of parasitism but no parasitism was recorded in tomato and tobacco pairs.

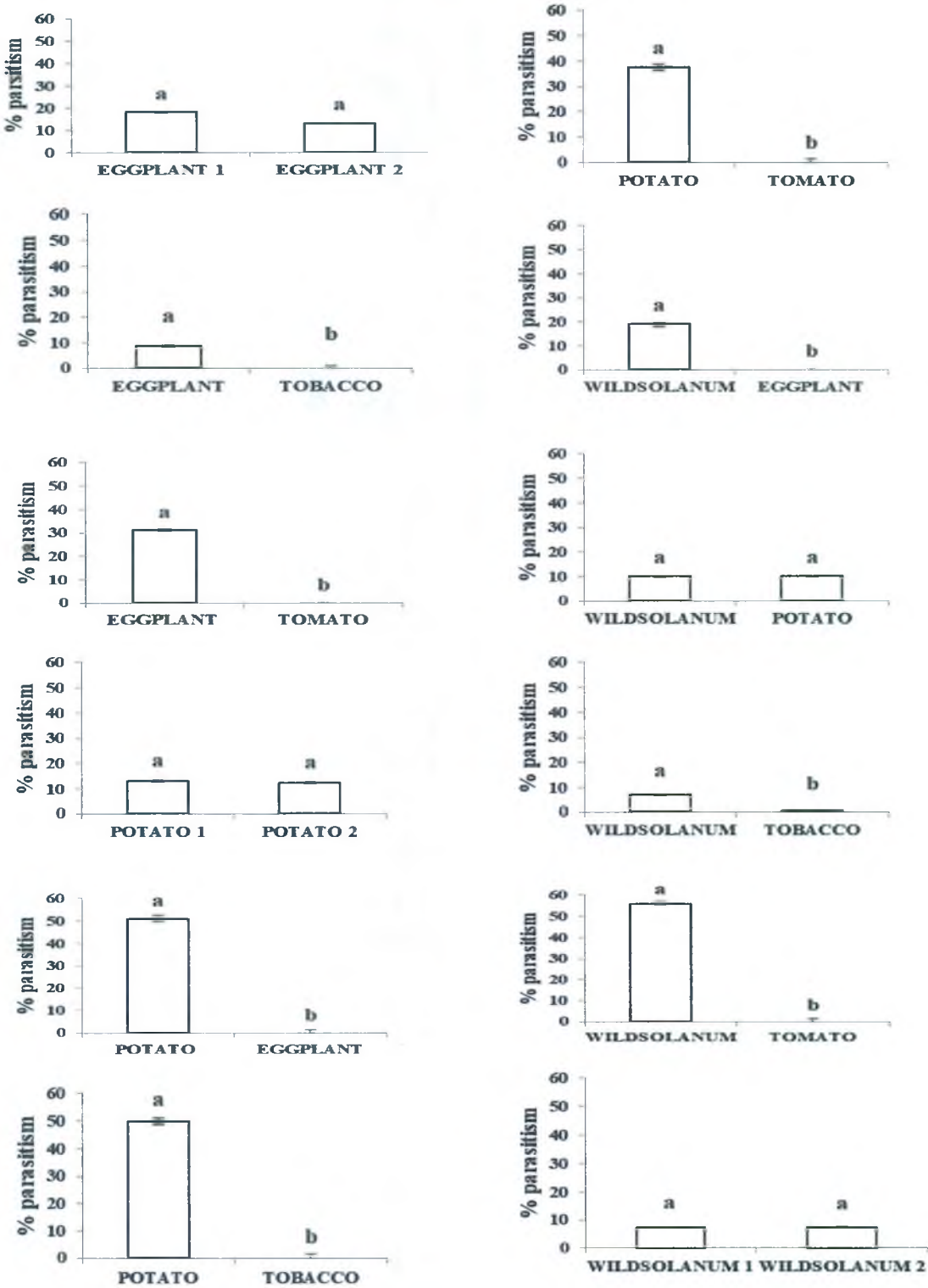


Figure 3. Mean (\pm SE) percent parasitism in field cages. Significant difference between bars within a bar chart is indicated by different lower cases (Paired sample T-test, $p < 0.05$).

Open field larval density and parasitism

Pure stand

In the pure stands there was significant difference in larval infestation rates between plant species ($p < 0.001$) (Table 1). There was no leaf infestation in tomatoes and larvae were abundant on the potato and tobacco plants. The larvae collected from potato, tobacco and wild solanum were not statistically significant. Similarly, no variation was detected in number of larvae recorded on eggplant and wild solanum (Table 1).

Means followed by the same letter (s) are not significantly different from each other at 5%, Tukey–Kramer Test.

Variability was detected in the number of parasitoids emerged in the PTM larvae collected from the five host species ($F = 5.02$ $p < 0.0009$) (Fig 4). The observed parasitoids were *D. mollipla* and one unidentified species. Peak parasitism was observed in wild

solanum, potato, and eggplant. No parasitism was observed in tomato. In tobacco, parasitism was detected in the field, but the parasitoids emerged were not *D. mollipla* rather the unidentified species.

Table 1. Mean (\pm SE) of number of PTM larvae collected from five different solanaceous species in pure stands

Plant species	Mean \pm SE larvae per plant species
Tomato	0.00 \pm 0.00a
Eggplant	0.30 \pm 0.06b
Potato	0.61 \pm 0.50c
Wild solanum	0.45 \pm 0.07bc
Tobacco	0.60 \pm 0.08c
F value	19.16
P- value	< 0.0001

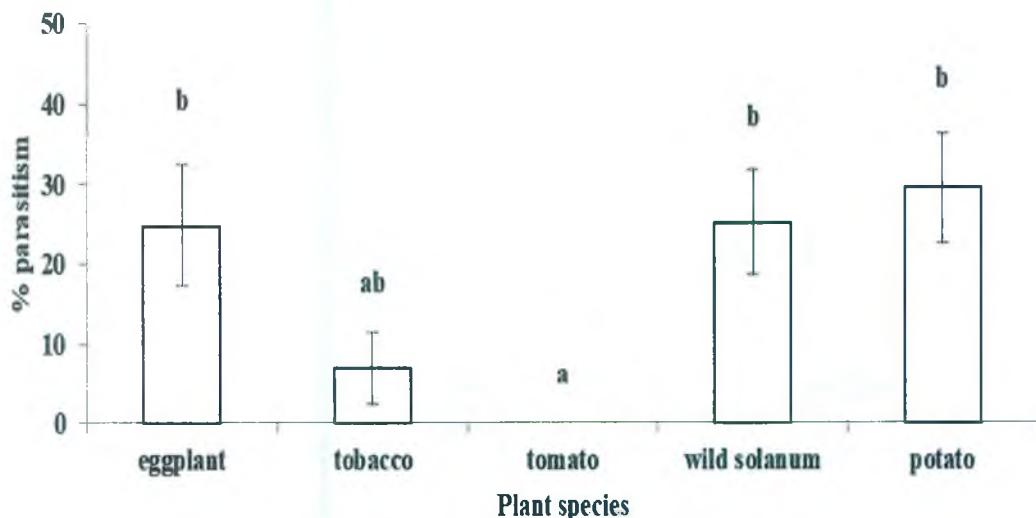


Figure 4. Mean (\pm SE) percentage parasitism in the open field pure stands

Mixed stand

There was significant difference ($p < 0.0001$) in the number of PTM larva recorded between the solanaceous species (Table 2). The overall mean infestation per species was highest in tobacco followed by wild solanum and potato, however; no variability was observed with each other. Number of larvae recovered from tobacco, wild solanum and potato plants was significantly higher than that of tomato and eggplant.

Similar to the pure stand, significant parasitism was detected between the different plant species in the mixed stand and no parasitism was observed in tomato ($p < 0.0001$). The observed parasitism was from two parasitoids, *D. mollipla* and one unidentified species and parasitism in tobacco was from by the unidentified species. Parasitism in wild solanum and eggplant was found to be significantly different from tobacco and tomato (Figure 5)

Table 2. Mean (\pm SE) of number of PTM larvae collected from five different solanaceous species in mixed stands

Plant species	Mean + SE larvae per plant species
Tomato	$0.03 \pm 0.02a$
Eggplant	$0.51 \pm 0.06b$
Potato	$0.80 \pm 0.05c$
Wild solanum	$0.81 \pm 0.08c$
Tobacco	$0.82 \pm 0.07c$
F value	32.59
P- value	< 0.0001

Means followed by the same letter (s) are not significantly different from each other at 5%, Tukey- Kramer Test

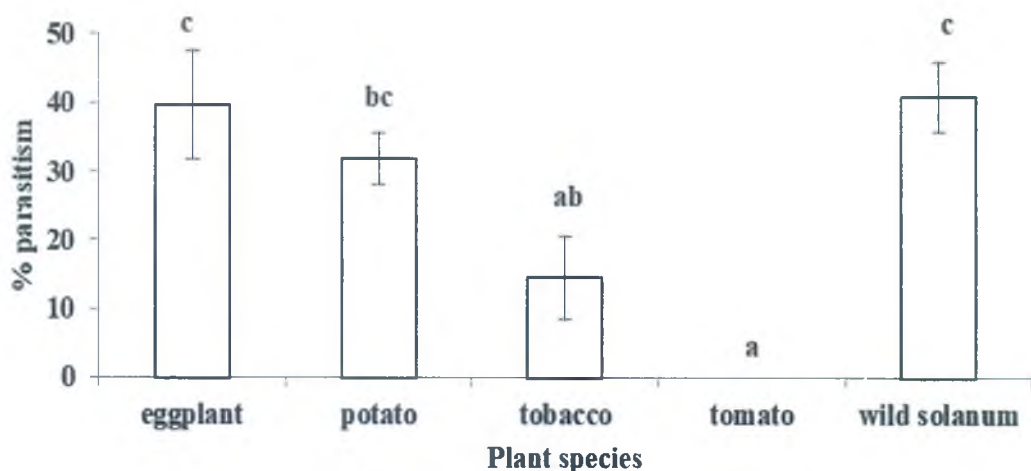


Figure 5. Mean (\pm SE) percentage parasitism in the open field mixed stands

Discussion

Preference of PTM and foraging preference and efficiency of the major parasitoids under cage and field conditions were studied. In the cages where the same plants were paired, even though the number of larvae recovered varied between plant species, PTM adult females were found to oviposit in all of the plant species. This might be due to the absence of other suitable host under no choice condition. For instance under field condition no larva was seen on tomato which might be due of the presence of other more preferred hosts. Alternatively, PTM preference changed when paired with other hosts, more larvae were collected in potato, wild solanum, eggplant and tobacco as each paired separately in a cage with tomato. Similarly, planting tomato mixed with other solanaceous hosts in an open field resulted in a low PTM larval population buildup in tomato plants.

These results suggest that PTM preference towards a host is affected by the presence of other more preferred host plants. This is consistent with the earlier findings of Bayeh *et al.* (2007), who reported a very low larval PTM population buildup in tomato plants, when compared to potato, during the vegetative stage. Tomato was also reported to be inconsistent PTM host as compared to other solanaceous plants potato, eggplant and tobacco (Fenemore, 1980). In addition, tomatoes leaves are found to be suboptimal host for PTM larvae and more PTM eggs were recorded on the leaves of potato than that of tomato (Bayeh *et al.*, 2007). These findings indicated that PTM failed to oviposit on tomato plants in the presence of more suitable companion plant. This might largely be related to the low performance

of PTM larvae on tomato leaves (Bayeh *et al.*, 2007), variability in allelochemical profile of host plants, and visual plant attributes such as growth form, leaf shape or color between the plants species which might influence the host location process and oviposition (Prokopy and Owens, 1983, Tosh *et al.*, 2003; Das *et al.*, 2007). Non-volatile secondary metabolites, leaf trichomes and cuticular waxes on plant surfaces are known to trigger acceptance or rejection of plants for feeding and/or oviposition (Muller and Riederer, 2005).

PTM larvae that tunneled in the leaves of tomato and tobacco were not parasitized by *D. mollipla*; this might be due to the presence of an enemy free space for *D. mollipla* in tomato and tobacco. A number of previous works have reported the presence of enemy-free space. Bayeh *et al.* (2004) reported the presence of enemy free space in tomato. In another study, they have concluded the reason behind the EFS provided by tomato to be linked with the tomato leaf traits such as glandular trichome (Bayeh *et al.*, 2006). They have further showed the parasitoid *D. pulchripes* to equally accept PTM larvae fed on both potato and tomato when provided in the absence of the host. Non-host plants may also emit repellent volatile compounds or volatiles that mask the odours of the host plant (Mauchline *et al.*, 2005; Amarawardana *et al.*, 2007).

In contrast, in potato, eggplant and wild solanum parasitism was detected when each was paired with themselves as well as with tomato and tobacco. This idea is in concurrence with Onzo *et al.* (2009) who stated that, plants can attract the natural enemies of herbivores by emitting specific volatile chemicals when attacked by herbivores. These volatile chemicals are among the main information-conveying

agents available to predatory arthropods when searching for prey. Here it is important to note that both PTM and *D. molipla* used in the field cage experiment were reared on potato which could affect their preferences and primed adults to prefer potato (Proffit *et al.*, 2015).

The absence of parasitism by *D. molipla* by tobacco plants while the unidentified parasitoid was able to parasitize is an interesting finding, which implies that the responsible plant factor in tobacco that prevented *D. molipla* from parasitizing PTM might be morphological such as leaf trichomes (both glandular and non-glandular). *Apanteles subandinus* and *Orgilus lepidus*, parasitoids of PTM, had been shown to have variable preference to PTM larvae in different hosts (Salehi and Keller, 2002). *A. subandinus* preferred PTM in potato, tomato or eggplant whereas, *O. lepidus* female landed more frequently on PTM infested potato than eggplant or tomato. In addition, when the parasitoids were provided with potato, tomato or eggplant with PTM larvae *O. lepidus* showed more preference to potato-PTM complex than tomato or eggplant.

Conclusions

The findings of this study showed that PTM has a varying preference to the tested solanaceous plants with higher number of PTM larvae observed on eggplant, potato, tobacco, and wild solanum than tomato under both semi-field and field condition. Likewise, parasitoids showed variability in preference and the extent of parasitism. In general, PTM behavioural response to host plants can be manipulated through intercropping or border cropping of the main crop with two or more companion crop in order to reduce damage in the

main crop. Future studies should focus on investigating the chemical profile of the tested or other solanaceous host plants that could be used to develop super attractant for the management PTM and the underlying reason for the difference in parasitism.

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References

- Adhanom Negasi, Tsedeke Abate, Geti E. 1985. Research on insect pests of root and tuber crops in Ethiopia, in A Review of Crop Protection Research in Ethiopia. Proceedings of the First Ethiopian Crop Protection Symposium, Institute of Agricultural Research (IAR). 422-431 pp.
- Amarawardana L, Bandara P, Kumar V, Pettersson J, Ninkovic V, Glinwood R. 2007. Olfactory response of *Myzus persicae* (Homoptera: Aphididae) to volatiles from leek and chive: Potential for intercropping with sweet pepper. *Acta Agriculturae Scandinavica Section B -Soil and Plant Science* 57: 87-91.
- Andow, DA. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36: 561-586.
- Bayeh Mulatu, Applebaum SW, Coll M. 2004. A recently acquired host plant provides an oligophagous insect herbivore with enemy-free space.

- OIKOS* 107: 231–238.
- Bayeh Mulatu, Applebaum SW, Coll M. 2006. Effect of tomato leaf traits on the potato tuber moth and its predominant larval parasitoid: A mechanism for enemy-free space. *Biological Control* 37: 231–236.
- Bayeh Mulatu, Shalom WS, Moshe C. 2007. Biological performance of potato tuber moth on leaves of tomatoes. *Pest Management Journal of Ethiopia* 11: 61–67.
- Cook SM, Khan ZR, Pickett JA. 2007. The Use of Push-Pull Strategies in Integrated Pest Management. *Annual Review of Entomology* 52: 375–400.
- Das PD, Raina R, Prasad AR, Sen A. 2007. Electroantennogram responses of the potato tuber moth, *Phthorimaea operculella* (Lepidoptera; Gelechiidae) to plant volatiles. *Journal of Biological science* 32: 339–349.
- Daud MF, Fauziah I, Mohd Rasdi Z, Fairuz K, Abu Zari U, Syed Abdul Rahman SA, Ismail R, Hanysyamn MN, Norazliza R. 2014. Asymmetry effect of intercropping non host crops between cabbage and climatic factor on the population of the diamondback moth (*Plutella xylostella* L.) and yield. *Agriculture, Forestry and Fisheries* 3: 171–177.
- Fenemore PG. 1980. Oviposition of potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae); identification of host-plant factors influencing oviposition response. *New Zealand Journal of Zoology* 7: 435–439.
- Fenemore PG. 1988. Host-plant location and selection by adult moth, *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae): a review. *Journal of Insect Physiology* 3: 175–177.
- Golizadeh A, Esmaeili N. 2012. Comparative life history and fecundity of *Phthorimaea operculella* (Lepidoptera: Gelechiidae) on leaves and tubers of different potato cultivars. *Journal of Economic Entomology* 105: 1809–1815.
- Kfir R. 2003. Biological control of the potato tuber moth *Phthorimaea operculella* in Africa. pp. 77–85. In: Neuenschwander P, Borgemeister C, Langewald J. (Eds.), *Biological Control in IPM Systems in Africa*, CABI Publishing, Wallingford, UK.
- Kroschel J, Kaack HJ, Fritsch E, Huber J. 1996. Biological control of the potato tuber moth (*Phthorimaea operculella* Zeller) in the Republic of Yemen using granulosis virus: Propagation and effectiveness of the virus in field trials. *Biological Science and Technology* 6: 217–226.
- Lithourgidis AS, Dordas CA, Damalas CA, Vlachostergios DN. 2011. Annual intercrops: an alternative pathway for sustainable agriculture. *Australian Journal of Crop Science* 5: 396–410.
- Mauchline AL, Osborne JL, Martin AP, Poppy GM, Powell W. 2005. The effects of non-host plant essential oil volatiles on the behaviour of the pollen beetle *Meligethes aeneus*. *Entomologia Experimentalis et Applicata* 114: 181–188.
- Mishra A. 2014. Effect of winter maize-based intercropping systems on maize yield, associated weeds and economic efficiency. *Communicata Scientiae* 5: 110–117.
- Mousavi SR, Eskandari H. 2011. A General Overview on Intercropping and Its Advantages in Sustainable Agriculture. *Journal of Applied Environmental and Biological Sciences* 1: 482–486.
- Müller C, Riederer M. 2005. Plant surface

- properties in chemical ecology. *Journal of chemical ecology* 31: 2621-2651.
- Onzo A, Rachid H, Maurice WS. 2009. The predatory mite *Typhlodromalus aripo* prefers green-mite induced plant odours from pubescent cassava varieties. *Experimental Application Acarol* 58: 359-370.
- Ouma G, Jeruto P. 2010. Sustainable horticultural crop production through intercropping: The case of fruits and vegetable crops: A review. *Agriculture and biology journal of North America* 1: 1098-1105.
- Pimentel D. 1961. Species Diversity and Insect Population Outbreaks. *Annals of the entomological society of America* 54: 76-86.
- Proffit M, Khallaf MA, Carrasco D, Larsson MC, Anderson P. 2015. 'Do you remember the first time?' Host plant preference in a moth is modulated by experiences during larval feeding and adult mating. *Ecology letters* 18: 365-374.
- Prokopy RJ, Owens ED. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28: 337-364.
- Rondon SI. 2010. The potato tuberworm: A literature review of its biology, ecology, and control. *American Journal of Potato Research* 87: 149-166.
- Root RB. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecologia Monographs* 43: 95-124.
- Salehi L, Keller A. 2002. Investigation on Host Finding Behavior of the Two Parasitoids of Potato Tuber Moth in a Flight Tunnel. *Journal of Agricultural Sciences Technology* 4: 95-102.
- Tewodros Mulugeta, Bayeh Mulatu, Habte Tekie, Mohammed Yesuf, Andreasson E, Alexandersson E. 2018. Phosphite alters the behavioral response of potato tuber moth (*Phthorimaea operculella*) to field-grown potato. *Pest Management Science* 75: 616-621.
- Tosh RC, Glen P, Neil D, Jim H. 2003. Reproductive response of generalist and specialist aphid morphs with the same genotype to plant secondary compounds and amino acids. *Journal of Insect Physiology* 49: 1173-1182.
- Tsedeke Abate, Gashawbeza Ayalew. 1994. Progress in vegetable pest management research. pp. 187-193. In Herath E, and Desalegne L. (eds), *Horticultural Research and Development in Ethiopia*, Addis Ababa, Ethiopia.