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Diet effects on survivorship and developmental parameters of tufted apple bud moth, *Platynota idaeusalis* (Walker) (Lepidoptera: Tortricidae).

Efectos de la dieta en la supervivencia y parámetros de desarrollo de la polilla de la manzana *Platynota idaeusalis* (Walker) (Lepidoptera: Tortricidae).

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Abstract

Survival of larvae, developmental time, pupal and adult weights of the tufted apple moth *Platynota idaeusalis* (Walker) (Lepidoptera: Tortricidae), were monitored in the laboratory for a comparison of performance among a lima bean-based synthetic diet and four different host plant species: apple, *Malus domestica* (Bork.) cv. Red Yorking; black raspberry, *Rubus occidentalis* L.; broad-leaved plantain, *Plantago major* L.; and dandelion, *Taraxacum officinale* Wiggers. Artificial diet proved to be the best diet for *P. idaeusalis* in survivorship and in all the developmental parameters studied. Excluding artificial diet, survivorship was highest when feeding on apple, and lowest on dandelion at pupation, and at adult eclosion. Black raspberry and plantain were intermediate in their effects. Developmental time on apple was about the same as dandelion-fed larvae, whereas larvae feeding on plantain had the longest developmental time taken to pupation and adult eclosion among all diets. Female larvae reared on black raspberry emerged 2.6 days later than males, compared with 0.3 days for apple-reared *P. idaeusalis*. Larvae reared on plantain produced the heaviest pupae and adult female among host plant species, followed by apple, dandelion, and black raspberry.

Key words: development, interaction diet-insect, *Platynota idaeusalis*, apple.

Resumen

Supervivencia de las larvas, tiempo de desarrollo, pesos de la pupas y adultos de la polilla de la manzana fueron comparados entre una dieta artificial y cuatro diferentes especies de plantas hospederas: manzana, *Malus domestica* (Bork.)

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cv. Red Yorking; mora, *Rubus occidentalis* L.; llantén, *Plantago major* L.; y diente de león, *Taraxacum officinale* Wiggers. La dieta artificial fue la mejor para *P. idaeusalis* en todos los parámetros de desarrollo estudiados, pero hubo también un efecto significativo de las plantas hospederas. Supervivencia hasta pupación y eclosión del adulto fue mayor en larvas que se alimentaron de manzana y en cambio más baja en diente de león. Tiempo de desarrollo fue mas corto en larvas que se alimentaron en manzana y diente de león, mientras las larvas que se alimentaron de llantén tuvieron el tiempo de desarrollo más largo hasta pupación y eclosión de adultos. La eclosión de las hembras fue siempre posterior que la de los machos, pero la magnitud de la diferencia varió de acuerdo al hospedero. Las larvas criadas en llantén produjeron las pupas y adultos hembras más pesadas, en cambio mora produjo las más livianas.
Palabras claves: desarrollo, interacción dieta-insecto, *Platynota idaeusalis*, manzana.

Introduction

The tufted apple bud moth, *Platynota idaeusalis* (Walker) (Lepidoptera: Tortricidae) is a native polyphagous herbivore that is the most significant direct insect pest for many apple growers in Pennsylvania (16, 19) and other apple-producing areas along the Atlantic seaboard (18).

P. idaeusalis is a highly polyphagous species [attacking at least 17 plant families (20)], there is a high probability for this insect to feed on a wide range of plants with unique secondary compounds. Second generation larvae overwinter as second through fourth instars in larval shelters such as rolled leaves and decaying fruit in apple, peach, cherry, and pear orchards (8, 24) and complete development in the spring on a variety of herbaceous species and apple root suckers (8). Knight and Hull (19) found that adult and larval populations were often on a wide variety of herbaceous plant species beneath host apple, pear, peach, nectarine, and cherry trees. They also noted that knowledge of *P. idaeusalis* biology on hosts other than apple, e. g., on ground cover within orchards, would be extremely useful in considering the allocation of control measures.

Though often found on other crops, such as peach, pear, and sweet and sour cherry, *P. idaeusalis* is not considered an important pest other than on apple (19, 28). However, populations of *P. idaeusalis* that feed on these alternate hosts can be a source of reinfestation into apples.

Although *P. idaeusalis* can feed on many different host plant species (20), there is currently little knowledge on feeding preference. In a neonate and fourth instar multi-choice assay, Dominguez-Gil *et al.* (11) found that the number of neonates moving to apple and black raspberry leaf disks was higher than on dandelion and plantain. Plantain leaf disks were significantly less preferred by neonates than those of apple, black raspberry, and dandelion. However, significantly more leaf tissue was consumed by fourth instar larvae from apple and dandelion than from black raspberry and plantain. They concluded that apple is a preferred host for both newly-hatched and older larvae, while young larvae preferred black raspberry over dandelion and plantain and older larvae prefer. dandelion equally to apple, but more than either black raspberry or plantain.

Simelane (28), working with a field strain of *P. idaeusalis* reared on apple, peach and cherry leaves, and synthetic diet, found that host has an influence on the survivorship and developmental time to adulthood. Larvae reared on apple and cherry were not significantly different in time to pupation or adult eclosion or in pupal weights. *P. idaeusalis* larvae fed on peach developed faster and reached higher pupal weight, whereas larvae feeding cherry took longer to develop and achieved the lowest pupal weights. Survivorship was highest when feeding on apple and lowest on peach. He concluded that the type of host has an influence on the developmental time, fitness, and mortality of *P. idaeusalis*. Developmental rates may be different in cherry and peach orchards so that population dynamic predictions and possibly timing of control actions would have to be shifted to account for these differences (28).

The host plant has long been recognized as an important factor affecting the population dynamics of phytophagous insects (23). Although few studies of *P. idaeusalis* have focused on the role of the host plant, the species, condition, and quantity of available food plants may be of great significance in determining insect population levels (31). Potential host plants differ in their suitability, their effects on larval development rate, pupal weight, female fecundity, survivorship, and behavior (2, 4) and in their acceptance by larvae in laboratory choice tests and in the field. The choice of food plant and the composition of plant species may interact with various environmental factors to influence the population biology of *P. idaeusalis*.

The interaction of this pest with most of its non-crop host plants has not been thoroughly studied, but affects many components of pest management. Because of these plant species are common weeds and contribute to *P. idaeusalis* population in the orchard, it is important to understand the influence of plant allelochemical on the *P. idaeusalis* survival and development, pesticide resistance, and detoxification ability. Little is known about the effect these plants may have on the development and reproductive performance of *P. idaeusalis*.

This study was designed to examine the larval performance of *P. idaeusalis* on four different host plant species: apple, *Malus domestica* (Bork.) cv. Red Yorking; black raspberry, *Rubus occidentalis* L.; broad-leaved plantain, *Plantago major* L.; dandelion, *Taraxacum officinale* Wiggers; plus a lima bean-based synthethic diet. Performance was measured as larval survival to pupation and adult eclosion, development times, pupal weight, and adult body mass.

Materials and methods

Host-plants. Host-plant species (table 1) were raised in a greenhouse at the Pennsylvania State University, University Park. Apple is the economically important host of *P. idaeusalis*; the other three species are present in the apple orchard and surrounding vegetation. The apple trees were cultivar Red Yorking on Emla 7 root stock. Black raspberries were started from cuttings. The remaining host species were reared from seed in potting soil. All plants were transplanted to pots filled with Terra Lite Metro-Mix 250® Growing medium (E. C. Geiger, Harleysville, PA). Plants were fertilized every two months with water-soluble 15-30-15 (N-P-K) fertilizer (4.0 g/L). Plants were watered as needed and grown under a 16-h photophase and ambient relative humidity. Whitefly, thrips, mite and aphid infestations in the greenhouse necessitated the use of 2.5 % Safer insecticidal soap (50.5 % potassium salts of fatty acids, Agro-Chem, Jamul, CA). As a precaution, all host species were treated at the same time.

Test plants were selected arbitrarily from a group of individual plants that were similar in height and phenology. For comparison with previous studies, *P. idaeusalis* larvae were also reared on a lima bean-based artificial diet (21).

Insects. The genotype resistant to azinphosmethyl used in this experiment is a near isogenic line derived from resistant larvae collected in an apple orchard in Adams Co., Pa. The main objective of having created this strain was to select a strain resistant specifically to azinphosmethyl. Progeny from this collection were crossed with a laboratory susceptible line, and backcrossing to the lab susceptible line was carried out for four additional generations. At each backcross the portion of the genome that was susceptible increased by 50 %, so that after four generations *P. idaeusalis* had genomes approximately 94 % that of the susceptible strain. Repeated backcrossing essentially creates an "isogenic" strain by gradually diluting the fraction of the genome coming from the resistan parent (26). This method is used to move a major resistance gene into a susceptible genetic background and thereby isolate it from other genes that affect the resistant phenotype. The azinphosmethyl-resistant strain was selected with azinphosmethyl in three generations (F_4 ,F_7, F_{10}).

Homozygosity of the resistant strain was increased by selection of larvae. Beginning with the first laboratory generation, the strain was exposed to selection pressure through four generations by exposing neonates to 25 ppm azinphosmethyl diet incorporation assay. Selection was made with neonates using 25 ppm azinphosmethyl diet incorporation assay. This dose represents the LC99 for the susceptible colony (6). The selection protocol followed Biddinger (6). Formulated azinphosmethyl was applied (0.5 mL) in diluted aqueous solution to the surface of 7-10 mL of lima bean-based synthetic diet in plastic cups and allowed to air-dry for 2-3 h. Test larvae

Table 1. Plant species used in fitness study for *Platynota idaeusalis*.

Common name	Scientific name	Source	Variety	Family
Apple	*Malus domestica* (Bork.).	Adams County Nursery, Aspers, PA.	Red Yorking	Rosaceae
Black raspberry	*Rubus occidentalis* L.	Miller Nurseries, Canandaigua, NY.	Allen	Rosaceae
Broad-leaved plantain	*Plantago major* L.	B. McPheron house, Port Matilda, PA.		Plantaginaceae
Dandelion	*Taraxacum officinale* Wiggers	Stokes Seeds, Inc., Fredonia, NY.		Asteraceae

were introduced into diet cups in groups of four. The larval exposure period to the treated diet was until pupation or death.

Bioassay. Larvae used in this experiment were reared on a lima bean-based artificial diet (21) at 26.7 °C, 60 % relative humidity with a photoperiod of 16:8 (L:D) h. Fourth instar larvae (12 days old) were removed from artificial diet and transferred to each host to complete larval development. Larvae of the diet treatment were transferred to new cups with diet. Larvae from generation F_{19} were used for these experiments.

Fifty-five 14-day old larvae were transferred onto caged, potted pple and black raspberry and 50 onto plantain and dandelion in sleeve cages (5 or 10 larvae per cage) in a walk-in type growth chamber. The growth chamber was set at 26.7 °C, day length: 16:8 (L:D) h and 50-80 % R.H. The cages were made of fine pore nylon mesh and sealed with parafilm. Another set of 50 14-day old larvae were transferred singly in 28 mL plastic cups containing semi-synthetic lima bean diet (21). All cages and cups were checked every two days for date of pupation and eclosion. The pupae from all treatments were weighed, sexed and transferred from the cages singly into plastic cups until adult eclosion. Pupae and adults were weighed using an electronic balance accurate to 0.1 mg. Development time to pupation and adult eclosion, pupal fresh weight, adult dry weight, sex ratio and survivorship on each host species were measured.

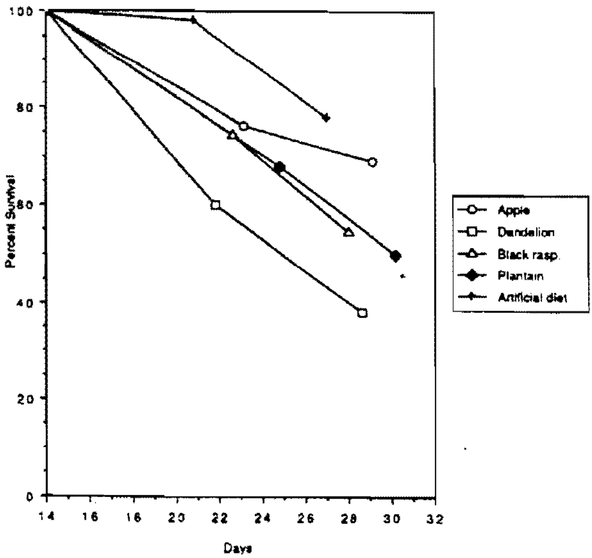
Statistical analyses. Survivorship, development time to pupation and adult eclosion, and pupal and adult weights were analyzed by two way analysis of variance (ANOVA) using the Statview statistical program (1) followed by Fisher's protected least significant difference (PLSD) mean separation tests (22). Factors for the two-way analyses were diet and sex. Specific comparisons between males and females within each host were evaluated by 2-tailed t-tests. χ^2 tests were used to determine if there was departure from an expected 1:1 sex ratio.

Results and discussion

Survivorship. All insects were reared for 13 days on artificial diet. Any difference in survivorship, development time, pupal and adult weight occurred after 14 days, the time when the larvae were transferred to the hosts.

Survival to pupation (98 %) and adulthood (78 %) was highest on synthetic diet-reared larvae (figure 1). Feeding on apple resulted in the highest survivorship among the host plant species (76 % at pupation, 69 % at adult eclosion) (figure 1). *P. idaeusalis* showed the lowest survival rate on dandelion (60 % at pupation, 38 % at adult eclosion) (figure 1). The percentage of larvae surviving to pupation and adult eclosion for black raspberry (74.5 %, 54.5 %) and plantain (68 %, 50 %) had intermediate values.

Development time. The type of food consumed by larvae, sex, and the interaction between host and sex



Data points show survival and development time at pupation, and adult eclosion. Initial cohort at neonate on apple and black raspberry n = 55; dandelion, plantain, and artificial diet n = 50.

Figure 1. Survivorship curves for *P. idaeusalis* larvae transferred from artificial diet onto different diets at 14-days after egg hatch, plotted as the percent of the initial cohort alive at neonate.

each had a significant influence on pupal and adult weight, the number of days from neonate (14 days old) to pupation, and days from 14-day old to adult eclosion for both males and females, although the main effect of sex on days to adult eclosion was not significant (table 2). Male larvae fed dandelion and black raspberry developed significantly faster than did their female counterparts in pairwise comparisons (table 3, figure 2). Although not significantly different, male larvae fed apple and plantain developed faster than did the females on those hosts (table 3, figure 2). Males reared on artificial diet developed fastest to the pupal stage, followed by dandelion, black raspberry, apple and plantain (table 3, figure 2). Females fed on artificial diet developed faster, followed by apple, dandelion, black raspberry, and plantain (table 3, figure 2). Both males and females developed significantly more slowly than on other hosts (table 3, figure 2).

Host again had a significant effect on the number of days to adult eclosion, with sex and the interaction between host and sex ratio also significant (table 2). Adult males emerged significantly earlier than females from larvae reared on black raspberry (table 3, figure 3). In fact, males in the artificial diet and black raspberry treatments emerged first among all hosts followed by dandelion, apple, and plantain. Although not significantly differ-

Table 2. Two-way analysis of variance indicating source of variation, degrees of freedom, F, and P values for data from fitness study of *P. idaeusalis*.

Source of variation	Diet		Gender		Interaction (Diet X Gender)	
	df	F	df	F	df	F
Pupal weight	4.172	16.9***	1.172	107.9***	4.172	9.9***
Adult weight	4.130	10.4***	1.130	91.3***	4.130	10.1***
Days from neonate to pupation	4.173	13.5***	1.173	13.4***	4.173	2.4*
Days from neonate to adult eclosion	4.131	10.7***	1.131	1.5	4.131	3.7**

* F is significant at $P < .05$. ** $P < .01$. *** $P < .0001$

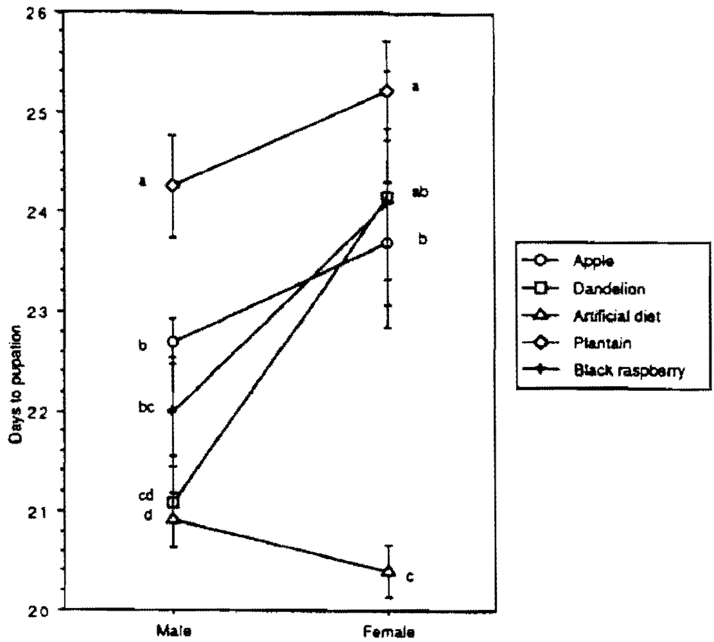


Figure 2. Interaction line plot of the influence of dietary host on the mean of days from neonate to pupation for each sex.

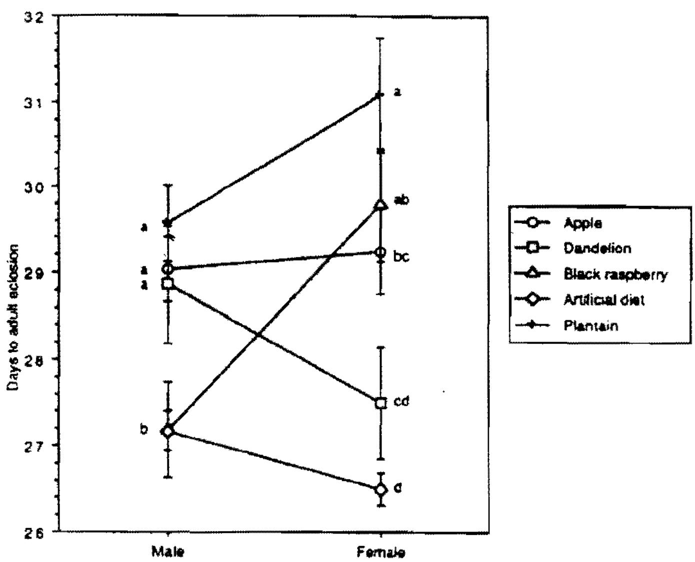


Figure 3. Interaction line plot of the influence of dietary host on the mean days from neonate to adult eclosion.

ent, adult males reared on dandelion took longer to eclose than did females (table 3, figure 3). Females in the black raspberry treatment were one of the last to emerge among the five different diets (figure 3). Artificial diet females were the first to emerge among all hosts (figure 3). Feeding on artificial diet and dandelion resulted in the fastest development to female adult eclosion, followed by apple, black raspberry, and plantain (table 3, figure 3).

Pupal and adult weights. Female pupae weighed significantly more than males on all diets (table 3, figures 4 and 5). Feeding on artificial diet resulted in the highest female pupal weight among all hosts, followed by plantain, apple, dandelion, and black raspberry (table 3, figures 4 and 5). Pupal weights did not differ significantly among males (table 3, figures 4 and 5). Adult weights were significantly lower in males than females on artificial diet, plantain, and apple.

Female adults were heavier when they were reared on artificial diet than when they fed the other hosts (table 3, figures 6 and 7). Black raspberry appeared to have the most detrimental effect on female adult weights, resulting in the lowest weights among the different diets for females (table 3, figures 6 and 7). Apple resulted in the highest male adult weight among the different diets (table 3, figures 6 and 7).

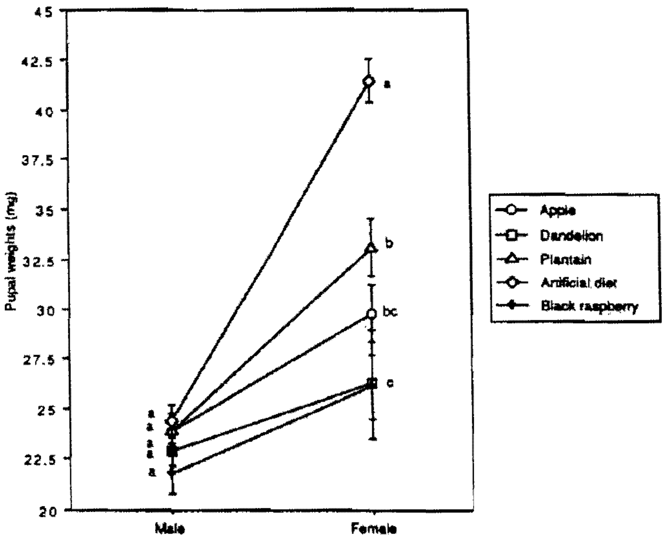
Host effects on sex ratio. Although sex ratio was not known to be equal at the beginning of the experiment (14-day old larvae) the individuals were distributed randomly among treatments, so the treatments should have started with similar sex ratios. More dandelion-fed larvae developed signnificantly into male than female pupae (table 4). Black raspberry had the second highest male-biased sex ratio (table 4). Meanwhile, larvae reared on plantain, artificial diet, and apple yielded about the same number of males and females, both at pupation and eclosion.

Stephens & Krebs (30) considered special features of herbivores that make them unusual consumers. While attempting to fulfill their nutritional requirements by consuming plant tissues and products, however, herbivores face problems regarding foraging strategies and being subjected to potentially deleterious factors that may reduce their performance and probability of survival (29). For example, allelochemicals form one major line of plant defense with which herbivores must cope during both feeding and the postingestive processing of food (5, 13, 14, 25). Because most, if not all, plants and plant parts contain both nutrients and allelochemi-cals, the consumption, and utilization of food by herbivores usually involves their interaction (29). As a result, diets are often characterized by partial consumption of a few or many plant species (27) because food quality of any one food type is relatively low (when compared with food quality for carnivores), and one food type rarely will provide all essential nutrients for survival (5, 9, 30).

The host plant consumed has an influence on survivorship and fitness of *P. idaeusalis*. Survivorship and development rates of *P. idaeusalis* larvae are host specific (17). This study

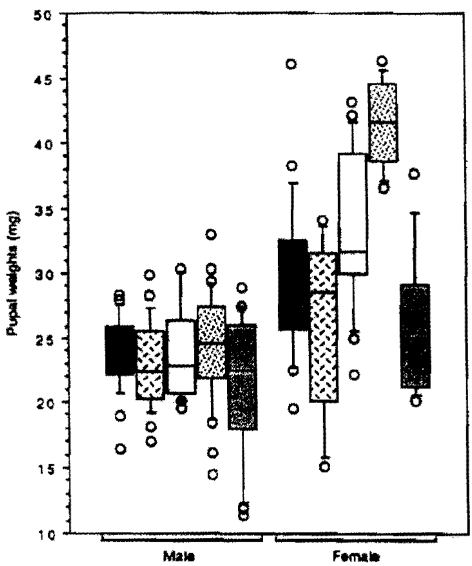
Table 3. Effect of diet on the mean pupal and adult dry weights, and development times (± SEM; n) of *P. idaeusalis*.

Diet	Sex	Days to pupation	Days to eclosion	Pupal weight (mg)	Adult dry weight (mg)
Artificial diet	F	20.4 (0.3;10)	26.5 (0.2;8)	41.5 (1.1;10)	7.4 (0.2;9)
P-level (t-test)	M	20.9 (0.3;26)	27.2 (0.2;23)	24.4 (0.8;26)	3.3 (0.1;20)
		0.2821	0.1132	0.0001	0.0001
Apple	F	23.7 (0.6;19)	29.3 (0.5;12)	29.8 (1.5;18)	5.3 (0.4;15)
P-level (t-test)	M	22.7 (0.2;24)	29.0 (0.4;23)	23.9 (0.6;24)	4.0 (0.2;21)
		0.1099	0.7426	0.0001	0.0035
Black raspberry	F	24.1 (0.8;12)	29.8 (0.7;10)	26.1 (1.6;12)	3.9 (0.4;10)
P-level (t-test)	M	22.0 (0.6;29)	27.2 (0.6;21)	21.8 (1.0;29)	3.2 (0.2;21)
		0.0414	0.0087	0.0253	0.1014
Plantain	F	25.2 (0.5;18)	31.1 (0.7;11)	33.1 (1.4;18)	5.4 (0.5;12)
P-level (t-test)	M	24.3 (0.5;16)	29.6 (0.4;14)	23.9 (0.9;16)	3.2 (0.2;13)
		0.1888	0.0611	0.0001	0.0002
Dandelion	F	24.1 (1.3;7)	27.5 (0.6;4)	26.2 (2.7;7)	4.3 (0.7;6)
P-level (t-test)	M	21.1 (0.5;22)	28.9 (0.7;15)	22.9 (0.7;22)	3.2 (0.2;13)
		0.009	0.3324	0.0977	0.0712



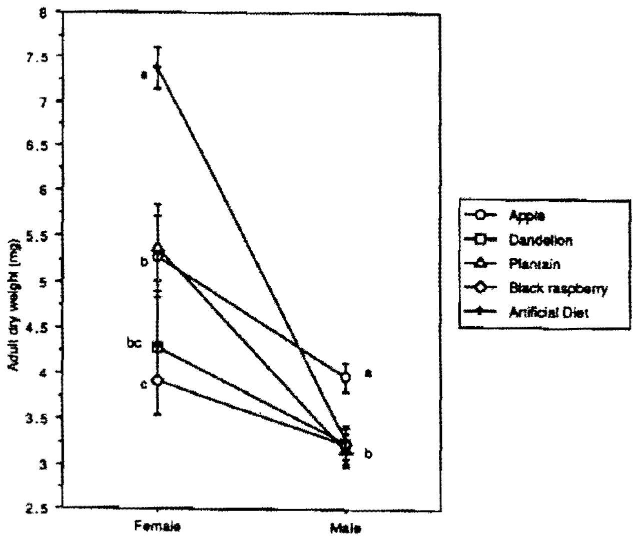
Means within each sex indicated by the same letter are not significantly different from each other (P < .05, Fisher's protected LSD).

Figure 4. Interaction line plot of the influence of dietary host on mean pupal weights of *P. idaeusalis* males and females.



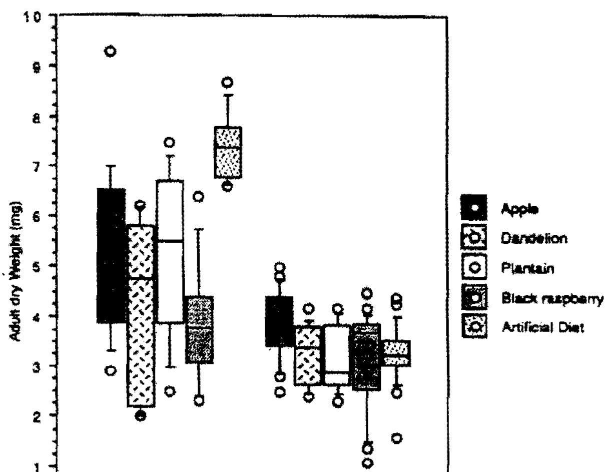
Box is middle 50 % of observations. Horizontal line in box is the median. Ehen it is necessary, the boxplot displays the 10th, 25th, 50th, 75th and 90th percentiles of a variable. All values for variables above the 90th percentile and below the 10th percentile are plotted separately.

Figure 5. Boxplots of pupal weights of *P. idaeusalis* fed different diets.



Means within each sex indicated by the same letter are not significantly different from each other ($P < .05$, Fisher's protected LSD).

Figure 6. Interaction line plot of the influence of dietary host on the mean adult dry weights of *P. idaeusalis* males and females.



Box is middle 50 % of observations. Horizontal line in box is the median. Ehen it is necessary, the boxplot displays the 10th, 25th, 50th, 75th and 90th percentiles of a variable. All values for variables above the 90th percentile and below the 10th percentile are plotted separately.

Figure 7. Boxplots of adult dry weights of *P. idaeusalis* fed different diets.

Table 4. Sex ratio for *P. idaeusalis* reared on different diets.[1]

	At Pupation		At Adult eclosion	
Diet	n	Male:female	n	Male:female
Apple	42	1.3:1	38	1.4:1
Black Raspberry	41	2.4:1**	30	2.0:1*
Dandelion	30	3.3:1**	19	3.8:1**
Plantain	34	0.9:1	25	1.3:1
Artificial diet	49	1.1:1	39	1.2:1

1. Sex ratio was not known to be 1:1 at the beginning of the experiment, but should be similar among diet treatments. *, $P < .001$. **, $P < .0001$, by χ^2.

demonstrated that *P. idaeusalis* can complete development on several host plants and that different hosts led to different developmental outcomes. Groundcover weeds and wild hosts adjacent to cultivated orchards have the potential to serve as reservoirs of *P. idaeusalis* populations (10, 12, 19).

Artificial diet proved to be the best host for *P. idaeusalis* survivorship and for all the developmental parameters studied in the present study. Felland & Hull (13) reported that larvae reared on artificial diet survived better, developed faster, and produced heavier male and female adults. David *et al.* (10) also showed that *P. idaeusalis* developed faster on semi-synthetic diet compared to feeding on excised leaves of strawberry, apple, and dewberry in the laboratory.

Among host plants, survivorship was highest when feeding on apple and lowest on dandelion. Black raspberry and plantain display intermediate values in both survival at pupation and at adult eclosion (figure 1).

This finding has control implications for *P. idaeusalis*. Even though, *P. idaeusalis* survival is lower when the insect feed on weeds (dandelion and plantain) or surrounding vegetation (black raspberry), feeding on those hosts could still have important contribution to the pest population in the orchards.

Developmental time on dandelion was about the same as apple-fed larvae, whereas larvae feeding on plantain had the longest time taken to pupation and adult eclosion among all diets. In the field prolonging the developmental period might represent an important factor for fitness reduction and affect the nutritional suitability of the host plant, the susceptibility of the larva to predators and parasitoids, the availability of mates, and prolonged exposure to abiotic factors. Female larvae reared on black raspberry emerged 2.6 days later than males, compared with 0.3 days for apple-reared *P. idaeusalis*. In the case of plantain-fed larvae, females emerged 1.5 days later than males. The difference in total development time between the sexes might lead to a shortage of males for female moths developing on black raspberry or plantain in nature.

Larvae reared on plantain produced the heaviest pupae and adult females among the host plant species, followed by apple, dandelion, and black raspberry. These results indicate that extended development of plantain-fed female larvae allows them to grow somewhat larger and form heavier pupae; pupal weight directly correlates with higher fecundity in terms of number of eggs produced for other lepidopterans (8, 16).

These results are thus consistent with those of Simelane (29), who also determined that apple and cherry were not significantly different from one another in developmental time taken to pupation and adult eclosion or pupal weights. Excluding the synthetic diet, which resulted in the best performance, *P. idaeusalis* larvae feeding on peach developed fastest and achieved the highest pupal weights, whereas larvae feeding on cherry took longer to develop and had the lowest pupal weight. Survivorship was highest when feeding on apple and lowest on peach. Simelane (29) used a similar methodology (potted trees) and the same set of environmental conditions.

Hunter *et al.* (18) reported that densities of *P. idaeusalis* larvae varied significantly in both larval generations among leaf types within trees and among cultivars. The highest densities of *P. idaeusalis* were observed on 'Delicious' and lowest on 'Yorking,' while terminal shoot leaves supported higher larval densities than either fruiting or nonfruiting spurs. Furthermore, Hunter *et al.* (18) found that the relationship between larval density and phloridzin concentration varied among leaf types. Larval densities on shoot leaves increased as phloridzin concentrations in those leaves increased in the first generation. However fruiting spurs supported higher larval densities than either nonfruiting spurs or shoot leaves.

Host effects on individual larvae, such as those reported here, and by Felland & Hull (13), Simelane (29), Hunter *et al.* (18), are undoubtedly important factors affecting *P. idaeusalis* in nature. *P. idaeusalis* can feed on many different host plants, leading to different rates of development, fitness, and mortality. Such effects must be considered in studies of the population dynamics of the insect over large areas.

Therefore, additional studies are needed to determine *P. idaeusalis* population biology outside of apple, on groundcover within orchards, and on different apple cultivars. This knowledge could be useful in timing of control actions.

Since fruit production is intermixed in Pennsylvania, the variability in the life cycle of *P. idaeusalis* will be high due to the many host species available. Recommendations for the timing of control applications due to the different phenologies will have to be more refined if the selection pressure which results in the development of resistance is to be reduced. For example, insecticide spray programs may have to be adjusted to take into account the delayed emergence due to feeding on plantain.

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