Performance effects of Californian host plants on the Light Brown Apple Moth, *Epiphyas postvittana* (Walker) [Lepidoptera: Tortricidae]

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Abstract The light brown apple moth (LBAM) of Australia is a recent invasive pest to California. Little is known about the ecology of the LBAM in California. Since the moth is a generalist herbivore known to feed on a remarkably long list of plant species, LBAM will likely feed on novel host plants, including symbolic native species of coastal California. The purpose of this study was to compare the effects of several potential host plant species available in the Bay Area on the fitness of the light brown apple moth. Two experimental lab studies were conducted to assess both direct and indirect effects of locally available plant hosts on LBAM fitness. Results indicate that LBAM fitness is adversely impacted by a diet of the California native plants tested, but positive fitness effects of the plant host that is an invasive species slightly surpassed the known host, a cultivated species. Adult moths did not prefer the crop plant or the invasive plant host for oviposition, which could reflect their similar, positive effects on larval fitness. The native host plants tested most likely serve as inferior host plants when compared to crops and herbaceous weeds, yet there likely are significant differences in fitness effects among native plant species and some could still be capable of supporting populations. Furthermore, since there is a multitude of untested novel plant species that could also serve as hosts, it is possible that LBAM populations could grow even if excluded from agricultural zones.

Introduction

As people and commodities travel greater distances with globalization, natural biogeographic barriers are effectively reduced since plants, animals, and pathogens can "hitchhike" along the way (Yoshida *et al*. 2007, Metcalf 1995). While there are impediments that reduce the odds of successful establishment, such as resource availability or a requisite population threshold for population growth, these hitchhikers occasionally do gain a foothold as observed in cases ranging from zebra mussels in the Great Lakes (Berkman *et al.* 1994) to the cane toad in Australia (Barton 1997). In successful invasions, the exotic organism may be at an advantage in the face of a novel set of resources or biota that pose little threat through competition or predation. These biological invasions may have negative ecological impacts by displacing native species, for example, but can also have significant economic impacts because of damage to crops and native species and the need for expensive control efforts (Sanders *et al*. 2003, Johnson *et al*. 2007).

Although most phytophagous, or plant-eating, insects are specialists (Cain *et al*. 2008), meaning that they can forage on only a select few plant species, the phytophagous insects that are generalists, or polyphagous, can consume a variety of plants and are therefore more likely to find suitable plants in a new environment. Insect generalists have two primary advantages over specialists: greater resource availability and the ability to consume a better balance of nutrients by feeding from different plants (Bernays and Menkenberg 1997). Pupulations of invasive herbivores that are generalists may easily grow out of control, especially when the range of suitable plant hosts is vast and natural enemies are lacking (Metcalf 1995; Johnson *et al*. 2007). California's geographic location, array of habitat types and climates, and role in world agricultural production and trade render the state particularly prone to invasions by unwanted pests (Metcalf 1995). In fact, it is estimated that 50% of crop losses from insect damage in California are due to exotic pests (Metcalf 1995). As a result, there has been a long history of pest exclusion and eradication attempts, which extends from the creation of inspection stations to intercept alfalfa weevil in the late 19th century (Leifson 1989) through the ongoing attack on the medfly, *Ceratitis capitata*. The state has been "eradicating" medfly since the early 1980s with a range of techniques, including the controversial spraying of malthion over urban centers, yet the pest has persisted at diminished levels for over twenty years (CDFA 2008). Lepidopterans, such as the codling moth and other indigenous leafrollers, have also been targets of eradication or control programs because of their devastating impacts on the agricultural industry (Metcalf 1995).

An exotic leafroller, the light brown apple moth (LBAM), has recently invaded the central coast of California from Santa Cruz to the Bay Area. The moth is native to Australia and also has become established in New Zealand, New Caledonia, Hawaii, and the United Kingdom (Johnson *et al*. 2007). LBAM has been deemed a Class-A pest by the California Department of Food and Agriculture (CDFA), which is an organism considered to pose a high risk of invading and having significant consequences when this occurs (Johnson *et al*. 2007). Part of the reason for this classification is the moth's purported ability to attack a huge range of plants, including important cash crops and culturally significant species, such as grape and coastal redwood respectively (CDFA 2007). LBAM has been reported feeding on over 2,000 host plant species (USDA 2008a), including more than 250 crop plants (Danthanarayana *et al*. 1995), and this figure may grow as the insect's range expands into new locations with new plant species. Economic damage attributed to LBAM in its native range, Australia, has mainly been limited to pome fruits, stone fruits, grape, and citrus (Danthanarayana 1975, Danthanarayana *et al.* 1995). In Australia, LBAM has damaged up to 85% of crop yields during the worst outbreaks. While LBAM has been reported on native species in California, such as manzanita (Mills 2008, pers. comm.) and redwood (CDFA 2007), there is no formal data on the effects of this new diet on the moth's fitness and its preference for these new species over traditional plant hosts. Some of these reported host plants seem unlikely to be ideal hosts that can sustain LBAM populations. For example, despite opposite claims by the CDFA and the USDA (CDFA 2007), it seems unlikely that the moth could survive and grow substantially on redwood or Monterey cypress since it usually builds protective structures by rolling up the edge of a leaf as a larva (USDA 2008a, 2008b). However, based on this information, state and federal agencies estimate economic impacts from agricultural losses could exceed $100 million annually if eradication fails (Fowler *et al.* 2007). To reduce losses, costly control measures and accompanying quarantines and trade restrictions have already been employed (Johnson *et al.* 2007, Fowler *et al.* 2007).

The legitimacy of these impact projections has been questioned in legal and political arenas because of scientific uncertainty in the underlying assumptions (Laird 2008). There are still many unanswered questions regarding the population ecology of this moth in its new environment that would inform predictions about its likely impacts (Johnson *et al*. 2007, USDA 2008). Despite the lack of data, the arrival of this insect pest has already elicited a sensationalized eradication campaign (Pesticide Action Network North America 2008, elect. comm.). The paucity of data on the ecology of the moth in this novel environment exemplifies an inherent problem with managing an exotic pest since this often leads to speculative predictions and inappropriate methods of control (Perkins 1989). In the case of LBAM, the knowledge gap is especially relevant because the extent of damage it causes on a particular host species appears to vary widely depending on other ecological factors, including the availability of alternative host plants. In Hawaii, for example, LBAM has not posed an economic threat since it arrived over a century ago (Danthanarayana 1975, USDA 2008a). There, LBAM is only a minor pest at worst and beneficial at best for its ability to suppress certain weeds like Himalayan blackberry (HDA 2007). Likewise, LBAM is usually not an economic pest in the United Kingdom, where it feeds on a multitude of non-crop plants (Danthanarayana *et al*. 1995). The insect's range and population growth are apparently limited by climate in both of these environments (Johnson *et al*. 2007). The potential range and impact of LBAM in the U.S. thus depends on environmental conditions, such as climate, in combination with biotic factors, like the range and diversity of host plant species. Since little is known about the effects on LBAM of these factors locally, the degree of risk LBAM poses in California is unknown and disputed (Johnson *et al*. 2007, Harder and Rosendale 2008).

Several past studies have been conducted with LBAM in Australia, including investigations of how plant host species affect LBAM fitness and preference, that suggest LBAM is capable of adapting to a range of conditions yet may be affected positively or negatively by the local conditions (Danthanarayana 1975, 2000, Danthanarayana *et al.* 1995). Although LBAM is known to feed on a variety of plant species, it seems likely that it would still exhibit preferences based on underlying host plant effects on fitness. Clear preferences have been demonstrated by other generalist moth species (Shields *et al*. 2003) and can arise due to the need to adapt physiologically to the quality of available food plants given the local biodiversity and seasonality (Hebert *et al*. 2006) or to avoid natural enemies (Singer 2008). For example, as it relates to host plant quality, local plant phenology may provide strong evolutionary pressure in nascent populations of similar polyphagous moth species in order to synchronize hatching with the budburst of the dominant preferred species (Tikkanen and Lyytiainen-Saarenmaa 2002).

Previous work on LBAM suggests that the high level of intraspecific variability observed for several traits, including feeding behavior, correlates to the heterogeneity of environments within its range (Geier and Springett 1976, Gu and Danthanarayana 2000). Furthermore, this variability seems to have a genetic basis that enhances LBAM's adaptive potential (Danthanarayana 2000). These results indicate that LBAM can adjust feeding behavior according to the local conditions and resource pool. Other lepidopteran larvae are known to self-regulate nutrient intake by adjusting foraging behavior (Simpson *et al*. 2004). It therefore seems likely that LBAM would adjust its foraging patterns to reflect the nutritional quality of plants in terms of effects on LBAM fitness. Previous studies demonstrate that the intrinsic rate of population growth varies according to diet for LBAM since the larval host plant affects growth and fecundity (Danthanarayana 1975, Danthanarayana *et al.* 1995). It is essential to know what factors influence the insect's foraging behavior in order to gauge its response to locally available resources and refine methods of detection and control accordingly (Prokopy 1995). Several ecological factors could influence the LBAM's feeding behavior and, in turn, its fitness and population dynamics in California.

In light of the regional abundance and diversity of California native plants and thus potential food sources on the central coast, it seems possible that LBAM may thrive here. Therefore, I ask the question: Is LBAM fitness affected by potential novel host plants found in the Bay Area? I investigated direct effects of host plant on larval fitness as well as the indirect effect of oviposition, or egg-laying, preference by adult moths. Plant damage is only caused by LBAM in the larval stage as they feed on and construct shelters for pupation using the host plant on which they hatch. Oviposition behavior has an indirect effect on LBAM fitness since the oviposition site significantly affects the larvae's host plant selection (Price 1997, Gibbs *et al*. 2006). The moths are thus involved in food plant selection by choosing a plant on which to deposit eggs although larval preferences still have a role in plant host selection because the larvae of this species are relatively mobile (Foster and Howard 1999). Also, there may be a learning component to oviposition behavior that could facilitate a host shift in light of a new environment, particularly in generalist herbivores (Barron 2009). Through an experimental growth study, I compared larval success on five novel host plants, or those that were not present in its native range, that could serve as larval food for the light brown apple moth in California. To test larval performance, I compared larval survivorship, development time to pupation, and pupal weight among larvae reared on native and naturalized plants of the Bay area (Table 1). I also studied the influence of plant species on oviposition by conducting an experimental choice test between two plant species: the control, which was a cultivated species and known host, and the novel host plant that was the highest quality LBAM forage in terms of effects on larval performance. I hypothesized that larvae raised on novel host plants would exhibit reduced survivorship, increased development time, and lower pupal weight compared to the control, and moths would prefer for oviposition the host plant on which larval performance was greatest. While these results do not provide a basis for predictions regarding LBAM's impacts on California plants generally, analyzing the effects of the plants on LBAM allowed me to assess the relative suitability of particular potential hosts of interest.

Methods

Since host plant affects LBAM performance directly and indirectly, there were two components to this study: comparative biology of larvae and preference of ovipositing females.

Part I: Larval performance A colony of LBAM was reared in the lab of Environmental Science, Policy, and Management Professor Nick Mills at the Natural Resources Laboratory on the UC Oxford Tract. A group of five locally available, novel host plants were selected (Table 1) that fall into either category: 1) significant exotic, invasive weeds of California that originate from regions outside the native range of LBAM, or 2) potential novel hosts in California that are culturally or economically significant natives. These plants were compared to grape, which served as a control since it is a crop plant that is a known host (Danthanarayana *et al.* 1995) prevalent both in LBAM's native range and coastal California. Of particular interest was the manzanita species tested, which seemed to be supporting LBAM populations in the Santa Cruz area based on observations in the field (Mills 2008, pers. comm.). This varietal was also one of the most commonly cultivated ornamental manzanitas. Blackberry, the invasive plant tested, was rated severe by the California Invasive Plant Council in terms of its impact, invasiveness, and distribution (Cal-IPC 2008).

Five to seven newly-hatched larvae, progeny of lab-reared females, were placed in each of 15 Petri dishes containing only the cut foliage for each host plant species tested. The larvae ate only the experimental host plants. The foliage was collected at sites around Berkeley and immediately transferred to water-filled, cotton-stoppered vials. Material was replaced as used or after four to six days. The experiment was maintained under constant temperature (23°C) and light cycles (14L:10D). Three parameters were measured to test the effects of these host plants on LBAM caterpillar performance: survivorship, duration of larval development, and pupal weight. These life history traits are commonly used to evaluate larval performance generally and as indicators of host plant suitability in similar studies (Price 1997, Bernays and Menkenberg 1997, Sznajder and Harvery 2003, Vanbergen *et al*. 2003). Larvae were monitored every two to four days for mortality or pupation, which took approximately four to six weeks, and I recorded survivorship as the percent of larvae to pupate. I also recorded development time from hatching until pupation. A longer development period has negative implications for performance since the exposure time of larvae to natural enemies is effectively extended and a lower body weight is typically attained (Price 1997). Pupae were then collected in individual centrifuge tubes and dried in an oven at 55°C until they reached constant mass, which took several days. Oven dried pupal weight was used as a measure of both growth efficiency and as an indicator of potential reproductive capacity since a strong correlation between pupal weight and fecundity has been previously demonstrated (Danthanarayana 1975). Sets of two or three novel plant species were tested at approximately the same time, and grape was tested as the control treatment with each trial. Data collection for each trial overlapped since development time varied depending on plant species, and data for part I was collected from late June through early January.

Table 1. Experimental host plant list

Scientific name	Common name	Category
Rubus armeniacus	Himalayan blackberry	Invasive
Sequoia sempervirens	Coast redwood	Native
Quercus agrifolia	Coast live oak	Native
Cupressus macrocarpa	Monterey cypress	Native
Arctostaphylos densiflora X	Vine Hill Manzanita 'Howard McMinn'	Native/ Ornamental
Vitis vinifera	Grape	Crop (Control)

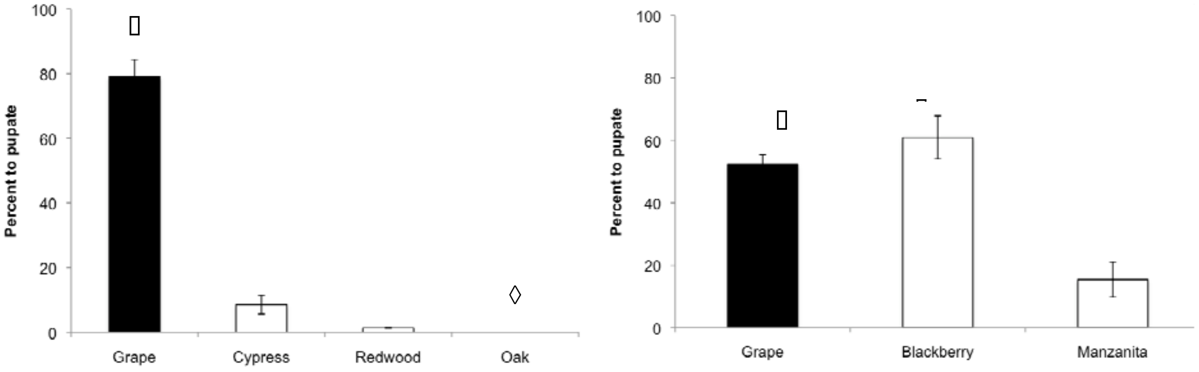
Part II: Oviposition preference Choice tests are often performed to gauge insect preferences for host plants (Price 1997). Grape, the control plant, was compared to the most suitable novel host plant based on the results of Part I (i.e., that on which overall performance was greatest). A host plant preference test was administered to mated, adult females. I conducted the paired choice test in 15 replicates of plastic containers (12 cm x 16 cm), covered with netting, holding two stems of foliage in cotton-stoppered glass vials (4 cm), one of each test species, and two mated female moths, two to three days old. The moths were left in the container for five days, by which time they had oviposited (Danthanarayana 1975). After five days, I recorded the total number of eggs laid on each plant species. This experiment was carried out under controlled temperature conditions (approximately 20 ºC) and exposed to natural light cycles, and was completed in April.

Data Analysis The independent variable throughout the study was host plant species. All statistical analysis was performed in JMP 7 (Statistical Analysis Software, Cary, NC, 2007). In Part I, I tracked development time (days), survivorship (percent of larvae to pupate), and oven-dried pupal weight (milligrams) to test host species effects on larval performance. I used a Tukey-Kramer HSD to identify what species within each trial differed significantly in terms of effects on development time and pupal weight (Quinn and Keogh 2002). Survivorship data was heavily zero-inflated and could not be transformed to meet assumptions of normality and equal variance, so I utilized nonparametric tests (Quinn and Keogh 2002). Within each trial, I performed pairwise Mann-Whitney tests to distinguish what plant species differed in terms of effect on survivorship, using the normal approximation of the test for samples of $n \geq 25$ (Zar 1996). I also did regression analyses of the log-transformed data to determine if survivorship or pupal weight varied with development time or if survivorship varied with pupal weight. Part II of the experiment was a paired choice test conducted with adult moths in which I tracked number of eggs laid per plant. Egg count data was also heavily zero-inflated, so no transformations attained a normal distribution. Therefore, I used a Wilcoxon signed rank test for a significant difference in mean rank (Quinn and Keogh 2002).

Results

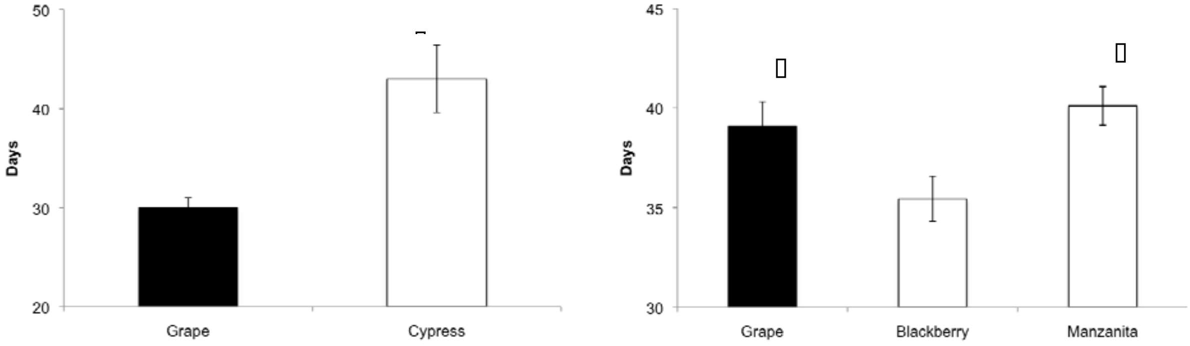
Part I: Larval performance Survivorship of larvae raised on California native host plants was significantly lower than survivorship on the invasive plant (blackberry) or the control (grape) by at least a factor of four (Fig. 1). In Trial 1 (Fig. 1a), larval survivorship on a diet of grape ($n=15$, $\mu=79.1\%$) was at least nine-fold greater than on cypress ($n=30$, $\mu=8.5\%$), redwood (n=15, μ=1.3%), or coast live oak (n=15, μ=0%). Only one caterpillar reared on a redwood diet pupated, and no larvae survived on oak. In Trial 2 (Fig. 1b), larval survivorship on grape (n=15, μ=52.4%) or blackberry (n=15, μ=70.0%) diet was significantly greater than on a diet of manzanita (n=25, μ=15.4%) by almost four times (grape/manzanita: P<0.0001, S=414.5, Z=4.06344; blackberry/manzanita: P<0.0001, S=435, Z=4.68449). There was no significant difference in effects of grape and blackberry on survivorship. While not all native plant species could be directly compared since I conducted two trials, some significant differences among native species were still detected. Survivorship on cypress was significantly higher than on oak (P=0.0316, S=285, Z=-2.14947), but not significantly higher than on redwood (P=0.0946, S=296, Z=-1.67149).

Part I: Survivorship through larval stage



a) Trial 1 b) Trial 2

Figure 1. Mean larval survivorship of LBAM expressed as a percent for a) Trial 1 and b) Trial 2. In both trials, host species significantly affected percent survivorship based on pairwise Mann-Whitney tests. Symbols indicate significant differences (P≤0.05). Bars indicate ±1 S.E. Part I: Larval development time

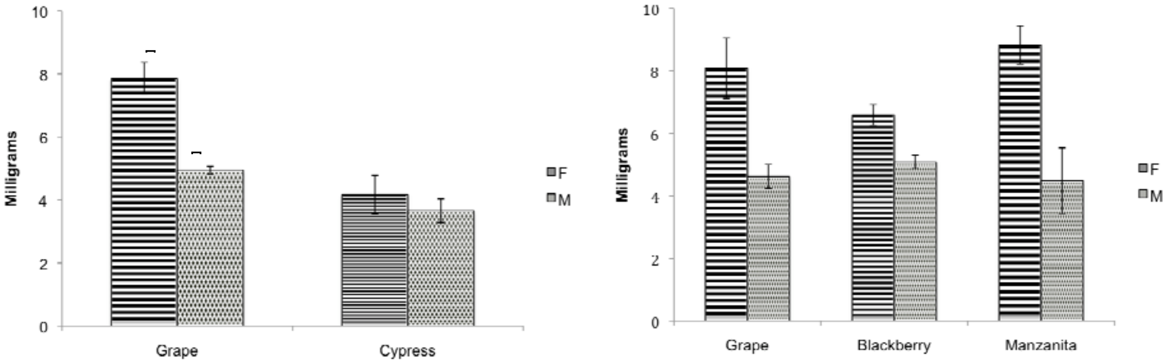


a) Trial 1 b) Trial 2

Figure 2. Mean development time in number of days to pupation for a) Trial 1 and b) Trial 2. In both trials, host species significantly affected development time based on a t test (Trial 1: t=-4.67, df=21, P<0.0001) or an ANOVA and Tukey-Kramer HSD (Trial 2: F=4.98, df=2, P=0.0116). Symbols indicate significant differences (P≤0.05). Bars indicate ±1 S.E. Redwood was excluded since only one data point was obtained.

Development time was at least as long on California natives as on the control and was shorter on the invasive plant relative to the control (Fig. 2). Number of days from hatching to pupation ranged from 22-66, which was the minimum value for grape (n=15, μ=30.1) and maximum value for cypress (n=8, μ=43.0) respectively. Among the first set of plants, development time was almost 45% longer on cypress compared to grape (Fig. 2a). However, development time was approximately 10% shorter on blackberry (n=15, μ=35.5) than on grape (n=14, μ=39.1) or manzanita (n=15, μ=40.1) in Trial 2 (Fig. 2b).

Part I: Pupal weight



a) Trial 1 b) Trial 2

Figure 3. Pupal weight was grouped by sex since females are heavier on average than males. a) In Trial 1, host species significantly affected mean pupal weight based on a t test (female: t=4.64, df=9.73, P=0.001; male: t=3.28, df=6.17, P=0.0161). b) An ANOVA revealed no significant host plant effect in Trial 2 (female: F=3.06, df=30, P=0.0628; male: F=0.24, df=29, P=0.7908). Symbols indicate significant differences (P≤0.05). Bars indicate ±1 S.E. Redwood was excluded because only one data point was obtained.

Pupal weight was significantly lower than the control only for LBAM raised on cypress (Fig. 3). In Trial 1, pupal weight varied by host plant species for both female and male LBAM, and pupal weight of LBAM raised on grape (female: n=13, μ=7.86; male: n=15, μ=4.95) was about 35-90% greater than those raised on cypress (female: n=5, μ=4.17; male: n=6, μ=3.67) (Fig. 3a). In Trial 2, there was no significant effect of host plant species on pupal weight (Fig. 3b, Table 2).

None of the three fitness parameters tested was strongly correlated based on regression analyses of the log-transformed data. Survivorship was most strongly correlated to development time ($r^2=0.36$), with poor survivorship associated with a longer development period, but was not correlated with pupal weight ($r^2<0.15$), except for female pupal weight in Trial 1 ($r^2=0.42$). Pupal weight was also very weakly correlated to development time ($r^2<0.27$).

Part II: Adult moth preference LBAM adults did not prefer either the control or novel host plant for oviposition (Fig. 4). The average number of eggs was almost three times greater on grape (n=15, μ=86.1) than on blackberry (n=15, μ=26.5), but this difference was not statistically significant (P=0.2324).

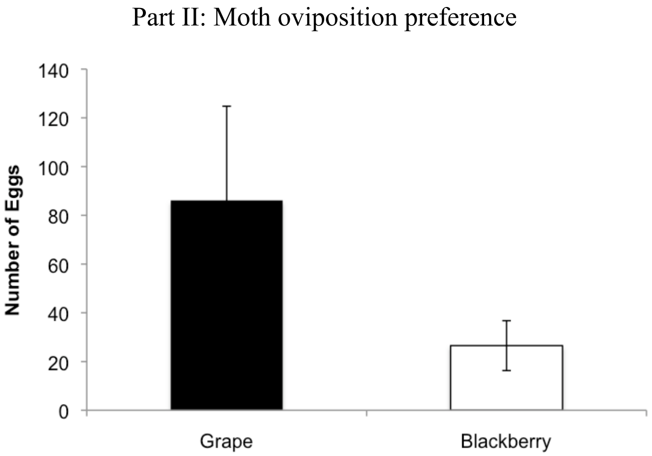


Figure 4. Mean number of eggs laid for grape and blackberry. Based a Wilcoxon signed-rank test, there was no significant preference for either plant (W=12.5, df=14, P=0.2324). Bars indicate ±1 S.E.

Discussion

Because the Bay Area is botanically diverse, there is much potential forage for the LBA moth outside of agricultural zones. However, based on my results, LBAM performance is negatively affected by a strict California native plant diet for the few plants I tested. Performance of LBAM larvae varied with host plant species, with the clearest difference between native and non-native host plants (Figs. 1-4). Adult moth oviposition preference reflected the relative quality of these plants in terms of their effects on larval performance. Results from parts I and II both revealed significant differences between effects of California natives versus non-natives, but little difference within these groups. These results provide insight on the current invasion of California, but also point to further avenues of research to investigate multi-trophic plant host interactions of LBAM in California.

Results from part I support the hypothesis that larvae raised on novel host plants would have reduced survivorship, a longer development period from hatching to pupation, and lower pupal weight compared to the control. Most novel plant species did have a detrimental effect on larval fitness with respect to these life history parameters. However, larvae displayed the greatest overall performance on Himalayan blackberry, a locally invasive plant that is a close relative of cultivated blackberry, since it was comparable to grape in all performance parameters (Figs. 1-3) and slightly surpassed grape in its positive effect on development time (Fig. 2). This host plant was also the plant for which LBAM was cited to be a bio-control agent in Hawaii (HDA 2007). Moreover, blackberry is the most similar in many respects to the agricultural crop control, grape. These results are consistent with previous studies, which indicate that LBAM is a pest primarily on certain agricultural crops, including both grapevine and berryfruit (Danthanarayana *et al.* 1995). This preference for agricultural crops is common since crop plants are a product of artificial selection for certain traits and thus tend to have fewer innate defenses against herbivory (Robinson 2004). Part I results also support the previous finding that herbaceous plants are superior larval food for LBAM compared to woody plants (Danthanarayana 1975). No larvae survived on coast live oak, and both Monterey cypress and coast redwood were inferior to the control, an herbaceous plant. In the second trial, manzanita was also inferior when compared to the herbaceous plants, blackberry and grape. The manzanita varietal was the second most suitable novel host plant overall and is also the plant on which LBAM has been most often observed along the Central Coast (Mills, pers. comm. 2008).

While the patterns for each individual host plant were consistent, i.e., lower survivorship was associated with longer development times and lower pupal weight, I did not observe very strong correlations of these three performance parameters in the regression analysis. The weakest correlation was the variance of pupal weight with development time, but it is possible that the relationship between these traits varied by plant. Host plant species can each affect different components of larval fitness, which is a phenomenon observed in insect herbivores (Gibbs *et al.* 2006). Both positive and negative correlations dependent on host plant species have been found for other lepidopterans, reflecting a tradeoff between survivorship and fertility (Braby and Jones 1994, Fischer and Fiedler 2002, Agosta 2008).

The second hypothesis, that moths would prefer the plant for oviposition on which larval performance was greatest, was also upheld based on the results of part II. There was no significant difference in number of eggs laid on grape or blackberry (Fig. 4), just as there was little difference in larval performance on these plants (Figs. 1-3). Although larvae did have a faster development rate on blackberry, blackberry and grape served as comparable quality larval hosts overall, which was consistent with the fact that adults did not appear to prefer either plant for oviposition. Part II results revealed no significant difference between the most suitable host plants in terms of oviposition preference, but I only tested a choice between two potential plant hosts. Therefore, while the results do not refute my hypothesis, they are certainly not conclusive. In fact, adults of generalist leafroller moths tend to oviposit on fewer plant species than the larvae may actually eat as they lay eggs mainly on the primary larval food sources (Tomkins *et al.* 1991, Price 1997), and prior studies indicate this may be expected for LBAM (Wearing 1998). Adult LBAMs do not usually disperse more than a couple hundred meters, so oviposition is also limited by plant community composition in the immediate environs (USDA 2008). Still, my results do not preclude a strong oviposition preference-larval performance linkage (Price 1997).

To date, there are few data on LBAM specifically that investigate how plant suitability with respect to performance relates to larval foraging behavior; yet applying my results implicitly requires that there is a performance-preference link. In general, the strength of this link is quite variable among insect species (Price 1997). I was able to examine plant species effects on LBAM fitness directly since only one food source was provided, but did not determine whether or not wild LBAM would prefer to eat the plants I tested. This knowledge gap is important since some phytophagous, or plant eating, insects have been shown to prefer forage in the field that does not optimize performance as measured in lab studies (Reavey 1991). In Part II of this study, I attempted to gain some insight to the preference-performance link for LBAM by relating oviposition behavior to larval performance. But, as mentioned above, oviposition preference may not perfectly align with food preferences of the larvae themselves (Wearing 1998). Also, adult LBAM may prefer a plant for oviposition regardless of larval survivorship on that plant like other moth species (Agosta 2008). Although oviposition preference could have reflected differential effects on larval performance in this study, more research needs to be done to establish the strength of this link for LBAM.

Given the limitations of this study, caution must be taken when extrapolating these results to the field. First, only a very small number of plants were tested, so there is a multitude of other potential host plants that LBAM may prefer over any of the plants I tested. While my results may be consistent with other findings about LBAM and host effects generally, it is not appropriate to generalize about what plant groups will be affected by the moth. Also, I could not compare all species since seasonality is known to play a significant role in the chemistry and thus the nutritional quality of food sources for LBAM and other insects (Danthanarayana *et al*. 1995, Bernays and Chapman 1989, Bentancourt *et al*. 2003), and I tested different plant species in separate trials. Plants tested may have served as better or poorer larval forage at a different time of year. Lastly, only three life history traits were examined, and negative effects on one parameter could have been compensated for by another trait not considered in this study. Decreased fecundity (pupal weight) could be offset by an increase in egg size and fertility, for example (Moreau *et al*. 2006). This possibility underscores limitations to interpreting my results.

Most importantly, the lab setting of my study ignored important ecological interactions, which could even mediate the relative host plant effects on performance I found in the lab. Not only is it important to investigate direct host plant effect on LBAM life history traits, but also to analyze the indirect effects of host plants that may occur in the field through ecological interactions. Multi-trophic interactions could alter a primary host plant effect by also affecting the fitness of the herbivores' natural enemies and their efficacy in parasitizing larvae (Teder and Tammaru 2002), as in the case of the cabbage looper caterpillar (Caron *et al.* 2008) or Glanville fritillary butterfly (Van Nouhuys and Hanski 1999). The effect on the parasitoid of the larval host diet may primarily be due to the presence of secondary plant compounds, or those compounds not used in primary metabolic processes, which are consumed by the herbivores (Sznajder and Harvey 2003, Van Nouhuys and Hanski 1999, Price 1997). However, these secondary compounds also typically serve as a defense against herbivory, to which generalist insects like the LBAM are particularly susceptible (Price 1997). Thus in addition to having direct negative effects on LBAM populations, a relatively toxic host plant that leads to prolonged development time could also effectively increases exposure time to natural enemies in the field (Lill and Marquis 2000). Host plant species was also demonstrated to affect diapause and voltinism, or number of generations, in multivoltine moth species such as LBAM (Hunter and McNeil 1997), which has major implications for the pest's population dynamics. Complexity of plant architecture can even influence larval performance in the field, by interfering with predators, for example (Konvicka *et al*. 2003, Kaitaniemi *et al.* 2004). Since my experiment was carried out in Petri dishes using only small individual sprigs of each plant, my results could have been affected by the artificiality of removing the cutting from the context of the whole plant.

Although this study indicates how certain host plant species affect LBAM performance, it is still unclear what specific plant traits, such as plant nutrient profiles or secondary compound content, primarily influence LBAM fitness. This information could reveal the mechanisms by which certain plants had a given effect on LBAM and would be useful for establishing a methodology to better predict the suitability of a potential novel host. In general, suitability of a host plant in terms of herbivorous insect performance is determined largely by the presence of secondary plant compounds. These compounds serve as a defense for the plant, but in many cases insects have specialized on a particular host as they evolved the ability to withstand the plant's toxins (Price 1997). These specialist insects can therefore utilize plants that are generally unsuitable to other species because they contain more potent and unique secondary compounds (Price 1997). Generalist herbivore fitness tends to be maximized on plants that contain another class of secondary compounds, which are does-dependent and common to a broader range of plants (Price 1997). This is because the ability to feed on numerous plants comes with the tradeoff that specific toxic plant compounds cannot be specially metabolized. These types of compounds are typically found in late successional species, which tend to be woody species (Price 1997). Interestingly, LBAM performance has been found to be higher on herbaceous plants (Danthanarayana 1975), which are usually attacked by specialists, a finding supported by this study. Plant nutrient content, e.g., nitrogen and moisture content, may also affect larval performance to an extent, but many insects apparently compensate for lacking nutrients by adjusting intake (Simpson *et al*. 2004, Lavoie and Oberhauser 2004, Janssen 1993). New leaves may be superior to old leaves, which have higher secondary compound concentrations and poor nutritional quality (Bittencourt-Rodrigues and Zucoloto 2009) Understanding what plant characteristics create a high-quality food source for LBAM would therefore enhance our ability to predict impacts on a potential host.

While capture patterns indicate that LBAM is surviving in California outside of an agricultural context (CDFA 2009), the moth's fitness, with respect to three performance measures, was optimal on the non-native, herbaceous plant species in this lab study. The results of this experiment provide a good indication that Monterey cypress, coast live oak, or coastal redwood are unlikely to serve as LBAM hosts, although the CDFA has reported LBAM feeding on evergreens, including redwood (CDFA 2007). There may be incidental herbivory on these less than ideal host plants, but the results suggest that it is unlikely that these plants could actually support LBAM populations. However, to understand the implications of host plant effects on LBAM's impacts as an economic or ecological pest, all ecological factors must be considered since interactions with other organisms or conditions in the field may influence the plant host effects.

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