

Seasonal host shifts based on midgut residues of *Protaetia brevitarsis*

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Abstract

White-spotted flower chafer adult (*Protaetia brevitarsis*), a serious omnivorous pest in regions with multiple fruits and crops, to gain a deeper understanding of its harmful patterns, we used DNA molecular tracking technology to identify host plant residues in the midgut of adult and determined their preferred plant species during the growing season. The combined results for 2019 and 2021 show that adults fed on 32 plant species among 23 families in multi-cropped regions, with a preference for grapes (*Vitis vinifera*; 40%), peach (*Prunus perisica*; 23%), and mulberry (*Morus alba*; 14%). Some adults fed on multiple plant hosts, with four species detected in one adult and two to three species detected in one-third of adults. Adults shifted among host species during the season, from mulberry or grape to peach and then back to grape. These results provide a scientific basis for in-depth research to develop green integrated control technologies against *P. brevitarsis* adults.

Background

At least half of the more than 10 million insect species worldwide are phytophagous insects that feed on living plant tissue, and they have developed a variety of feeding habits [1]. Phytophagous insects can be monophagous, oligophagous, or polyphagous according to the types and amounts of plants on which they feed [2]. The morphological, physiological, and biochemical adaptations of insect feeding habits have been well studied [3, 4]. Monophagous insects such as grape phylloxera (*Daktulosphaira vitifoliae*), which specialize in feeding on grapes and generally feed on specific plant species or genera, always have a relatively fixed diet [5]; oligophagous insects mainly feed on a specific plant group, as in the case of the diamondback moth (*Plutella xylostella*), which feeds only on cruciferous vegetables [6, 7]. Polyphagous insects have a more complicated relationship with host plants; they can infect diverse hosts and do not typically develop specific adaptations for a particular host. For example, the white-spotted flower chafer (*P. brevitarsis*) damages crops, fruits, flowers and trees [8, 9]. One of the greatest obstacles to multihost feeding is the toxic metabolites produced by plants, which limit their feeding range and cause many herbivorous insects to specialize for a plant species [10, 11]. Multiple hosts feeding habits can still be caused passively by external factors or actively by insects themselves. For instance, chrysomelid leaf beetles that switched host plants were able to reduce their synthesis of compounds that attracted natural enemies and predators [12, 13].

Some insects also have the ability to flexibly use host information to locate seasonal food sources [14]. One case in point is the mirid bug adults (*Apolygus lucorum*), according to the flowering order of host plants and regularly undergo seasonal host shifts, adults have their broadest range of hosts in early spring; by summer, they prefer hosts such as *Helianthus annuus*, *Ocimum basilicum* and *Agastache rugosus*; and in autumn, they migrate to *Artemisia* spp. [15, 16]. In addition, although herbivorous insects typically have a polyphagous diet, some polyphagous insects have clear feeding preferences for specific plants. For instance, green peach aphids (*Myzus persicae*) have a wide range of hosts and can pose a threat to more than 50 plant families during the summer, but they overwinter only on certain hosts, such as peach trees or other plants in the Rosaceae family [17]. A study of four species of Scarabaeoidae on

their preferences among six host plants indicated that *Holotrichia oblita* preferred pear; *H. parallela* preferred hawthorn, pear and elm; and *Metabolus flavescens* and *Brahmina faldermanni* preferred lilac [18].

P. brevitarsis is an important polyphagous pest of horticultural crops and some field crops in northwestern China, where livestock manure in pastoral areas provides an ideal breeding ground for larvae, and abundant fruit trees provide ripe fruits preferred by adults [9, 19, 20]. Survey results for *P. brevitarsis* during its reproductive period in Xinjiang showed that its lifespan is approximately 90–130 days in wild areas and that in vineyards, the adult stage lasts from late May to early August [21, 22]. These studies indicated that although *P. brevitarsis* adults have a long lifespan, the mature fruits favored by adults are present only for a short period. Therefore, how do the adults survive through their long adult stage, and what do adults eat when their preferred fruits are not available?

Common field monitoring methods for tracking insects and their hosts have limitations for studying hosts of *P. brevitarsis* adults. Adults have long lifespans, frequently move between hosts, and feed at unpredictable times, making it difficult to accurately identify hosts through direct field observation. However, DNA-based molecular tracking based on DNA barcoding is now a powerful tool for studying the relationships between herbivorous insects and host plants [23]. The Consortium for the Barcode of Life recommends the combined use of *rbcL* and *matK* as plant barcodes to achieve a 72% success rate for identifying plants to the species level. To study host species of *P. brevitarsis* adults, Cai used *rbcL* to identify multiple host species [24].

We also wanted to determine what hosts were eaten by *P. brevitarsis* adults during different seasons and whether they preferred specific hosts like other Scarabaeidae do. We collected adults from an orchard with multiple specifically cultivated species, used DNA barcoding technology to identify the plant species in the midguts, and studied the proportion of the adults that contained each plant species. Knowledge of the changes over time in the preferred plant species of *P. brevitarsis* adults provides a scientific basis for developing environmentally safe preventive measures and controls for the integrated management of adults.

Methods

Insects

P. brevitarsis adults were collected from the ~ 7-ha Hailiqihan Orchard in the Xinjiang Uygur Autonomous Region (42.95° N, 89.16° E), where grape is the main crop, but peach, apricot, Chinese date, fig and other fruit are also grown. Insect samples were collected using bucket traps (Beijing), odor attractants [25] and bait cores (Fig. 1). Given that adult infestations in Xinjiang are greatest in late May to late August, we sampled insects from June to August in 2019 and 2021. We sampled every 7 days to ensure that we collected at least 30 live adults each time. Each individual was placed in a separate centrifuge tube and stored at -20°C until use.

PCR amplification and cloning of plant DNA barcodes

Plant genomic DNA was extracted from the midguts of the adults and used as a template to amplify *rbcL*; the optimal PCR system, product recovery, linkage and transformation methods for *rbcL* were previously established to generate a potential host DNA barcode information library for the adults. If the host could not be identified based on *rbcL*, then the *trnL* and *trnH-psbA* gene fragments were amplified as described previously [24, 26]. The amplified products were separated using 1% agarose gel electrophoresis and placed in a gel image system (Tanon, Shanghai) for detection after approximately 30 minutes and then recovered using a gel extraction kit (Tiangen, Beijing), the recovered products were ligated to the cloning vector (pGEM-T) and inserted into *Escherichia coli* DH5α. The cells were incubated overnight at 37°C on a Luria-Bertani agar plate containing 0.1% mg/mL ampicillin (Solarbio, Beijing), and the next day, colony PCR was used to determine the presence/absence of the construct. Then the samples were sent to Sangon Biotech (BBI LIFE SCIENCES, Shanghai) for sequencing [27]. Geneious (Dotmatics, New Zealand) was used to capture the target fragments, and these fragments were identified in the sequence data and for sequence alignments using the Basic Local Alignment Search Tool (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) [28].

Statistical analyses

After identifying the plant species in the midgut of each *P. brevitarsis* adult, we used one-way analysis of variance (ANOVA) in SPSS 25.0 (IBM, Armonk, NY, USA) to determine significant differences in the number of adults that fed on 1–4 plant species and the number of adults that fed on each plant species during different time periods.

Results

Gene amplification

In the midgut of adults collected from June 9 to August 5, 2021, *rbcL* was amplified from plant DNA from an average percentage of 37% of the adult insects. The lowest percentage of adults with *rbcL* was 18% on June 16 and the highest percentage (58%) was on June 23 (Fig. 2).

Number of plant species fed on by *P. brevitarsis* adults

We identified the plant species found in the midgut of adults collected from June 9 to August 5, 2021, and found that the adults habitually fed on multiple plant species. Wherein, 67% of the adults contained only one plant species ($F_{3,24} = 56.07, P < 0.0001$), 31% contained two plant species, 4% contained three species, and only one adult insect contained four plant species.

Plant species eaten by *P. brevitarsis* adults in 2019 and 2021

In 2019, 17 species in 14 families were identified from the midguts of adults, among them, 16 species were identified at the species level, and one species was identified at only the genus level (Fig. 3a).

Grape (*Vitis vinifera*) was the most preferred species, being found in 60% of the insects, followed by peach (23%, *Amygdalus persica*) and narrow-leaved oleaster (9%, *Elaeagnus angustifolia*).

In 2021, 21 species in 18 families were identified in adults; among them, 10 species were identified to the species level and 11 species were identified to the genus level only. Mulberry (*Morus alba*) was found in the most adults (25%), followed by peach (24%) and grape (23%) (Fig. 3b).

For both 2019 and 2021, 32 plant species belonging to 23 families were identified in adults (Fig. 3c). Grape was found in the most adults (40%), followed by peach (23%), mulberry (14%), narrow-leaved oleaster (7%) and purslane (5%, *Portulaca*).

Plant species eaten by *P. brevitarsis* adults from June-August

In 2019, on June 1, 74% of all adults had grape (*Vitis vinifera*) in the midgut, significantly more than the percentage that had other plant species ($F_{6,14} = 7.993$, $P = 0.001$) (Fig. 4). On June 13, peach was found in the most adults (73%) ($F_{4,10} = 7.745$, $P = 0.004$). On June 20, peach was still the most preferred species (52%) ($F_{6,14} = 8.111$, $P = 0.001$). On June 27, peach (44%) and grape (42%) were equally identified in adults ($F_{4,10} = 10.255$, $P = 0.001$). On July 3, 63% of the total sample were adults with grape in the midgut ($F_{4,10} = 9.714$, $P = 0.002$). On July 18, grape was found in the most adults (61%) ($F_{2,6} = 26.607$, $P = 0.001$), followed by narrow-leaved oleaster (35%) and peach (4%). On July 25, grape was still the significantly preferred species (63%) ($F_{3,8} = 34.472$, $P < 0.001$), followed by peach (18.07%), narrow-leaved oleaster (17%) and jujube (2%). In August, a total of 45 adults were collected, and *rbcL* was detected only from grape. The results for 2019 indicated that most adults fed on grape in early June, most favored peach in mid-June, some included narrow-leaved oleaster in late June and early July, and most again fed on grape in August. Thus, adults went from grape to peach to grape and narrow-leaved oleaster during June-August as their preferred host plants.

In 2021, on June 9, 65% of the adults had mulberry (*Morus alba*) in their midgut ($F_{3,8} = 8.727$, $P = 0.007$) (Fig. 5). On June 16, grape was found in the most adults (59%) ($F_{3,8} = 2.291$, $P = 0.155$). On June 23, mulberry was the most identified species again (59%), which was significantly greater than the percentage of other plant species ($F_{7,16} = 13.574$, $P < 0.001$). On July 11, peach was found in the most adults (64%), significantly more than the percentage that had other plant species ($F_{11,24} = 4.371$, $P = 0.001$). On July 21, mulberry was found in the most adults (53%), significantly more than other plant species ($F_{11,24} = 6.509$, $P < 0.001$). On July 28, among the 11 plant species we detected, there was no significant difference in their proportion ($F_{9,20} = 0.511$, $P = 0.849$). On August 5, grape was found in the most adults (75%), significantly more than other plant species ($F_{5,12} = 4.761$, $P = 0.013$). These results indicated that the adults shifted their hosts from mulberry and grape to mulberry and peach to grape (in June-August) as their preferred hosts.

Discussion

In this study, to learn more about plant hosts preferred by *Protaetia brevitarsis* from June through August at their peak population in Xinjiang, based on plant DNA in midgut contents, we determined that (1) adults fed on 32 plant species in 23 families but most preferred grape and peach. (2) One-third of the adults fed on more than one plant species (2–4 species), but only one adult consumed four. (3) Over time, adults shifted from grape to peach to grape and narrow-leaved oleaster in 2019, and from mulberry and grape to peach to grape in 2021. This information furthers our understanding of the feeding plant species for *P. brevitarsis*, shifts in the preferred hosts during their growing season, and provides a basis for exploring why *P. brevitarsis* preferences apparently changed and how they locate host plants.

Notably, the feeding preferences of *P. brevitarsis* adults were not entirely consistent across years, with different preferences for grape and peach early in 2019 and for grape and oleaster late in 2019; but for mulberry and grape early in 2021 and for mulberry with grape or peach late in 2021. The preference of phytophagous insects for specific hosts seems to be ubiquitous. Although tomato leaf miner (*Tuta absoluta*) feeds on various Solanaceae hosts, it prefers tomato [29]. These changes in preferences may be due to biotic factors (e.g., pathogens and natural enemies), for instance, the oriental fruit moth (*Cydia molesta*) also shifts during their growing season from peach and apple to pear, perhaps because larval development differs on different species. Another example is when *Impatiens balsamina* plants are severely infected with powdery mildew, *A. lucorum* adults move to other species that provide a better food source [15, 30–32]. Abiotic factors (e.g., temperature, rainfall) often affect herbivorous insect feeding indirectly by influencing the condition of plants and causing insects to switch to less preferred plant species [16, 33, 34].

Although omnivorous insects can feed on different plant species, their life parameters can differ significantly depending on the plant species [35–37]. *P. brevitarsis* adults laid fewer eggs after eating only grape, and although eating mulberry alone maintained adult survival, their fecundity was lower than that of adults fed only on peach, apricot, watermelon, or tomato [22]. Compared with feeding on other plants, feeding on elm (*Ulmus pumila*) had a significant impact on the fecundity of *Holotrichia parallela*, as the ovaries of this species had the greatest development and highest egg production [38]. Thus, the multihost diet of *P. brevitarsis* adults could significantly supplement nutrients to optimize reproductive capacity; a single plant species might not meet developmental or reproductive needs [22, 39]. However, interestingly, in the present study, nearly two-thirds of the *P. brevitarsis* adults fed on one plant species during its peak period, while the other one-third fed on 2–4 plant species. Although malnutrition early in life can negatively impact insect health, nutritional supplementation later in life can offset or compensate for the early negative impact [40–42]. Therefore, feeding on multiple species might provide missing nutrients to help adults survive their long adult stage and reproduce. In fact, the adult population is greater when *A. lucorum* feeds on multiple species rather than one [43]. These findings highlight important areas for subsequent research on the effects of diets comprising one or multiple plant species.

Various plant volatiles serve as important chemical signals for phytophagous insects to locate food [14, 44, 45]. *Maladera orientalis* has a significant preference for the volatiles *trans*-3-hexenol and *cis*-3-

hexenol released by peach leaves [46], and *P. brevitarsis* adults have strong electroantennography responses to various host volatiles of alcohols and aldehydes, particularly 4-methylisole, which attracts males and females [47–49]. Other plant species release specific volatiles after damage that attract insects. The mechanically damaged leaves of *Fagus sylvatica* L., *Quercus robur* L. and *Carpinus betulus* L. release volatiles that attract *Melolontha melolontha* males [50], and certain insect-infested grape varieties are more attractive than healthy varieties to *P. brevitarsis* adults [27]. Our findings on the preferred hosts during the growing season and peak population of *P. brevitarsis* provide an important basis for the study of the plant odorants used by *P. brevitarsis* adults to locate preferred plant species and how adults recognize these cues and develop new alternatives for the safe integrated management of these polyphagous pests.

Conclusion

We used DNA molecular tracking technology to identify plant residues in the midgut of *Protaetia brevitarsis* adults and determined their preferred plant species during the growing season. The results showed that adults fed on 32 species from 23 families, and that grapes and peaches were most preferred, followed by mulberry. Some adults also fed on 2–4 plant species. Adults shifted their preference from grape to peach to grape and narrow-leaved oleaster in 2019, and from mulberry and grape to peach to grape in 2021. On the basis of our findings and those of previous studies by Cai (2021) and Cui (2023), we conclude that these host shifts likely provide better nutrition to enable the optimal development and reproduction of *P. brevitarsis* adults. Our current work provides an important foundation for developing methods to suppress early-season adult populations and for subsequent research on the mechanism for localizing preferred plant species.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could influence the work reported in this paper.

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Author Contribution

Hui Wu: writing original draft, editing, software, visualization, formal analysis, investigation, validation, data curation. Zhuangzhi Cui: software, visualization, formal analysis, investigation, validation, data curation. Xiaoqing Huang: methodology, supervision. Fanfang Kong: methodology, supervision. Zhongyue Wang: funding acquisition, resources, supervision. Yongqiang Liu: conceptualization, methodology, resources, funding acquisition, supervision, project administration, review, editing.

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Availability of data and materials

Not applicable.

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Figures



Figure 1

Barrel traps used to collect adult *Protaetia brevitarsis*.

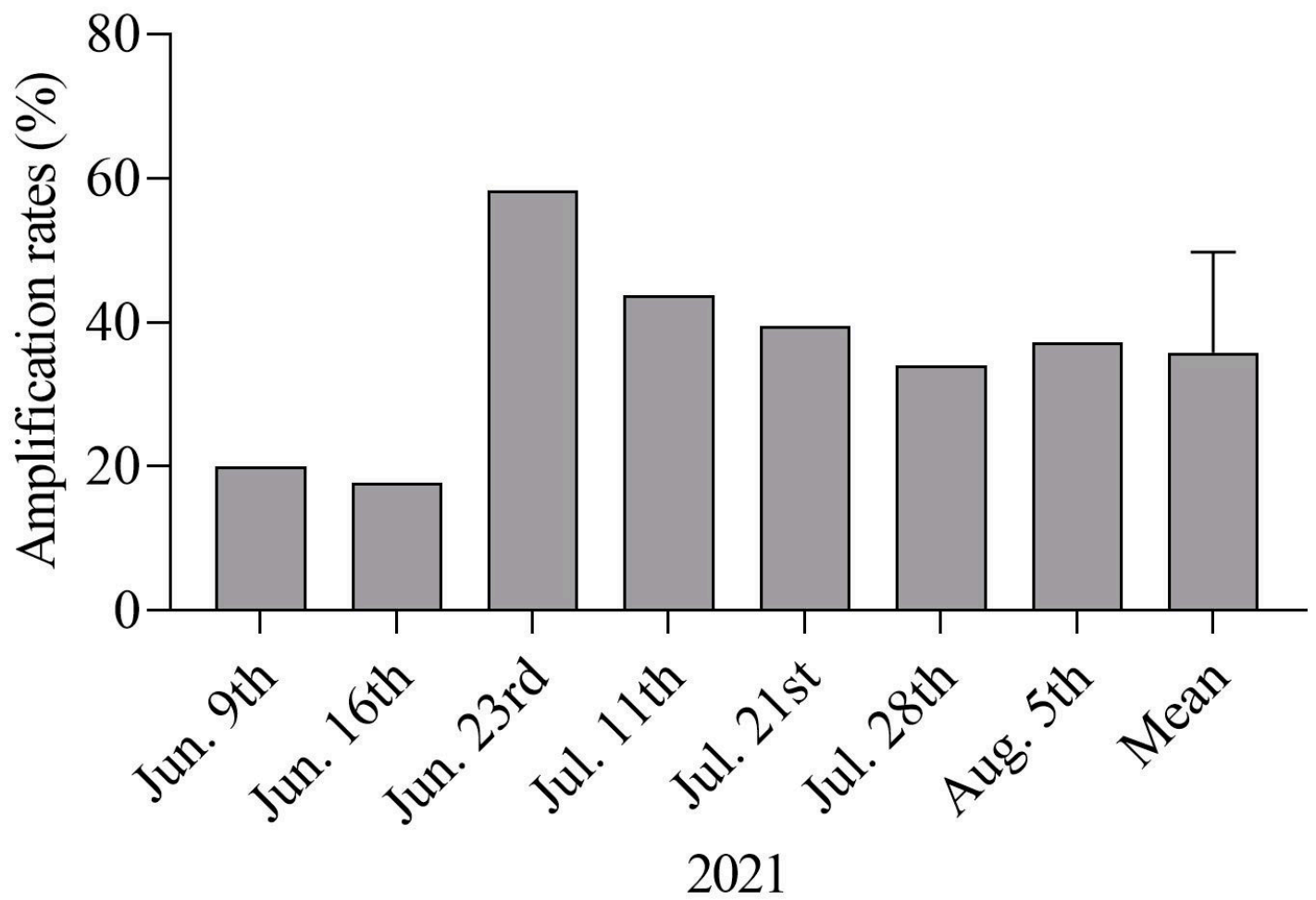


Figure 2

Percentage of *Protaetia brevitarsis* adults with midgut containing *rbcL* from plants. Bar for SE is given for mean.

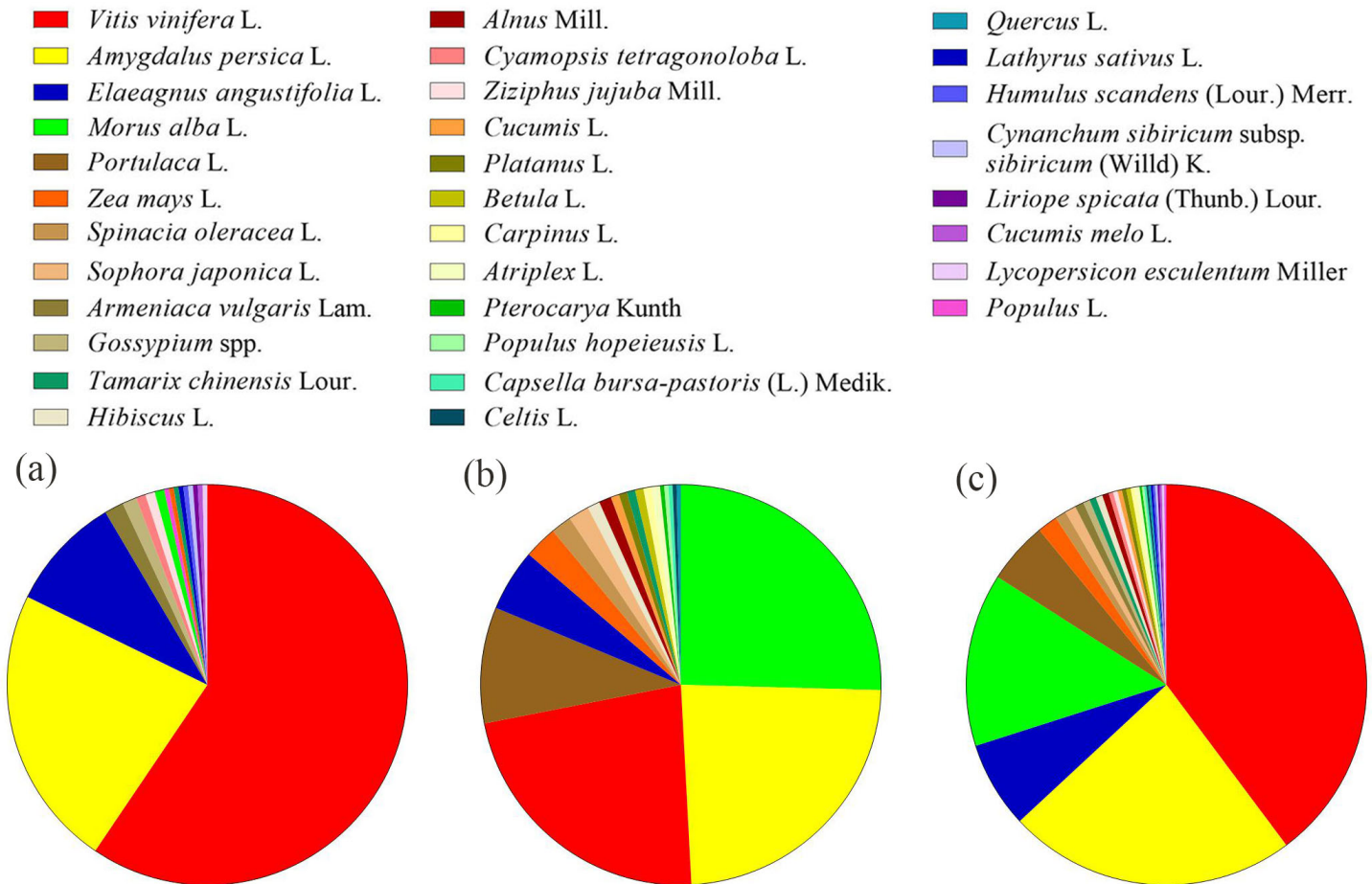


Figure 3

Proportion of each plant species in total eaten by *Protaetia brevitarsis* adults in (a) 2019 and (b) 2021 and (c) 2019 and 2021.

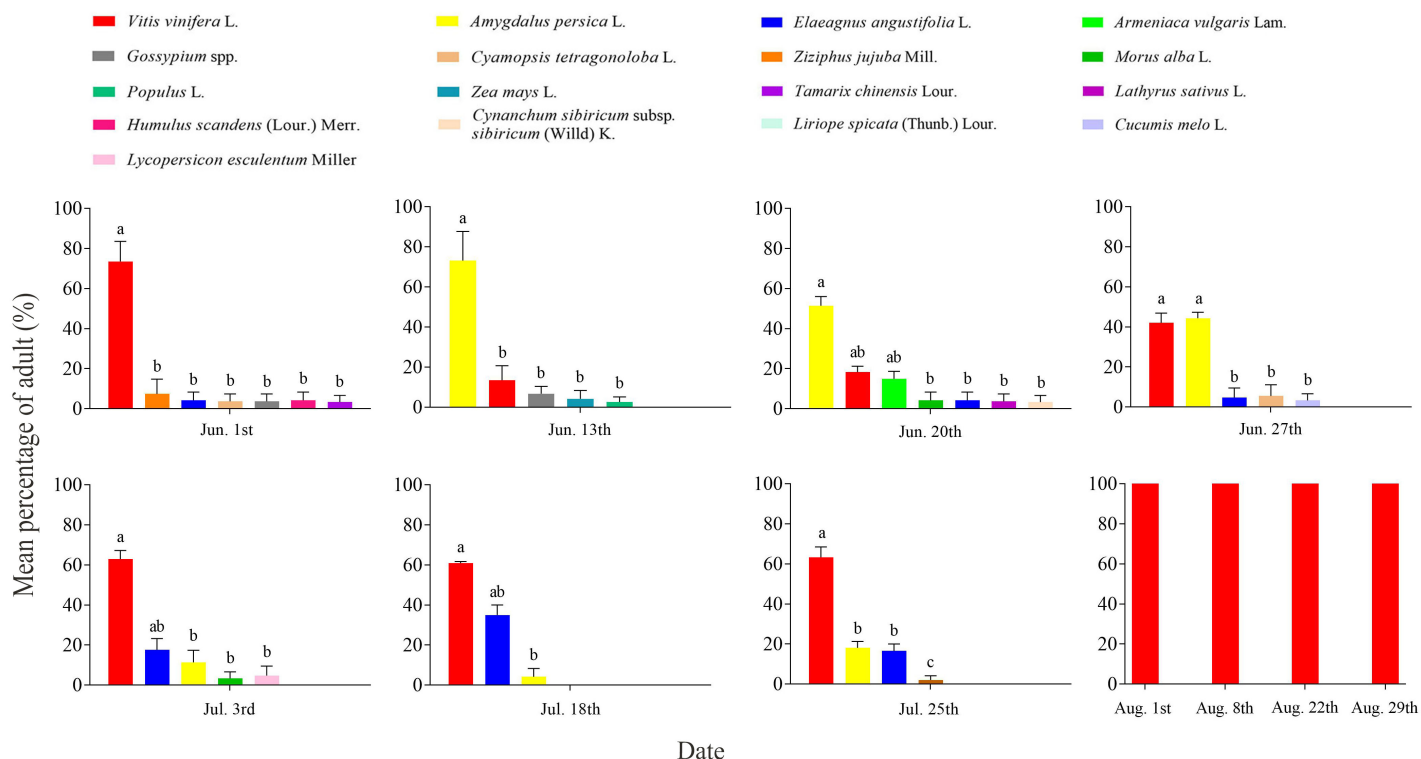


Figure 4

Plant species percentages of *Protactia brevitarsis* adults from June through August 2019. Lowercase letters indicate significant differences among means at $P < 0.05$; vertical line at the top of each histogram indicates standard error.

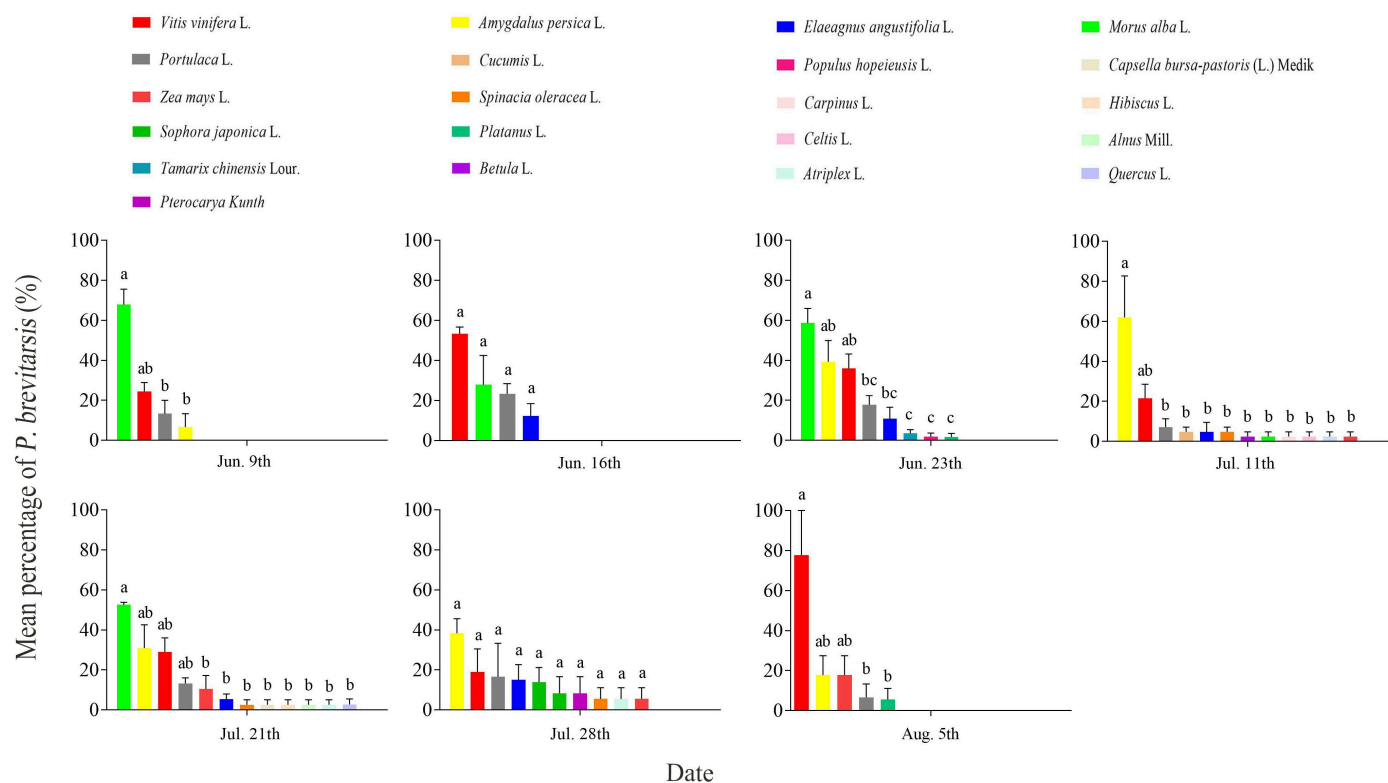


Figure 5

Plant species percentages of *Protaetia brevitarsis* adults and trends in different periods in 2021. Lowercase letters indicate significant differences among means at $P < 0.05$; vertical line at the top of each histogram indicates standard error.