

Kudzu-deprived First-generation *Megacopta cribraria* (F.) (Heteroptera: Plataspidae) Are Capable of Developing on Alternative Legume Species¹

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ABSTRACT The biology of *Megacopta cribraria* (F.) (Heteroptera: Plataspidae) is not well understood in its new North American distribution, especially its development on alternative host plant species. We investigated whether overwintered *M. cribraria* could directly feed and oviposit on other legume species (Fabales: Fabaceae) without feeding on kudzu, *Pueraria montana* (Loureiro) Merrill var. *lobata* (Willdenow) Maesen & S. Almeida, and subsequently complete a first-generation on these species in no-choice greenhouse assays. Overwintered *M. cribraria* successfully oviposited on mung bean, *Vigna radiata* (L.) R. Wilczek; black-eyed pea, *Vigna unguiculata* (L.) Walp; lima bean (=butter bean), *Phaseolus lunatus* L.; soybean, *Glycine max* L. Merrill; and kudzu. There were no differences in oviposition or the hatch rates on different legume species, although hatch rate was highest for soybean followed by kudzu, lima bean, mung bean, and black-eyed pea, respectively. First-generation *M. cribraria* developed on all legume species except black-eyed pea in 55.6 ± 1.6 d with little variation in developmental time of the instars. However, there were significantly more first instars molting to second instars on kudzu (19.6 ± 3.3), soybean (14.7 ± 3.0), and mung bean (19.0 ± 1.0) than on lima bean (5.3 ± 2.4). Mean developmental days of the first, second, and fourth instars were consistent at about seven days, while the third and fifth instars took longer to develop. Mortality from egg to adult was greatest on black-eyed pea, followed by lima bean, kudzu, mung bean, and soybean. These results indicate that overwintered *M. cribraria* adults are able to bypass kudzu to directly develop on soybean, lima bean, and mung bean crops.

KEY WORDS kudzu bug, *Vigna radiata*, *Phaseolus lunatus*, *Glycine max*, *Pueraria montana*

Megacopta cribraria (F.) (Heteroptera: Plataspidae) is an invasive agricultural and residential pest species that was first detected in the United States in 2009 (Eger et al. 2010). Since then, it has greatly expanded its U.S. distribution and is now found in at least 13 southeastern states (Gardner et al. 2013, Gardner 2015). This herbivorous insect likely feeds on plant phloem by probing stems and petioles of various legume species (Fabales: Fabaceae) (Eger et al. 2010, Zhang et al. 2012, Seiter et al. 2013). The preferred hosts of *M. cribraria* are

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kudzu, *Pueraria montana* (Loureiro) Merrill var. *lobata* (Willdenow) Maesen & S. Almeida, and soybean, *Glycine max* (L.) Merrill (Tayutivutikul & Yano 1990, Li et al. 2001, Wang et al. 2004, Xing et al. 2008). It is considered an agricultural pest of legume crops including soybean and vegetable beans in many Asian countries (Ishihara 1950, Wang et al. 1996, Wu & Xu 2002). *M. cribraria* undergoes five nymphal instars lasting approximately 24–56 d in its native range before eclosing into the adult (Eger et al. 2010).

In the southeastern U.S.A., *M. cribraria* completes two generations per year (Zhang et al. 2012). Depending on location, overwintering adult *M. cribraria* may spend up to six months without food when sheltered in overwintering sites (authors observations), and they become active once temperatures increase in the spring. Overwintered adults will either stay in kudzu patches or disperse to alternative hosts (Zhang et al. 2012), such as soybean, where they can cause tremendous damage (Seiter et al. 2013). Overwintered adult *M. cribraria* feed on multiple leguminous and a limited number of non-leguminous plants (Zhang et al. 2012, Hu & Carroll 2012). However, they display a restrictive reproductive host range (i.e., able to develop from egg to adult) that is limited to legumes, such as kudzu (Zhang et al. 2012, Medal et al. 2013); soybean (Zhang et al. 2012, Del Pozo-Valdivia & Reisig 2013); pigeon pea, *Cajanus cajan* L.; black-eyed pea, *Vigna unguiculata* L.; lima bean (=butter bean), *Phaseolus lunatus* L.; and pinto bean, *Phaseolus vulgaris* L. (Medal et al. 2013). This biological trait, a broad host range yet limited reproductive range, is common of many native and invasive Pentatomoidea (Panizzi 1997), and is most likely the result of differences in adult and nymphal characteristics, which may include mobility (Panizzi et al. 1980, Schumann & Todd 1982), nutritional demands (Kehat & Wyndham 1972, Kester & Smith 1984), and differing stylet morphologies of nymphs and adults (Moizzuddin & Ahamd 1975).

Due to observations of *M. cribraria* overwintering in or near kudzu patches (Waldvogel & Alder 2012), which are usually available before cultivated soybean crops (authors observations), it has been anecdotally thought that *M. cribraria* must initially feed on kudzu to gain essential nutrients before dispersing to alternative feeding and reproductive host plants. However, Smith (2013) and Seiter et al. (2013) reported that overwintered *M. cribraria* could infest early-planted soybeans, and Del Pozo-Valdivia & Reisig (2013) suggested that the first-generation is able to bypass kudzu and develop on soybean. Previous studies, however, have not demonstrated in-full if kudzu is necessary in the diet of *M. cribraria*, since adults that produced eggs or nymphs for these studies had been reared on or initially fed on kudzu (Del Pozo-Valdivia & Reisig 2013), or they were obtained from kudzu patches or field locations when it was likely that kudzu was already available (Zhang et al. 2012, Medal et al. 2013, Blount et al. 2015).

To investigate if first-generation *M. cribraria* can develop on alternative host plants in the absence of kudzu, a no-choice greenhouse assay was conducted utilizing economically important legume species and starved overwintered adult *M. cribraria* before the onset of spring feeding.

Materials and Methods

Plants and insects. Mung bean, *Vigna radiata* (L.) R. Wilczek, black-eyed pea (Cranford, NJ), lima bean (butter bean, Alabama Farmer's Cooperative), and

soybean ('93Y92', DuPont-Pioneer, Des Moines, IA) were grown from seeds beginning 10 February 2014, while kudzu was grown from field-collected root crowns (Lee Co., Auburn, AL). Seeds and root crowns were placed in individual 3.7-liter black plastic pots containing Sunshine Pro Premium Potting Soil (SunGro Horticulture Canada Ltd., Seba Beach, Alberta). Plants were grown and maintained under natural light conditions, $23 \pm 3^\circ\text{C}$, 50–70% RH, and provided with water as needed in a greenhouse on the Auburn University campus (Auburn, AL). Four plants of each legume species were used in this experiment. Before they had migrated to food plants, overwintered adult *M. cribraria* were collected from tree bark and leaf-litter near a kudzu patch at Park Town Creek (Auburn, Lee Co., AL) (32.609111 N, 85.391889 W), and an area of fragmented forest adjacent to Route 14 near E. Glenn Ave. (Auburn, Lee Co., AL) (32.609111 N, 85.500739 W) on 19 March 2014. Adults were separated by sex and stored in large glass containers with mesh lids (10×12 cm) under room temperature of $22 \pm 2^\circ\text{C}$ and ambient light conditions before introducing them to plants in the greenhouse.

No-choice experiment. On 21 March 2014, a single plant of each legume species was placed individually inside a $24.5 \times 24.5 \times 63.0$ cm cage (Bug dormTM, BioQuip Products, Rancho Dominguez, CA) and 10 pairs (10 males & 10 females) of field-collected *M. cribraria* were introduced into each cage. Adults were allowed to feed on a legume plant until seven days after no new egg masses were observed on it. At this time, adults were removed from their host plants. Plants were then inspected and the number of egg masses and individual eggs per mass were counted. Upon hatching, neonate nymphs were allowed 24 h to ingest the endosymbiont capsule contents, after which time they displayed wandering behavior away from the egg mass. Then, 20 neonates were randomly selected to remain on their respective host plant per replicate. There were three replicates, so 60 neonates for each plant species were tested. Egg masses were deposited on both the mesh cage material and the plant itself. If nymphs were on the mesh cage material, they were transferred to the adaxial leaf surface with a fine-haired paintbrush (size 3/0, Royal Brush Manufacturing, Inc., Merrillville, IN) until each plant had 20 neonates at the end of 24 h. When plants reached the flowering stage after about 30 d (R1 stage), a plant of the same species in a vegetative growth stage (V2–V3) was placed inside the cage and nymphs were encouraged to wander to the immature plant by gently touching them with the fine-haired paintbrush. Kudzu plants did not reach maturity during the experiment and were not replaced. Plants were evaluated every other day, and the average percentage of eggs hatching per plant, time required for completion of each instar, total days required for development from egg to adult, and mortality were determined. Due to low survivorship in the three lima bean replicates, the remaining fourth instars ($n = 9$) were transferred to a single lima bean plant, and only observational results were recorded thereafter for the duration of the experiment.

Data analysis. Days until oviposition, number of egg masses, eggs per mass, egg hatch rate, duration of larval development from egg to adult, numbers of adults, sex ratios, and mortality on each plant species were analyzed and subjected to separate one-way analysis of variance (ANOVA) tests (IBM SPSS Statistics for Window, Version 21.0, 2013; IBM Corp., Armonk, NY) with plant species as the lone (fixed) effect in the model. Mean duration of nymphal instars

and mean numbers of nymphs on each bean species were separated using Tukey's Honestly Significant Difference (HSD) procedure ($P = 0.05$) where appropriate. A Chi-squared ($\alpha = 0.05$) test was performed to compare differences in the overall sex ratio per bean species by using the total number of males and females produced on all three plants.

Results

Oviposition and egg hatch rates. In the no-choice assays, it took an average of 21.5 ± 0.4 d for oviposition to occur, and time from introduction until oviposition of *M. cribraria* did not differ significantly among the five legume species ($F = 0.458$; $df = 4, 10$; $P = 0.985$). There were no significant differences in the number of egg masses ($F = 0.951$; $df = 4, 10$; $P = 0.474$) or total eggs ($F = 0.647$; $df = 4, 10$; $P = 0.642$) laid on the five legume species during the observation period (Table 1). The mean duration of the egg stage did not differ significantly among the legume species ($F = 0.647$; $df = 4, 10$; $P = 0.381$) (Table 2). Likewise, there were no significant differences in percentage of eggs hatching among the five legume species ($F = 0.761$; $df = 4, 10$; $P = 0.574$), although the hatch rate was numerically greatest on soybean followed by kudzu, lima bean, mung bean, and black-eyed pea (Table 1).

Duration of instars. No neonates ($n = 60$) survived for more than about two days on black-eyed pea. The mean duration of the first instar did not differ significantly among the other four legume species ($F = 0.167$; $df = 3, 8$; $P = 0.916$), nor was the duration of second instar significantly different ($F = 2.867$; $df = 3, 8$; $P = 0.104$) (Table 2). However there were significantly greater mean numbers of first instars molting to second instars on mung bean, soybean, and kudzu than on lima bean ($F = 11.140$; $df = 3, 8$; $P = 0.003$) (Table 1). Mean development of the third instar took significantly longer on lima bean than on mung bean, soybean, or kudzu ($F = 21.700$; $df = 3, 8$; $P < 0.001$), and only nine third instars molted to the fourth instar on lima bean (Table 2). However, there were no significant differences in the mean number of third instars on mung bean, lima bean, soybean, or kudzu ($F = 3.438$; $df = 3, 8$; $P = 0.072$) (Table 1). There were no significant differences in mean developmental time for fourth instars on mung bean, soybean, or kudzu ($F = 3.00$; $df = 2, 6$; $P = 0.125$) (Table 2), or in the mean number of fourth instars among these three legume species ($F = 0.063$; $df = 2, 6$; $P = 0.940$) (Table 1). Development of the fifth instar took significantly longer on kudzu than on mung bean, but developmental time on soybean was not significantly different from kudzu or mung bean ($F = 6.500$; $df = 2, 6$; $P = 0.032$) (Table 1). Development of *M. cribraria* from egg to adult was completed in 49–55 d on mung bean, followed by kudzu (51–60 d), and soybean (55–59 d). Development regardless of host plant averaged about 52–58 d (Table 2). Mean developmental time from egg to adult did not differ among mung bean, soybean, or kudzu ($F = 1.855$; $df = 2, 6$; $P = 0.236$) (Table 2).

Adults. There were no significant differences in the mean number of adults that developed on kudzu, soybean, or mung bean ($F = 0.268$; $df = 2, 6$; $P = 0.774$) (Table 2). Additionally, there were no significant differences in the sex ratios (M:F) produced on mung bean (1.07:1.00) ($\chi^2 = 0.333$; $df = 1$; $P = 0.564$), lima bean (1.00:1.00) ($\chi^2 = 0.200$; $df = 1$; $P = 0.655$), soybean (1.00:0.94) ($\chi^2 = 0.030$; $df = 1$; $P = 0.862$), or kudzu (0.58:1.00) ($\chi^2 = 1.316$; $df = 1$; $P = 0.251$).

Table 1. Mean (\pm SE) numbers of egg masses, eggs, mean hatch rate, and mean number of first, second, third, fourth and fifth instars, and adults.

Parameter ^a	Legume common name				
	Mung bean	Black-eyed pea	Lima bean	Soybean	Kudzu
No. egg masses	6.3 \pm 2.6 a	3.0 \pm 0.58 a	6.6 \pm 0.3 a	9.0 \pm 1.0 a	8.0 \pm 2.1 a
No. eggs	67.3 \pm 19.2 a	67.6 \pm 8.5 a	62.3 \pm 5.9 a	67.3 \pm 10.7 a	42.6 \pm 11.5 a
Hatch rate (%)	41.3 \pm 13.9 a	33.7 \pm 17.2 a	51.3 \pm 20.0 a	68.2 \pm 9.8 a	52.0 \pm 11.0 a
No. 1 st instar ^c	22.6 \pm 0.7 a	21.7 \pm 9.8 a	29.7 \pm 10.3 a	45.3 \pm 6.8 a	23.3 \pm 8.0 a
No. 2 nd instar	19.0 \pm 1.0 a	0.0	5.3 \pm 2.4 b	14.7 \pm 3.0 a	19.6 \pm 3.3 a
No. 3 rd instar	12.6 \pm 4.0 a	0.0	3.3 \pm 1.2 a	12.0 \pm 3.1 a	16.6 \pm 3.3 a
No. 4 th instar	10.3 \pm 5.2 a	0.0	9.0 ^b	11.3 \pm 3.5 a	12.3 \pm 2.8 a
No. 5 th instar	10.0 \pm 5.5 a	0.0	9.0 ^b	11.3 \pm 3.5 a	11.0 \pm 3.5 a
No. adults	9.0 \pm 5.7 a	0.0	6.0 ^b	11.0 \pm 2.3 a	6.3 \pm 3.5 a
Pooled nymph to adult mortality (%)	55.0 \pm 0.3	100.0 \pm 0.0 ^d	91.7 \pm 0.8 ^d	45.0 \pm 0.2	68.3 \pm 0.2

^aDifferent letters within a row indicate a significant difference using Tukey's HSD ($\alpha = 0.05$).

^bDue to low survivorship in the three replicates of lima bean, raw numbers are given past the third instar.

^c60 neonates (n = 20 per replication) were transferred to each legume species 24 h after hatching.

^dValues were not included in one-way ANOVA analysis due to 100% mortality in black-eyed pea and only one replication of lima bean eclosing to adults (observational results only).

Table 2. Mean developmental days (\pm SE) of the egg stage and the five nymphal instars (I–V) of *M. cribraria* on mung bean, black-eyed pea, lima bean, soybean, and kudzu.

Legume common name	Egg stage	Mean developmental time (days \pm SE) ^a					Total days
		I	II	III	IV	V	
Mung bean	9.7 \pm 1.3 a	5.7 \pm 0.9 a	6.7 \pm 0.3 a	11.3 \pm 1.8 a	8.0 \pm 1.1 a	11.0 \pm 0.0 b	52.3 \pm 1.8 a
Black-eyed pea	6.0 \pm 0.6 a	—	—	—	—	—	—
Lima bean	9.0 \pm 2.0 a	6.0 \pm 1.7 a	7.0 \pm 0.6 a	20.7 \pm 0.7 b	2.0 ^b	14.0 ^b	58.7 \pm 2.9 ^b
Soybean	9.7 \pm 1.4 a	7.0 \pm 1.5 a	6.7 \pm 0.3 a	10.0 \pm 1.1 a	10.0 \pm 2.0 a	14.3 \pm 0.9 ab	57.7 \pm 1.3 a
Kudzu	8.7 \pm 1.8 a	6.7 \pm 1.7 a	8.0 \pm 2.0 a	10.0 \pm 0.0 a	5.0 \pm 1.0 a	18.3 \pm 2.3 a	56.7 \pm 2.8 a
Mean irrespective of host plant	8.6 \pm 0.7	6.3 \pm 0.3	7.8 \pm 0.3	13.0 \pm 2.6	7.7 \pm 1.4 ^b	14.5 \pm 2.1 ^b	55.6 \pm 1.6 ^b

^aDifferent letters within a column indicate a significant difference using Tukey's HSD ($\alpha = 0.05$).

^bDue to low survivorship, lima bean is not included in analyses for fourth instars, fifth instars, total days, or mean development irrespective of host plant.

Mortality. Pooled percent mortality from nymph to adult was greatest on black-eyed pea, followed by lima bean, mung bean, and soybean (Table 1). Excluding black-eyed pea ($100.0 \pm 0.0\%$ mortality) and lima bean (incomplete replication), there were no significant differences in mortality among the three bean species (mung bean, soybean, and kudzu) on which *M. cribraria* was able to successfully develop ($F = 0.263$; $df = 2, 6$; $P = 0.774$).

Discussion

Previous experiments (Zhang et al. 2012, Medal et al. 2013, Del Pozo-Valdivia & Reisig 2013, Blount et al. 2015) used either *M. cribraria* that were reared on kudzu with first instar offspring being transferred to selected legume species or adults that were collected in the field after feeding on kudzu. However, our study utilized overwintering *M. cribraria* that were starved and deprived of kudzu for approximately five months (late October through March) before experimentation in no-choice greenhouse tests. Overwintered adult *M. cribraria* oviposited on all of the caged legume species, including those that were not suitable developmental hosts for the first-generation, an observation that is consistent with reports from other researchers (Zhang et al. 2012, Medal et al. 2013, Blount et al. 2015). The percentage of eggs hatching did not differ significantly on any of the five legume plants, indicating no effect of host plant on this life-stage parameter. First-generation adults were able to develop on soybean, kudzu, and mung bean, and to a lesser degree on lima bean. The successful development on mung bean represents a new host record in the U.S.A.

The lack of development of adult *M. cribraria* on black-eyed pea and the successful development on mung bean contradict the observations by Medal et al. (2013). They found that *M. cribraria* could be reared from egg to adult on black-eyed pea, but not on mung bean. However, the result of our experiment agrees with Zhang et al. (2012) and Blount et al. (2015) in that no adult development was recorded on black-eyed pea. Recent host range testing by Blount et al. (2015) found that *M. cribraria* were not able to develop to adults in choice, no-choice, or field trials on lima bean (butter bean) and mung bean directly, which directly contradicts our findings. Differences in the developmental success on alternative legume species could be because previous researchers utilized field-collected adults from locations where kudzu was available already. Additional factors could be differences in the variety/cultivar of black-eyed pea, lima bean, and mung bean used in their experiments, as well as in the rearing procedures of the insects.

In its native geographical distribution, 24–56 d are needed for *M. cribraria* to transition from egg to adult on various host species (Eger et al. 2010). In the present study, *M. cribraria* developed 5–9 d slower on soybean compared to no-choice experiments by Del Pozo-Valdivia & Reisig (2013). This result is likely due to a difference in rearing conditions and/or soybean variety. The experimental temperature used by Del Pozo-Valdivia & Reisig (2013) was 28°C, while we used $23 \pm 3^\circ\text{C}$, which also could have contributed to differences in our results.

Mortality was significantly greater on both black-eyed pea and lima bean, suggesting that these two legume species are not suitable developmental hosts for *M. cribraria*. However, mung bean and soybean were adequate developmental hosts for this insect, as mortality was lower on these plant species than on kudzu. The overall high rates of mortality (greater than 45.0% for all plant species)

observed in the no-choice experiments could have been induced by restricting nymphal *M. cribraria* to small cages, preventing their access to shade or higher quality host plants. Researchers have previously had difficulties rearing this insect in controlled environments (Zhang et al. 2012, Del Pozo-Valdivia & Reisig 2013).

Mean developmental times for the first, second, and fourth instars were consistent among mung bean, soybean, and kudzu at approximately 7.0 d for each instar. However, the third and fifth instars developed slower, lasting about 10.0 d and 14.6 d, respectively, when fed mung bean, soybean, or kudzu. Slower development of the fifth instar has been recorded previously (Tayutivutikul & Yano 1990), however this is the first report of slower developmental times of third instar *M. cribraria*. During this instar, *M. cribraria* nymphs undergo a physiological change developing functional dorsal abdominal scent glands opening through ostia on tergites 3–4 and 4–5 (Moizuddin & Ahmad 1975). A consequence of this morphological change may be a trade-off between nutrient reallocation to favor the secondary development of defensive features over gaining body mass (Tollrian & Harvell 1999, Steiner & Pfeiffer 2007, Brönmark et al. 2012).

Although mortality was greater than 90%, a small number of nymphs of *M. cribraria* ($n = 5$) were able to successfully develop into adults after 59 d on lima bean. Noteworthy is the developmental time of the third instar on lima bean, which took an average of 21 d. This result indicates that there could be a plant factor inhibiting or delaying nymphal development on this plant. This could be due to plant nutritional quality, such as varying quantities of elements like nitrogen, which are known to retard the development of immature insects (Mattson 1980, Scriber & Slansky 1981). Future research should investigate these limiting plant factors that may have significantly delayed the development of *M. cribraria*.

While this study was limited to no-choice greenhouse experiments, it indicates that overwintered *M. cribraria* can migrate directly from overwintering sites to early-planted soybean fields. Additionally, it corroborates previous field observations suggesting that kudzu is not an obligatory host for this insect (Del Pozo-Valdivia & Reisig 2013, Seiter et al. 2013, Smith 2013). However, feeding on kudzu and/or other supplementary plant species, or host-switching from adult to nymph, may benefit the overall development of *M. cribraria*. For instance, supplemental feeding on legumes that are high in lipids, such as soybean, has been shown to increase starvation tolerance and reproductive fitness in the southern green stinkbug, *Nezara viridula* (L.) (Panizzi & Hirose 1995). Additionally, host switching from nymph to adult *N. viridula* has been indicated to increase fitness (Panizzi & Saraiva 1993). Perhaps *M. cribraria* receives similar benefits and/or trade-offs from this behavior, and subsequent investigations should address how host switching and supplementary feeding may affect certain biological and life history traits of *M. cribraria*.

Previous reviews (Panizzi 1997) have emphasized the importance that nutritional ecology plays in the life cycles of Pentatomoidea of agricultural concern. Few studies have examined the effects of host plant and developmental host plant switching between nymphal stages and on adults of subsequent generations. Further research should address these topics, since a better understanding of host and developmental host plant use, the sequence in which these plants are used, and the dispersal from which wild to cultivated crops takes

place (Panizzi 1997) could improve control methods against *M. cribraria* in the southeastern U.S.A.

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