The Biology and Preliminary Host Range of *Megacopta cribraria* (Heteroptera: Plataspidae) and Its Impact on Kudzu Growth

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ABSTRACT The bean plataspid, *Megacopta cribraria* (F.), recently was discovered in the United States feeding on kudzu, *Pueraria montana* Lour. (Merr.) variety *lobata* (Willd.), an economically important invasive vine. We studied its biology on kudzu and its impact on kudzu growth. We also tested its ability to use other common forest legumes for oviposition and development. Flight intercept traps operated from 17 May 2010 to 31 May 2011 in a kudzu field near Athens, GA showed three peaks of adult flight activity suggesting there are two generations per year on kudzu. Vine samples examined for eggs from April 2010 to April 2011 and June to October 2011 showed two periods of oviposition activity in 2010, which coincided with the peaks in adult activity. In 2011, the second period of oviposition began on or before 24 June and then egg abundance declined gradually thereafter until late August when we recovered <2 eggs/0.5 m of vine. Samples of the five nymphal instars and adults on vines did not show similar trends in abundance. Adults did not lay eggs on the various legume species tested in 2010 in a no-choice test possibly because the cages were too small. In the 2011 field host range experiments conducted in a kudzu field by using 12 legume species, *M. cribraria* preferentially oviposited on kudzu over soybean, *Glycine max* Merrill., but they still laid 320 eggs per plant on soybean. *Lespedeza hirta* (L.) Hornem. and *Lespedeza cuneata* (Dum. Cours.) G. Don had 122.2 and 108.4 eggs per plant, respectively. Kudzu and soybean were the only species *M. cribraria* completed development on. Plots protected from *M. cribraria* feeding by biweekly insecticide applications had 32.8% more kudzu biomass than unprotected plots. Our results show that *M. cribraria* has a significant impact on kudzu growth and could help suppress this pest weed.

KEY WORDS bean plataspid, kudzu bug, host preference, invasive, exotic

Large numbers of *Megacopta cribraria* (F.) (Hemiptera: Heteroptera: Plataspidae) were first discovered on kudzu, *Pueraria montana* Lour. (Merr.) variety *lobata* (Willd.), in northeast Georgia in October 2009 (Suiter et al. 2010). This was the first time *M. cribraria* or any member of the family Plataspidae were reported in North America. The potential pest status of this exotic insect in the United States was uncertain at the time; however, it was deemed a nuisance pest because adults aggregate on houses seeking overwintering sites in the vicinity of kudzu patches. How the insect arrived in the United States and where it came from is still unknown but it has spread quickly. In 2009 only nine Georgia counties were infested but by August 2011 almost all of Georgia and South Carolina and over half of North Carolina counties were infested (W. Gardner, University of Georgia, personal communication).

M. cribraria is native to Asia and the Indian subcontinent (Srinivasaperumal et al. 1992, Hua 2000, Hosokawa et al. 2007). It feeds primarily on leguminous plants such as kudzu and soybean (*Glycine max* Merrill.) sucking sap from stems, petioles and leaves, but it is also listed as a pest of Chinese fruit trees including peach (*Amygdalus persica* Linn.), plums (*Prunus* spp.), and jujube (*Ziziphus jujube* Mill.) (Wang et al. 1996, Li et al. 2001, Wang et al. 2004). Eger et al. (2010) provided detailed information on the reported host plants of *Megacopta* spp. in Asia. Although *M. cribraria* is an exotic insect with potential to affect the growth of kudzu, an economically important invasive weed, it also poses a threat to soybean and other legume crops. *Megacopta cribraria* has caused serious damage to soybeans in central and southern China (Wang et al. 1996, 2004; Li et al. 2001; Wu and Xu 2002) where both nymphs and adults feed on tender stems or leaves resulting in purple spots on leaves. Heavy feeding can result in some defoliation and sooty mold growing on the excretions of *M. cribraria;* it also covers leaves and stems, reducing photosynthesis. Although *M. cribraria* has not been reported to feed on seed pods, the combination of stem and foliar damage, and reduced photosynthesis from sooty mold, leads to improperly developed pods, undersized seeds, and eventual yield loss (Xing et al. 2006). So far, insecticides are the preferred method to control *M. cribraria* in soybean fields in China. Appli-

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cation of beta-cypermethrin, deltamethrin, or sumicidin targeting nymphs and application of methamidophos and beta-cypermethrin targeting adults resulted in over 85% control (Wang et al. 2004). Similar studies showed that application of organophosphate or pyrethroid insecticides, especially to control nymphs, provided good results as well (Wu et al. 1992, Zhang and Yu 2005).

Megacopta cribraria in the United States has been identified from both morphological (Eger et al. 2010) and COI sequence characters (Jenkins et al. 2010). Eger et al. (2010) reviewed recent literature on the biology, host range, and distribution of this insect, whereas Suiter et al. (2010) provided information on the discovery and distribution of *M. cribraria* in northeast Georgia. Horn and Hanula (2011) demonstrated an effective trap for monitoring *M. cribraria* populations in the field. Here we report on the life history, seasonal activity, and preliminary host range of *M. cribraria* on plants in the United States with a focus on forest legumes. In addition, we measured its impact on kudzu and its potential to suppress growth of this invasive vine.

Materials and Methods

Biology and Seasonal Activity of *M. cribraria*. We monitored the various life stages of *M. cribraria* in a kudzu patch within a residential neighborhood in Athens, GA. Sampling began in late April 2010, when large numbers of adults and eggs already were present in the field. Surveys were conducted weekly from 26 April to 8 November 2010 and in 2011 from 22 March to 27 April and 24 June through 21 October. Sampling was started earlier in 2011, just after kudzu plants began sprouting, to determine when oviposition began and to complete 1 yr of sampling. Sampling was initiated again on 24 June, at the beginning of the second period of adult emergence based on 2010 sampling, to better differentiate the second peak in oviposition. Samples were collected weekly and consisted of 10 randomly selected 0.5-m lengths of kudzu vine. In 2010 and from March to April 2011, five cuttings were taken from the growing tips of kudzu vines and the other five were cut from older parts of the vine. Vines were disturbed as little as possible during collection and the samples immediately were placed individually in zip lock bags for transport to the laboratory where all life stages were counted and recorded. From June to October 2011 we were interested in sampling eggs. Because previous sampling showed that eggs were laid almost exclusively on new buds and leaf nodes near the growing vine tip, we randomly collected ten 0.5-m samples of new vine tips and examined them for new and hatched eggs.

In 2010, to determine if parasitoids were attacking eggs, all egg masses were counted, cut from the rest of the sample, and then transferred with the corresponding plant material to 1,000-ml glass beakers with moistened filter paper on the bottom and polyester cloth covering the openings to prevent potential parasitoids from escaping. Eggs were held at 24–26°C, 40–60% RH, and a photoperiod of 14:10 (L:D) h, and observed daily for the emergence of parasitoids or bug nymphs. After eggs were removed, the remaining portions of the samples were returned to the zip lock bags and placed in a freezer to kill the insects and aid in separating them from the plant material for sorting and counting. Adults and various instar nymphs were sorted and counted for each sample and the body length, body width, and width across the eyes of thirty nymphs of each instar was measured using a calibrated ocular micrometer mounted within a dissecting microscope. Body sizes of 15 randomly selected male and 15 female adults, as well as the size of eggs, also were measured.

Horn and Hanula (2011) found that white and yellow traps were attractive to adult *M. cribraria* so we used the same traps to monitor adult activity throughout the year. Traps consisted of white or yellow Plexiglas cross-vanes (20 cm by 30 cm) with a gray bucket (diameter 20 cm, 10 cm deep) filled with soapy-water solution attached beneath to capture bugs flying into the cross-vanes and dropping down. In total, eight traps were deployed in four rows 50 m apart with two traps per row spaced 5 m apart. Samples were collected weekly from 17 May 2010 to 31 May 2011 in an ≈30-ha kudzu field near Athens, GA.

No-choice Host Test of *M. cribraria*. We were interested in obtaining information on *M. cribraria*'s ability to use some common forest legumes to determine if it might become a pest in forests and whether it could use other hosts besides kudzu. If not, then controlling kudzu in the vicinity of soybean fields might be a pest management option for this insect.

An adult no-choice survival and oviposition test was conducted in a stand-alone, single-level insectary building in Athens, GA. The room used for the experiment had six windows that were left open during the experiment and was lighted with Osram Sylvania (Danvers, MA) Sun Stick fluorescent lights in June and July 2010. Kudzu is in the order Fabales, family Fabaceae, subfamily Papilionoideae, tribe Phaseoleae, and subtribe Glycininae. All plant species chosen for the no-choice test and the subsequent field host range tests were from the same subfamily as kudzu. Tables 2-4 provide information on the classification of the various plants tested. In the no-choice test, nine species were chosen for comparison to kudzu including four trees: *Cladrastis kentukea* (Dum. Cours.) Rudd (American yellowwood), *Robinia pseudoacacia* L. (black locust), *Albizia julibrissin* Durazz. (mimosa, non-native), *Cercis canadensis* L. (redbud); and five herbaceous plants: *Lespedeza hirta* (L.) Hornem. (hairy lespedeza), *Lespedeza cuneata* (Dum. Cours.) G. Don (sericea lespedeza, non-native), *Lablab purpureus* (L.) Sweet (lablab, non-native), *Baptisia australis* (L.) R. Br. (wild indigo), and *Erythrina herbacea* L. (coral bean). Kudzu plants were established in 2-gal plastic pots by collecting rooted nodes from nearby patches (Frye et al. 2007). All plants were kept under similar nursery conditions with irrigation and fertilizer as needed. *Megacopta cribraria* were collected as newly emerged adults from a field in June. One male

Table 1. Measurements (means ± SE, mm) of *Megacopta cribraria* nymphs ($N = 30$)

	Nymph				
	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Body length	1.09 ± 0.13	1.47 ± 0.13	2.29 ± 0.20	2.97 ± 0.50	4.45 ± 0.36
Body width	0.68 ± 0.09	1.01 ± 0.12	1.62 ± 0.11	2.47 ± 0.36	3.45 ± 0.35
Width across eyes	0.36 ± 0.01	0.48 ± 0.01	0.66 ± 0.02	0.89 ± 0.02	1.19 ± 0.05

and one female were paired and caged in a fine mesh polyester cloth cage (25 cm by 15 cm) that was securely tied over a randomly selected branch of each test plant. Ten plant replicates were used for each test species. The number of surviving adults and the number of eggs deposited were recorded every other day until the adults died.

Nymphal no-choice development was tested using the same plant species but the trial was conducted in full sunlight at Whitehall Forest, Athens, GA from 27 May to 20 June. Eggs of *M. cribraria* were collected in the field and maintained under constant conditions (24–26°C, 40–60% RH, and a photoperiod of 14:10 [L:D] h). Once hatched, neonates were left around the egg shell for 1 d so they could acquire their obligate symbiotic bacteria that females deposited beneath egg masses. Ten neonates then were transferred to a test plant branch by using a paint brush and caged as above. Ten plants of each species were used. Plants were watered and observed daily for development to adults.

Field Host Range Tests of *M. cribraria*. To determine if *M. cribraria* used other hosts under seminatural conditions, a field test was conducted for 1 wk from 18 to 25 April 2011 in a 30-ha kudzu patch near Athens, GA by using eleven legume species. We used the same plants as in the no-choice test with the exception of coral bean. However, we added a native woodland vine purchased from a local nursery, *Wisteria frutescens* (L.) Poir. (American wisteria), and two agricultural legumes, soybean and blackeyed pea, *Vigna unguiculata* (L.) Walp., which were grown from seeds. To use kudzu as our control and to expose plants naturally to large numbers of *M. cribraria,* we placed all 11 test plants within 3-m- by 3-m-square areas located in the middle of the kudzu patch. Each replicate was surrounded by a 1.5-m-tall plastic mesh fence to keep out deer and groundhogs. Five kudzu vines equal in size to our plants were randomly selected as controls and marked with tags. *Megacopta cribraria* already had begun ovipositing on kudzu so we examined each kudzu vine and removed all eggs that were present. Potted plants were watered every day during the study. The experiment was replicated five times with replicates spaced at least 30 m apart. At the end of the test, the number of adults and eggs on each test plant were counted. To monitor the development of nymphs, test plants were moved to Whitehall Forest, covered with black fine mesh cloth cages to keep eggs and nymphs undisturbed, and placed in full sunlight. Plants were watered every day and checked for developing nymphs. Soybean was used as a surrogate for kudzu in this trial because the rapid growth rate of kudzu made it difficult to maintain in a small cage over an extended period of time. Soybean is in the same subtribe as kudzu, and it is a known host of *M. cribraria* in China and in the United States (P. Roberts, University of Georgia, Tifton, personal communication).

An additional host range test was conducted in a small (≈2-ha) kudzu field in a residential neighborhood in Athens from 27 April to 4 May 2011. This site was selected because two non-native legumes, *Vicia sativa* L. (garden vetch) and *Wisteria sinensis* (Sims) DC. (Chinese wisteria, non-native), were growing adjacent to it. We also tested another common native forest legume, *Amphicarpaea bracteata* L. Fernald (hog-peanut), because it was found to be an acceptable host for two other Asian insects that were tested as biological controls for kudzu (Frye et al. 2007). Hog-peanut plants were grown from seeds in pots. Potted hog-peanut was placed together with tagged kudzu and garden vetch plants. Five locations were selected ≈10 m apart, and five branches of the Chinese

Table 2. Adult longevity of *Megacopta cribraria* in adult no-choice survival test on some common forest legumes. Adults were caged on branches of the test plants and held in an insectary

Plant species (common name) [Tribe (subtribe)]	Mean (± SE) Longevity (d)
Cladrastis kentukea (Dum. Cours.) Rudd (yellowwood) [Sophoreae]	24.6 ± 4.4 a
Lespedeza cuneata (Dum. Cours.) G. Don (sericea lespedeza) [Desmodieae]	13.5 ± 1.7 ab
Pueraria montana variety *lobata* Willd. (kudzu) [Phaseoleae (Glycininae)]	12.6 ± 1.6 ab
Lespedeza hirta (L.) Hornem. (hairy lespedeza) [Desmodieae]	10.9 ± 1.3 abc
Albizia julibrissin Durazz. (mimosa) [Ingeae]	10.2 ± 1.7 abc
Erythrina herbacea L. (coral bean) [Phaseoleae (Erythrininae)]	8.9 ± 1.6 abc
Robinia pseudoacacia L. (black locust) [Robinieae]	8.5 ± 1.0 abc
Lablab purpureus (L.) Sweet (lablab) [Phaseoleae (Phaseolinae)]	7.8 ± 0.9 abc
Cercis canadensis L. (red bud) [Cercideae]	7.2 ± 1.2 bc
Baptisia australis (L.) R. Br. (wild indigo) [Thermopsideae]	6.3 ± 0.8 c
	$F_{9,\ 182} = 5.10$; $P < 0.0001$

Means followed by the same letter are not significantly different ($P < 0.05$; ANOVA, Tamhane's T2 test, SPSS Inc. 2001).

Table 3. Mean (± SE) number of adults and eggs of *Megacopta cribraria* on various potential hosts, and the number of adults developed from eggs deposited in a field choice test with 11 test plant species in 2011

Plant species (common name) [Tribe (subtribe)]	Number of adults	Number of eggs	Number of adults developed from eggs
Pueraria montana variety *lobata* Willd. (kudzu) [Phaseoleae (Glycininae)]	75.0 ± 15.5 ab	528.8 ± 57.4 a	N/A
Glycine max (L.) Merr. (soybean) [Phaseoleae (Glycininae)]	0.4 ± 0.2 c	320.0 ± 135.2 b	14.2 ± 5.7
Lespedeza hirta (L.) Hornem. (hairy lespedeza) [Desmodieae]	0.6 ± 0.6 c	122.2 ± 12.6 c	0
Lespedeza cuneata (Dum. Cours.) G. Don (sericea lespedeza) [Desmodieae]	0.8 ± 0.6 c	108.4 ± 57.0 c	0
Wisteria frutescens (L.) Poir. (American wisteria) [Millettieae]	0.8 ± 0.5 c	18.8 ± 11.8 c	0
Cladrastis kentukea (Dum. Cours.) Rudd (Yellowwood) [Sophoreae]	105.2 ± 23.5 a	5.0 ± 3.5 c	0
Vigna unguiculata (L.) Walp. (Blackeyed pea) [Phaseoleae (Phaseolinae)]	0	2.2 ± 2.2 c	0
Lablab purpureus (L.) Sweet (Lablab) [Phaseoleae (Glycininae)]	0	1.6 ± 1.6 c	0
Robinia pseudoacacia L. (Black locust) [Robinieae]	72.2 ± 19.2 b	0	0
Cercis canadensis L. (Red bud) [Cercideae]	0.2 ± 0.2 c	0	0
Albizia julibrissin Durazz. (Mimosa) [Ingeae]	0.4 ± 0.4 c	0	0
Baptisia australis (L.) R. Br. (Wild indigo) [Thermopsideae]	0.4 ± 0.2 c	0	0
	$F_{9, 40} = 14.7$ $P < 0.0001$	$F_{7, 32} = 11.3$ $P < 0.0001$	N/A

Means followed by the same letter are not significantly different ($P < 0.05$; ANOVA, LSD, SPSS Inc. 2001).

wisteria growing nearby were randomly selected and tagged. Eggs found on selected plants were removed to start the test as before. The numbers of adults present on each plant and the numbers of eggs deposited were counted after 1 wk of exposure.

Impact of *M. cribraria* on Kudzu. The impact of *M. cribraria* on kudzu was assessed by treating plots with insecticide and comparing them to unsprayed plots. The study was conducted in three kudzu fields near Athens, GA where we established five sets of study plots (two fields had two sets of plots each). Each site or location within a field contained two adjacent 5-m by 5-m plots (≈5–10 m apart). We mowed the border (≈1 m wide) around each plot every 2 wk from 5 May to 20 September 2010 to prevent kudzu encroaching from outside the plots. On the same days that we mowed, we also sprayed lamda-cyhalothrin insecticide (Cyonara 9.7, 6.3 ml/L, 0.06% a. i.) on half of the plots and left the other plots as untreated controls. Insecticide was applied using a Solo back-pack mist blower (Stihl model SR 320, VA Beach, VA) to ensure penetration into the tangle of vines within the plot. At the end of the study we sampled *M. cribraria* abundance in each plot by taking 10 sweeps per plot with a sweep net and by taking ten 0.5-m cuttings of kudzu vine per plot to determine how effective the insecticide was in protecting the plots.

Kudzu biomass within each plot was measured to determine the impact of *M. cribraria* on seasonal growth. We harvested all kudzu vines and leaves growing above ground in a 1-m-wide strip across the middle of each plot on 20 September. However, the first meter in from the edges was not included in the samples because bugs moving into the plots between sprays tended to accumulate along the edges. Therefore, only the central 3 m^2 of kudzu in each plot was measured. Leaves and stems from each plot were separated, dried in an oven at 40°C for 6 d, and weighed. Samples of dried leaves from each plot were analyzed by the Soil, Plant, and Water Laboratory of the University of Georgia to determine if *M. cribraria* affected their carbon and nitrogen content.

Data Analysis. Data are expressed as untransformed means ± SE. Adult longevity data were log transformed to normalize it, and then it was analyzed using analysis of variance (ANOVA) followed by Tamhane's T2 test (because equal variance was not assumed) to evaluate differences between plant species. The number of adults and eggs in the multiple-choice tests were analyzed with ANOVAs followed by least significant difference (LSD) to evaluate differences between plant species. An independent sample *t*-test was used to compare the leaf, stem, and total biomass, as well as the percent carbon content, nitrogen content, and carbon to nitrogen ratio of kudzu from control plots and insecticide sprayed plots. An independent sample *t*-test also was used to compare the numbers of adults and nymphs of *M. cribraria* in sprayed and unsprayed plots (SPSS Inc. 2001).

Table 4. Mean (± SE) number of adults and eggs of *Megacopta cribraria* in a field host range test with three test plant species in 2011

Plant species [Tribe (subtribe)]	Number of adults	Number of eggs
Pueraria Montana variety *lobata* Willd. (Kudzu) [Phaseoleae(Glycininae)]	42.8 ± 10.4	180.4 ± 19.4 a
Amphicarpaea bracteata L. Fernald (hog-peanut) [Phaseoleae(Glycininae)]	0	10.6 ± 3.4 b
Vicia sativa L. (garden vetch) [Fabeae]	0	54.0 ± 17.6 b
Wisteria sinensis (Sims) DC. (Chinese wisteria) [Millettieae]	0	0
	N/A	$F_{2, 12} = 33.49$ $P < 0.0001$

Means followed by the same letter are not significantly different ($P < 0.05$; ANOVA, LSD, SPSS Inc. 2001).

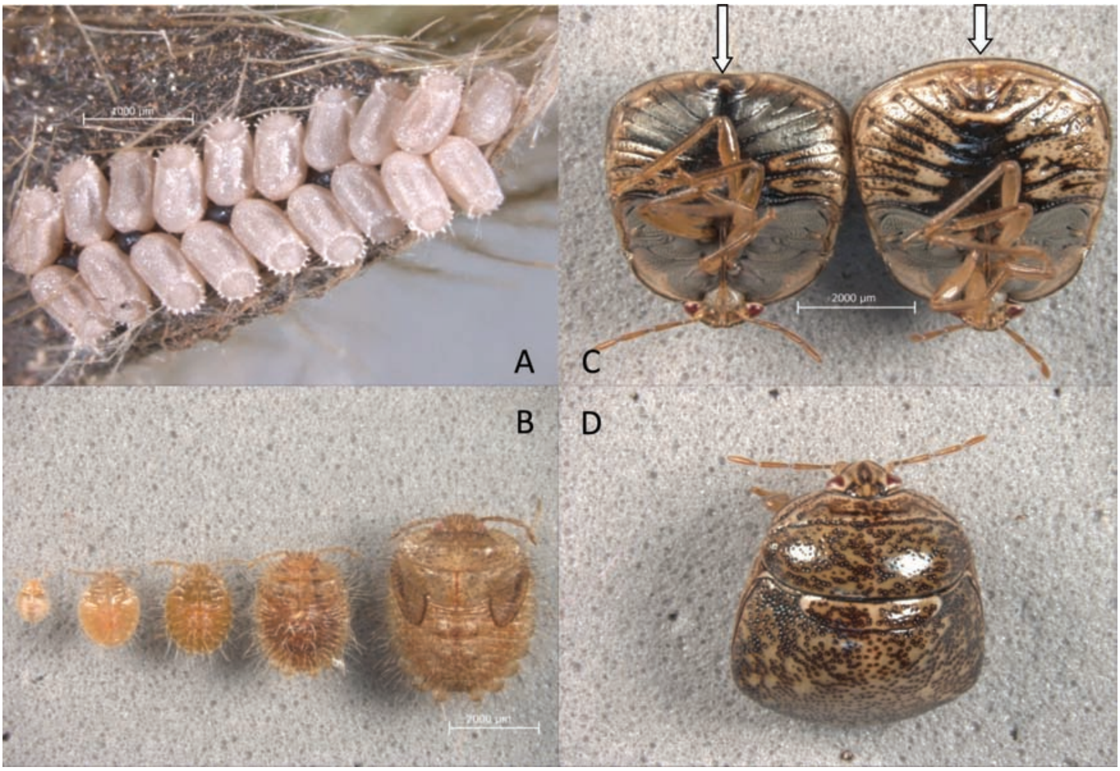

Fig. 1. Eggs (A), five nymphal instars (B), ventral view of male (left) and female (right) (C), and dorsal view of an adult *M. cribraria* (D). (Online figure in color.)

Results

Biology and Seasonal Activity of *M. cribraria*. Eggs of *M. cribraria* were most commonly found on the tender leaf sheaths of the growing vine tips of kudzu but a few also were found on the underside of leaves and older vines of kudzu. They were laid in groups of two or occasionally three parallel rows (Fig. 1A), but occasionally eggs were laid in small, irregular groups or individually. We observed an average of 15.64 ± 0.58 eggs per egg mass ($N = 200$). Individual eggs were 0.86 ± 0.01 mm long and 0.47 ± 0.01 mm wide ($N = 10$), oval in shape and white when freshly laid but turned off-white or pink soon after. The operculum is round and surrounded by short spine-like projections. Eggs are attached to plant substrates with a blackish material deposited under them by females. No parasitoids were detected in any of the eggs collected.

Megacopta cribraria undergoes five nymphal instars (Fig. 1B). The body length, body width, and width across the eyes of each instar are shown in Table 1. The width across the eyes was the most stable parameter for distinguishing instars in addition to overall size. First-instar neonates are reddish and turned brown after several hours. Newly hatched nymphs aggregated near the egg masses, but dispersed quickly when disturbed. Second- and third-instar nymphs dispersed from the vicinity of eggs and were yellowish green. Fourth and fifth instars had well defined wing buds and were greenish to greenish brown.

Newly emerged adults were whitish and tender, but hardened and turned a mottled brown color within several hours (Fig. 1C and D). They are somewhat square in shape. Females averaged 4.47 ± 0.28 mm long and 3.86 ± 0.42 mm wide, whereas males were 3.99 ± 0.81 mm long and 3.54 ± 0.37 mm wide ($N = 15$). Males and females are easily separated by the shape of their terminal sternites. In males the sternite is rounded, whereas in females it is v-shaped with a distinct suture (Fig. 1C). Adults are active, strong fliers, and readily fly when disturbed. The sex ratio of male to female from the whole-year samplings was 1.1: one (2887: 2621). However, the sex ratio of male to female from the flight intercept traps in early spring 2011 was 1: 1.8 (154: 272).

We recovered nearly 100 eggs/0.5 m of vine on our initial sampling date of 26 April 2010 (Fig. 2). Egg abundance declined to nearly zero in late June and early July. A second period of oviposition activity occurred in July and August although the number of eggs per 0.5 m of vine was much lower than in the spring. In 2011, egg-laying began during the first week of April and increased rapidly to an average of ≈140 eggs/0.5 m of vine by late April. We initiated egg sampling again in late June based on the previous year's adult flight and oviposition results. The second peak in egg laying in 2011 began on or near 24 June as indicated by the high number of eggs that were all newly laid (white in color) and the lack of hatched

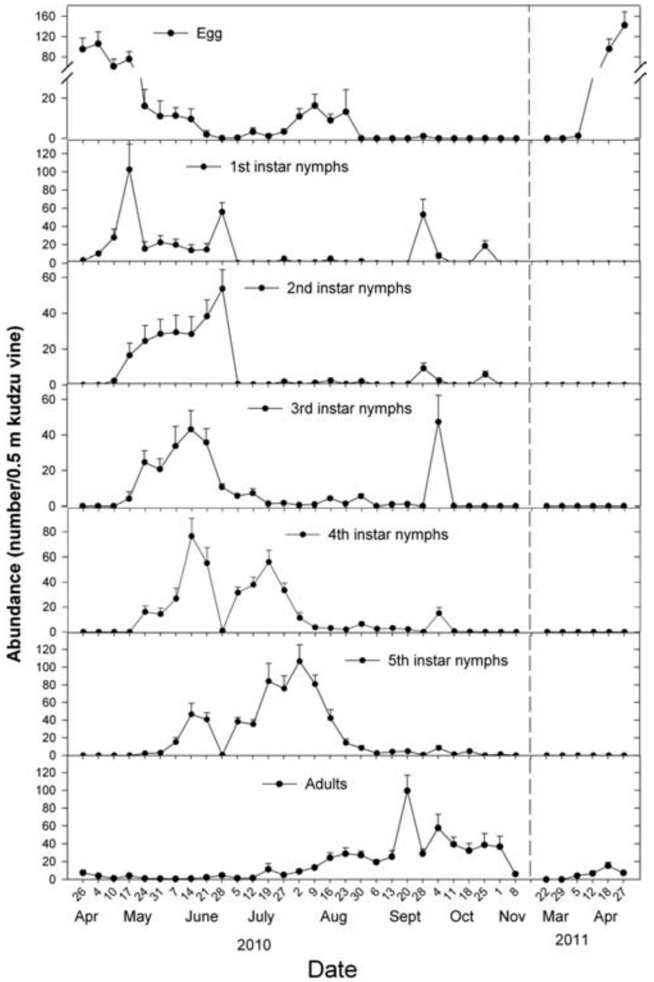

Fig. 2. Abundance of eggs, nymphs, and adults on 0.5-m lengths of kudzu vine ($N = 10$) collected from a patch of kudzu in Athens, GA from 26 April 2010 to 27 April 2011.

eggs (Fig. 3). This was almost a month earlier than the 2010 midsummer peak of adult flight activity and second oviposition period. Numbers of newly laid eggs gradually decreased until late August and then remained at low numbers through late October. Hatched eggs were observed on almost every sample after 24 June until early October.

The first nymphs were recovered 4 May 2010 and none were recovered in early spring 2011 (Fig. 2). First-instar nymphs then were present almost throughout the year. Second instars first appeared 10 May and gradually increased until 28 June after which low numbers were recovered throughout the summer. Third instars first were detected 17 May, 1 wk after second instars were detected, and peaked in abundance on mid-June. They then declined to low levels until early October when nearly 50 third instars/0.5 m of vine were detected. Fourth-instar nymphs first were detected 24 May. They exhibited two peaks in abundance in mid-June and mid-July and were abundant from then until early August after which numbers were low. Fifth instars first were detected 24 May and had two peaks in abundance in mid-June and again early August.

Megacopta cribraria overwintered as adults. No eggs or nymphs were detected in early spring 2011 when new kudzu growth was examined (Fig. 2) and we found no nymphs remaining once plants died after the first frost in early November. We used two methods of monitoring adult activity, vine cuttings (Fig. 2) and flight intercept traps (Fig. 4), which provided very different results. Vine cuttings taken from 26 April through late June 2010 yielded low numbers of adults. The first newly emerged adults were collected on 21 June after which adult abundance gradually increased until it peaked on 20 September and remained at high levels until the first frost. Vine samples in 2011 also had very low numbers of adults in March and April. Adult abundance was low in vine samples taken in the spring of both years although large numbers of eggs were found.

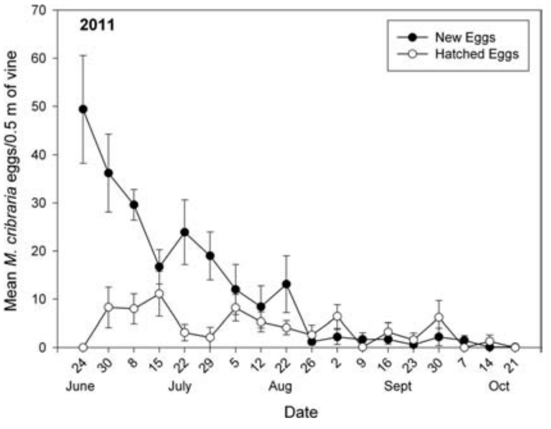

Fig. 3. Mean (±SE) ($N = 10$) number of newly laid and hatched eggs of *M. cribraria* per 0.5-m-long sections of kudzu vine tip from 24 June to 21 October 2011.

Flight intercept trap captures demonstrated a different pattern of adult activity (Fig. 4). Traps placed in the field 17 May 2010 caught very low numbers until 21 June when we first noticed newly emerged adults on kudzu. Adult captures then increased, peaked, and remained high from 27 July to 11 August after which numbers declined sharply. This peak in adults coincided with the second period of egg laying (Fig. 2). Captures remained low for several weeks until mid-September when they began to increase again peaking in October. The last adults were caught in traps on 1 December. Overwintered adults began flying again in mid-March 2011. We caught over 2,000 adults per trap from 6 to 13 April and trap captures remained high until 2 May after which numbers declined to relatively low levels by the last week of May.

No-choice Host Test of *M. cribraria*. In the adult no-choice survival and oviposition test in 2010, most eggs were deposited on the surface of the polyester cages instead of on the test plants so we did not analyze the oviposition data. Although kudzu was the presumed best host of *M. cribraria*, adults lived longest on American yellowwood, *C. kentukea*, but not significantly longer than on most other plant species tested except redbud, *C. canadensis*, and wild indigo, *B. australis* (Table 2). Neonates placed on different plant species did not complete development on any of them including lablab, *L. purpureus*, which is a host in Asia (Eger et al. 2010).

Field Host Range Tests of *M. cribraria*. In the field host range tests in spring 2011, kudzu and American yellowwood had the largest number of adults present. Black locust had fewer adults than yellowwood and kudzu, but significantly more than all other species tested (Table 3). No adults were found on blackeyed pea, or lablab. Not surprisingly, significantly more eggs were deposited on kudzu than any other test species. Soybean had fewer eggs than kudzu, but significantly more than the other species. Excluding kudzu, which was not included in the development study because it is the main host in Georgia thus far, soybean was the only other test plant that successfully supported complete development from egg to adult (Table 3). In the second host range test adults were only found on kudzu. Although *M. cribraria* laid eggs on some of the other plants, significantly more eggs were found on kudzu (Table 4) compared with Chinese wisteria, garden vetch, and hog-peanut (Table 4).

Impact of *M. cribraria* on Kudzu. Lamda-cyhalothrin insecticide maintained populations of *M. cribraria* at low levels (Fig. 5). Unsprayed control plots had ≈40 times the number of *M. cribraria* adults as treated plots. Likewise, no nymphs were recovered from sprayed plots.

Megacopta cribraria feeding reduced the biomass of kudzu (Fig. 6). Leaf ($t = -2.55$, df = 8, $P = 0.034$);

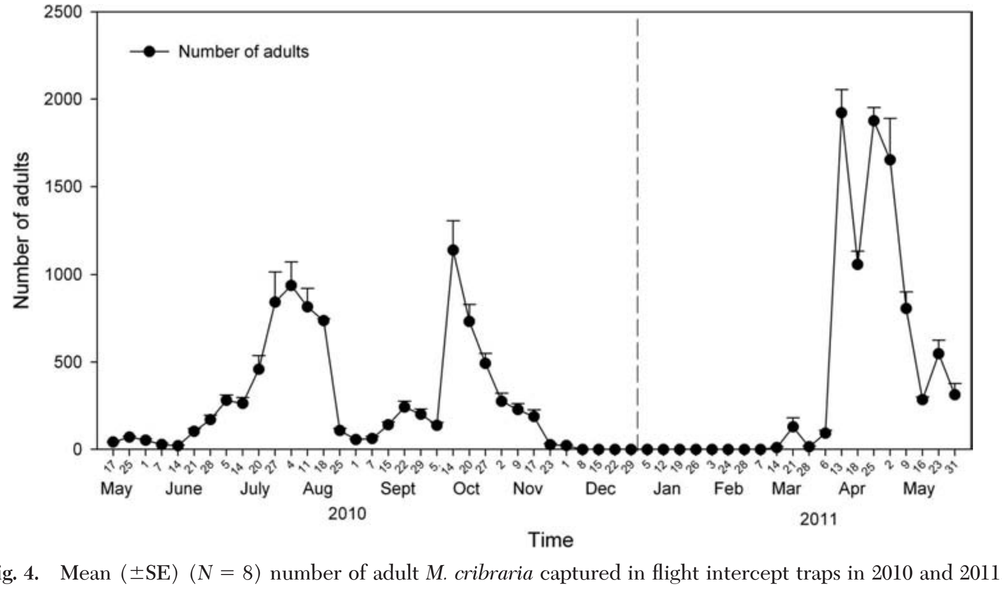

Fig. 4. Mean (±SE) ($N = 8$) number of adult *M. cribraria* captured in flight intercept traps in 2010 and 2011.

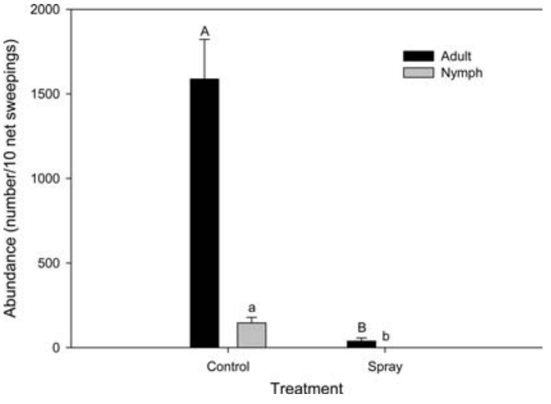

Fig. 5. Mean (±SE) ($N = 5$) number adults and nymphs per 10 sweeps with a sweep net in unsprayed control plots and insecticide sprayed plots.

stem ($t = -3.51$, df = 8, $P = 0.008$); and total kudzu biomass ($t = -4.49$, df = 8, $P = 0.002$) were significantly lower in unsprayed plots (Fig. 6). Bug feeding throughout the year resulted in 32.3%, 32.6%, and 32.5% reductions in leaf, stem, and total biomass, respectively. However, they had no effect on carbon content ($t = 0.11$, df = 8, $P = 0.912$); nitrogen content ($t = 0.53$, df = 8, $P = 0.612$); or carbon to nitrogen ratio ($t = -0.54$, df = 8, $P = 0.603$) of leaves. During the summer we noticed that deer fed preferentially on the sprayed plots. This was evident from their characteristic feeding damage but we did not attempt to measure the extent of the damage, so the impact of deer feeding on overall biomass is unknown.

Discussion

Megacopta cribraria feeds primarily along the main stems or vines, on leaf petioles and on leaf veins, but early instars also appear to feed on leaves. Overwintering adults began laying eggs during the week of 5–12 April 2011 and, based on 2010 results, first generation eggs were abundant until 17 May. Egg abundance increased again from 5 July to 23 August 2010 but we did not observe large numbers per 0.5 m of vine, possibly because the much greater numbers of new vines to oviposit on and because we sampled both old and new vines. Because females lay very few eggs on older vines the average number of eggs per length of vine was reduced. This was evident in 2011 when we only sampled growing tips of vines and had approximately twice the number of eggs per 0.5 m of vine as we did in 2010. In 2011 a second peak in oviposition beginning on or near 24 June was observed, which was earlier than the previous year. The occurrence of second generation eggs during summer 2010 was consistent with flight trap results, which showed that first generation adults began emerging in late June and they were present from then until late August. However, vine sampling in 2010 showed no peak of adult activity in the summer. It is unclear why this occurred. Newly emerged adults initially were whitish in color,

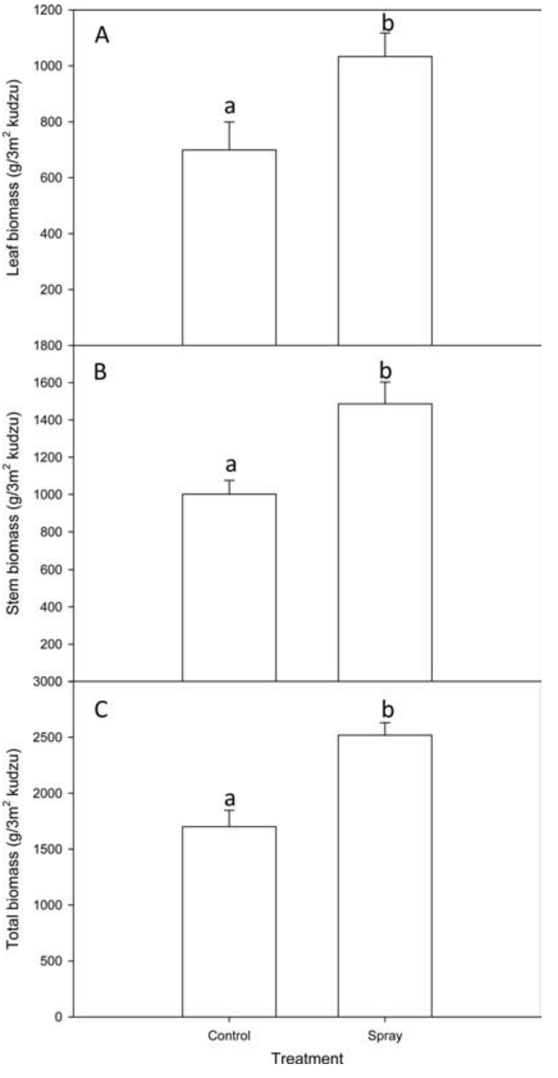

Fig. 6. Mean (±SE) ($N = 5$) leaf (A), stem (B), and total biomass (C) of kudzu per 3 m^2 in unsprayed control plots and insecticide sprayed plots.

so they were easy to recognize, and we started collecting them by 21 June 2010. However, we never collected adults in large numbers from vine samples until mid-August, after which we observed an increase in adults on kudzu that coincided with increased catches of second generation adults in flight intercept traps. The low abundance of adults on vines in summer may be related to dispersal behavior. At least some first generation adults leave kudzu to find new hosts. This was shown when large numbers of adults arrived in soybean fields during the early summer where they then completed a generation on soybeans (P. Roberts, University of Georgia, personal communication), which is consistent with observations on soybean in China (Chen et al. 2009).

What triggers this dispersal behavior or what portion of the population disperses is unknown, but previous studies indicated that host plants were most susceptible to stink bugs that primarily feed on seeds during fruit and pod formation (Hall and Teetes 1982, Schumann and Todd 1982, Riley et al. 1987, Bundy and McPherson 2000), and as fruit of host plants reach maturity and harden, plants become less attractive, and stink bugs disperse to more succulent plants (Toscano and Stern 1976, Todd and Herzog 1980, Hall and Teetes 1982, Jones and Sullivan 1982). This is unlikely to occur with kudzu because it grows continuously throughout the summer so new vines and leaves always are present. Overcrowding may be a factor. The high populations of first generation nymphs may result in newly emerged adults being predisposed to disperse. Thus, first generation adults may lay some eggs on kudzu, accounting for the relatively low numbers of eggs observed after overwintering generation oviposition is completed, and then disperse to find other patches of suitable host plants. Regardless, at least some of the population leaves kudzu during the summer in search of other hosts or locations. This is similar to *M. cribraria* behavior in China where overwintered adults also were active in March and April feeding and ovipositing on kudzu, black locust, and kidney bean (*Phaseolus vulgaris* L.), but eventually some overwintered and first-generation adults migrated to soybean (Wang et al. 1996, Chen et al. 2009).

It is clear that *M. cribraria* is capable of completing two generations per year on kudzu. Flight trapping results showed three distinct peaks of activity. The first, in early spring was because of the emergence of overwintering adults that coincided with peaks in egg abundance in spring of 2010 and 2011. This was followed by two additional peaks in trap captures that were the adults of the first and second generations. Second generation adults then overwinter. Captures of first generation adults from late June through mid-August 2010 also coincided with increased numbers of eggs on kudzu vines. The increase in abundance of early-instar nymphs late in the season at the time when second generation adults were emerging suggests that at least a partial third generation may occur. Whether they successfully complete development to adults may be dependent upon the timing of the first freeze. In China *M. cribraria* is reported to have two or three generations per year. For example, Li et al. (2001) reported two and rarely three generations in Yugan county (28° 21′ N) of Zhejiang Province. Wu et al. (1992) found three generations in Lanxi (29° 28′ N) and Zhejiang Provinces, and two to three generations occurred in Zhumadian (32° 98′ N) (Zhang and Yu 2005) and Luohe (33° 34′ N) of Henan Province (Chen et al. 2009).

Results of the no-choice tests of both adults and neonates showed that enclosing small branches with polyester cages was not effective. Wu et al. (1992) reported that adults of *M. cribraria* were very active, so restricting them with small cages may affect their behavior because they laid eggs on the cages rather than plant tissue. Studies in China indicated that first generation adult *M. cribraria* lived 1.5–3 mo, and second generation overwintering adults lived 9–10 mo (Zhang and Yu 2005). In our tests first-generation adults survived an average of 25 d on yellowwood and only 13 d on kudzu, even though they were collected in mid-June right after molting to the adult stage. Thus, conditions probably were not optimal for *M. cribraria* survival in this trial.

Kudzu was the best host for *M. cribraria* oviposition in both field host range tests. Adults were found in large numbers on the stems of yellowwood and black locust. Both tree species have been reported to attract large numbers of adults (D. Suiter, University of Georgia, and J. Johnson, Georgia Forestry Commission, personal communications). Despite the large numbers of adults found on them, no eggs were laid on black locust and only five eggs per plant were found on American yellowwood, indicating that neither is preferred for oviposition when kudzu is available. Other than kudzu, soybeans were the only host on which *M. cribraria* completed development from egg to adult although survival was low. Whether this is an indication that soybean is a poor host or the bugs do poorly when caged on plants is unclear. Relatively large numbers of eggs were laid on *Lespedeza* spp. but no development occurred on them under our test conditions.

We used relatively small tree saplings in our tests so response of *M. cribraria* to mature trees is unknown, but our results with trees and herbaceous plants suggest that *M. cribraria* may not be a serious pest of forest legumes. However, a large number of species of legumes occur in North American forests, some of which may prove to be acceptable hosts, and there are over 100 species of legumes that are listed as threatened, endangered, or sensitive species (Birdsall and Hough-Goldstein 2004). How this insect will impact them is unknown but thus far it appears to have a restricted host range.

Kudzu is a serious invasive plant in the United States with over 1.2–2.8 million ha infested (Corley et al. 1997, Everest et al. 1999) and an estimated increase of 50,000 ha/yr (Mitich 2000). After being introduced as an ornamental vine at the Philadelphia Centennial Exposition from China in 1876 (Winberry and Jones 1973), kudzu was used as a forage crop at the beginning of the 20th century (Piper 1920). Then its role changed from being a soil erosion control plant in the 1930s and '40s (Tabor and Susott 1941), to being recognized as a weed by 1953, to finally being listed as a common weed in the southeastern United States by 1970 (Everest et al. 1999). Several surveys for kudzu biocontrol agents have been conducted in Japan and China (Tayutivutikul and Kushigemati 1992, Britton et al. 2002, Sun et al. 2006, Imai et al. 2010). *Megacopta cribraria* was one of 116 phytophagous insects feeding on kudzu in China but it has not been considered for biological control because of its wide host range, particularly its ability to feed on and cause substantial damage to soybean. However, now that *M. cribraria* is in the United States it might play a beneficial role in controlling kudzu.

Megacopta cribraria clearly impacted kudzu growth, reducing biomass by almost 33%. However, this may underestimate their impact because deer preferentially fed on insecticide sprayed plots, possibly because the large numbers of bugs on unsprayed vines. Sweep net sampling showed that untreated plots had over 1,500 adults per 10 sweeps compared with ≈20 adults per 10 sweeps on insecticide treated plots (Fig. 5). The insects produce a strong odor when disturbed and they also may be distasteful if ingested. Regardless of the reason deer chose the sprayed plots, they reduced biomass as well. Without deer feeding, *M. cribraria*'s overall impact may have been greater than we observed.

Kudzu is a perennial vine that grows quickly during the growing season but dies back to the ground after a hard freeze. The plant depends on its large starchy roots, which can reach up to a 4-m depth in the soil and weigh up to 136 kg, to provide energy in the spring for the rapid initial growth, reported to be up to 0.3 m per day and 20 m per year (Everest et al. 1999). Ball et al. (1979) reported that grazing kudzu with goats or cows can eliminate it if 80% of the foliage is consumed continuously for 2 yr. Likewise, close mowing every month for 2 yr is effective in eliminating an infestation (Ball et al. 1979). However, at forest edges all vines climbing up trees also must be cut or the area will be reinfested from the edges (Miller and Edwards 1983). No studies have been done to determine the effects of lower levels of defoliation. Forseth and Innis (2004) suggest that fall mowing or grazing would be most effective because fall translocation of carbon to the roots is critical for establishment of plants.

Megacopta cribraria is not a defoliator, but large numbers of adults arrive in kudzu patches in the spring, where they and their offspring feed continuously throughout the year, resulting in at least 33% reduction in overall plant growth. Whether repeated years of *M. cribraria* feeding will affect kudzu growth further may depend on whether or not the growth reduction has a cumulative effect, i.e., it helps deplete the root reserves. If so, then *M. cribraria* may benefit forests because kudzu vines along forest edges grow up and over the tops of nearby trees, eventually killing them by shading. Over time kudzu can cover large areas of potentially productive forest and farm land resulting in estimated losses of $100–500 million per year (Forseth and Innis 2004). If *M. cribraria* can deplete kudzu's root reserves and reduce its ability to climb, it may benefit southern forests as well as farmers, utility companies, and railroads that deal with kudzu encroaching on their land, climbing utility poles, and growing across their tracks.

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