BIOLOGY, HOST PREFERENCES, AND POTENTIAL DISTRIBUTION OF *CALOPHYA TEREBINTHIFOLII* (HEMIPTERA: CALOPHYIDAE), A CANDIDATE FOR BIOLOGICAL CONTROL OF BRAZILIAN PEPPERTREE, *SCHINUS TEREBINTHIFOLIA,* IN FLORIDA

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Abstract

Brazilian peppertree, *Schinus terebinthifolia* Raddi (Anacardiaceae), a perennial woody plant native to Brazil, Argentina, Uruguay and Paraguay, has become one of the most invasive weeds in Florida. A leaflet pit galling psyllid, *Calophya terebinthifolii* Burckhardt & Basset (Hemiptera: Calophyidae), has been identified as a potential biological control agent for Brazilian peppertree. However, biological information on the psyllid, including its life history, rearing procedures and potential distribution, is lacking. This type of information is essential when importing an insect for biological control purposes. From May-Aug 2009, field and laboratory research was conducted in Gaspar, Santa Catarina, Brazil with psyllids collected from the Atlantic coastal region of Santa Catarina. Laboratory studies on the psyllid in Brazil focused on: female fecundity (55.3 ± 8.9 eggs/female), the number and size of the immature stages, age-specific survivorship, and mean generation time (43.7 ± 1.2 days). Preliminary evidence from feeding trials suggests this psyllid from the Atlantic coastal region of Santa Catarina is locally adapted to Brazilian peppertree plants of haplotype A, which is one of the genetic types that invaded Florida. Ecological niche modelling with MaxEnt confirmed there was climatic overlap between Florida and the native range of the psyllid in South America. Using collection and survey locations of the psyllid in its native range and point locations for haplotype A plants in Florida, a map was created that predicted Volusia, coastal Pasco and Hernando counties, and a small section of southwestern Polk county as suitable locations for establishment of the psyllid if it is approved for release as a biocontrol agent.

Key Words: weed biocontrol, psyllid, life history, niche modeling

Resumen

Brazillian peppertree, *Schinus terebinthifolia* Raddi (Anacardiaceae), un árbol perenne nativo de Brasil, Argentina, Paraguay y Uruguay, es una de las plantas más invasoras en la Florida. El psílido formador de agallas en las hojas, *Calyophya terebinthifolii* Burckhardt & Basset (Hemiptera: Calophyidae), ha sido identificado como un agente potencial de control biológico de Brazillian peppertree. Sin embargo, información biológica sobre el psílido, incluyendo su historial de vida, procedimientos de crianza y distribución potencial no existe. Este tipo de información es esencial cuando se importa un insecto con propósitos de control biológico. De mayo a agosto del 2009, investigaciones de campo y en laboratorio fueron llevadas a cabo en Gaspar, estado de Santa Catarina, Brasil con insectos colectados en la región costera atlántica de Santa Catarina. Los estudios de laboratorio con el psílido en Brasil se concentraron en la fecundidad de las hembras (55.3 ± 8.9 huevos/hembra), el número y tamaño de los estadíos inmaduros, sobrevivencia a diferentes edades, y duración promedio de una generación (43.7 ± 67 1.2 días). Resultados preliminares de los ensayos de alimentación indican que los psílidos originarios de la región costera atlántica de Santa Catarina están adaptados localmente a plantas de Brazillian peppertree haplotipo A, el cual es uno de los tipos genéticos que ha invadido la Florida. El modelo de nicho ecológico utilizando 'MaxEnt' confirmó

que existe una similaridad climática entre la Florida y el rango nativo del insecto en América del Sur. Utilizando los datos de las localidades donde se colectó el insecto en su rango nativo y las localidades del haplotipo A en la Florida, se generó un mapa que predijo el condado de Volusia, la región costera de Pasco, el condado de Hernando, y una pequeña sección del suroeste del condado de Polk como localidades adecuadas para el establecimiento del psílido si éste llega a ser aprobado para ser liberado como agente de control biológico.

Palabras Clave: control biológico de malezas, psílidos, historia natural, modelo del nicho

Brazilian peppertree, *Schinus terebinthifolia* Raddi (Sapindales: Anacardiaceae) is a perennial woody shrub/tree native to Brazil, Argentina, Uruguay and Paraguay (Barkley 1944, 1957). It was originally introduced to Florida in the 1840s as an ornamental (Mack 1991), but has since naturalized becoming an invasive weed occupying more than 283,000 ha in central and south Florida (Cuda et al. 2006; Rogers et al. 2012) and is expanding its range northward (Anon. 2007a,b; Mukherjee et al. 2012). Brazilian peppertree having numerous invasive properties such as fast growth, prolific seed production, tolerance to shade, fire, drought, salinity, and vigorous resprouting (Ewel 1979; Nilsen & Muller 1980; Doren et al. 1991; Ewe & Sternberg 2005), displaces native vegetation and reduces the biodiversity of native plants and animals (Bennett et al. 1990). Furthermore, Brazilian peppertree populations in Florida are the result of 2 separate introductions from different parts of the native range resulting in the establishment of 2 cpDNA haplotypes (A and B) and their hybrids (Williams et al. 2005).

In 2011, the South Florida Water Management District spent almost $1.8 million controlling Brazilian peppertree (Rodgers et al. 2012). Because of its invasive characteristics and resistance to conventional control methods, Brazilian peppertree was targeted for classical biological control in Florida in the late 1970s (Delfosse 1979; Campbell et al. 1980). The lack of native congeners minimizes the risk of damage to nontarget plants from introduced natural enemies, making it a good candidate for biological control (Pemberton 2000). Biological control of Brazilian peppertree could provide a more cost effective and sustainable approach for managing this invasive weed, especially when it is integrated with conventional control methods (Cuda et al. 2006). Several insect biological control agents have been studied for release in Florida (e.g., Medal et al. 1999; Martin et al. 2004; Cuda et al. 2005, 2008, 2009; Manrique et al. 2008; Moeri et al. 2009; Mound et al. 2010; Wheeler et al. 2010; Oleiro et al. 2011; McKay et al. 2012; Rendon et al. 2012). *Calophya terebinthifolii* Burckhardt & Basset (Hemiptera: Calophyidae), a leaflet galling psyllid of Brazilian peppertree (Vitorino et al. 2011), is the focus of this study.

Because local climatic conditions can play an important role in the distribution and effectiveness of a weed biocontrol agent (McClay & Hughes 1995; Julien 2000; Robertson et al. 2008), matching ecoclimatic conditions for optimal development of *C. terebinthifolii* in its native range is likely to increase the likelihood of its establishment post-release (Geiger & Gutierrez 2000). Ecological niche modelling is a tool for predicting the fundamental niche of a species (where a species could occur) by establishing a statistical relationship between species known occurrences and relevant predictor variables (for example, climatic variables) (Phillips et al. 2006). Several methods have been developed to model climate based species distributions (reviewed in Franklin 2009). The Maximum Entropy Species Distribution Model (MaxEnt) is a presence only modelling approach that predicts the ecological niche of a species using known occurrence data (latitude/longitude point locations of the species) and environmental layers (Phillips et al. 2006). Using the input data for *C. terebinthifolii*, MaxEnt can generate a prediction of geographical locations climatically suitable for the psyllid to establish persistent populations in Florida.

The objectives of this research were to accelerate testing of *C. terebinthifolii* as a biological control agent for Brazilian peppertree in Florida by 1) investigating the biology of *C. terebinthifolii* in Brazil (fecundity, number/size of instars, and survivorship); 2) comparing the performance of *C. terebinthifolii* on the genotypes of Brazilian peppertree that occur in Florida; and 3) using ecological niche modelling to identify potential release areas in Florida that overlap climatically with the insect's native distribution in South America and locating additional sites in Brazil for collecting *C. terebinthifolii* adapted to Florida Brazilian peppertree genotypes.

Materials and Methods

The study was conducted from 11 May-8 Aug 2009 in Gaspar, Santa Catarina, Brazil at the Laboratório de Monitoramento e Proteção Florestal (LAMPF) (S -26.9110° W -48.9362°). LAMPF is affiliated with the Forest Protection and Surveillance Laboratory that is part of the Universidade Regional de Blumenau.

Fecundity, Instar Verification, Size, and Survivorship

A colony of psyllids was established in the laboratory by collecting individuals from the field. Geoposition, corresponding weather conditions (i.e., relative humidity, temperature, wind speed, and precipitation), site description, and number of psyllids collected were recorded for each site. Adults were captured individually in clear gelatin capsules (size "000") from Brazilian peppertrees located along the eastern coast of Santa Catarina, Brazil. The gelatin capsules containing adult psyllids were stored in coolers, and then transported back to LAMPF within 3-5 h of capture. Field collected adults were then released on Brazilian peppertree seedlings. The seedlings used in the studies were grown in 1 liter nursery pots under ambient conditions in a greenhouse at LAMPF and were all approximately 40 cm in height with at least 3 flushes of new leaflets.

To measure fecundity, 1 female and 1 male (newly emerged from the established colony) were released on a Brazilian peppertree seedling ($n = 28$) covered with a 30×60 cm mesh bag and secured at the base of the seedling stem with 2 vinyl-coated twist ties. Leaves were checked daily for eggs. Temperature and relative humidity also were recorded. Female wing length (mm), body length (mm), and head width (mm) were measured at death. Fecundity was regressed against female wing length to examine the relationship between egg production and body size (Geiger & Gutierrez 2000).

To verify the number of instars from laboratory reared ($n = 18$) and field collected nymphs ($n = 177$), the following parameters were measured under a dissecting microscope: body length, body width, and head capsule width (mm). Based on previous studies, this sample size of 195 nymphs was adequate for generating a histogram of instars and size range of each instar for cecidogenous psyllids (Devi & Prabhoo 1995; Alvarez-Zagoya & Cibrian-Tovar 1999). Measurements were compared to those of *Calophya schini* Tuthill recorded by Alvarez-Zagoya and Cibrian-Tovar (1999) as a point of reference and comparison between the 2 congeners.

Using the eggs produced from the female fecundity study, egg cohorts were followed through their development with survivorship and temperature recorded daily. Psyllids were allowed to complete their development on a Brazilian peppertree seedling using the same procedure described for the aforementioned fecundity study. Psyllid eggs ($n = 157$) were kept in environmental growth chambers at 21.9 ± 2.6 °C; RH, $67.9 \pm 7.6\%$; and 16:8 h (L:D).

Data were analyzed with SAS© software, Version 9.0 (SAS 2002). Sample means ± SEM were determined for all parameters. After confirming that the data were normally distributed, a linear regression was performed to correlate fecundity with female size. A frequency distribution was created to determine number of instars. A significance level of $\alpha = 0.05$ was used for all statistical analyses. The means of body length of male and female adult *C. terebinthifolii* and of *C. terebinthifolii* and *C. schini* were statistically compared with t-tests using Proc t-test (SAS 2002). A survivorship curve of the laboratory population was produced and a life table was constructed. Population statistics were calculated using standard techniques (Price 1997).

Performance on Brazilian Peppertree Haplotypes Established in Florida

To test the hypothesis that *C. terebinthifolii* performs better on natal genotypes of Brazilian peppertree, terminal buds were taken from laboratory plants ($n = 22$) in Brazil and preserved in silica gel. Chloroplast haplotype was determined by D. A. Williams, Texas Christian University, Ft. Worth, Texas. Sampled plants were categorized as either a success (females laid eggs, instars developed and emerged as adults) or failure (no eggs were laid or psyllids failed to develop into adults). Categorical data were analyzed with the *G*-test of independence (Sokal & Rohlf 1995) at $\alpha = 0.05$.

Ecological Niche Modeling

Two occurrence datasets were used for the ecological niche modelling. The first dataset included the geolocations of *C. terebinthifolii* in its native South American range ($n = 47$) with points obtained from surveys by Ms. Lindsey Christ, Dr. Greg Wheeler and Mr. Fernando McKay (personal communication), and from Burckhardt & Basset (2000). The second dataset included 50 point locations of Brazilian peppertree (haplotype A) found in Florida provided by Dr. William Overholt (personal communication). Two bioclimatic (bioclim) variables obtained from the WORLDCLIM database (http://www.worldclim.org) were used to model the insect's fundamental niche. The climate layers were generated using average climate data collected from weather stations worldwide (Hijmans et al. 2005). ESRI 2.5 arcminute resolution grids of current climate data were used to run the model (Environmental Systems Research Institute, Inc., Redlands, California). The 2 bioclim variables included were bio14 (precipitation during the driest month) and bio4 (temperature seasonality-standard deviation of monthly temperature).

Data partitioning is a technique used to provide test points for model verification and accuracy (Phillips et al. 2006). Both niche models generated in MaxEnt were statistically verified by running 10 random partitions of the dataset with 80% of the points as training data to generate the

models and the remaining 20% as independent test data for extrinsic verification of predictive accuracy. Each training set was run in MaxEnt with the random seeded sub-sampling procedure using 10 replications with 10% as random test percentage for intrinsic model testing. A minimum training threshold dependent one-tailed binomial test was conducted to verify the models generated by the MaxEnt predictions performed significantly better than random (Phillips et al. 2006). The test was based on omission rate (test points falling in pixels predicted as not suitable) and Fractional Predictive Area (FPA, fraction of pixels predicted suitable) (Phillips et al. 2006). Because MaxEnt generates continuous predictions, the minimum training threshold (minimum value received by any training data) was used to perform the threshold dependent binomial test because the binomial test requires the data to be binary (presence / absence), not continuous. The proportion of test points (n_{test}) predicted not suitable (out$_{test}$) was used as the extrinsic omission rate (out$_{test}$/n_{test}) (Anderson et al. 2003). The binomial test was performed using Proc Freq in SAS© 9.0 (SAS 2002).

MaxEnt used presence data and randomly generated "pseudo-absences" from the study area (also referred to as model background) to generate the predicted distribution. For native occurrences, all of South America was used as the background; for predictions using Florida occurrences of Brazilian peppertree haplotype A, Florida was used as the background. A prediction map showing the potential distribution of *C. terebinthifolii* in Florida was developed by combining the predictions generated using 10 randomly partitioned datasets.

To identify areas in Florida climatically similar to the native distribution of the psyllid, predictions generated using the 2 occurrence datasets were overlapped. The overlapped distribution was classified into 4 major categories: 1) not suitable (absent), 2) suitable based on *C. terebinthifolii* occurrence data from South America, 3) suitable based on Florida distribution of Brazilian peppertree type A plants, and 4) overlap between 2 and 3.

RESULTS AND DISCUSSION

Fecundity, Instar Verification, Size, and Survivorship

In total, 18 of 28 females (64.3%) in cages containing mating pairs of adult *C. terebinthifolii* deposited eggs. Mean number of eggs laid per female was 55.3 ± 8.9 (*n* = 18) with a range of 16-139 eggs (excluding the 10 females that did not lay eggs). These values are similar to those reported for *C. schini*; the average number of eggs laid for this species was 50 (no SEM was given) with a range of 25-110 eggs based on 10 oviposit-

ing females (Alvarez-Zagoya & Cibrian-Tovar 1999). The oblong shaped eggs of *C. terebinthifolii* are 0.212 ± 0.002 mm in length (Table 1) and are a milky, translucent cream color when first laid then turn a black, iridescent color within 24 h. Similar to *C. schini* (Downer et al. 1988), the females laid their eggs on the new leaf flush along the leaflet margins, midribs, leaflet petiolules, and leaf buds. The number of eggs laid by a female increased with wing length (*F* = 5.15; df = 9; *P* = 0.0494; Fig. 1). The low R² value (0.364) reflected the high variability in the data. In total, 11 of the 18 females that laid eggs (61.1%) were recovered for measurement.

To determine the number of instars, a histogram of body length was constructed and examined for distinct peaks. The histogram (Fig. 2) confirmed 5 instars for *C. terebinthifolii*. Automontage images of the different instars and adults are shown in Fig. 3 in black and white and in color in Suppl. Fig. 3. The measurements of all life stages of *C. terebinthifolii* (body length, body width, and head capsule width) are provided in Table 1 and were compared with its congener *C. schini* in Fig. 4. Female body lengths for *C. terebinthifolii* were significantly larger than males (*t* = 3.65; df = 38; *P* = 0.008), which is typical for most psyllids (Hodkinson 2009). By comparison, *C. schini* is significantly larger than *C. terebinthifolii* in the following stages: egg (*t* = 10.85; df = 52; *P* < 0.0001), 3rd instar (*t* = 3.62; df = 42; *P* = 0.0008), 5th instar (*t* = 7.63; df = 157; *P* < 0.0001), and adult (*t* = 3.54; df = 68; *P* = 0.0007).

A survivorship curve (Fig. 5) was developed using daily observations on survivorship from 4 of the cages (*n* = 157 eggs) held in the environmental growth chambers. Eclosion of 1st instars commenced on day 9, and there was a sharp decrease in survival during the first wk after hatching when the nymphs are in the vulnerable crawler stage. Survivorship leveled off after the crawlers settled into pit galls and then survival gradually decreased during the 3rd, 4th, and 5th instars until adults began to emerge around day 43. The average duration from egg to adult stage was 43.7 ± 1.2 days, which was similar to the 43 days reported for *C. schini* (Alvarez-Zagoya & Cibrian-Tovar 1999).

Performance on Brazilian Peppertree Haplotypes Established in Florida

The results from the DNA analysis are shown in Table 2. From this test sample, psyllids only developed to adults on haplotype A and haplotype O plants, with the best performance on haplotype A plants. A *G*-test comparing all other haplotypes (O, K, D, and M), with haplotype A plants showed the psyllids performed significantly better on A than other haplotypes (*G* = 7.63; *P* < 0.01). Recent studies on the Brazilian peppertree invasion

TABLE 1. DIMENSIONS OF ALL LIFE STAGES OF THE LEAFLET GALLING PSYLLID *CALOPHYA TEREBINTHIFOLII*.

| Stage	n	$\bar{x} \pm$ SEM (mm)
Egg	30	0.212 ± 0.002 length 0.099 ± 0.002 width
1st instar	18	0.228 ± 0.005 length 0.183 ± 0.012 width 0.108 ± 0.004 head capsule width
2nd instar	67	0.307 ± 0.002 length 0.298 ± 0.002 width 0.155 ± 0.002 head capsule width
3rd instar	14	0.446 ± 0.010 length 0.442 ± 0.009 width 0.222 ± 0.006 head capsule width
4th instar	24	0.674 ± 0.015 length 0.665 ± 0.015 width 0.320 ± 0.009 head capsule width
5th instar	72	0.962 ± 0.006 length 0.942 ± 0.006 width 0.398 ± 0.002 head capsule width
Adult	40	1.251 ± 0.020 body length 1.509 ± 0.018 wing length 0.441 ± 0.007 head capsule width
Female	28	1.293 ± 0.021 body length 1.542 ± 0.020 wing length 0.453 ± 0.008 head capsule width
Male	12	1.154 ± 0.013 body length 1.432 ± 0.025 wing length 0.415 ± 0.009 head capsule width
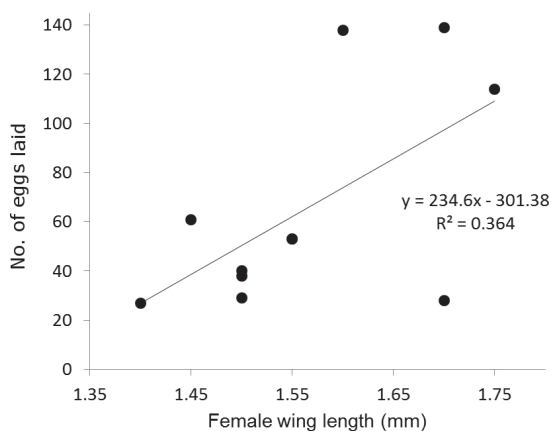
Fig. 1. The relationship between wing length and laboratory fecundity of female *Calophya terebinthifolii* (*n* = 11).
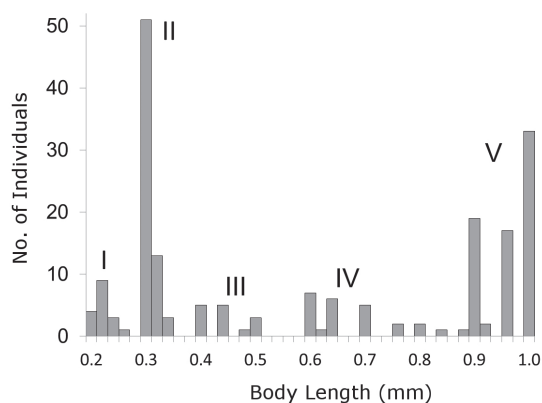
$y = 234.6x - 301.38$
$R^2 = 0.364$

Fig. 2. Frequency distribution of nymphal length measurements of *Calophya terebinthifolii*. Peaks within groupings indicate 5 instars.

in Florida (Geiger et al. 2011; Mukherjee et al. 2012) and 'fine scale' adaptation by several of its natural enemies (Cuda et al. 2012) suggest that it may be necessary to introduce multiple biotype-specific control agents into Florida to achieve the desired impact.
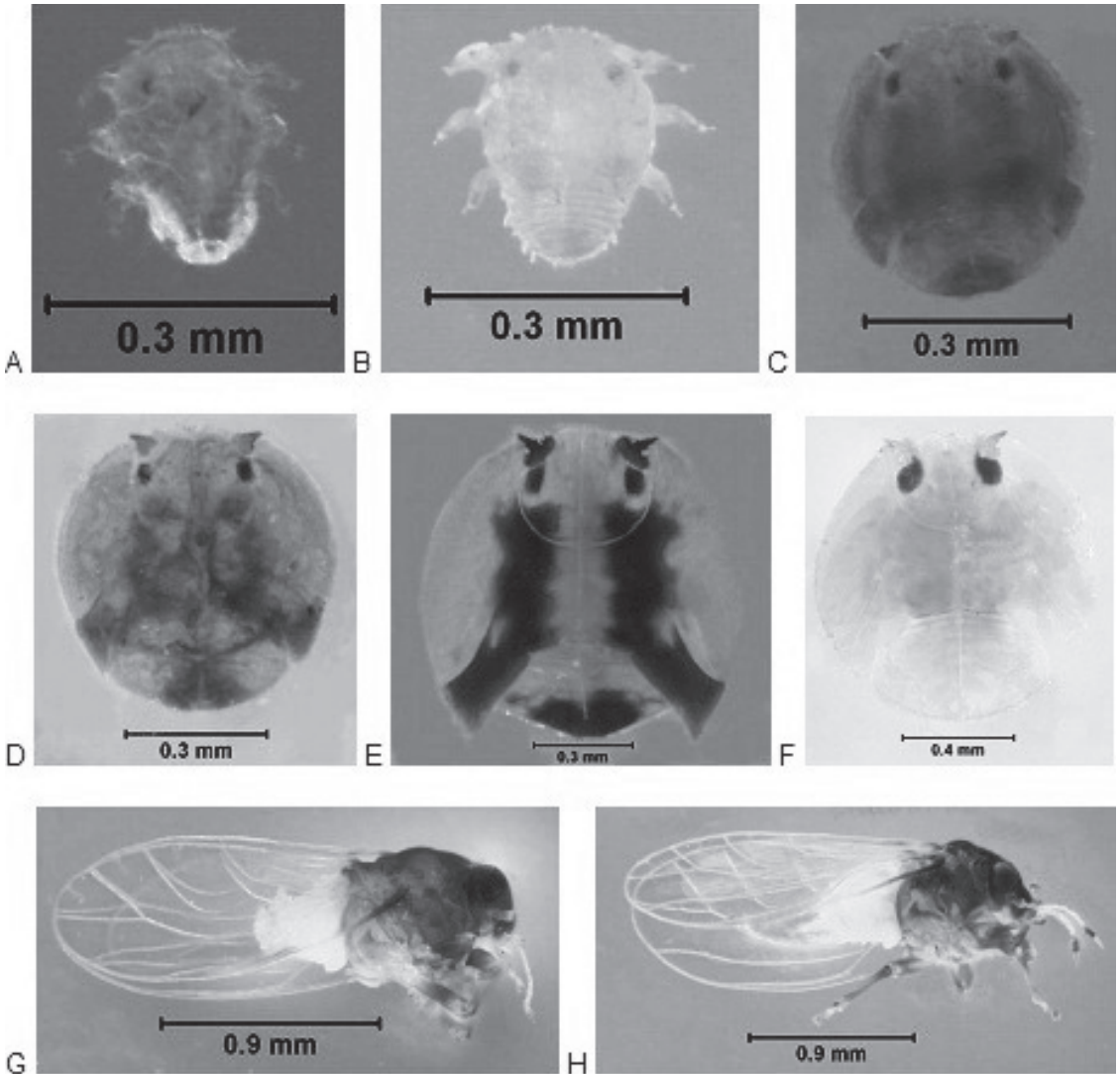
Fig. 3. Automontage images of *Calophya terebinthifolii.* A) 1st instar, B) 2nd instar, C) 3rd instar, D) 4th instar, E) 5th instar, F) 5th instar prior to darkening, G) adult male, and H) adult female. Photo credit L. R. Christ.

Ecological Niche Modelling

Tropical psyllids are especially vulnerable to cold temperatures and drought (Hodkinson 2009). Waring & Cobb (1992) reported that in 73% of published studies, gall-forming species reacted negatively to drought. Young nymphs of several species of gall-inducing psyllids often suffer high mortality before gall formation due to low humidity (Ferreira et al. 1990; personal observation). Because *C. terebinthifolii* reproduces continuously in Brazil, precipitation during the driest month (bio14) is a critical factor to include in the model as reflected by this variable's overall contribution to the model prediction. It is noteworthy that Weins et al. (2006) found that temperature seasonality (bio4) was an important climate variable for predicting the distribution of tropical tree frogs in temperate North America.

The minimum training threshold dependent binomial test results for Florida (validated using Florida type A Brazilian peppertree points) were highly significant for all the data partitions (Table 3; z = 3.1623; P = 0.0008). The average FPA (Fractional Predictive Area) was 0.448. The extrinsic omission rates were zero for all partitions. Likewise, the results for the South American tests were similar (Table 4; z = 2.5-3.2; P < 0.0001), with all data partitions being highly significant. The average FPA for the South American
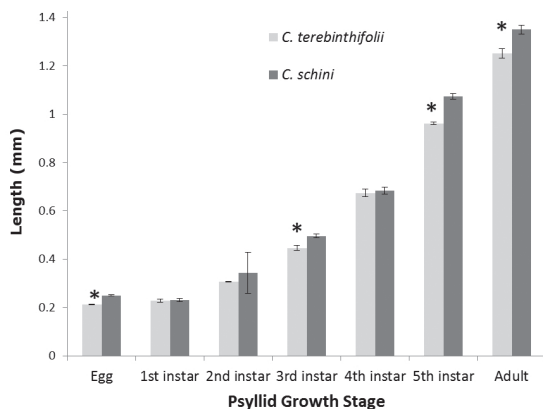
Fig. 4. Comparison of the body lengths of the life stages of *Calophya terebinthifolii* and *C. schini*. Measurements for *C. schini* obtained from Alvarez-Zagoya & Cibrian-Tovar (1999).

tests was 0.173. The extrinsic omission rates were slightly higher with an average of 4%. Overall, the models generated by MaxEnt were accurate with predictions being significantly better than random.

The predicted distribution of *C. terebinthifolii* in Florida is shown in Fig. 6 in black and white and in color in Suppl. Fig. 6. Establishment of *C. terebinthifolii* is expected to occur in a few coastal regions along the panhandle, west coast, and along the east coast in Florida. Areas of overlap where Brazilian peppertree haplotype A plants were known to occur and predicted to be suitable for establishment of *C. terebinthifolii* included the following Florida counties: Volusia, coastal Pasco and Hernando, and a small section of southwestern Polk. These counties should be targeted for planned releases of *C. terebinthifolii* if it is ap-
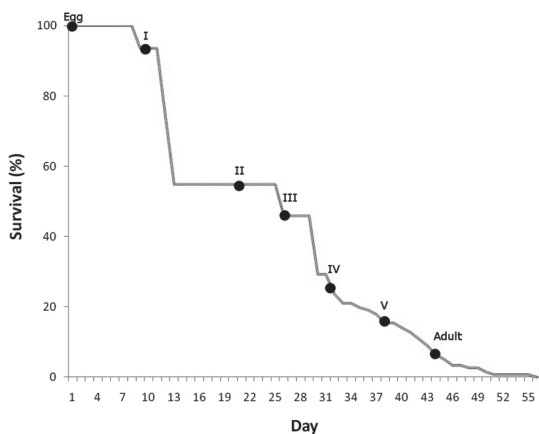
proved for release as a biological control agent of Brazilian peppertree. It is noteworthy that the psyllid is predicted to establish in Franklin Co. in the panhandle where Brazilian peppertree was recently discovered (EDDMaps 2012).

Using the known locations of *C. terebinthifolii*, another map was generated in MaxEnt to predict other areas in South America likely to support psyllid populations. The map for South America (available upon request) predicted *C. terebinthifolii* to occur in the following countries: 1) southern Chile, 2) central Bolivia, 3) southeastern Paraguay, 4) Uruguay, and 5) southern Brazil in the states of Rio Grande do Sul, Santa Catarina, Paraná, and coastal São Paulo. These areas (except for Chile and Bolivia where Brazilian peppertree has not been reported) would be good locations to survey for *C. terebinthifolii* because the full native range for the psyllid is still unknown.

Conclusions

Results of this research provide baseline biological data for evaluating *C. terebinthifolii* as a candidate for biological control of Brazilian peppertree. The 5 instars observed for *C. terebinthifolii* in this study differed from the number reported by Downer et al. (1988) for *C. schini* in California. They observed this congener had only 4 distinct peaks after measuring 1,000 field-collected nymphs in all stages of development over a 10 wk period. More recently, Alvarez-Zagoya & Cibrian-Tovar (1999), who studied *C. schini* in Mexico, found evidence of 5 instars when nymphs were studied in a laboratory setting. It is conceivable that Downer et al. (1988) focused their field sampling efforts on nymphs that had already initiated gall formation, and simply overlooked the first instar crawler stage because of its small size and mobility (Table 1).

Three different studies on both species of *Calophya; C. schini* in Chapingo, Mexico (Alvarez-Zagoya & Cibrian-Tovar 1999), *C. schini* in Ventura County, California (Downer et al. 1988), and *C. terebinthifolii* in Santa Catarina, Brazil (Vitorino et al. 2011; personal observation) found the insects to have continuous generations. The polyvoltinism exhibited by *Calophya* psyllids makes them good candidates for biological control because they can provide year round control. Although not gall-forming, other psyllids such as *Boreioglycaspis melaleucae* Moore and *Heteropsylla spinulosa* Muddiman, Hodkinson and Hollis have been successfully used as biological control agents (Kuniata & Korowi 2004; Rayamajhi et al. 2007; Center 2007; Rayamajhi et al. 2008). Additionally, *C. terebinthifolii* may reach higher densities in Florida than Brazil because of escape from specialist parasitoids (Christ 2010).

Brazilian peppertree haplotypes suitable for psyllid development were unknown prior to the

Fig. 5. Survivorship curve of *Calophya terebinthifolii* in laboratory environmental growth chambers in Brazil at 21.9 ± 2.6 °C, RH 67.9 ± 7.6% and 16:8 h L:D.

TABLE 2. REARING OF *CALOPHYA TEREBINTHIFOLII* ON 5 DIFFERENT BRAZILIAN PEPPERTREE HAPLOTYPES AT LAMPF, SANTA CATARINA, BRAZIL, MAY-AUG 2009. REARING SUCCESS EXPRESSED AS A PERCENTAGE OF THE TOTAL NUMBER OF PLANTS WITHIN EACH HAPLOTYPE PRODUCING NORMAL ADULTS.

Brazilian peppertree cpDNA haplotype	N	Success	Failure	% Success
A	12	8	4	67%
O	5	1	4	20%
K	2	0	2	0%
D	2	0	2	0%
M	1	0	1	0%

TABLE 3. MINIMUM TRAINING THRESHOLD DEPENDENT BINOMIAL TEST RESULTS OF OMISSION FOR PREDICTING THE DISTRIBUTION OF THE LEAFLET GALLING PSYLLID *CALOPHYA TEREBINTHIFOLII* IN FLORIDA WITH MAXENT.

Data Partition	Fractional Predictive Area	Points Not Suitable (out_{test})	Test Points (n_{test})	Extrinsic Omission Rate (out_{test}/n_{test})	Z
Part – 1	0.406	0	10	0	3.1623**
Part – 2	0.410	0	10	0	3.1623**
Part – 3	0.356	0	10	0	3.1623**
Part – 4	0.475	0	10	0	3.1623**
Part – 5	0.463	0	10	0	3.1623**
Part – 6	0.517	0	10	0	3.1623**
Part – 7	0.419	0	10	0	3.1623**
Part – 8	0.506	0	10	0	3.1623**
Part – 9	0.413	0	10	0	3.1623**
Part – 10	0.510	0	10	0	3.1623**
Average	0.448	0		0	

** P = 0.0008

TABLE 4. MINIMUM TRAINING THRESHOLD DEPENDENT BINOMIAL TEST RESULTS OF OMISSION FOR PREDICTING THE DISTRIBUTION OF THE LEAFLET GALLING PSYLLID *CALOPHYA TEREBINTHIFOLII* IN SOUTH AMERICA WITH MAXENT.

Data Partition	Fractional Predictive Area	Points Not Suitable (out_{test})	Test Points (n_{test})	Extrinsic Omission Rate (out_{test}/n_{test})	Z
Part – 1	0.222	0	10	0.0	3.1623**
Part – 2	0.058	1	10	0.1	2.5298**
Part – 3	0.078	1	10	0.1	2.5298**
Part – 4	0.232	0	10	0.0	3.1623**
Part – 5	0.237	0	10	0.0	3.1623**
Part – 6	0.255	0	10	0.0	3.1623**
Part – 7	0.260	0	10	0.0	3.1623**
Part – 8	0.077	1	10	0.1	2.5298**
Part – 9	0.233	0	10	0.0	3.1623**
Part – 10	0.075	1	10	0.1	2.5298**
Average	0.173	0.400		0.04	

** P< 0.0001

laboratory rearing experiments in Brazil. Few replicates were used for some of the haplotypes (K, D, and M) and no type B plants were included, making it difficult to draw clear conclusions regarding the possible suitability of Florida genotype plants. However, it is noteworthy that type O

is most closely related to haplotype B (Mukherjee et al. 2012). If *C. terebinthifolii* is indeed locally adapted to haplotype A, it may have difficulty developing on the novel genotypes in Florida created by the hybridization of haplotypes A and B. In Brazil, these 2 haplotypes do not occur sym-
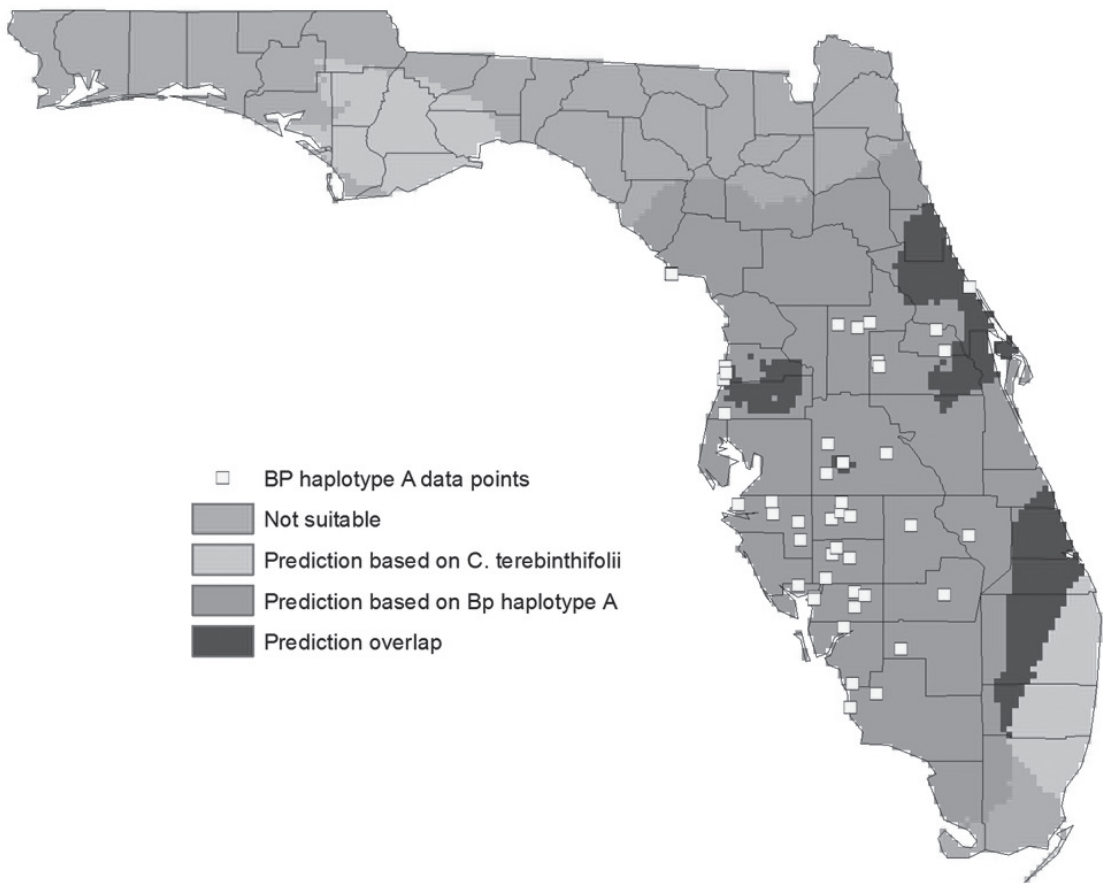
Fig. 6. Map of predicted climatic suitability for the leaflet galling psyllid *Calophya terebinthifolii*, its host plant Brazilian peppertree haplotype A, and their predicted overlap in Florida. Open squares (*n* = 50) indicate locations of Brazilian peppertrees identified as haplotype A through DNA analysis (D. A. Williams, unpubl. data).

patrically (Williams et al. 2005; Mukherjee et al. 2012)). However, if *C. terebinthifolii* from coastal Santa Catarina, Brazil can develop on both haplotypes A and O, it may accept haplotype B as well. Because our preliminary data suggest that *C. terebinthifolii* is locally adapted to specific Brazilian peppertree genotypes, evidence of 'fine scale' adaptation to its host plant is consistent with other small natural enemies of Brazilian peppertree having limited dispersal capability (see Cuda et al. 2012).

The 2 predicted distribution maps produced in this study were constrained by the paucity of data points for *C. terebinthifolii* in its native range. Consequently, the maps generated should be considered preliminary. One of the assumptions made when generating niche models is that the entire native range of the species is known and is accounted for in the point locations (Phillips et al. 2006). However, the complete native range of *C. terebinthifolii* is still unknown. As more information about the native range distribution of the

psyllid becomes available, a more accurate model can be developed. Nevertheless, these preliminary models are reasonable for selecting locations for future surveys in South America and potential habitats in Florida where the psyllid could be released as a biocontrol agent for Brazilian peppertree.

Finally, the most compelling argument for using *C. terebinthifolii* as a biological control agent for Brazilian peppertree in Florida is based on the discovery of the adventive *C. schini* in California in the mid 1980s (Downer et al. 1988). *Calophya schini*, which was first reported from Los Angeles County, California in Jul 1984, dispersed rapidly from San Diego County to the San Francisco Bay (a distance of about 800 km) in less than 4 yr (Downer et al. 1988). This congener of *C. terebinthifolii* caused extensive damage on Peruvian peppertree, *Schinus molle* L. In southern California where both *Schinus* species co-occur, Downer et al. (1988) reported that *C. schini* attacked only Peruvian peppertree but not its close relative

Brazilian peppertree. Assuming *C. terebinthifolii* would respond similarly if it were introduced into Florida without its natural enemies, this leaflet galling psyllid may be a promising candidate for the biological control of Brazilian peppertree.

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