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Diversity and impact of herbivorous insects on Brazilian peppertree in Florida prior to release of exotic biological control agents

Ganesh P. Bhattarai[a,b], Rodrigo Diaz[a,c], Veronica Manrique[a,c], William W. Turechek[d], Lyle Buss[e], Bernardette Stange[a] and William A. Overholt[a]

[a]Indian River Research and Education Center, University of Florida, Fort Pierce, FL, USA; [b]Department of Entomology, Kansas State University, Manhattan, KS, USA; [c]Department of Entomology, Louisiana State University, Baton Rouge, LA, USA; [d]United States Department of Agriculture, Agricultural Research Service, Horticultural Research Laboratory, Fort Pierce, FL, USA; [e]Department of Entomology and Nematology, University of Florida, Gainesville, FL, USA

ABSTRACT

Brazilian peppertree, *Schinus terebinthifolia* Raddi (Anacardiaceae), is a South American plant that is highly invasive in Florida. The impact of insect herbivores on the performance of Brazilian peppertree was evaluated at two locations in Florida using an insecticide exclusion method. Although 38 species of insect herbivores were collected on the invasive tree, there were no differences in growth or reproductive output of insecticide protected and unprotected trees, providing evidence that insect feeding had no measurable impact on tree performance. The majority of insects collected on Brazilian peppertree were generalists, and several were serious agricultural pests.

1. Introduction

Schinus terebinthifolia Raddi (Anacardiaceae), commonly referred to as Brazilian peppertree, is one of the most aggressive terrestrial invasive plants in Florida. The native South American distribution of Brazilian peppertree includes Brazil, Argentina, Paraguay, and Uruguay (Barkley, 1944, 1957; Mc Kay, Oleiro, Vitorino, & Wheeler, 2012). In Brazil, it is considered a pioneer species (Lorenzi, 2002; Nogueira, Martinez, Ferreira, & Prado, 2004) and is used for reforestation of degraded landscapes (Hüller, Coelho, Lucchese, & Schirmer, 2009). In Florida, Brazilian peppertree colonises disturbed habitats, but also intact natural communities including mangrove forests, saw-grass marshes, slash pine forests, tropical hardwood hammocks, palmetto prairies, cypress savannas, and sand pine scrub oak (Doren & Jones, 1997; Ewel, Ojima, Karl, & Debusk, 1982; Loope & Dune-vitz, 1981; Woodall, 1982). In the early 1990s, it was estimated that >280,000 ha, primarily in south and central Florida, were infested with Brazilian peppertree (Cuda, Ferriter, Manrique, & Medal, 2006), but there is recent evidence of a northward expansion (Mukherjee et al., 2012). Characteristics which contribute to the invasiveness of Brazilian peppertree

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CONTACT William A. Overholt ✉ billover@ufl.edu 🖃 Indian River Research and Education Center, University of Florida, Fort Pierce, FL 34945, USA

include a high reproductive output, an effective mechanism of dispersal by birds (Panetta & McKee, 1997), tolerance to shade (Ewel, 1978), fire (Doren, Whiteaker, & LaRosa, 1991), drought (Nilsen & Muller, 1980a) and saline conditions (Ewe & Sternberg, 2002), and allelopathic effects on neighbouring plants (Gogue, Hurst, & Bancroft, 1974; Morgan & Overholt, 2005; Nilsen & Muller, 1980b; Overholt, Cuda, & Markle, 2012).

The introduction history of Brazilian peppertree into Florida is fairly well documented (Morton, 1978; Mukherjee et al., 2012; Nehrling, 1944; Williams, Overholt, Cuda, & Hughes, 2005, 2007). The first record of the tree in Florida is from Barkley (1944) where he mentions specimens collected at unspecified locations by Ferdinand Rugel in the 1840s. Next, seeds from Algeria and France were sent to the USDA Plant Introduction Center in Miami in 1898 and 1899 (Morton, 1978). The original provenance of these seeds is unknown. A third introduction occurred in 1926 when seeds collected 'somewhere in Brazil' were planted in Punta Gorda in southwestern Florida (Nehrling, 1944). Recent molecular studies support historical records of introductions into Miami and Punta Gorda, with evidence of two chloroplast haplotypes in Florida; one found primarily on the west coast, arbitrarily designated as haplotype A, and a second on the southern east coast, designated as haplotype B (Williams et al., 2005). The two types have hybridised extensively since arriving (Mukherjee et al., 2012; Williams, Muchugu, Overholt, & Cuda, 2007), and there is evidence that hybrid seedlings have higher survival, growth rates and biomass accumulation than the parental types (Geiger, Pratt, Wheeler, & Williams, 2011). The source populations of the two types introduced into Florida are southeastern Brazil and Bahia State in northern Brazil (Mukherjee et al., 2012; Williams et al., 2005). These two source populations are widely separated in Brazil, and therefore, have not had the opportunity to hybridise in the native range. Thus, Florida's hybrid trees are genetically distinct from trees that occur in in the native range.

In the practice of weed biological control, it is recommended to conduct prerelease surveys in the invaded region to determine whether herbivorous insects may already be having an impact the target plant (Costello, Pratt, Rayamajhi, & Center, 2003; Olckers & Hulley, 1995). Cassani (1986) cataloged insects found associated with Brazilian peppertree on the southwestern coast of Florida and listed 46 phytophagous species, but stated that 'no significant herbivory was observed on *S. terebinthifolia* at any time during the survey'. A later survey added 10 species of phytophagous Lepidoptera, with *Paectes abrostoloides* (Guenée.) (Eutellidae) being the most commonly encountered species. *P. abrostoloides*, and a congener, *P. obrotunda* Guenée, were found to feed on tender apical foliage, but caused little damage due to their low density (Cassani, Maloney, Habeck, & Bennett, 1989). No attempts to quantify the impact of insect herbivores on Brazilian peppertree growth have been made.

Biological control of Brazilian peppertree has been under investigation for several years and a number of insect natural enemies have been identified and evaluated (Cuda et al., 2012; Manrique, Cuda, & Overholt, 2013; Wheeler et al., 2016), but none have yet been released due to potential for non-target damage (Davis, McKay, Oleiro, & Wheeler, 2011; Mc Kay et al., 2012; Oleiro, Mc Kay, & Wheeler, 2011; Wheeler et al., 2011), or in one case, the presence of compounds toxic to birds and mammals (Dittrich, Macedo, Cuda, & Biondo, 2004). However, two insects have recently been recommended for release by the USDA/APHIS Technical Advisory Group on Biological Control (TAG); a leaf galling psyllid, *Calophya latiforceps* Burckhardt (Hemiptera: Calophyidae), and a

thrips, *Pseudophilothrips ichini* Hood (Thysanoptera: Phlaeothripidae). The psyllid has been shown to be highly specialised on Brazilian peppertree (Diaz, Moscoso, Manrique, Williams, & Overholt, 2014, 2015), and greenhouse studies demonstrated that the psyllid reduced plant height by 31% and biomass accumulation by 11% over a three-month exposure period (Prade et al., 2016). *Pseudophilothrips ichini* feeds at the apical meristems causing dieback of new growth and reduced growth by 89% over an one-month feeding period. It is anticipated that one or both of these insects will be released in Florida in the near future.

The objectives of the current study were to use an insecticide exclusion method to: (1) quantify the impact of insect herbivory on growth and reproductive output of Brazilian peppertree prior to the release of exotic biological control agents, (2) examine whether different haplotypes of Brazilian peppertree differ in growth rates and experience differential herbivore pressure in Florida, and (3) provide baseline data on performance of Brazilian peppertree for comparison with data collected after biological control agents are established in the field.

2. Material and methods

2.1. Field study

Field plots of three genetic types of Brazilian peppertree were established in Fort Pierce (27.4324, −81.4112) and Immokalee (26.4620, −81.4438), Florida. Brazilian peppertree seeds were collected from three areas in Florida: (1) Miami where haplotype B is dominant, (2) Punta Gorda where haplotype A is dominant, and Fernandina Beach where hybrids are most common (Williams et al., 2007). At each location, seeds from 10 mother trees were collected and comingled prior to planting. Seeds were planted in trays in a germination potting soil mixture (Fafard® Super-fine Germination Mix, Sungro, Agawam, MA), and then transplanted into 1 gallon pots with Fafard® 3B potting soil when 5–10 cm tall. The plants were grown in a greenhouse for three months and then transplanted in the field in Fort Pierce and Immokalee in November 2014. At each site, we established 12 plots consisting of two rows of Brazilian peppertrees, three plants per row in Fort Pierce ($N = 72$) and four plants in Immokalee ($N = 96$). One of the haplotypes (A, B, or hybrid) was randomly assigned to each plot within a site. In this way, there were four plots for each haplotype in each site. One row of plants in each plot was randomly assigned to insecticide treatment while the other received water. All plants in the rows designated to receive insecticide were treated with a soil drench of the neonicotinoid insecticide imidacloprid 2F (Adonis 2F, Envincio LLC, Cary, NC; hereafter insecticide treated) at the recommended rate of 6 ml per 30.5 cm of plant height, diluted in 250 ml of water. The untreated plants (hereafter, water treated) received an equal volume of water. The dosage of insecticide was increased in relation to average plant height following the insecticide label recommendations. Plants were separated by 4.9 m within and between rows.

All trees were inspected every three months from November 2014 to August 2016. Plant height, basal stem diameter, number of branches, and number of fruits were recorded. In addition, a visual estimate of the proportion of leaves with insect chewing damage was made on a scale of 0–10 with 0 = no damage, 1 = 1–10%, 2 = 11–20%, and so on with 10 = 91–100% of leaves with damage.

2.3. Imidacloprid ELISA bioassay

To determine whether trees receiving insecticide or water treatments had quantifiably different levels of insecticide, we measured the titre of imidacloprid in leaf tissue using a direct competitive ELISA (Abraxis LLC, Warminster, PA). Leaves were collected on four of the eight sampling occasions (February 2015, August 2015, February 2016, and August 2016). We chose these dates to represent winters when conditions are typically driest at the two field sites, and summers when conditions are typically wettest. During each of the four field samplings, seven leaves were collected from each of four randomly selected insecticide treated plants and four plants that had received only water for each haplotype ($N = 12$ for each treatment). An effort was made to select leaves of different ages and from different heights and directions. Leaves were placed in resealable plastic bags and transported in coolers with ice packs to a -50°C freezer where they were maintained until analysis.

To perform the ELISA, all leaflets from the 84 leaves collected from each treatment and sampling date were stripped from the midrib and placed, along with the midrib, in a stack. Two grams of leaf and midrib tissue (76.4 cm^2 ± 3.0, mean ± SE) was cut from the centre of the stack and homogenised in 18 ml of methanol in a Kleco Tissue Pulverizer (Kinetic Laboratory Equipment Co., Visalia, CA). An 8-fold dilution series was then made from the homogenate in sample diluent buffer included in the ELISA kit. Because spectrophotometric readings must be within the range of the standard curve to accurately estimate imidacloprid concentration, preliminary testing was conducted where it was determined that dilutions from 8^{-4} through 8^{-7} and 8^{-6} through 8^{-8} were sufficient for detection of imidacloprid in the water and insecticide treatments, respectively. Standard curves were prepared using the imidacloprid standards provided with the ELISA kit and were created for each 96-well plate run according to manufacturer's instructions. Within 15 minutes of applying the stop solution, ELISA plates were read at an absorbance of 450 nm using a MRX II plate reader (Dynex, Chantilly, VA). All samples and standards were run in triplicate.

2.4. Data analysis

We tested for differences in herbivory and plant growth (plant height, basal diameter, and number of branches) between insecticide protected and unprotected plants of different haplotypes growing in different sites over time. To account for the non-independence of the plants within a plot, we calculated the mean values for each response variable (herbivore damage and plant growth measurements) for each treatment and survey date and used these values in the analyses. For each response variable, a separate linear mixed-effects model was run with site, treatment (insecticide, water), haplotype (A, B, hybrid), survey time (eight sampling occasions), and all possible two-way interactions between these variables treated as fixed effects. Pseudo-replication caused by repeated-measure on the experimental plants was controlled by treating plant id as a random effect. Similarly, plot id was included in the model as a random effect to account for the paired structure of treatments in each plot. Plant height and basal diameter were square-root transformed and number of branches were *ln*-transformed to meet the normality assumption. We used quantile-quantile plots to examine the distribution of residuals and detect

observations with undue influence. In the case of influential observations, we re-ran the analysis excluding those observations. Exclusion of influential observations did not qualitatively alter the results. Therefore, we retained all observations in the analyses. In the cases with significant interactions involving site (site × treatment or site × haplotype or site × time), separate mixed-effect models were run for each site. When haplotype effect was significant, a Bonferroni-corrected post-hoc analysis was run to test for the difference in response variable between haplotypes. All analyses were run in R 3.3.2 (R Core Team, 2016) using the nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2016).

We determined the total number of fruits produced by each female tree during the period of data collection and the average number of fruits produced per female tree within a plot. We used a general linear model to evaluate the effect of site, treatment, haplotype, and all two-way interactions between these predictor variables on the average number of fruits produced. Number of fruits were *ln*-transformed to meet the normality assumption.

For ELISA testing, mean absorbances and their standard deviations were calculated across the triplicates for each of the standards and the samples. Standard curves were created by dividing the mean absorbance value for each standard (B) by the mean absorbance of the zero standard (B_0 – the standard containing no imidacloprid) and then plotting B/B_0 by the logarithm of the imidacloprid concentration. For this ELISA, the intensity of the colour is inversely proportional to the concentration of imidacloprid. B/B_0 was calculated for the samples and the concentration of imidacloprid in ppb is determined by interpolation and back calculation. Only samples whose dilutions yielded a B/B_0 within the range of the standard curve were used for back calculations. In the case where more than one dilution was usable, an average concentration was calculated. A general linear model with site, treatment and year as main effects was used to compare insecticide concentration between insecticide protected and unprotected plants grown at different sites.

3. Results

3.1. Field study

A number of herbivores (38 species, 5 orders) were found to feed on the experimental Brazilian peppertree plants at the study sites (Table 1). However, the incidence of foliar herbivory pooled for all sites and sampling dates was extremely low ($1.25 \pm 0.14\%$ [mean ± SE] of leaves). More importantly, chewing damage on untreated plants ($1.25 \pm 0.20\%$ [mean ± SE]) was not different from the plants protected by insecticide ($1.24 \pm 0.19\%$; $F_{1,\,38} = 0.001$, $P = .97$, Figure 1). Herbivory also did not differ between sites ($F_{1,\,38} = 0.32$, $P = .56$) or plant haplotypes ($F_{2,\,38} = 2.25$, $P = .11$). Frequency of chewing damage was significantly greater in November 2015 and February 2016 than on all other survey occasions ($F_{7,\,301} = 16.41$, $P < .0001$, Figure 1).

Protection from herbivory did not have a significant effect on plant height ($F_{1,\,38} = 1.42$, $P = .24$, Figure 2(A)) or basal stem diameter ($F_{1,\,38} = 0.13$, $P = .71$, Figure 2(B)). Interestingly, the number of branches was 17% lower in the plants treated with insecticide than the control plants ($F_{1,\,38} = 3.61$, $P = .06$, Figure 2(C)).

Brazilian peppertrees in Fort Pierce were 96% taller ($F_{1,\,38} = 175.62$, $P < .0001$, Figure 2(A)), had 39% greater stem diameter ($F_{1,\,38} = 30.67$, $P < .0001$, Figure 2(B)), and produced

Table 1. Insect herbivores collected from Brazilian peppertrees at study sites in Fort Pierce and Immokalee, Florida.

Species	Common name	Native/Exotic to Florida	Host range/feeding behaviour
Coleoptera			
Anthribidae			
Toxonotus cornatus (Say)	Snout nose weevil	Native, Eastern U.S.A, Mexico (Valentine, 1998)	Previously collected from *Diospyros* sp. in Florida (Valentine, 1998). Most anthribids feed on fungi in dead wood
Chrysomelidae			
Altica sp.	N/A[a]	N/A	N/A
Curculionidae			
Diaprepes abbreviates (L.)[¥]	Diaprepes root weevil	Exotic, Caribbean, first reported in Florida in 1964 (Weissling et al., 2012)	Polyphagous, adults chew leaves, larvae feed on roots (Weissling et al., 2012).
M. undecimpustulatus undatus Marshall	Sri Lankan weevil	Exotic, Sri Lanka, first reported in Florida in 2000 (Neal, 2013)	Polyphagous, adults chew leaves, larvae feed on roots (Neal, 2013)
Notolomus basalis LeConte[§]	No common name	Native, southeastern U.S.A	Polyphagous, adults feed on flowers, larval hosts unknown. (Henderson, 1986).
Hemiptera			
Alydidae			
Hyalymenus tarsatus (F.)	Texas bow-legged bug	Native (Henry & Froeschner, 1988)	Polyphagous, sucking on seeds and fruits (Schaefer, 1980)
Aphididae			
A. gossypii Glover [¥]	Melon/cotton aphid	Cosmopolitan (Luo et al., 2016)	Polyphagous, sucking on leaves (Ebert & Cartwright, 1997)
Cicadellidae			
Homalodisca vitripennis (Germar)	Glassy winged sharpshooter	Southeastern U.S.A (Conklin & Mizell, 2013)	Polyphagous, sucking (Hoddle, Triapitsyn, & Morgan, 2003)
Curtara insularis (Caldwell)	Ringspot leafhopper	Exotic, Caribbean (Halbert, 2009)	Host range unknown, sucking, previously collected in Florida on *Citrus* spp. (Halbert, 2009; Halbert, 2010)
Coccidae			
Ceroplastes cirripediformis Comstock [¥]	Barnacle scale	Cosmopolitan (Hodgson & Hilburn, 1991)	Polyphagous, sucking (Miller & Miller, 2003)
Coreidae			
Leptoglossus gonagra (F.) [¥]	Passion vine bug	Native, Florida, West Indies, southward to Argentina (Koerber, 1963).	Polyphagous, sucking (Leonard, 1931)
L. phyllopus (L.) [¥]	Florida leaf-footed bug	Native, North and South America, but also occurs in Africa, Asia and Australia (Brailovsky, 2014)	Polyphagous, sucking (Stansley & Rogers, 2016)
Flatidae			
Metcalfa pruinosa (Say)	Citrus flatid planthopper	Native (Strauss, 2010)	Polyphagous, sucking (Wilson & McPherson, 1981)
Pentatomidae			
Diolcus chrysorrhoeus (F.)	Shield back bug	Native (Eger & Baraonowski, 2002)	Polyphagous, sucking collected from trees and shrubs (McPherson, 1982)
Euschistus servus (Say)	Brown stink bug	Native (Gomez & Mizell, 2009)	Polyphagous, sucking (Rolston & Kendrick, 1961)
	Lesser brown stink bug	Native, Neotropical (Panizzi & Slansky, 1985)	Polyphagous, sucking (Brennan, Eger, & Liburd, 2013)

Euschistus quadrator (Rolston)			
Piezodorus guildinii (Westwood)	Small green stink bug	Native, Neotropical (Panizzi & Slansky, 1985)	Polyphagous, primarily on legumes, sucking (Panizzi & Slansky, 1985)
Proxys punctulatus (Palisot)	Black stink bug	Native, Neotropical (Gomez & Mizell, 2009)	Polyphagous, can also be predaceous, sucking (Gomez & Mizell, 2009)
Thyanta perditor (F.)	Neotropical red-shouldered stink bug	Native, Neotropical (Panizzi & Herzog, 1984)	Polyphagous, sucking (Panizzi & Herzog, 1984)
Nezara viridula (L.)	Southern green stink bug	Exotic, Africa (Sequiter, 2013)	Polyphagous, sucking (Sequiter, 2013)
Hymenoptera			
Torymidae			
M.transvaalensis (Hussey)[§]	Brazilian peppertree drupe feeder	Exotic (Wheeler et al., 2001)	Specialist in Florida, feeding in Brazilian peppertree drupes (Wheeler et al., 2001)
Lepidoptera			
Arctiidae			
U.ornatrix (L.)	Bella moth	Native, Neotropical (Dinez-Filho et al., 2010)	Specialist on *Crotalaria* spp., defoliator (Cogni, 2010)
Crambidae			
Parapediasia decorellus (Zinchen)	Graceful grass-veneer	Native, North America (Scholtens & Solis, 2015)	Host range unknown, feeding behaviour unknown
Eribidae			
Estigmene acrea (Drury)	Salt marsh moth	Native, North America (Hill & Roelofs, 1981)	Polyphagous, defoliator (Dussourd & Denno, 1994)
Geometridae			
Melanchroia chephise (Stoll)	White-tipped black moth	Native (Heppner, 2003)	Polyphagous, defoliator, hosts in the Anacardiaceae, Euphorbiaceae and Rutaceae (Heppner, 2003)
Oxydia vesulia (Cramer)	Spurge spanworm moth	Native, neotropical (Fung & Wheeler, 2016)	Polyphagous, defoliator (Fung & Wheeler, 2016)
Noctuidae			
Bagisara repanda (F.)	Wavy lined mallow moth	Native, Neotropical (Ferguson, 1997)	Hosts in Florida unknown (Heppner, 2003). In Barbados 'broomweed' (Bennett & Alam, 1985), defoliator
S. ornithogalli (Guenée)*	Yellow-striped armyworm moth	Native, North and Central America (Todd & Poole, 1980)	Polyphagous defoliator (Tallamy & Shropshire, 2009)
Spodoptera albula (Walker)*		Native, North, Central and South America (Pogue, 2002)	Polyphagous, defoliator (Montezano et al., 2013)
Spodoptera latifascia (Walker)	Velvet armyworm	Native, southern U.S.A and the Caribbean (Pogue, 2002)	Polyphagous, defoliator (Portillo, Pitre, Meckenstock, & Andrews, 1996)
Spodoptera sp.	N/A	N/A	Defoliator
Euteliidae			
P.fuscescens (Walker)			Host range unknown, defoliator, previously collect from Brazilian peppertree in Florida (Manrique et al., 2012)

(*Continued*)

Table 1. Continued.

Species	Common name	Native/Exotic to Florida	Host range/feeding behaviour
Psychidae			
Cryptothelea nigra (Barnes & McDunnough)	Nigrita bagworm moth	Native, southeastern U.S.A (Sobczyk, 2011)	Host range unknown, defoliator.
Sphingidae			
Xylophanes tersa (L.)*	Tersa sphinx moth	Native, New World (Heppner, 2003)	Rubiaceae, defoliator (Torres, 1992)
Protambulyx strigilis (L.)*	Streaked sphinx moth	Native, Neotropical (Heppner, 2003)	Anacardiaceae in Florida (Heppner, 2003), defoliator. Recorded from Brazilian peppertree in Argentina (Mc Kay et al., 2009)
Orthoptera			
Acrididae			
Chortophaga viridifasciata (DeGeer)	Southern green-striped grasshopper	North and Central America (Pfadt, 1994)	Gramnivore, defoliator (McClenaghan, Gibson, Shokralla, & Hajibabaei, 2015)
S. Americana (Drury)	American grasshopper	North America, Bahamas and Mexico (Sequiter & Capinera, 2014)	Polyphagous, defoliator (Sequiter & Capinera, 2014)
Tettigonidae			
Scudderia sp.	N/A	N/A	N/A

Notes: Species identified by * completed their life cycle on Brazilian pepper plant in the lab. Species marked with § emerged from seeds collected from the experimental plants. Species previously collected from Brazilian peppertree by Cassani (1986) and Cassani et al. (1989) are marked with ¥.

[a]Since the species was not determined, it was not possible to identify common names, ranges or host specificity.
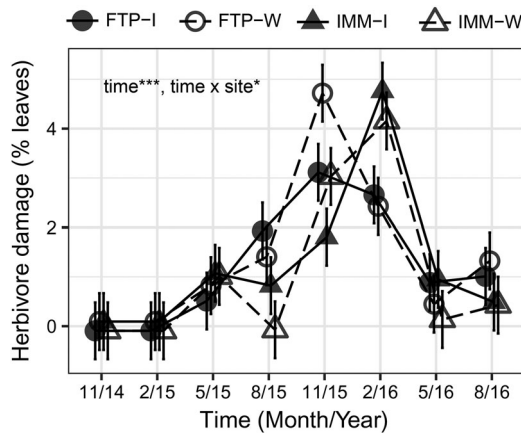
Figure 1. Effect of site and insecticide treatment on herbivore damage on Brazilian peppertrees over time. Means (± SE) for herbivore damage (% leaves with chewing damage) are shown for the insecticide (I) and water (W) treated plants growing in experimental plots at Fort Pierce (FTP) and Immokalee (IMM), Florida. Significant effects in the linear mixed-effect model for each response variable are indicated by **$(P < .01)$ or ***$(P < .001)$.

78% more branches ($F_{1, 38} = 36.68$, $P < .0001$, Figure 2(C)) than those growing in Immokalee. Furthermore, all three measurements exhibited significant site × time interactions (height: $F_{7, 301} = 56.79$, $P < .0001$; diameter: $F_{7, 301} = 12.20$, $P < .0001$; number of branches: $F_{7, 301} = 50.47$, $P < .0001$) indicating greater rates of plant growth over time in Fort Pierce than in Immokalee (Figures 2 and 3).

As indicated by significant site × haplotype interactions, effects of haplotype on plant height differed between Fort Pierce and Immokalee ($F_{2, 38} = 3.83$, $P = .03$, Figure 3(A)). In Fort Pierce, haplotype A was 17% and 13% shorter than haplotype B ($P = .005$) and hybrid trees ($P = .06$), respectively. Haplotype B and hybrid plants were similar in plant height ($P = .49$). However, there was no significant difference in height of haplotype A, B and hybrid plants at Immokalee. In addition, basal stem diameter did not differ between the haplotypes ($F_{2, 38} = 0.97$, $P = .38$, Figure 3(B)).

After controlling for the effect of the study sites and time, plants belonging to haplotype A produced 29% and 39% more branches than those belonging to haplotype B ($P = .08$) or hybrid plants ($P = .02$, Figure 3(C)), respectively. Haplotype B and hybrids produced statistically equivalent number of branches ($P = 0.79$). As indicated by a non-significant site × haplotype interaction ($F_{2, 38} = 0.16$, $P = .85$), differences among the haplotypes followed similar pattern at both sites (Figure 3(C)).

A total of 68 plants (41%) produced fruits during the two-year study. Since Brazilian peppertree is dioecious, this value probably represents the proportion of female trees in the study. However, number of fruits produced per fruiting plant was highly variable, ranging from 3 to 32,133. Consistent with the plant growth measurements, plants in Fort Pierce produced 680% more fruits than those in Immokalee ($F_{1, 30} = 24.29$, $P < .0001$, Figure 3(D)). Fruit production did not differ between insecticide treatment ($F_{1, 30} = 0.025$, $P = .88$) or plant haplotype ($F_{2, 30} = 2.94$, $P = .07$, Figure 3(D)).
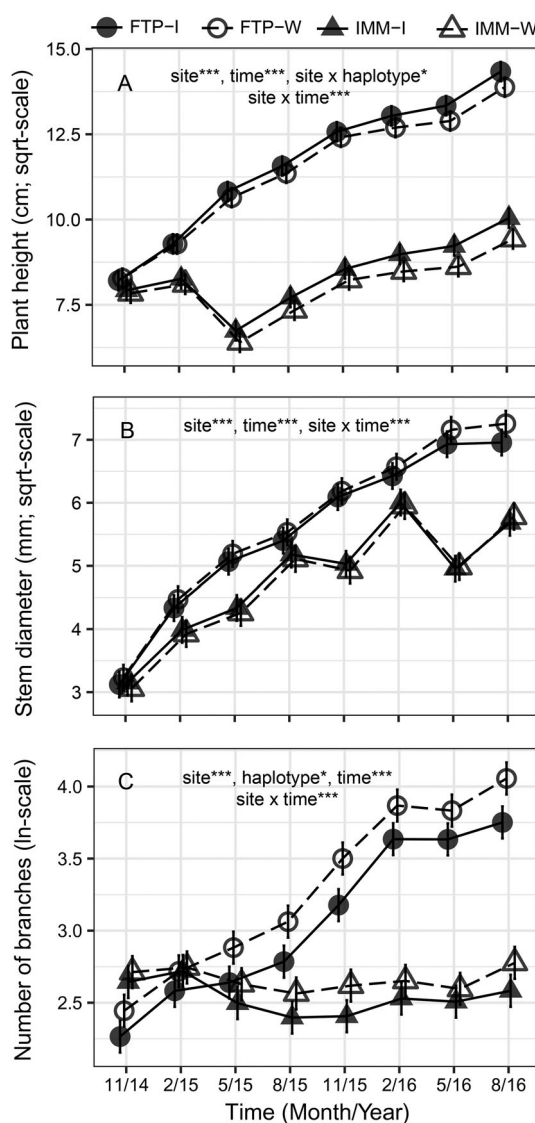
Figure 2. Effect of site and insecticide treatment on the growth of Brazilian peppertrees over time. Least-square means (± SE) for (A) plant height, (B) basal diameter, and (C) number of branches are shown for the insecticide (I) and water (W) treated plants growing in experimental plots at Fort Pierce (FTP) and Immokalee (IMM), Florida. Least-square means (± SE) for each treatment at each site were computed from linear mixed-effect models. Significant effects in the linear mixed-effect model for each response variable are indicated by *($P < .05$), or ***($P < .001$).

3.3. Imidacloprid ELISA bioassay

The foliage of insecticide treated plants contained 32 times higher concentration of insecticide (2.98 ± 0.22 μg/cm2 leaf tissue [mean ± SE]) than the plants treated with water (0.09 ± 0.22 μg/cm^2 leaf tissue; $F_{1, 12} = 86.10$, $P < .0001$, Figure 4). Insecticide concentration was about 60% higher in the leaf tissues of plants growing at Immokalee than those at Fort Pierce ($F_{1, 12} = 5.15$, $P = .04$, Figure 4).
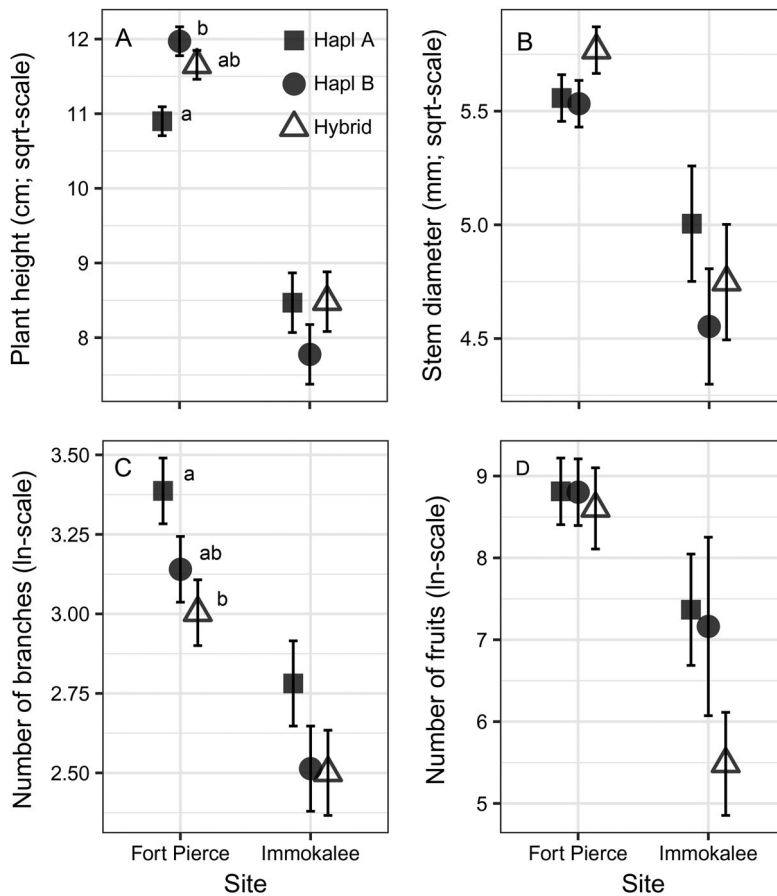
Figure 3. Growth measurements and fruit production among different haplotypes of Brazilian pepper-trees in experimental plots at Fort Pierce and Immokalee, Florida. Least-square means (± SE) of (A) plant height, (B) basal diameter, (C) number of branches, and (D) number of fruits are shown for haplotypes A, B, and A × B hybrid. Least-square means (± SE) were computed for each haplotype from linear mixed-effect models performed for each response variable within a site. Data were pooled across the treatments for each response variable. Significant differences between haplotypes within a site are indicated by different letters.

4. Discussion

This is the first field study to quantify damage to Brazilian peppertree due to insect herbivory. Regardless of insecticide treatment, the plants received an extremely low level of herbivory (1.25% leaves) from leaf-chewing insects in the field sites. Consequently, there was no discernible influence of insecticide treatment on plant height, basal stem diameter or reproductive output of Brazilian peppertree. This result strongly suggests that insect herbivores have little or no effect on Brazilian peppertree performance in Florida, providing support for the 'enemy release hypothesis' that posits a decrease in suppression by natural enemies when an organism is moved outside of its native range (Cronin, Bhattarai, Allen, & Meyerson, 2015; Darwin, 1859; Elton, 1958; Keane & Crawley, 2002). Moreover, invasive plants in the introduced range have also been shown to
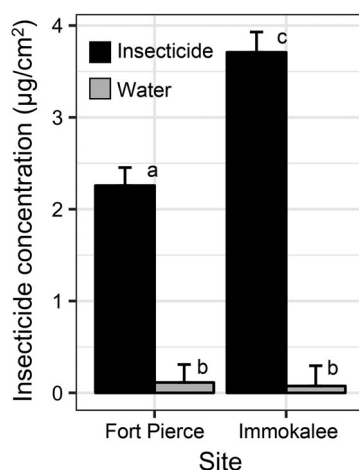
Figure 4. Mean concentration (± SE) of insecticide (µg/cm² leaf tissue) in Brazilian peppertree foliage collected from experimental plots at Fort Pierce and Immokalee, Florida over two years. Significant differences between insecticide and water treated plants are indicated by different letters.

receive relatively lower herbivore pressure than co-occurring native competitors (e.g. Bhattarai et al., 2017a; Cronin et al., 2015). Despite finding several herbivorous insects with chewing mouthparts, there was extremely low foliar damage to Brazilian peppertree, in agreement with the results of Cassani's (1986) survey in which he concluded that 'no significant herbivory was observed on *S. terebinthifolius* at any time'. Losses due to sucking insects, several of which were collected (Table 1), could not be directly estimated, but the lack of difference in plant height and trunk diameter between insecticide and water treated plants suggests that they also caused minimal damage to Brazilian peppertree.

It would be informative to compare the lack of impact of insect herbivores on Brazilian peppertree in Florida with data from the native range, but we are not aware of any open field estimates of herbivory from South America. Vitorino, Christ, Barbieri, Cuda, and Medal (2011) measured the effect of the specialist psyllid *Calophya terebinthifolii* in the laboratory, and found a 40% reduction in biomass accumulation after three months. Similarly, Prade et al. (2016) found an 11% reduction in biomass of plants infested by *C. latiforceps* after three months in a study conducted in a quarantine greenhouse in Florida. Feeding damage by the specialist thrips, *P. ichini*, was more dramatic in a greenhouse study, resulting in an 89% reduction in growth rate after a one-month exposure period (Manrique et al., 2014). Based on the levels of damage found in these laboratory and greenhouse studies, coupled with the lack of invasiveness in its native range, we hypothesise that insect herbivory has a greater effect on the performance of Brazilian peppertree in South America than in Florida.

As might be expected for an exotic plant, the majority of herbivorous insects found on Brazilian peppertree were generalists. However, a few specialised feeders were also collected. The seed feeding wasp, *Megastigmus transvaalensis* (Hussey), is a native of South Africa where its hosts include several native species in the genus *Rhus*, as well as the exotic hosts *S. terebinthifolia* and *Schinus molle* (Grissell & Prinsloo, 2001). This wasp was first reported in Florida in 1988, and is thought to have been introduced in

drupes of *Schinus* spp. imported as a spice (pink peppercorns) from Reunion Island (Habeck, Bennett, & Grissell, 1989). During a two-year study in the late 1990s, Wheeler, Massey, and Endries (2001) found that *M. transvaalensis* was widespread in Florida, infesting 23.5–38.5% of drupes during the winter and 76.3–74.8% during the spring. In Florida, the wasp appears to be monophagous, having only been found in Brazilian peppertree drupes (Wheeler et al., 2001).

Another herbivore, *Paectes fuscescens* Walker (Lepidoptera: Euteliidae), may have a limited host range. Several species in the genus *Paectes* have previously been collected from Brazilian peppertree in Florida, including *P. abrostoloides* (Guenée), *P. devincta* (Walker), *P. nana* (Walker), and *P. fuscescens* (Cassani et al., 1989; Manrique, Diaz, Pogue, Vitorino, & Overholt, 2012). In addition, other *Paectes* spp. have been collected in Brazil from Brazilian peppertree (Manrique et al., 2014; Mc Kay et al., 2009; Pogue, 2013). Only the host range of one species, *P. longiformis* Pogue, has been investigated in the laboratory. This moth completed development equally well on Brazilian peppertree and *S. molle*, and to a lesser degree on six other members of the Anacardiaceae (Manrique, Diaz, Condon, & Overholt, 2014). The only host record for *P. fuscesens* in Florida is Brazilian peppertree (Manrique et al., 2012), although since the moth is putatively native to Florida, it would seem certain that it also feeds on one or more native plants.

Another specialist collected, the sphingid *Utetheisa ornatrix* (L.), feeds on *Crotalaria* spp. (Cogni, 2010). This moth was collected as an adult, and only on one occasion, and therefore it is very likely that it was simply using Brazilian peppertree as a substrate for resting while in transit between oviposition sites.

Many of the insect herbivores we collected from Brazilian peppertree are pests of agricultural crops in Florida. Two exotic weevils, *Diaprepes abbreviates* (L.) and *Myllocerus undecimpustulatus undatus* Marshall, attack citrus and several other crops (Neal, 2013; Weissling, Pena, Giblin-Davis, & Knapp, 2012). *Aphis gossypii* Glover is a cosmopolitan pest that attacks a wide range of plants, including various cucurbits, other vegetable crops, citrus and cotton (Capinera, 2009). The leaf-footed bug, *Leptoglossus phyllopus* (L.), feeds on several crops in Florida, but is primarily a concern due to the damage it causes to ripening citrus fruit (Stansley & Rogers, 2016). *Spodoptera ornithogalli* (Guenée) is a highly polyphagous pest attacking a wide range of vegetables and field crops in Florida and elsewhere (Capinera, 2005). The American grasshopper, *Schistocerca americana* (Drury), attacks many plants and is particularly a concern in Florida due to defoliation of citrus seedlings (Sequitier & Capinera, 2014). Brazilian peppertree is extremely widespread in south/central Florida, occupying an estimated 3000 km^2, and often grows in close proximity to citrus groves and other agricultural fields (Cuda, Medal, Gillmore, Habeck, & Pedrosa-Macedo, 2009). The presence of agricultural insect pests on Brazilian peppertree (Cuda et al., 2009) suggests that the invasive weed may provide refuge, and thus exacerbate crop damage through apparent competition (Bhattarai, Meyerson, & Cronin, 2017b). Alternatively, if population growth of these insects is negative on Brazilian peppertree, the exotic weed may serve as a trap plant and result in population declines (Shelton & Nault, 2004).

Brazilian peppertree, particularly at the Fort Pierce site, grew very rapidly during the two-year study, with stem diameter increasing 400%, and height increasing by 200%. At the Immokalee site, growth was less dramatic, with stem diameter increasing 300% and height by about 150%. The poor performance of trees in Immokalee was likely due, at

least in part, to two factors; herbivory by deer was severe during the first winter of the study, with 77% trees exhibiting signs of feeding in February 2015. This was coupled with a freeze on 20 February 2015 that damaged the foliage on 100% of the trees.

The results from Fort Pierce, in particular, demonstrate the high growth potential of Brazilian peppertree in Florida. These growth rates are similar to the values of 30–50 cm/year for Brazilian peppertree seedlings reported by Ewel et al. (1982) in the Everglades National Park. Fruit production was also high with an average of about 8700 fruits per tree during the study period in Fort Pierce, and a maximum of more than 32,000 fruits for one tree. The earliest fruits were present six months after transplanting to the field (nine-month-old trees). Although we did not determine the viability of seeds, Ewel et al. (1982) reported a germination rate of 30–60%. Panetta and McKee (1997) reported much higher germination (80–100%) for seeds from which the exocarp was removed, or had been consumed and defecated by birds.

Plant genotype influenced Brazilian peppertree performance, but the effect was inconsistent between sites. Haplotype B and hybrids outperformed haplotype A plants in Fort Pierce, whereas there were no differences at Immokalee. Haplotype A plants dominate in the western peninsula Florida, where Immokalee is located, whereas haplotype B is more common on the east coast, including the Fort Pierce area (Mukherjee et al., 2012; Williams et al., 2007;). This pattern is thought to be associated with the introduction history of Brazilian peppertree into Florida, with Haplotype A introduced on the west coast around 1926 and Haplotype B introduced into Miami in the late 1890s (Williams et al., 2007). One possible explanation for the differential performance of the two types in Fort Pierce is that there has been some adaptation to local conditions since the introduction of Brazilian peppertree into Florida. Mukherjee et al. (2012) suggested that hybridisation, followed by selection was a factor in the northward spread of Brazilian peppertree in Florida. Our results do not support Geiger et al.'s (2011) finding of hybrid vigour in Florida Brazilian peppertree, albeit his result was based on variables we did not measure, seed germination and early seedling survival.

The ELISA results were generally as expected with an average of 32 times more imidacloprid in treated plants than in untreated plants. The detection of imidacloprid in water treated plants was unanticipated. Insecticide and water treated plants were separated by 4.9 m, whereas similar studies have separated treated and untreated trees by approximately the same distance (5 m in Sétamou et al., 2010 and in Stricker & Stiling, 2012). We believe that heavy rainfall events transported small amounts of imidacloprid from treated to untreated trees. It is possible that the concentrations found in untreated trees may have caused some insect mortality, but it is unlikely that it was at the same level as in treated plants.

In summary, we identified a number of insect herbivores associated with Brazilian peppertree in Florida, the majority of which were polyphagous. Despite the number of herbivores encountered, insect herbivory was extremely low and had no measurable influence on plant growth and reproductive output of Brazilian peppertree, consistent with the 'enemy release' hypothesis. We predict that the introduction of specialised natural enemies from the native range of Brazilian peppertree will provide increased top down suppression the Brazilian peppertree in Florida, thereby decreasing its invasiveness.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Barkley, F. A. (1944). *Schinus L. Brittonia*, 5, 160–198.

Barkley, F. A. (1957). A study of *Schinus L. Lilloa Revista de Botanica*, 28 (1–110). Universidad Nacional del Tucumen, Argentina.

Bennett, F. D., & Alam, M. M. (1985). An annotated check-list of the insects and allied terrestrial arthropods of Barbados. Caribbean Agricultural Research and Development Institute, St. Augustine, Trinidad and Tobago.

Bhattarai, G. P., Meyerson, L. A., Anderson, J., Cummings, D., Allen, W. J., & Cronin, J. T. (2017a). Biogeography of a plant invasion: Genetic variation and plasticity in latitudinal clines for traits related to herbivory. *Ecological Monographs*, 87, 57–75.

Bhattarai, G. P., Meyerson, L. A., & Cronin, J. T. (2017b). Geographic variation in apparent competition between native and invasive *Phragmites australis*. *Ecology*, 98, 349–358.

Brailovsky, H. (2014). Illustrated key for identification of the species included in the genus *Leptoglossus* (Hemiptera: Heteroptera: Coreidae: Coreinae: Anisoscelini), and descriptions of five new species and new synonyms. *Zootaxa 3794*, 143–178.

Brennan, S. A., Eger, J., & Liburd, O. E. (2013). A stink bug *Euschistus quadrator* Rolston (Insecta: Hemiptera: Pentatomidae). Institute of food and agricultural sciences, University of Florida Document EENY-523. Retrieved from http://edis.ifas.ufl.edu/in937

Capinera, J. L. (2005). Yellowstriped armyworm, *Spodoptera ornithogalli* (Guenee) (Insecta: Lepidoptera: Noctuidae). Institute of Food and Agricultural Sciences, University of Florida and Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Document EENY216. Retrieved from http://edis.ifas.ufl.edu/in373

Capinera, J. L. (2009). *Aphis gossypii* Glover (Insecta: Hemiptera: Aphididae). Featured creatures, Institute of Food and Agricultural Sciences, University of Florida and Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Retrieved from http://entnemdept.ufl.edu/creatures/veg/aphid/melon_aphid.htm.

Cassani, J. R. (1986). Arthropods on Brazilian peppertree, *Schinus terebinthifolius* (Anacardiaceae) in south Florida. *The Florida Entomologist*, 69, 184–196.

Cassani, J. R., Maloney, D. R., Habeck, D. H., & Bennett, F. D. (1989). New insect records on Brazilian peppertree, *Schinus terebinthifolius* in South Florida. *The Florida Entomologist*, 72, 714–716.

Cogni, R. (2010). Resistance to plant invasion? A native specialist herbivore shows preference for and higher fitness on an introduced host. *Biotropica*, 42, 188–193.

Conklin, T., & Mizell, R. F. (2013). Glassy-winged sharpshooter, *Homalodisca vitripennis* (=*coagulata*) (Germar) (Insecta: Hemiptera: Cicadellidae: Cicadellinae). Institute of Food and

Agricultural Sciences, University of Florida. Document EENY-274. Retrieved from http://edis.ifas.ufl.edu/in552

Costello, S. L., Pratt, P. D., Rayamajhi, M. B., & Center, T. D. (2003). Arthropods associated with above-ground portions of the invasive tree, *Melaleuca quinquenervia*, in South Florida, USA. *Florida Entomologist*, 86, 300–322.

Cronin, J. T., Bhattarai, G. P., Allen, W. J., & Meyerson, L. A. (2015). Biogeography of a plant invasion: Plant-herbivore interactions. *Ecology*, 96, 1115–1127.

Cuda, J. P., Christ, L. R., Manrique, V., Overholt, W. A., Wheeler, G. S., & Williams, D. A. (2012). Role of molecular genetics in identifying 'fine tuned' natural enemies of the invasive Brazilian peppertree, *Schinus terebinthifolius*: a review. *Biocontrol*, 57, 227–233.

Cuda, J. P., Ferriter, A. P., Manrique, V., & Medal, J. C. (2006). Florida's Brazilian peppertree management plan. Recommendations from the Brazilian Peppertree task force. Florida Exotic Pest Plant Council, 2nd Edition. Retrieved from http://fleppc.org/Manage_Plans/2006BPmanagePlan5.pdf.

Cuda, J. P., Medal, J. C., Gillmore, J. L., Habeck, D. H., & Pedrosa-Macedo, J. H. (2009). Fundamental host range of *Pseudophilothrips ichini* s.l. (Thysanoptera: Phlaeothripidae): a candidate biological control agent of *Schinus terebinthifolius* (Sapindales: Anacardiaceae) in the United States. *Environmental Entomology*, 38, 1642–1652.

Darwin, C. R. (1859). *The origin of species*. New York: Literary Classics, Inc.

Davis, D. R., McKay, F., Oleiro, M. Vitorino, & Wheeler, G. S. (2011). Biology and systematics of the leafmining Gracillariidae of Brazilian pepper tree, *Schinus terebinthifolius* Raddi, with descriptions of a new genus and four new species. *Journal of the Lepidopterists' Society*, 65, 61–93.

Diaz, R., Manrique, V., Munyaneza, J. E., Sengoda, V. G., Adkins, S., Hendricks, K., … Overholt, W. A. (2015). Host specificity testing and examination for plant diseases reveal that the gall-forming psyllid, *Calophya latiforceps* (Hemiptera: Calophyidae), is safe to release for biological control of *Schinus terebinthifolia* (Sapindales: Anacardiaceae). *Entomologia Experimentalis et Applicata*, 154, 1–14.

Diaz, R., Moscoso, D., Manrique, V., Williams, D., & Overholt, W. A. (2014). Native range density, host utilization and life history of *Calophya latiforceps* (Hemiptera: Calophyidae): An herbivore of Brazilian Peppertree (*Schinus terebinthifolia*). *Biocontrol Science and Technology*, 24, 536–553.

Dinez-Filho, J. A. F., Ferro, V. G., Santos, T., Nabout, J. C., Dobrovolski, R., & De March Jr.P. (2010). The three phases of the ensemble forecasting of niche models: geographic range and shifts in climatically suitable areas of *Utetheisa ornatrix* (Lepidoptera: Arctiidae). *Revista Brasileira de Entomologica*, 54, 339–349.

Dittrich, R. L., Macedo, J. H. P., Cuda, J. P., & Biondo, A. W. (2004). *Brazilian peppertree sawfly larvae toxicity in bovines. Proceedings of the Joint Annual Meeting of the American College of Veterinary Pathologists (55th) and American Society for Veterinary Clinical Pathology (39th)*, Abstract 29. 13–17 November, Orlando, FL.

Doren, R. F., & Jones, D. T. (1997). Management in everglades national park. In D. Simberloff, D. C. Schmitz, & T. C. Brown (Eds.), *Strangers in paradise: Impact and management of nonindigenous species in Florida* (pp. 275–286). Washington, D.C: Island Press.

Doren, R. F., Whiteaker, L. D., & LaRosa, A. M. (1991). Evaluation of fire as a management tool for controlling *Schinus terebinthifolius* as secondary successional growth on abandoned agricultural land. *Environmental Management*, 15, 121–129.

Dussourd, D. E., & Denno, R. F. (1994). Host range of generalist caterpillars: Trenching permits feeding on plants with secretory canals. *Ecology*, 75, 69–78.

Ebert, T. A., & Cartwright, B. (1997). Biology and ecology of *Aphis gossypii* Glover (Homoptera: Aphididae). *Southwestern Entomologist*, 22, 116–153.

Eger Jr., J. E., & Baraonowski, R. M. (2002). *Diolcus variegatus* (Heteroptera: a Caribbean species established in South Florida. *Florida Entomologist*, 85, 267–269.

Elton, C. S. (1958). *The ecology and invasion by animals and plants*. Chicago, IL: University of Chicago Press.

Ewe, S. M. L., & Sternberg, S. L. (2002). Seasonal water-use by the invasive exotic, *Schinus terebinthifolius* in native and disturbed communities. *Oecology*, 133, 441–448.

Ewel, J., Ojima, D., Karl, D., & Debusk, W. (1982). *Schinus in successional ecosystems of Everglades national park* (South Florida Research Center Report T-10 676). Homestead, FL: U. S. National Park Service.

Ewel, J. J. (1978). Ecology of *Schinus*. In *Proceedings of techniques for control of Schinus in South Florida* (pp. 7–21). Sanibel, FL: The Sanibel Captiva Conservation Foundation, Inc.

Ferguson, D. C. (1997). Review of the new world Bagisarinae with description of two new species from the southern United State (Noctuidae). *Journal of the Lepidopterists Society*, 51, 344–357.

Fung, J., & Wheeler, G. S. (2016). Life history and host range of *Oxydia vesulia transpeneus*, an unsuitable biological control agent of Brazilian peppertree. *Biocontrol Science and Technology*, 26, 298–304.

Geiger, J. H., Pratt, P. D., Wheeler, G. S., & Williams, D. A. (2011). Hybrid vigor for the invasive exotic Brazilian Peppertree (*Schinus terebinthifolius* Raddi., Anacardiaceae) in Florida. *International Journal of Plant Sciences*, 172, 655–663.

Gogue, G. J., Hurst, C. J., & Bancroft, L. (1974). Growth inhibition *by Schinus terebinthifolius*. *HortScience*, 9, 301.

Gomez, C., & Mizell III, R. F. (2009). Black stink bug *Proxys punctulatus* (Palisot) (Insecta: Hemiptera: Pentatomidae). Document EENY-432. Institute of Food and Agricultural Sciences, University of Florida. Retrieved from http://edis.ifas.ufl.edu/in795

Grissell, E. E., & Prinsloo, G. L. (2001). Seed-feeding species of Megastigmus (Hymenoptera: Torymidae) associated with Anacardiaceae. *Journal of Hymenoptera Research*, 10, 271–279.

Habeck, D. H., Bennett, F. D., & Grissell, E. E. (1989). First record of a phytophagous seed chalcid from Brazilian peppertree in Florida. *The Florida Entomologist*, 72, 378–379.

Halbert, S. E. (2009). Entomology section. P. J. Anderson & G. S. Hodges (Eds.). *Tri-logy*, 48(3), 8.

Halbert, S. E. (2010). Entomology section. P. J. Anderson & G. S. Hodges (Eds.). *Tri-logy*, 49(2), 8.

Henderson, A. (1986). A review of pollination studies in the Palmae. *The Botanical Review*, 52, 221–259.

Henry, T. J., & Froeschner, R. C. (1988). *Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States*. New York, NY: Brill Academic Publishers.

Heppner, J. B. (2003). *Lepidoptera of Florida, Part I Introduction and Catalog*. Gainesville, FL: Florida Department of Agriculture and Consumer Services. Retrieved from http://freshfromflorida.s3.amazonaws.com/arthropods-of-florida-vol-17.pdf

Hill, A. S., & Roelofs, W. L. (1981). Sex pheromone of the saltmarsh caterpillar moth, *Estigmene acrea*. *Journal of Chemical Ecology*, 7, 655–668.

Hoddle, M. S., Triapitsyn, S. V., & Morgan, D. J. W. (2003). Distribution and plant association records for *Homalodisca coagulate* (Hemiptera: Cicadellidae) in Florida. *Florida Entomologist*, 86, 89–91.

Hodgson, C. J., & Hilburn, D. J. (1991). An annotated checklist of the Coccoidea of Bermuda. *The Florida Entomologist*, 74, 133–146.

Hüller, A., Coelho, G. C., Lucchese, O. A., & Schirmer, J. (2009). Comparative study of four tree species used in riparian forest restoration along Uruguay River, Brazil. *Revista Arvore*, 33, 297–304.

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17, 164–170.

Koerber, T. W. (1963). *Leptoglossus occidentalis* (Hemiptera: Coreidae), a newly discovered pest of coniferous seed. *Annals of the Entomological Society of America*, 56, 229–234.

Leonard, M. D. (1931). *Leptoglossus gonagra* Fab. injuring *Citrus* in Porto Rico. *Journal of Economic Entomology*, 24, 765–767.

Loope, L. L., & Dunevitz, V. L. (1981). *Investigations of early plant succession on abandoned farmland in Everglades National Park*. (South Florida Research Center Report T-644). Homestead, FL: U.S. National Park Service.

Lorenzi, H. (2002). *Arvores brasileiras: manual de identificacao e cultivo de plantas arboreas do Brazil* [Brazilian trees: manual for identification and cultivation of Brazilian trees] (2nd ed.). Sao Paulo: Instituto Plantarum.

Luo, J.-Y., Zhang, S., Wang, L., Lv, L.-M., Wang, C.-Y., Li, C. H., … Cui, J. J. (2016). The distribution and host shifts of cotton-melon aphids in China. *PLoS One*, *11*, e0152103.

Manrique, V., Cuda, J. P., & Overholt, W. A. (2013). Brazilian peppertree: A poster child for invasive plants in Florida landscapes. *Journal of Florida Studies*, *1*, 1–14.

Manrique, V., Diaz, R., Condon, T., & Overholt, W. A. (2014). Host range tests reveal *Paectes longiformis* is not a suitable biological control agent for the invasive plant *Schinus terebinthifolia*. *BioControl*, *59*, 761–770.

Manrique, V., Diaz, R., Erazo, L., Reddi, N., Wheeler, G. S., Williams, D., & Overholt, W. A. (2014). Comparison of two populations of *Pseudophilothrips ichini* (Thysanoptera: Phlaeothripidae) as candidates for biological control of the invasive weed *Schinus terebinthifolia* (Sapindales: Anacardiaceae). *Biocontrol Science and Technology*, *24*, 518–535.

Manrique, V., Diaz, R., Pogue, M. G., Vitorino, M. D., & Overholt, W. A. (2012). Description and biology of *Paectes longiformis* Pogue (Lepidoptera: Euteliidae), a new species from Brazil and potential biological control agent of Brazilian peppertree in Florida. *Biocontrol Science and Technology*, *22*, 163–185.

McClenaghan, B., Gibson, G. B., Shokralla, S., & Hajibabaei, M. (2015). Discrimination of grasshopper (Orthoptera: Acrididae) diet and niche overlap using next-generation sequencing of gut contents. *Ecology and Evolution*, *5*, 3046–3055.

Mc Kay, F., Oleiro, M., Cabrera Walsh, G., Gandolfo, D., Cuda, J. P., & Wheeler, G. S. (2009). Natural enemies of Brazilian peppertree (Sapindales: Anacardiaceae) from Argentina: Their possible use for biological control in the USA. *Florida Entomologist*, *92*, 292–303.

Mc Kay, F., Oleiro, M., Vitorino, M. D., & Wheeler, G. S. (2012). The leafmining *Leurocephala schinusae* (Lepidoptera: Gracillariidae): Not suitable for the biological control of *Schinus terebinthifolius* (Sapindales: Anacardiaceae) in continental USA. *Biocontrol Science and Technology*, *22*, 477–489.

McPherson, J. E. (1982). *The Pentatomoidea (Hemiptera) of Northeastern North America with Emphasis on the Fauna of Illinois*. Carbondale, IL: Southern Illinois University Press.

Miller, G. L., & Miller, D. R. (2003). Invasive soft scales (Hemiptera: Coccidae) and their threat to U. S. agriculture. *Proceeding of the Entomological Society of Washington*, *105*, 832–846.

Montezano, D. G., Specht, A., Bortolin, T. M., Fronza, E., Sosa-Gómez, D. R., Roque-Specht, V. F., … Barros, N. M. (2013). Immature stages of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae): Developmental parameters and host plants. *Anais da Academia Brasileira de Ciências*, *85*, 271–284.

Morgan, E. C., & Overholt, W. A. (2005). Potential allelopathic effects of Brazilian pepper (*Schinus terebinthifolius* Raddi, Anacardiaceae) aqueous extract on germination and growth of selected Florida native plants. *Journal of the Torrey Botanical Society*, *132*, 11–15.

Morton, J. F. (1978). Brazilian pepper - its impact on people, animals and the environment. *Economy Botany*, *32*, 353–359.

Mukherjee, A., Williams, D. A., Wheeler, G. S., Cuda, J. P., Pal, S., & Overholt, W. A. (2012). Brazilian peppertree (*Schinus terebinthifolius*) in Florida and South America: Evidence of a possible niche shift driven by hybridization. *Biological Invasions*, *14*, 1415–1430.

Neal, A. (2013). Sri Lankan weevil, *Myllocerus undecimpustulatus undatus* Marshall. Institute of Food and Agricultural Sciences, University of Florida. Document EENY-579. Retrieved from http://edis.ifas.ufl.edu/in1016.

Nehrling, H. (1944). *My garden in Florida, volume I*. Estero, FL: American Eagle.

Nilsen, E. T., & Muller, W. H. (1980a). A comparison of the relative naturalization ability of two *Schinus* species in southern California. I. Seed germination. *Bulletin of the Torrey Botanical Club*, *107*, 51–56.

Nilsen, E. T., & Muller, W. H. (1980b). A comparison of the relative naturalizing ability of two *Schinus* species (Anacardiaceae) in southern California. II. Seedling establishment. *Bulletin of the Torrey Botanical Club*, *107*, 232–237.

Nogueira, A., Martinez, C. A., Ferreira, L. L., & Prado, C. H. B. A. (2004). Photosynthesis and water use efficiency in twenty tropical tree species of differing succession status in a Brazilian reforestation. *Photosynthetica*, *42*, 351–356.

Olckers, T., & Hulley, P. E. (1995). Importance of preintroduction surveys in the biological control of *Solanum* weeds in South Africa. *Agriculture, Ecosystems and Environment*, 52, 179–185.

Oleiro, M., Mc Kay, F., & Wheeler, G. S. (2011). Biology and host range of *Tecmessa elegans* (Lepidoptera: Notodontidae), a leaf-feeding moth evaluated as a potential biological control agent for *Schinus terebinthifolius* (Sapindales: Anacardiaceae) in the United States. *Environmental Entomology*, 40, 605–13.

Overholt, W. A., Cuda, J. P., & Markle, L. (2012). Can novel weapons favor native plants? Allelopathic interactions between *Morella cerifera* (L.) and *Schinus terebinthifolius* Raddi. *The Journal of the Torrey Botanical Society*, 139, 356–366.

Panetta, F. D., & McKee, J. (1997). Recruitment of the invasive ornamental, *Schinus terebinthifolius*, is dependent upon frugivores. *Australian Journal of Ecology*, 22, 432–438.

Panizzi, A. R., & Herzog, D. C. (1984). Biology of *Thyanta perditor* (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America*, 77, 646–650.

Panizzi, A. R., & Slansky Jr, F. (1985). New host records for the stink bug *Piezodorus guildinii* in Florida (Hemiptera: Pentatomidae). *The Florida Entomologist*, 68, 215–216.

Pfadt, R. E. (1994). Greenstriped Grasshopper, *Chortophaga viridifasciata* (DeGeer). Wyoming Agricultural Experiment Station Bulletin 912. Retrieved from http://keys.lucidcentral.org/keys/grasshopper/nonkey/html/FactSheets/greenstr.htm.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2016). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-128. Retrieved from http://CRAN.R-project.org/package=nlme.

Pogue, M. (2002). A world revision of the genus *Spodoptera* Guenée (Lepidoptera: Noctuidae). *Memoirs of the American Entomological Society*, 43, 1–202.

Pogue, M. G. (2013). A review of the *Paectes arcigera* species complex (Guenée) (Lepidoptera, Euteliidae). *ZooKeys*, 264, 126–163.

Portillo, H. E., Pitre, H. N., Meckenstock, D. H., & Andrews, K. L. (1996). Oviposition preference of *Spodoptera latifascia* (Lepidoptera: Noctuidae) for sorghum, maize and non-crop vegetation. *The Florida Entomologist*, 79, 552–562.

Prade, P., Diaz, R., Vitorino, M. D., Cuda, J. P., Kumar, P., Gruber, B., & Overholt, W. A. (2016). Galls induced by *Calophya latiforceps* Burckhardt (Hemiptera: Calophyidae) reduce leaf performance and growth of Brazilian peppertree. *Biocontrol Science and Technology*, 26, 23–34.

R Core Team. (2016). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*. Vienna: Austria. URL https://www.R-project.org/.

Rolston, L. H., & Kendrick, R. L. (1961). Biology of the brown stink bug, *Euschistus servus* Say. *Journal of the Kansas Entomological Society*, 34, 151–157.

Schaefer, C. W. (1980). The host plant of the Alydinae, with a note on heterotypic feeding aggregations (HemipteraL Coreoidea: Alydidae. *Journal of the Kansas Entomological Society*, 53, 115–122.

Scholtens, B. G., & Solis, M. A. (2015). Annotated check list of the Pyraloidea (Lepidoptera) of America North of Mexico. *Zookeys*, 535, 1–136.

Sequiter, J. M. (2013). Southern green stink bug, *Nezara viridula* (Linnaeus) (Insecta: Hemiptera: Pentatomidae). Institute of Food and Agricultural Sciences, University of Florida. Document EENY016. Retrieved from http://edis.ifas.ufl.edu/in142.

Sequitier, J. B., & Capinera, J. L. (2014). American grasshopper, *Schistocerca americana* (Drury) (Insecta: Orthoptera: Acrididae). Institute of Food and Agricultural Sciences, University of Florida. Document EENY-024. Retrieved from http://edis.ifas.ufl.edu/in130.

Sétamou, M., Rodriguez, D., Saldana, R., Schwarzlose, G., Palrang, D., & Nelson, S. D. (2010). Efficacy and uptake of soil-applied imidacloprid in the control of Asian citrus psyllid and a citrus leafminer, two foliar-feeding citrus pests. *Journal of Economic Entomology*, 103, 1711–1719.

Shelton, A. M., & Nault, B. A. (2004). Dead-end trap cropping: A technique to improve management of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Crop Protection*, 23, 497–503.

Sobczyk, T. (2011). *World catalogue of insects 10. Psychidae (Lepidoptera)*. Stenstrup, Denmark: Apollo Books.

Stansley, P. A., & Rogers, M. E. (2016). Plant bugs, chewing insect pests, Caribbean fruit fly and thrips. In *2016 Florida citrus pest management guide*. Institute of Food and Agricultural Sciences, University of Florida. Document EENY-004. Retrieved from http://edis.ifas.ufl.edu/cg005.

Strauss, G. (2010). Pest risk analysis of *Metcalfa pruinosa* in Austria. *Journal of Pest Science*, 83, 381–390.

Stricker, K. B., & Stiling, P. (2012). Herbivory by an introduced Asian weevil negatively affects population growth of an invasive Brazilian shrub in Florida. *Ecology*, 93, 1902–1911.

Tallamy, D. W., & Shropshire, K. J. (2009). Lepidopteran host use of native and alien ornamental plants. *Conservation Biology*, 23, 941–947.

Todd, E. L., & Poole, R. W. (1980). Keys and illustrations for the armyworm moths of the noctuid genus *Spodoptera* Guenée from the Western Hemisphere. *Annals of the Entomological Society of America*, 73, 722–738.

Torres, J. A. (1992). Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. *Journal of Tropical Ecology*, 8, 285–298.

Valentine, B. D. (1998). A review of the Nearctic and some related Anthribidae (Coleoptera). *Insecta Mundi*, 12, 251–296.

Vitorino, M. D., Christ, L. R., Barbieri, G., Cuda, J. P., & Medal, J. C. (2011). *Calophya terebinthifolii* (Hemiptera: Calophyidae), a candidate for biological control of *Schinus terebinthifolius* (Sapindales: Anacardiaceae): Feeding preferences and impact studies. *Florida Entomologist*, 94, 694–695.

Weissling, T. J., Pena, J. E., Giblin-Davis, R. M., & Knapp JR, J. L. (2012). *Diaprepes* root weevil, *Diaprepes abbreviates* (Linnaeus) (Insecta: Coleoptera: Curculionidae). Institute of Food and Agricultural Sciences, University of Florida. Document EENY-024. Retrieved from http://edis.ifas.ufl.edu/in151.

Wheeler, G. S., Massey, L. M., & Endries, M. (2001). The Brazilian peppertree drupe feeder *Megastigmus transvaalensis* (Hymenoptera: Torymidae): Florida distribution and impact. *Biological Control*, 22, 139–148.

Wheeler, G. S., Geiger, J., Mc Kay, F., Rendon, J., Chawner, M., & Pratt, P. D. (2011). Defoliating broad-nosed weevil, *Plectrophoroides lutra*; not suitable for biological control of Brazilian pepper (*Schinus terebinthifolius*). *Biocontrol Science and Technology*, 21, 89–91.

Wheeler, G. S., Mc Kay, F., Vitorino, M. D., Manrique, V., Diaz, R., & Overholt, W. A. (2016). Biological control of the invasive weed *Schinus terebinthifolia* (Brazilian peppertree): A review of the project with an update on the proposed agents. *Southeastern Naturalist*, 15(sp8), 15–34.

Williams, D. A., Muchugu, E., Overholt, W. A., & Cuda, J. P. (2007). Colonization patterns of the invasive Brazilian peppertree, *Schinus terebinthifolius*, in Florida. *Heredity*, 98, 284–293.

Williams, D. A., Overholt, W. A., Cuda, J. P., & Hughes, C. R. (2005). Chloroplast and microsatellite DNA diversities reveal the introduction history of Brazilian peppertree (*Schinus terebinthifolius*) in Florida. *Molecular Ecology*, 14, 3643–3656.

Wilson, S. W., & McPherson, J. E. (1981). Life histories of *Anormenis septentrionalis*, *Metcalfa pruinosa*, and *Ormenoides venusta* with descriptions of immature stages. *Annals of the Entomological Society of America*, 74, 299–311.

Woodall, S. L. (1982). *Herbicide tests for control of Brazilian-pepper in Florida*. Asheville, NC: USDA Forest Service Research Note SE314, Southeastern Forest Experiment Station.