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EFFECTS OF RELATIVE HOST PLANT ABUNDANCE, DENSITY AND INTER-PATCH DISTANCE ON ASSOCIATIONAL RESISTANCE TO A COASTAL GALL-MAKING MIDGE, *ASPHONDYLIA BORRICHIAE* (DIPTERA: CECIDOMYIIDAE)

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ABSTRACT

Associational resistance (AR) is an emergent property of ecological communities and may play an important role in their assembly and structuring. Gall densities of the midge *Asphondylia borrichiae* Rossi & Strong (Diptera: Cecidomyiidae) on the coastal plant *Iva frutescens* L. (Asteraceae) are reduced in the presence of a second host, *Borrchia frutescens* (L.) (Asteraceae). In this system associational resistance is mediated by parasitoid natural enemies that emerge from *Borrchia* galls and attack galls on *Iva*, thereby reducing gall densities on *Iva*. We quantified distances between patches of *Iva* and *Borrchia* and the relative abundances of both plant species and predicted that gall densities would be reduced and parasitism rates elevated on *Iva* closer to *Borrchia* compared with more distant patches and on *Iva* occurring with relatively greater *Borrchia* abundance in comparison to reduced ratios of *Borrchia* to *Iva* abundance. Although gall densities were elevated on *Iva* more distant from *Borrchia*, as compared with *Iva* adjacent to *Borrchia*, parasitism rates were unaffected by patch distance in this system. Increasing relative abundance of *Borrchia* was found to significantly reduce gall densities on *Iva*, though parasitism rates on *Iva* galls were unaffected by *Borrchia* abundance. These results suggest other factors, e.g., environmental quality, host plant genotype, etc., may swamp out the effects of parasitoid-mediated AR in this system as *Iva* becomes more distant from *Borrchia* or as the abundance of *Borrchia* relative to *Iva* is reduced.

Key Words: parasitoid-mediated associational resistance, enemies hypothesis, *Asphondylia borrichiae*, *Iva frutescens*, *Borrchia frutescens*

RESUMEN

La resistencia asociativa (RA) es una propiedad emergente de las comunidades ecológicas y puede jugar un papel importante en su montaje y estructura. Se reduce la densidad de agallas del mosquito cecidomida, *Asphondylia borrichiae* a las plantas costeras de *Iva frutescens* en presencia de un segundo hospedero, *Borrchia frutescens*. En este sistema la resistencia asociativa está controlada por los enemigos naturales parasitoides que emergen de las agallas sobre *Borrchia* y atacan las agallas sobre *Iva*, lo que reduce la densidad de las agallas sobre la *Iva*. Hemos cuantificado la distancia entre los parches de *Iva* y *Borrchia* y la abundancia relativa de las dos especies de plantas y predcimos que la densidad de las agallas sería elevada y la tasa de parasitismo reducida en plantas de *Iva* más distantes de *Borrchia* en comparación con parches adyacentes y sobre plantas de *Iva* que ocurren con relativamente mayor abundancia de *Borrchia* en comparación a una reducción en la proporción de abundancia de *Borrchia* y *Iva*. Aunque la densidad de agallas fue elevada en plantas de *Iva* más distantes de *Borrchia*, en comparación con *Iva* adyacente a *Borrchia*, la tasa de parasitismo no fue afectada por la distancia entre los parches en este sistema. Se encontró que el aumento en la abundancia relativa de *Borrchia* redujó significativamente la densidad de las agallas sobre *Iva*, aunque la tasa de parasitismo en las agallas sobre *Iva* no fue afectado por la abundancia de *Borrchia*. Estos resultados sugieren que otros factores pueden eliminar los efectos de RA controlada por los parasitoides en este sistema así como *Iva* se localiza más distante de *Borrchia* o como la abundancia relativa de *Borrchia* a *Iva* se reduce.

Palabras Clave: resistencia asociativa mediada por parasitoides, enemigos hipótesis, *Asphondylia borrichiae*, *Iva frutescens*, *Borrchia frutescens*

Associational resistance (AR) occurs when there is a reduction in herbivore load or attack rate on a plant species growing in a mixed community relative to the herbivore load on that species when grown in monoculture. The converse phenomenon is known as associational susceptibility (AS) and has been found to occur more frequently in plant-insect interactions than AR (Barbosa et al. 2009). A number of mechanisms for AR have been hypothesized, among them the resource concentration hypothesis, the enemies hypothesis, the semiochemical diversity hypothesis, the repellent plant hypothesis and the attractant decoy hypothesis (Tahvahnainen & Root 1972; Root 1973; Atsatt & O'Dowd 1976; Russell 1989; Jactel et al. 2011). Parasitoid-mediated AR has previously been observed in the interactions of the gall midge *Asphondylia borrichiae* Rossi & Strong (Diptera: Cecidomyiidae) with 2 of its host species, *Borrichia frutescens* (L.) DC. (Asteraceae) and *Iva frutescens* L. (Asteraceae) (Stiling et al. 2003). The relatively larger *A. borrichiae* galls on *B. frutescens* produce relatively larger parasitoids. The parasitoids produced in such galls are more capable of parasitizing the relatively smaller *A. borrichiae* galls produced on *I. frutescens*, which are susceptible by dint of a size effect.

On small offshore spoil islands near the west coast of central Florida, *I. frutescens* gall parasitism rates were higher and galling rates lower in the presence of neighboring *Borrichia*, but the converse effect was not observed (Stiling et al. 2003). A follow-up study on the same islands, subsequent to large-scale additions and reductions of *B. frutescens* from different spoil islands supported earlier observational studies (Stokes & Stiling, in press). Because *Iva* gall densities were reduced and parasitism rates were higher where *B. frutescens* was added, while the reverse was observed where *B. frutescens* was removed, spillover of parasitoids from *Borrichia* to *Iva* is likely the most important mechanism of AR in this system. The parasitoid *Torymus umbilicatus* is likely the member of the parasitoid guild most responsible for the AR effect observed, given that this species' specific parasitism rate increases in the presence of or increased abundance of *Borrichia*, which is facilitated by its possession of an ovipositor over 2X longer than those of other guild members, permitting hyperparasitism later in gall development (Stiling & Rossi 1994). The attractant decoy hypothesis and other explanatory mechanisms requiring host switching by the gall midge are unlikely, given that host choice experiments showed minimal cross-genus oviposition by *A. borrichiae* (Rossi et al. 1999) and a molecular population genetic study supported the results of the host choice experiment and provided evidence in favor of genetic divergence among host-species-associated populations at two locales (Stokes et al. 2012). Thus, *I. frutescens* and *B. frutescens* are host to distinct populations with little migration between hosts.

Here we present data from 3 additional studies where we seek to quantitatively model response variables (i.e., galling rate and parasitism rate on *I. frutescens*) with factors that are likely to affect parasitoid-mediated AR: distance separating host plant species, relative abundance of host plant species, and gall densities and parasitism rates on *B. frutescens*. We expect gall densities to increase and parasitism rates to decrease on *Iva* with increasing distance from *Borrichia*. Further, we predict the relationship between the ratio of *Borrichia* to *Iva* abundance and *Iva* gall densities to be negative, while the abundance ratio should have a positive relationship on *Iva* gall parasitism rates.

MATERIALS AND METHODS

Effect of Host Patch Distance on Coastal Islands

This study was conducted on 6 spoil islands, part of a series of spoil islands spaced at intervals no less than 0.8 km off the Gulf Coast of Florida, near Clearwater and Tarpon Springs (Pinellas County) (Fig. 1). The islands are the result of a dredging operation by the U.S. Army Corps of Engineers in the 1960s and have subsequently been naturally colonized by coastal plants and their insect herbivores. All islands had two patches of *I. frutescens*, one adjacent to (< 1 m) *Borrichia* in island centers and one distant from (typically > 10 m) patches of *B. frutescens*, on island edges, near water and susceptible to tidal input. Monthly counts of galls were conducted from Apr 2009 through Jan 2010 to estimate galling rates in patches of *I. frutescens* adjacent to and distant from patches of *B. frutescens*, as well as on *B. frutescens*. During each sampling period, gall counts were taken of 100 haphazardly-selected leaf buds on each of 5 different *I. frutescens* bushes in patches near and far from *B. frutescens* patches, as well as gall counts on 400 haphazardly-selected *B. frutescens* leaf buds. Mature galls were collected from near and distant *I. frutescens* patches on all islands and returned to the lab for culturing of the gall community to determine parasitism rates.

Aggregate mean differences in galling rate, total parasitism rate, and *T. umbilicatus*-specific parasitism rates between patches of *I. frutescens* near to and far from *B. frutescens* were compared using paired-sample *t*-tests, using islands as replicates. We predicted galling rates on *Iva* close to *Borrichia* to be lower, and parasitism rates higher, than on *Iva* distant from *Borrichia*.

Effect of *B. frutescens* Abundance on AR-Courtney Campbell Causeway East

The Courtney Campbell Causeway (CCC) is a roadway which extends across northern Tampa Bay from Tampa, Hillsborough County, Florida to Clearwater, Pinellas County, Florida. On the

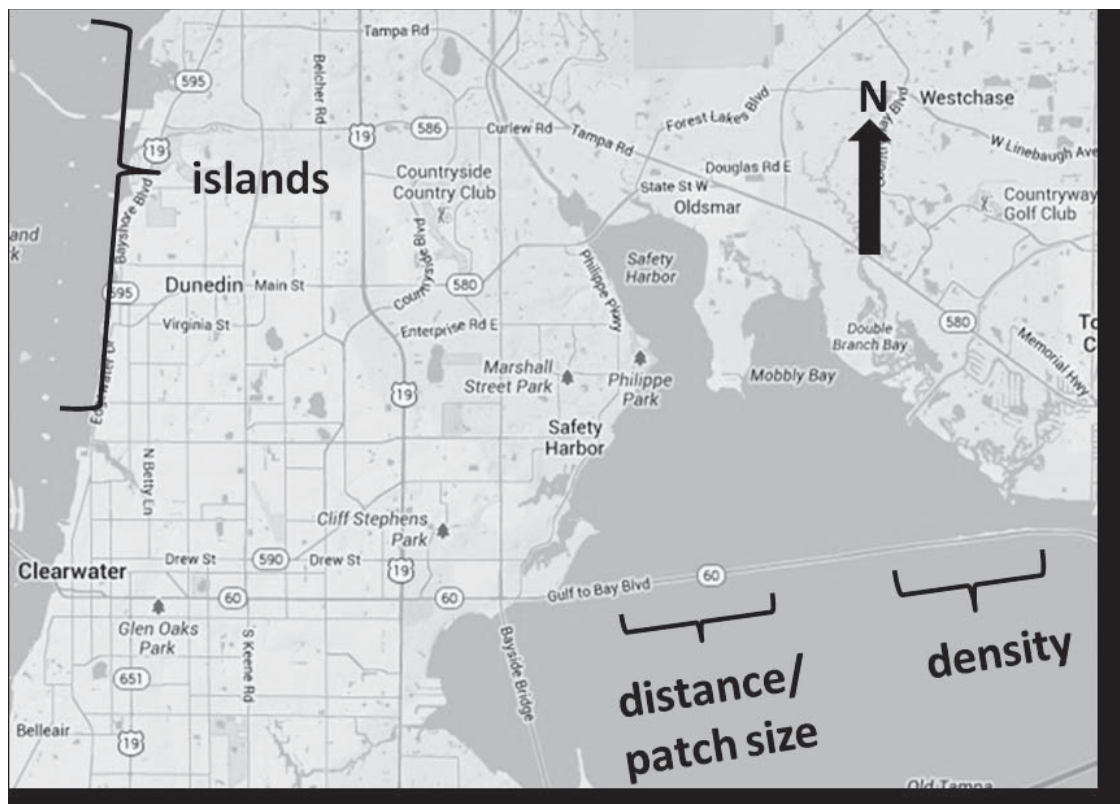


Fig. 1. Map showing overview and relative location of each of the 3 studies. Tampa (Hillsborough County), Florida is to the east.

east side of the CCC bridge is an extensive area of *B. frutescens* forming a continuous ground cover matrix with *I. frutescens* shrubs emerging intermittently, such that the distance between the host species is zero; moreover, relative host plant abundances vary with varying *Borrchia* stem density (Fig. 2). Monthly gall counts were performed from Jan 2009 to Sep 2009 to determine gall densities on *I. frutescens* and *B. frutescens*. Additionally, areal density of potential oviposition sites (leaf buds) on *Borrchia* on both sides of each *I. frutescens* shrub in the study was measured and the local average determined. Emergence holes were counted concurrently on both species and classified according to whether they were the result of emerging gall midges or parasitoids (Stiling & Rossi 1997). Linear regression analysis was performed using *I. frutescens* gall density and parasitism rate as response variables and *B. frutescens* gall density, oviposition site areal density and parasitism rate as independent variables influencing *Iva* gall density. We predicted *Iva* gall density to be lower and parasitism rate higher as *Borrchia* gall density, oviposition site density and parasitism rate increased.

Effect of Host Patch Distance and Relative Abundance – Courtney Campbell Causeway West

On the western side of the CCC bridge, discrete patches *Borrchia* and *Iva* of various relative abundances occur in a narrow band at random intervals, in effect a linear transect, approximately 4 km distant at the nearest sampling point to the CCC-East density study (Fig. 1). These patches were used to study both the effects of relative host species abundance and the effects of inter-patch distance on gall densities and parasitism rates on *I. frutescens*. Monthly censuses were performed from Feb 2009 to Oct 2009 to determine gall densities on *I. frutescens* and *B. frutescens*. Gall parasitism rates were determined by counting emergence holes and classifying them according to whether they were the result of emerging gall midges or parasitoids. Additionally, both *Iva* and *Borrchia* patch sizes and areal densities of potential oviposition sites (i.e., leaf buds) were determined to estimate the total number of potential oviposition sites per patch (*Borrchia*) or per bush (*Iva*) and the ratios of the abundances were log-transformed to standardize the scale as the host which is more abundant switches from one

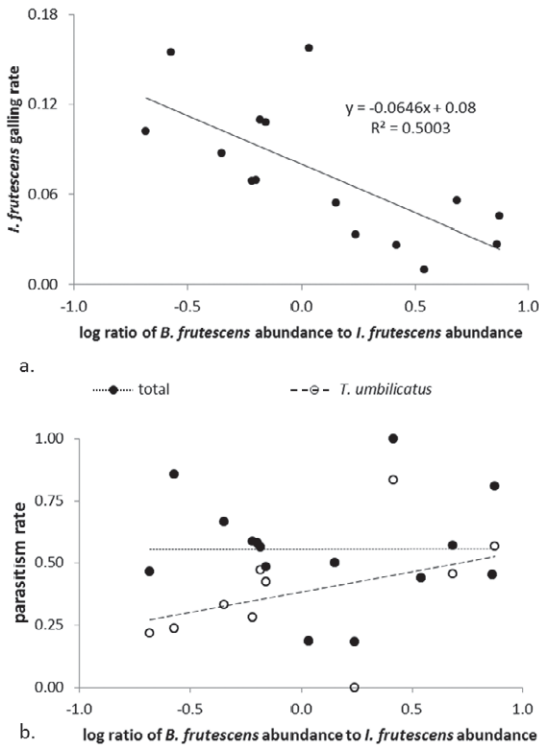


Fig. 2. Relationship between log-10-transformed *B. frutescens* to *I. frutescens* relative abundance and (a.) *Iva frutescens* galling rate and (b.) total and *Torymus umbilicatus*-specific parasitism rates.

host species to the other. Distances between edges of adjacent patches were measured to obtain a minimum inter-patch distance for each pair of patches. To quantitatively model the effects of *Iva-Borrichia* inter-patch distance and relative oviposition site abundance on AR, linear regressions were conducted on 3 *I. frutescens* response variables for parasitoid-mediated AR: galling rate, total parasitism rate and *T. umbilicatus*-specific parasitism rate.

RESULTS

Effect of Host Patch Distance on Coastal Islands

Although differences in mean galling rates between near and distant patches of *I. frutescens* were statistically significantly different, with galling rates much higher on *Iva* bushes distant from *Borrichia* ($t = 4.261$, $df = 5$, $P < 0.01$; Fig. 3a), overall parasitism rates were not significantly different ($t = 1.816$, $df = 5$, $P > 0.05$; Fig. 3b). Furthermore, *T. umbilicatus*-specific parasitism rates were significantly greater on *Iva* patches distant from *Borrichia* in comparison to near *Iva* patches ($t = 3.548$, $df = 5$, $P < 0.01$; Fig. 3c).

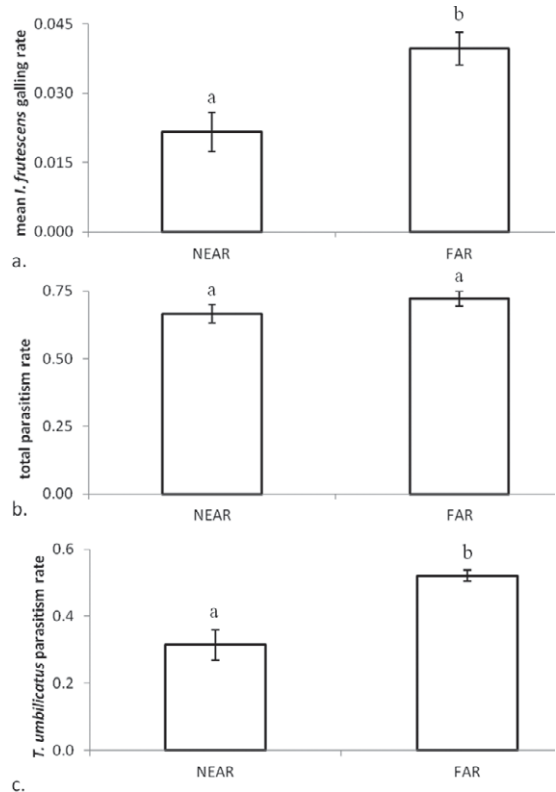


Fig. 3. Comparison of (a.) mean galling rates (± 1 SEM) (b.) mean total parasitism rates and (c.) mean *Torymus umbilicatus*-specific parasitism rates (± 1 SEM) on *Iva frutescens* patches adjacent to and distant from *Borrichia frutescens* patches on spoil islands.

Effect of *B. frutescens* Abundance on AR – Courtney Campbell Causeway East

Of the 4 comparisons performed by linear regression (*B. frutescens* galling rate on *I. frutescens* galling rate, *B. frutescens* leaf bud areal density on *I. frutescens* galling rate, *B. frutescens* parasitism rate on *I. frutescens* parasitism rate, and *B. frutescens* parasitism rate on *I. frutescens* galling rate), none were statistically significant (Table 1).

Effect of Host Patch Distance and Relative Abundance – Courtney Campbell Causeway West

Linear regressions were performed to measure the effect of each of 3 variables (*B. frutescens* galling rate, distance between host species patches, and relative host abundance) on 3 response variables: *I. frutescens* galling rate, overall parasitism rate on *Iva* and *T. umbilicatus*-specific parasitism rate on *Iva*. Of these 9 comparisons (Table 2), the only significant relationship was a negative correlation between *I. frutescens* galling rate and log-transformed relative host abundance, which

TABLE 1. RESULTS OF LINEAR REGRESSIONS IN THE DENSITY STUDY AT COURTNEY CAMPBELL CAUSEWAY-EAST. NO SIGNIFICANT RESULTS WERE DETECTED.

Predictor variable	Response variable	R	P
<i>B. frutescens</i> galling rate	<i>I. frutescens</i> galling rate	0.39	0.09
<i>B. frutescens</i> leaf bud areal density	<i>I. frutescens</i> galling rate	0.22	0.36
<i>B. frutescens</i> parasitism rate	<i>I. frutescens</i> galling rate	< 0.01	0.99
<i>B. frutescens</i> parasitism rate	<i>I. frutescens</i> parasitism rate	0.34	0.20

explained approximately 50% of the observed variation ($F = 13.017$, $r = 0.7073$, $P < 0.01$; Fig. 2).

DISCUSSION

In a prior study, Stiling and colleagues (2003) found a strong effect of *B. frutescens* galls on *I. frutescens* gall densities, which they attributed to parasitoids, especially *T. umbilicatus*, from *B. frutescens* spilling over and attacking *A. borrichiae* galls on *I. frutescens*. A follow-up study involving large scale experimental additions and removals of *Borrichia* on coastal spoil islands found additional support for the existence of parasitoid-mediated AR in this system (Stokes & Stiling, in press). However, the data presented here cannot further clarify the effects of inter-patch distance or patch sizes on the strength of AR operating in the system. Although *Iva* galling rates were significantly lower on spoil islands when *Iva* was adjacent (< 1 m) to *Borrichia* in comparison to when *Iva* was located distant (> 10 m) from it, parasitism rates showed no such pattern and *T. umbilicatus* parasitism rates were significantly higher on patches of *I. frutescens* distant from *B. frutescens*. One possible explanation for these observed patterns is that there may be a high dispersal rate of both gall makers and parasitoids from islands. Following a flight of at least 0.8 km over open water, all immigrating insects, gall makers and parasitoids alike, may oviposit extensively on the first appropriate plants encountered, which happen to be the *Iva* bushes occurring at a distance from *Borrichia*, on island edges.

It was expected that distance between patches would affect the strength of AR along the western side of the Courtney Campbell Causeway. Such an effect would possibly weaken quickly, with AR rapidly dropping off after short distances, as in the case of the repellent plant hypothesis because of diffusion of noxious odors (Tahvanainen & Root 1972; Atsatt & O'Dowd 1976). Surprisingly, no effect of distance between patches on AR was detected in the study, possibly because the study design did not exceed the cruising range of the natural enemies, which is unknown. However, *B. frutescens* gall densities were generally low in the area examined, reducing the ability to detect distance effects on parasitoid-mediated AR.

Despite the inability to detect an effect of inter-patch distance on AR mediated by natural enemies, *Iva* galling rates strongly declined (by >5x) with increasing relative abundance of *Borrichia*, corresponding to general predictions of AR and accounting for 50% of the variation in *Iva* gall density. However, overall parasitism rates and *T. umbilicatus*-specific parasitism rates were unaffected by relative abundance of *Borrichia*. An increase in *Borrichia* oviposition site availability may indicate conditions favorable to *Borrichia* and, possibly, less favorable for *Iva*. Decreased microenvironmental favorability for *Iva* may, in turn, decrease *Iva* plant quality and, thereby, depress galling rates.

In summary, these results shed little light on the effects of inter-patch distance and relative host abundance on the strength of parasitoid-mediated AR in the *Asphondylia borrichiae*-*Borrichia frutescens*-*Iva frutescens* system. Plant

TABLE 2. RESULTS OF LINEAR REGRESSIONS BETWEEN 3 PREDICTOR AND RESPONSE VARIABLES AT COURTNEY CAMPBELL CAUSEWAY-WEST. VALUES PROVIDED ARE THE REGRESSION COEFFICIENT AND THE P-VALUE OF THE MODEL, RESPECTIVELY. BOLD-FACE TYPE INDICATES A SIGNIFICANT RELATIONSHIP.

Response variable	Predictor Variable		
	<i>B. frutescens</i> galling rate	Host patch distance	Log relative host plant abundance
<i>I. frutescens</i> galling rate	0.33, 0.24	0.07, 0.82	0.71, < 0.01
Total <i>Iva</i> parasitism rate	0.04, 0.88	0.02, 0.95	< 0.01, 0.99
<i>T. umbilicatus</i> -specific parasitism rate on <i>Iva</i>	0.10, 0.73	< 0.01, 0.99	0.41, 0.13

genotype of *Borrchia* and local environmental conditions are both known to affect gall densities on *Borrchia* (Stiling & Rossi 1996). *Iva* gall densities are also likely to be influenced by environment and *Iva* genotype. A mosaic of *Iva* and *Borrchia* genotypes on coastal islands and along the Courtney Campbell Causeway, together with a varied range of microenvironmental factors could obscure distance and relative abundance effects in this system. More detailed studies are needed to disentangle the relative strengths of the effects of *Iva* and *Borrchia* relative abundance, plant quality, genotypic susceptibility and environmental quality to galling and inter-patch distance on parasitoid-mediated AR in this system.

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