PROCEEDINGS

OF THE

FORTEENTH SYMPOSIUM

ON THE

NATURAL HISTORY OF THE BAHAMAS

Edited by

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Gerace Research Centre

San Salvador Bahamas

2011

Cover photograph – “Iggie the Rock Iguana” courtesy of Ric Schumacher

Printed at the Gerace Research Centre

ISBN 0-935909-95-8

BEETLE (COLEOPTERA: BRUCHIDAE: *ACANTHOSCELIDES MACROPHTHALAMUS*) SEED PREDATION ON *LEUCAENA LEUCOCEPHALA* (FABACEAE: MIMOSOIDEAE) SEEDS AND PODS IN TWO HABITATS ON SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT

Leucaena leucocephala (Jimbay) is an invasive legume native to Central America and has been introduced by humans into tropical regions worldwide. *Acanthoscelides macrophthalmus* (Coleoptera) is a seed predator with high host specificity to Jimbay and has been considered as a biological control agent. On San Salvador Island, Bahamas, the seeds of Jimbay are subject to a substantial amount of predation by *A. macrophthalmus*. Jimbay pods from two locations near the Gerace Research Centre were collected: a sparse open patch of growth in the centre of the paved catchment basin, and a dense section of forest at the edge of the catchment. Two types of insect predation and one type of parasitoid damage in the pods from both locations were found. Seed predation was predominately due to *A. macrophthalmus*, and there was significantly more beetle seed damage in pods collected from the open catchment. A hymenopteran parasitoid was reared from *Acanthoscelides* larva and was more abundant in the open catchment site. The second form of predation was less common and the result of lepidopteran larvae.

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INTRODUCTION

Leucaena leucocephala (Lam.) de Wit (Fabaceae: Mimosoideae), common name Jimbay, is listed as a significant invasive plant threat in warmer climates worldwide (ISSG 2006). *Leucaena leucocephala* is native to Mexico and Central America. Due to its nutritional value and versatility, *L. leucocephala* has been introduced as cattle fodder throughout the world since the 17th century and today the species is present in over 100 countries (Walton 2003).

Leucaena leucocephala has many characteristics common in invasive plants: it continually produces an abundance of seeds allowing it to spread easily, it relies on generalist pollinators as well as selfing, and it is resilient to drought and fire (Walton 2003). Additionally, it possesses allelopathic compounds that reduce competition from surrounding vegetation (Midori et al. 2009). All of these characteristics contribute to what may be a considerable threat to the biodiversity of ecosystems (Walton 2003).

The bruchid beetle, *Acanthoscelides macrophthalmus*, is a specialist seed predator of *L. leucocephala.* The *Acanthoscelides* genus is referred to as the ‘bean weevils’ (Godfrey and Long 2008), due to the significant damage they inflict on leguminous seeds. Adult beetles lay eggs on the pods and when the eggs hatch the first instar larvae burrows through the pod and into the seed. Within the seed the larval stages develop, consuming the embryo and leaving the seed unviable (Effowe *et al.* 2009). The larvae pupates within the remnants of the seed and the emerging adult burrows out of the pod in search of mates. *Acanthoscelides macrophthalamus* has high host specificity to Jimbay (Shoba and Olckers 2010), although a recent study has indicated a potential host shift to *Falctaria moluccana* (Fabaceae: Mimosoideae) is possible where present (Midori *et al.* 2009). *Acanthoscelides macrophthalamus* has already been introduced to South Africa as a biological control agent of Jimbay (Shoba and Olckers 2010), and has been considered for use in integrated pest management on several other continents. Despite the high selectivity of *A. macrophthalamus* to the legume and high predation rates (Effowe *et al.* 2009), Raghu *et al.* (2005) suggest that bruchid populations may not be effective control agents due to the fact that Jimbay seed maturation and dispersal is more rapid than the generation time of the insect.

On San Salvador Island, Bahamas, a high level of seed predation, including the characteristic predation patterns of *A. macrophthalamus*, was observed on local Jimbay pods. Here we explore whether the level of predation on the Jimbay pods is associated with the plant's immediate surroundings. Specifically, we examined the distribution of seed predators and their densities along transects of Jimbay in two different habitats. Pod samples were taken from Jimbay located in dense monocultures and from Jimbay growing in sparse, exposed areas. We hypothesized that dense communities of Jimbay would be subject to higher predation levels as a result of greater pod numbers.

MATERIALS AND METHODS

On 5 May 2009 Jimbay seed pods were collected from 2 transects at the Gerace Research Centre water catchment. The water catchment is a concrete slope with an area of about 2 ha. located directly behind the Gerace Research Centre. The catchment directs water runoff to the collecting drain at the base of the slope. Cracks and thickets of weedy growth are scattered along the concrete surface. The first transect was along the northeast lower edge of the catchment. This transect was 52.8 m long and ran 326°N to 130°S (N24° 07.025' W074° 27.869' to N24° 07.005' W074° 27.848').

This catchment edge was almost completely Jimbay, with 38 m of diverse habitat east of the catchment to the New World Trail. Average tree height was 5 m and was determined using a sextant.

The second transect was in the open catchment near the wooden tower. This site was 3.05 meters higher in elevation than the first transect. This transect was 74 m long and ran 293°N to 167°S (N24° 06.982' W074° 27.876' to N24° 06.965' W074° 27.853').

This part of the catchment is predominately exposed concrete and receives full sunlight throughout the day. Tree height was determined with a meter tape. This transect was 2 m wide, and followed a fissure in the concrete through which plants were rooted.

A random numbers table was used to select points along the transects from which Jimbay fruits were collected. Fruits were collected if they were brown and dry, but not yet dehisced.

The relative coverage was calculated for the 3 different plant species growing along the catchment edge transect (Table 1). Along the open catchment transect, plants were much shorter and less dense which allowed for a greater number of parameters to be measured including the relative density, relative coverage, relative frequency, and relative importance values of the many species that grew in along this transect (Table 2).

Samples from each transect distance were separated into plastic storage bags on 5 May 2009. The pods were frozen from 9-16 June 2009 to kill insects. During the time the bags were stored, insects were allowed to emerge from the seeds and pods.

Pods collected from each transect were individually examined under a dissecting scope. The lengths of the pods were measured to the nearest half-centimeter. Evidence of predation on the pods was recorded. The type of predation was attributed to a coleopteran, lepidopteran, or hymenopteran. Each insect inflicted characteristic damage to the seed and pod. The pod was split open and the seeds were counted. Predation on the seeds was determined as above. For seeds with multiple holes, each hole was counted as a separate predation event. The seeds that did not develop were labeled 'aborted'.

Some pods dehisced while in storage and no longer possessed a portion of their seeds. These pods were indicated as being previously dehisced and were excluded from statistical tests. Any insects found emerging or in the pod were collected and preserved in ethanol.

RESULTS AND DISCUSSION

Plant Community Analysis

Plants were smaller and less dense in the open catchment (Table 3). Jimbay occurred sporadically along the transect and were separated by several other plant species and exposed concrete. Other common plant species found along the transect included Granny Bush (*Croton linearis*), Butterfly Pea (*Centrosema virginianum*), and *Tridax procumbens* (Table 2). Relative linear coverage of Jimbay (percentage of transect covered by a plant species) was 0.38 and average height was 1.5 m. Jimbay along the catchment edge had a relative coverage of 0.93 and averaged 5.0 m in height (Table 3). Gumbo Limbo (*Bursera simaruba)* and Manchineel (*Hippomane mancinella*), were established along this transect but had limited coverage in comparison to Jimbay (Table 1). During this experiment the forest along the catchment edge extended at least 25 m in depth and was predominately Jimbay. Recent bulldozing has removed this stand of Jimbay. Depth along the open catchment transect was negligible as it was an entirely linear section of growth. Thus, for comparison of current and future locations, the catchment edge is classified as a dense monoculture of Jimbay, while the open catchment is a sparse polyculture in an open area (Tables 1 and 2).

Plant size and density may be directly related to water availability, heat stress, and soil fertility. Plants growing along the open catchment transect grew in concrete fractures along a north facing slope in full sunlight. Conversely, plants along the catchment edge grew at the much flatter base of the sloped basin in forest soil where rainwater runoff and nutrients collect. Manure is one source of nutrient in this case, as the basin serves as a source of fresh water for feral cows. Therefore, Jimbay growth may be competition limited along the catchment edge, but stress limited in the open catchment. Likely as a result of the growing conditions, pods were more available and abundant along the edge. An average of 13.5 pods per transect location were collected from the catchment edge, versus 7.7 for the open catchment (Table 3). In Australia and Pacific Asia, Jimbay trees range from 3-15 m in height. Pods grow in clusters from 5-45 and average 10-19 cm long. Anywhere from 8 to 30 seeds are produced per pod (Walton 2003, ISSG 2006, Sankaran 2007). Pods in both locations of this study were consistent with the literature's description.

Fruit Analysis

There was a positive correlation between number of seeds and pod length for both locations (R^2=0.67 catchment edge, R^2=0.71 open catchment), making pod length an indicator of seed number. Pod length itself was not site specific, nor was the average number of seeds per pod (t-test, n=10, 2 tailed, P>0.05). This suggests that, regardless of growing conditions, Jimbay plants invest the same amount of energy per pod in fruiting. Nutrient deficiencies may be compensated for by a decreased number of ovules or flowers per plant. The difference in average number of aborted seeds was significant (t-test, n=10, 2 tailed, P=0.056), with a greater number of aborted seeds occurring along the catchment edge. Seeds may be aborted for a number of reasons, but higher abortion levels along the catchment edge may be the result of pollination failure. Jimbay are capable of self-pollinating and are visited by a number of generalist pollinators (Walton, 2003). Pollinator availability may be greater in open areas, although this hypothesis was not tested in this study.

Seed Predation Analysis

Two distinct types of seed predation were observed on Jimbay seeds. These included damage from a beetle (Coleoptera: Bruchidae) and an unidentified moth (Lepidotera). A parasitoid wasp (Hymenoptera: Pteromalidae) was also recovered. These insects were found preserved in the frozen pods and seeds, while exiting the pod, and loose within the bags containing the pods. The coleopteran was identified by Warren Steiner (Smithsonian) as *Acanthoscelides macrophthalmus*, while the hymenopteran and lepidopteran species are currently unidentified. The wasp is a parasitoid of *A. macrophthalmus* although its host specificity is unknown without identification. Each type of predation was easily distinguishable based on characteristic damage patterns on both seed and pods. *Acanthoscelides macrophthalmus* create circular exit holes averaging 1.7 mm in diameter in both seed and pod. Seeds that were preyed upon by bruchids were hollow with endosperm and embryo almost entirely consumed. Wasp seed damage is identical to bruchid damage due to the parasitoid life cycle. Holes in pod and seed resulting from the wasp were neatly circular in shape and appeared similar to the bruchid exit hole but smaller, averaging 0.6 mm in diameter. The lepidopteran produced irregularly shaped exit holes averaging 1 mm in diameter in the pod. However, the lepidopteran seeds were left unchewed, substantially diminished, and surrounded by frass and silk.

Significantly more bruchid predation was observed in the open catchment (Table 4, t-test, n=10, 2 tailed, P=0.047). No correlation between bruchid predation and pod length was found. However, there was a higher average level of coleopteran predation across all pod sizes in the open catchment (Figures 1 and 2; Table 4). This difference in bruchid predation may relate to pod accessibility and apparency in the same way pollination did. The pods in the open catchment are much more exposed than they are along the catchment edge. As a result, predators may locate the host seeds more easily. Isolation may also influence predation. Assuming an equal distribution of adult beetles across both areas, Jimbay along the catchment edge exist in populations large enough that bruchids have the option of ovipositing on pods at a variety of locations nearby. Conversely, bruchids in the open catchment are confined to the limited number of Jimbay plants growing there. *Acanthoscelides macrophthalmus* preferentially oviposit on seeds that do not have *A. macrophthalmus* eggs on them unless oviposition sites are limiting (Shoba and Olckers 2010).

In those pods with bruchid predation, the open catchment had significantly higher levels of the hymenopteran parasitoid (Table 4, t-test, n=10, 2 tailed, P= 0.0035). Factors that could influence wasp numbers are: beetle availability, beetle apparency, pod apparency, environmental conditions, and perhaps hill-topping (flighted insects moving upwards along an inclined surface). Further study will be necessary to determine which influences are affecting the distribution of these parasitoids.

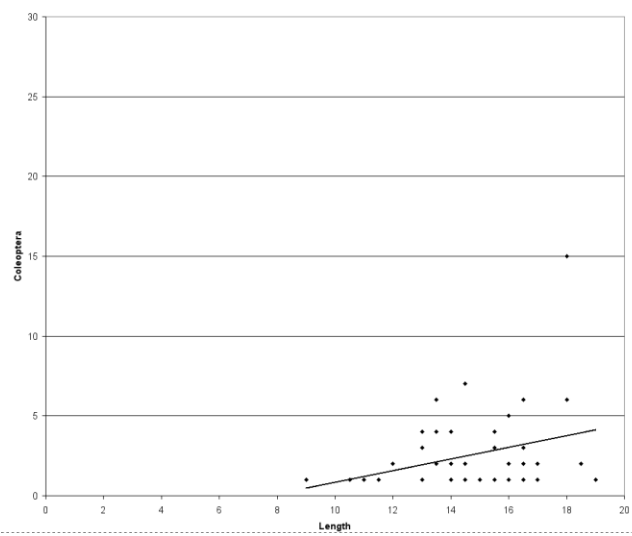

Figure 1. Coleoptera predation as a function of pod length along the catchment edge.

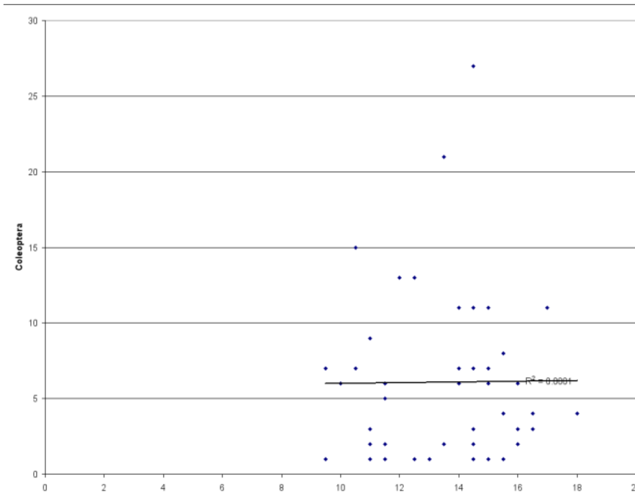

Figure 2. Coleoptera predation as a function of pod length in the open catchment.

No transect-specific patterns were observed in lepidopteran predation of Jimbay seeds. While the bruchid is largely confined by its host range, the lepidopteran may not be, making Jimbay location and pod numbers less relevant. Identification of this insect is needed for further analysis. These data, although limited by a small sample size and limited statistical power, will be useful in future studies on San Salvador to further determine which factors influence seed predation on *Leucaena leucocephala,* a highly invasive plant around the globe.

ACKNOWLEDGMENTS

We would like to thank Elmira College, Dr. Thomas A. Rothfus and the staff of the Gerace Research Centre all of whom made this research possible. We would also like to thank Dr. Maya Patel for her comments, patience, and support.

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Table 1. Relative coverage values along the catchment edge transect.

Species	Relative Coverage
Leucaena leucocephala	0.93
Bursera simaruba	0.03
Hippomane mancinella	0.04

Table 2. Relative line intercept values along open catchment transect.

Species	Density	Coverage	Frequency	Importance
Leucaena leucocephala	23.75	38.21	23.75	23.87
Croton linearis	22.50	24.15	22.50	19.26
Centrosema virginianum	15.00	4.31	15.00	9.56
Tridax procumbens	8.75	2.27	8.75	5.51
Poaceae 1	5.00	2.04	5.00	3.35
Poaceae 2	1.25	0.34	1.25	0.79
Passiflora pectinata	5.00	4.88	5.00	4.14
Urechites lutea	2.50	3.29	2.50	2.31
Smilax auriculata	2.50	3.29	2.50	2.31
Solanum bahamense	1.25	0.91	1.25	0.95
Melanthera aspera	1.25	0.45	1.25	0.82
Stachytarpheta jamaicensis	3.75	1.36	3.75	2.47
Exposed Concrete	7.50	14.51	7.50	24.66

*Table 3. Jimbay (*Leucaena leucocephala*) pod, seed and plant characteristics at the two sample sites.*

Transect	Average No. Pods Collected	Pod Length (cm)	Average Seeds per Pod	Coverage of Transect by Jimbay (%)	Plant Height (m)
Catchment edge	13.5	13.54	14.67	0.93	5.05
Open Catchment	7.7	13.43	14.75	0.38	1.5

Table 4. Significantly more Acanthoscelides macrophthalmus*, Hymenoptera, and fewer aborted seeds were found in the open catchment.*

	Catchment edge	Open catchment	Sig. (*P*)*
Aborted seeds	3.1903	2.2379	0.0562
Coleoptera	0.6891	2.548	0.0468
Hymenoptera	0.4565	1.3333	0.0035
Lepidoptera	0.948	1.4573	0.3

*Significance is based on a two-tailed t-test, n = 10.