2006

Comparing the effects of the exotic cactus-feeding moth, Cactoblastis cactorum (Berg) (Lepidoptera: Pyralidae) and a native cactus-feeding moth, Melitara prodenialis (Walker) (Lepidoptera: Pyralidae) on two species of Florida Opuntia

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Comparing the Effects of the Exotic Cactus-Feeding Moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) and a Native Cactus-Feeding Moth, *Melitara prodenialis* (Walker) (Lepidoptera: Pyralidae) on Two Species of Florida *Opuntia*.

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Sciences
University of South Florida

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Date of Approval:
November 14, 2006

Keywords: plant-insect interactions, invasive species, native species, insect ecology, biological control, prescribed fire

Acknowledgments

I would like to thank my advisor; Peter Stiling and the rest of my advisory committee, Gordon Fox and Gary Huxel for all of their advice and particularly for not allowing me give up when the end was so near. Thank you also to Henry Mushinsky for agreeing to serve on my committee at the last minute.

For their encouragement and friendship, I would like to thank my fellow lab mates, Maria Albarracin, Laura Altfeld, Mark Barrett, Tatiana Cornelissen and Rebecca Forkner. For their help in the field, I would like to acknowledge Patrick Fiore, Tatiana Cornelissen and Rebecca Forkner.

I would like to thank Dr. Gordon Fox and those at the USF Botanical Gardens, Laurie Walker, Kim Hutton and Bob Koehler for allowing me space and equipment to grow *Opuntia* on campus. Large thanks must go to the nurseries who generously donated *Opuntia* plants for on-campus experiments: Mountain States Wholesale Nursery, Glendale, AZ; Arizona Cactus Sales, Chandler, AZ; and Desertland Nursery, El Paso, TX. I would also like to thank those managers that allowed me the opportunity to work on their land: Sally Braem, Honeymoon Island State Park, Robert Browning, Fort DeSoto Park, Anne Malatesta, Lake Wales Ridge State Forest, Eric Menges, Archbold Biological Research Station, Gaye Sharpe, Polk County Environmental Lands Program, and George Tatge, Sarasota County Parks and Recreation.

Special appreciation goes to Tatiana Cornelissen. Without her support, knowledge and more importantly, her friendship, this research would not have been possible. Inspiration for this graduate work is due to Amy Arnett and Edward Beals, who both believed in and encouraged me, even when I did not believe in myself. Thank you.

Thank you to Patrick Fiore. His presence, assistance and love were essential to this entire process. Finally, I would like to thank my parents who forever support me; no matter which path I choose to follow. They are truly the best parents in the world.

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ABSTRACT

Exotic species are a great concern because of the possibility of negative effects once they become established. The exotic cactus moth, *Cactoblastis cactorum* has a reputation for being detrimental to *Opuntia* populations throughout Florida and the southeastern United States. Multiple projects are currently underway to attempt to contain and eradicate this species before it can migrate to the *Opuntia*-rich desert southwest and the agricultural *Opuntia* fields in the Mexican highlands. These projects have been undertaken without previous studies to determine what negative effects, if any, the moth is having on the common native *Opuntia* species. This is understandable; since it was earlier suggested that *C. cactorum* was doing great harm to rare and endangered species in the Florida Keys (Stiling et al. 2004). This study looks at the effects of the native moth borer, *Melitara prodenialis* and the exotic invader, *Cactoblastis cactorum* on two common *Opuntia* spp. within central Florida. Throughout the duration of this study, the coastal plants were subjected to damage solely by *C. cactorum* and the inland plants by *M. prodenialis.* The amount of moth damage was compared between three inland and three coastal sites, as well as between plants subjected to prescribed fire and those that were

not within these sites. Plant mortality was determined for both the sites and burn treatments. The number of eggsticks was also compared between inland and coastal sites and burned and unburned treatments. The results of this study show that although there is a significant difference in plant mortality between inland and coastal sites (higher mortality was shown at inland locations), there is no difference in moth damage at these sites. This suggests that the exotic moth is doing similar or less damage to the cactus than is the native moth. The number of eggsticks was also greater at coastal sites. This indicates that although the exotic moth is more prolific than the native, it is still unable to cause higher cactus mortality rates. None of the data was significant between burned and unburned treatments, indicating that prescribed fire does not have any effect, negative or positive on the *Opuntia*.

Introduction

The introduction and establishment of non-indigenous species in new locations is of major concern, for they often become troublesome once they have established. Examples of nonnatives in the United States that have subsequently become pests include the Japanese beetle (*Japonica popillia*), the invasive fire ant (*Solenopsis invicta*) and plants such as purple loosestrife (*Lythrum salicaria*), St. John's wort (*Hypericum perforatum*) and Brazilian pepper (*Schinus terebinthifolius)*. Many exotic species that establish are generalists, effective dispersers and good competitors. They often lack natural enemies in their new habitats that would serve to keep their numbers low (DeLoach 1991; Drea 1991; Hight and Drea 1991). Exotics can influence their new communities by interfering with the community dynamics either directly or indirectly.

Direct effects may include the introduction of disease (such as parasites or pathogens), and predation of native species. Indirect effects include displacement of native species or the interference in the dynamics of two or more native species (for example, an insect invader may feed on another insect that is important to the local plant community, thereby affecting the local plants). Due to the possibility of negative effects, it is important to study exotic species to determine their impacts on the communities into which they become established.

Some locations seem to harbor a larger number of exotics than others. Florida is one of the most vulnerable areas to invaders within the United States, ranking number two in established exotic species (Hawaii is number one) (Simberloff 1997). Many factors can contribute to this. Florida is essentially an island, bordered by water on three sides and limited by frost to the north, there is a large amount of disturbance of natural communities (due to rapid urban growth) and high movements in and out of the state (largely due to tourism) (Simberloff 1997). One of the more recent invaders into the United States is the South American cactus moth, *Cactoblastis cactorum*.

Insect Life History

Cactoblastis cactorum (Berg) is a pyralid moth, native to South American countries such as Uruguay, Paraguay, Argentina and possibly parts of Brazil (Mann 1969). The moth is reported to specialize on the platyopuntia subfamily of cacti (Dodd 1940; Mann 1969), which are known as the prickly pears. The eggs of the adult moth are laid in a stick (one on top of another), often at the tip of a cactus spine (Hoffmann and Zimmermann 1989) but they may also be adhered directly to a cladode or a fruit (pers. obs.). The female will lay more than one eggstick before her death in approximately 10 days. The number of eggs found in an eggstick can range from 5 – 100 with an average of about 50 eggs (Hoffmann and Zimmermann 1989). Once hatched, the tiny, gray larvae cooperatively chew through the tough outer cuticle of the cladode and enter the pad. The larvae are gregarious and feed inside the cladodes, consuming all but the vascular tissues (pers. obs.). As they feed, the larvae push frass out of holes in the cladode. This dripping or weeping may be used as a good indicator of active plant infestation in the field. During the day, it is common to see *C. cactorum* larvae congregated on the outside of the cactus plant (Dodd 1940), presumably to escape the hot internal temperatures that can be greater than 55 degrees Celsius when exposed to sunlight (Gibson and Nobel 1986).

When the larval development is complete, larvae often drop into the soil or litter at the base of the plant to pupate, although they may also use an empty cladode "shell" (Habeck and Bennett 1990). Once the adult moths emerge, they will begin to mate. The females will then oviposit prior to their death in approximately 10 days. In subtropical

Florida, *C. cactorum* shows its peak activity between March and October, but larvae are visible at other times throughout the year in much lower densities (pers. obs.). The generation time in Florida has not been determined, but Australian moths have two generations per year varying between 100 to 165 days, depending on the season (Habeck and Benett 1990; Mann 1969).

Melitara prodenialis (Walker) is a pyralid moth native to Florida and the eastern United States. This is another cactus borer specializing on the platyopuntia family of cactus. Mann (1969) describes differences between the species in Texas compared with the Florida race. In Florida, the moth has three generations per year. The adults first emerge in March or April, generation two occurs in June, and the last generation appears between August and October (Mann 1969).

Melitara prodenialis adult females also lay their eggs in a "stick" similar to *Cactoblastis cactorum*. The eggsticks of *M. prodenialis* are shorter than eggsticks of *C. cactorum.* They contain between 30-50 eggs, with an average of 30 (Mann 1969). *Melitara prodenialis* eggsticks are oviposited to most parts of the plant; directly on a cladode, at the end of a spine, on a fruit and even at a segment joint (pers.obs.).

The larvae of *M. prodenialis* range from a light gray to a bright blue color when mature. The early instar larvae can be distinguished from those of *C. cactorum* because of the difference in the color of the head capsule; *M. prodenialis* has a brown head capsule while *C. cactoblastis* has a black head capsule. *Melitara prodenialis* larvae also collectively feed on the internal tissues of the prickly pear, but they are rarely seen on the outside of the plants (pers. obs.). The larvae will pupate in the same manner, as does *C. cactorum*, in an empty cladode or at the base of the plant in the litter (Mann 1969).

Melitara prodenialis is known to feed on Florida cactus, including *Opuntia stricta, O. humifusa and O. pusilla* (Mann 1969), but prefers the low-growing species, unlike *Cactoblastis cactorum*, which will feed on the taller, woody species (Carlton and Kring 1994). Although it feeds on multiple species of *Opuntia*, *M. prodenialis* shows a preference for *O. humifusa* (Carlton and Kring 1994).

Background of Study Insects

Florida was the entry point into the United States for *Cactoblastis cactorum*, which was first noticed in the Florida Keys in 1989 (Habeck and Bennett 1990). The moth is renowned for its success as a biological control agent against exotic *Opuntia* in Australia; it is responsible for eradicating cacti from millions of acres of rangeland and providing control of cacti on many more (Dodd 1940). Biological control advocates have heralded the Australian prickly pear biological control campaign for many years as the best example of safe, effective biological control. However, this is not to say that this particular campaign can be predictive of the moth's behavior in other locations. When *C. cactorum* was subsequently used for biological control in South Africa, it was unable to produce the stunning results that it had in Australia (Pettey 1947). In the Caribbean, the moth has been used with moderate success against native cacti (Simmonds and Bennett 1966). There has been much speculation in the literature about this differential success between countries. Factors such as differences in moisture, temperature and seasonality have been suggested, but the true reason for the variations in the moth's success remains unidentified.

In Florida, there appears to be heavy damage to the native *Opuntia* species due to the activities of *C. cactorum*. It is likely that *C. cactorum* is having a detrimental effect on the more rare cacti in the Florida keys (Stiling *et al*. 2004), but there is less known about the impact the moth is having on the two most common and widespread species of *Opuntia* in Florida, *O. stricta* and *O. humifusa.* While visiting field sites used by Johnson and Stiling for earlier research on *Cactoblastis cactorum*, it has been observed that many of the areas no longer contain the large numbers of cactus they had during the time of the earlier studies (early to mid 1990's), possibly as a result of moth activity (pers. obs.). This suggests that the moth might be having a strong negative effect on the more common *Opuntia* as well as on the more rare species.

There has been little attempt to quantify the damage that *Melitara prodenialis* does to the Florida *Opuntia*. In one study done at Florida Atlantic University in Boca Raton, FL done to examine infestation of cacti by moth borers, it was shown that *Opuntia stricta* plants had a larger number of *Meltiara prodenialis* larvae than *Cactoblastis cactorum* larvae with co-infestation of plants occurring (Pierce 1995). This study also showed that *M. prodenialis* showed a preference for tertiary pads, while *C. cactoblastis* showed no preference of pad type (Pierce 1995). The lack of attention given to the effects of *M. prodenialis* may be because the moth is native to the area and likely to be co-evolved with its host species. Another reason could be that the moth does not appear to be having a strong negative affect on any rare or endangered cactus species.

It is important that both moth species be investigated if we wish to learn as much as possible about their behavior and their effects on cacti. Both moth species were shown to behave differently in trials done for the biological control program for cactus in Australia (Dodd 1940). These trials showed that *Cactoblastis cactorum* outperformed *Melitara prodenialis* and therefore became the control organism used in that highly successful program (Dodd 1940). So far, *Cactoblastis cactorum* has not had the same effects in Florida as it had in Australia. Currently there are numerous programs in effect to help delay or halt the spread of *C. cactoblastis* out of Florida and possibly control it throughout its range. Comparisons between the native and the exotic moths could allow researchers to more completely understand their similarities and their differences. This information could be used to help improve the programs that are aimed at control of the invasive species.

Study Plants

Opuntia stricta is a large plant species that grows erect and is found only along coastal areas, often among sea oats and other dune vegetation and along shell mounds. The cladodes can be quite large, up to 25cm in length (Wunderlin and Hansen 2003). The cladodes are often slightly ovate with rounded edges. The spines are short, yellow, often clustered and can be up to 4cm long (Figure 1). An older plant can grow up to 1.5m tall and can have a mostly woody "trunk".

Opuntia humifusa is much shorter than *O. stricta* and can be found along coastal dunes and shell mounds as well as inland sandhill and scrub areas. The cladodes of *O. humifusa* are more round when compared with *O. stricta* cladodes and measure between 4 and 16cm in length (Wunderlin and Hansen 2003). The spines are longer, usually singular and can be gray, white or darkly colored (Figure 1). Spines may occasionally be absent. *O. humifusa* tends to grow more recumbent than *O. stricta*, but seems to have a slightly more erect presentation in inland areas than along the coast, growing up to 30cm in height (pers. obs.). This species can also have woody pads when older. The formation of lignified woody tissue in cacti naturally occurs with age, but might also be induced by injury to the tissue, including that caused by insects (Gibson and Nobel 1986). Both species may have plants ranging from only a few pads up to greater than two hundred.

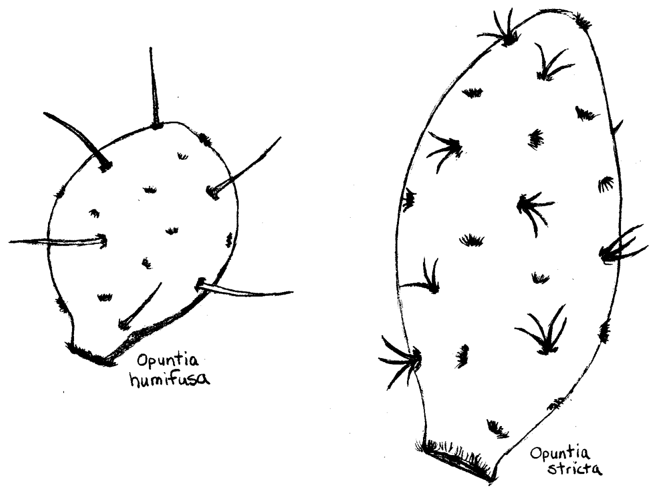

Figure 1. Illustration to demonstrate key differences between cladodes: shapes and spines (figure not to scale).

Study Sites

Coastal Sites:

Honeymoon Island State Park, Dunedin, Florida: Honeymoon Island is a barrier island located on the Gulf coast of Florida just west of the city of Dunedin, connected to the mainland by a causeway (Figure 2). The habitats that include *Opuntia* species are slash pine, scrub and sand dune communities. Both *O. humifusa* and *O. stricta* are found at this site, *O. humifusa* is more common in the pine and scrub communities, whereas *O. stricta* is found under the pines, but dominates in the "sugar sand" scrub. Coastal site soils in this study are likely composed of Entisols and Histosols, but dunes are more often associated with Entisols, which is a well-drained sandy soil (Myers and Ewel 1990). Barrier islands contain the most recent deposits of sand compared with other Florida communities. The soil found in these habitats is comprised primarily of sand mixed with shell (Myers and Ewel 1990). The park maintains the area with prescribed fire. Common vegetation among the prickly pear includes sea oat (*Uniola paniculata*), sea grape (*Coccoloba uvifera*), cabbage palm (*Sabal palmetto*) and weeds such as beggar's tick (*Bidens alba*) and beggar weed (*Desmodium tortuosum*) in the dune habitat. In the pineland, common plants include poison ivy (*Toxicodendron radicans*), cabbage palm (*Sabal palmetto*), slash pine (*Pinus elliottii*) and honeylocust (*Gleditsia triacanthos*).

Fort DeSoto Park, Mullet Key, Florida: Fort DeSoto is a Pinellas County Park located between the Gulf of Mexico and Tampa Bay. The park consists of Mullet Key just south of St. Petersburg. Both *Opuntia humifusa* and *O. stricta* can be found among the many sand dune areas within the park, although *O. humifusa* seems to be more common here. The soil consists of sand with some shell material. The location of the *Opuntia* varies in their distance from the shore and some plants may be impacted by salt spray, although not likely by wave action. The park maintains the vegetation with prescribed fire, but many areas are currently overdue for fire (Robert Browning, pers. comm.). Plants that can be found among the cacti include numerous sandspurs (*Cenchrus incertus*), railroad vine (*Ipomoea pes-caprae*), sea oat (*Uniola paniculata*) and sea grape (*Coccoloba uvifera*).

North Lido Beach, Sarasota, Florida: North Lido Beach is located on the northern end of Lido Key, a barrier island located on the Gulf coast of Florida. There is a large area consisting of sand dune habitat, containing both *Opuntia humifusa* and *O. stricta*. A wall of Australian pine (*Casuarina equisetifolia*) separates the beach from developed areas on the eastern border of this dune habitat. Other vegetation includes sea oat (*Uniola paniculata*), sea grape (*Coccoloba uvifera*), railroad vine (*Ipomoea pes-caprae*) and nonnative beachberry (*Scaevola sericea*).

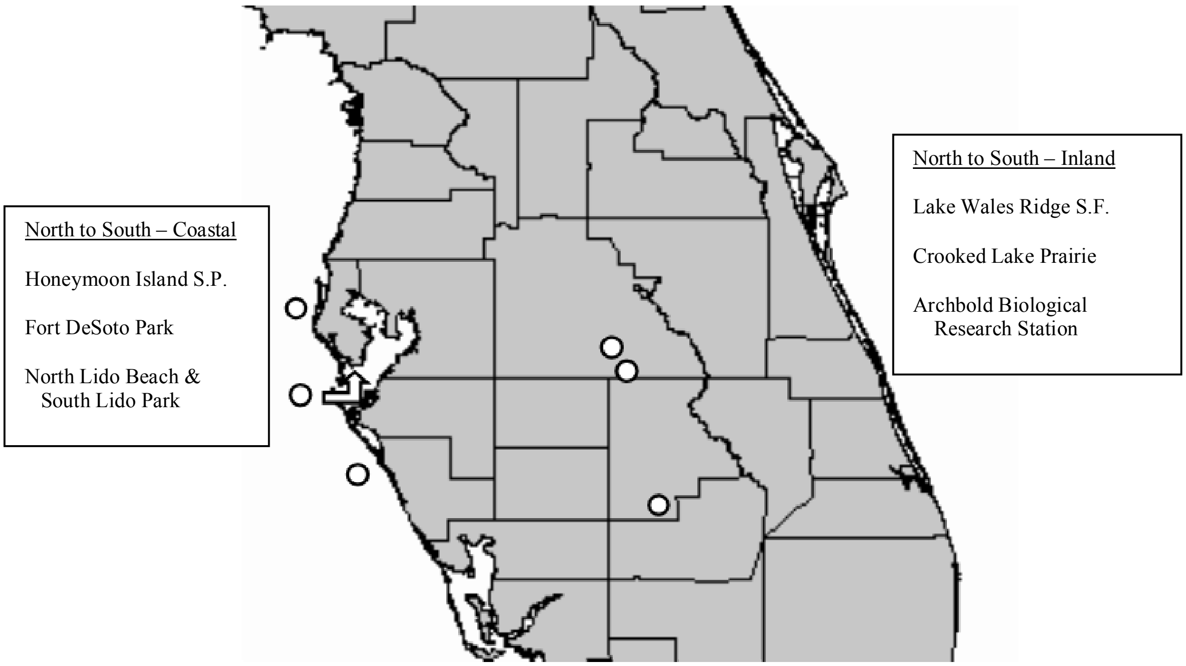

Figure 2. Map of central Florida to demonstrate the approximate locations of study sites.

South Lido Park, Sarasota, Florida: South Lido Park is along the southern end of Lido Key on the inland (east) side of the key. Development to the west and a mangrove-dominated inlet to the east border the park. There is no beach or dune area in this park and plants are located in a sandy, sunny area not in close proximity to the water. The plants here are not likely impacted by salt spray, wave action or even extreme windy conditions. South Lido Park contains only one *Opuntia stricta* plant and numerous *O. humifusa*. Surrounding vegetation here includes cabbage palm (*Sabal palmetto*), beggar's tick (*Bidens alba*) and various grasses.

Inland Sites:

Inland sites are located along the Lake Wales Ridge. Lake Wales Ridge is an area of relatively high elevation (up to 50 m.) that is oriented north-south in the center of the

Florida peninsula. The ridge transects five Florida counties: Highlands county, Lake county, Orange county, Osceola county and Polk county, with the majority located in Highlands, Lake and Polk counties. The ridge is made up of ancient dunes that once represented shoreline during the pre-Pleistocene era and was occasionally isolated due to fluctuations in sea level. Due to this isolation, many species evolved to be endemic to the ridge communities and many are now listed as threatened or endangered. The soils of the ridge are mostly Entisols, which are highly drained thick sand (Myers and Ewel 1990).

Archbold Biological Station, Lake Placid, Florida: Archbold Biological Station is located along the southern end of the Lake Wales Ridge. *Opuntia humifusa* is the only *Opuntia* species identified on the property. The plants in this study are located in scrub, and flatwoods habitats, both of which contain soil that is characteristically low in nutrients (Myers and Ewel 1990). Some of the more common vegetation found among the cacti include sand live oak (*Quercus geminata*), Saw palmetto (*Serenoa repens*), gopher apple (*Licania michauxii*), natal grass (*Rhynchelytrum repens*) and some scrub hickory (*Carya floridana*).

Hickory Lake Scrub, Frostproof, Florida: Hickory Lake Scrub is part of the Polk County Environmental Lands Program and is located just south of downtown Frostproof along highway 17. Hickory Lake Scrub is a small tract of land made up of 57 acres and is home to many threatened and endangered plants. The cacti on this property are *Opuntia humifusa* and they are located in scrub habitat. Polk County maintains the vegetation using prescribed fire, but they have only had ownership of the land since 1997. Other vegetation found among the cacti includes sand live oak (*Quercus geminata*), gopher apple (*Licania michauxii*), some sand pine (*Pinus clausa*) and a large amount of ground lichen (*Cladinia* sp.).

Lake Wales Ridge State Forest, Frostproof, Florida: Lake Wales Ridge State Forest is separated into two tracts of land. The area containing cacti is located along route 630 in the Walk-in-the-Water tract (Lake Weohyakapka) and plants are found in scrub habitats on sandy soils. The Department of Forestry maintains the property with prescribed fire, although part of the walk-in-the-water tract was scheduled to be burned in 2003, but was actually burned in spring 2005. The species present is *Opuntia humifusa*. Vegetation that occurs among the cacti is abundant and includes numerous sand live oak (*Quercus geminata*), slash pine (*Pinus elliottii*), and St. John's wort (*Hypericum* sp.).

Crooked Lake Prairie, Babson Park, Florida: Crooked Lake Prairie is part of the Polk County Environmental Lands Program that was acquired by the county in 1997. Since its acquisition, it has been maintained with prescribed fires. The prairie is a 525-acre preserve along the eastern shore of Crooked Lake on Cody Villa Rd. off Florida's highway 17. The habitat of interest is scrub habitat that has little vegetation and lots of "sugar sand". This area has an abundance of *Opuntia humifusa* on a large majority of the property due to previous management practices. The land was once used for cattle grazing. The land would be roller-chopped in preparation of planting grains suitable for cattle and this process (repeated over multiple seasons) led to an abnormally high abundance of cacti (Gayle Sharpe, Polk County Environmental Lands Program, pers.comm.). The process caused the "chopping" of cactus plants and subsequent propagation of the chopped pieces.

Chapter One

What is the Response of *Opuntia humifusa* and *Opuntia stricta* in Florida After Attack by *Cactoblastis cactorum* and *Melitara prodenialis*?

Introduction

The arrival of *Cactoblastis cactorum* into North America has caught the attention of many individuals. There is concern of how the moth will affect the ornamental cactus industry in the desert southwest (Irish 2001), what levels of damage the moth will inflict upon the commercial agriculture crops throughout Mexico (Soberon *et al.* 2001) and what impact it will have on the natural communities that contain prickly pear cactus (Stiling 2002).

The response of plants to herbivory has been a highly debated topic in much of the literature. There are studies that have demonstrated no effect, negative effects and positive effects on plants due to herbivory (or simulated herbivory) and that plant response is highly dependent upon other conditions (Paige and Whitham 1987, Maschinski and Whitham 1989). Some of the conditions that can influence the response of a plant to herbivory include the seasonal timing of herbivory, the extent of the damage, and the amount of nutrients available to the plant (Paige and Whitham 1987). Genetic variation may also contribute to some plants being more tolerant to herbivore damage (Strauss and Agrawal 1999). Numerous studies have been conducted that demonstrate plants are indeed capable of compensating for herbivore damage (Hendrix 1979, Paige and Whitham 1987, Obeso 1998, Thomson *et al.* 2003). Since *Opuntia* spp. often reproduce vegetatively as well as sexually, compensation may occur in response to damage from both herbivores and prescribed fire (which is a common land management practice in many southern pine communities).

During preliminary observation of the two species of *Opuntia* in this study, it seemed that *Cactoblastis cactorum* attacks *O. stricta* more frequently than it does *O. humifusa* in the field (pers. obs.), although Johnson and Stiling (1996) were unable to show any preference between the two in laboratory host-choice studies. If there is truly a preference, it may be a preference of host species, the suitability of habitat (*O. stricta* has not been documented inland) or some combination of the two. It is most likely due to preference of host and not the moth's ability to survive in inland habitats, or its preference for coastal habitats, for *C. cactorum* has been documented at two inland locations (Crooked Lake Prairie , Polk County, Florida and Archbold Biological Research Station, Highlands County, Florida). The spatial distribution of the plants could play a role in this as well, but is less likely because *C. cactorum* is capable of long-distance flight, up to15 miles (Dodd 1940).

To date, there has been little attempt to quantify the damage to and the mortality of *Opuntia humifusa* and *O. stricta* plants that are attacked by *C. cactorum.* Johnson and Stiling (1998) were able to demonstrate an increase in the number of dead and damaged *O. strica* pads due to *C. cactorum* over a two-year period, 1991 through 1993, but their sample sizes were very small. The Florida populations of *O. humifusa* and *O. stricta* have now been exposed to *C. cactorum* for more than ten years, therefore it is important to better quantify the effects to have a stronger understanding of this association.

A commonly found native moth borer is *Melitara prodenialis* whose larvae also feed on the internal tissues of prickly pear cladodes. The damage appears similar to that caused by *Cactoblastis cactorum*. *Melitara prodenialis* larvae are easily distinguished from *Cactoblastis cactorum* larvae by opening infested pads. *Cactoblastis cactorum* larvae are bright orange with black spots and a black head capsule. *Melitara prodenialis* larvae are a dark indigo blue and have a brown head capsule. The early instars of both species can be pale in color with small black spots, but the color of the head capsules allow for accurate identification at these stages. The eggsticks of *M. prodenialis* are also easily distinguished from those of *C. cactorum* in the field, for they are usually found in shorter chains and the eggs are more squat or flattened than those of *C. cactorum*.

Methods

Damage and Mortality Levels:

Two hundred *Opuntia* plants were marked at each study site, except at Fort DeSoto, which only had 100 plants marked due to area restrictions. We walked through each site, dropping flags when a plant was encountered, regardless of plant species, after which the plant was assigned a number and drawn on with a permanent marker. This occurred at each site until 200 plants were marked (100 at Fort DeSoto). All plants were monitored for two years. Site visits occurred monthly from July 2003 through July 2005. At these visits the total number of woody pads, the number of medial pads and the number of new pads (primary, secondary and tertiary, respectively) were counted on each plant. The cause of mortality was noted if it was due to something other than *Cactoblastis cactorum* activity (such as trampling, etc.). The number of pads with true bug damage, the number of pads with active/recent moth damage, and the presence of old moth damage were also counted at each visit. Old moth damage was more difficult to measure, since damage from old prescribed burning could sometimes mimic old moth damage.

In order to address the possibility of turnover, 15 *Opuntia* sp. plants with approximately 10 – 20 pads were chosen at Honeymoon Island State Park. Each pad was marked in order to monitor plants for pad turnover in the field. Ideally, this would be done to assess turnover in the absence of moth activity. When encountered at monthly censuses from 2004 through 2005, eggsticks were removed from these marked plants. However, despite these efforts all plants were still attacked by *Cactoblastis cactorum*. Larvae presumably had crawled from infested neighboring plants. Although all plants were attacked and turnover could not accurately be determined, no mortality was observed over the year they were followed. This experiment could be repeated with the plants protected (such as in cages) to give an accurate representation of turnover. However, past experiments have shown that turnover does not occur frequently in this system (Peter Stiling, pers. comm.).

On all other plants the presence of stem-boring larvae of both native and exotic species was noted and species identified. When eggsticks were present, the number of eggs was counted using a hand lens and notation was made if an eggstick was hatched or unhatched. When larvae were present at census, the number of pads that showed active damage was obtained. Determination of number of pads with old larval damage was not as simple, especially in sites that have an active burn history. Burned pads often can appear gray, white and papery, appearing similar to those that have been eaten by caterpillars; therefore, old burn damage data was not collected. If the plant had old larval damage this was noted without the number of pads being determined.

The presence of other insect herbivores was noted and individuals counted if they were observed using (or are known to use) the cacti as a food source. There are numerous other native insects that are known to feed on *Opuntia* cactus (Mann 1969), and both heteropterans and coleopterans have been noted at the field sites (pers. obs.). Oviposition by insects was noted, species identified and number of eggs obtained, if possible. One insect that was not possible to count in the field but whose presence was noted is the cochineal insect, *Dactylopius* sp. that is found infesting many *Opuntia* throughout Florida. The mature homopterans exude a white, waxy covering over their sessile bodies and whole pads can be almost entirely covered in this residue, making identification of individuals difficult (pers. obs.).

The number of primary (woody), tertiary (new growth) and secondary (all other) cladodes were counted on each plant. A plant that has a large amount of woody tissue may be less likely to sustain larval feeding compared with a plant that is composed of mostly succulent parts. A large amount of woody tissue should make that particular plant less vulnerable to insect damage as the tissue will be much more difficult for the larvae or bug proboscis to penetrate.

An examination of cuticle toughness was conducted for *Opuntia humifusa* pads in order to identify differences by pad type. If larval preference is demonstrated, cuticle toughness may provide a potential explanation for this preference since newly hatched larvae must penetrate the cuticle in order to feed on the tissues. The cuticle toughness is likely one reason for the gregarious behavior of larvae; cooperation may be required to first gain entry into the food source. A minimum of 15 primary, secondary and tertiary pads was collected from unmarked *Opuntia humifusa* plants at three inland and one coastal site during the active season and measures of cuticle toughness were made in the laboratory using a penetrometer. Comparison of pad toughness was conducted by pad type (primary, secondary and tertiary).

Nitrogen is one important nutrient for plant growth and its availability in plant tissue can be a limiting factor for insects (Strauss and Zangerl 2002). This must be considered an important variable in the cactus moth – *Opuntia* relationship. Measurements of soil nitrogen were obtained for each location during the wet portion of the active moth season. According to Gibson and Noble (1986), the *Opuntia* roots are primarily horizontal and between 5 – 15 cm underneath the soil surface, therefore, a 10 cm soil sample should be representative of what the roots are exposed to. Soil cores were collected approximately 10cm deep within 6 inches from the base of 30 randomly selected plants at each location (except Fort DeSoto, which had only 15). The samples were brought back into the lab and the nitrogen content was analyzed using a CE Instruments NC 2100 CN Analyzer (CE Elantech, Lakewood, NJ, USA). Comparison of soil nitrogen was made by site.

All data were tested for normality with a Kolmogorov-Smirnov test, and all variables met the assumptions of normality except for the number of plants with larval damage, the number of plants with no mortality, and the number of woody (primary) pads. All normal variables were compared between inland and coastal sites (essentially comparing *Cactoblastis cactorum* and *Melitara prodenialis*) using a Student's t-test. The pad toughness data were compared with a single-factor ANOVA. The number of plants with no mortality and the proportion of primary (woody) pads were compared with Mann-Whitney tests due to their lack of normality.

Further analyses were performed to compare *Opuntia humifusa* only between coastal and inland sites. Data were again tested for normality using a Kolmogorov-Smirnov test, all meeting assumptions of normality. Variables were then compared using Student's t-tests.

Comparison was also made between *Opuntia humifusa* and *Opuntia stricta* at coastal sites only. Normality was tested with a Kolmogorov-Smirnov test and all data met these assumptions except for the amount of plant mortality. This variable responded to square root transformation. All variables were compared using Student's t-tests.

All statistical analysis was performed using Systat 11.0 (Systat Software, Inc. 2004) and statistical figures created with Sigma Plot 8.02 (SPSS, Inc. 2002).

Results

Of the comparisons performed, only two showed significant differences; the first in the overall mortality of plants, which was higher at the inland sites, than coastal sites. The second was the number of moth eggsticks counted which was higher at coastal sites (Table 1, Figure 7). The samples sizes for the two locations varied slightly, inland N = 600 and coastal N = 500.

Table 1. Summary of Student's t- test for all data between coastal and inland sites. * Nonparametric Mann-Whitney U-test. Significant results are highlighted.

VARIABLE	**t**	**p**
Average number of pads	2.107	0.103
Plant mortality	-4.142	0.014
Moth damaged plant mortality	0.336	0.754
Damaged pads	2.231	0.090
Damaged plants	1.932	0.126
True bug damaged plants	-0.371	0.729
Old damaged plants	2.417	0.073
Average number of tertiary pads	0.098	0.927
Average number of eggsticks	6.539	0.000
Pad toughness	F = 13.144	0.002
Soil nitrogen	1.673	0.170
Average number of woody pads*	U = 4.00	p = 0.827
Damaged plants, no mortality*	U = 4.00	p = 0.822

The average number of total pads did not differ significantly when compared by location, coastal vs. inland ($t = 2.107$, $p = 0.103$), although coastal sites had a few plants with very large numbers of pads (300+). However, when averaged, the mean coastal number of pads is 39.83 and the mean number of inland pads is 18.67 (Figure 3).

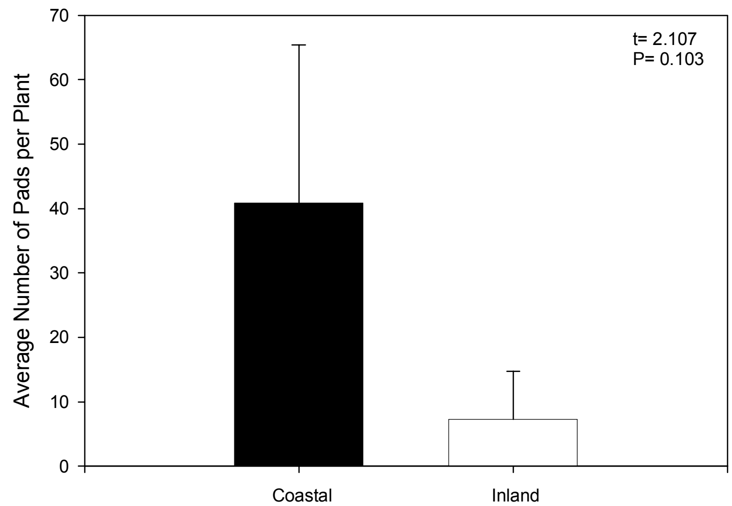

Figure 3. The number of pads averaged by location (coastal vs. inland).

When comparing the average proportion of plants that died throughout the duration of the study, there was a significant difference between inland and coastal sites ($t = -4.142$, $p = 0.014$). Inland sites showed a higher level of mortality than did coastal sites, indicating that there was greater mortality associated with plants attacked by *Melitara prodenialis* than those attacked by *Cactoblastis cactorum* (Figure 4). Mortality of plants that had shown previous attack by the moths was not different between the two locations ($t = 0.336$, $p = 0.754$) with an average percentage of inland plants mortality at 10% and coastal plant mortality at 14%.

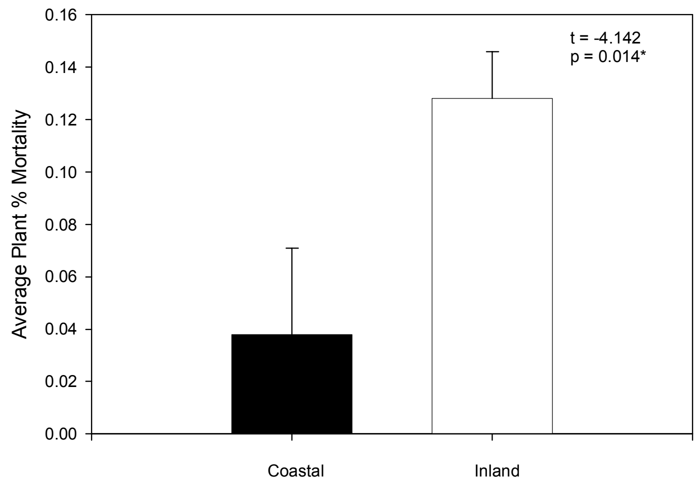

Figure 4. Proportion of plant mortality by coast vs. inland. * Indicates a significant result.

The average proportion of damaged pads by site was not statistically different (t = 2.231, p = 0.090), but there was a slightly higher average for coastal plants vs. inland (5% and 1%, respectively). This result is likely an accurate representation of moth activity since the sample sizes were 7,852 on the coast and 8,857 inland (Figure 5).

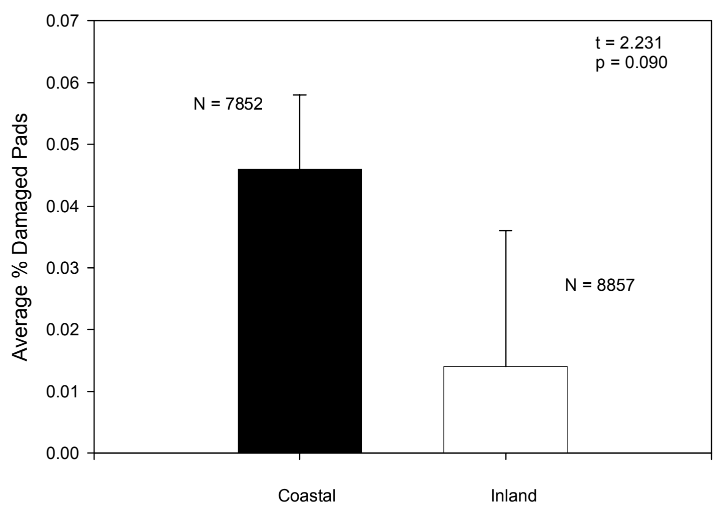

Figure 5. The proportion of damaged pads by location.

The average number of damaged plants by location was also not significant (t = 1.932, p = 0.126); however, there was a trend toward coastal sites showing a greater number of damaged plants than inland sites (41% and 14%) (Figure 6).

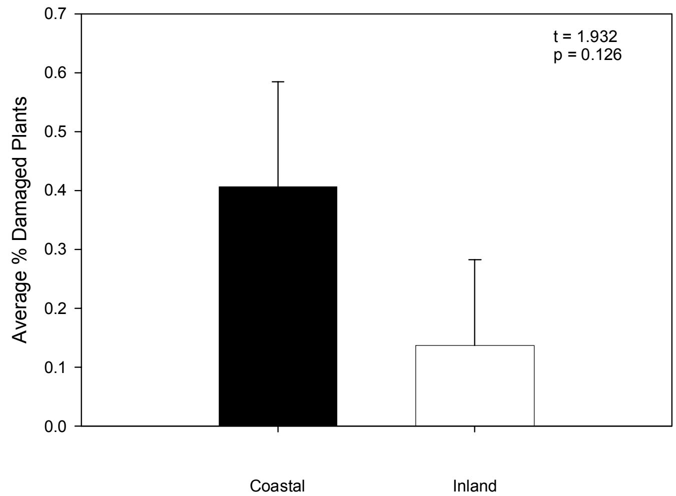

Figure 6. Proportion of damaged plants by location.

The average proportion of pads with true bug damage was also not significantly different between locations ($t = -0.371$, $p = 0.729$). This is interesting, given that true bugs and eggs were noted regularly at all inland sites and less frequently at coastal sites.

The average proportion of plants with old moth damage was not significantly different ($t = 2.417$, $p = 0.073$), but again the trend was toward more old damage at coastal sites vs. inland sites (average of 63% and 18%, respectively).

The proportion of tertiary pads was not significantly different among locations ($t = 0.098$, $p = 0.927$). This would suggest that if compensation is occurring because of moth damage, it is consistent regardless of moth species and habitat. The average proportion of primary pads was also not different by location ($U = 4.00$, $p = 0.827$).

The average number of plants with moth damage and no mortality could not be analyzed with a t-test, because the data did not meet the assumptions of normality. Therefore, the nonparametric Mann-Whitney U-test was used. This showed that there was no significant difference in damaged plants between the two sites that survived throughout this study (U = 4.00, p = 0.822).

There was a significant difference among the number of eggsticks noted at the two locations, with a higher average at coastal sites than inland sites ($t = 6.539$, $p < 0.001$). This suggests that *Cactoblastis cactorum* either lays a greater number of eggs, or simply has a much larger population than does *Melitara prodenialis* (Figure 7).

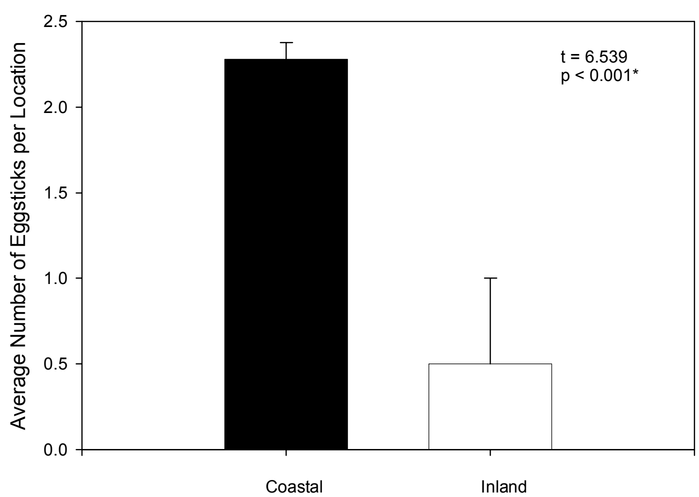

Figure 7. Average number of eggsticks by location. * Indicates a significant result.

Pad toughness was significantly different between pad types ($F = 13.144$, $p = 0.002$). The toughness averages fit well with our prediction; the toughest being primary pads, then secondary and lastly tertiary (new growth) (Figure 8). The least tough was 0.44 lb/mm^2 and the toughest 3.5 lb/mm^2.

Soil nitrogen also did not differ between the coast and inland, and total content was very low overall, less than 1% nitrogen ($t = 1.673$, $p = 0.170$).

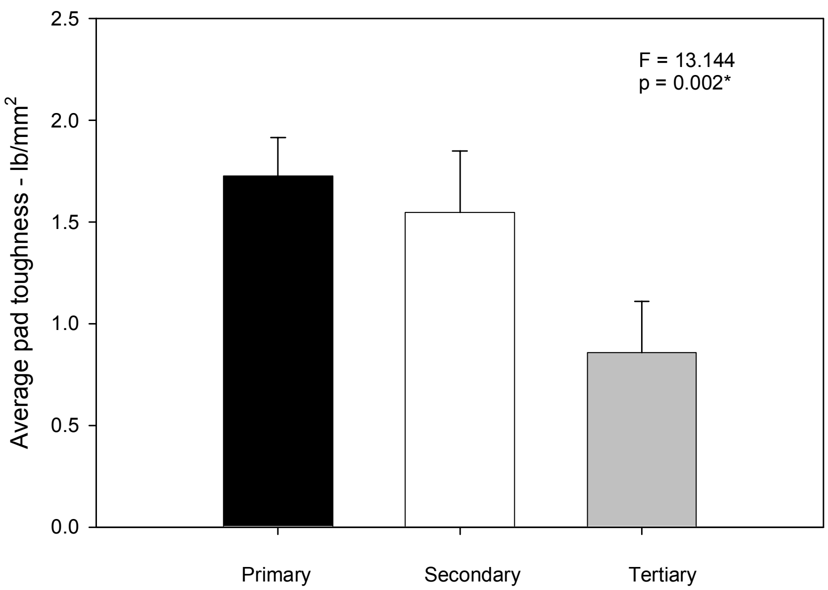

Figure 8. Chart demonstrating the average pad toughness of *Opuntia humifusa* pads by pad type. *Indicates a significant result.

Analysis was also performed to compare *Opuntia humifusa* only between coastal and inland sites. Sample sizes for *Opuntia humifusa* were as follows, inland sites N 600 and coastal sites N 331. Significant results include the proportion of plant mortality, the number of tertiary pads, the number of moth eggsticks and the level of soil nitrogen (Table 2).

The average total number of pads was not statistically different between the two locations ($t = 2.496$, $p = 0.067$). However, plants located on the coast had more pads overall with a mean of 37.24 with the inland plants averaging 17.89 pads (Figure 9).

Table 2. Summary of Student's t-test for *Opuntia humifusa* between coastal and inland sites. Significant results are highlighted.

Variable	**t**	**p**
Average number of pads	2.496	0.067
Plant mortality	-3.127	0.035
Moth damaged plant mortality	0.307	0.774
Damaged pads	0.691	0.528
Damaged plants	1.410	0.231
True bug damaged pads	-2.710	0.054
Old damage plants	1.993	0.117
Average number of tertiary pads	2.981	0.041
Average number of eggsticks	3.237	0.032
Average plant nitrogen	-2.652	0.057
Average soil nitrogen	3.488	0.025
Damaged plant, no mortality	1.375	0.241

The proportion of plant mortality was greater inland than along the coast (12.8 % and 3.9% respectively) (Figure 10). This difference was statistically significant ($t = -3.127$, $p = 0.035$). Mortality may be higher in sites associated with *Melitara prodenialis* than sites that contain *Cactoblastis cactorum.* However, mortality of plants documented with current or recent moth damage was not different between the two sites ($t = 0.307$, $p = 0.774$). This indicates that mortality of plants at inland sites may not be related to moth activity.

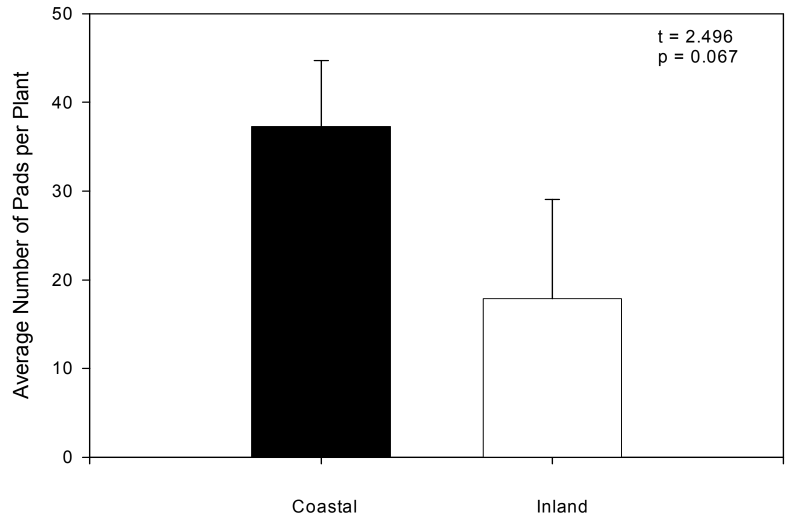

Figure 9. Average number of total *Opuntia humifusa* pads compared by location.

Both the number of damaged pads and the proportion of damaged plants were not different between the two locations. Both species of moth may be feeding on *Opuntia humifusa* similarly, regardless of plant location and habitat.

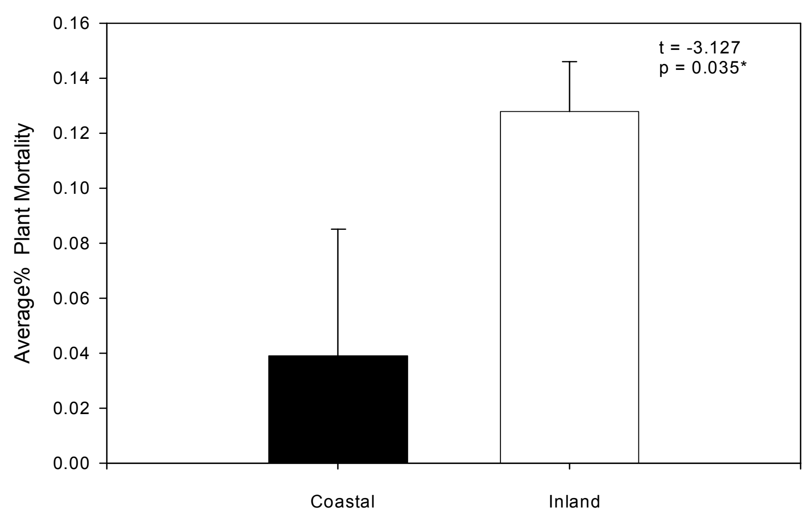

Figure 10. *Opuntia humifusa* plant mortality between coastal and inland sites. *Indicates a significant result.

The amount of true bug damage was compared between the coastal and inland sites. This comparison was not significant ($t = -2.170$, $p = 0.054$), however the proportion of plants that were damaged was greater inland (93%) than along the coast (43%) (Figure 11).

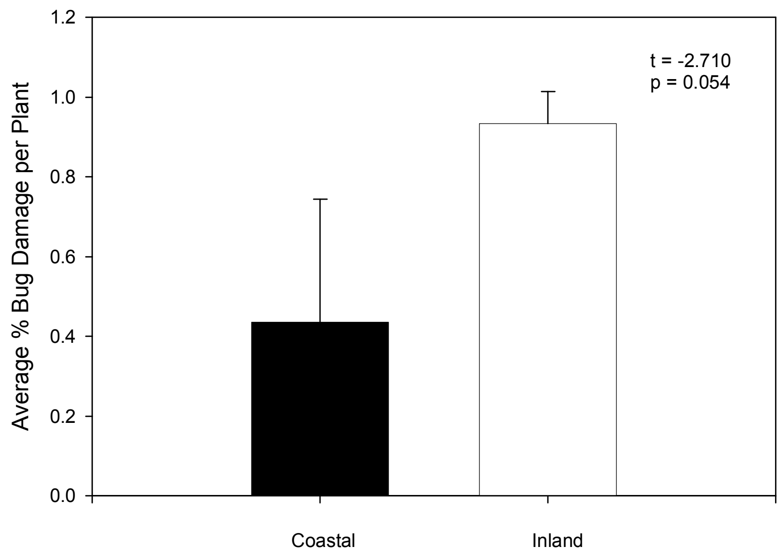

Figure11. The proportion of true bug damage on *Opuntia humifusa* when compared by site location.

The proportion of plants with old larval damage was also not significant between the two locations (t = 1.993, p = 0.117). This is consistent with the results for the number of damaged pads and the proportion of damaged plants.

There was a significant difference in the number of tertiary pads (new growth) (t = 2.981, p = 0.041). Coastal plants put out more new growth when compared with growth of the inland plants (Figure 12).

When nitrogen was compared, there was no significance in the amount of plant nitrogen between the two locations (t = -2.652, p = 0.057), although nitrogen content was higher at inland sites when compared with coastal sites (0.81% and 0.53%, respectively). In contrast, the amount of soil nitrogen was different between the two locations. The soil nitrogen available was greater at coastal sites (0.18%) than at inland sites (0.09%) (t = 3.488, p = 0.025).

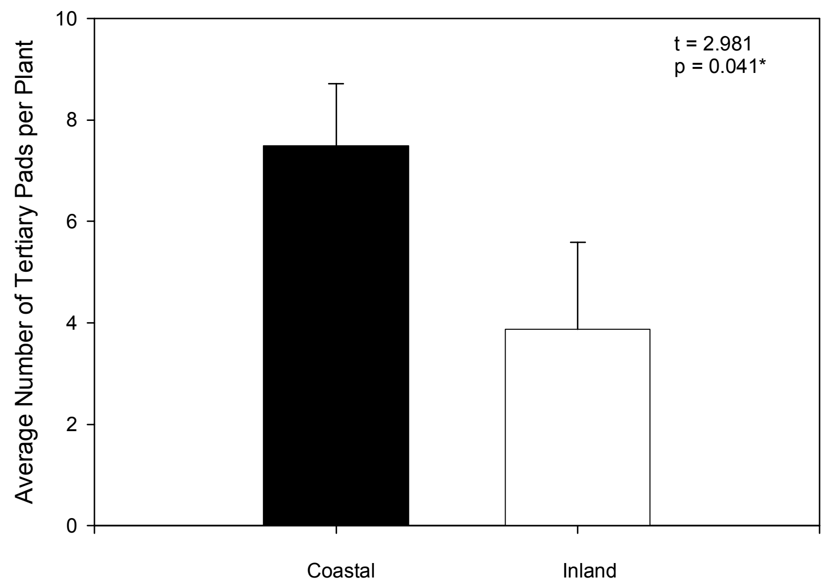

Figure 12. The average number of *Opuntia humifusa* tertiary pads when compared by location. *Indicates a significant result.

There was also a significant difference between the coastal sites and inland sites when the average numbers of moth eggsticks were compared ($t = 3.237$, $p = 0.032$). This comparison shows that there is a greater number of eggsticks deposited on plants along the coast (2.24) than those inland (0.5) (Figure 13).

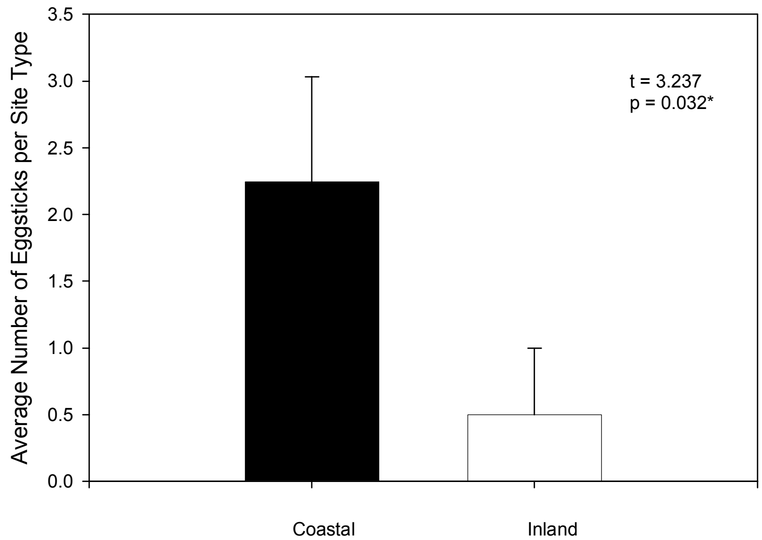

Figure 13. Comparison of the average number of moth eggsticks laid on *Opuntia humifusa* at coastal sites and inland sites. *Indicates a significant result.

Comparisons within the coastal sites were calculated comparing *Opuntia stricta* and *Opuntia humifusa* at these sites only. Sample size of *Opuntia stricta* was N = 169 and *Opuntia humifusa* was N = 331. There were some significant differences between variables at the coast. These include the proportion of damaged plants and the proportion of damaged plants that did not die during this study (Table 3).

The average number of pads was not different between the two species of plants (t 0.248, p = 0.817) (Figure 14). This result is likely due to the large standard deviation of *Opuntia stricta* at coastal sites.

Mortality of plants that had active larval feeding was not significantly different between the two species of cactus (t = -0.405, p = 0.706) at coastal sites. In this group overall, mortality was low (1.8% for *Opuntia stricta* and 2.9% for *Opuntia humifusa*.

The number of pads damaged by moth larvae was not different between the two species (t = 1.577, p = 0.190). However, the proportion of damaged plants was different between the two species (t = 7.981, p = 0.001). *Opuntia stricta* had 96% of the plants attacked during the study, while *Opuntia humifusa* had only 32% of plants attacked (Figure 15).

Table 3. Summary of Student's t-tests comparing *Opuntia humifusa* and *Opuntia stricta* at coastal sites only. Significant results are highlighted.

Variable	**t**	**P**
Average number of pads	0.248	0.817
Plant mortality	-0.818	0.459
Moth damaged plant mortality	-0.405	0.706
Damaged pads	1.577	0.190
Damaged plants	7.981	0.001
True bug damage	-1.896	0.131
Old damage	2.296	0.083
Average number of tertiary pads	0.468	0.664
Average number of eggsticks	-0.775	0.482
Average plant nitrogen	-0.573	0.598
Average soil nitrogen	0.027	0.980
Damaged plants, no mortality	4.006	0.016

The proportion of plants with damage by true bug feeding was not significant between the two plant species (t = -1.896, p = 0.131); however, the mean for *Opuntia stricta* was 8% and the *Opuntia humifusa* was 44%.

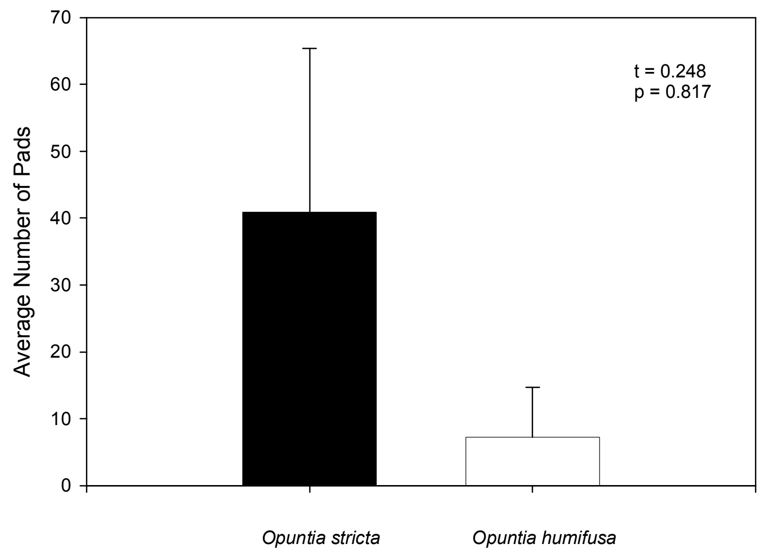

Figure 14. The difference in the average number of pads between the two cactus species at the coast.

The proportion of plants that showed evidence of old moth damage was also not significant (t = 2.296, p = 0.083), although *Opuntia stricta* showed a trend of sustaining more moth damage than did *Opuntia humifusa* (78% and 48%, respectively).

No difference was shown in regards to the number of tertiary pads counted between the two plant species (t = 0.468, p = 0.664). No significance was found when nitrogen levels were compared in plant tissues (t = -0.573, p = 0.598) nor in soil samples (t = 0.027, p = 0.980).

The proportion of plants that had some active moth damage during this study but did not die was different between the two cactus species (t = 4.006, p = 0.016) with damage being greater to *Opuntia stricta* than to *Opuntia humifusa* (Figure 16).

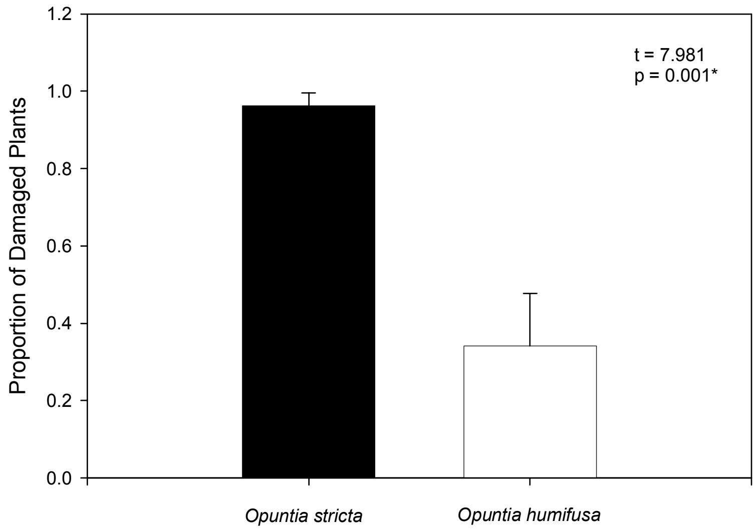

Figure 15. The proportion of damaged plants when compared by cactus species at the coast. *Indicates a significant result.

The average number of eggsticks that were counted on plants were not different between the two species (t = -0.775, p = 0.482), although they were slightly higher on *Opuntia humifusa* (mean = 2.24) than on *Opuntia stricta* (mean = 1.81).

Because the data for plant mortality did not conform to the assumptions of normality, a square root transformation was performed and a t-test performed on these data. This test showed no significant difference in mortality between the two cactus species (t = -0.818, p = 0.459).

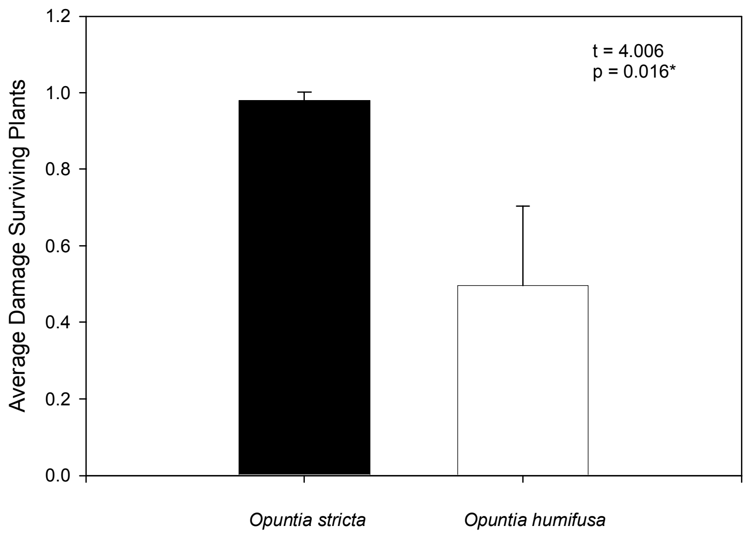

Figure 16. Comparison of the proportion of damaged plants surviving the duration of the study by cactus species.

*Indicates a significant result.

Discussion

It does seem that *Cactoblastis cactorum* is having a negative impact on the populations of the common prickly pear species in Florida with high levels of damage and even mortality of large plants (Stiling, pers. comm. and pers. obs). This may be due, in part, to repeated damage from *C. cactorum* feeding combined with prescribed burns and damage from other native herbivores. The addition of the new enemy into the community may push the plants beyond the point at which they are able to compensate for the losses.

Damage from *Cactoblastis cactorum* appears clumped in the field, with some plants showing heavy damage while neighboring plants show little or no damage (pers. obs.). This can be due to differences in palatability of different genotypes; however, due to the high amount of vegetative reproduction, neighboring plants have a large probability of being clones. Plants that have previous damage may be more likely to sustain future attack. It has been noted that a plant could contain many more eggs than will be capable of surviving on the amount of tissue available, yet its neighboring plants are free from any eggs (Monro 1967 and pers. obs.). This could be because of visual or chemical cues from previously attacked plants that adult females use to locate hosts. It has been suggested that this "overloading" is a way to conserve resources for future generations (Monro 1967).

Cactoblastis cactorum shows a definite preference for coastal plants vs. inland plants. *Cactoblastis cactorum* was noted at two inland study locations (Archbold Biological Research Station and Crooked Lake Prairie) and one location not included in the study (Hickory Lake Scrub, Frostproof, FL). *Cactoblastis cactorum* did not attack any plants marked at these inland locations throughout the duration of this study. At the coastal sites, *Cactoblastis cactorum* was the only moth-borer identified. It is not clear whether this preference is for habitat or for plant species, although Johnson and Stiling (1996) were unable to show a preference between *Opuntia stricta* and *Opuntia humifusa* in laboratory studies. There may be many factors that contribute to this apparent preference. One could be the possibility that the exotic moth favors coastal locations due to slightly lower mid-day temperatures as a result of ocean breezes. Another contributor might be that it might be easier for *C. cactorum* adults to identify new stands of plants as coastal plants seem to occur in more open areas (dune habitats primarily), while inland plants can be in forested land. These factors could be tested in the future using laboratory studies to corroborate field data.

Plant mortality was predicted to be higher at the coastal sites (sites that include the exotic moth). To our surprise, inland sites showed a higher proportion of plant mortality attributed to the native moth, *Melitara prodenialis* (coastal = 4% and inland = 13%). The percentage of damaged plants along the coast was 44% and inland was 13%. When the proportion of plant mortality was separated by whether or not the plants had previous moth damage there was no significant differences between coastal and inland sites. This could indicate that it is not the activity of the moth borers contributing to the demise of the plants. Throughout the duration of the study, the hurricane seasons were very active. The inland sites were heavily affected by hurricanes, although this did not contribute to the mortality of large amounts of plants directly. In particular, a category four hurricane passed through the inland area in August of 2004. The hurricane activity led to there being a much longer period of standing water present at some sites. This alone, may have led to higher rates of plant mortality at these sites. Another factor that might contribute to there being greater mortality of inland plants is the high levels of mealybug infestation (*Dactylopius* spp.). This data was not subjected to analysis, but this insect occurred at much greater levels at inland sites (pers. obs.). Also, feral hogs (*Sus scrofa*) are present at inland sites, with rooting activity observed regularly. Feral hog activity was not noted at any coastal site. This could also contribute to the inland plants having higher mortality. It seems as though inland plants may be exposed to higher levels of stress due to factors other than insect damage, which may make them less likely to recover from additional damage from moth larvae. On the coast, the primary stress would likely be the moth activity, which may not be enough to lead to high levels of mortality.

Plant damage was not significantly different between coastal sites and inland sites. However, there was a strong trend for coastal sites to show higher levels of damage on pads, plants and even documented old damage (Table 4). This is very interesting. Inland plants show higher levels of mortality, have no *Cactoblastis cactorum* damage and coastal plants have higher levels of *Cactoblastis cactorum* damage, with lower rates of mortality. This indicates that while the exotic cactus moth is doing more damage to plants along the coast, it is not leading to higher levels of plant mortality than is seen with the native cactus moth. This is likely a true representation of what is happening in the system for the sample size was very large (1100 plants followed over a two-year period). Perhaps a longer study would paint a different picture if it takes a longer period of time for the plants to respond to repeated damage from the moth larvae.

Table 4. The proportion of plants with moth damage by site location (coastal vs. inland).

Variable	**Site**	**Mean**
Damaged pads	Coastal	0.046
Damaged pads	Inland	0.014
Damaged plants	Coastal	0.407
Damaged plants	Inland	0.137
Old damage	Coastal	0.625
Old damage	Inland	0.177

There was no difference between the average number of pads on coastal versus inland plants. This was surprising due to the coastal sites having some individual *Opuntia stricta* plants with well over 300 pads. The average number of primary and tertiary pads was also similar at both locations. The trend for coastal plants to have higher damage due to moth activity cannot be attributed to the amount of pads or the type of pads available for them to feed upon. There was also no significant difference in cuticle toughness, meaning that both sites had plants that were equally easy or difficult for the early instar larvae to penetrate.

There was no difference observed in the amount of damage sustained on either coastal or inland plants from true bug feeding, which would be expected given that there is no difference in the toughness of plant cuticles (Hemipteran species noted were *Chelinidea vittiger aequoris* and another unidentified species). At inland sites (primarily Lake Wales Ridge State Forest) there was a large amount of blister beetles (*Epicauta fabricii*) noted on flowers and leaf buds. These beetles were observed feeding on both the leaf buds and pollen, but were never documented along the coast. There is the possibility that these insects could contribute to the higher mortality noted inland, although it is unlikely that this factor alone is responsible.

There was no difference in the soil nitrogen available between coastal and inland sites. Overall, nitrogen levels were extremely low, but this is to be expected since the soil in which the *Opuntia* are found is primarily sand. Nitrogen levels are probably not a determining factor affecting host choice for the moth borers.

The average number of eggsticks counted was greater on the coast than inland. This suggests that *Cactoblastis cactorum* either has a much larger population than does *Melitara prodenialis* or is capable of higher reproductive rates. While the exotic moth may be more prolific, it is not having a negative effect on the plants for the mortality was higher on inland plants, where *M. prodenialis* is active. Throughout the study at least one hundred *C. cactorum* eggsticks were collected from coastal field sites to rear in the laboratory and not once were parasitoids reared from these eggs. Therefore, it is not likely that the higher reproductive effort is to overcome egg parasitism.

When coastal and inland comparisons were made for *Opuntia humifusa* alone, plant mortality was again higher at inland sites. This was not associated with moth damage, for moth-damaged plant mortality was not significant between locations. This indicates that there must be some other factor contributing to the loss of inland plants. Loss could be due to differences in moth behavior, maybe *Melitara prodenialis* moths do not move on to new hosts in a manner to conserve food sources for future generations. Loss could be related to the presence of feral hogs and their activity or simple weather patterns, such as the active hurricane season that occurred during this study.

The amount of new growth (tertiary pads) was greater on the coast than inland. However, there was no significant difference in the nitrogen in the plant tissue or in the soil between the two sites. Therefore, nitrogen availability is not driving this difference in growth rates. Plant nitrogen is not significantly different between locations but was slightly higher inland and soil nitrogen was not different between locations but was higher on the coast. Nitrogen was low overall (less than 1% at both sites, foliar and soil). This may simply be a reflection of slight inherent differences between the two habitats or variation in rates of nitrogen cycling in the two habitats.

There was a significant difference in the number of eggsticks between the two locations. Eggsticks were more numerous at coastal sites (*Cactoblastis cactorum*) when compared with inland sites (*Melitara prodenialis*). This can be a reflection of differences in the reproductive rates, viability of eggs, survivorship of larvae or even population size between the two species of moth.

When plant species were compared at coastal sites only, no statistical difference was found in the average number of pads between species. Of all *Opuntia stricta* plants followed there was only one individual with 300+ pads and 11 individuals with more than 100 pads. The rest of the plants (157) had less than 100 pads. The *Opuntia humifusa* plants had five individuals with 200+ pads and 17 individuals with 100+ pads, the rest of the plants (309) had less than 100 pads each.

There was no significant difference found in the amount of new growth each species of plant produced throughout this study. This is interesting, because there was a significant difference between the coastal and inland plants. Therefore, that result must be a function not of the plant species, but of the site location.

The levels of foliar nitrogen and soil nitrogen were also not significant between the two plant species. This is not surprising since nitrogen has been shown to be at low levels and not significantly different in other comparisons.

The level of true bug damage was not statistically different between *Opuntia* species, but was slightly higher in *Opuntia humifusa*. True bugs were noted more often at inland sites (pers. obs.).

There was no significant difference in mortality levels of the two species at the coastal locations. However, the mortality of plants that had been attacked by *Cactoblastis cactorum* was higher in *O. stricta*. This indicates that the moth may have some larger effect on this plant species than on the other species present although this was not consistent in this study. The total number of moth-damaged pads did not differ between the two plant species, but the proportion of damaged plants was higher in *O. stricta*. This would indicate that the larvae may be more congregated on these plants than they are on the *O. humifusa* individuals. Another result that supports this idea is that the mortality of plants that have active *Cactoblastis cactorum* attack was also higher in *O. stricta* than in *O. humifusa*. However, the number of eggsticks does not support this, because eggsticks were not found to be significantly different in their distribution between the two species of plants. Unless, hatched *C. cactorum* eggsticks are fragile and are easily blown, brushed or otherwise removed from the plant compared with *M. prodenialis* eggsticks, it would seem that if more larvae were doing more damage to plants proportionally it would be supported by the eggstick data. The possibility of hatched eggsticks being easily removed may explain this anomaly.

A second possibility is that the moths laid more eggs on *O. stricta* than *O. humifusa*. This could not be assessed with the data collected because eggsticks were not removed after being counted at each census. In order to determine if this is happening, eggsticks would need to be removed after they were tallied so they would not be counted repeatedly.

Chapter Two

What is the effect of prescribed fire on the relationship between Florida *Opuntia* populations and attack by cactus moths?

Introduction

Fire can play an important role in many natural ecosystems, being a requirement for maintenance of natural community structure. In many ecosystems, natural fires once served to remove understory vegetation and cycle nutrients among its other benefits. Long-leaf pine communities of Florida are one type of ecosystem that was historically subjected to natural cycles of fires, which helped to maintain a healthy ecosystem. Human tendency to suppress fires led to the encroachment of many areas by invasive plant species as well as degradation of the vegetation as those species that are dependent upon fire were no longer exposed to it. Now that the importance of fire is realized for the maintenance and overall health of these ecosystems, prescribed burning is conducted periodically on tracts of managed land throughout the state of Florida.

Some of the benefits of fire include the release of nutrients that are trapped in vegetation back into the system, the removal of canopy, the removal of competitive vegetation and the removal of ground litter (Whelan 1995). After a fire occurs there are changes in the daily temperature of the soil (temperature increases) and there are also changes in the water relations (possible increased runoff leading to increased erosion, increased evaporation and decreased water holding capacity) (Whelan 1995). Cacti seem to be well adapted to many of these possible post-fire changes for they can withstand intense heat/sunlight and prolonged periods with little water.

If a fire is not too severe, there seems to be an increase in nutrients available to new growth (Smith 1996). At first, nitrogen is not in the form plants can use and it must first be fixed by nitrogen-fixing plants (legumes) and soil organisms before it can be made available to plants (Smith 1996).

Since prescribed fire does not kill the underground portions of *Opuntia* plants in Florida habitats and these plants subsequently show tremendous new growth (pers. obs.). The prediction is that plants subjected to prescribed fire will show a subsequent increase in herbivory by *Cactoblastis cactorum*. This is likely because new tissues may be easier for the larvae to penetrate, and the burned soil (and subsequently plants) may have an increase in macronutrients making these plants more attractive to adult moths for oviposition. Preliminary work has shown that all aboveground tissues are not destroyed during a fire and late-instar *C. cactorum* larvae have been noted in cladodes one month after a burn (pers. obs.). Therefore, it is possible that prescribed burning may enhance the spread and intensity of attack of cacti by *Cactoblastis cactorum*.

Methods

At the same sites used for the damage and mortality studies, 100 of the marked plants were not burned during the study and 100 were exposed to prescribed fire. This excludes Fort DeSoto, which did not have a prescribed fire over the duration of the study and had 100 plants marked unexposed to fire. Sites with burned treatments include Crooked Lake Prairie (burned December 2001 and February 2004), Honeymoon Island State Park (burned May 2003), Archbold Biological Station (burned July 2003), and Lake Wales Ridge State Forest (burned May 2005). Visits were made to census plants once per month from July 2003 through July 2005.

The number of pads including the number of primary, secondary and tertiary pads was counted at each visit. The number of damaged pads (showing active larvae feeding), the number of pads with true bug damage, and the number of eggsticks including the number of eggs and if the eggs were hatched or unhatched was counted at each visit.

Soil samples were collected during the wet season to determine nitrogen content. A soil core approximately 10cm deep within 6 inches from the base of the plant was collected from 15 randomly selected plants within each burn treatment. Samples were then analyzed in a CE Instruments NC 2100 CN Analyzer (CE Elantech, Lakewood, NJ, USA) to obtain total nitrogen content.

Any other insects observed using the *Opuntia* were counted and identified. If these insects were utilizing *Opuntia* as a host, this was also noted.

All data were tested for normality using a Kolmogorov-Smirnov test. All data met the assumptions of normality, except for plant mortality of plants with previous moth damage. All variables were compared between burned and unburned treatments using a

Student's t-test, except for plant mortality with previous moth damage, which was compared using the nonparametric Mann-Whitney U-test.

Comparison was also made between coastal sites and inland sites for the first year following fire. Since prescribed burning occurred at different times at the sites throughout the study, only three sites were burned early enough in this study to be followed for a minimum of one year. These sites include Honeymoon Island State Park, Archbold Biological Research Station and Crooked Lake Prairie (data for Crooked Lake were the year following the second fire 2004 through 2005).

The data were subjected to normality testing using a Kolmogorov-Smirnov test. Those that did not meet assumptions of normality include: average pads, damaged plants, true bug damage, old moth damage, and average eggsticks. None of these data responded to transformation, except for the average number of pads. Normal data were compared using a Student's t-test and non-conforming data were compared with a nonparametric Mann-Whitney U-test.

An attempt to compare burned *Opuntia humifusa* and non-burned *O. humifusa* at inland sites only (Archbold and Crooked Lake) in the first year after fire was made. All data were tested for normality using a Kolmogorov-Smirnov normality test. All variables met the assumptions of normality. Because of the low replication and the presence of zero data, not all variables were comparable. Those that were successfully compared with Student's t-tests include: average pads, plant mortality, true bug damage, old moth damage, tertiary pads, average plant nitrogen, and average soil nitrogen. Because of low replication and zero values, comparison of *Opuntia humifusa* between inland sites and coastal sites after one year since the fire was not possible.

All statistics were calculated using Systat 11.0 (Systat Software, Inc., 2004) and all statistical figures were constructed using Sigma Plot 8.02 (SPSS, Inc., 2002).

Results

There were no significant results within the analysis of all plants between burned and unburned treatments, summarized in Table 5.

Table 5. Summary of Student's t-test results between burned and unburned treatments. *Nonparametric Mann-Whitney U-test.

Variable	**t**	**p**
Average pads	0.267	0.796
Plant mortality	0.865	0.409
Dam pads	-0.870	0.407
Dam plants	-0.091	0.929
True bug dam plants	0.705	0.498
Old dam plants	-0.238	0.817
Dam no mortality	-1.637	0.136
Tertiary pads	-0.044	0.966
Primary pads	-0.526	0.612
Average eggsticks	-1.576	0.149
Soil nitrogen	1.039	0.329
Moth mortality*	U = 15.500	p = 0.770

The average number of pads was not significantly different between burned and unburned treatments ($t = 0.267$, $p = 0.796$) with mean pads for burned and unburned 29 and 26, respectively. The proportion of damaged plants is not different by burn treatment ($t = -0.091$, $p = 0.929$) (Figure 17).

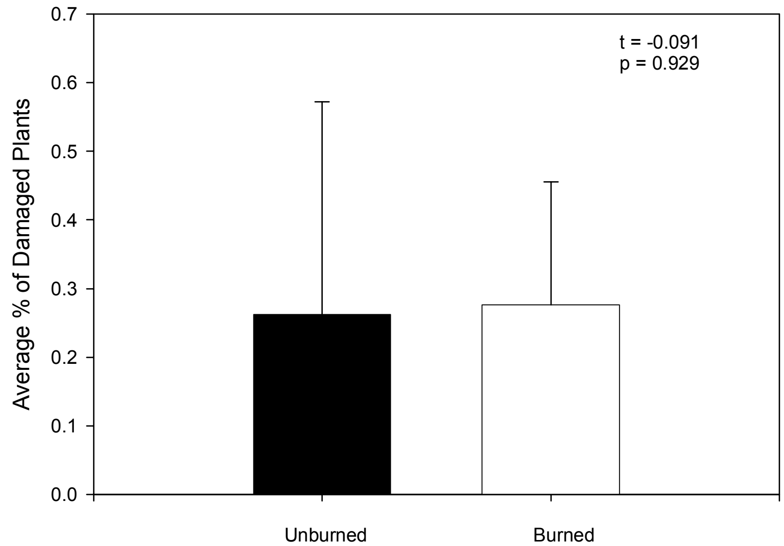

Figure 17. Proportion of damaged plants by burn treatment.

There was no difference in plant mortality when compared by burn treatment ($t = 0.865$, $p = 0.409$). Plants that were damaged by moths but survived were not significantly different between treatments ($t = -1.637$, $p = 0.136$). Plants that had old moth damage also did not differ ($t = -0.238$, $p = 0.817$). Plants that sustained moth damage and perished during the study was analyzed with the nonparametric Mann-Whitney U test and showed no difference by treatment ($U = 15.500$, $p = 0.770$). Therefore, prescribed fire does not seem to have an overall effect on the resilience of plants.

The proportion of tertiary pads did not differ between the burned and unburned treatments ($t = -0.044$, $p = 0.966$). The average number of moth-damaged pads was also not statistically significant between the two treatments ($t = -0.870$, $p = 0.407$) (Figure 18).

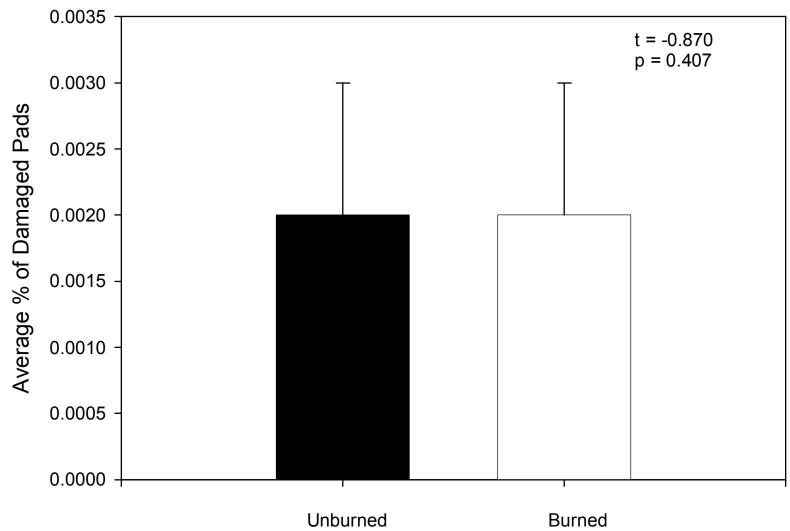

Figure 18. Proportion of damaged pads by burn treatment.

The proportion of plants that sustained true bug damage was not significant by treatment ($t = 0.705$, $p = 0.498$). The average number of eggsticks also did not differ by treatment ($t = -1.015$, $p = 0.337$) (Figure 19).

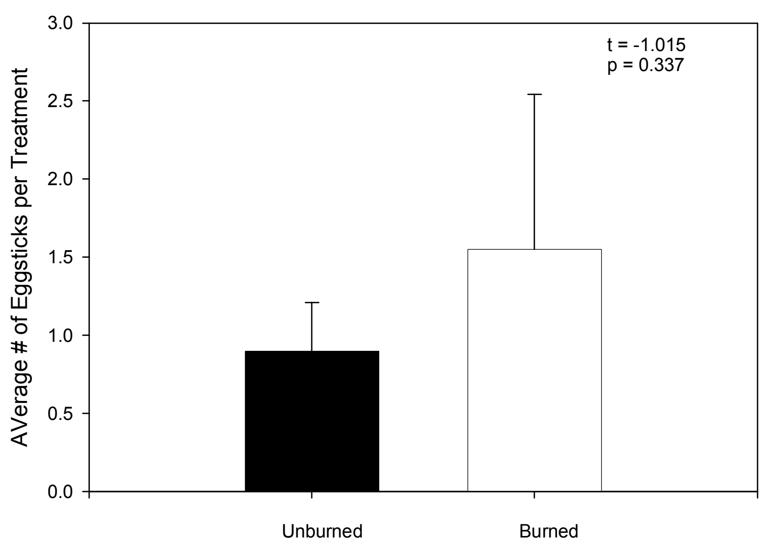

Figure 19. The average number of eggsticks by burn treatment.

The number of primary pads was not significantly different between burn treatments (t = -0.526, p = 0.612). The amount of soil nitrogen also did not differ by treatment (t = 1.039, p = 0.329).

When burned plots were compared after only one year of fire, four variables showed a significant difference using parametric statistics. However, one variable compared with a Mann-Whitney U-test showed significance (Table 6).

Table 6. Summary of statistics performed comparing burned inland and coastal sites one year following prescribed burn. *Mann-Whitney U-test. Significant results highlighted.

Variable	**t**	**p**
Average number of pads (Square root transformed)	6.475	0.003
Plant mortality	-1.562	0.193
Damaged pads	2.915	0.043
Damaged plants	U = 8.00	p = 0.060
True bug damage	U = 0.00	p = 0.064
Old damage	U = 8.00	p = 0.060
Number of tertiary pads	4.572	0.010
Average plant nitrogen	-0.047	0.965
Average soil nitrogen	2.312	0.082
Average number of eggsticks	U = 8.00	p = 0.028

There was a significant difference in the average number of pads when compared by site location (t = 6.475, p = 0.003). The plants along the coast had an average of 34.42 pads and the inland plants averaged 12.94 pads (Figure 20).

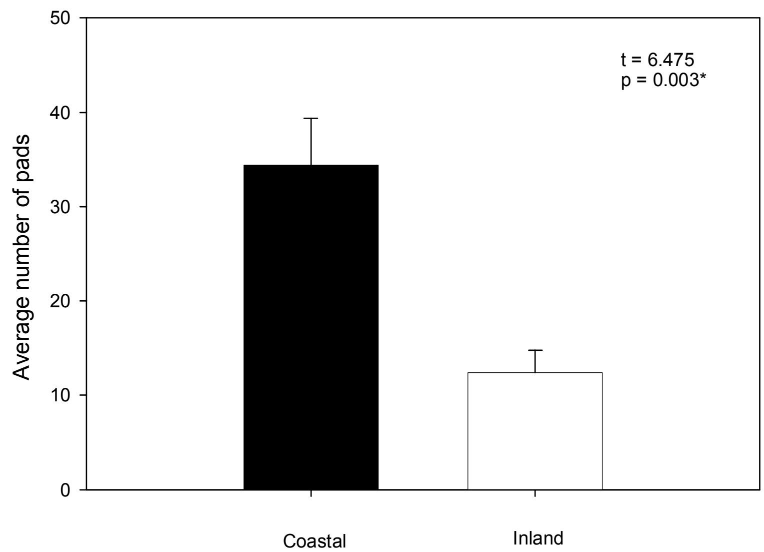

Figure 20. Comparison of the average pads in the first year following a fire by inland and coastal location. *Indicates a significant result.

There was no difference in plant mortality when this was compared between the two locations ($t = -1.562$, $p = 0.193$). However, there was a higher amount of mortality inland, which has been consistent throughout this study. Inland plants have a mortality of 9% and coastal, 0.5%. Data for the mortality restricted to the plants attacked by larvae were not sufficiently replicated to permit testing. Therefore it is unknown whether moth activity is contributing to the mortality of plants or not.

The amount of damaged pads was statistically different between the locations ($t = 2.915$, $p = 0.043$). Damage was higher at the coast (average = 5.65) than at the inland sites (average = 1.11) (Figure 21). This suggests that *Cactoblastis cactorum* may be a more voracious feeder, damaging more plants along the coast than *Melitara prodenialis* does at inland sites.

Different amount of tertiary pads were counted at the two locations (t = 4.572, p = 0.010). Twice as many tertiary pads were noted at coastal sites than at inland sites (Figure 22). This was consistent with the results that were obtained in chapter one, combining burned and unburned treatments for two years. Plants along the coast put out a greater number of new pads than did those at inland sites.

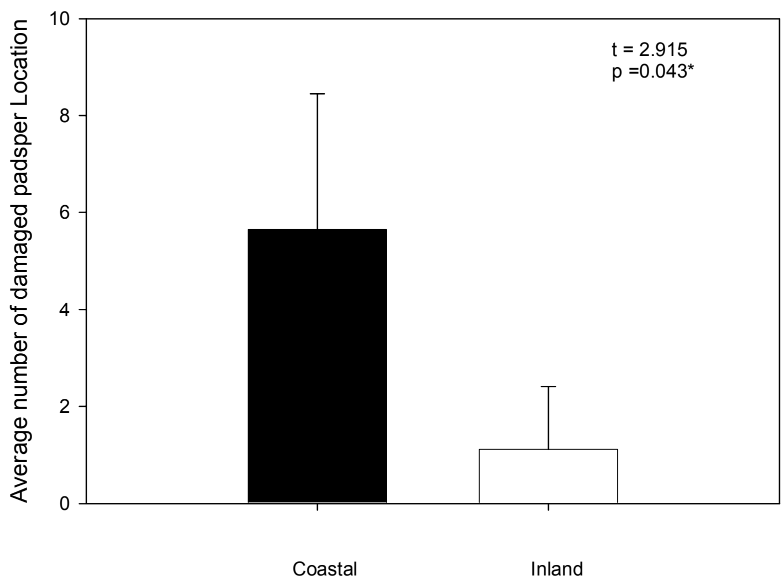

Figure 21. Average damaged pads when compared by location one year following prescribed fire. *Indicates a significant result.

There was no difference noted in the amount of plant (t = -0.047, p = 0.965) or soil nitrogen (t = 2.312, p = 0.082). Plant foliar nitrogen was very low and similar between the two locations, inland plants had 0.584% and coastal plants had 0.569% nitrogen. Soil nitrogen was also less than 1% at both locations, but it was slightly higher along the coast (0.210%) than inland (0.096%).

The proportion of damaged plants was tested using a nonparametric Mann-Whitney U-test and this showed no difference between the coastal and inland burn sites (U = 8.00, p = 0.060). True bug damage was also tested with a Mann-Whitney U-test and showed no significance between the two burn locations (U = 0.00, p = 0.064).

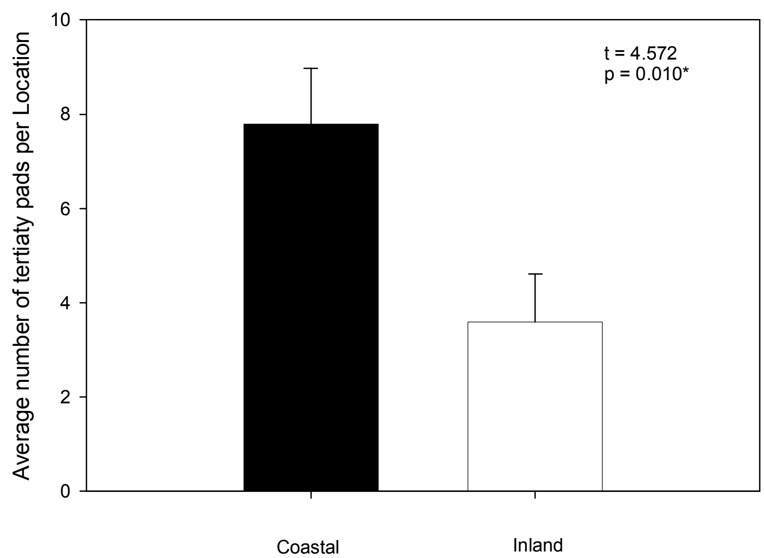

Figure 22. Average number of tertiary pads by location one year after fire. *Indicates a significant result.

The average number of plants that had old larval damage was not statistically different at coastal sites than inland sites (U = 8.00, p = 0.060).

The average number of eggsticks was different between the coastal and inland burn treatments (U = 8.00, p = 0.028). There was an average of 10 eggsticks laid on coastal plants and zero eggsticks laid on inland plants in burn treatments.

Comparison was made for the first year following prescribed fire between burned and unburned treatments at inland sites only. Again, because of low replication and zero values, all variables were not tested. The variables compared between treatments include the average number of pads, plant mortality, true bug damage, and old moth damage, number of tertiary pads, average foliar nitrogen, and average soil nitrogen, summarized in Table 7.

Table 7. Summary of Student's t-test performed on *Opuntia humifusa* in burned and unburned plots at inland sites, one year following prescribed fire. Significant results are highlighted.

Variable	**t**	**p**
Average number of pads	0.248	0.827
Plant mortality	-0.141	0.901
True bug damage	0.542	0.642
Old damage	-0.447	0.698
Number of tertiary pads	1.079	0.393
Average plant nitrogen	-2.082	0.173
Average soil nitrogen	1.220	0.347

None of the variables tested have shown any significant differences between the inland burn treatments and inland non-burned treatment, the first year following fire. Average pads were similar ($t = 0.248$, $p = 0.827$) in both treatments averaging 12.04 in unburned treatments and 12.75 in burned treatments.

Plant mortality in the two treatments was also not significant ($t = -0.141$, $p = 0.901$), averaging 8% in burned plots and 10% in non-burned plots. The proportion of plants that exhibited true bug damage was approximately 80% in both treatments ($t = 0.542$, $p = 0.642$). The proportion of plants with old larval damage was also similar in the two treatments ($t = -0.447$, $p = 0.698$), averaging 0.5% in burned plots and 1% in unburned plots.

The average number of tertiary pads was not statistically different between the two inland treatments ($t = 1.079$, $p = 0.393$) with burned plants averaging slightly higher at an average of 4.13 and unburned averaging 3.06.

The percent of foliar and soil nitrogen were also not significant among the treatments ($t = -2.082$, $p = 0.173$; and $t = 1.220$, $p = 0.347$, respectively). It is interesting that the foliar nitrogen was slightly higher in unburned plots, but the soil nitrogen was higher in burned plots (Figures 23 and 24).

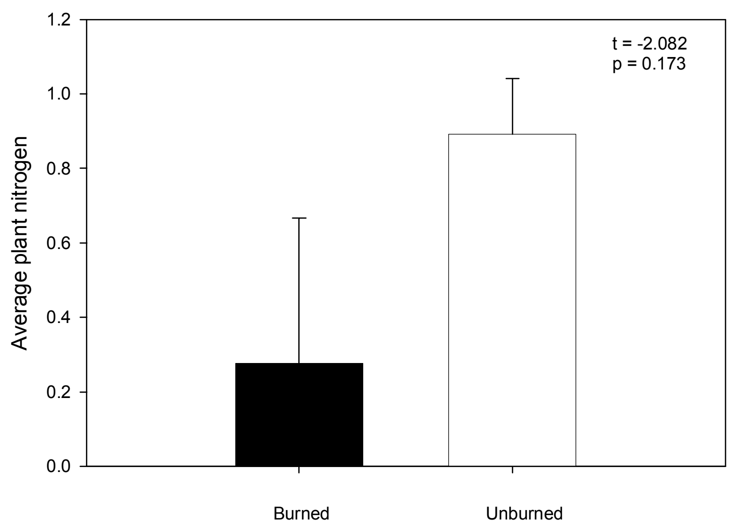

Figure 23. Average percentage of foliar nitrogen in burned and unburned inland plots

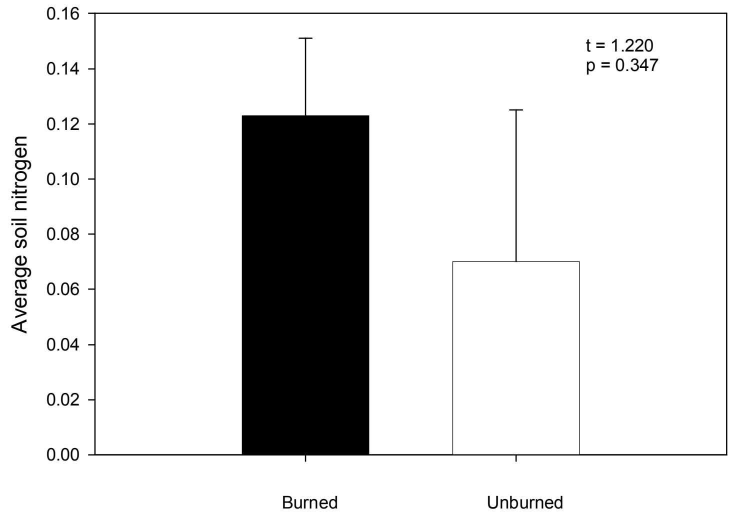

Figure 24. Average percentage of soil nitrogen in burned and unburned inland plots.

Discussion

Cactoblastis cactorum was not observed at Lake Wales Ridge State Forest and did not attack any marked inland plants, although it was noted at Archbold Biological Research Station and Crooked Lake Prairie and another site not used in this study but within close proximity to field sites (Hickory Lake Scrub, Frostproof, FL). *Melitara prodenialis* was the dominant species at all inland sites, while *Cactoblastis cactorum* dominated at the coastal sites. No co-occurrence of moth species within marked plants at any site was observed throughout the duration of this study.

All field sites, except for North Lido Beach, South Lido Park and Fort DeSoto were subjected to a prescribed fire at some point during the course of this study. Ideally, fire would have occurred at approximately the same time at each site, but unfortunately the burn cycle varied by site. The burn treatments were completed on the following dates: Archbold Biological Research Station was burned July 2003, Lake Wales Ridge State Forest was burned May 2005, Crooked Lake Prairie was burned March 2004 and Honeymoon Island was burned May 2003.

When the results were compared by burn treatment, there was no difference in plant mortality. This suggests that the plants are well adapted to a natural fire regime and can easily withstand its occurrence. It would be interesting to note if this tolerance would change if the fire regime were altered so that it is outside of the natural fire cycle.

There was no difference in the average number of pads between burn treatments. This suggests that there is no overcompensation in response to fire. Since both coastal and inland sites had similar amounts of larval damage, the addition of fire exposure was not enough to cause overcompensation in this system.

The number of primary pads was not different in burned areas vs. unburned areas. No induction of woody changes to the stems is caused by exposure to fire. There were also no differences in the amount of tertiary pads between the two treatments. It seems as though *Opuntia* puts out a certain amount of new growth regardless of damage due to fire or cactus moths. This is an interesting find, because observing the process of regeneration post-fire, it appears that tissue exposed to the fire often dies and rots, but the plant survives, putting out a large amount of tertiary growth.

There were no differences in proportions of plant damage or pad damage between the two treatments. Possibly, because there is no increase in new tissue, there is also no increase in larval feeding. This would also suggest that nutritional quality remains similar regardless of whether or not the plant has been subjected to a prescribed burn.

The proportion of pads with true bug chlorotic spots was not different in the burned treatments and unburned treatments. It was presumed that an increase in tertiary pads would coincide with an increase in true bug feeding. Since the tertiary tissue was not different, neither was the bug damage.

There was no difference in eggsticks between the burn treatments. Again, this hypothesis was based upon the idea that greater tertiary tissue would lead to greater reproductive effort since it would be easier for newly hatched larvae to enter the plants. Although the amount of eggsticks was greater on the coast (see Chapter 1), when the sites were separated by burn treatment this result was not repeated. This is also interesting because three of the coastal sites did not have any exposure to fire, while all the inland sites did. It would seem that there would still be a larger amount of eggs laid at coastal sites, and this is the trend, although it was not statistically different (Table 8).

Table 8. The mean proportion of eggsticks laid by burn treatment.

Burn Treatment	**Mean Proportion of Eggsticks**
Burned	0.897
Unburned	1.550

There was no statistical difference in the amount of nitrogen available in the soil when compared by treatment. Again, this could be due to the simple fact that there is inherently little nitrogen available in the system. Another possibility is that there is no initial "flush" of nitrogen released after prescribed fire in Florida ecosystems as suggested by Whelan (1995).

Comparisons were made for the first year following fire to assess if results may be different when fire was recent and regeneration was occurring. If areas revert back to "unburned" status quickly then a longer study might mask significant results.

When coastal and inland burn sites were compared, it was found that the average amount of pads were higher on the coast. The one coastal site had only 7 plants with 100+ pads (the highest was one individual at 205) and a sample size of 100, while inland sites had 4 plants with 100+ pads and a sample size of 200. This may be a reflection of differences due to the combination of plant species, *Opuntia stricta* and *Opuntia humifusa,* along the coast and only one species, *O. humifusa* inland.

Mortality was slightly higher at inland sites, consistent with earlier results. This may, in part, be due to differences in the effects from moth species, but other variables not measured could lead to this result as well. Inland sites had much evidence of feral pig (*Sus scrofa*) activity that can uproot and knock over plants. Another possibility was the category four hurricane (Charley) that passed through the inland sites in August 2004 and led to flooding and standing water that may have affected the ability of the plants to survive.

Damaged plants and eggsticks were higher at the coastal site. This may be a result of a larger population of *Cactoblastis cactorum* than *Melitara prodenialis.* If this is not the case, it may simply reflect greater reproductive effort and/or survival of *C.cactorum* than the native moth borer.

Coastal sites showed higher amounts of tertiary (new) growth, which may be an effect of the coast having the combination of plant species, rather than only *Opuntia humifusa.*

An attempt was made to compare burned plots and unburned plots at inland sites and coastal sites separately the first year following a fire. Because of low replication and many zero values, only some variables were comparable with a t-test at inland sites.

There were no significant results among any of the variables compared between burned and unburned plots. The variables tested included: average number of pads, plant mortality, proportion of true bug damage, proportion of old moth damage, the number of tertiary pads and the percentage of foliar and soil nitrogen. No significant difference in these variables supports earlier analyses suggesting that fire has little negative or altering effects on the *Opuntia* or the insects that uses it as a host.

Differences (although not statistically significant) between the levels of nitrogen are interesting. Foliar nitrogen was slightly higher in unburned plots and soil nitrogen was slightly higher in burned plots. It may be possible that nitrogen is trapped in the plant tissues until it can be released into the soil by an event such as fire (Whelan 1995). This may have been more significant if the system was not inherently low in nitrogen to begin with. Another study including the fertilization of plants and exposing them to prescribed fire may provide more information.

Summary

The plant stress hypothesis (White 1974) states that plants may have higher levels of nitrogen (a limiting factor for insects) when under high levels of stress and that this would correlate with higher levels of insect damage. It appears that inland plants were under higher levels of stress than were coastal plants throughout this study (fire, flood, hurricanes, insects and feral hogs). Inland plants also showed a higher rate of cactus mortality. This could be supportive of the plant stress hypothesis. However, this is not likely the cause, since there were no correlating increases in moth damage. Also, since plants subjected to fire (presumably higher stressed plants than those not burned) did not show higher rates of moth attack, this hypothesis can be ruled out.

The higher proportion of inland plant mortality vs. coastal plant mortality may be attributed to levels of stress that the plants simply could not recover from and not due to insect feeding.

Currently, there are many programs in effect aimed at controlling the spread, reducing the effects of, and eradication of *Cactoblastis cactorum* in southeastern *Opuntia* populations. These studies are based on the premise that the exotic cactus moth is causing great damage and mortality to the native cactus populations. The results of this study suggest that over the short-term (two years) the exotic moth is not harming the cactus any more than are the native moths. It is possible that *C. cactorum* is doing similar damage to plants as is *Melitara prodenialis.* In 1998, Johnson and Stiling found *M. prodenialis* along with *C. cactorum* at the same coastal sites that were used in this study, although *M. prodenialis* was not documented throughout this study at these locations. It is likely that *C. cactorum* is a more damaging species than the native moth and is excluding the native in locations where it becomes well established. While this may not have serious effects at this time, the types of negative impacts it could have in the future are unknown. Perhaps over a longer time period, negative effects will be realized. This could include a greater amount of damage and mortality to the cactus or possibly competitive exclusion of native moths. Until these effects can be demonstrated quantitatively, perhaps research should focus on monitoring and assessment of the spread and damage due to *Cactoblastis cactorum*, rather than its containment and eradication.

Literature Cited

Burger, J.C. and S.M. Louda. 1994. Indirect versus direct effects of grasses on growth of a cactus (*Opuntia fragilis*): insect herbivory versus competition. Oecologia 99 (1-2): 79-87.

Carlton, C.E. and T.J. Kring. 1994. *Melitara prodenialis* Walker on prickly pear in Arkansas. Southwestern Naturalist 19(1): 23-31.

DeLoach, C.J. 1991. Past successes and current prospects in biological control of weeds in the United States and Canada. Natural Areas Journal 11(3): 129-142.

Dodd, A.P. 1940. The biological campaign against prickly-pear. The Commonwealth Prickly Pear Board, Brisbane, Australia.

Drea, Jr., J.J. 1991. The philosophy, procedures, and cost of developing a classical biological control of weeds project. Natural Areas Journal 11(3): 143-150.

Gibson, A.G. and P.S. Nobel. 1986. The Cactus Primer. Harvard University Press, Cambridge, MA.

Habeck, D.H. and F.D. Bennett. 1990. *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae),a Phycitine new to Florida. FL Dept. of Agric. and Consumer Services, Div. of Plant Industries, Entomol. Circ. No. 333.

Hendrix, S.D. 1979. Compensatory reproduction in a biennial herb following insect defloration. Oecologia 42: 107-118.

Hight, S.D. and J.J. Drea, Jr. 1991. Prospects for a classical biological control project against purple loosestrife (*Lythrum salicaria* L.). Natural Areas Journal 11(3): 151-157.

Hight, S.D., J.E. Carpenter, K.A. Bloem, S. Bloem, R.W. Pemberton and P. Stiling. 2001. Expanding geographical range of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. Florida Entomologist 85(3): 409-535.

Hoffmann, J.H. and H.G. Zimmermann. 1989. Ovipositional and feeding habits in cactophagous pyralids: predictions for biological control of cactus weeds in southern Africa. Proc. VII. Int. Symp. Biol. Contr. Weeds., 6-11March 1988, Rome, Italy. Delfosse, E.S. (ed.) 1st Sper. Patol.Veg. (MAF), pp: 395-399.

Irish, M. 2001. The ornamental prickly pear industry in the southwestern United States. Florida Entomologist 84(4): 484-485.

Johnson, D.M. and P.D. Stiling. 1996. Host specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. Environmental Entomology 25(4): 743-748.

Johnson, D.M. and P.D. Stiling. 1998. Distribution and dispersal of *Cactoblastis cactorum* (Lepidoptera: Pyralidae),an exotic *Opuntia*-feeding moth, in Florida. Florida Entomologist 81(1): 12-22.

Mann, J. 1969. Cactus-feeding insects and mites. Bulletin 256, Smithsonian Institution, Washington, D.C.

Maschinski, J., and T.G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. The American Naturalist 134(1): 1-19.

Mellink, E. and M.E. Riojas-López. 2002. Consumption of platyopuntias by wild vertebrates *in* Cacti: Biology and Uses. (Nobel, P.S., ed). University of California Press, Berkeley, CA. pp: 109-123.

Monro, J. 1967. The exploitation and conservation of resources by populations of insects. Journal of Animal Ecology 36: 531-547.

Myers, R.L. and J.J. Ewel. 1990 Ecosystems of Florida. University of Central Florida Press, Orlando, FL.

Obeso, J.R. 1998. Effects of defoliation and girdling on fruit production in *Ilex aquifolium*. Functional Ecology 12: 486-491.

Paige, K.N. and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. The American Naturalist 129(3): 407-416.

Pettey, F.W. 1947. The biological control of prickly pears in South Africa. Science bulletin 271, Union of South Africa Government Printer, Pretoria.

Rebman,J.P.and D.J. Pinkava. 2001. *Opuntia* cacti of North America – an overview. Florida Entomologist 84(4): 474-483.

Sáenz-Hernandez, C, J. Corrales-Garcia and G. Aquino-Pérez. 2002. Nopalitos, mucilage, fiber and chochineal *in* Cacti: Biology and Uses. (Nobel, P.S., ed). University of California Press, Berkeley, CA. pp: 211-234.

Simberloff, D. 1997. The biology of invasions *in* Strangers in Paradise (Simberloff, D., D.C. Schmitz, and T.C. Brown, eds.). Island Press, Washington, D.C. pp: 3-17.

Simmonds, F.J. and F.D. Bennett. 1966. Biological control of *Opuntia* spp. by *Cactoblastis cactorum* in the Leeward Islands (West Indes). Entomophaga 11(2): 183-189.

Smith, R.L. 1986. Ecology and Field Biology, 5th ed. Harper Collins College Publishers, New York, NY.

Soberon, J., J. Golubov and J. Sarukhan. 2001. The importance of *Opuntia* in Mexico and routes of invasion and impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Florida Entomologist 84(4): 486-492.

Stiling, P. 2002. Potential non-target effects of a biological control agent, prickly pear moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), in North America, and possible management actions. Biological Invasions 4(3): 273-281.

Stiling, P., D. Moon, and D. Gordon. 2004. Endangered cactus restoration: mitigating the non-target effects of a biological control agent (*Cactoblastis cactorum*) in Florida. Restoration Ecology 12(4): 605-610.

Stiling, P., D. Moon, and D. Gordon. Non-target effects of *Cactoblastis cactorum* (Berg) Lepidoptera: Pyralidae) on *Opuntia corallicola* Small in the Florida Keys. Unpublished manuscript.

Strauss, S.Y. and A.A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology and Evolution 14(5): 179-185.

Strauss, S.Y. and A.R. Zangerl. 2002. Plant-insect interactions in terrestrial ecosystems *in* Plant Animal Interactions: An Evolutionary Approach (Herrera, C.M, and D. Pellmyr, eds.). Blackwell Publishing, Malden, MA. pp: 77-106.

Thomson, V.P., S.A. Cunningham, M.C. Ball, and A.B. Nicotra. 2002. Compensation for herbivoryby *Cucumis sativus* through increased photosynthetic capacity and efficiency. Oecologia 134(2): 167-175.

Valiente-Banuet, A., and H. Godínez-Alvarez. 2002. Population and community ecology *in* Cacti: Biology and Uses (P.S. Nobel, ed.). University of California Press, Berkeley, CA. pp:91-108.

Vigueras G., A.L. and L. Portillo. 2001. Uses of *Opuntia* species and the potential impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in Mexico. Florida Entomologist 84(4): 493-498.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press, New York, NY.

White, T.C.R. 1974. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia 16(4): 279-301.

Wunderlin, R.P. and B.F. Hansen. 2003. Guide to the Vascular Plants of Florida, 2nd ed. University Press of Florida, Gainesville, FL.