THE ECOLOGY AND MORPHOLOGICAL VARIATION OF *OPUNTIA*

(CACTACEAE) SPECIES IN THE MID-SOUTH, UNITED STATES

By

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Opuntia species have been poorly studied ecologically and taxonomically in the eastern United States. This study deals with the ecology of *Opuntia* species in the mid-south United States and covers not only the high degree of morphological variation exhibited by taxa, but also the taxonomy and distributions of the group for Mississippi. The taxa in the mid-south have distinct habitat preferences and can be separated based on habitat characterization. Information from this work provides valuable data useful in predicting possible routes that an invasive species, *Cactoblastis cactorum* (the cactus moth), might use in its potential westward migration. Phenotypic plasticity exhibited by *Opuntia pusilla* subjected to experimental conditions exemplifies the care that should be taken when making species delineations. Spine production in certain species is more a function of abiotic environmental pressures than genetic heritage. Two taxa that previously were put into synonymy with other species are recognized from this work.

DEDICATION

I would like to dedicate the work that has culminated in the production of this thesis to my father, Terrence C. Majure. Without his training from a very young age, I would not have had the tools necessary to complete such a project. He is an amazing naturalist, and I owe a large portion of my knowledge of the natural world to him. He always was willing to take the time to teach me concepts and point out minute details that most other people neither see, nor understand. I am greatly indebted to my father for making me who I am today.

ACKNOWLEDGMENTS

a part of his lab. In working with him, I have greatly improved my capabilities as a

scientist and hope to continue collaborating with him in the future.

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CHAPTER I

INTRODUCTION

There are five different types of Opuntioids (Cactaceae within the subfamily

Opuntioideae). These consist of the genera *Cylindropuntia*, *Grusonia*, *Opuntia*, *Nopalea*

and *Consolea*. The *Cylindropuntia* and *Grusonia* are collectively termed "chollas,"

whereas the genera *Opuntia*, *Nopalea*, and *Consolea* are known as the "platyopuntias," so

named for their flat stems (Figure 1.1; Benson 1982, Rebman & Pinkava 2001).
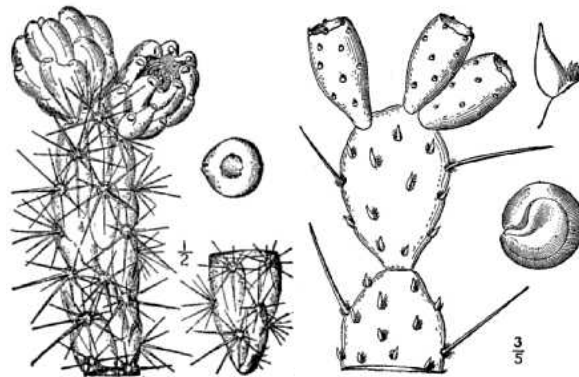
Fig. 1.1. Examples of cylindropuntia (left) and platyopuntia (right). Left:
Cylindropuntia imbricata; right: *Opuntia humifusa*, one of the
focal species of this research. Images from the USDA PLANTS
database (http://plants.usda.gov/), originals from Britton, N.L.,
and A. Brown. 1913. *Illustrated flora of the northern states and
Canada*. Vol. 2: 571, 573.

In Mississippi however, only one of these genera exist, *Opuntia*. The species that occur naturally in Mississippi are all part of one major complex, the *O. humifusa* complex (Doyle 1990). The major species of this group, *O. humifusa* (Raf.) Raf., is considered by some to be the most prominent species in the eastern United States and mostly ubiquitous over the area with one major variety, variety *humifusa* (Benson 1982, Wallace & Fairbrothers 1987, Pinkava 2003), except for the coastal areas. Here several other forms, varieties, or species (depending on the author) can be found (Small 1933, Britton & Rose 1963, Benson 1982, Weakley 2003, Pinkava 2003).

The three main species of *Opuntia* within the mid-south United States are *O. humifusa* (Raf.) Raf.*, O. pusilla* (Haw.) Haw. and *O. stricta* (Haw.) Haw. Another species that occurs in the Mississippi deltaic plain, which is much less common than the latter three, tentatively will be called *O*. aff. *allairei* Griffiths. This species has not been studied ecologically as have the other species and so will only be mentioned in "The Opuntia of Mississippi" (Chapter 3 of this work).

Understanding the habitats in which these taxa survive is necessary for a variety of reasons. The typification of habitats where *Opuntia* species can be found in the mid-south is an essential process by which the potential routes for the invasive moth, *Cactoblastis cactorum* Berg., can be predicted. *Cactoblastis cactorum* is arguably one of the most effective biological control agents. Originally from Argentina, Paraguay, Uruguay, and southern Brazil (Mann, 1969), this moth has been used successfully in Australia, South Africa, and the Caribbean Islands to control non-native, invasive populations of *Opuntia* (Mahr 2001, Pemberton & Cordo 2001, Perez-Sandi 2001, Zimmermann et al. 2001). Possibly, its most exemplary usage is demonstrated by its

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introduction into Australia in the 1930s, where millions of hectares of *Opuntia*-infested

lands were quickly controlled by the moth (Mahr 2001).

Unfortunately, *Cactoblastis* is now threatening the native *Opuntia* species in the

southeastern United States. It was found in the Florida Keys in 1989 and has since

migrated rapidly through coastal areas where it has been found as far north as South

Carolina (Hight et al. 2002), and as far west as southwestern Alabama. It is essential to

halt the spread of the cactus moth before it reaches *Opuntia*-rich areas in the

southwestern United States and in Mexico, where it would presumably have an adverse

effect on species diversity and the Mexican economy (Mahr 2001, Perez-Sandi 2001,

Soberon et al. 2001, Zimmermann et al. 2001, Hight et al. 2002).

Habitat typification also provides for an opportunity to understand more fully the

ecological processes influencing the distribution and survival of native populations of

Opuntia species in this region. Due to the arduous and painstaking process of specimen

collection, many botanists and/or ecologists may note the presence of *Opuntia* species in

a site, but they are rarely collected. For example, at the beginning of this project, a total

of approximately 30 specimens from native *Opuntia* had been collected among the four

predominant herbaria in the state of Mississippi. We now know of more than 100

locations with native *Opuntia* populations within Mississippi. This reflects the lack of

attention or interest paid to this group in this area. Also, the general consensus about site

parameters is that they are areas with sandy, well-drained soils and an open canopy which

reduces shading. Otherwise, their physical, environmental variables and other biotic

factors have not been investigated rigorously for this region. The basic ecological

parameters were measured among native populations in order to determine possible plant

species associations and habitat conditions necessary for the survival of species of *Opuntia* in the mid-south.

It is quite simple to understand the degree of phenotypic plasticity that is ever-present in *Opuntia* species by merely growing and observing natural or planted populations. Due to their outstanding morphological plasticity, many atypical populations of certain species repeatedly have described as new species or varieties of already described taxa. This is easy to see by the long list of synonyms commonly associated with most species now accepted within the *Opuntia* genus (also reviewed in Chapter 3). However, morphological plasticity generally is not quantified or tested experimentally.

The morphological plasticity in *Opuntia* was demonstrated using *Opuntia pusilla* as an experimental organism. This species was grown experimentally under shaded and full light conditions to induce phenotypic plasticity in new growth on cladodes obtained from a natural population. Vast differences were seen between the shade and light treatments. The facility in morphological change by manipulating microclimate was shown in this experiment and has implications in terms of defining species boundaries using morphometric data. *Opuntia* taxa should be well evaluated before making species delimitations, as environmental variability can cause exaggerated morphologies divergent from classical species boundaries.

Due to the plasticity in the morphological behavior of *Opuntia* species, it is necessary to re-evaluate characteristics displayed by the few native species available for study in this region. Comparisons of morphological characteristics among the species found in this area will help establish a more solid foundation in which to delineate species. Although the *Opuntia* from this region have been studied since the early 1800s

with the species typification of *Opuntia humifusa* as *Cactus humifusus* by Rafinesque (1820), and various treatments by Engelmann (1856), Small (1903, 1913, 1933), and Benson (1982), they have not been studied in great detail. For example, in the Flora of North America (Pinkava 2003), the *O. pusilla* distribution only extends to Forrest County in the southern third of Mississippi which is also the northernmost population that Benson mentions in The Cacti of the United States and Canada (1982). I and other investigators have found populations of *O. pusilla* as far inland as northeast Mississippi along the Tenn-Tom Waterway in Lowndes County. Also D. Pinkava (personal communication) was unaware that an *Opuntia* species with red-centered flowers occurs in this region and therefore did not include it in his treatment in the Flora of North America.

Commonly used morphological characteristics to make species delimitations are sometimes ambiguous among populations. This could be due to hybridization between taxa, or it could be due to habitat variables that cause shifts in morphology, making species delineation more inconclusive. Tuberous roots have often been a taxonomic character used to delineate certain species of *Opuntia* in the *O. humifusa* complex. Tuberous roots however, can be formed by growing specimens on differing substrates. In Radford et al. (1968), *O. pusilla* and *O. humifusa* are separated by nodal disarticulation and the presence of more than one spine per areole. *Opuntia humifusa* can show a small degree of nodal disarticulation under the right circumstances (e.g., stress). I have seen numerous populations of *O. humifusa* where more than one spine would be present per areole. Contrarily, I have observed numerous plants of *O. pusilla*, when grown in the shade, to produce 0-1 spine per areole. In Wunderlin (1998), these two species are

separated by spines being retrorsely barbed or not and nodal disarticulation. In *O. humifusa* var. *humifusa*, I have observed that young spines are extremely retrorsely barbed. Also, in many instances, older spines of *O. pusilla* lose the characteristic retrorse barbs normally seen, especially on more basal cladodes, but as well on terminal cladodes.

Hybridization is said to be rampant in the Cactaceae and especially within the genus *Opuntia* (Grant & Grant 1979, Benson 1982, Rebman & Pinkava 2001, Griffith 2003 & 2004); however, no one has demonstrated conclusively that hybridization occurs between *O. humifusa* and *O. pusilla*. It has only been noted from natural populations (Radford 1968, Benson 1982, Weakly 2003). Populations of a potential hybrid taxon were studied in detail. Along with habitat descriptions, morphological characteristics are described in order to help better understand the underlying mechanisms involved in the origin of this taxon. This information will be useful in conjunction with molecular data at a later date to see whether these populations actually represent hybrids.

Morphological data, taken from natural populations in this study, are used carefully as a basis for developing a descriptive key for the native *Opuntia* of Mississippi. A general key for the flora of Mississippi is still unfinished and therefore unavailable; however, this will provide a preliminary guide to one of the more ambiguous groups.

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CHAPTER II

HABITAT TYPIFICATIONS FOR THE *OPUNTIA* (CACTACEAE)

OF THE MID-SOUTH

Abstract

The ecology of *Opuntia* species in the eastern United States has been poorly studied. Available information has usually been anecdotal or observational without the necessary testing of parameters of habitat structure that predict species' distributions. This work deals with the associate plant species and soil characteristics that are useful in identifying habitat requirements for *Opuntia* in the southeastern United States. Twenty-one sites were chosen from Mississippi and coastal Alabama among five *Opuntia* taxa, *O. humifusa* var. *humifusa, O. humifusa* var. *cespitosa, O. pusilla, O. stricta,* and *O.* "hybrid". Abiotic and biotic parameters were measured to identify habitat and community structure. *Opuntia humifusa* var. *humifusa, O.* "hybrid", and *O. pusilla* all were more similar in habitat characteristics than the other two taxa. *Opuntia humifusa* var. *cespitosa* was correlated with more mesic environments and heavier soils than the other taxa. *Opuntia stricta* was found in higher pH soils. A variety of associate species were found with the *Opuntia* taxa. This information can be used as a framework for those interested in working in habitats where *Opuntia* species occur. Such information also may prove useful as *Cactoblastis cactorum* becomes more of a threat to southeastern *Opuntia*

populations and continues spreading westward. This information will be helpful for developing a predictive model of *Opuntia* species occurrences.

Introduction

The ecology and taxonomy of prickly pear cacti (*Opuntia* species) of the eastern United States have been poorly studied. Hanks and Fairbrothers (1969) described ecological aspects of populations *Opuntia humifusa* (Raf.) Raf. (sensu *Opuntia compressa* (Salisb.) Macbr. in the northeastern United States. Benson (1962), a recognized authority on North American cacti, provided anecdotal descriptions of habitats in which *Opuntia* could be found along the Atlantic and Gulf coasts. Doyle (1990) minimally described habitats where species within the *O. humifusa* complex might be found. General information on habitat characteristics of eastern *Opuntia* has been provided by Radford et al. (1968), Wunderlin 1997, Pinkava 2003, and Weakley 2003, but this information has been extrapolated from collections and not actually from testing habitat requirements.

Most eastern *Opuntia* species in the southeastern United States (e.g., *O. cubensis, O. humifusa, O. pusilla, O. stricta* and *O. triacantha*) are more abundant in sandy, slightly disturbed xeric areas (e.g., barrier islands, coastal sand dunes, and inland coastal plain sand deposits) which provide suitable habitats for *Opuntia* (Benson 1962). Several of these species are sympatric, and reportedly hybridize (Snow 1981, Benson 1982, Doyle 1990). *Opuntia* are renowned for hybridization (Benson 1982, Rebman & Pinkava 2001, Pinkava 2003, Powell & Weedin 2004). The southwestern species, *Cylindropuntia leptocaulis* (D.C.) F.M. Knuth, has been found to hybridize in up to 14 different

combinations (Donald Pinkava, Desert Botanical Garden, personal communication). One taxon in this study appears to be of hybrid origin and will be referred to as O. "hybrid."

The most common species of *Opuntia* in Mississippi are *O. humifusa* (Raf.) Raf., *O. pusilla* (Haw.) Haw., and *O. stricta* (Haw.) Haw. *Opuntia humifusa* and *O. pusilla* can be found from the barrier islands to quite some distance inland. *Opuntia stricta* is restricted to coastal areas in Mississippi (e.g., barrier islands, shell middens), except for where it has been transplanted as an ornamental. I have recently identified a new variety of *Opuntia* for Mississippi, named here as *O. humifusa* var. *cespitosa* (Raf.) Majure (comb. nov., under consideration), which is commonly found in the Black Belt Prairie physiographic region, but with some outlying populations. This variety differs from *O. humifusa* var. *humifusa* in several characters and also differs from the similar *O. macrorhiza* Engelm. (Donald Pinkava, personal communication).

Cactoblastis cactorum Berg (cactus moth) is an invasive species that recently has become a threat to our native populations of *Opuntia* (Hight et al. 2001). This species, native to Argentina was originally introduced into Australia for control of introduced *Opuntia* and, following its success there, introduced into South Africa, Hawaii, Mediterranean areas, and elsewhere as a biological control agent (Zimmermann et al. 2000). This moth was introduced into the Caribbean island of Nevis in 1957 (Stiling 2000), and it subsequently dispersed to other islands (Habbeck & Bennett 1990, Pemberton 1995, Johnson & Stiling 1996). In contrast to native species of cactophagous moths, *C. cactorum* has gregarious larvae that can destroy the whole plant instead of a single cladode, with subsequent generations eliminating large stands of *Opuntia*. This moth was first detected on Big Pine Key in south Florida in 1989 (Habbeck & Bennett

1990). In addition to its dispersal from the Florida Keys, evidence has been provided based on DNA that it has been introduced into the southeastern United States more than one time (Simonsen et al, personal communication). Currently this invasive species occurs in coastal areas from Dauphin Island, Mobile County, Alabama (where efforts are in progress to eradicate it) to South Carolina. In addition it was recently detected on Isla Mujeres and Cancun, Mexico (USDA 2007).

The cactus moth is thought to have been introduced into Florida through natural dispersal or unintentional human introduction (Mahr 2001). In the case of the recent Mexican detection, *Cactoblastis* may have been dispersed by previous meteorological events, that carried it from Cuba and other Caribbean Islands where it had been released as a biocontrol agent (Habeck & Bennett 1990, Pemberton 1995, Johnson & Stiling 1996).

As so little is known about our native *Opuntia* species, the cactus moth potentially could "devour" knowledge of the species before we fully understand them ecologically and taxonomically. The potential impact of the cactus moth on our native species requires more understanding of the ecology and taxonomy of our native *Opuntia* species. In addition, ecological data could prove useful in predicting areas where *Opuntia* might be found in the eastern United States as well as monitoring areas where the invasive *Cactoblastis* could colonize. This study provides ecological and distributional data on *Opuntia* species in the Midsouth and identifies habitat characteristics of novel (or poorly studied) taxa, such as *O. humifusa* var. *cespitosa*.

Materials and Methods

Study sites and data collection

      Sites throughout the state of Mississippi and southwestern Alabama with *Opuntia* species were located using the scarce amount of existing herbarium data, soils data from county soil surveys, personal communication, and from other sources (e.g., floristic surveys, theses and dissertations, and plant community reports). Of the 40 sites identified, twenty-one were subjectively chosen for this work based on *Opuntia* species present, the size and health of the population, and physiographic region (sites were stratified among different physiographic regions in order to account for biotic and abiotic heterogeneity that could been found with respect to geographic location; Fig. 2.1).
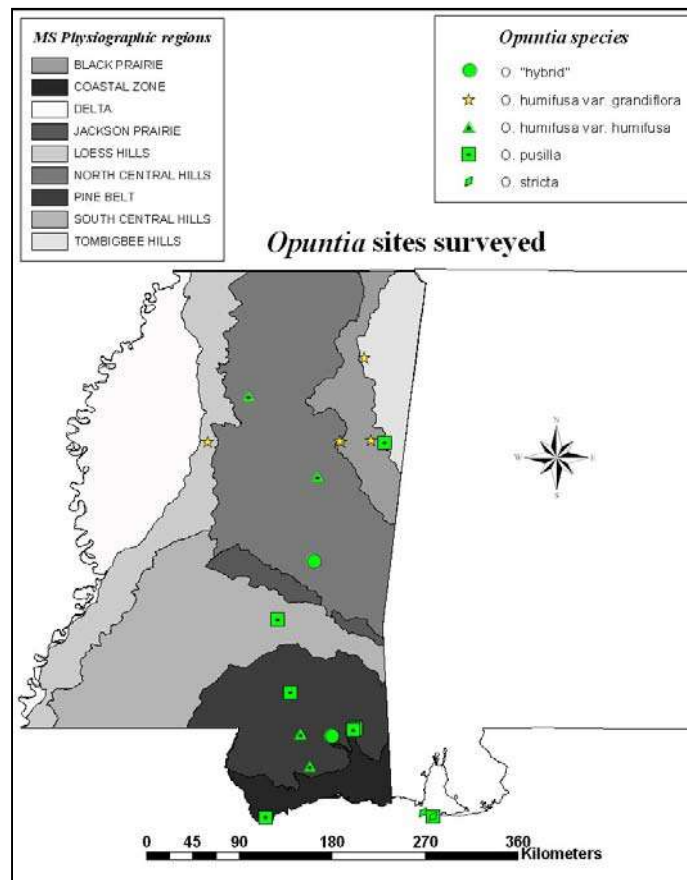
Figure 2.1. The twenty-one sites surveyed in Mississippi were located among seven physiographic regions. The sites in southwestern Alabama consisted of only one physiographic region (coastal zone) along the gulf coast. Some points are located in close proximity to others and therefore are difficult to separate on the map.

Within each site, transects were placed so that they would be located within the densest portions of the population, considering that these areas should be most exemplary of the population. Transects for each site were of varying lengths since populations were of different sizes. Along each transect, 1m^2 plots were set up at 4 m intervals. The plots were centered around the closest, mature *Opuntia* plant at least 4 m from the last plot along the transect. Morphological characteristics were measured only for mature plants in each plot. The percent cover of the *Opuntia* species as well as all other associate plant species within each plot, was subjectively determined on a 100 point scale. Two soil cores were taken to a depth of 15cm for determining pH and soil particle percent composition.

Associate canopy species were surveyed using a 2.5m radius plot originating from the center of the *Opuntia* plant within the 1 m^2 plot. Every stem per species was counted within the 5 m plot. Those stems counted included only woody species (shrubs, trees, vines) found within the 19.6m^2 plot. In some cases, the highest population densities for the *Opuntia* species were in open areas with few to no canopy species. In those cases, canopy survey plots were placed in areas adjacent to the larger population (within 5-10m), with an *Opuntia* plant still serving as the axis for the plot.

Analyses

Indicator species analysis (ISA) was used to determine plant species that were associated quantitatively with *Opuntia* in these twenty-one study areas. Data used for these analyses consisted of associate species that made up the ground-cover and a separate data set of canopy species associated with *Opuntia* populations. The ISA

analysis was conducted by guidelines of McCune and Grace, 2002 using PcOrd (version

4). This analysis uses relative species abundance based on species frequency data per site

to determine the level at which a particular species was found within the site (i.e., if

found in only one site, it would indicate 100% relative abundance for the site although

low abundance levels might make this species have insignificant values). Relative

frequency is the proportional frequency for that species located within a certain site.

Indicator values are determined as a product of the relative frequency and relative

abundance, and a Monte Carlo test of significance is used to determine whether the

indicator values for species are significant (i.e., is one species located in one area over

another by more than just random coincidence) at $\alpha = 0.05$.

Simple linear regressions were carried out in SAS 9.0 to test for relationships

between the abiotic variables and percent *Opuntia* coverage within the plots. A multi

response permutation procedure (MRPP) was run in PcOrd 4 to test for actual significant

differences among and between sites based on overall community data (e.g., pH, soil

particle size composition, associate plant species). Soil particle size composition data

were arcsin√ transformeu and then standardized ($z_i \equiv \dfrac{x_i - \overline{x}}{\sigma}$) with the pH data in

SYSTAT 10. The standardization of pH and soil data adjusts the scale between different

types of quantitative data but relationships remain the same. Therefore, pH data does not

overpower soil data by having greatly differing values. The Sorensen (Bray-Curtis)

distance measure was used to calculate the distance matrix. Groups were defined by the

Opuntia species present. The output for MRPP includes an A-value and a p-value. The A-

value describes the amount of "within-group homogeneity." For example, a group is

more homogeneous the closer the A-value is to 1 or more heterogeneous the further A

diverges from 1. The p-value is a measure of statistical probability testing the null hypothesis that groups do not differ more than would be expected at random (McCune and Grace 2002).

In order to determine the mechanisms driving differences between sites and relationships among abiotic variables and species percent cover data, a Canonical Correspondence Analysis (CCA) was applied using PcOrd 4. This is an ordination used to determine community structure based on measured environmental variables. As we were more interested in abiotic forces driving the community framework of different *Opuntia* species, this analysis seemed most appropriate. The analysis was based on two data matrices. The first matrix consisted of plot- and site-wise species data; the second matrix consisted of the environmental variables measured. Two analyses were performed. The first consisted of all *Opuntia* species presence data and their associate species within the primary matrix. The second analysis was based on *Opuntia* species presence data within the primary matrix. For both analyses, 1000 runs were chosen for the Monte Carlo test to test for no linear relationship between matrices. Scores used for graphing purposes were the LC scores or the linear combinations of environmental variables.

Results

The ISAs demonstrate a variety of indicator species for these *Opuntia* species. Indicator species are those that had high relative abundance within plots of a certain *Opuntia* species and also were found to be correlated with that *Opuntia* species by more than just chance alone (i.e., they had significance values of $p \leq 0.05$; Table 2.1 & 2.3). Most of the indicator species were more indicative of sites rather than species of *Opuntia*,

as many also could be found in sites with other *Opuntia* species despite their not occurring within the plots. For example, *Carex tenax* was an indicator species for *O. humifusa* var. *humifusa*, but it also was seen with *O. pusilla* on numerous occasions. Thus, because most of the *Opuntia* taxa are sympatric, with the exception of *O. humifusa* var. *cespitosa*, associate plant species among the *Opuntia* studied also are useful for understanding plant assemblage structure (Table 2.2). Many of the associated taxa are found in moderately disturbed areas and suggest a level of disturbance that is suitable for the sustained existence of *Opuntia* species in areas where interspecific competition levels could be reduced.

Although found with all other *Opuntia* species in the state, *Juniperus virginiana* was the most abundant canopy species associated with *O. humifusa* var. *cespitosa,* and subsequently was an indicator species for this taxon (*O. humifusa* var. *cespitosa* is often found in cedar barrens and glades). *Baccharis halimifolia* was one of very few canopy species found in the areas surveyed with *O. stricta* and the only canopy indicator species for *O. stricta*. Indicator canopy species for *Opuntia humifusa* included: *Pinus palustris, Quercus falcata, Serenoa repens,* and *Vaccinium elliottii*. Neither the putative hybrid, *O. "hybrid"*, nor *O. pusilla* had any canopy species as indicators. As with ground cover, indicative canopy species also could be found with other *Opuntia* species than those for which they were indicators, so those canopy species that were found to co-occur with multiple *Opuntia* taxa will provide more useful information when trying to locate *Opuntia* (Table 2.4).

Table 2.1. *Opuntia* taxa are given along with their indicator ground-cover species. Indicator species are chosen by those ground-cover species having a p-value ≤ 0.05 based on a Monte Carlo Test.

Opuntia species	Indicator Ground-cover Species
Opuntia "hybrid"	*Andropogon sp., Callicarpa americana, Conyza canadensis, Dichanthelium aciculare* ssp. *aciculare, Eupatorium capillifolium, Galactia volubilis, Gelsemium sempervirens, Lechea tenuifolia, Parthenocissus quinquefolius, Pinus taeda, Pityopsis aspera, Rhynchospora megalocarpa, Schizachyrium scoparium, Smilax smallii, Tragia urens*
Opuntia pusilla	*Aristida dichotoma* var. *curtissii, Aristida tuberculosa, Chrysoposis mariana, Croptilon divaricatum, Dichanthelium oligosanthes, Hypericum gentianoides, Oenothera laciniata, Stipulicida setacea var. setacea, Triplasis americana*
Opuntia humifusa var. *humifusa*	*Carex tenax, Dichanthelium sphaerocarpon, Krigia virginica, Lonicera japonica, Stenotaphrum secundatum, Wahlenbergia marginata*
Opuntia humifusa var. *cespitosa*	*Centrosema virignianum, Chamaechrista fascicularis, Cynodon dactylon, Dichanthelium acuminatum* ssp. *lindheimeri, Dichondra caroliniensis, Helenium amarum, Iva annua, Medicago lupulinus, Oenothera speciosa, Oxalis stricta, Paspalum dilatatum, Pyrus communis, Ranunculus sardous, Salvia lyrata, Schedonorus phoenix, Trifolium repens, Verbena brasiliensis*
Opuntia stricta	*Campsis radicans, Conradina canescens, Cynanchum palustre, Galium hispidulum, Hydrocotyle bonariensis, Ipomoea sagittata, Panicum repens, Rubus trivialis, Smilax bona-nox, Solidago sempervirens, Tradescanthia roseolens*

Table 2.2. *Opuntia* species are coded as: 0=putative hybrid, 1=*O. pusilla*, 2=*O. humifusa* var. *humifusa*, 3=*O. humifusa* var. *cespitosa* and 4=*O. stricta*. Their associate ground-cover species are given in the right-hand column.

Opuntia species	Associate species
0,1,2,3,4	*Ambrosia artemesiifolia*
0,1,2,3	*Gamochaeta falcata, Schizachyrium scoparium*
1,2,3,4	*Cynodon dactylon, Smilax bona-nox*
0,1,2	*Bulbostylis ciliatifolia* var. *coarctata, Commelina erecta, Conyza canadensis, Dichanthelium aciculare* ssp. *aciculare, Gelsemium sempervirens, Hypericum gentianoides, Lechea minor, Lonicera japonica, Rumex hastatulus, Stylisma humistrata, Stylisma pikeringii, Trichostema dichotomum, Vaccinium arboreum*
0,2,3	*Andropogon* spp.
0,1,3	*Dichanthelium ovale* ssp. *villosissimum*
1,2,3	*Oxalis stricta, Vulpia myuros*
1,3,4	*Rubus trivialis*
2,3,4	*Stenatophrum secundatum*
1,2	*Acalypha gracilens, Andropogon virginicus, Clitoria mariana, Croptilon divaricatum, Dichanthelium sphaerocarpon, Diodia teres, Ilex vomitoria, Krigia virginica, Lechea mucronata, Nuttallanthus canadensis, Paspalum notatum, Plantago virginica, Pseudognaphalium obtusum, Smilax auriculata, Toxicodendron pubescens, Triodanis perfoliata, Vulpia ocotoflora*
2,3	*Carex muhlenbergii, Centrosema viriginiana, Cerastium glomeratum, Dichondra caroliniensis, Erigeron annus, Euphorbia corollata, Juniperus virigniana, Quercus falcata, Q. pagoda, Q. stellata, Salvia lyrata, Schedonorus phoenix, Solidago odora, Symphyotrichum patens, Trifolium campestre, Vicia sativa*
0,2	*Lechea tenuifolia, Pinus taeda, Polypremum procumbens, Rhynchosia cytisoides, Toxicodendron radicans*
1,3	*Chamaechrista fasciculata, Dichanthelium acuminatum* ssp. *lindheimeri, Solanum carolinianum*
1,4	*Lepidium virginicum, Panicum repens, Physalis angustifolia, Silene antirrhina*

Table 2.2 Continued.

2,4	*Dichanthelium acuminatum* ssp. *fasciculatum, Dichanthelium portoricense*
3,0	*Galactia volubilis*
3,4	*Medicago lupulinus*

Table 2.3. *Opuntia* species are given along with their indicator canopy species. Indicator species are chosen by those canopy species having a p-value $<$or$=$ 0.05 based on a Monte Carlo Test.

Opuntia species	Indicator Canopy Species
Opuntia humifusa var. *humifusa*	*Pinus elliottii, Quercus falcata, Serenoa repens, Vaccinium elliottii*
Opuntia humifusa var. *cespitosa*	*Juniperus virginiana*
Opuntia stricta	*Baccharis halimifolia*

Table 2.4. Associate canopy species present with more than one species of *Opuntia* are
presented in the following table. *Opuntia* species are coded as: 1=*O. pusilla*,
2=*O. humifusa* var. *humifusa*, 3=*O. humifusa* var. *cespitosa* and 4=*O. stricta*.
Canopy data was not recorded for the putative hybrid.

Opuntia species	Associate canopy species
1, 2, 3, 4	*Juniperus viriginana*
1,2,3	*Diospyros virginiana, Ilex decidua, Liquidambar styraciflua, Lonicera japonica, Quercus falcate, Quercus hemisphaerica, Quercus nigra, Vaccinium arboreum, Vitis rotundifolia*
1,2	*Albizia julibrissin, Ilex vomitoria, Pinus palustris, Prunus serotina, Quercus incana, Quercus laevis, Quercus margarettiae, Quercus virginiana, Vaccinium elliottii, Vaccinium stamineum*
1,3	*Campsis radicans, Ulmus alata*
2,3	*Carya pallida, Carya tomentosa, Cercis canadensis, Fraxinus americana, Quercus alba, Quercus stellata, Quercus velutina*

Opuntia pusilla percent cover was negatively correlated with pH (p=0.0002,
R^2=0.28) and the amount of sand present (p<0.0001, R^2=0.39), but was positively
correlated with percent clay (p=0.002, R^2=0.20) and percent silt (p=0.004, R^2=0.18)
(Figure 2.2 A-D). Percent cover of the putative *Opuntia pusilla × humifusa* hybrid also
was correlated negatively with percent sand concentration (p=0.03, R^2=0.39) and
positively correlated with the percent silt concentration within the soil (p=0.04, R^2=0.37;
Fig. 2.2 E-F). The other three species were not significantly correlated with any of the
abiotic parameters measured.
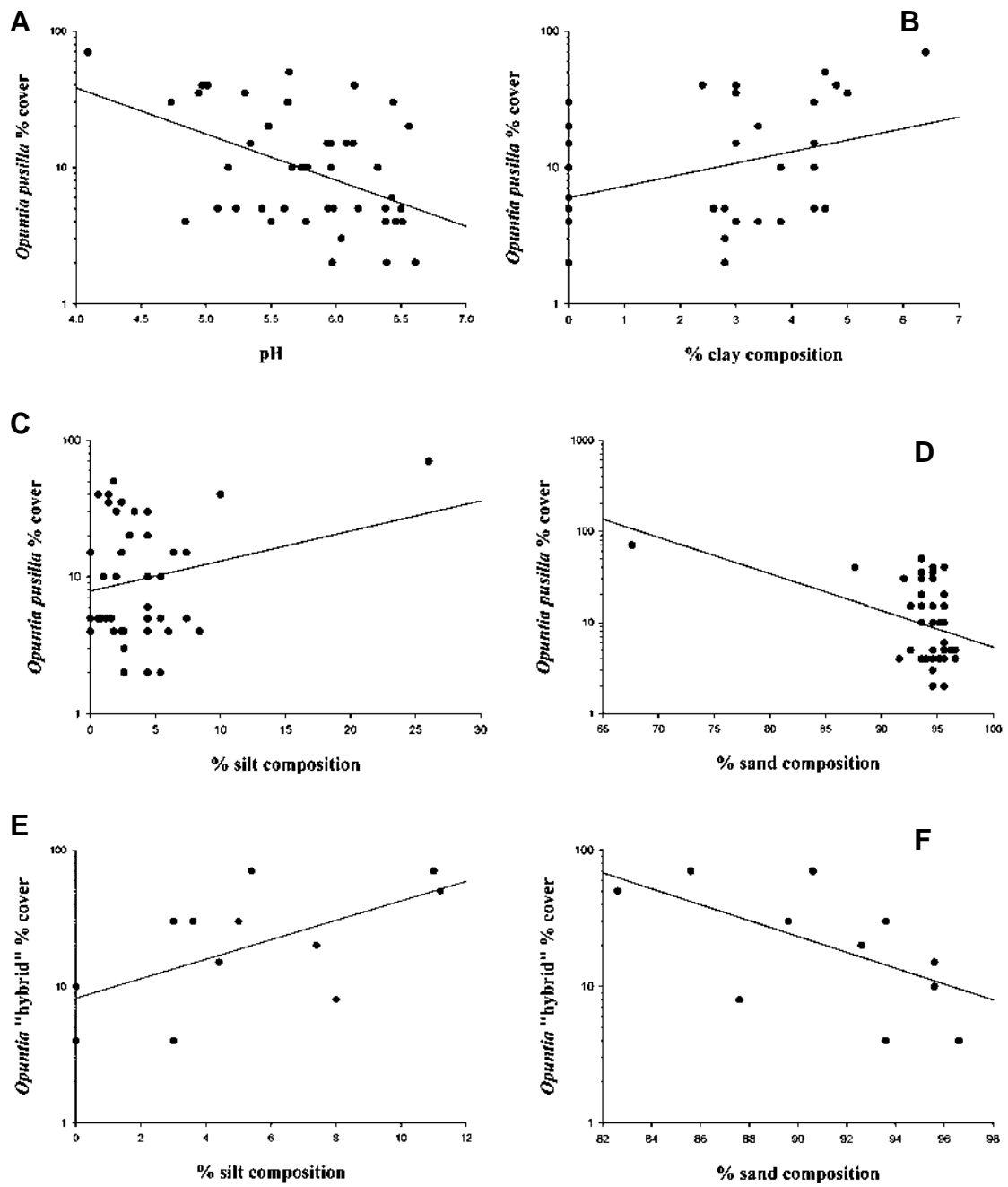
Figure 2.2. A-F. Regression analyses indicating relationships among *O. pusilla* and the putative hybrid with environmental variables.

The MRPP analysis demonstrated there to be a statistically significant relationship among the abiotic data and the *Opuntia* species (p<0.000001, A=0.08). Pairwise comparisons were run between all of the species and their habitat data to determine which groups may have been causing significant effects. All of the pairwise comparisons revealed significant relationships among the *Opuntia* species and the environmental data, signifying that certain underlying biotic or abiotic variables were the cause for these relationships (Table 2.5).

Table 2.5. MRPP analyses showed significant differences among all of the
Opuntia species and their environmental variables, as well as differences
when compared pairwise. High between group heterogeneity was
observed among all of the pairwise comparisons. Because of multiple
comparisons (n=10), the pairwise comparisons are significantly different
at p<0.005.

Opuntia species	p-value	A-value
Among all groups	<0.00000001	0.08
O. "hybrid"& *O. pusilla*	<0.000001	0.03
O. "hybrid"& *O. humifusa* var. *humifusa*	<0.0003	0.03
O. "hybrid"& *O. humifusa* var. *cespitosa*	<0.00001	0.06
O. "hybrid"& *O. stricta*	<0.0001	0.13
O. pusilla & *O. humifusa* var. *humifusa*	<0.00000001	0.04
O. pusilla & *O. humifusa* var. *cespitosa*	<0.00000001	0.04
O. pusilla & *O. stricta*	<0.00000001	0.06
O. humifusa var. *humifusa* & *O. humifusa* var. *cespitosa*	<0.000005	0.04
O. humifusa var. *humifusa* & *O. stricta*	<0.0000007	0.07
O. humifusa var. *cespitosa* & *O. stricta*	<0.00006	0.09

Clear relationships among abiotic variables and the different *Opuntia* species

were shown by CCA when carried out without associate species. Axis 1 was the most

significant at p=0.001 and explained 22 percent of the variance among the data. *Opuntia*

humifusa var. *humifusa, O. pusilla,* and their putative hybrid all were correlated strongly

with a high percent sand content. *Opuntia humifusa* var. *cespitosa* was correlated

positively with percent clay and silt concentration, whereas *O. stricta* was correlated with

increasing pH (Fig. 2.3A). When CCA was carried out with associate species, clear

patterns still were seen and were nearly identical to the previous analysis, although only 4

percent of the variance was explained (Fig. 2.3B).
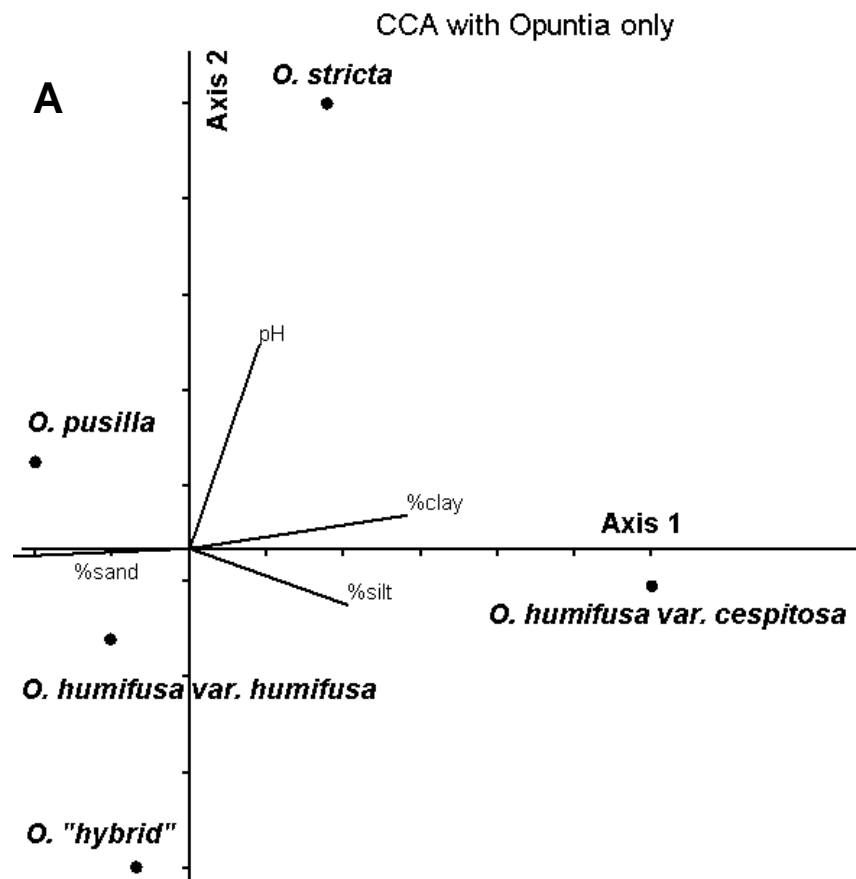
Figure 2.3. A&B. CCA results showing the relationships among *Opuntia* spp. and
environmental variables; in (A) the environmental variables were only
constrained against *Opuntia* spp. presence data explaining 22 % variance; in
(B) all associate species and *Opuntia* species were run in the analysis
explaining 4 % variance. In Figure 3B, *Opuntia* spp. are coded as in the
previous tables, where O=*O.* "hybrid," 1=*O. pusilla,* 2=*O. humifusa* var.
humifusa, 3=*O. humifusa* var. *cespitosa,* and 4=*O. stricta.*
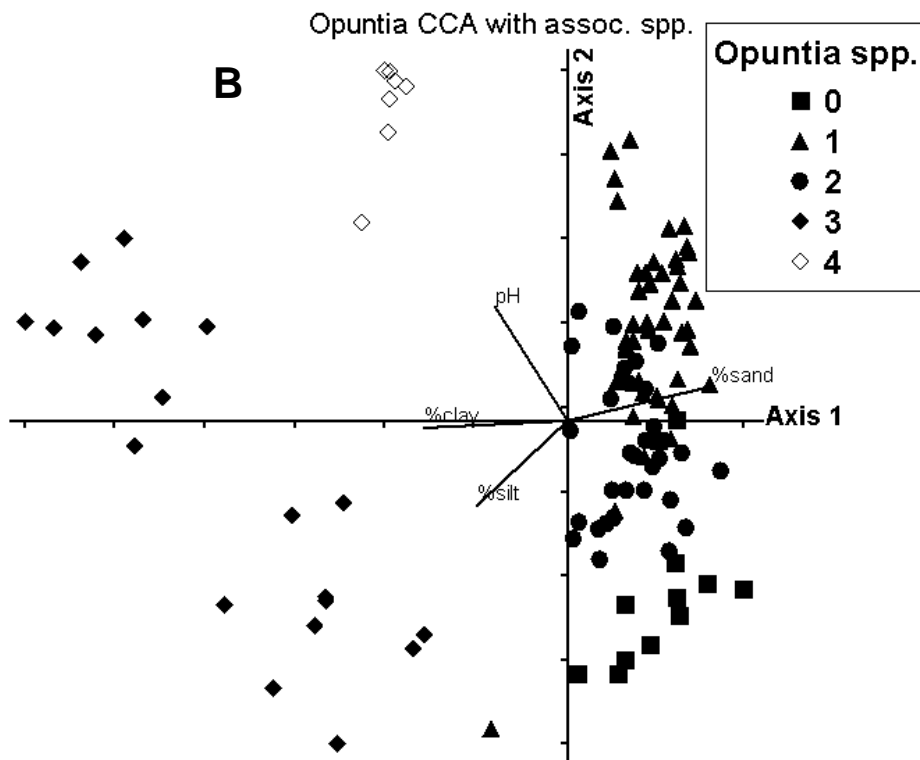
Figure 2.3. continued.

Discussion

The *Opuntia* taxa surveyed in this study can be separated to some extent based on their habitat characteristics. This holds true although several of the species are sympatric. *Opuntia humifusa* var. *cespitosa* is being recognized as a different taxon from typical *O. humifusa* var. *humifusa* based on morphological characteristics. The results of these analyses demonstrate that this plant also differs greatly in habitat characteristics from *O. humifusa* var. *humifusa*. While *O. humifusa* var. *humifusa* is more restricted to areas with higher percent sand composition and a lower pH, *O. humifusa* var. *cespitosa* is more often found in habitats with a higher percent clay and silt content, and a slightly higher pH. Associate vegetation also can be quite different between those two entities, as *O. humifusa* var. *cespitosa* is more typical of mesophytic vegetation and *O. humifusa* var.

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humifusa is more commonly associated with xerophytic vegetation. This is noteworthy as *O. humifusa* var. *cespitosa* appears to be more closely related to *O. macrorhiza* than is *O. humifusa* var. *humifusa,* the former of which also is more commonly found with mesophytic vegetation (Powell & Weedin 2004).

  Opuntia humifusa, *O. pusilla*, and *O. stricta* can occur sympatrically in coastal populations. However, most of the populations surveyed were inland except for those at Fort Morgan, AL. Thus, the large differences among habitat structure observed for *O. humifusa* and *O. pusilla,* as compared with *O. stricta* could be attributed to site selection. However, *O. stricta* often is found slightly segregated from *O. humifusa* and *O. pusilla,* whereas the latter two are frequently seen growing closely together, even in coastal habitats (e.g., Horn Island, Jackson Co., MS). The different growth forms of these species also could play a role in where these species tend to occur or where they can occur. *Opuntia stricta*, being more frutescent, can tolerate taller and denser stands of associate vegetation (e.g., dense canopy produced by forbs and small shrubs). *Opuntia humifusa* and *O. pusilla*, on the other hand, need sites that are more open or free from a dense understory canopy produced by shrubs, vines, and the taller herbaceous species.

  The regression analysis showed that percent cover of the putative hybrid and *O. pusilla* were correlated negatively with a high percent sand composition. However, CCA results indicate that these taxa most often occur in areas containing higher amounts of sand. The analyses thus indicate that these taxa, although negatively affected by higher amounts of sand, are also more restricted to areas with higher amounts of sand. *Opuntia pusilla* occurs most frequently in areas containing between 40% and 70% sand, but the highest percent cover was observed at a 50% level of sand concentration. *Opuntia pusilla*

is smaller than the other species and presumably would be more vulnerable to interspecific competition effects. The higher sand content within the soil could lower the amount of interspecific competition this species would be subjected to *O. pusilla* did have the lowest average species richness/plot overall, n=7.9. The lowest average percent cover of associate vegetation was recorded from *O. pusilla* plots as well (47%), however, other species were very close to that average (e.g., *O. humifusa* var. *cespitosa* = 48% and *O. stricta* =49%).

One factor that could constrain results from these analyses is the low sample size for certain species, namely *O. stricta* and the putative hybrid. *Opuntia stricta* is only found naturally in coastal areas. Natural populations of this species in Mississippi are restricted to barrier islands, shell middens, and the coastal mainland. The largest local populations of *O. stricta*, although covering small areas, were in southwestern Alabama, thus their selection for survey. The resultant data contained very few plots. Few putative hybrid populations were known during at time of survey, so only a limited number of sites were available.

Conclusions

The sympatric species *O. humifusa, O. pusilla,* and their putative hybrid in Mississippi have, as one might presume, very similar habitat characteristics. Generally they occur in acidic, sandy soils in areas that receive a certain degree of disturbance, and they are associated more frequently with xerophytic plant assemblages. *Opuntia stricta*, which also is sympatric with *O. humifusa* and *O. pusilla*, thrives in some of those same habitats but might rely on other microhabitat features for successful establishment or may

just be able to tolerate a wider range of habitat features. It can occur in low depressions on shell middens and barriers islands and was seen to occur in more alkaline soils than *O. humifusa* or *O. pusilla*. *Opuntia* aff. *cespitosa* is considerably different from the other species in habitat characteristics. It generally occurs in less acidic soils having a higher percent silt and sand content subsequently causing reduced filtration and a more mesophytic habitat. The habitat characteristics of all of the taxa studied here can be applied to modeling efforts in order to better predict where *Opuntia* species can be located in the mid-south. This is especially important in areas that have been undersurveyed for *Opuntia* and will help fill in the gap when trying to locate "stepping stones" for *Cactoblastis*.

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CHAPTER III

THE MORPHOLOGICAL PLASTICITY OF *OPUNTIA PUSILLA* (HAW.) HAW.

(CACTACEAE) INDUCED THROUGH MICROCLIMATIC

DIFFERENTIATIONS

Abstract

The morphological characteristics of *Opuntia* species can be highly variable in relation to environmental pressures. This often can lead to taxonomic difficulties when delineating species. Several *Opuntia* species planted in a greenhouse setting were seen to diverge greatly in their morphology, as compared to the natural populations from which they were obtained. Natural populations of *O. pusilla* and greenhouse grown plants seemed to demonstrate the greatest amount of morphological plasticity. This species subsequently was used to test the induction of phenotypic changes by modifying microclimatic variables (light and heat quantities). Notable and statistically significant morphological changes were recorded as a result of our experimental treatments. Plants grown in the full light treatment produced 99.8% more spines than those in the shade treatment. Also, root diameter, cladode volume to area ratio and biomass produced were significantly greater for those plants grown in the full light treatment. Plants from the full light treatment produced significantly more and longer spines than plants from the natural population. Results also suggest that temperature plays a key role in spine production. This experiment demonstrates the ease in which the morphology of *O. pusilla* can be

manipulated depending on direct environmental pressures and exemplifies the care that must be taken when delimiting *Opuntia* species in the field.

Introduction

Morphological variability of *Opuntia* species is thought to be influenced by environmental pressures (Rebman & Pinkava 2001). Benson (1982) noted the change from an extremely spiny *O. macrorhiza* Engelm. collected in the field, to a plant that subsequently produced spine-free cladodes after being grown in cultivation. Presumably, that morphological change was correlated with a change in environmental characteristics from the natural environment into cultivation. Likewise, I observed considerable phenotypic plasticity in greenhouse-grown *Opuntia* species. This variability included increased density and lengths of spines, increased cladode thickness, and renewed growth of mature spines in greenhouse plants, in comparison with natural populations.

Lewis and Nobel (1977) found for cacti with dense spine coverage, such as *Ferocactus acanthodes*, that a simulated reduction in the number of spines caused an increase in stem surface temperatures due to an exaggerated convection coefficient. In simulations where the spines were added and even increased over their normal densities, stem surface temperatures were greatly reduced, especially at the apex. In a separate study, Nobel (1978) found that the surface temperature of *Mammillaria dioica* also was impacted through spine coverage by reducing the convection coefficient, reducing the amount of solar radiation reflected onto the stems, intercepting short-wave radiation during the day, and via the expulsion of long-wave radiation at night. The reduction of spines in this case increased the maximum temperatures and decreased minimum

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temperatures for this species. Therefore, not only were spines found to inhibit high temperatures during the day, but they also were seen to maintain higher stem apex temperatures at night which could potentially aid in the tolerance of cold temperatures. Nobel found that in cases where stem pubescence and spines were removed, spines had the greatest effect on temperature regulation.

In another experiment by Nobel (1983), spines for *O. bigelovii* and *F. acanthodes* influenced the stem surface temperature by absorbing short-wave radiation, which was subsequently reflected onto the stem surface by giving off long-wave radiation, by affecting the convection coefficient through air current regulation, and by heat conductance to or from the surface of the stem. He suggests that spines act as "long-wave radiators" for thermoregulation of stem surface temperatures. Within that experiment, those plants where spine coverage was reduced manually were shown to produce more biomass than those where spines were left on the plant. Paradoxically, spines not only reduced stem surface temperatures, but they also diminished plant productivity by decreasing the amount of PAR (photosynthetically active radiation) reflected onto the stem surface. Therefore, a "tradeoff" was exhibited between thermoregulation and overall plant production.

In natural populations of *O. pusilla*, from an observational perspective, spine production seems to be reduced in areas that are shaded and would experience lower temperatures. I wanted to test this hypothesis in a greenhouse study where ambient temperatures would be significantly decreased through the use of shade treatments and normal, ambient temperatures would be increased substantially in full light treatments due to the greenhouse setting. I expected that new growth from the shade treatment

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would produce fewer spines and also that cladode sizes would be different than new growth in the light treatment. New growth in the light treatment was expected to produce numerous spines, as well as exhibit different cladode morphology from the new growth in the shade treatment.

Materials and Methods

Study species

Opuntia pusilla is one of the more spinose, low growing *Opuntia* species in the southeastern United States and can be quite variable morphologically from population to population (pers. obs.). Due to natural characteristics of *O. pusilla* (e.g., easily disarticulating cladodes), terminal cladodes were easily gathered from parent plants with very limited disturbance to the environment. This species also was seen to be more environmentally reactive and faster growing, in preliminary observational studies, than *O. humifusa* or other eastern taxa.

Opuntia pusilla, as the name implies, is a relatively small prickly pear cactus (cladodes 8 x 2.5cm; Pinkava 2003) found in the southeastern United States from North Carolina to Texas among the coastal states (Benson 1982, Pinkava 2003, Weakly 2003). Generally, it is considered to be mainly coastal, being found in sand dune systems (Radford 1968, Snow 1977, Benson 1982, Wunderlin 1998, Pinkava 2003, Weakly 2003), open, deciduous forest edges in coastal areas and Caribbean Tropical Forest (Benson 1982), sandy openings and rock outcrops (Pinkava 2003), and sandy, pine-scrub forests (Radford 1968, Pinkava 2003). This cactus has sub-cylindric and/or flat cladodes, the latter being more typical of the genus (Rebman & Pinkava 2001), and is typically

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very spiny with 1-4 spines per areole (Radford 1968, Snow 1977, Pinkava 2003). The spines typically are strongly retrorsely barbed and the cladodes disarticulate with ease (Radford 1968, Snow 1977, Benson 1982, Wunderlin 1998, Pinkava 2003, Weakly 2003). These characteristics aid in the vegetative dispersal of this species, as the cladodes commonly become stuck to anyone who passes through a patch of *O. pusilla* (Radford 1968, Benson 1982, Weakly 2003). This is seen frequently in the *Cylindropuntia* (chollas) and is one of the primary means of vegetative propagation by that genus, as their present distributions may be attributed to this form of dispersal (Rebman & Pinkava 2001).

Study design and analysis

One hundred and twenty terminal cladodes of *Opuntia pusilla* were obtained from a natural population of this species from an historic, riverine sand deposit along the Tennessee-Tombigbee Waterway in Lowndes County, MS, USA (33.4970°N, 88.4468°W). Each cladode was gathered from a different plant to maximize any variation among the samples taken and hopefully reduce confounding morphological factors that might be associated with a single genotype. Two shade treatments and two light treatments were prepared in a greenhouse on the Mississippi State University campus. Shade treatments were made by using multiple layers of mosquito netting to simulate natural shading by overstory vegetation. For each shade and light treatment, 20 cladodes were chosen randomly from the 120 gathered. Ten of these were despined to test for productivity increases due to spine removal, while the other 10 were left natural. These were placed randomly on tables within the greenhouse.

The soil used was taken from the parent population (average pH = 5.9; average particle size composition = 95.4% sand, 3.6% clay, and 1.0% silt) to control for any extraneous problems that might occur using a different soil type. The other forty cladodes were despined and planted in the natural population, from which they were taken, to serve as an ambient reference group. Twenty of these were planted in full sunlight, while the other twenty were planted in some degree of shade (under shrubs, trees, etc.). All of the cladodes used were planted in mid-February to permit establishment before the growing season which begins in late March to early April. Cladodes planted in the greenhouse were watered twice weekly. Those planted in the natural population received only natural precipitation. Hobo data loggers were used to make temporal measurements of the microclimatic environment within each treatment in the greenhouse. Measurements were taken each hour from February until early September. The natural population was surveyed monthly beginning in May and lasting through September. A LICOR Quantum/Radiometer/Photometer (Model LI-250 Light Meter) and a digital pocket thermometer (ERT600; CE) were used monthly to record environmental characteristics at the field site. However, after the first two months, during a substantial drought, comparative microclimatic data collection was discontinued, as essentially no new growth was observed at the field site.

At the beginning of September, 2006, all of the newly produced cladodes from the full light and shade treatments were collected both from the greenhouse and the natural population. The number of new spines produced was counted and measured. Initially two spines, one shorter and one longer, often are produced from one areole, so these were separated into a long and short category. The longer spines generally are the first spines

produced. The size of the new cladodes was measured by length, width, and thickness. Fresh and dry biomass of each new cladode also was determined. Diameter and fresh and dry biomass were measured for the new roots produced. Volume and area were calculated for the cladodes, where a=length, b=width and c=height. The cladodes were considered as ellipsoids with; (Volume) $V = 4/3\ \pi\ (a)(b)(c)$ (Weisstein 2006) or scalene ellipsoids with (Area) $A \approx 4\pi(a^p b^p + a^p c^p + b^p c^p/3)^{1/p}$, where p =1.6075 (Michon 2006). One-way ANOVAs were run on the data, using SAS 9.1, to test for differences between the treatment measurements. I wanted to see if there were significant differences in the average dry biomass, cladode length, width, thickness, root diameter, and volume to area ratio between treatments. I also wanted to see if the new cladodes from the light treatment produced more numerous and longer spines than those produced by the parental population. Spines lengths and numbers were compared between the new greenhouse-grown cladodes and the parental cladodes (those from which the new growth was produced), which had developed in the natural population.

Results

Greenhouse plants

As would be expected higher values for sunlight intensity were recorded from the greenhouse light treatment, and night values were the same. The Hobo dataloggers used became saturated at light levels of 161 $\mu mol/m^2 s^{-1}$ (764 lum/ft^2) for both treatments, so daytime data was nearly useless after 8:00 a.m. until 4:00 p.m. To account for this a subsample of the data was taken twice a day at 7:00 a.m. and 5:00 p.m. (before and after saturation) for the two treatments. The difference of these samples was calculated. The

shade treatment sunlight intensity was on average 81.4 μmol/m^{2}s^{-1} less than the shade

treatment. The light treatment light intensity mean was 103.5 μmol/m^{2}s^{-1}, and the shade

treatment light intensity mean was 22.1 μmol/m^{2}s^{-1} based on the values from the Hobo

data loggers. So there was a 21.4% reduction in light intensity from the unshaded to

shade treatment. Greenhouse temperatures were much different between the light and

shade treatments (Fig. 3.1). In the full light treatment, as might be expected, temperatures

were more variable having a minimum temperature of 0.73°C at 6:00 a.m. on March 26,

2006 and a maximum temperature of 57.24°C at 1:00 p.m. on May 29, 2006. The

minimum and maximum temperatures of the shade treatment were 1.17°C also at 6:00

a.m. on March 26, 2006 and 56.6°C at 1:00 on August 10, 2006, respectively.
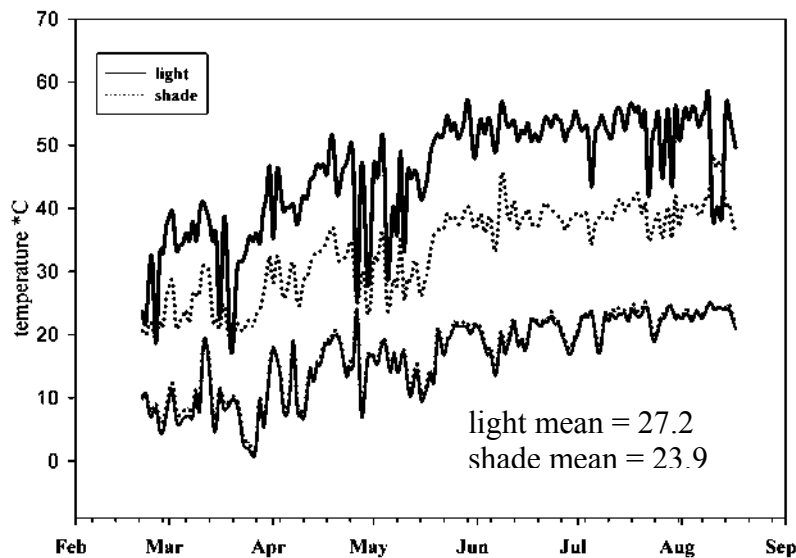
Fig. 3.1. Temperatures consistently were higher, as expected,
in the light treatment during daytime hours, and occasionally
lower during nighttime hours.

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The length and width of new cladodes from the shade treatment were significantly greater than for the light treatment (p<0.0001, F_{df} =79.88, df=116 and p<0.0082, F_{df}=7.24, df=116), respectively. However, cladodes were significantly thicker in the light treatment (p<0.0001, F_{df} =220.85, df=116; Fig. 3.2).
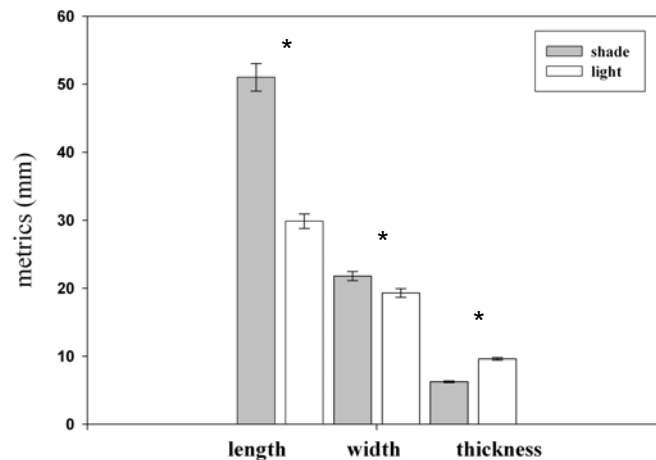
Fig. 3.2. Average cladode metrics per treatment with shade-grown plants being longer and wider, while light-grown plants are thicker. Asterisks indicate significant differences.

There was significantly more aboveground and belowground biomass produced by those plants subjected to the full light treatment (p<0.0001, F_{df}=39.57, df=79 and p<0.009, F_{df} = 7.15, df=79; Fig. 3.3) than in the shade treatment. Spine removal did not affect biomass production in either treatment (p=0.7025, F_{df}=0.15, df=39 for shade trt.& p=0.4621, F_{df}=0.55, df=39 for light trt.).
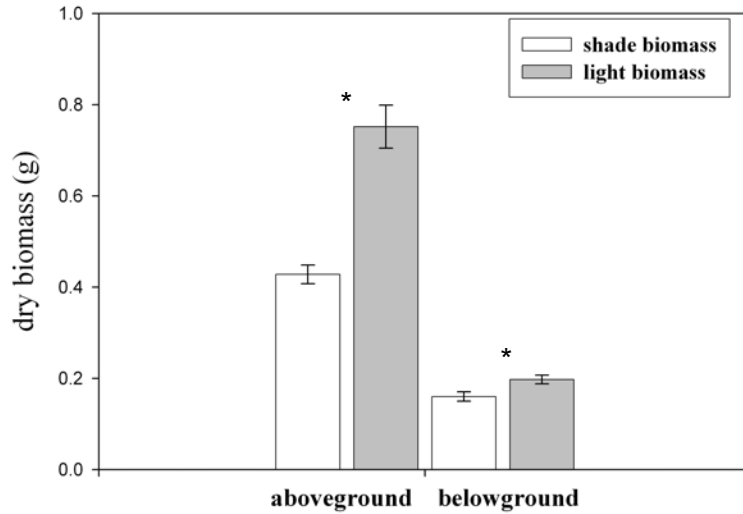
Fig. 3.3. Average above and belowground biomass compared between the shade and light treatment. Asterisks indicate significant differences.

The volume to area ratio (V:A) was significantly greater for those plants grown in the full light treatment (p<0.0001, F_{df}=133.71, df=115; Fig. 3.4).
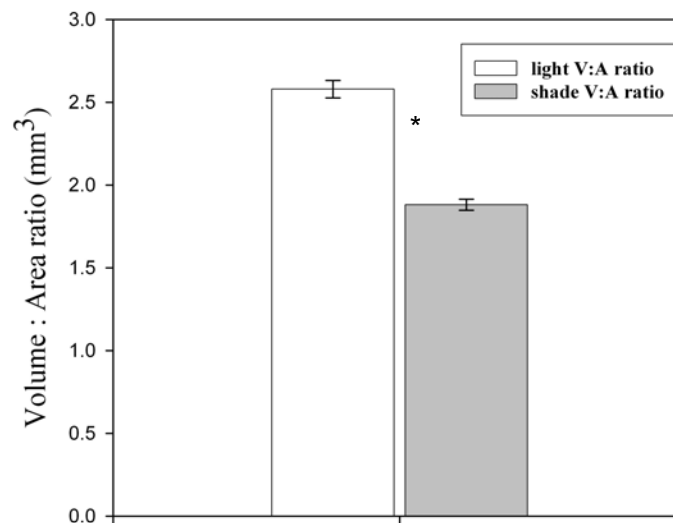
Fig. 3.4. Light treatment volume to area ratio was greater than the shade treatment. Asterisks indicate significant differences. Root diameter also was significantly greater in the full light treatment (p<0.0001, F_{df}=59.33, df=79; Fig. 3.5).
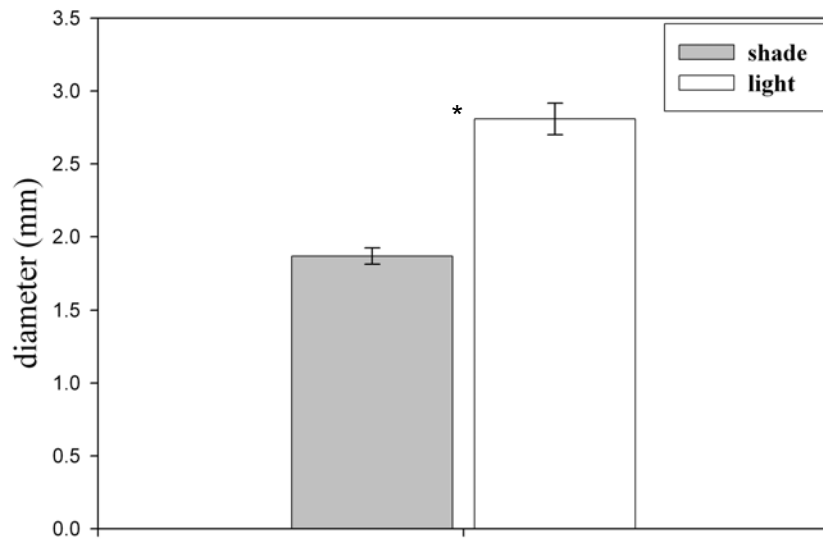
Fig. 3.5. Average root diameter per treatment. Asterisks indicate significant differences.

All of the new cladodes formed from those plants in the full light treatment produced numerous spines (Fig. 3.6). Only one new cladode produced from within one of the shade treatments produced one spine.
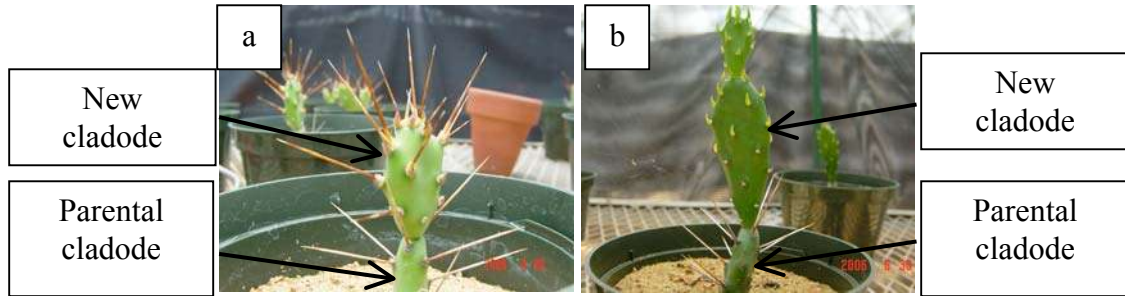
Fig. 3.6. This figure represents full light and shade grown plants with the new cladode in the full light treatment having produced numerous spines (a), while the new cladodes in the shade treatment produced no spines (b). The parental cladodes represented here are those that were not despined.

The new cladodes within the light treatment produced significantly more spines per cladode than those produced by the parental cladodes that were taken from the natural population ($p<0.0001$, $F_{df}=23.48$, df=29). The long, new spines produced were significantly longer than those produced by the parental cladodes ($p=0.045$, $F_{df}=4.06$, df=229) However, the parental cladode short spines were significantly longer than the short, new spines produced from the greenhouse plants ($p=0.038$, $F_{df}=4.4$, df=144; Fig. 3.7).
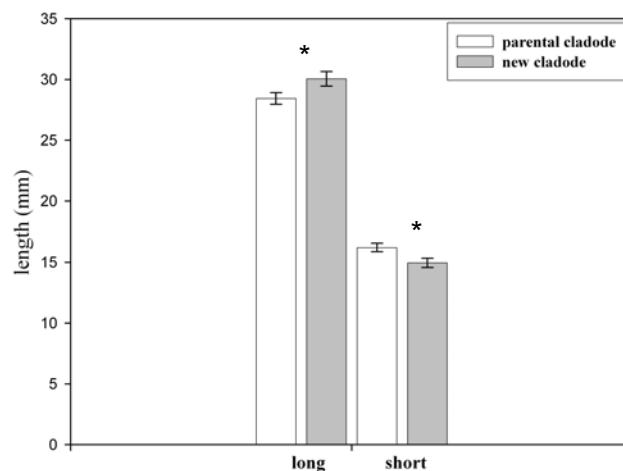
Fig. 3.7. Parental vs. new cladode spine lengths. Asterisks indicate significant differences.

Field plants

Cladodes planted within the natural population were subjected to extreme conditions during the growing season, as a major drought had affected the area. Growth therefore was extremely limited on all of the transplants. Only 48% (19) of the cladodes planted produced new cladodes, 40% (16) produced no new cladodes, and 12% (5)of those planted died during the experiment. Spines were produced on new cladodes from both the shade and light treatments, but more and longer spines were produced in the light treatment. Light and temperature data were significantly higher in the light treatment, as expected.

Discussion

Morphology

Morphological characteristics of *O. pusilla* were influenced heavily by differential heat and light levels between treatments. Cladode thickness, mean above and belowground biomass, root diameter, spine production and the volume to area ratio all were significantly greater in the full light treatment. Far more spines were produced in the full light treatment than in the shade treatment (99.8% more). Long spine lengths, and the overall number of spines produced per cladode were significantly greater in the greenhouse population, as compared to the parental population.

Larger cladode length and width in the shade treatment should be a function of decreased light availability, wherein plants increase leaf surface area and chlorophyll quantity to maximize light uptake. Lichtenthaler et al. (1981) observed the same results investigating the difference in sun and shade leaves of *Fagus sylvatica*. The sun leaves

were thicker and had a larger dry biomass, but leaf area was larger and contained higher amounts of chlorophyll in shade leaves. These are common changes observed between shade grown and light grown leaves (Gurevitch et al. 2002). Although cladodes are not leaves, they are photosynthetic stems and perform the same function.

The significantly shorter spines observed in the greenhouse plants for the "short spines" measured can easily be attributed to their degree of maturation. Glochids had not yet exerted either because of the degree of maturation (e.g., some new growth still had leaves at the time of collection). If plants were grown for more than one year, significantly longer "short" spines should be observed for the greenhouse plants, as well as the exertion of glochids. Of course, natural population biomass production could also be limited by water availability. Those cladodes planted in the natural population produced minimal amounts of biomass compared to the greenhouse plants, and some produced no biomass at all. The lack of water in the natural population likely constrained the production of fleshy biomass as well as spine production.

The difference in root diameter and overall biomass production between greenhouse treatments could be a result of increased photosynthesis in the light treatment and to subsequently, a larger store from which to obtain water and nutrients. Although the plants in both treatments were watered equally, soils in the full light treatment should have lost water more rapidly which could have driven the production of water storing roots. There are numerous genera and species of cacti that produce water storing roots (Dubrovsky & North 2002). I have found in many *Opuntia* populations that tuberous roots are produced in several species depending on the substrate in which they grow. Thus this characteristic, which is sometimes used as a diagnostic character in taxonomic

studies, seems to be a function of substrate attributes where the plants are growing.

Weniger (1970) found fibrous and tuberous rooted individuals of *O. macrorhiza* Engelm.

from the type locality for the species. Other authors also have found tuberous rooted

plants in species other than *O. macrorhiza* (Doyle 1990, Powell & Weedin 2004, D.J.

Pinkava, personal communication).

Biomass production was not influenced significantly by the removal of spines.

Other species in which a notable change in productivity has been measured (e.g., Nobel

1983) are taxa that are densely covered with spines. Spines would therefore have more of

an effect on PAR reflection from the stem surface and photosynthesis in those species

than in a species like *O. pusilla*, which is not as densely covered in spines.

Temperature is a highly selective evolutionary force. As Nobel and Hartstock

(1984) point out, "Temperature influences nearly all aspects of the physiology and

ecology of plants." It is thought that spine production can be influenced by the removal

or addition of light (D.J. Pinkava, personal communication). Spines can aid in

thermoregulation (Lewis & Nobel 1977, Nobel 1978, 1980; Rebman & Pinkava 2001,

Powell & Weedin 2004) but also may cause a reduction in photosynthesis (Nobel 1983,

Powell & Weedin 2004). So, does light or temperature play a more important role in

spine production and in increasing spine lengths? The greenhouse used in this experiment

is covered by a thin layer of translucent plastic, so the amount of available sunlight

should be reduced as compared to an open, natural scenario. In fact, light measurements

taken on one day with a LICOR Quantum/Radiometer/Photometer (Model LI-250 Light

Meter) from 4:00-4:30 p.m. were on average 510.5 $\mu mol/m^2s^{-1}$ less in the greenhouse

than outside of the greenhouse and values were statistically different (p<0.0001; SE +/-

64). Contrarily, maximum temperatures in the greenhouse are much higher than would be observed in a natural population in this area (e.g., 57°C). Accordingly, if light were the only factor in spine production, then natural populations should produce the higher number of spines with longer spine lengths than those observed in the greenhouse plants.

The amount of light only negatively affects cacti when associated with extreme temperatures or if light availability is limited (Nobel & Bobich 2002), so why would they produce numerous spines other than for temperature regulation? Certainly spines play a major role in the deterrence of herbivory, but this may only be an indirect advantage of spine production. Abrahamson and Rubinstein (1976) found no significant difference in spine coverage between a natural population of *O. humifusa* in a Florida sandridge habitat and a population subjected to frequent grazing by cattle. Spines are reduced bud scales and leaves of axillary buds (Salgado & Mauseth 2002). These reductions in structure are classical examples of xerophytic structural adaptations used for decreasing surface area and therefore transpiration rates of the plant (Gurevitch et al. 2002). However, we have shown that only under certain conditions are they developed. More work will be necessary to separate or link the effects of light and temperature on spine production, as well as other environmental catalysts that could be influential (e.g., precipitation).

Taxonomic Implications

The phenotypic plasticity of *O. pusilla* presents many problems. In trying to identify material in the field or herbarium specimens, identifications are highly dependent on the "classic" characteristics of a species. However, where material is collected from a single individual in a population, such characteristics may not be present. If individual

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plants, or the majority of the population is grown under less than ideal conditions (e.g., heavy shading, drought), the resultant morphologies can easily lead to errors in identification. Some of the main characteristics of *O. pusilla* are its small size, copious production of spines and growth habit. Therefore, an individual collected from the shade where fewer spines have been produced and cladode size has increased could easily be misidentified. Care should be taken that characteristics of the whole population are taken into account when determining this and other *Opuntia* species. As for herbarium material, annotations should be made only when sufficient information is available to produce a correct identification. Sometimes even plants with typical morphological characteristics for the species can become widely distorted through specimen preparation.

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CHAPTER IV

THE *OPUNTIA* (CACTACEAE) OF MISSISSIPPI

Abstract

Only a scarce amount of literature is available dealing with distributions, habitat characteristics, and keys to the southeastern species of *Opuntia*. These treatments often are ambiguous and are based on limited studies of the taxa. This work provides a descriptive key to the *Opuntia* of Mississippi along with the distribution of taxa and habitat descriptions. Herbarium material was examined from all of the herbaria in the state, as well as from other repositories. An in depth literature review was conducted to minimize interpretive error while making species designations and to understand characteristics of other species that should potentially be recognized. Observations, collections and measurements were made from natural populations within Mississippi and other parts of the southeastern United States. Plants also were planted in a greenhouse for a period of close to two years for observation. The following work is based on all of the information gained from the two year study, which includes six taxa and nearly 150 natural populations.

Introduction

The *Opuntia* species occurring in Mississippi and the eastern United States are a complex group, and the taxonomy of the species has never been resolved because they

are extremely morphologically plastic, poorly studied ecologically, and are difficult to preserve correctly. This treatment deals with the ecology, morphological variation, and taxonomy of the group for Mississippi. As the flora for Mississippi has not been completed yet, this also provides a preliminary treatment of the diversity and distribution of the Cactaceae for the state.

Opuntia species (Caryophyllales: Cactaceae; Stevens, 2005) are biologically complex xerophytes. The genus is native to the Americas, and species can be found from Canada in North America to the southernmost portion of the South America (Powell & Weedin 2004). However, Mexico has the highest diversity of species (DeFelice, 2004), where *Opuntia* species flourish in desert-like habitats due to their numerous xerophytic adaptations. These include thick, waxy cuticles that reduce the amount of water lost through transpiration and modified leaves and bud scales in the form of spines and glochids (Mauseth 2006) that decrease plant surface area and transpiration rates that further reduces water loss. Spines also have been shown to affect thermoregulation of cacti (e.g., Lewis & Nobel 1977, Nobel 1978, 1983). A large degree of spine coverage can affect the convection coefficient by forming a protective layer of air around the plant body and by reflecting sunlight. This decreases water loss and helps maintain or decrease plant body temperatures, but also affects photosynthetic rates and subsequently productivity (Nobel 1983). *Opuntia* species can grow roots with extreme rapidity to maximize the amount of water uptake after long periods of drought are broken by rain. They generally have shallow root systems as well, to take advantage of ephemeral, natural showering events. Also, like many other cacti, they exhibit crassulacean acid metabolism (CAM) type photosynthesis that enables them to reduce water loss by

opening their stomata only at night and utilizing stored CO_2 during the day for photosynthesis. Finally, *Opuntia* contain cells rich in polysaccharides that form mucilage, which easily binds to water molecules, thus making evaporation more difficult if the plant is injured. This mucilage also produces a firm, filmy layer over a wound that rapidly seals it off to avoid extra water loss. Fast forming scar tissue aids in this process at eliminating sources of moisture loss (Benson 1982, Rebman & Pinkava 2001).

The platyopuntias, or genera of Opuntioid cacti with flat stems (cladodes, cladophylls, or pads), commonly are known as "nopales" or "prickly pear cacti" (Benson 1982, Wallace & Fairbrothers 1987, Hanselka & Paschal 1991, Mohamed-Yasseen 1996, Rebman & Pinkava 2001, DeFelice 2004). They can grow at or near the ground surface, or they can form shrubs and even small trees. Generally, they produce an abundance of many seeded fruits, but also they are easily propagated from stem fragments. Many species easily disarticulate at the nodes, and form large colonies of clones from parent plants simply by vegetative reproduction (Benson 1982, Rebman & Pinkava 2001).

Opuntia species are hosts to a variety of insect and mite species (Mann, 1969) and also are utilized by many other animal species, including humans (Kalmbacher 1975, Benson 1982, Hanselka & Paschal 1991, Mohamed-Yasseen et al. 1996, Melink & Riojas-Lopez 2001, Perez-Sandi 2001, DeFelice 2004). In most of their range, prickly pears are used as fodder for livestock (Hanselka & Paschal 1991, Mohamed-Yasseen 1996, Nefzaoui & Salem 2001, DeFelice, 2004). Often they are grown for human consumption as well, where the young pads are collected and made into a variety of consumable products. The fruit can be made into beverages, syrup, a cheese-like product, or can be consumed raw (Benson 1982, Mohamed-Yasseen 1996, Pimienta 1997). The

seeds were used by early California natives to produce a "seed meal" (Benson 1982, Mohamed-Yasseen 1996). Species of *Opuntia* also are used ornamentally, medicinally, and commercially to make a red dye produced by the cochineal insect (*Dactylopius coccus* Costa) that feeds on species of *Opuntia* (Benson 1982, Pimienta 1997, Vigueras & Portillo 1997, DeFelice, 2004).

Opuntia are widely distributed in the southeastern US, where some species are planted for ornamental purposes. Many ornamental species are imported from the southwestern United States, e.g., the southwestern species, *Opuntia engelmannii* Salm-Dyck ex Engelm., or other areas in the Americas (e.g., *O. ficus-indica* (L.) P. Mill.). Natural dispersal of Opuntia is not well known, although Barlow (2001) suggested that extinction and population reductions of vertebrates have affected active dispersal. Bison, for example, are thought to have been major dispersers of *O. fragilis,* which has an extensive geographical range in the western United States (Mitch 1970). Jansen (1986) suggested that ancient megafauna consumed *Opuntia* fruit, and therefore would have been important dispersal agents. A great number of extant animals, such as deer, rabbits, coyotes, birds, and numerous reptiles, feed on *Opuntia* fruit and contribute to the dispersal of sexually produced propagules (e.g., Timmons 1941, Dean & Milton 2000, Melink & Riojas-López 2001). In addition, *Opuntia* species probably can be dispersed through hurricanes and other natural meteorological events (Majure et al. 2007). Cladodes could be transported by water to shell middens, barrier islands, and shorelines where they then would root and develop into new plants. Frego and Staniforth (1985) suggested that *O. fragilis* also could be transported along riparian systems by water.

Current status of the taxonomy of eastern US *Opuntia*

The current status of the taxonomy on eastern *Opuntia* is a work in progress. After nearly 200 years since *Cactus humifusus* was described by C. S. Rafinesque (1820), there still is confusion about what species even exist in the eastern United States. Questions of hybridization, varietal level status, specific status, as well as numerous morphological and physiological attributes remain unanswered. Based on Pinkava (2003), five species of *Opuntia* currently occur in the eastern United States. These are *O. cubensis* Britton & Rose, *O. humifusa* (Raf.) Raf., consisting of varieties *humifusa* and *ammophila* Small, *O. pusilla* (Haw.) Haw., *O. stricta* (Haw.) Haw., and *O. triacantha* (Willdenow) Sweet. However, according to the Plants Database (2007), based on taxonomic information from John Kartesz (Biota of North America Program; USDA 2007), there are nine species. These include *O. ammophila* Small*, O. austrina* Small*, O. x cubensis, O. dillenii* (Ker Gawler) Haw.*, O. humifusa, O. macrorhiza* Engelm.*, O. pusilla*, *O. stricta* and *O. triacantha.* Kartesz included certain taxa at the specific level, e.g., *O. austrina* and *O. dillenii,* apparently based on a 1990 dissertation by J.D. Doyle (Kartesz personal communication), which in no way conclusively segregates these taxa as separate species or even varieties (Doyle 1990). In my personal opinion, and in line with Pinkava (2003), I do not see the distinction between *O. humifusa* var. *humifusa* and *O. austrina* in Mississippi and consider them both within variety *humifusa*. There could be valid *O. austrina* in Florida from where it was described (Small 1903).

After having seen specimens and live material in the field, I do agree with the separation of *O. ammophila* as a separate species and not merely a variety of *O. humifusa*. Pinkava (personal communication) wanted to combine this species with *O.*

humifusa var. *humifusa*. He believes this species to be merely an ecotype due to its location below the frost line. I do not think that this taxa represents only an ecotype because typical, decumbent *O. humifusa* var. *humifusa* occurs adjacent to and farther south than locations of *O. ammophila*, although much more research on this question is needed.

I have only seen what would be considered *O. dillenii* from the Yucatán Peninsula, so I do not have enough experience with this taxon to comment on the inclusion or separation of it with or from *O. stricta*. However, considering the vast amount of morphological variation in the group, this taxon could easily be considered synonymous with *O. stricta*.

Benson had identified *O. macrorhiza* Engelm. from Wisconsin and Illinois (Benson 1982), but he also combined *O. tortispina* with *O. macrorhiza* (Powell & Weedin 2004). Pinkava (2003) has *O. macrorhiza* limited in distributionmuch farther to the south and west. Another species, *O. tortispina* which is considered conspecific with *O. macrorhiza* by the Plants Database (USDA 2007), most likely is the plant inhabiting those areas of the Midwest (Powell & Weeedin 2004) and apparently as far east as Ohio (USDA 2007). After examining specimens of *Opuntia* from Wisconsin, I could not be absolutely sure of the species, but they shared characteristics of both *O. macrorhiza* and *O. tortispina*. Much work is needed on this group from the Midwest and Eastcentral United States.

Opuntia triacantha is quite rare in the US with populations only on Big Pine Key, Florida. This species is more common in the Caribbean, where it hasn't been extirpated by *Cactoblastis cactorum*.

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Opuntia cubensis is treated as a species by Pinkava (2003), but it is referred to as a hybrid species between *O. dillenii* and *O. triacantha* according to the Plants Database (2007). Benson (1982) mentioned finding intergrades between *O. triacantha* and *O. cubensis* but still accepted it as a species. Britton and Rose (1963) also considered the taxon to be of hybrid origin. More work will be needed to understand this taxon.

Opuntia pusilla is relatively common in the eastern United States in coastal states from North Carolina to Texas (Louisiana is not confirmed yet). Most collections are from barrier islands and directly adjacent to coastal areas (Benson 1982, Pinkava 2003).

Mississippi *Opuntia*

The four native or naturalized species of *Opuntia* within Mississippi are *O. humifusa* (Raf.) Raf*., O.* aff. *allairei* Griffiths*, O. pusilla* (Haw.) Haw., and *O. stricta* (Haw.) Haw. A putative hybrid also occurs within Mississippi but will not be treated in the key, as more information will be needed to determine the taxonomic level at which this entity should be recognized. The four main taxa, and varieties thereof, are treated below. Cladode characteristics are typical of live material. Herbarium specimens are much more difficult to determine, as cladode characteristics and flower color generally are poorly preserved. It is advisable always to use live material for identifications, and when possible, specimens that are in flower. Flower color and general characteristics of the plants and the population should be noted, as single plants within a community might not have the typical characteristics of the species. Sterile specimens often can be misleading and result in misidentification, especially in herbarium specimens. Glochid color generally is distorted in age or in those most heavily subjected to environmental

stresses. True glochid color can sometimes be seen by extracting the inner glochids from the areoles. It is best to use younger cladodes when determining glochid colors.

Another morphological trait that historically has been used in species determinations is the presence or absence of tuberous root thickenings. Of the *Opuntia* species that occur in Mississippi, *O. humifusa, O. pusilla*, and *O*. aff. *allairei* have been observed with thickened, tuberous roots (Fig. 4.1). This characteristic has been used by many authors to distinguish *O. macrorhiza* (Engelmann 1850, 1856; Benson 1944, 1969, 1982; Gleason 1952, Lundell 1969) and *O. pollardii* Britton & Rose (syn. *O. humifusa* var. *austrina* or *O. humifusa* var. *humifusa*; Small 1903, 1913) from other species, such as *O. humifusa* and *O. pusilla*. However, tuberous roots often are found in plants growing in more well-drained substrates, independent of the species (e.g., Weniger 1970, Doyle 1990, Powell & Weedin 2004, Pinkava personal communication). Environmental factors are most likely the primary cause of this phenomenon, but this needs to be tested further.

Figure 4.1. Tuberous roots of *O*. aff. *allairei*, *O. humifusa*, and *O. pusilla.*

All voucher specimens made during this study are housed in the Mississippi State University Herbarium (MISSA). Specimens were collected from each location given for the distribution of the taxa represented here, which includes over 130 specimens.

The following is a treatment of the known *Opuntia* taxa in Mississippi, based on a thorough review and reconciliation of extant taxonomic works on the genus in North America.

Key to the *Opuntia* of Mississippi

1. Cladodes large, plants forming shrubs to sub-shrubs, erect or decumbent, cladodes not easily disarticulating, tepals yellow or basally tinged red, spines usually 0-2 per areole…………………………………………………………………….…………. 2

1'. Cladodes small, ellipsoid, obovate, or rotund, subcylindrical or flat, 1-4 (11)cm long, 0.7-2.2 (5.1)cm wide, 3-9 (16)mm thick, easily disarticulating at the upper nodes, stems decumbent or slightly ascending, spines usually strongly retrorsely barbed especially on terminal cladodes, 0-4 per areole……...………………………………………………………….….. *O. pusilla* (3)

2. Plants low, stems decumbent or ascending, spines white, brown, or gray, cylindrical in cross-section, sometimes twisted longitudinally, tepals wholly yellow or basally tinged red………………………………………………………………………...……….…3

2'. Plants erect, sub-shrubs to shrubs, spines yellow or brown in age, flattened in cross section, twisted, tepals wholly yellow, plants restricted to coastal areas or occasionally planted as ornamentals……………………………………………...………….…….……O. stricta (4)

3. Cladodes 7.0-13.6 (32.5)cm long, 4.0-6.8 (8.5)cm wide, 5-15mm thick, usually strongly tuberculate, mostly elliptical, generally strongly ascending, spines mostly wanting, if present, one per areole, white or brownish, 15-18mm long, cylindrical, straight, spreading or ascending, not retrorsely barbed to the touch, glochids bright yellow to orange-brown in age, tepals yellow tinged red basally ………………………………………………………………...*O.* aff. *allairei* (5)

3'. Cladodes 3.1-10.5 (18.7)cm long, 2.0-8.0 (11.3) cm wide, 4-10 (19)mm thick, +/- tuberculate, elliptical, rotund, or obovate, ascending or most often lying on the ground,

spines wanting or to 2 (rarely 3) per areole, yellowish or castaneous when young, aging white then gray, 5-71mm long, cylindrical, straight, spreading, ascending, or deflexed, +/- retrorsely barbed to the touch, glochids clear, light yellow, light brown, or crimson red, tepals wholly yellow or yellow with red bases…………………………………………………………………...……………4

4. Cladodes dark green to bluish-green, slightly glaucous, rotund to obovate, generally slightly tuberculate, 3.8-10.5 (18.7)cm long, 3.2-8.0 (11.3)cm wide, 4-10 (19)mm thick, tepals yellow, basally tinged dark red to red-orange, glochids crimson, reddish-brown, dark or light brown in age, spines 0-2(3) per areole, or wanting, bony white or gray in age, not retrorsely barbed, erect, spreading, or deflexed, …………...…..*O. humifusa* var. *cespitosa* (2)

4'. Cladodes yellow-green, lime-green, to dark green, mostly ellipsoid, rotund, or obovate, +/– tuberculate, cladodes 3.1-8.5 (17.7)cm long, 2.0-5.2 (9.0)cm wide, 4-10 (19)mm thick, tepals wholly yellow, glochids yellow to tan or light brown (sometimes nearly colorless), spines 0-2 per areole sometimes wanting, white or gray in age, oftentimes retrorsely barbed; erect, spreading, or deflexed……………………………………………….*O. humifusa* var. *humifusa* (1)

1. *Opuntia humifusa* (Raf.) Raf. var. ***humifusa***

Opuntia humifusa var. *humifusa* is the most widespread taxon in Mississippi

occurring naturally in four physiographic regions; the North Central Hills, the South

Central Hills, the Pine Belt, and the Coastal Zone (Fig. 4.2). This *Opuntia* has many

different morphological forms and, therefore, has been given many different names for

many years (e.g., *O. austrina* Small; *O. calcicola* Wherry; *O. compressa* var. *austrina*

(Small) L. D. Benson; *O. humifusa* var. *ammophila* (Small) L.D. Benson; *O. humifusa*

var. *austrina* (Small) Dress; *O. impedata* Small ex Britton & Rose; *O. rafinesquei*

Engelmann; Pinkava 2003). Two varieties have been recognized for Mississippi, *O.*

humifusa var. *humifusa* and *O. humifusa* var. *austrina*. In this treatment, only *O.*

humifusa var. *humifusa* is recognized. The variety *austrina* is supposed to be much larger,

more erect, and have longer spines than the more common variety *humifusa.* Also, *O.*

humifusa var. *austrina* is referred to as the variety occurring along coastal areas in deep sands of sand dunes and barrier islands (Benson 1982, Weakley 2003). This delineation however is ambiguous, and other plants found farther inland share most of the same features as coastal populations. The degree of spine coverage, spine length and diameter, and pad turgidity probably are more a function of environmental variables acting on phenotype rather than genetic dissimilarity. Morphological variation also seems to coincide with latitude. However, because inland *Opuntia* populations typically are highly disjunct from one another, a high degree of interpopulational genetic diversity might be expected.
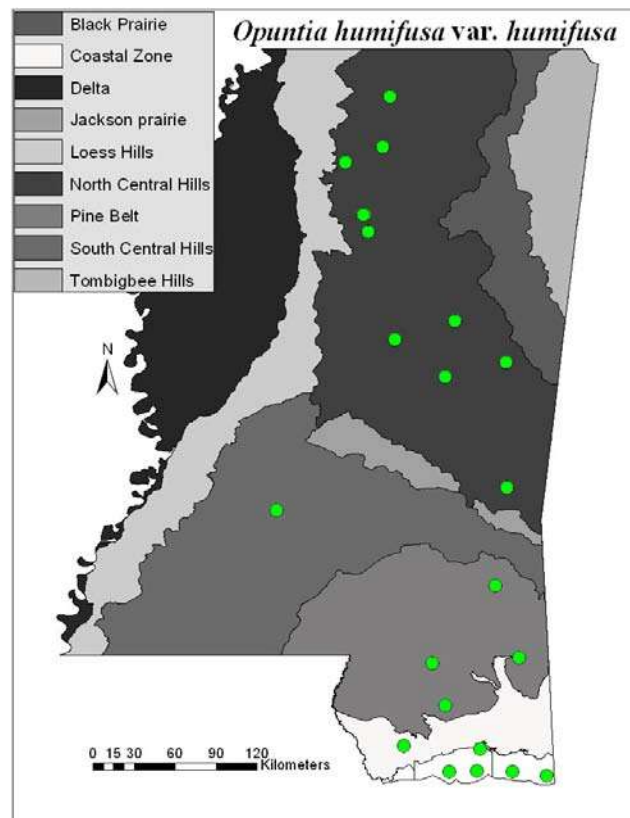
Fig. 4.2. Distribution of *Opuntia humifusa* var. *humifusa* in Mississippi.

Opuntia humifusa var. *humifusa* is found on sandy substrates in pine forests, on barrier islands, low areas behind primary or secondary sand dunes, and scrub oak forests. Unlike inland populations of *Opuntia pusilla*, localities for this taxon are removed somewhat from riparian systems. It is associated with a variety of grasses, sedges, forbs, and woody vegetation common to sandhill communities. In southern Mississippi, it commonly is found associated with *Gopherus polyphemus* (the endangered gopher tortoise).

Morphological characteristics

Opuntia humifusa var. *humifusa* is generally a low, decumbent plant (Fig. 4.3), but it can reach heights of 30 to 40 cm in certain situations during the growing season when the cladodes
are turgid. It forms relatively small (<4 m²) to large populations (>5 hectares) depending on the quantity of suitable habitat.

Fig. 4.3. *O. humifusa* var. *humifusa* typical, decumbent growth form.

Cladodes

Cladodes generally are lime to dark green and become cross-wrinkled in the winter or under water stress. Cladode sizes are highly variable depending on microclimate. Sizes range from 3.1-8.5 (17.7)cm long, to 2.0-5.2 (9.0)cm wide, and 4-10 (19)mm thick. They can be obovate, ovate, orbicular, or elliptical in shape. Cladodes even from the same plant can exhibit greatly divergent morphology.

Spines

Spines are yellowish or cream and mottled with reds and browns generally in rings near the base of the spine when immature, then they turn a pale to bright white color with yellowish tips. Aged spines turn light or dark gray and have yellowish, brownish, or black tips. They range in lengths 5- 71mm, and 0.7-1.3mm in diameter and are strongly retrorsely barbed when immature, with barbs wearing in age. *Opuntia humifusa* var. *humifusa* has up to two spines per areole and oftentimes is spineless (Fig. 4.4). There is an outer chalky layer that covers the spines. In cases where this is rubbed off (e.g., after a hurricane), the spines appear light cream, light yellow, or even colorless. Spines can be erect, spreading, or slightly deflexed depending on the age of the cladode from which it is produced and the areole from which it is produced. For example, spines can become deflexed and appressed to a cladode if another cladode or flower is produced from the same areole effectively limiting available space. Generally spines are erect or spreading and are produced from the uppermost portion of the cladode (upper 1/3 of the cladode, apex, margins) or the portion of the cladode that receives the most sunlight.

Figure 4.4. *Opuntia humifusa* var. *humifusa* with and without spines.

Glochids

The glochids are light yellow, tan, or more commonly colorless (Fig. 4.5).

Glochids darken in age from being exposed to ambient effects (e.g., sunlight). Plants

grown in a greenhouse were seen to have a terrestrial alga cover the glochids and turn

them almost black. This also has been seen from natural populations. This could

inevitably lead to misinterpretations of glochid color. Glochids range in length up to

6mm.

Figure 4.5. Glochids of *O. humifusa* var. *humifusa.*

Flowers

The inner tepals in this variety are completely yellow. Outer tepals are green. The style and stigma are white. Filaments of the stamens are yellowish or creamy colored. The anthers are yellow (Fig. 4.6).

Figure 4.6. Flower of *O. humifusa* var. *humifusa.*

2. *Opuntia humifusa* (Raf.) Raf. var. *cespitosa* (Raf.) Majure
(comb. nov., under consideration)

Opuntia humifusa var. *cespitosa* occurs in Mississippi mainly in the Black Prairie

Physiographic Region, but plants have also been found in the Tombigbee Hills, North

Central Hills, and the Loess Hills (Fig. 4.7).
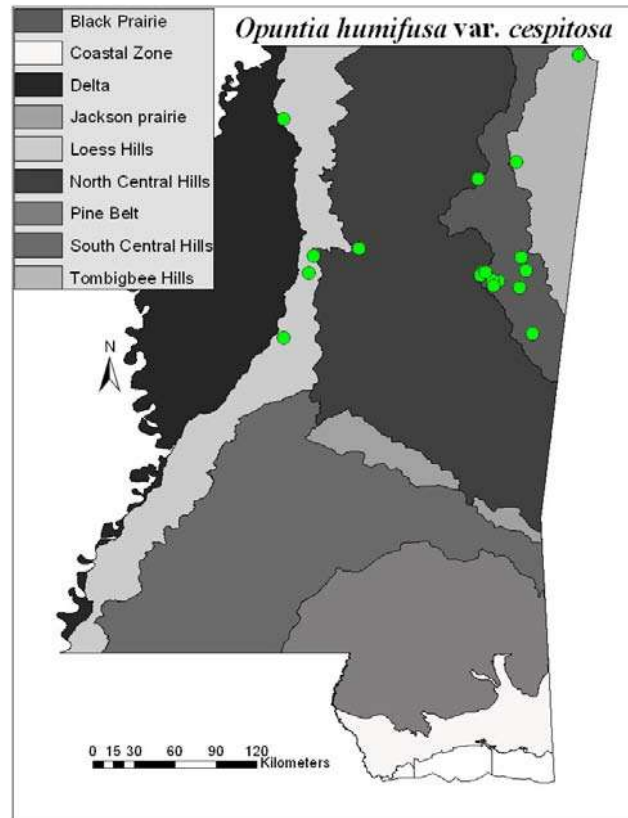
Figure 4.7. Distribution of *O. humifusa* var. *cespitosa* in Mississippi.

In the Black Prairie it most commonly is found in acidic soils overlying chalk

outcrops of the Pontotoc Ridge where *Juniperus virginiana* forms a dominant canopy

cover (Fig. 8). Where it is found outside of the Black Prairie, it occurs in upland mixed

pine and deciduous forests in dry clayey or silty-sandy soils or on sandy prairies. In

Tennessee this species is commonly found in Juniper glades and barrens growing beside

or over limestone outcrops. In Arkansas it occurs in shale barrens and granitic outcrops. Specimens of this species also have been seen from the black prairie and dolomite outcrops in Alabama, as well as portions of Kentucky and Virginia. In Missouri and Illinois this plant is found in sandy prairies. There is evidence that it also occurs in New York (Kalbacher 1975). This taxon in Mississippi tends to grow in areas that are slightly more mesic in nature (Fig. 4.8) than those of *O. humifusa* var. *humifusa*, *O. pusilla*, and *O. stricta*. It has been included as synonymous with *O. humifusa* var. *humifusa* for quite some time (Engelmann 1856, Small 1903, 1913, 1933; Weniger 1970), and has either been ignored as being different from typical *O. humifusa* var. *humifusa* (Benson 1982) or unseen by specialists (Pinkava 2003, Pinkava personal communication). Interestingly, although Benson (1982) excluded this taxon from his more recent treatment, he previously considered this eastern *Opuntia* as a possible separate variety of *O. humifusa* (*O. humifusa* var. *microsperma*; 1962) and even mentions that *O. macrorhiza* Engelmann is found within the eastern US. *Opuntia humifusa* var. *cespitosa* deviates morphologically from the original description of *Cactus humifusus* Raf. described in 1820 (Rafinesque 1820) in having yellow tepals that are basally tinged red, among other characteristics. Ironically, Engelmann's description of *O. macrorhiza* (1850) is nearly a perfect match for this variety. I am therefore treating this variety as separate from *O. humifusa* var. *humifusa* and maintaining that classical *O. humifusa* var. *humifusa* has wholly yellow tepals (Rafinesque 1820, Engelmann 1856 (as *O. vulgaris* Mill.), Radford et al. 1968, Benson 1982, Wunderlin 1997, Pinkava 2003). Habitat characteristics also are easily separable between the two varieties (Chapter 1).

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Figure 4.8. Examples of mesic and *Juniper* dominated habitat of *O. humifusa* var. *cespitosa.*

The name *cespitosa* comes from a species described by Rafinesque (1830) for a plant from the eastern United States. Although, no flower color is mentioned, he describes the plant as having really long spines and red glochids. The distribution he gives for the species is much more accurate than for other taxa that might be considered for this variety (e.g., *O. grandiflora* Engelm.). As well, this plant can be quite cespitose, so the name also is accurate in basic description. Of course more work will be necessary to determine whether this taxon should remain at the varietal level or if it should be elevated to specific status.

Morphological characteristics

At first glance, this variety can be mistaken for the more common *O. humifusa* var. *humifusa*. However, this taxon is easily separated from *O. humifusa* var. *humifusa* in having red-centered flowers. This variety also is decumbent and low growing (Fig. 4.9),

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although heights of 30 or more centimeters can be reached occasionally, especially when the plant is surrounding by supporting vegetation.

Figure 4.9. *O. humifusa* var. *cespitosa* growth form.

Cladodes

Cladodes are normally dark green to moderately glaucous (Fig. 4.10), obovate, orbicular, or elliptical. The cladodes consistently are more orbicular than the other variety. They range in size from 3.8-10.5 (18.7)cm long, 3.2-8.0 (11.3)cm wide and 4-10 (19)mm thick. Cladodes become cross wrinkled in this variety during winter or in times of stress as well. This variety also becomes more purplish during times of stress, especially around the areoles.

Figure 4.10. Moderately glaucous cladodes of *O. humifusa* var. *cespitosa.*

Spines

Spines of *O. humifusa* var. *cespitosa* are usually bony white with castaneous colored or maroon bases during development and right after maturity, which are strikingly similar to *Opuntia macrorhiza* as described by Powell & Weedin (2004). In age they become light to dark gray. Spine tips are light yellow or cream when young but usually darken in age, to almost black in certain specimens. Spine tips are never retrorsely barbed to the touch, although, they do possess microscopic barbs. These can easily be seen under moderate magnification. Spines range in size from 9.5-60mm long and 0.7-1.05mm in diameter.

Glochids

This species typically has crimson, reddish-brown, or dark brown glochids, although plants with light brown glochids are found. They range in length up to 7mm long.

Flowers

The flowers of this variety are quite striking in having dark yellow inner tepals that are dark red to orange-red basally extending to roughly 1/2 to 2/3 the length of the tepal (Fig. 4.11). The outer tepals are green. The stigma lobes are white or a light cream color. Filaments generally are reddish, orangish, or dark yellow. Anthers are yellow. Pollen of this variety is slightly larger than in variety *humifusa*, and its pollen contains more germinal pores than variety *humifusa*. This is another characteristic that needs to be studied in more detail.

Figure 4.11. Typical flowers of *O. humifusa* var. *cespitosa*.

3. *Opuntia pusilla* (Haw.) Haw.

Opuntia pusilla is most often considered to be a coastal species, as it is found on barrier islands, coastal shorelines, sand dunes, and shell middens (Radford et al.1968, Benson 1982, Wunderlin 1998) in the coastal states from North Carolina to Texas, with the exception of Louisiana (Benson 1982, Pinkava 2003). However, we have found many populations of *O. pusilla* much farther inland, generally occurring on well-drained, acidic sand deposits along river systems. In Mississippi this species is found in the Tombigbee Hills, Black Prairie, South Central Hills, North Central Hills, Jackson Prairie, Pine Belt, and the Coastal Zone physiographic regions (Fig. 4.12).
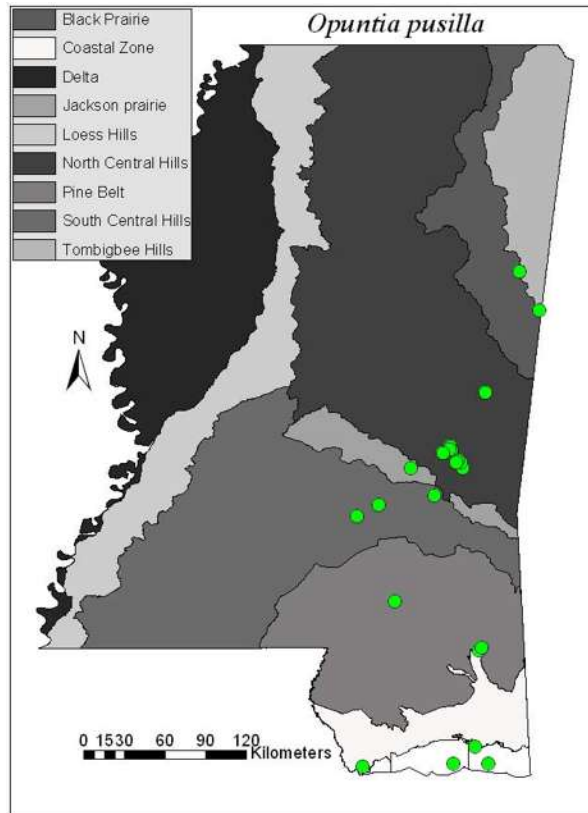
Figure 4.12. Distribution of *O. pusilla* in Mississippi.

Opuntia pusilla can be dispersed easily by animals due to easy disarticulation of the nodes and retrorsely barbed spines which hook into the fur, skin, or in the case of humans, clothing (Fig. 4.13). The fragments then root and form new plants if the environment is suitable for continued growth. Dispersal by flooding events also could play an important role in the movement of populations of this species. A similar species morphologically, *Opuntia fragilis* (Nutt.)Haw. is presumed to be spread along riparian areas by flooding events (Frego & Staniforth 1985).

Figure 4.13. *O. pusilla* clinging to shoe by retrorse barbed spines.

Opuntia pusilla is highly morphologically plastic (Majure & Ervin in preparation) like many other *Opuntia* species. Small (1933) recognized two species (*O. drummondii* Graham and *O. tracyi* Britton) based on cladode and fruit morphology, with one species having sub-cylindric cladodes and the other possessing flat cladodes. These are characteristics of cladodes that can be seen on the same plant, within and among populations, and most likely has something to do with environmental variables. However, larger forms of what appear to be intermediate between *O. pusilla* and *O. humifusa* have been found and moderately conform to the description of *O. drummondii*. It is treated here as *O.* x *drummondii* in the following description.

Morphological characteristics

Opuntia pusilla is a small plant as the name implies. It often forms small mounds or patches of cladodes from 5-15 cm tall that are easily hidden in grasses, forbs, and shrubs. Patch sizes increase as terminal cladodes disarticulate throughout the year and fall around the existing plant. These pads form new plants that maintain this cycle, steadily increasing the patch diameter. Of course, many cladodes fall back into the parent plant and increase the overall density of stems radiating from a central location, and many pads are dispersed away from the parent plant. Under prolonged periods of shading, this

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species tends to form smaller and smaller cladodes that eventually resemble juvenile plants (Fig. 4.14).

Figure 4.14. Etiolated pads of *O. pusilla* grown under heavy shade.

Only when the canopy cover is removed (e.g., after a flooding event, beaver activity, etc.) do the plants start to recuperate (Fig. 4.15; Majure in review). It is not known at what reduced light level does this species start to suffer effects from shading nor for how long etiolated plants can remain in this state. More work needs to be done to test this observation.

Figure 4.15. Pads of *O. pusilla* after the removal of dense canopy cover.

Cladodes

Cladodes range from 1.0-4.0 (11.0) cm long, 7-22 (51) mm wide, and 3-9 (16) mm thick. Cladode shapes tend to be ellipsoid, obovate, or rotund and are subcylindrical or commonly flat (Fig. 4.16). The most turgid cladodes are found along coastal areas, especially on the barrier islands. In winter the cladodes become transversely cross-wrinkled and turn a purplish color, especially at the areoles.

Figure 4.16. Growth forms of *O. pusilla* with pads sub-cylindric or flattened.

Spines

Spines on this species are strongly retrorsely barbed when immature but can lose this with age and weathering. They are 4-60 mm in length and 0.45-0.6mm in diameter. From 0-4 spines can be produced from a single areole. Spine production is a function of habitat characteristics, where degrees of shading and lower temperatures tend to decrease spine production and increase cladode length and width. High amounts of sunlight and subsequently high temperatures have the opposite effect and increase cladode thickness (Chapter 2). However, in natural populations typically 2-3 spines are produced when plants are in full sun. Younger spines can be maroon, creamy-yellow or pale white with yellow tips, while older spines tend to age bright white, then gray and have darker tips (brownish).

Glochids

The glochids of *O. pusilla* are the same color as in *O. humifusa* var. *humifusa* and can be up to 6mm long.

Flowers

Flowers of this species are bright yellow, where the inner tepals are wholly yellow and the outer tepals are green. The style and stigma lobes are white. The filaments of the stamens are yellowish or cream colored and the anthers are yellow as in *O. humifusa* var. *humifusa* (Fig. 4.17).

Figure 4.17. Flowers of *O. pusilla.*

4. *Opuntia* x *drummondii* (Graham) Majure (comb. nov., under consideration)

Opuntia x *drummondii* is found within the Jackson Prairie, North Central Hills, South Central Hills, and the Pine Belt physiographic regions in Mississippi (Fig. 4.18). It is typically found further disjunct from riparian systems than is *O. pusilla,* much like *O. humifusa* var. *humifusa.*. It's habitat characteristics are similar to both *O. humifusa* var. *humifusa* and *O. pusilla.*
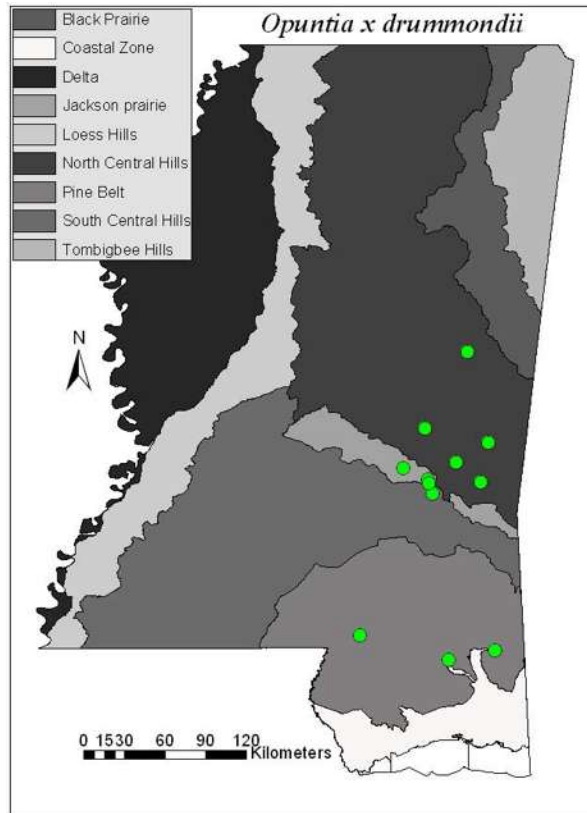
Figure 4.18. Distribution of *O.* x *drummondii* in Mississippi.

This taxon has characteristics intermediate between *O. humifusa* var. *humifusa* and *O. pusilla.* Other authors also have noted growth forms that appear intermediate between these two species (Benson 1944, 1982; Snow 1977, Doyle 1990), but all accounts have been observational and not empirically tested. Hybridization among *Opuntia* is not uncommon (e.g., Grant & Grant 1979, Benson 1982, Rebman & Pinkava 2001, Bobich & Nobel 2001, Griffith 2004). However, the name *O.* x *drummondii* will be applied tentatively until further evidence elucidates the actual relationships among these taxa. Molecular genetic analyses are currently underway to gain a better understanding of interrelationships among these taxa (Majure et al. in preparation).

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Morphological Characteristics

As mentioned previously, characteristics of this taxon are perceived to be intermediate between true *O. humifusa* var. *humifusa* and *O. pusilla*. Within populations of this taxon, plants can be found that are more similar to *O. humifusa* or *O. pusilla*. The basal pads generally are larger than in *O. pusilla*, but the terminal pads are smaller, freely disarticulate at the nodes, and are more spinose than *O. humifusa* (of course this varies with the population, plant, and environmental variables). Characteristics observed in the field are maintained when the plants are planted in an environmentally controlled greenhouse. This seems to imply that the morphological traits exhibited among these populations are a product of genetic dissimilarity from either *O. humifusa* or *O. pusilla*, a combination of those species' genetic identities, or a divergent entity of either *O. humifusa* or *O. pusilla*.

Cladodes

The cladodes of this taxon can be larger like *O. humifusa* or smaller like *O. pusilla*. Overall sizes range from 2.5-7.3 (16.2)cm long, 2.1- 4.5 (6.8)cm wide, and 5-9 (15)mm thick. The upper or terminal cladodes freely disarticulate at the nodes, so plants are easily spread by means of vegetative reproduction similarly to *O. pusilla*. Plants often form dense clumps produced by disarticulating cladodes that establish around the periphery and among older stems of the parental plant similar to *O. pusilla*. They also can form long chains of pads that produce widely sprawling plants that seem to grow more vigorously than *O. humifusa* or *O. pusilla* (Fig. 4.19). This could be a sign of hybrid vigor or just a response to habitat characteristics or environmental conditions.

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Figure 4.19. Vigorous growth of *O*. x *drummondii.*

Spines

Spines can be similar in size to *O. humifusa* or *O. pusilla*, where *O. pusilla* typically has smaller diameter spines. Their sizes range from 7-50mm long and 0.6-0.8mm in diameter. Up to 4 spines can be produced from an areole, although mostly 2-3 are produced. Spines are strongly retrorsely barbed, especially in immature spines. This can decrease as the spine ages and weathers. Younger spines can be maroon, creamy-yellow or pale white with yellow tips, while older spines tend to age bright white, then gray and have darker tips (brownish), as in *O. pusilla*.

Glochids

Glochids are the same for *O*. x *drummondii,* as they are for *O. humifusa* var. *humifusa* and *O. pusilla.* They range in length from 0-4mm.

Flowers

Flowers are identical to *O. humifusa* var. *humifusa* and *O. pusilla*, although they tend to be smaller, as in *O. pusilla.*

5. *Opuntia* aff. *allairei* **Griffiths**

Opuntia aff. *allairei* has been found in the floodplain of the Mississippi River in the Delta physiographic region and in the Loess Hills physiographic region (Fig. 4.20).
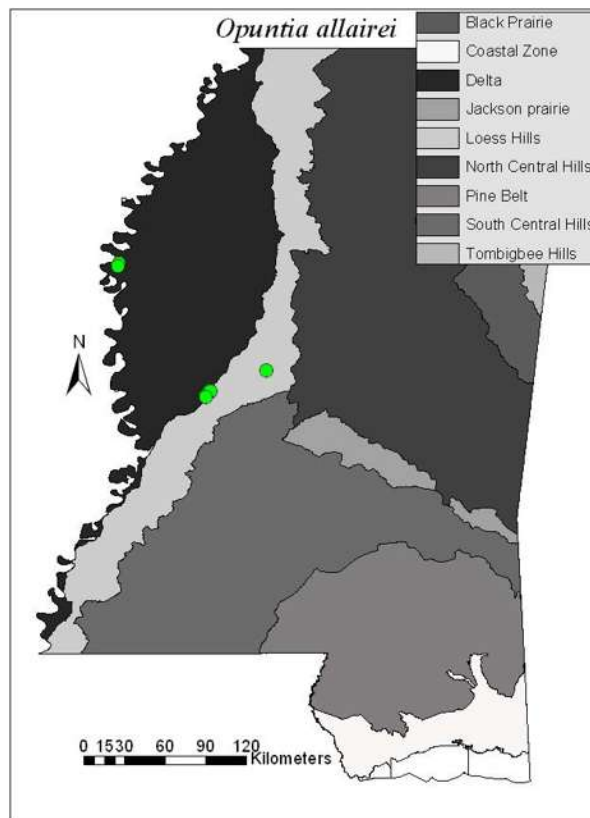

Figure 4.20. Distribution of *O*. aff. *allairei* in Mississippi.

In the Delta Physiographic region it occurs in an area that was heavily impacted by the "great flood" in 1927, when levees along the Mississippi River failed following months of almost continuous winter and spring rains (Barry 1997). There are hundreds of

hectares of sandy fields in that area inhabited by this species. Hilgard (1884) mentions seeing *Opuntia* along the Dogwood Ridge in the Mississippi floodplain that occurred from Coahoma County, which is adjacent to Bolivar County, down to Holmes County. Whether it is the same species is yet to be determined, and trips to locate Dogwood Ridge and any *Opuntia* species that might occur there have been unsuccessful. The other populations have been found only in one county in the Loess Hills. Through more investigation, more populations of this species should be found in the Loess Hill physiographic region. I have seen one specimen from Wilkinson County that most closely resembles this species.

This species is unlike any other *Opuntia* in the state regarding growth form, although flower color overlaps with *O. humifusa* var. *cespitosa*. It is obviously within the *O. humifusa* complex but probably is more closely related to *O. humifusa* var. *cespitosa* and *O. macrorhiza*, than to *O. humifusa* var. *humifusa*. *Opuntia allairei* is the closest taxon morphologically to this species among other species described from the southwestern United States, as far as I can tell. Weniger (1970, 1984) considered this species only a variety of *O. humifusa*, but it appears more divergent from that species, so here I will tentatively consider it as a separate entity close to (i.e., affinis) *O. allairei*. More work definitely will need to be done in order to fully understand the origin of this taxon, as well as its relationship with the other taxa.

Ecological data for this species is relatively limited. The populations observed in the Delta and Loess Hills were found only after most of my other fieldwork had been completed, so more ecological information is needed to aptly describe the habitat for this taxon in Mississippi.

Soils in the delta area are of the dundee-askew-sharkey series. The askew soils are the main component where the *Opuntia* is found and consist of a fine silty-loam, which is slightly acidic. The area resembles a mid-western grassland with sparse woody vegetation among a variety of forbs and grasses. Soils in the Loess Hills area are of the morganfield-adler-convent and the dundee-dubbs-sharkey series. The morganfield-adler-convent are silty to loamy soils formed from alluvium and are nonacid and moderate to well-drained. The dundee-dubbs-sharkey soils also were formed from alluvium. Dundee soils are well-drained and neutral, whereas the other two soils are acidic and poorly drained.

Associate species for this taxon in the delta area are those generally found in sandy, slightly disturbed areas, which in some cases are the same as those found for *O.* x *drummondii*, *O. humifusa* var. *humifusa* and *O. pusilla* (e.g., *Cenchrus spinifex, Chrysopsis gossypina, Triplasis purpurea*). Other associate species include: *Gleditsia triacanthos, Juniperus virginiana, Xanthoxylum clava-hercules, Ambrosia artemesiifolia, Ampelopsis arborea, Bromus arevensis, Brunnichia ovata, Chenopodium ambrosioides, Cocculus carolinus, Croptilon divaricatum, Croton glandolosus, Cynodon dactylon, Cyperus refractus, Paspalum setaceum*, and *Toxicodendron radicans*. Associate species for the Loess Hill population also are species more typical of dry environments, however with many exceptions of course (e.g., *Celtis laevigata, Diospyros virginiana, Juniperus virginiana, Rhus copallinum, Sassafras albidum*).

Morphological Characteristics

This plant can reach heights of 60cm in shaded conditions, but it generally is around 30-40cm tall with dark green to yellow-green pads. It forms large colonies of mostly ascending cladodes (sometimes slightly decumbent; Fig. 4.21). It is the largest of the naturally occurring, inland *Opuntia* in Mississippi.

Fig. 4.21. *O*. aff. *allairei* demonstrating ascending habit of cladodes and large size forming long chains of cladodes up to one meter in length.

Cladodes

Cladodes generally are 7.0-13.6 (32.5)cm long, 4.0-6.8 (8.5)cm wide and 5-25mm thick.

Spines

Spines are almost completely wanting in this species. When present they are relatively small ranging 15-18mm long and about 0.6mm in diameter. Only one spine per areole has been observed.

Glochids

Glochids can be up to 5mm long and are bright yellow to orange-brown in age.

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Flowers

The flowers of this species are showy with yellow tepals basally tinged red, as in

O. humifusa var. *cespitosa* (Fig. 4.22).

Figure 4.22. Flower of *O*. aff. *allairei.*

6. *Opuntia stricta* (Haw.) Haw.

Opuntia stricta generally is restricted to coastal areas (Benson 1982, Pinkava

2003, Wunderlin 1998). Benson (1982) mentions that *O. stricta* is found "even in jungles

along the Everglades, where the water table is only a few centimeters below the surface,"

implying that this species can survive in areas atypical for cacti. However, humans in

many cases have transported this species throughout the mid-south, transplanting it in

their yards and flower gardens. Cladodes often are taken from coastal populations for this

purpose. In Mississippi this species occurs naturally in two counties in the Coastal Zone

physiographic region (Fig. 4.23).
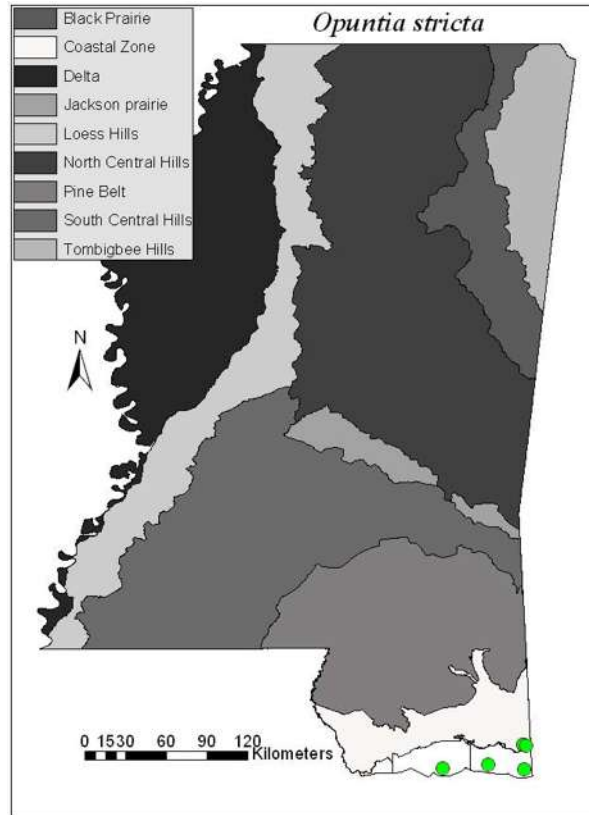
Figure 4.23. Distribution of *O. stricta* in Mississippi.

Records from Hancock County exist as well, but these have not been reconfirmed. It occurs on barrier islands, shell middens, and weedy areas along the coast. It has been seen occasionally in wrack and could potentially be dispersed by water during meteorological events, such as hurricanes (Majure et al. 2007).

     Opuntia stricta is most well known for its destructive invasion in Australia and parts of South Africa. These locations also have been the stages for use of the successful biological control agent, the cactus moth, *Cactoblastis cactorum* Berg (Zimmerman et al. 2000). In Australia this moth was released and eventually decimated millions of hectares of invaded rangeland by the non-native *O. stricta* and other *Opuntia* spp (Mahr 2001). Unfortunately, the moth also was released onto the Caribbean Islands and consequently

found its way to the continental United States. Here it has negatively affected populations of our native *Opuntia* (Stiling 2000, Stiling & Moon 2001, Zimmerman et al. 2001, Stiling et al. 2004). *Opuntia stricta* has been heavily affected in certain areas (e.g., Bon Secour and Dauphin Island, AL; Majure pers. obs.). Because *O. stricta* is relatively rare in Mississippi, the cactus moth could easily eliminate our populations of this species.

Morphological characteristics

      Opuntia stricta is a frutescent prickly pear that can grow up to 1m or more tall. It can form dense colonies in certain situations, but most often populations are composed of plants that are sparsely scattered throughout an area (Fig. 4.24).

Figure 4.24. *O. stricta* growth forms.

Cladodes

      Cladodes range in size from 11.0-20.4 (28.0)cm long, 6.3-11.4 (17.0)cm wide and 9-13

(19)mm thick. They are light lime green to yellow-green, moderately glaucous on younger growth and have slightly scalloped margins (Fig. 4.25).

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Figure 4.25. Scalloped margined cladodes of *O. stricta.*

Spines

Spines range in size from 20-27mm long and 1.05-1.3 in diameter. They are dark yellow or yellow orange and are flattened. Usually they curve and may be twisted. Spines are erect, spreading or commonly deflexed. From 0-3 spines per areole have been seen in material from Mississippi.

Glochids

The glochids of this species are dark yellow to brown in age and can be 0-6mm long.

The flowers of this species are completely yellow (Fig. 4.26).

Figure 4.26. Flower of *O. stricta.*

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CHAPTER V

CONCLUSIONS

Taxonomy and Ecology

Before the start of this research, the *Opuntia* of the Mississippi were poorly

represented in the state herbaria, with only about 30 specimens from a few counties.

The MISSA collection only had four specimens (it now has >120). Little was known

about the taxa (apparently) and habitat characteristics among the taxa that are present

here. Up to three new taxa will be recognized from this work, which at the time had

been overlooked and lumped in with all of the formerly accepted species. Only three

species of *Opuntia* were recognized in Mississippi prior to this project. This number

could increase to four or five species, and/or additional varieties, and/or a hybrid

species. The morphological plasticity of southeastern *Opuntia* species had been noted

(Benson 1982, Doyle 1990) but not experimentally tested in any way. *Opuntia pusilla*

was used in this work to quantify degrees of phenotypic plasticity based on

environmental variables.

Previously, *Opuntia humifusa* var. *austrina* (or *O. austrina*) was considered to

be included within the Mississippi flora, however, now (in agreement with Pinkava

2003) this taxon is considered to be synonymous with *O. humifusa* var. *humifusa,* at

least in Mississippi. This taxon could be valid, but if so, it does not occur in Mississippi. It was described from Dade County, Florida (Small 1903), so it could be better represented in Florida. All of our material includes only morphological variants of *O. humifusa* var. *humifusa*. Benson (1982) apparently was confused by the incredible diversity of morphological characteristics among coastal populations of this species, as he recorded both variety *humifusa* and variety *austrina* from the Mississippi coast.

The great amalgamation of morphological misinterpretations, and subsequently misguided descriptions of novel species among the *Opuntia* taxa of the mid-south, has led to quite a number of names now synonymous under currently accepted species. Early descriptions were oftentimes depauperate of reliable information and species characteristics (e.g., Rafinesque 1820, 1830; Engelmann 1850), so many interpretations for what the original authors meant have been proposed. This has led to a great deal of confusion about what species actually occupy portions of the mid-south and the ever-changing names do not ameliorate the situation. To increasingly confound this problem, most *Opuntia* authorities concentrate on western species, so in-depth studies of the eastern taxa are performed primarily with herbarium material. This leads to unfortunate errors in species interpretations. *Opuntia humifusa* var. *humifusa* is oftentimes considered ubiquitous throughout the eastern United States (Benson 1982, Wallace & Fairbrothers 1987, Pinkava 2003), but it is apparent that there is more than one variety occurring over this area. It seems that although Rafinesque's description (1820) of *O. humifusa* var. *humifusa* was correct, his distribution proposed for the species (from New York to

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Missouri) was applicable to two different varieties. *Opuntia humifusa* var. *humifusa* has been by some considered to have flowers that are yellow or yellow with red centers (Engelmann 1856, Small 1903, 1913, 1933) which is in contrast to the original description (Rafinesque 1820) and to current and previous authorities' view of the species (e.g., Benson 1982, Pinkava 2003). *Opuntia humifusa* var. *humifusa* should have, according to the original description, wholly yellow flowers. Therefore, the *Opuntia humifusa* with red-centered flowers that occurs in Mississippi will now be under consideration for a nomenclatural change. Not only does it differ from *O. humifusa* var. *humifusa* in morphology, but it also is found in contrasting habitats.

The Mississippi delta and loessial hill *Opuntia* before was only known from a floristic survey, where it was included as *O. humifusa* (Wiseman 1982). This taxon appears to differ from all of the other *Opuntia* taxa in Mississippi. It appears to be western in origin and actually fits the description of a western species, *O. allairei* Griffiths (or *O. compressa* var. *allairei*; Weniger 1970). More work will be necessary to classify this species.

Another taxon that appears intermediate between *O. humifusa* var. *humifusa* and *O. pusilla* is being studied. It has habitat characteristics that overlap the putative parental taxa, but generally parental taxa are absent within populations of this taxon. Work is being conducted to see if these populations actually are of hybrid origin or if they could represent a novel taxon.

The *Opuntia* of the mid-south occupy different habitats among inland populations (e.g., *O. humifusa* var. *humifusa, O. humifusa* var. *microsperma,* and *O. pusilla*) or several taxa (*O.humifusa* var. *humifusa, O. pusilla*, and *O. stricta*) can be

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sympatric along coastal areas. They all occupy acidic soils, although they can be found in circumneutral soils. Soils also are either well-drained or are thin and located atop harder substrates that provide for no accumulation but rather accelerated evaporation of moisture, thus soils become more xeric than in surrounding areas. All *Opuntia* species in the mid-south are found associated with vegetation more common to xeric habitats, and some of these associate species can be found among all of the *Opuntia* species. Other associates are more restricted to certain habitats along with certain *Opuntia* species.

Opuntia humifusa var. *humifusa*, *O. pusilla*, *O.* x *drummondii*, and *O. stricta* all are found in sandy soils. *Opuntia stricta* seems to be able to withstand a higher amount of soil moisture than the others and can even be found growing directly adjacent and partially into marshes along the coast. It also has been found on nearly neutral soils. *Opuntia humifusa* var. *humifusa*, *O. pusilla*, and *O.* x *drummondii* are all found in highly acidic, well-drained, sandy soils. Inland populations of *O. humifusa* var. *humifusa* and *O.* x *drummondii* generally are found on sandhills which are highly disjunct, typically, from riparian systems. In contrast, most populations of *O. pusilla* are encountered directly adjacent to or within the floodplain of major river systems. This could be due to potential dispersal mechanisms of *O. pusilla*. *Opuntia humifusa* var. *microsperma* in contrast to the other taxa, is found in more mesic situations in heavier soils of the blackland prairies and other mixed deciduous or upland pine forests. There is a report of this taxon being found along riparian systems, but this has not yet been confirmed.

Opuntia aff. *allairei* is found in sandy, acidic soils of the Mississippi Delta, but only limited ecological information is available at present. More data on associate species, canopy cover and soil characteristics will be necessary to correctly identify generalized components of this species' habitat characteristics.

These taxa are found in other locations in the eastern United States (Table 1). Preliminary studies of herbarium specimens (from BRIT, IBE, NCU, TENN, USMS, and WISC), as well as my own collections have resulted in a small dataset that can be used to begin the next step, as a continuation of this project, which will be classifying the *Opuntia* species of the eastern United States. This will be done using a variety of morphological and molecular data. A treatment also will be developed for the southeastern taxa.

Table 5.1. *Opuntia* specimens from eastern states and county record numbers.

O. aff. *allairei*

Mississippi = 2 counties

O. *ammophila*

Florida = 10 counties
Georgia = 1 county

O. *fragilis*

Wisconsin = 1 county

O. *humifusa* var. *cespitosa*

Alabama = 7 counties
Arkansas = 6 counties
Illinois = 1 county
Kentucky = 6 counties
Michigan = 1 county

Mississippi = 10 counties
Missouri = 2 counties
Tennessee = 22 counties
West Virginia = 1 county

Opuntia *humifusa* var. *humifusa*

Alabama = 15 counties
Florida = 14 counties
Georgia = 9 counties
Louisiana = 3 counties
Mississippi = 18 counties
North Carolina = 29 counties
South Carolina = 29 counties
Tennessee = 1 county
Virginia = 11 counties

Table 5.1. Continued.

O. pusilla

Alabama = 5 counties
Florida = 4 counties
Mississippi = 11 counties

O. stricta

Alabama = 2 counties
Florida = 4 counties
Mississippi = 3 counties

O. tortispina

Wisconsin = 12 counties

Morphological plasticity

The incredible, sometimes overwhelming and highly surprising morphological plasticity of eastern *Opuntia* species was successfully tested using the highly variable species, *O. pusilla*. Under different microclimates (shade vs. full sun), this species produced significantly different growth forms. Under shaded conditions, and subsequently lower temperatures, new cladodes were longer, wider, and completely devoid of spines. Light grown plants, where temperatures also were higher, produced numerous spines, were thicker, and produced significantly more biomass than shade grown plants. Differing morphologies observed from this experiment exemplify the easily induced phenotypic plasticity that *Opuntia* species often demonstrate. Results have taxonomic and physiological implications. Taxonomically, care must be taken when determining species in the field, and potential environmental forces should be noted. Physiologically it is apparent that the amount of light and temperature have a

large effect on the production of spines. Spines are known to have effects on the

thermoregulation of plant body temperatures (Lewis & Nobel 1977, Nobel 1978,

1980, 1983; Powell & Weedin 2004), much like the trichomes on leaves of other

plants (Hopkins & Hüner 2004). More work most definitely will be needed to

separate the effects of light versus temperature, as well as available soil nutrients.

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