

# FINAL REPORT

*As Required by*

THE ENDANGERED SPECIES ACT, SECTION 6

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Grant No: E-1-7

ENDANGERED AND THREATENED SPECIES CONSERVATION

## Project No. 30: A Study of the Reproductive Biology of the Tobusch Fishhook Cactus (*Ancistrocactus tobuschii*)

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## ABSTRACT

This following study on the endangered Tobusch fishhook cactus (*Ancistrocactus tobuschii*) was conducted from 1991 through 1994 (and additionally 1995 for report finalization) on three study sites: The Walter Buck Wildlife Management area (BWM); Devil's Sinkhole (DSH); and, Kickapoo Caverns (KPC). Field pollination, seed ecology, annual mortality, reproductive effort, and changes in plant size were investigated.

The breeding system, potential pollinators, and effects of pollen donor proximity on reproduction were all investigated. The mean percent fruit set, number of seeds per treated flower, and percent seed germination were all much lower for hand self-pollinated flowers (5.0%; 1.1 seeds; 6.3%) than for hand cross-pollinated flowers (98.0%; 38.9 seeds; 22.7%), indicating that this species is self-incompatible with respect to pollination. Several species of halictid bees were the most commonly observed insect visitors at both sites during the four year field investigation, although a limited investigation into their effectiveness as pollinators indicates that they may effect little pollination per floral visit. A test of the relative effects of artificial pollination using "neighbor" pollen (i.e., from within the same colony) versus "distant" pollen (i.e., from another colony in the same population) on preemergent reproductive success at one population site showed that no significant differences exist between the two test groups with respect to fruit set, seed set and seed germinability, indicating that pollen transfer between closely proximal individuals (which have a higher probability of being closely related) may not be limiting reproductive success in this population.

The seed ecology was examined with respect to seed dispersal and predation; annual seed germinability; the period of germination in the field, and the relative field germination success within several different types of microsites; and the soil seed reserve. Removal by ants appears to be the most common fate for seeds of this species, perhaps initially affecting as much as 85% of annual production. The only species of ant observed moving Tobusch fishhook cactus seeds at all three sites during this investigation was a small reddish-brown ant (*Forelius foetidus*), which was observed to be very effective at removing most seeds from most fruits and into its ant mound. The fate of seeds following transport into the mound is unknown. For the 15-20% of seeds not immediately removed from fruits by ants, dispersal appears limited mostly to gravity and rainwater, as evidence by the common occurrence of seedlings surrounding mature adult plants. Successful dispersal of some seeds away from maternal parent plants may be effected by occasional ant droppage of seeds and infrequent vertebrate frugivory, but post-dispersal predation of such seeds by ants may impose additional limits to the actual effectiveness of this as a dispersal strategy for the cactus. Annual seed germinability varied widely during the four year course of this investigation, from a high of ca. 67% at one site to a low of ca. 1% at another site. With one exception, significant differences were only noted between years, and not between sites for each given year. Reasons for this wide variation in seed germinability between years are not yet understood. An overall average of ca. 20% of seeds placed within protective exclosures throughout each field study site germinated after nearly one year, although this varied somewhat between sites. Percentage germination was similar between each of three different microhabitat types where seeds were placed, although "beneath rocks" was slightly greater than "selaginella", which was slightly greater than "grass". A modest size reserve of germinable seeds was detected in the soil at two of the three sites which were sampled. While most samples did not contain seeds,

those seeds which were detected were from samples collected within several decimeters of reproductive-sized plants.

Mortality, reproduction, and changes in plant size were monitored. Individual plant diameter varied significantly between years, occasionally resulting in an average decrease between annual censusing periods. Its value as a measure of annual growth is therefore somewhat limited, but plant diameter does appear to have useful predictive value concerning the onset of sexual reproduction, reproductive output and, to an extent, of impending senescence. Plant diameter may therefore be useful in delineating different life stages for demographic analysis of populations. Annual mortality was high during all years at BWM and DSH, but was more modest at KPC. Of the plants monitored in 1991, 55% at BWM and 69% at DSH had died by the end of March, 1994. Grub infestation accounted for the majority of attributable mortality at all sites during all years, and was probably responsible for a large percentage of mortality for which a cause was not discernible. Grubs of two cactus-specialist coleopteran species were identified as causing such mortality: *Moneilema armata* LeConte and, especially, *Gerstaeckaria nobilis* LeConte. Herbivory by larger mammals accounted for a small but constant portion of the annual attributable mortality, although such activity was not always immediately fatal because many plants (especially at DSH) produced branches following mammal-associated damage to the main stem. For reasons which are not yet apparent, the annual flower, fruit, and seed production per plant decreased consistently and significantly at all populations during each year of this study. Annual fruit set (fruits/flower) was generally constant at near 70% throughout the course of this investigation, while average seed germinability varied widely between years, from populational annual averages of ca. 65% to ca. 1%.

If the trends observed during this investigation continue, the high mortality, decreasing reproductive effort and success, and apparently low seedling recruitment could lead to the rapid extinction of the study populations, especially at the BWM and DSH sites. While more information concerning the autecology of this cactus should be acquired prior at any attempts at development of a long-range management strategy, it may be necessary to employ stop-gap measures in the mean time, and control of the grub-related mortality seems like an obvious starting point.

# FINAL REPORT

STATE: TEXAS

PROJECT NO.: E-1-7

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PERIOD COVERED: January 1, 1991 through August 31, 1995

PROJECT NUMBER: 30

PROJECT TITLE: A Study of the Reproductive Biology of the Tobusch Fishhook Cactus (*Ancistrocactus tobuschii*)

PROJECT OBJECTIVE: To determine pollination mechanisms and vectors, reproductive success (percentage of flowers producing fruit), various seed biology studies (germination requirements, dormancy, and soil seed bank), means of dispersal, and demographic structure of several populations of Tobusch fishhook cactus (*Ancistrocactus tobuschii*).

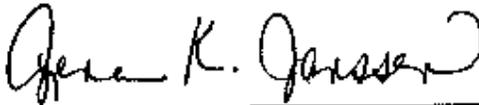
SEGMENT OBJECTIVE: Complete Ph.D. dissertation for submission as final report.

## ACCOMPLISHMENTS

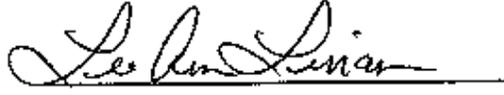
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## SIGNIFICANT DEVIATIONS

*None*

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29 Dec. 1995  
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**REPRODUCTION, MORTALITY, AND TEMPORAL CHANGES IN  
PLANT SIZE FOR THE ENDEMIC TOBUSCH FISHHOOK CACTUS**

*(Ancistrocactus tobuschii)*

by

Raymond Timothy Emmett, B.A., M.A.

**Dissertation**

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

**Doctor of Philosophy**

**The University of Texas at Austin**

December 1995

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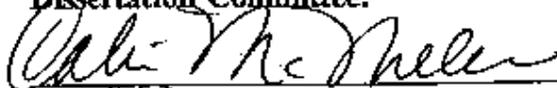
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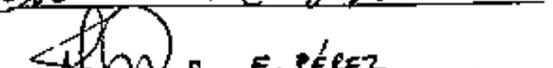
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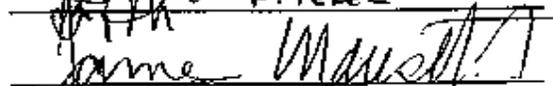
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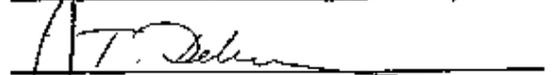
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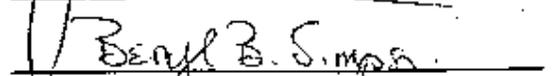
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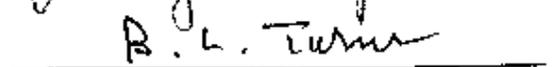
  
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## DEDICATION

This dissertation is dedicated to Dr. Calvin McMillan for his lifelong contribution to ecological science and, through his always popular classes on ecology and environmental issues, for helping to focus the eyes and open the minds of many diverse students toward the world they were preparing to inherit.

## ACKNOWLEDGMENTS

Little did I suspect during my first encounter with this inconspicuous little plant during an Austin Community College class field trip in 1983, that the Tobusch fishhook cactus would play such an important role in my later education. It seems appropriate, therefore, that my first "thank you" should go to the instructor of that memorably enjoyable and informative class, Dr. Steve Muzoz, for helping to start me down this long road.

Along the way, this research project has certainly proven testament to the fact that most substantial undertakings in life are completed only with the help of others. Insight provided by the Ph.D. committee has been of great value, so I would like to thank Dr. Calvin McMillan for his many years of friendly advice and support; Dr. Jim Mauseth for his encouragement and for stepping in to co-direct my committee after Cal retired; Dr. Francisco Perez for his especially close interest in this project; and Dr. Ted Delevoryas, Dr. Beryl Simpson, and Dr. Billie Turner for their constructive guidance.

It is with great appreciation that I acknowledge the assistance of the Texas Parks and Wildlife Department staff, in particular Kelly Bryan, Bill Carr, Wayne

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Finally, I reserve the greatest thanks for my friend and dedicated field assistant of the past four years, Burford L. Westlund. Burford's keen observational skills, practical and extensive knowledge of this cactus and of plants in general, and willingness to work hard even under adverse conditions have contributed immeasurably to this study. While I may have not always been the most receptive audience, Burford never gave up trying to teach me how the cow eats the cabbage. I also reserve a special "thank you" to Dorothy Westlund for kindly and patiently "loaning out" her husband on many weekends throughout the course of this study.

Thanks to you all!

RTE, 1995.

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**REPRODUCTION, MORTALITY, AND TEMPORAL CHANGES IN  
PLANT SIZE FOR THE ENDEMIC TOBUSCH FISHHOOK CACTUS**  
*(Ancistrocactus tobuschii)*

Publication No. \_\_\_\_\_

Raymond Timothy Emmett, Ph.D.  
The University of Texas at Austin, 1995

Co-Supervisors: Calvin McMillan and James D. Mauseth

Three naturally-occurring populations of the endangered Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) were utilized to investigate mortality, changes in plant size, and aspects of the reproductive biology. Two populations were monitored for four consecutive years, the third for two consecutive years. Data pertaining to plant diameter, reproductive effort and success, and mortality were gathered through regular censusing. Several manipulative field

and greenhouse trials were conducted to examine aspects of the pollination biology, seed dispersal, and seed germination.

Field pollination studies showed this cactus to be strongly self-incompatible; that fruit set, seed set, and seed germinability were not significantly different between within-colony and other-colony pollen donation; and that natural cross-pollination may be largely effected by small, solitary halictid bees.

Seed removal and short-distance dispersal appear to be largely effected at all three sites by the small ant *Forelius foetidus*, but the majority of these seeds may end up in the ant mound or in buried refuse piles. Evidence for occasional longer-distance dispersal by birds or mammals was also observed. Gravity and rain-wash dispersal probably also account for a small percentage of seed dispersal. Seed germinability was extremely variable between years, from ca. 1% to 65%. An average of 20% of seeds germinated after ca. one year of placement within field enclosures, with little difference noted in germination between three microhabitat types. A modest soil seed reserve was detected at two of the three sites, although this was limited to the direct vicinity of reproductive-size plants.

Annual census data indicate that populations at two of the three study sites may be in danger of extinction. Annual mortality was consistently high between years at these two sites, affecting ca. 20% to 35% of monitored plants. Two species of cactus-specialist beetle were responsible for the majority of attributable mortality, and probably for much of the nonattributable mortality. Annual flower, fruit, and seed production decreased consistently between years during the censusing period, while percent fruit set remained relatively constant. Average changes in plant diameter were generally small, indicating that previous speculation of rapid growth rate for this cactus may require reevaluation.

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## CHAPTER 1.0 INTRODUCTION

This dissertation presents the findings of a four-year field study and analysis of the reproductive biology, mortality, individual plant size changes within three naturally-occurring populations of the rare endemic Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) in Central Texas. This study was sponsored by the United States Fish & Wildlife Service, through a cooperative agreement with the Texas Parks & Wildlife Department and the University of Texas at Austin, to allow fulfillment of several task objectives presented in the species recovery plan (USFWS, 1987) for this federally-listed endangered cactus.

Chapter 1 of this dissertation provides a general description of the study plant; identification and a general description of the field study sites which were monitored; a brief mention of other facilities which were utilized during the course of the study; a note about limitations on sample sizes used in this investigation; and mention of the data management and statistical software which was used.

In Chapter 2, a brief overview of the general concepts associated with species rarity is presented. The nature of rarity in the Tobusch fishhook cactus is then assessed with regard to these general concepts. Finally, the goals of this particular

investigation are presented, including mention of their potential relevance to conservation of this rare species.

Chapter 3 provides a description of the protocol and results of an investigation of several features of the pollination biology which were performed using several naturally-occurring populations of *A. tobuschii*. Specifically, aspects of the breeding system, the potential pollinators and their relative effectiveness, and the relative effects of near versus far pollen donation were all investigated.

The fourth chapter details an investigation of the seed ecology of the Tobusch fishhook cactus. Specific features which were examined include the average annual seed production and seed germinability; seed dispersal mechanisms; field germination of seeds; and the soil seed reserve.

Chapter 5 provides a description of the field monitoring protocol used during annual censuses of natural populations of *A. tobuschii*; and a summary of the various data obtained during censuses and the analyses performed on these data. Two of the study populations were monitored for four consecutive years, while the third was monitored for two consecutive years. General features which were examined during

this investigation include individual plant size; sexual reproductive effort; mortality; and annual changes in each of these features.

## 1.1 STUDY PLANT

### Morphology and Phenology

The Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) is a small, tuberculate cactus which is endemic to the central and western portions of the southern half of the Edwards Plateau region of Central Texas. Adult plants typically grow, unbranched, to a height of 4.0 to 5.0 cm. and a diameter of 4.0 to 5.0 cm., although there are reports of plants as large as ca. 9.0 cm. in diameter (Weniger, 1970). The onset of vegetative growth, as evidenced by the apical production and expansion of new tubercles, becomes apparent in April and May of each year (pers. observ.). Branching appears to occur in only those plants which have suffered damage to the stem apical meristem (Marshall, 1952; pers.observ.). Each tubercle and its associated areole contains 7 to 9 radial spines and 3 to 5 central spines, one of which is hooked. Fibrous root systems (Benson, 1982) and short taproot systems (Weniger, 1970) have both been reported for this cactus.

Flowering occurs once per year from early February through mid-March, with the yellow/yellow-green flowers borne in the axils of tubercles formed during the most recent growing season. The largest plants may bear eight or more flowers in one season (pers. observ.). With the lack of successful pollination, individual flowers may open daily for up to a week. The green fruits, which are generally 2.0 to 3.0 cm. in length, reach maturity in mid to late May, at which time they may acquire a pink tinge. As fruits dry, a longitudinal slit forms to expose the black seeds, of which there are usually about 20 to 40 per fruit; seeds are papillate, and approximately 1.5 mm. long, 1.5 mm. broad, and 1 mm. thick (Benson, 1982). Reproduction in this species occurs exclusively from seeds (TPWD, 1984).

#### Distribution

The Texas Natural Heritage Program of the Texas Parks and Wildlife Department has documented the occurrence of forty-seven populations of this species, from the time it was first described in the early 1950's through May, 1995 (J. Poole, pers. comm., 1995). Texas counties from which this plant has been reported include Bandera, Edwards, Kerr, Kimble, Kinney, Real, Uvalde, and Val Verde (Figure 1.1). Wauer (1973) reports that this species also occurs in the Dead Horse Mountains, Big Bend National Park, Brewster County, Tx.; Weniger and Warnock

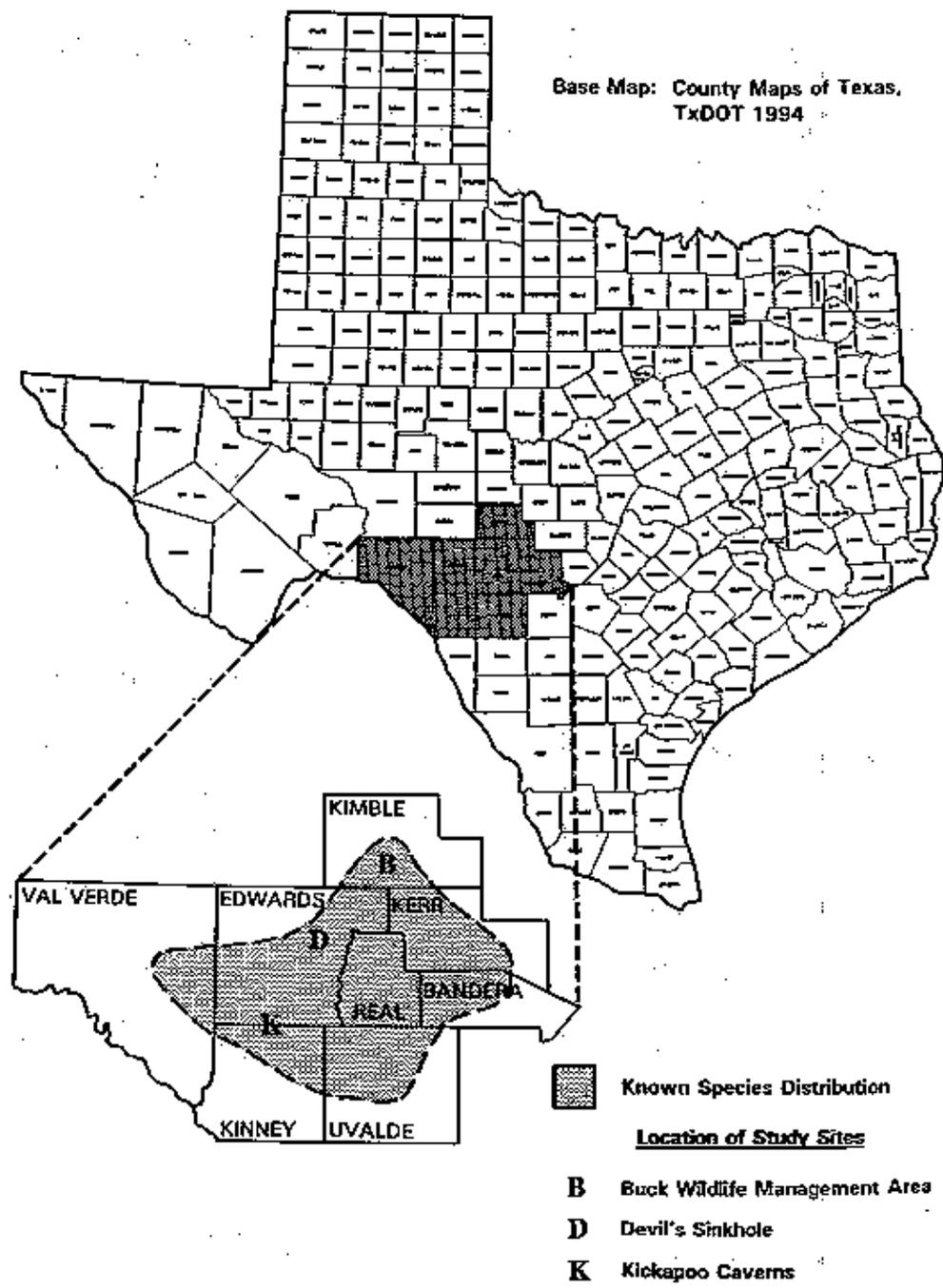


Figure 1.1. Distribution of *Ancistrocactus tobuschii*.

(USFWS, 1979a) and Zimmerman and Poole (TPWD, 1984) believe that this is certainly a misidentification, however, as these mountains are several hundred miles west of the nearest confirmed Tobusch fishhook cactus population, and possess very different habitat characteristics than areas where *A. tobuschii* is typically found.

### Taxonomy

This taxon was first discovered and described as a distinct species in the early 1950's (Marshall, 1952) although, with the original nomenclatural combination published as "*Mammillaria (Ancistrocactus) tobuschii* W.T.Marshall", there was obviously some confusion by the author as to the correct taxonomic affinity. Since that time, there have been additional confusion and disagreement as to the taxonomic status of this plant. Backeberg (1961) placed this species in the genus *Ancistrocactus*, but Weniger (1970) placed the Tobusch fishhook cactus (as well as its congeners and species from other closely related genera) into the genus *Echinocactus*. Weniger's nomenclatural combination for this species is reportedly invalid, however (TPWD, 1984; USFWS, 1987).

More recently, Zimmerman (pers.comm., 1992) has stated that the Tobusch fishhook cactus should be classified as only a variety of the closely-related species

*Ancistrocactus brevihamatus* Britton & Rose (which Benson (1982) claims is merely the mature adult form of *A. scheeri* Britton & Rose). To add ecological confusion to this taxonomic problem, the geographic ranges of *Ancistrocactus tobuschii*, *A. brevihamatus*, and *A. scheeri* overlap somewhat in Kinney and Val Verde Counties and, although these taxa usually occupy different types of habitat within this area of distributional overlap (J. Poole, pers.comm., 1995; pers.observ.), several closely sympatric populations of *A. tobuschii* and each of its congeners are known to occur (J. Poole, pers.comm., 1995). In a limited greenhouse investigation, Zimmerman (unpub. data) noted successful fruit and seed-set resulting from hand-cross pollination of *A. tobuschii* with its congeners, although seed germinability was not assessed. Poole (pers.comm., 1995) has observed some evidence of natural hybridization in closely sympatric *Ancistrocactus* populations.

In spite of these taxonomic and ecological problems, at this time "*Ancistrocactus tobuschii*" is still the most widely used scientific name for the Töbusch fishhook cactus. For this reason alone, this nomenclature is therefore followed throughout this dissertation, although its use should not be construed as an endorsement of this classification. Indeed, the author believes that the relationship between this plant and its congeners is in need of further research, although such an investigation is not within the intended scope of this study.

### Habitat, Ecology, and Population Characteristics

Most of the earliest-discovered populations of this species occurred on gravelly soils in flood-prone areas associated with rivers and streams (USFWS, 1987), but this type of habitat is now considered to be much less typical for this species. Presently, the great majority of known Tobusch fishhook cactus populations grow in full sun to moderate shade on rocky hilltops or mesa-tops in shallow, limestone-derived soils (J. Poole, pers. comm., 1995). The vegetational community type with which *A. tobuschii* populations are typically associated is the Ashe Juniper — Live Oak Woodland, although plants are usually found in the relatively clear, grass and herb dominated openings between wooded areas. In fact, because these inconspicuous and difficult to find cacti (e.g., see Sabo, 1978) somewhat resemble the clumps of bunchgrass with which they are often closely associated, it has been suggested that *A. tobuschii* may effectively be a grass mimic, and/or that grasses may function as nurse plants for developing Tobusch fishhook cactus seedlings and juveniles (TPWD, 1989).

Until fairly recently, fewer than two hundred Tobusch fishhook cactus plants were known in the wild (USFWS, 1979a). While more *A. tobuschii* populations have since been discovered, the majority of these are composed of few and/or widely-

spaced individuals, and the total number of known plants at this writing is still relatively low, only around two thousand (J.Poole, pers.comm., 1995).

Several known populations of this taxon are known to have gone extinct or have been drastically reduced in numbers (USFWS, 1979b; 1987; pers. observ.), including the population from which this species was first described. Known or probable causes of population extinctions include natural and/or man-caused habitat disturbance, and decimation of populations by commercial cactus collectors.

The small and apparently precarious nature of most populations and the largely unknown species biology of this cactus, coupled with known pressures such as persistent and increasing habitat alteration associated with such activities as land development and ranching, and large-scale collection of entire cactus populations to supply the domestic and foreign cactus trade (see TPWD, 1991), led to the addition of *Ancistrocactus tobuschii* to the endangered species list of the United States in 1979 (44 FR 64736), and the State of Texas in 1983. These and other factors which may be contributing to the rarity of this species are discussed further in Chapter 2 of this dissertation.

## 1.2 FIELD STUDY SITES

Naturally-occurring *A. tobuschii* at three separate sites were utilized for study during the course of this project. Before providing a description of each of the three study sites however, it is necessary first to briefly discuss the "plant grouping" terminology used throughout this dissertation. The majority of Tobusch fishhook cactus individuals at all three sites occur within fairly spatially distinct groups of several to many individuals, within which the majority of interaction (e.g., pollination and seed dispersal) occurs, and each of these groups is herein referred to as a "colony." In turn, some of these colonies occur in closely proximal groups, such that there is still a substantial likelihood of interaction between colonies within these groups. A group of closely proximal colonies with a high likelihood of frequent interaction is from here on referred to as a "population." Interactions between different populations at each site are probably much more infrequent, limited by such features as distance and topography. Still, occasional interaction between populations at each site does most likely occur, so the entirety of populations at each study site is described here as comprising a "metapopulation."

Tobusch fishhook cacti at two of the three study sites, i.e., the Walter Buck Wildlife Management Area (BWM), Kimble County, and the Devil's Sinkhole State

Natural Area (DSH), Edwards County, were monitored during the entire 1991 through 1994 duration of the field study. A site in Real County which had originally been chosen for field monitoring starting in 1991 could not be included in this study because the property owner recanted access permission. Beginning in 1993, and continuing through 1994, relatively newly-discovered populations of Tobusch fishhook cactus at Kickapoo Caverns State Natural Area (KPC), southern Edwards County and northern Kinney County were included into the study. Conditions at all of the monitored *A. tobuschii* populations within the three metapopulation sites are characteristic of the rocky hilltop "upland" type habitat which is most typical for this species.

In general, these three Tobusch fishhook cactus sites were chosen for inclusion in this study — with the help of Texas Natural Heritage Program personnel — because 1) they were known to contain a substantial number of individuals; 2) the three sites each occur in geographically different portions of the known range of this species (see Figure 1.1); and, 3) the sites occur on state-owned property, where continued access could be assured for the duration of the study. In addition to the above criteria, choice of these three metapopulation sites was also somewhat fortuitous, because the previously described taxonomic and ecological controversy concerning *A. tobuschii* and its congeners was able to be largely avoided. The BWM

and DSH sites are both just outside of the known distributional range of other *Ancistrocactus* taxa (Benson, 1982), and no other species in this genus were observed at these sites during the four year field investigation. Other *Ancistrocactus* taxa have been reported from Kinney County (Benson, 1982), however, and several *A. brevihamatus* have indeed been seen within the KPC property boundaries (J. Poole, pers. comm., 1995; pers. observ.). All of the *A. brevihamatus* observed at KPC were growing in lowland situations, however, while the *A. tobuschii* populations which were monitored at this site occur on rocky hilltops. No evidence of hybridization was observed within the *A. tobuschii* study populations at KPC during the course of this investigation.

The KPC site is located ca. 64 kilometers (ca. 40 miles) south/southwest of the DSH site, and ca. 116 kilometers (ca. 72 miles) southwest of the BWM site. The DSH site is located ca. 56 kilometers (ca. 35 miles) southwest of the BWM site. As shown on Figure 1.1, BWM lies nearer the northern and eastern boundaries of the present species distribution, while DSH is more centrally located within the known range, and KPC occurs nearest the southern and western distributional boundaries.

Unless noted otherwise, scientific nomenclature for cacti follows Benson (1982) and for all other types of plants follows Correll and Johnston (1970).

Dominant vegetation at all three sites is generally typical of that associated with upland-occurring populations of this species, and includes live oak (*Quercus fusiformis* Small), ashe juniper (*Juniperus ashei* Buchh.), Texas persimmon (*Diospyros texana* Scheele), elbowbush (*Forestiera pubescens* Nutt.) and agarito (*Berberis trifoliolata* Moric). Mexican pinyon pines (*Pinus cembroides* v. *remota* Little) are present at DSH and are common at KPC, but are not found at BWM. Other cacti which are found at one or more of the study sites include several species of prickly pear (*Opuntia lindheimeri* Engelmann and *O. phaeacantha* Engelmann), tasajillo (*O. leptocaulis* de Candolle), sulcate cory cactus (*Coryphantha sulcata* (Engelmann) Britton & Rose), lace cactus (*Echinocereus reichenbachii* v. *reichenbachii* (Tenscheck) Haage, f., ex Britton & Rose), pitaya (*E. enneacanthus* v. *enneacanthus* Engelmann), claretcup cactus (*E. triglochidiatus* Engelmann), biznaga de chilitos (*Mammillaria heyderi* Mühlenpfordt), button cactus (*Epithelantha micromeris* (Engelmann) Weber), and horse crippler (*Echinocactus texensis* Hopffer).

Although the location of many of the study plants at BWM, and of the general colony sites constituting the DSH and KPC metapopulations, had been previously mapped by Texas Parks and Wildlife Department personnel, much of the late winter and early spring of the initial year of the site investigation (BWM and DSH — 1991; KPC — 1993) was spent surveying these properties for additional plants and colonies.

In addition to those areas where *A. tobuschii* was found, there was a great deal of apparently suitable habitat at all three sites where no Tobusch fishhook cacti were found during surveys.

Once identified, individual plants were number-tagged and mapped to allow identification during subsequent censuses. Newly-discovered plants which were growing within or proximal to monitored colonies between the time of the initial site surveys and through 1993 were also number-tagged, mapped, and included in censuses. Details concerning the censusing protocol are presented in later chapters of this dissertation.

During the course of the field study, 162 plants were censused at BWM, 504 plants were censused at DSH, and 116 plants were censused at KPC. In addition to the censused plants, plants in several separate colonies or populations at DSH and KPC were also utilized for several other aspects associated with this study, but were not included in the annual censusing.

As shown in Figures 1.2, 1.3, and 1.4, six BWM colonies comprising two populations, three DSH colonies comprising one population, and two KPC colonies comprising two populations (respectively) were included in some portion of this

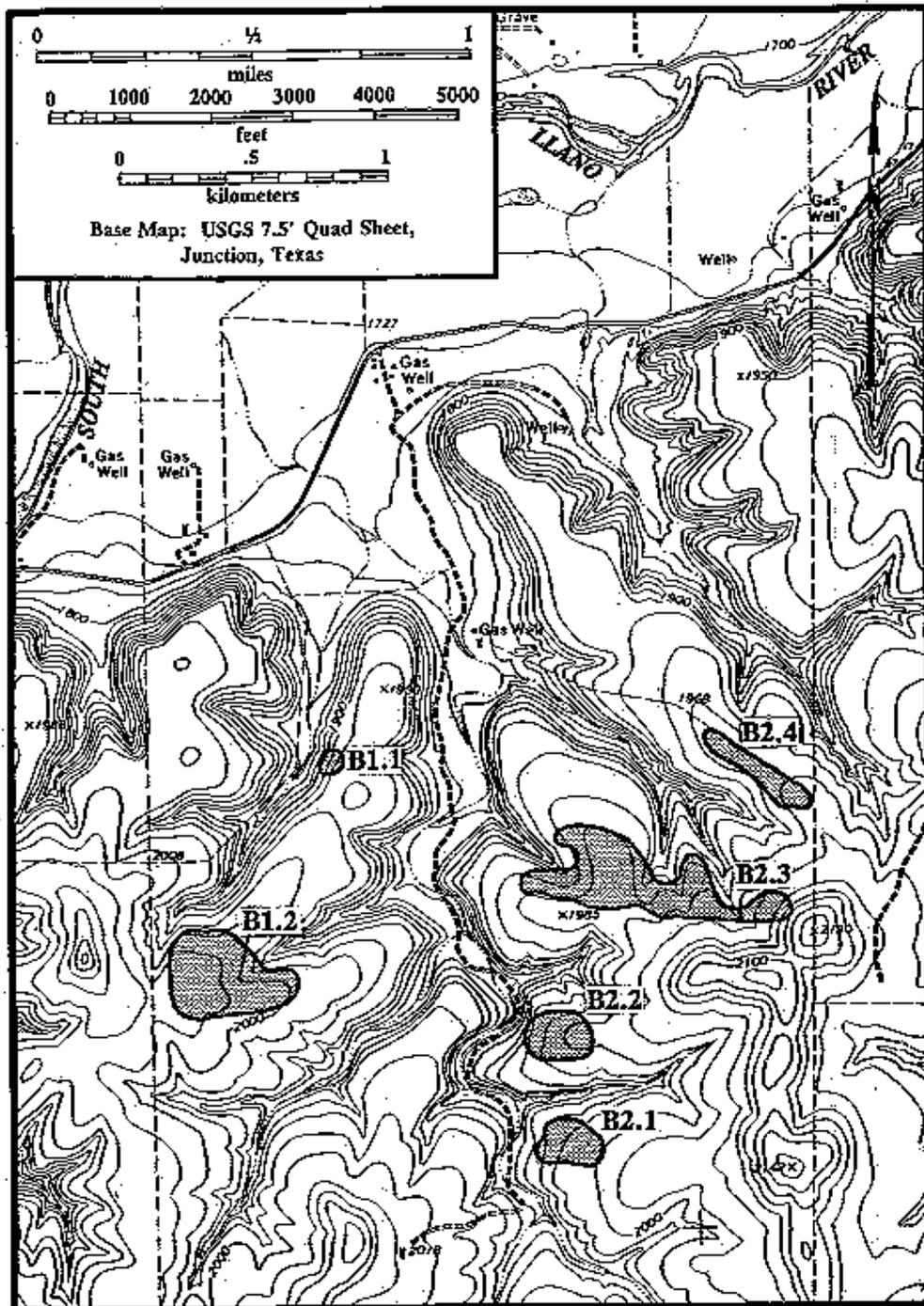


Figure 1.2. Approximate location and boundaries of study colonies at BWM site.

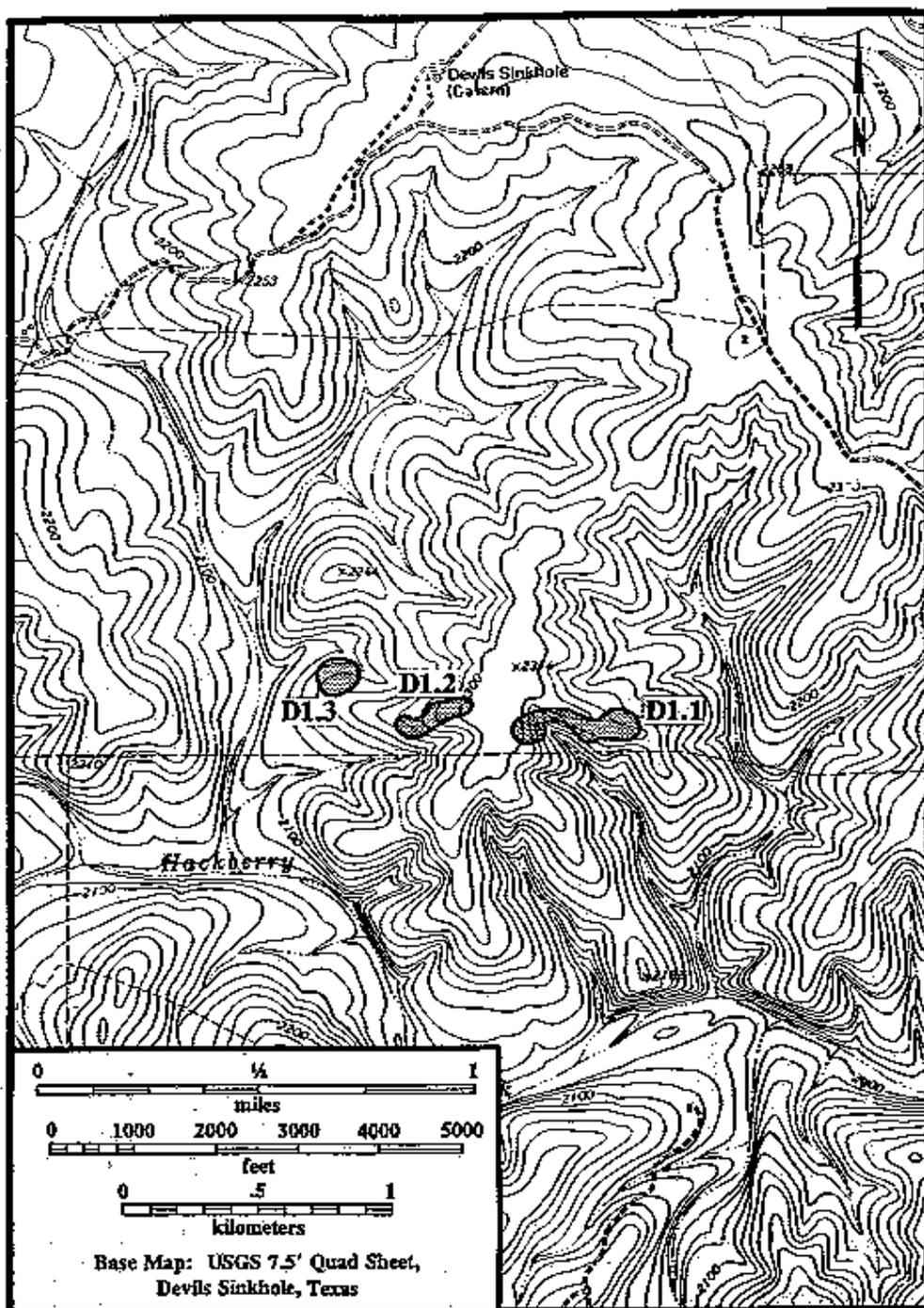


Figure 1.3. Approximate location and boundaries of study colonies at DSH site.

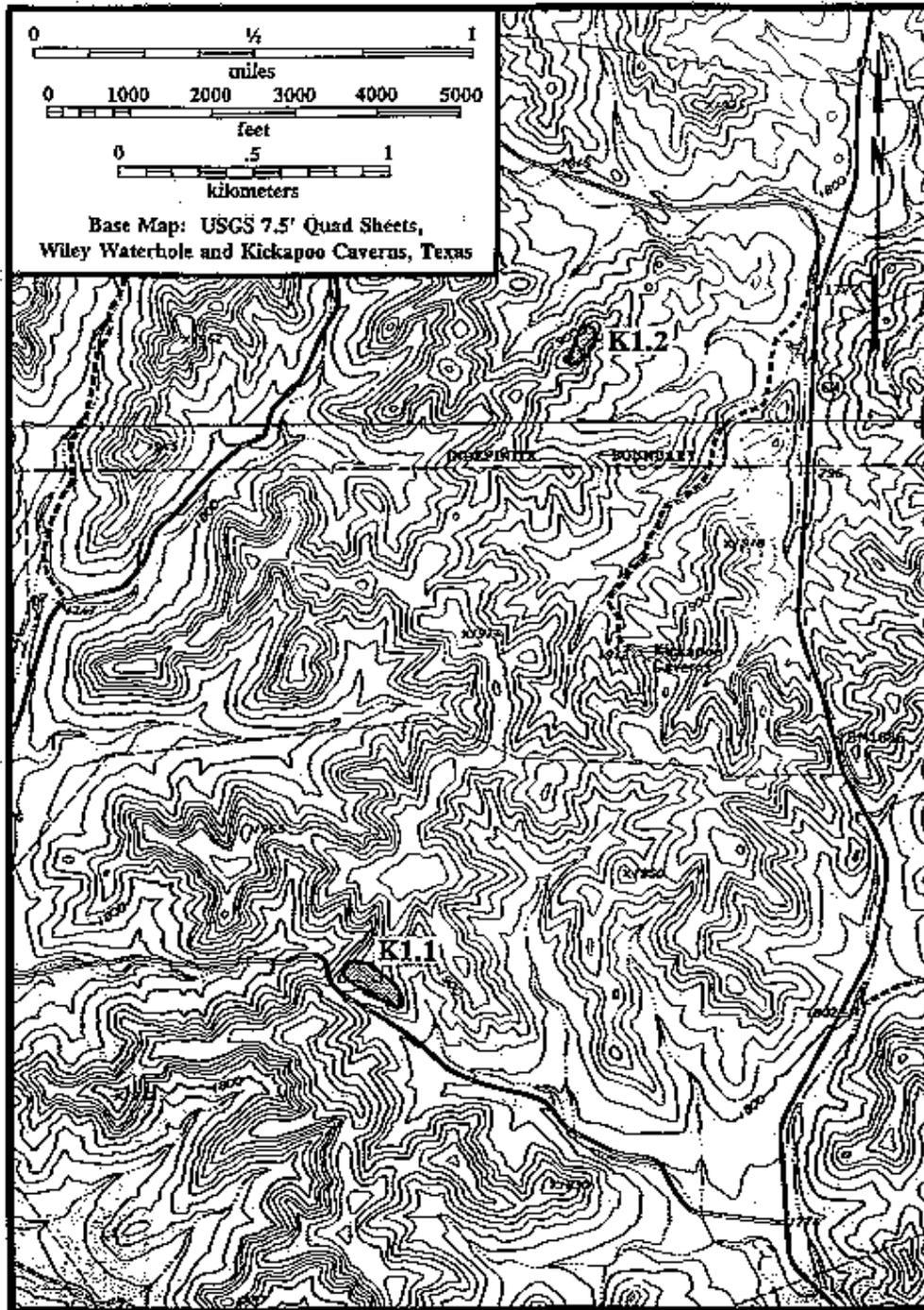


Figure 1.4. Approximate location and boundaries of study colonies at KPC site.

investigation. The boundaries of the colonies and populations were determined through intensive surveys.

It should be mentioned here that the study plant groups are not the only Tobusch fishhook cactus colonies and populations known to occur at each of the three study sites. Although large areas of all three sites were surveyed for *A. tobuschii* at the onset of this investigation, time, resources, and property boundaries constrained this survey to what was felt to be a practical limit. Other surveys not connected with this study have since discovered several additional individuals and colonies of Tobusch fishhook cactus at all three sites.

In an attempt to provide some quantification of obvious qualitative differences between colonies, and to allow some comparison of colony density between populations and between metapopulations, a very rough estimate of the average plant density within these groupings at each site was made. To accomplish this, colonies were surveyed to determine their approximate outer boundaries, i.e., the line beyond which no additional plants were found, plus a small buffer zone. The amount of apparently suitable habitat occurring within the colony boundaries was then evaluated. Criteria for the determination of apparently suitable habitat followed descriptions presented in the species recovery plan (USFWS, 1987) or provided by the Texas

Natural Heritage Program (TPWD, 1984), and, especially, by using knowledge gained through field experience. The approximate areal coverage of apparently suitable habitat within colony boundaries was then determined from direct field measurement. To roughly estimate the approximate density of a colony, the total number of plants of all sizes found within that colony at any time during the course of the field investigation was divided by the areal coverage of suitable habitat within the boundaries.

As shown in Table 1.1, there is a great difference in within-colony plant density between the three sites, but the within-colony plant density within sites is fairly consistent. While relatively small in areal coverage, the KPC colonies are far the most dense of all sites, containing an average of approximately one plant per square meter. The average plant density within the suitable habitat of colonies at DSH is approximately one plant per four square meters, while BWM colonies are the most diffuse relative to the other two metapopulations with an average colony density of approximately one plant per one hundred square meters.

As a note of caution, it should be reemphasized that information presented above and in Table 1.1 is only a rough estimate of "within colony" plant density at each site, and is largely intended for relative comparison of the three sites. No

Table 1.1. Approximation of "within colony" density (# plants/m<sup>2</sup>) at each site, including "within population" and "within site" averages. Approximations are based upon the total number of known plants encountered within each colony during the course of the field investigation, the field-surveyed boundaries of the colony (plus a small buffer zone), and the amount of apparently suitable habitat within the boundaries.

SITE	POPULATION	COLONY	# PLANTS	DENSITY
BWM	B1	B1.1	1	0.01
		B1.2	62	0.02
	B1 Average		63	0.02
	B2	B2.1	10	0.01
		B2.2	16	0.01
		B2.3	63	0.01
		B2.4	10	0.01
	B2 Average		99	0.01
	BWM Average		162	0.01
	DSH	D1	D1.1	337
D1.2			88	0.23
D1.3			79	0.24
DSH Average			504	0.24
KPC	K1	K1.1	116	1.00
	K2	K2.1	30	0.94
	KPC Average		146	0.99

inferences regarding such features as, e.g., actual between-plant distances should be attempted from this information.

### 1.3 CAMPUS FACILITIES

Germination of annually field-collected seeds and initial maintenance of the resulting seedlings was conducted within climate-controlled growth chambers on the University of Texas at Austin (UT) campus. More specific details concerning the protocol used during germination trials are presented in Chapter 4 but, unless otherwise noted, conditions in the growth chambers were maintained at 32°C, 90-100% relative humidity daytime (ca. 13 hours), and 20°C, 90-100% relative humidity nighttime (ca. 11 hours). Daytime artificial light intensity within growth chambers was measured with a hand-held digital light meter (Extech Instruments Model L246348), and averaged ca.  $200 \pm 10 \times 10^2$  Lux.

Seedlings were eventually transplanted from flats into 2-inch pots and removed into one room in a greenhouse complex on the UT campus. The temperature in the greenhouse complex was maintained at approximately 22°C day long. Light intensity and duration within the greenhouse room where the transplanted seedlings were stored was not closely controlled, and varied with the amount of available sunlight and with the occasional and inconsistent supplementation of artificial light from adjoining rooms within the greenhouse complex. Transplanted seedlings were thoroughly watered twice per week and fertilized monthly.

Specimens of *A. tobuschii* are reportedly quite difficult to maintain in cultivation (B.L. Westlund, pers. comm., 1990). For this reason, the greenhouse collection was periodically treated with fungicide (benomyl) and insecticides (e.g., *Bacillus thuringiensis*, diazanon, malathion). Even with this care, however, mortality among specimens in the greenhouse was quite high.

#### 1.4 A NOTE ABOUT SAMPLE SIZES USED IN THIS STUDY

The sample sizes which were used for manipulative trials, such as hand pollination, and during evaluative censusing, such as fruit collection, were necessarily modest for several reasons. First, each of the study populations consisted of a small to moderate number of individuals to begin with. Second, these populations were also being monitored to obtain annual demographic data, and it was felt necessary to limit the impact to plants from manipulative trials. Finally, the general rare status of this plant, and the need to lessen the impacts to the study populations for reasons of conservation, were also considered when deciding upon sample sizes for manipulative trials. For these reasons, the amount of flower-producing individuals utilized for field pollination trials each year was limited to no greater than 15% of the living monitored individuals, and the number of fruits collected was limited to approximately 20% of the total flower production noted within each metapopulation

at the last censusing date. While it could be argued that even the sample sizes utilized in this investigation could ultimately be seriously detrimental to the study populations, it was assumed that impacts caused by various field trials associated with this study could probably be mitigated by the continued existence and input from the unmonitored plants and populations known to exist at each site.

## **1.5 DATA MANAGEMENT AND STATISTICAL ANALYSIS**

All data collected during the course of this field and greenhouse investigation were managed and analyzed using several commercial programs written for use on IBM-PC compatible computers. Data management and basic statistics generation were accomplished using the Q&A version 3.0 (Symantec, Inc., 1988) database program. Statistical analysis of data was performed using SYSTAT version 5.0.3 (SYSTAT, Inc., 1990).

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## CHAPTER 2.0 SPECIES RARITY, AND THE GOALS OF THIS STUDY

### 2.1 INTRODUCTION

Before presenting the methodologies and results associated with the various studies which were conducted during the course of this project, consideration of the topic of "species rarity" and its relevance to this investigation is appropriate. Through a brief review of relevant literature on the subject, several general concepts associated with species rarity are first presented, including definitions of what constitutes a rare species, an overview of various causes which have been proposed to explain species rarity, and ideas for appropriate ways to proceed with investigations of rare species. Using these general concepts as a guide, the nature of rarity specific to the Tobusch fishhook cactus (*Ancistrocactus tobuschii*) is then examined. Finally, based on the potential causes of rarity in this cactus, the goals of the current investigation are presented, including brief mention of their potential relevance to the future conservation of this species.

## 2.2 SPECIES RARITY — GENERAL CONCEPTS

Issues related to endangered, threatened, and rare species and their conservation have received widespread attention during only the past several decades. As summarized in a review by Fiedler (1986) however, the scientific community has been considering the nature of species rarity for well over a century, having variously focused on such concepts as species age and area; species rarity as related to general frequency of occurrence probabilities; the relationship between genetic variability and species adaptability; and edaphic endemism, to explain the commonness or rarity of species.

As with the historical investigations, more current treatments of the nature of species rarity (e.g., Hodgson, 1986; Berg et al., 1994) have also failed to yield completely adequate generalizations which explain the nature of species rarity across broad taxonomic boundaries. In part, this may be due to inadequate and inappropriately broad definitions or descriptions of what constitutes a rare species. Drury (1980) proposes that rare species are simply those whose individuals are divided among somewhat reproductively isolated subpopulations. Rabinowitz (1981), building upon three criteria proposed by Drury (1980), provides an eight-celled categorical framework by which to delineate rare species from more common species

based upon size of the geographic range, degree of habitat specificity, and typical local population size. Based on their proposed criteria, both authors conclude that a minority of the world's species are common and the majority of species are rare. Drury (1980) does, at least, denote the term "endangered" to encompass extreme rarity.

In contrast to overly broad definitions of species rarity proposed in the scientific literature, criteria for governmental recognition as rare and in need of protection may be overly narrow (e.g., see Wilcove et al., 1993), and earlier recognition and protection of certain rare species could allow for more efficient and successful recovery efforts. In the United States, through August of 1994, the federal government had listed 388 rare plant taxa as endangered and 83 as threatened (USFWS, 1994), while several times this amount are currently classified as candidates for listing (K. Kennedy, pers.comm., 1995). In Texas, 28 plant taxa are currently federally listed as endangered or threatened, while approximately 190 more are candidates for listing (J. Poole, pers.comm., 1995; K. Kennedy, pers. comm., 1995).

The overwhelming majority of investigations of the nature of species rarity associated with particular species or narrow taxonomic groups have focused on only

one or a few factors. Much attention has been focused on genetic investigations of rare species, and most seem to confirm the idea that rare species suffer from relatively low genetic variability (e.g., see Dole and Sun, 1992; Kress et al., 1994; Godt et al., 1995; but also see, e.g., Meagher et al., 1978). Many investigations fail to consider adequately whether paucity of genetic variation is a cause, consequence, or both of the condition of species rarity, however (Babbel and Selander, 1974). Other investigations into the causes of rarity in various species or local groups include those which have focused on such features as plant breeding system (e.g., DeMauro, 1993), predators (e.g., Donnell, 1986), general life history (e.g., Fiedler, 1987), and taxonomic issues (e.g., Powell et al., 1991; Standley, 1992). Most species occur in somewhat variable environments and may, therefore, be subject to substantial periodic fluctuations in their numbers in response to, e.g., disturbance or competition. With this in mind, Harper (1981) points out the importance of considering species rarity in time as well as in space.

In contrast to the relatively narrow focus of most investigations of species rarity, Stebbins (1980) suggested the use of a synthetic approach which stresses the interaction of a unique environment, population genetic structure, and evolutionary history. Fiedler (1986) expanded upon Stebbins' synthetic approach, providing a more extensive framework of specific features to consider when investigating the

nature of rarity in a particular taxon of interest. This list consists of nine major categories of factors: species age, genetic health, evolutionary history, taxonomic position, associated ecological conditions, population biology, reproductive biology, land use history, and human use. An approach such as this is superior to other methods because it recognizes that rarity may be due to several contributory or interacting factors. Broad scope investigations of rare species are time and labor intensive, however, and so are relatively uncommon in practice (e.g., see Menges (1990) for complete documentation on the detailed investigation of the Furbish's lousewort).

### **2.3 A CATEGORICAL APPROACH TO PRELIMINARY ASSESSMENT OF RARITY IN THE TOBUSCH FISHHOOK CACTUS**

While few formal studies of *Ancistrocactus tobuschii* have been performed prior to this investigation, a substantial body of observational records from private and governmental entities spanning the ca. 40 years from the time of initial species description does exist. Information contained within these records allows limited speculation regarding some of the possible causes of rarity in this species and, based upon this information, it appears that rarity in *A. tobuschii* may be due to combined pressure from several factors.

Fiedler's (1986) list of nine assessment factors provides a good template by which to organize and assess the potential sources of rarity in a taxon, and also to determine areas which require additional investigation. Following each of the nine factors from this list, a preliminary assessment of rarity in the Tobusch fishhook cactus is presented below.

I. Age of Taxon

The age of this taxon, and of its congeneric species, is unknown. Uncertainty related to taxonomic age is typical of the Cactaceae in general, largely due to a nonexistent fossil record for this plant group (Benson, 1982).

II. Genotype of Taxon

Low genetic diversity could play a contributory role in the rarity of the Tobusch fishhook cactus although, as yet, this has not been investigated. Reports indicate that most of the known populations of *A. tobuschii* are widely separated and consist of relatively few individuals (TPWD, 1984; J. Poole, pers.comm., 1995). Small, relatively isolated populations are especially susceptible to genetic stochasticity associated with the founder effect, genetic drift, or inbreeding (Shaffer, 1987). The

resulting lack of genetic diversity could render populations unable to adapt over generations to changes in the environment.

There is some evidence that most known populations of the Tobusch fishhook cactus are not entirely devoid of genetic variation, however. Although *A. tobuschii* is apparently self-incompatible with respect to pollination (Zimmerman, unpub. manuscript) high fruit-set has been observed within most known populations of this plant, which indicates that at least some genetic variation exists within these populations. Still, while high fruit-set in a normally outcrossing species has been presented as evidence of genetic variability in previous studies (e.g., see Meagher et al., 1978), it does not provide quantification of the amount of variation which is present. Electrophoretic studies are needed to assess the extent of genetic variability for the Tobusch fishhook cactus, especially relative to differences in population size, and to genetic variation in its more common congeners. Such studies were not included within the scope of this project, however.

### III. Evolutionary History

Due to the lack of a fossil record, and of information from molecular investigation within the genus, family and possibly related families, an assessment of the possible ancestry of this taxon has not been attempted.

### IV. Taxonomic Position

As discussed in Chapter 1, taxonomic confusion has plagued the Tobusch fishhook cactus from the beginning, as this taxon was first described as "*Mammillaria (Ancistrocactus) tobuschii*" (Marshall, 1952). Since that time, there has been additional confusion and disagreement as to the taxonomic status of this plant. Weniger (1970) lumps all species of the genus *Ancistrocactus* (as well as species from several other genera) into the genus *Echinocactus*, and refers to the Tobusch fishhook cactus as *E. tobuschii*. This nomenclatural combination is reportedly invalid, however (TPWD, 1984; USFWS, 1987).

More recently, Zimmerman (pers. comm., 1992) has stated that the Tobusch fishhook cactus should be classified as only a variety of the closely-related species *Ancistrocactus brevihamatus* (which Benson (1982) claims is merely the mature adult

form of another closely-related species, *A. scheeri*), because the only reliable difference between the congeners is flower color. To add ecological confusion to this taxonomic problem, the geographic ranges of *Ancistrocactus tobuschii*, *A. brevihornatus*, and *A. scheeri* overlap somewhat in Kinney and Val Verde Counties and, within the few known sympatric populations, possible evidence of natural hybridization has been observed (J. Poole, pers. comm., 1995).

Taxonomic questions continue to exist for the Tobusch fishhook cactus and, based on the current level of information concerning the relationship of this taxon and its congeners, rightfully so. Additional investigations into this matter, perhaps using molecular techniques to determine the degree of relatedness of these taxa, seem very appropriate.

## V. Ecology

### *Habitat*

Most of the earliest-discovered populations of this species occurred on gravelly soils in flood-prone areas associated with rivers and streams (USFWS, 1987), but this type of habitat is now considered to be much less typical for this

species. Presently, the great majority of known Tobusch fishhook cactus populations grow in full sun to moderate shade on rocky hilltops or mesa-tops in shallow, limestone-derived soils (J. Poole, pers. comm., 1995). The vegetational community type with which *A. tobuschii* populations are typically associated is the Ashe Juniper — Live Oak Woodland, although plants are usually found in the relatively clear, grass and herb dominated openings between wooded areas.

This type of situation is extremely common on the Edwards Plateau, and there is a large amount of superficially similar but uncolonized habitat within the known range of this cactus. A detailed comparative habitat analysis should be conducted to investigate whether subtle differences exist between occupied and similar unoccupied sites.

#### *Edaphic Factors*

The Tobusch fishhook cactus typically grows on shallow, often rocky limestone-derived upland soils, or on gravelly limestone alluvium along floodplains associated with streams and rivers (USFWS, 1987). While soils at all population sites appear superficially similar to other limestone-derived soils found in comparable situations throughout most of the southern half of the Edwards Plateau, no detailed

edaphic analyses have yet been performed at *A. tobuschii* population sites to determine if these soils somehow differ from soils at other apparently suitable habitat where no Tobusch fishhook cacti occur.

### *Symbioses*

There are several reports that *A. tobuschii* grows in close association with clumps of short bunchgrasses (Marshall, 1952; TPWD, 1989; but see USFWS, 1979a). Other species of cactus have been shown to require nurse plants for protection of developing seedlings and juveniles (e.g., McAuliffe, 1984; Franco and Nobel, 1989; and Valiente-Banuet and Ezcurra, 1991), and Poole (TPWD, 1989) has suggested that bunchgrasses may function in such a capacity for developing Tobusch fishhook cactus seedlings. Due to the superficial similarity in appearance between some bunchgrasses and more mature *A. tobuschii*, it has also been suggested that the cactus may effectively be a grass mimic (TPWD, 1984). Further investigation of these possible relationships is necessary, as forces which negatively impact the bunchgrass populations (e.g., overgrazing) could also be contributing to rarity of the Tobusch fishhook cactus.

### *Predation*

In addition to the potential threats to this species from trampling or ingestion by domesticated livestock or their feral counterparts, several native faunal constituents which are known to utilize *A. tobuschii* habitat may also play an at least occasional predatory role on this plant. Native herbivores which are fairly common within the known range of this cactus include jackrabbits, cottontail rabbits, porcupines, and javelinas. There have also been reports (TPWD, 1984; A. Zimmerman, pers. comm., 1992) that the larvae of *Gerstaeckaria* sp., a cactus specialist weevil, and *Yosemitia* sp., a nocturnal Pyralid moth, feed and develop to adulthood within the stems of *A. tobuschii* plants, and that this eventually results in the death of the host plant. Zimmerman (pers. comm., 1992) believes that, from a predator-prey standpoint, sparse populations of *A. tobuschii* are the most secure kind, because diffuse spacing may limit the percentage of the population which the predatory insects impact at any one time. Although the extent to which herbivores/predators limit this cactus is not yet known, factors which favor the growth in numbers of *A. tobuschii* predators, such as (e.g.) suppression of their natural predators, could in turn eventually negatively impact the cactus.

### *Competition*

The Tobusch fishhook cactus occurs in several habitat types (i.e., gravelly areas within the floodplain of watercourses; and upland hilltops and mesa tops), each of which is naturally subject to occasional disturbance. It has been suggested (USFWS, 1987; A. Zimmerman, pers. comm., 1992) that this plant may function as a successional species, i.e., that this cactus may colonize only appropriately disturbed habitat, or persist in habitat which is maintained through periodic disturbance. If this is indeed the case, reasons for decline of *A. tobuschii* populations in areas deficient of periodic disturbance could be due at least in part to increased competition from species characteristic of later seral stages.

### VI. Population Biology

Prior to this investigation, no detailed, comparative, repeated monitoring of populations of Tobusch fishhook cactus had been conducted, so information related to life history and demographic characteristics concerning plant growth rate; reproductive rate; mortality; population size, structure, and changes in size and structure; and factors which could affect these features, is sketchy at best. Based on observations of several natural populations, there has been speculation (TPWD, 1984)

that *A. tobuschii* may reach reproductive maturity as early as 3 years from the time of germination, and that most plants die within 10 years following the onset of reproduction. If correct, this short life span (relative to most other cacti) could substantially contribute to rarity in this species if, e.g., successful reproduction occurs only during an occasional or rare year when certain optimum conditions for seedling establishment exist, such as seen in other cacti (e.g., Steenbergh and Lowe, 1977).

Several cactus specialist insects — a weevil (*Gerstaeckaria* sp.) and a moth (*Yosemitia* sp.) — have been observed to contribute to mortality in this cactus (A. Zimmerman, pers. comm., 1992), although the extent of insect-related mortality remains uninvestigated. It appears that there may be great differences in reproductive success (i.e., seedling establishment) both between populations, and/or during different years or groups of years within populations. Various reports have described populations in which all sizes of cactus were observed, including seedlings (Marshall, 1952; TPWD, 1984), and populations within which no seedlings were observed during a period of many years (USFWS, 1979b). Potential causes of the reported differences in reproduction between populations have yet to be explored, however.

## VII. Reproductive Biology

Typical of the majority of the cactus family (see Ross, 1981), the Tobusch fishhook cactus is reported to be an obligate outcrosser (Zimmerman, 1981). The principal pollinators in at least some populations may be small, solitary halictid bees and honey bees (*Apis mellifera*) (Zimmerman, 1981; Lockwood, in press), although the relative success at pollination for these organisms has not yet been directly assessed.

The seed ecology of this species remains largely unexplored. Seeds of this species are reportedly of high germinability (Marshall, 1952), and seedlings have been observed in some populations of Tobusch fishhook cactus (TPWD, 1984), but more specific information concerning seed production, seed germinability, seed dispersal, and seed germination in habitat is lacking. The presence of a soil seed reserve has been reported for other cactus species (e.g., Emmett, 1989), but has not yet been studied for this species. Poor reproduction could be contributing to the rarity of this species, so each of these features requires investigation.

## VIII. Land Use History

Humans have had a large impact on the character of the Edwards Plateau region during the past century and a half, and this alteration of habitat may be viewed on two scales. On a smaller, more localized scale, the direct modification of occupied or potential cactus habitat sites for construction of human habitations or associated structures; damming or channelization of streams and rivers; and, especially, clearing of land for rangeland and/or feeding and trampling by domesticated grazing or rooting animals and their feral counterparts (e.g., cattle, goats, sheep, and hogs), have all been reported as real or potential threats to this cactus (Marshall, 1952; USFWS, 1979b; 1987; 1988; TPWD, 1984).

On a larger scale, there is evidence that man has significantly altered the vegetational character of much of the Edwards Plateau during the past century and a half (Doughty, 1983). Many areas which were once reportedly dominated by grassland or savanna are now dominated by live oak and juniper woodland; it has been proposed that this change has resulted largely due to the combined effects of the higher grazing pressure associated with the widespread introduction of livestock, and with the suppression of natural fires (Amos and Gehlbach, 1988). Such changes may have substantially decreased the amount of suitable habitat available to *A. tobuschii*

although, because there are no historical records of the distribution or frequency of occurrence of this species prior to the mid-twentieth century, this idea remains as speculation.

The Tobusch fishhook cactus is typically found in areas currently and/or historically subject to periodic disturbance (i.e., floods — floodplain areas; fires — upland areas) (TPWD, 1984; USFWS, 1987). While no formal investigations of the relationship between disturbance and the Tobusch fishhook cactus have yet been completed, studies of the effects of juniper (*Juniperus* spp.) clearing, livestock grazing, and controlled burning on *A. tobuschii* are either in the proposal phase or have been recently begun.

A recent disturbance event at the population site at Devil's Sinkhole State Natural Area (DSH), Edwards County, may serve as an example (albeit uncontrolled) of the effects of disturbance on this cactus. DSH is the largest known *A. tobuschii* population, having recently contained over 400 individuals within an ca. 2000 m<sup>2</sup> area (pers. obs., 1992). During a widespread wildfire at this site in April, 1988, the entire area within which Tobusch fishhook cacti now occur in relatively high numbers is reported to have burned (TPWD, 1988; K. Bryan, pers.comm., 1990). While fire has been reported to be generally detrimental to living cacti (Bunting et al., 1980;

Steenbergh and Lowe, 1983), a substantial number of moderately-sized Tobusch fishhook cacti were observed within heavy ash at the site within several months of the fire (Westlund, pers.comm., 1990). Unfortunately, an in-depth survey had not been conducted prior to occurrence of the fire, so the pre-fire extent of the *A. tobuschii* population at this site is unknown. During censuses associated with the current investigation in the early 1990's, many of the plants which were observed were of a size which indicates that their existence probably predated the above fire.

If occasional disturbance is indeed required by *A. tobuschii* to maintain and/or allow the establishment of populations, human-caused suppression of natural disturbance factors such as fires and floods may be limiting the amount of suitable habitat available for *A. tobuschii* colonization and persistence.

#### IX. Recent Human Uses

The U.S. Endangered Species Act does not restrict the collection of listed plants on private land or the interstate commerce in these plants, although the State of Texas does at least require that written permission from the private property owner be obtained prior to collection, and that identification tags be attached to plants which are offered for sale (USFWS, 1987). The large-scale decimation of entire

populations by certain commercial plant collectors to supply the domestic and foreign cactus trade has been identified as a problem for many cactus species (TPWD, 1991). Many cactus enthusiasts are especially eager to add rare species to their collections, and are willing to pay handsomely for these specimens, so over-collection by cactus dealers to supply this market has become an even more serious problem for rare species such as the Tobusch fishhook cactus (USFWS, 1987). For this reason, governmental agencies are usually protective of locality information for rare species, although recent publication of several sites of occurrence for the Tobusch fishhook cactus (Weisman, 1995) indicates that this is not always the case.

#### **2.4 GOALS OF THIS STUDY**

Many factors were identified in the previous section which are potentially contributory to the rarity of this taxon. This preliminary analysis also shows that very little is yet known about the Tobusch fishhook cactus, but it would take many years to fill in all or most of these gaps in knowledge about the species. Because the unfortunately precarious status of many rare species such as this cactus call for near immediate preservational action, however, it has become necessary to place emphasis on the identification and investigation of certain key features which are most critical to the development of a potential conservation strategy.

Information relating to the demographic status of populations, and of the relationship of the species with its environment is almost always crucial to the development and implementation of successful species protection and management strategies (Primack, 1993). Following the categorical guideline presented in the previous section, an investigation of the Tobusch fishhook cactus should, therefore, focus on features included within the categories ecology, population biology, and reproductive biology, although consideration to features within other categories would also be appropriate. With this in mind, and with the concurrence of the relevant governmental agency sponsors (J. Poole, pers.comm., 1990), the decision was made to design this study to include: a four-year demographic monitoring program of several different populations of this cactus; an investigation of the reproductive biology of this taxon; and a comparative analysis of several aspects of the habitat and potential habitat with which this species is most commonly associated. The habitat analysis investigation is still in progress, and is not included in the scope of this dissertation.

More specifically, the general life history, population structure, changes in individual plant size over time (used here as an approximation of plant growth rates), mortality rates, causes of mortality, reproductive effort and success, breeding system, potential pollinators, seed germinability, seed dispersal, seed germination in habitat,

and the soil seed reserve were studied during a four-year field investigation using three geographically separated natural metapopulations of this cactus.

The above investigations can be useful in identifying at least short-term trends within populations, as well as apparent causes for observed changes. Information gathered from these investigations can be used to perform predictive analyses on the future persistence of populations. Ultimately, the results of this and associated studies should allow development of a management plan to protect and allow recovery of this species. If successful, various methodologies used in this investigation may also be used as a blueprint for the study and recovery efforts of other rare taxa.

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**CHAPTER 3.0 FIELD POLLINATION STUDIES OF THE  
TOBUSCH FISHHOOK CACTUS (*ANCISTROCACTUS TOBUSCHII*  
W.T. Marshall ex Backeberg) IN WEST CENTRAL TEXAS**

**3.1 ABSTRACT**

Several aspects associated with the pollination biology of the Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) were investigated at two natural population sites. The breeding system, potential pollinators, and effects of pollen donor proximity on reproduction were all investigated. The mean percent fruit set, number of seeds per treated flower, and percent seed germination were all much lower for hand self-pollinated flowers (5.0%; 1.1 seeds; 6.3%) than for hand cross-pollinated flowers (98.0%; 38.9 seeds; 22.7%), indicating that this species is self-incompatible with respect to pollination. Several species of halictid bees were the most commonly observed insect visitors at both sites during the four year field investigation, although a limited investigation into their effectiveness as pollinators indicates that they may effect little pollination per floral visit. A test of the relative effects of artificial pollination using "neighbor" pollen (i.e., from within the same colony) versus "distant" pollen (i.e., from another colony in the same population) on preemergent reproductive success at one population site showed that no significant

differences exist between the two test groups with respect to fruit set, seed set and seed germinability, indicating that pollen transfer between closely proximal individuals (which have a higher probability of being closely related) may not be limiting reproductive success in this population.

### 3.2 INTRODUCTION

The Tobusch Fishhook Cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) is a small, tuberculate member of the Cactaceae which is endemic to the south central and western portions of the Edward's Plateau region of Texas. Several naturally occurring populations of *A. tobuschii* at two locales — the Buck Wildlife Management Area (BWM), Kimble County, Tx.; and the Devil's Sinkhole State Natural Area (DSH), Edwards County, Tx. — were utilized to conduct an investigation of several facets of the pollination biology of this taxon.

An understanding of the reproductive biology of a rare plant species is crucial to development of a potential management or recovery strategy. With the increased interest and urgency to preserve and protect endangered species during the past several decades, pollination studies of rare species have become more common (e.g., Macior, 1978; Dieringer, 1991), and have elucidated contributory pressures on rare

species associated with such features as the breeding system (e.g., DeMauro, 1993) and insufficient pollinator populations (Suzan et al., 1994). Prior to this study, several investigations of the reproductive biology of the Tobusch fishhook cactus had been conducted. In an admittedly informal investigation of the floral and pollination biology of *A. tobuschii* in which sample sizes were small, Zimmerman (unpub. manuscript) indicates that this species appears to be self-incompatible with respect to pollination; that cross-pollination likely occurs entirely by insect vectors; and that the physical characteristics of the flowers probably leads to near exclusive pollination of this species by small bees. Lockwood (1995) has recently collected and identified several species of bees (as well as three other types of insects) from *A. tobuschii* flowers over the course of three years at Kickapoo Caverns State Natural Area (KPC), Kinney and Edwards Counties, Tx., and reports that honeybees (*Apis mellifera*) and a solitary halictid bee (*Dialictus comulus*) were the most common floral visitors at that site. Although the relative effectiveness at pollination of these insects was not directly assessed, Lockwood (1995) has proposed that successful pollination of each flower may occur with few pollinator visits.

To test the previous determination that *A. tobuschii* is self-incompatible with respect to pollination (Zimmerman, unpub. manuscript), hand pollination trials were performed on plants growing in naturally-occurring populations at the BWM and

DSH sites, using somewhat larger sample sizes than were used in the above-cited investigation. To gather additional information regarding the potential pollinators of this species, insect visitors to flowers of *A. tobuschii* were observed and voucher specimens of each type were collected for identification at BWM and DSH during each of the four field seasons encompassed by this investigation.

Previous reports (TPWD, 1984; Marshall, 1952; Zimmerman, unpub. manuscript) and preliminary observations associated with this study indicate that a substantial amount of pollen and seed dispersal may occur over a relatively small distance for *A. tobuschii*. Bees, which appear to be the most common floral visitors to *A. tobuschii*, typically optimize foraging by limiting interflight distances between potential food sources (see Levin, 1981). Seed dispersal in this cactus appears to be largely affected by gravity, rainwater, and ants (TPWD, 1984; Chapter 4, this dissertation). The occurrence of these two factors increases the likelihood that a large amount of pollen transfer could occur between closely related individuals, possibly leading to a high frequency of inbreeding within populations of this taxon, especially in relatively densely-spaced groups such as the several study colonies at DSH. Inbreeding depression (due, e.g., to increased incidence of homozygosity of deleterious recessive alleles) is a potential consequence of self-mating or mating between closely related organisms, resulting in reduced fitness in offspring (e.g.,

Darwin, 1900; Schoen, 1983; Levin, 1984; DeMauro, 1993; but see Billington, 1991). Inbreeding may effect a decrease in preemergent reproductive success, i.e., a decrease in fruit set, seed set and germination percentage (Wiens et al., 1987; Levin, 1989), especially in outcrossing species (e.g., Menges, 1991; Heschel and Paige, 1995).

During the first year of this study (1991), substantial differences in fruit set, seed set, and seed germinability were noted between BWM and DSH (See Chapters 4 and 5). In the much more densely-populated DSH metapopulation, seed germinability was significantly lower than that at BWM in 1991 (paired t-test,  $P < 0.001$ ), and fruit set and seed set were also noticeably lower at DSH in 1991, although these differences were not statistically significant. Mean fruit set, seed set, and seed germinability were more similar between BWM and DSH in 1992 and 1993, however.

Hand-pollination trials were conducted in 1994 to determine if the lower reproductive output noted at DSH in 1991 could have been associated with the much higher plant density at this site relative to BWM, i.e., that a higher percentage of pollen would be transferred between densely grouped plants, which would have a higher degree of relatedness due to limited-distance seed dispersal. The test was

designed to compare fruit set, seed set, and seed germinability resulting from pollination using pollen from within the same colony (neighbor) versus pollen collected from a spatially disjunct colony (distant) at the same metapopulation site.

### 3.3 MATERIALS AND METHODS

#### Overview of Floral Biology and Phenology

The period of anthesis for this cactus typically occurs between early to mid February through mid to late March of each year, with the peak blooming period usually occurring in late February through early March. Flowers of this species are hermaphroditic, contain numerous stamens which produce copious amounts of pollen, but produce little or no nectar (Zimmerman, unpub. manuscript). Protandry has been observed for Tobusch fishhook cactus flowers (TPWD, 1984; pers. observ.), but this may not constitute true temporal dioecism (see Cruden and Hermann-Parker, 1977) such as has been reported for a species of hedgehog cactus (*Echinocereus fasciculatus*) (Grant and Grant, 1979a) because hand pollination of flowers prior to stigma lobe unfolding still results in apparently normal fruit and seed set (Zimmerman, unpub. manuscript; pers. observation). Stamens usually exhibit a thigmotropic response (pers. observ.), which is typical in the Cactaceae. All flower

parts of this taxon are yellow in color, except for the outermost tepals and the stigma lobes, which are pale and bright green, respectively.

Tobusch fishhook cactus flowers are diurnal and, because flowers have been shown to be a major source of water loss for other species of xerophytic cacti (Nobel, 1977), this is interpreted to be a water conservation strategy. Flowers of this species open only during periods when sufficient sunlight and warmth are available (which also usually coincides with periods conducive to pollinator activity), and remain closed in the absence of these conditions. Without adequate pollination, individual flowers may reopen daily (given the proper environmental conditions) for up to a week (USFWS, 1987; TPWD, 1984; pers. observ.).

#### Breeding System

The compatibility status of *A. tobuschii* was investigated by comparing the effects of self versus cross pollination on fruit set, seed set, and seed germinability. To perform this investigation, it was necessary to prevent access to flowers on subject plants by potential pollinating insects. Exclusion devices were designed to cover entire plants, rather than just individual flowers. These were made from pieces of standard metal mesh window screening which was formed into the shape of a cone;

this was then covered with a cone-shaped piece of shear window drapery fabric, to insure that access was prevented from even very small potential pollinators. "Cones" were placed over individual plants and held in place by several aluminum nails pushed into the ground around the basal edges. A preliminary test of the cones in Spring, 1991, indicated that this design allowed for adequate light penetration and air flow, while effectively preventing flying insects from reaching flowers.

In mid-February, 1992, nineteen bud-forming plants at BWM and thirty bud-forming plants at DSH were fitted with the above-described cones just prior to anthesis. Plants were chosen for this study from a stratified random sample of plants which were of sufficient flower-producing size (i.e., 2.0 cm plant diameter or greater), based upon 1991 stem diameter census data. When primary plants were found not to be producing flower buds that season, substitute plants were chosen for this trial from a back-up list.

Plants were then assigned to one of two groups — hand self-pollination and hand cross-pollination — with both groups consisting of an approximately equal number of plants and an equivalent distribution of plant diameter. Manipulations were carried out on each test plant when a flower was observed to be open during one of four field visits made on four consecutive weekends in late February through

early March, 1992. If more than one flower was open, manipulations were performed on each open flower. In order to maintain the independence of samples, the resulting fruit set, seed set and germinability from plants on which more than one flower was treated were averaged and reported as one sample. Manipulations were performed on each flower using a two inch steel hardware nail to brush pollen from its own anthers (self), or from the anthers of four to six other plants also in anthesis within the metapopulation (cross) onto the stigma. Nails were disposed of after completion of one stigmatal pollination to avoid possible pollen contamination of subsequent flowers. Nails were used for the manipulations because they were readily available in sufficient quantities and, especially, because *A. tobuschii* pollen readily adhered to and was easily visible on the surface of the nail, but was easily brushed off onto the stigmatic surface with gentle contact. Following the pollination treatment, several tepals of each manipulated flower were marked on the outer surface with a blue (self) or green (cross) paint pen, to allow later distinction of hand-manipulated flowers (and resultant fruits) from others on the same plant. Cones were immediately replaced over each plant following treatment, and were permanently removed after one to two weeks, when manipulated flowers had obviously senesced.

All fruits which resulted from hand pollination were collected upon maturation in late April or early May, as was one fruit each from a subset of the naturally-pollinated plants throughout the metapopulation site. Fruits were each placed into individual labeled envelopes and transported to the laboratory in Austin for further processing.

In the laboratory, fruits were carefully split open and allowed to air-dry at room temperature for a period of one to two months. Seeds were then removed from each dried fruit and were counted, treated with a commercial fungicide (Fertilome with benomyl), and dry-stored in individual labeled, capped bottles in refrigeration (ca. 8°C) until performance of the germinability assessment.

Germinability of seeds from each fruit was assessed by sowing and maintaining the seeds in controlled conditions within a growth chamber, and monitoring and recording the percentage germination. The germination trial was begun in July, 1992, and was concluded in April, 1993, which was approximately one month after the last noted germination of a seed. Seeds were removed from refrigeration and sown into a 2:2:1 mixture of commercial potting soil:sharp sand:perlite in compartmentalized seedling flats, one seed per compartment. Twenty seeds from each fruit were utilized for this test except when a fruit yielded less than

twenty seeds, in which case all of the seeds from that fruit were used. Flats were kept covered with clear plastic lids in the climate-controlled growth chamber at 30°C, 100% relative humidity daytime (13 hrs.), and 21°C, 100% relative humidity nighttime (11 hrs.). Trays were thoroughly watered ca. every 2-3 days, and were monitored weekly for germination during the first two months of the trial, then monthly thereafter. Germinability was determined as the percentage germination of seeds from each fruit.

The mean, range, and standard error of the mean were determined for fruit set, seed set, and seed germinability among selfed and outcrossed groups using SYSTAT version 5.0.3 (SYSTAT, Inc., 1990). Summary statistics for the above characters resulting from naturally-pollinated (i.e., unbagged and not hand-manipulated) flowers throughout each metapopulation site were also generated and are presented for comparison but, because the goal of this investigation was to examine self- versus cross-pollination and not to compare the success of hand versus natural pollination, the natural pollination category does not represent a true experimental control in this instance. Because very few nonzero values were obtained for fruit set and seed set resulting from the "self" treatment at both sites, and because the associated seed germination values were nonexistent (i.e.,

germinability assessment of zero seeds is meaningless), additional statistical comparison of these data is not appropriate.

#### Floral Visitors, and Their Relative Effectiveness at Pollination

In order to gather information about the potential pollinators of *A. tobuschii*, all insect visitors which were observed on flowers at BWM and DSH during 1991 through 1994 were recorded. The abundance of the different flower-visiting insects of this cactus was not known (potential pollinating insects were never observed in large numbers during the four field years of this investigation), so voucher specimens were only periodically collected of each noticeably different type, to minimize possible negative impacts to insect populations. In an independent investigation, Lockwood (1995) was concurrently monitoring insect visitation on Tobusch fishhook cacti at Kickapoo Caverns State Natural Area, Kinney County and Edwards County, Tx.

In general, pollinator activity was noted only on days when conditions were sunny to partly cloudy, with temperatures of at least 16°C, and with calm to gentle wind conditions. The erratic and unpredictable nature of the weather during the typical flowering period for this species (February-March) somewhat limited the

number of field visit days on which conditions were actually conducive to floral opening and insect activity. Still, at least some insect activity was observed during each year, and at least one voucher specimen was collected of each noticeably different type of insect that was observed visiting Tobusch fishhook cactus flowers during the four year field study. Insects were collected into a net as they left the flower and were then placed into a kill jar charged with ethyl acetate. Specimens were returned to the laboratory in Austin where they were pinned and labeled.

During the 1993 and 1994 field seasons, randomly chosen bud-forming plants were covered with exclusion cones in preparation for trials designed to compare the relative pollination effectiveness of various types of natural insect visitors to *A. tobuschii* flowers. The test was designed to compare fruit set, seed set, and seed germinability resulting from flowers receiving a single visit from one of the various potential pollinating insects. Cones were to be removed and the open flower watched until visitation by an insect. Insects were to be collected following floral visitation, and cones replaced to insure against additional visitation to the insect-manipulated flower. Unfortunately, weather conditions proved too cloudy, cold, and/or windy to facilitate floral opening, insect activity, or both during most field visit days designated for performance of this task. Fair weather conditions did allow performance of the insect visitation procedure on ten plants at DSH during one

afternoon in early March, 1993, but none of the ten visited flowers produced a mature fruit. Insects which were observed during this trial were collected and prepared as above, then pooled with other voucher specimens. Specimens were distributed to several entomological experts for identification.

#### Relative Reproductive Success Using Near Versus Far Donor Pollen

This investigation was performed to determine if the proximity of pollen donors to the recipient plant within a population has an effect on reproductive fitness. Specifically, fruit set, seed set, and seed germinability were compared between flowers which were hand-pollinated using donor pollen from within the same dense colony (i.e., "neighbor" pollen) and flowers which received pollen from plants within another colony within the same population (i.e., "distant" pollen). To accomplish this, pollinator exclusion cones were placed (as for "Breeding System" above) on fifteen randomly chosen bud-forming plants within each of two spatially distinct colonies (i.e., thirty plants total) at DSH in February, 1994. The distance between the two colonies, from here on referred to as "East" and "West", is ca. 700 m. (see Figure 3.1).

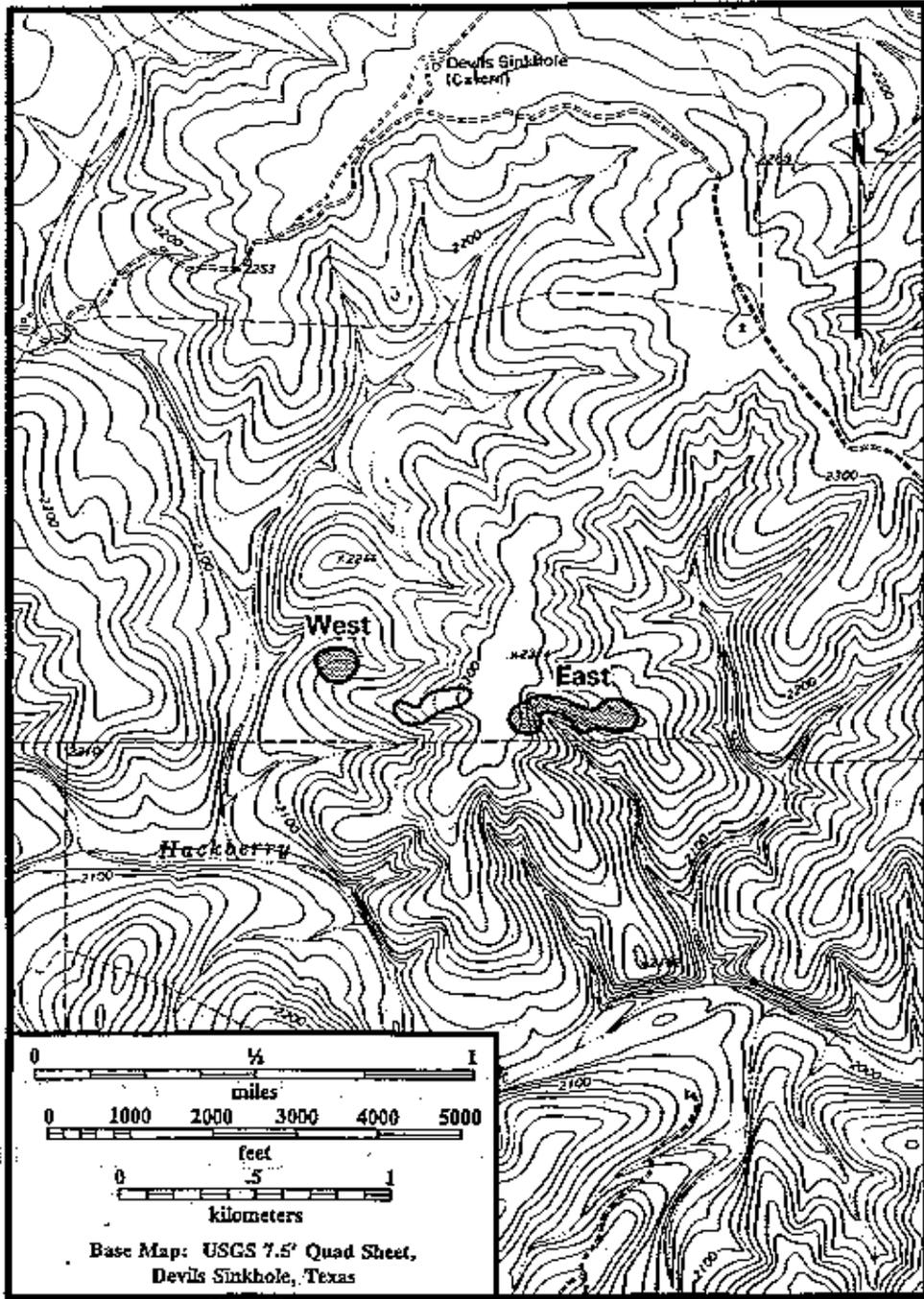


Figure 3.1. Approximate location and boundaries of the "east" and "west" colonies at DSH. The intermediate colony site is also shown.

Complete reproductive isolation probably does not exist between the two colonies. One substantial colony is known to occur between the East and West colonies, ca. 250 m. west of the East colony; several scattered individual plants are also known to occur between the two study colonies. The modest distance between the two colonies coupled with the occurrence of the intermediate colony and individuals between the two study colonies probably ensures that at least occasional gene exchange occurs between the East and West colonies. Still, considering the typically optimal foraging behavior of bees (the most commonly observed floral visitor), the apparently limited typical dispersal distance of Tobusch fishhook cactus seeds (see Chapter 4); and the existence of several topographic and vegetational obstructions between the two colonies, the majority of gene exchange probably takes place within each colony.

In early March, 1994, one flower on each of approximately one-half of the test plants at both colonies were hand-pollinated (using hardware nails as described in "Breeding System" above) with "neighbor" pollen from three nearby plants with open flowers, while a flower on each of the remaining test plants at each colony were hand-pollinated with "distant" pollen gathered from three plants at the other study colony. In order to distinguish manipulated flowers (and resultant fruits) from nonmanipulated flowers on each plant, several tepals on near-pollinated flowers were

spot-painted orange, while those on far-pollinated flowers were spot-painted blue. Cones were immediately replaced over each plant following treatment to prevent possible additional pollination by insects. Cones were removed after one to two weeks, when manipulated flowers had obviously senesced. In April or May, 1994, mature fruits resulting from manipulations, as well as a subset of the naturally-produced fruits at DSH, were collected into individual labeled envelopes and transported to the laboratory in Austin for processing and eventual greenhouse seed germinability testing, as described in "Breeding System" above.

Statistical analyses were performed to compare the test groups with respect to mean fruit set, seed set, and germinability. Each of these features were compared using a Kruskal-Wallis test. The mean and standard error of the mean of the data from naturally-produced *A. tobuschii* fruits from throughout the DSH site (i.e., all colonies at this site) are included for comparison. It was not the goal of this investigation to compare the relative success of the hand manipulations to natural pollination, however, so the latter does not constitute a true experimental control for this trial, and these data were not included in statistical analyses.

A nonparametric test was used for analysis of the two test groups because neither the data nor residuals for each of the dependent variables were normally

distributed, even after employment of each of several types of data transformation (i.e., log, arcsine, and square root) (Sokal and Rohlf, 1981). Differences between the two study sites for the "within test group" data for each character were not statistically significant, so data for the two sites were pooled for analysis to compensate for small sample sizes.

### **3.4 RESULTS**

#### Breeding System

Not all of the test plants chosen for this investigation were able to be utilized, because flowers on several plants were not open during field visit days, and because "cones" were found pulled off of some plants before treated flowers had fully senesced (leaving open the possibility that flowers received additional "natural" pollination). Such plants were removed from this study. Hand self-pollination was successfully accomplished on nine plants at BWM and thirteen plants at DSH, while hand cross-pollination was followed through to completion for nine plants at BWM and fourteen plants at DSH.

Results of the breeding system trials were similar at both sites, and appear to confirm an earlier report of pollen self-incompatibility for the Tobusch fishhook cactus (Zimmerman, unpub. manuscript). Fruit set, seed set, and seed germinability are clearly much lower for the hand self-pollination group than for the hand cross-pollination group (Figures 3.2, 3.3, and 3.4). Only ca. 5.0% of hand self-pollinated flowers resulted in formation of fruits and seeds, while almost 98% of the hand cross-pollination at both sites resulted in formation of fruits and seeds. Hand cross-pollinated flowers at both sites also resulted in more seeds per treatment (1.1 — self; 38.9 — cross) and higher germinability of these seeds (6.3% — self; 22.7% — cross) than self-pollinated flowers.

Hand cross-pollinated flowers had comparable or superior fruit set, seed set, and seed germinability to naturally pollinated flowers (Figures 3.2, 3.3, and 3.4). Naturally-pollinated flowers at both sites (combined) in 1992 resulted in 67.4% fruit set, 16.0 seeds per flower, and 24.5% seed germinability.

#### Insect Visitors, and Their Relative Effectiveness at Pollination

During each of the four years of this study, eight to ten field visit days were spent at study sites from mid-February through late March, the typical peak blooming

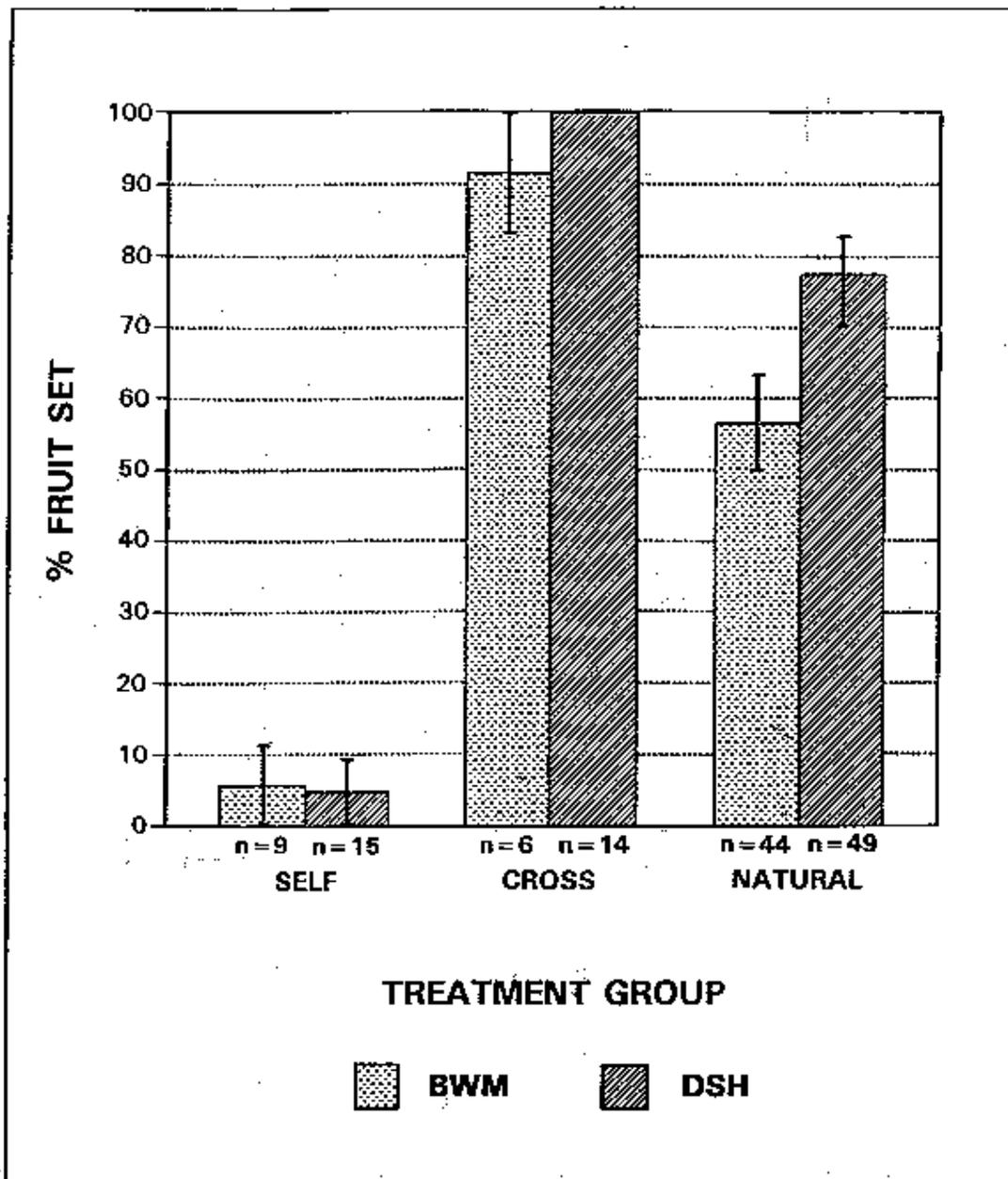


Figure 3.2. Mean percent fruit set at BWM and DSH resulting from hand self-pollination and hand cross-pollination. Mean percent fruit set for naturally-pollinated flowers at both sites is included for comparison. Vertical bars represent  $\pm$  standard error of the mean.

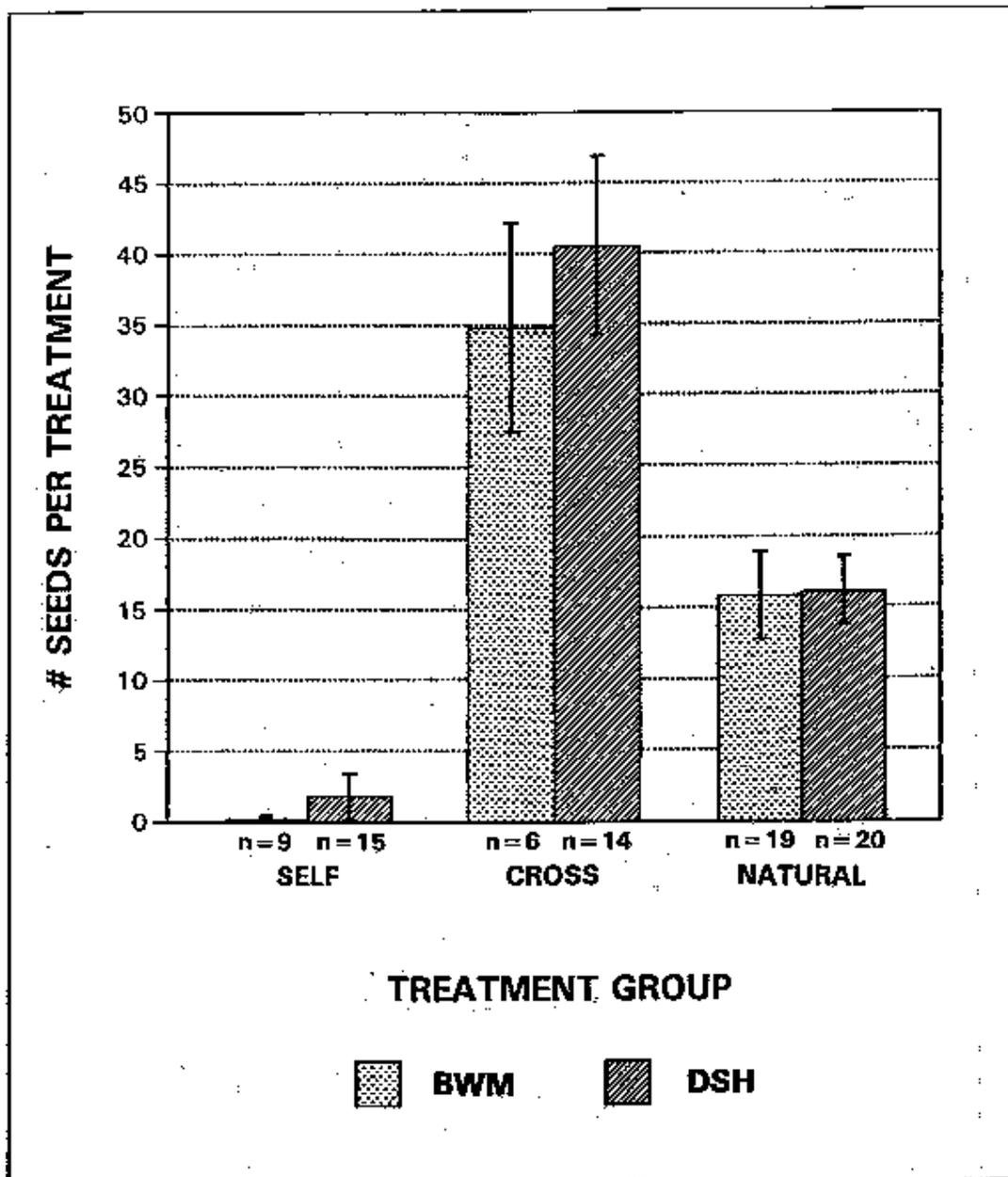


Figure 3.3. Mean number of seeds produced per treatment at BWM and DSH for hand self-pollination and hand cross-pollination. Mean number of seeds/flower for naturally-pollinated flowers at both sites is included for comparison. Vertical bars represent  $\pm$  standard error of the mean.

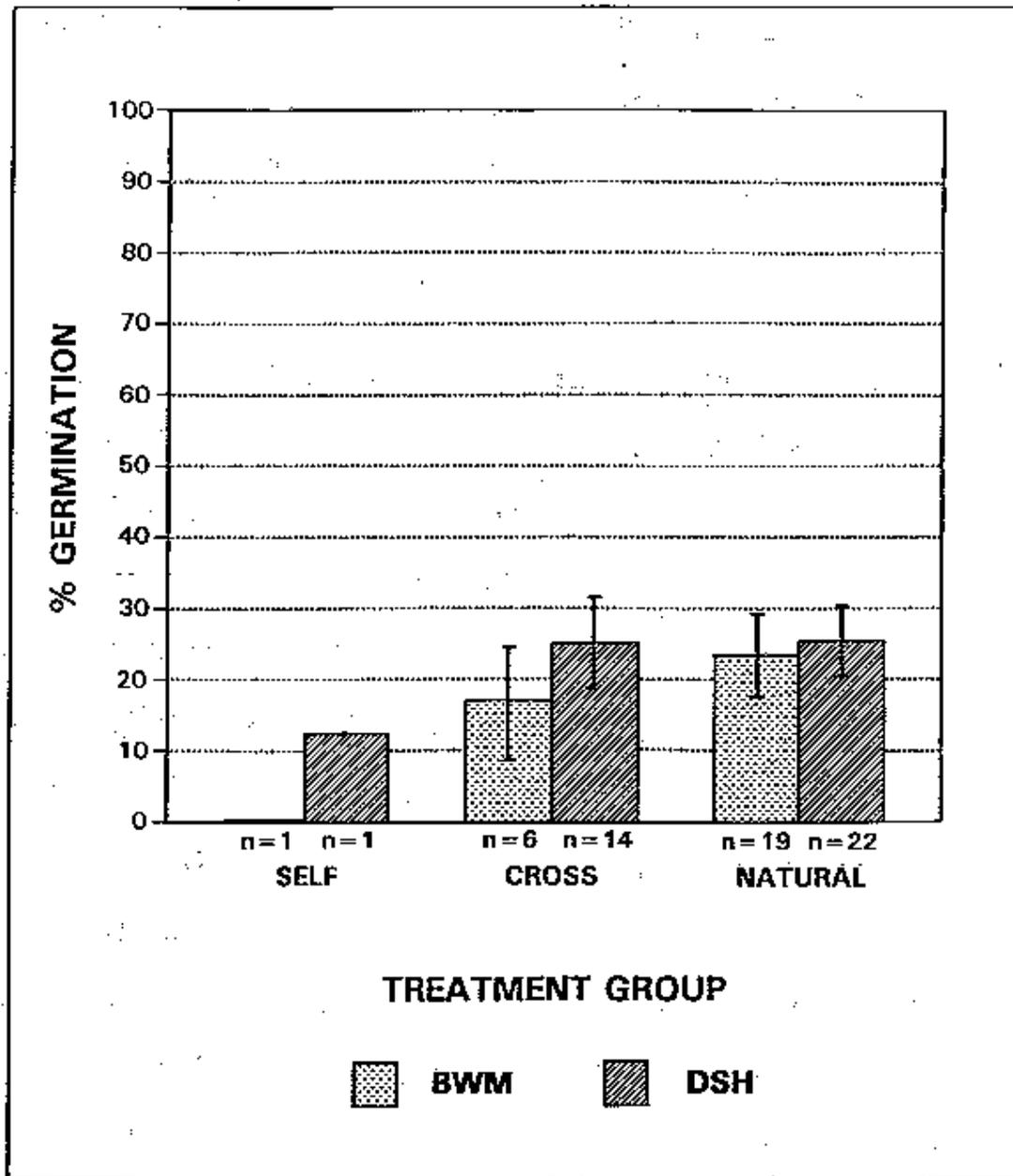


Figure 3.4. Mean percent seed germination at BWM and DSH resulting from hand self-pollination and hand cross-pollination. Mean percent seed germination from naturally-pollinated flowers at both sites is included for comparison. Vertical bars represent  $\pm$  standard error of the mean. The number of fruits (n) from which seed germinability was assessed is also provided.

period of this cactus. Potential pollinating insect activity was noted on only ca. 20% of those days, and the lack of observed pollinator activity was usually associated with weather conditions which included some combination of low temperature, high cloud cover, and high wind.

Table 3.1 lists the insect species which were observed visiting Tobusch fishhook cactus flowers at BWM and DSH during the four year field investigation, as well as those from an independent concurrent investigation at KPC (Lockwood, 1995), which is included for comparison. At least six different bee species (two *Lasioglossum (Dialictus)* vouchers which are unidentifiable to species appear to be conspecific) and two other species of insects were observed visiting *A. tobuschii* flowers at BWM and DSH during this study. *Lasioglossum (Dialictus) morrilli* was by far the most commonly observed visitor to *A. tobuschii* flowers at DSH (9 visits), although the majority of those observed visits (7 visits) occurred during one afternoon in 1993. No *L. morrilli* were seen at the BWM site and, in fact, few insect visitors at all were noted on *A. tobuschii* flowers at this site during the four year field study. Many of the same insect species are also reported from Tobusch fishhook cactus flowers at the KPC population site (Table 3.1). The frequency with which these insects were observed visiting Tobusch fishhook cactus flowers appears to be different between sites, however. Lockwood (in press) reports that, over the entire

three-year monitoring period at KPC, honeybees (*Apis mellifera* L.) and *Dialictus comulus* were the most commonly observed floral visitors. Only one honeybee visitation was witnessed at each of BWM and DSH during the entire four years of this investigation, however, and no *D. comulus* were observed and collected at either of these two sites during this period.

At least two species of floral visitor — *Lasioglossum morrilli* and *Lasioglossum (Dialictus)* sp. — were active during the field test of relative pollinator effectiveness conducted at DSH during the afternoon of 6 March, 1993. Although each of the insect visitors was permitted to manipulate the flower for as long as it wanted before capture, the single visit treatments to each of ten flowers resulted in the production of zero fruits. There are several possible explanations for the complete lack of fruit set resulting from this trial. On the day that the field access and capture investigation was conducted, favorable climatic conditions for pollinator activity had arisen only just prior to allowing floral access to the insects. The potential pollinators may therefore have visited no or few other open Tobusch fishhook cactus flowers before visiting the test plant from which they were captured and, because this and other investigations have shown *A. tobuschii* to be an obligate outcrosser, the complete lack of fruit set and seed set could be indicative of the lack of sufficient cross-pollination. It is also possible that the two types of insects which

Table 3.1 Insects observed visiting flowers of *A. tobuschii*, by study site. Check mark denotes occurrence at that site; the numbers of voucher specimens collected are indicated in parentheses. BWM and DSH observations are from this investigation, while KPC information is from Lockwood (1995).

Insect Species	SITE AND YEARS OF OBSERVATION/COLLECTION		
	BWM 1991-1994	DSH 1991-1994	KPC 1992-1994
<b>BEEES</b>			
<i>Apis mellifera</i>	✓ (1)	✓ (1)	✓
<i>Agapostemon angelicus</i> or <i>texanus</i>		✓ (2)	
<i>Agapostemon</i> sp.			✓
<i>Lasioglossum morrilli</i>		✓ (9)	✓
<i>Lasioglossum (Dialictus) connexus</i>	✓ (2)	✓ (1)	
<i>Lasioglossum (Dialictus) pruinasiformis</i>	✓ (1)	✓ (1)	✓
<i>Lasioglossum (Dialictus) sp.</i> (undetermined)	✓ (1)	✓ (3)	
<i>Dialictus comulus</i>			✓
<i>Osmia subfaciata</i>			✓
<b>OTHER INSECTS</b>			
<i>Toxomerus marginatus</i> (Syrphid fly)		✓ (1)	
<i>Diabrotica undecimpunctata howardi</i> (Chrysomelid beetle)		✓ (2)	✓
<i>Eurema nicippe</i> (Sulfur butterfly)			✓
Small black ants			✓

were active during this investigation may not provide adequate pollen to stigma transfer, and/or that several to many pollinator visits are necessary to each flower before sufficient pollen has been deposited on the stigma to cause fruit and seed production. Still, during the course of this four-year field investigation, several

naturally-produced fruits were collected which contained only one seed, indicating that only minimal successful pollination may be needed to effect fruit and seed set.

#### Relative Reproductive Success Using Near Versus Far Pollen

Similar to the situation experienced during the breeding system investigation, some bagged plants were unable to be used because flowers on some plants were not open during field visit days and because "cones" were found pulled off of some plants before treated flowers had fully senesced (leaving open the possibility that flowers received additional "natural" pollination). Such plants were removed from this study. Several plants which had been fitted with cones for another investigation were used to supplement the test group for this trial. Hand pollination with neighbor pollen was successfully followed through to completion for nine plants at the East colony and seven plants at the West colony, while hand pollination using distant pollen was successfully accomplished for six plants each at the East and West sites.

The proximity of pollen donors had no significant effect on fruit set, seed set, and seed germinability at DSH in 1994 (Figures 3.5, 3.6, and 3.7). Although fruit set was somewhat lower for the neighbor pollen group (58.1%) versus the distant pollen group (79.2%), the average number of seeds obtained per treatment and the

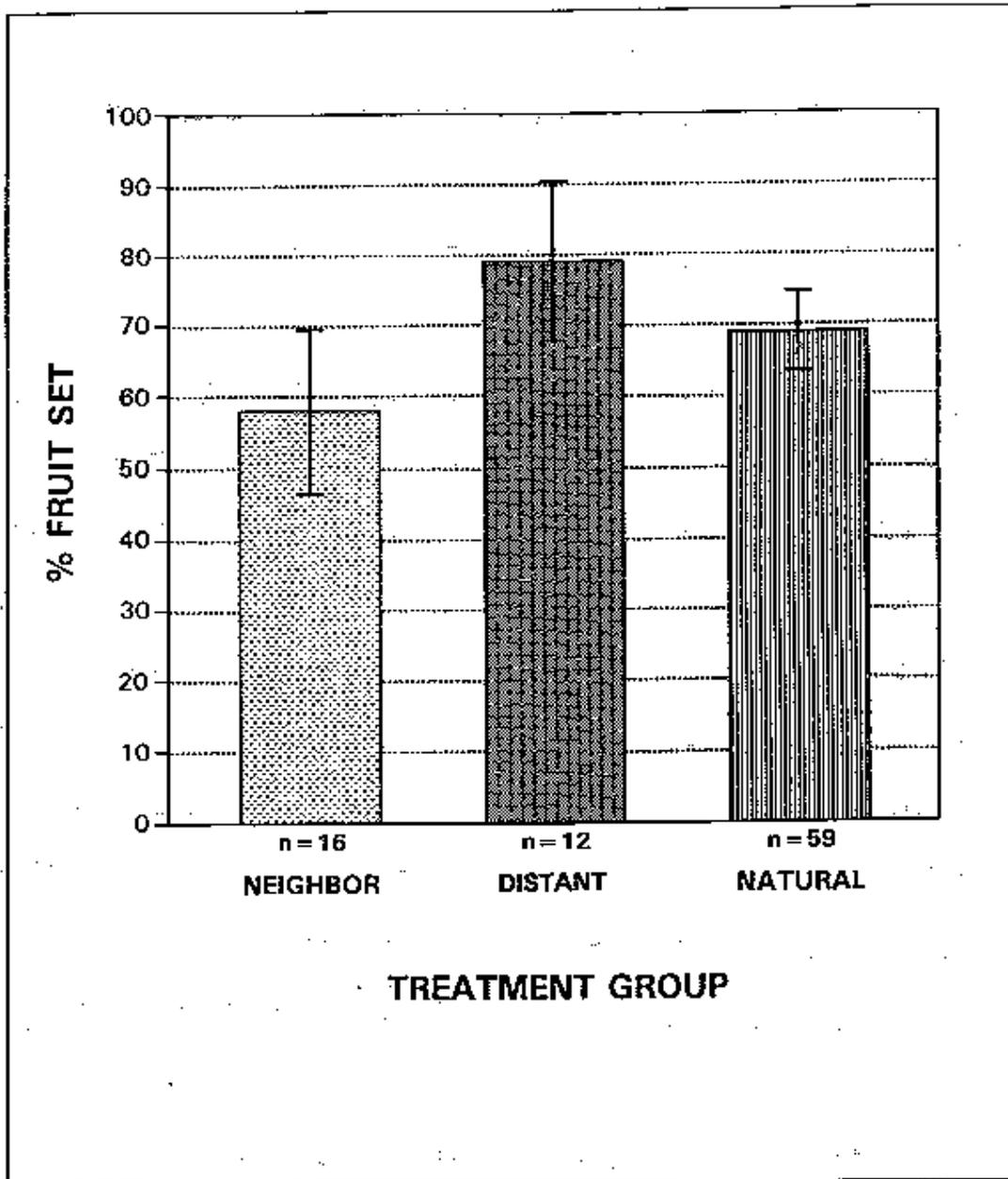


Figure 3.5. Mean percent fruit set for East and West colonies (combined) resulting from hand pollination using neighbor or distant pollen. The Kruskal-Wallis test detected no significant differences between the two test groups ( $P=0.201$ ). Mean percent fruit set for naturally-pollinated flowers throughout DSH is included for comparison. Vertical bars represent  $\pm$  standard error of the mean.

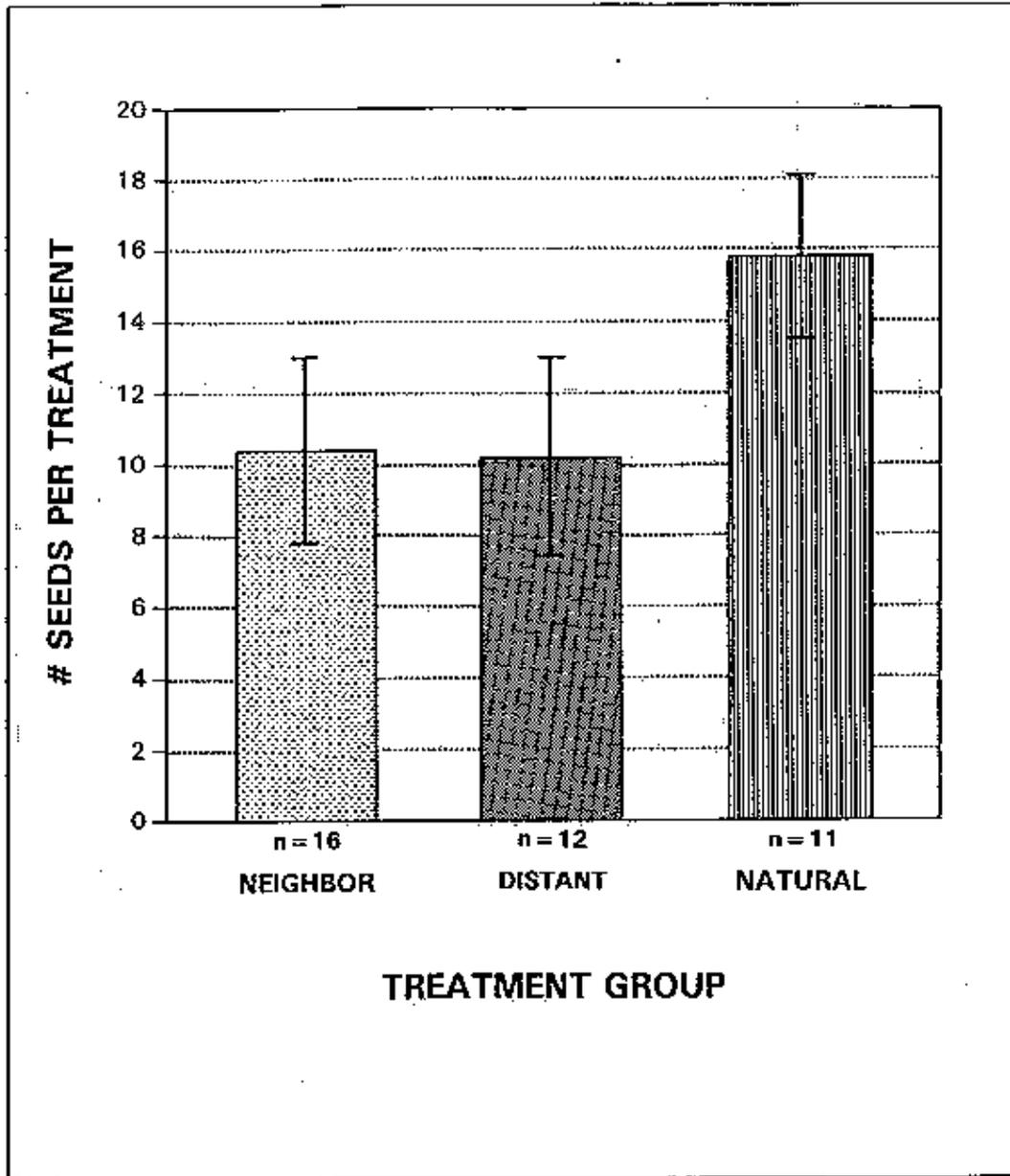


Figure 3.6. Mean number of seeds produced per treatment for East and West colonies (combined) resulting from hand pollination using neighbor or distant pollen. The Kruskal-Wallis test detected no significant differences between the two test groups ( $P=0.833$ ). Mean number of seeds produced per naturally-pollinated flower throughout DSH is included for comparison. Vertical bars represent  $\pm$  standard error of the mean.

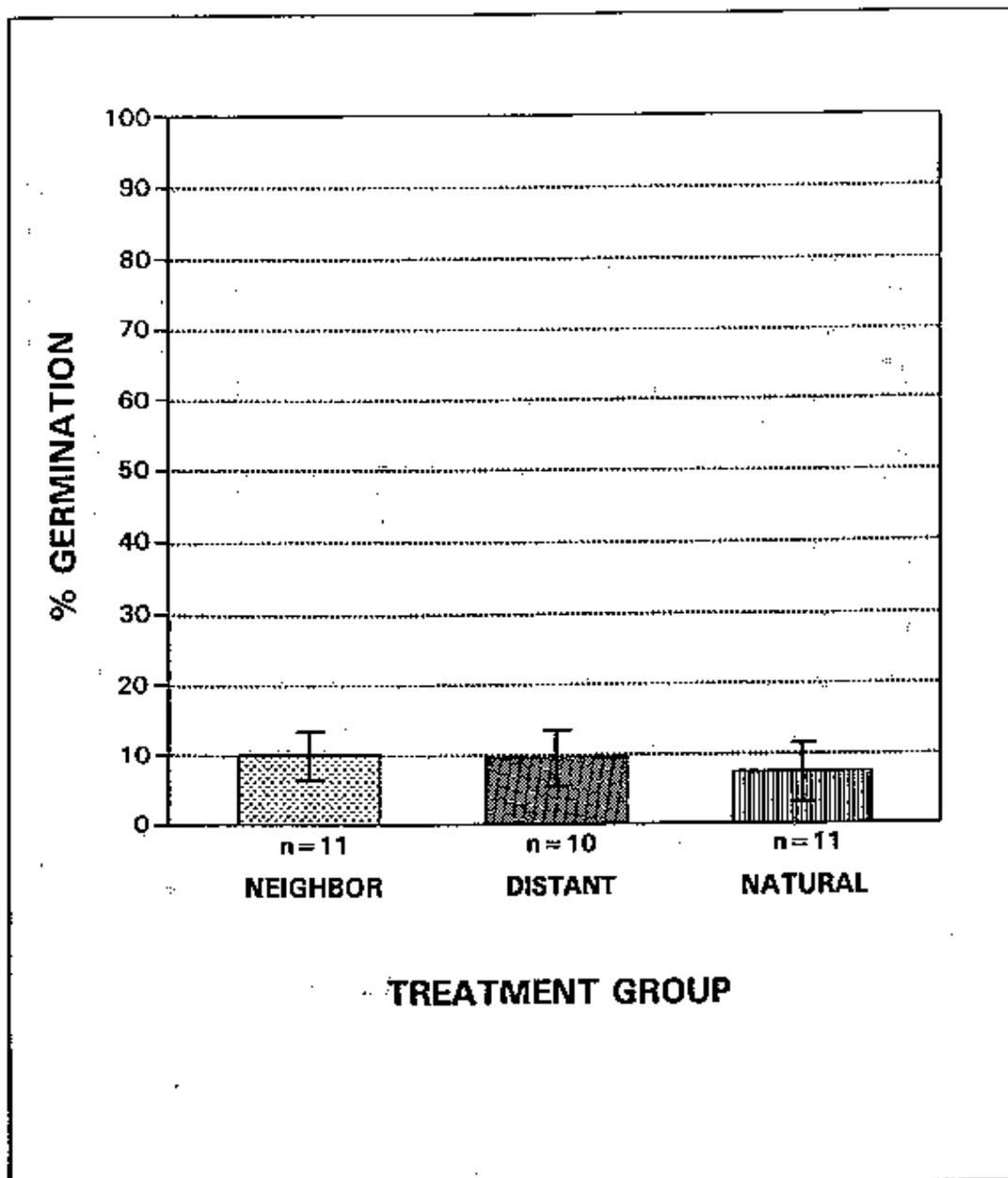


Figure 3.7. Mean percent seed germination for East and West colonies (combined) resulting from hand pollination using neighbor or distant pollen. The Kruskal-Wallis test detected no significant differences between the two test groups ( $P=0.325$ ). Mean percent seed germination for naturally-pollinated flowers throughout DSH is included for comparison. Vertical bars represent  $\pm$  standard error of the mean.

germinability of those seeds was nearly identical between the two groups (neighbor — 10.4 seeds/treatment, 10.1% germination; distant — 10.2 seeds/treatment, 9.6% germination).

Mean fruit set and germinability for both test groups were comparable to those resulting from naturally-pollinated flowers (69.0% fruit set, 7.3% germination), but mean seeds per treatment was slightly greater for naturally-pollinated flowers (15.8 seeds/flower).

### 3.5 DISCUSSION

The pollination biology of the Cactaceae has been investigated by numerous authors (e.g., Alcorn et al., 1961; 1962; Breckenridge and Miller, 1982; Grant and Grant, 1967; 1979a; 1979b; 1979c; Schmidt and Buchmann, 1986). For the most part, pollen self-incompatibility seems to be the more typical situation in this plant family. In an investigation of fifty-five taxa in the tribes Cereae (in which *A. tobuschii* is placed) and Pereskieae, Ross (1981) reports that approximately eighty percent of these species are self-incompatible with respect to pollination, including the congener *Ancistrocactus scheeri*. In several recent investigations, pollen self-incompatibility was demonstrated for the cardon (Cereae: *Pachycereus pringlei*)

(Fleming et al., 1994), acuna cactus (*Echinomastus erectocentrus* v. *acunensis*) (Johnson, 1992), and several members of the genus *Opuntia* (tribe Opuntieae) (Spears, 1987; Osborn et al., 1988).

Based on the results of hand self- versus cross-pollination conducted in this investigation, as well as those from a previous investigation (Zimmerman, unpub. manuscript), it appears that *A. tobuschii* should be classified as "heteromorphic", i.e., producing flowers which are hermaphroditic but which are self-incompatible with respect to pollination. As reported above, this situation appears to be typical of members of the Cereae, and of the Cactaceae in general. While self-incompatibility may help limit the occurrence of inbreeding and its potentially negative effects (Levin, 1981), it may also severely limit or totally prevent reproduction within small, isolated populations within which the number of different mating types are few or one (DeMauro, 1993), thus leading to a greater probability of rapid local population extinction. This may, in part, help to explain the relatively short-lived nature of Tobusch fishhook cactus populations, which are typically small and are apparently locally isolated.

Rowley (1980) provides an analysis and breakdown of some of the more common cactus genera by floral syndrome, which indicates that the majority of

temperate North American cacti produce flowers which are specialized for bee pollination or which are nonselective. Many pollination studies of temperate North American cactus species confirm that bees are indeed important pollen vectors for this group (e.g., Grant and Grant, 1979c; McFarland et al., 1989; Hoffman, 1992; Johnson, 1992). Notable exceptions to bee pollination include reports of bat and dove pollination in the saguaro (*Cereus giganteus*) (Alcorn et al., 1961) and cardon (*Pachycereus pringlei*) (Fleming et al., 1994); moth pollination in a night-blooming cereus (*Peniocereus striatus*) (Suzan et al., 1994); and hummingbird pollination in the claretcup cactus (*Echinocereus triglochidiatus*) (Grant and Grant, 1967). Although several other types of insect visitors to the Tobusch fishhook cactus have been observed and vouchered, bees are by far the most commonly reported insect visitors to flowers of this plant. The types and relative frequency of visitation by different bee types appears to vary between sites (Zimmerman, unpub. manuscript; Lockwood, 1995; this investigation). As foragers, the types of bees observed and collected during this investigation probably gather pollen and nectar from a wide number of different plant types and should therefore be classified as generalists in this regard (J.L. Neff, pers. comm., 1995). Few other plant species are in flower during the first several weeks of the Tobusch fishhook cactus flowering season, however, so this small cactus may act as an important food source for these insects during this period.

The relative effectiveness of the different species of insect visitors and, especially, the effects that pollinator limitation has on reproductive success in this species require further investigation. Small to medium-sized halictid bees were observed to be common visitors to *A. tobuschii* flowers during this and other investigations (Zimmerman, unpub. manuscript; Lockwood, 1995), but the limited examination of the pollination effectiveness of these insects conducted in this study indicates that they may be inadequate or inferior pollinators of this taxon. The most common visitors to flowers are not always the most effective at successful pollination (Schemske, 1984), and this may be the case with *A. tobuschii*. Honey bees, which were rarely observed visitors to Tobusch fishhook cactus at BWM and DSH during this investigation, but which were common at KPC during Lockwood's (1995) investigation, may actually effect more successful pollination than the solitary halictids. European honey bees were absent from this part of the world until fairly recent times (Winston, 1987). If pollination of the Tobusch fishhook cactus has historically relied upon native solitary bees, and if the native bees are indeed not especially effective pollinators of this species, then pollinator limitation could have been contributory to the historical rarity of this species. While honey bees may provide effective cross-pollination in those areas where they are very active, inconsistent and/or infrequent visitation by these insects in other areas could result

in local pollinator limitation. The relative effectiveness of different insect floral visitors to this cactus requires further investigation, however.

A comparison of seed set resulting from hand cross-pollination treatments which saturate stigmatic surfaces with pollen versus that resulting from natural pollination can be used as a test of pollinator limitation (Bierzuchudek, 1981). While emphasis was not placed on stigmatic saturation with pollen in this investigation (i.e., the goal of field hand-pollination trials conducted for this study was to transfer a fairly consistent amount of pollen to treated stigmas, to potentially enable at least modest seed set), a cursory comparison of natural and hand-cross data from 1992 (see Figure 3.2) shows that mean seed set is over twice as large for the hand cross-pollination group at both BWM and DSH. This could be indicative of pollinator limitation at both sites during 1992. Mean seed set was lower for the hand-cross treatments compared to naturally-pollinated flowers at DSH in 1994 (see Figure 3.5), however, and this could indicate that overall pollinator numbers and/or relative effectiveness may vary from year to year. This underscores the need to consider impacts to pollinator populations when devising rare plant management strategies (Sipes and Tepedino, 1995), especially for self-incompatible species.

Because studies of bee foraging behavior indicate that bees typically move between closely associated groups of open flowers before flying off to search for other, more distant flowers (e.g., Schmitt, 1980), there is a higher likelihood of pollen transfer between individuals within a closely-spaced group of plants. Previous reports (TPWD, 1984) and observations from this study (see Chapter 4) indicate that the majority of seed dispersal in this species is affected by ants, rainwater and/or gravity, with only occasional longer distance dispersal by mammals and birds, so dispersal of seeds usually occurs over only a relatively short distance. A high degree of interrelatedness probably exists within a dense group of Tobusch fishhook cactus individuals, such as within colonies at DSH.

With a higher degree of near-neighbor interrelatedness comes a high chance of inbreeding through cross-pollination if bees are the principal pollinator. Occasional pollination by butterflies, which often skip over nearest neighbors when foraging, can help improve gene flow throughout plant populations, however (Schmitt, 1980). While inbreeding depression can result when frequent inbreeding occurs in more isolated populations, other populations can actually become genetically adapted to cope with their environmental situation, even to the extreme that the importation of genetic variation may actually result in a reduction in fitness (i.e., outbreeding depression) (Ellstrand, 1992).

Results from the Spring, 1994, investigation show no significant differences in preemergent reproductive success between the neighbor and distant pollen donor groups. For a species with a strong pollen self-incompatibility system such as *A. tobuschii*, the near normal fruit set and seed set shown for the neighbor pollen group indicates that there are at least several mating types (and, hence, some genetic diversity) present within each of the densely-spaced study colonies at DSH. The lack of significant differences in preemergent reproductive success between the neighbor and distant test groups could indicate that the general degree of interrelatedness of plants within each colony is not that great; the self-incompatibility system is functioning adequately to reduce the level of inbreeding; there is sufficient genetic diversity within the colonies; and/or that *A. tobuschii* at this site are not especially prone to the potentially negative effects of inbreeding. The results of the Spring, 1994, trial indicate that the lower fruit set, seed set and seed germinability noted at DSH relative to BWM in 1991 may not have been due to high pollen transfer between densely-spaced individuals with a high likelihood of relatedness.

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CHAPTER 4.0 AN INVESTIGATION OF THE SEED ECOLOGY OF THE  
TOBUSCH FISHHOOK CACTUS (*ANCISTROCACTUS TOBUSCHII*  
W.T. Marshall ex Backeberg) IN WEST-CENTRAL TEXAS

4.1 ABSTRACT

The seed ecology of the Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg), a rare central Texas endemic species, was examined with respect to seed dispersal and predation; annual seed germinability; the period of germination in the field, and the relative field germination success within several different types of microsites; and the soil seed reserve.

Removal by ants appears to be the most common fate for seeds of this species, perhaps initially affecting as much as 85% of annual production. The only species of ant observed moving Tobusch fishhook cactus seeds at all three sites during this investigation was a small reddish-brown ant (*Forelius foetidus*), which was observed to be very effective at removing most seeds from most fruits and into its ant mound. The fate of seeds following transport into the mound is unknown. For the 15-20% of seeds not immediately removed from fruits by ants, dispersal appears limited mostly to gravity and rainwater, as evidenced by the common occurrence of seedlings

surrounding mature adult plants. Successful dispersal of some seeds away from maternal parent plants may be effected by occasional ant droppage of seeds and infrequent vertebrate frugivory, but post-dispersal predation of such seeds by ants may impose additional limits to the actual effectiveness of this as a dispersal strategy for the cactus.

Annual seed germinability varied widely during the four year course of this investigation, from a high of ca. 67% at one site to a low of ca. 1% at another site. With one exception, significant differences were only noted between years, and not between sites for each given year. Reasons for this wide variation in seed germinability between years are not yet understood.

An overall average of ca. 20% of seeds placed within protective enclosures throughout each field study site germinated after nearly one year, although this varied somewhat between sites. Percentage germination was similar between each of three different microhabitat types where seeds were placed, although "beneath rocks" was slightly greater than "selaginella," which was slightly greater than "grass."

A modest-sized reserve of germinable seeds was detected in the soil at two of the three sites which were sampled. While most samples did not contain seeds, those

seeds which were detected were from samples collected within several decimeters of reproductive-sized plants.

## 4.2 INTRODUCTION

The Tobusch Fishhook Cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) is a small, tuberculate member of the Cactaceae which is endemic to the south central and western portions of the Edward's Plateau region of Texas. Several naturally occurring populations of *A. tobuschii* at three locales — the Buck Wildlife Management Area (BWM), Kimble County, Tx.; the Devil's Sinkhole State Natural Area (DSH), Edwards County, Tx.; and Kickapoo Caverns State Natural Area (KPC), Kinney and Edwards Counties, Tx. — were utilized to conduct an investigation of several facets of the seed ecology of this taxon.

The seed ecology of the Tobusch fishhook cactus had not been closely investigated prior to this investigation. Reports for this species indicate that information relating to seed dissemination, germinability, features of the soil seed reserve, and period of germination in habitat is either completely lacking or exists solely from casual observation (TPWD, 1984; USFWS, 1987). Such information is crucial to development of a successful management strategy, however, because

inadequate seed germinability and dispersal, heavy seed predation, and the lack of suitable habitat for seed germination and seedling establishment can all greatly impact the survival of local populations (Menges et al., 1986; Fowler, 1988). A reserve of buried seeds in the soil can provide a buffer against periods of adversity by providing local populations with the means for replenishment of individuals and genetic diversity (Baskin and Baskin, 1980; Moore, 1985, 1988; Coffin and Lauenroth, 1989; Levin, 1990).

The method(s) of dispersal of seeds for the Tobusch fishhook cactus is largely unknown. Seedlings have been noted around the base of several plants in one population (Marshall, 1952), and this suggests that short distance, passive seed distribution effected by gravity and/or rainwater may occur. Zimmerman and Poole (TPWD, 1984) have reported the rapid disappearance of fruits from some plants, which could be indicative of bird or small mammal frugivory. Preliminary observations from the current investigation indicate that gravity, rainwater, and frugivory may all contribute to seed dispersal. In addition, ants also appeared to be involved in seed removal and predation from recently dehisced fruits of *A. tobuschii*. To determine the dispersal vectors and predators, and their relative importance for this species, fruit maturation and seed dispersal were closely monitored during the 1992, 1993, and 1994 field seasons. This investigation included several field trials

to examine more closely the role of ants in the fate of Tobusch fishhook cactus seeds, and the type(s) of ants involved in this activity. Also, a trapping effort was conducted to determine if and what kind of small mammals might be involved in frugivory-related seed removal.

Marshall (1952) reported that seeds of *A. tobuschii* are of high germinability, but did not elaborate upon this. In order to quantify seed germinability, naturally-produced fruits were collected annually from field study sites, and the seeds contained within were assessed for germinability under greenhouse conditions.

There has been speculation that bunchgrasses may act as "nurse plants" during germination and establishment of *A. tobuschii* (TPWD, 1984), but this and other microhabitat features related to natural seed germination, as well as the yearly period of germination, are in need of investigation (USFWS, 1987). To determine the relative germination success of seeds placed in different types of microhabitat, and to note the approximate period of seed germination in habitat, field-collected seeds were sown within different microhabitat types within exclosures which were constructed throughout each of the three metapopulation sites.

A previous investigation of one population of another rare cactus in Texas has reported the existence of a modest soil seed reserve associated with that species (Emmett, 1989). Because of the potentially important role of a seed reserve in allowing for post-disturbance population recovery, and because the nature of the soil seed reserve has not been investigated for *A. tobuschii* (USFWS, 1987; TPWD, 1984), several sampling strategies were utilized to determine whether the Tobusch fishhook cactus maintains a reserve of buried, viable seeds in the soil within the population sites.

#### 4.3 MATERIALS AND METHODS

##### Biology and Phenology of Fruit Maturation and Seed Dispersal

Annual fruit maturation for this species occurs from late April through May, at which time the green fruits often acquire a pink tinge. Eventually, the fruit pulp and seeds are exposed by dehiscence along one to several irregular longitudinal lines on the fruit wall. Fully developed Tobusch fishhook cactus seeds are black in color and finely papillate in texture, and are ca. 1.5 mm long, 1.5 mm broad, and 1.0 mm thick (Benson, 1982).

Observations made during field visits to each study site in early to mid June of each year showed very few or no whole or nearly whole fruits to remain on plants, and no evidence of seeds on the ground surrounding the plants was noted during those visits. Persistent basal portions of one to several fruits were observed on a few plants at each site during all times of the year and during all field years, and these usually contained one to several apparently normal seeds.

#### Frugivory, Seed Predation, and Seed Dispersal

In late April and May of each field year (1991-1994), the fate of maturing fruits and seeds of the Tobusch fishhook cactus were closely monitored. In almost all cases, fruits remained on the maternal plant until dehiscence, but several instances where predehiscent fruit removal was apparent were noted. Nearly all of the dehisced fruits observed at all sites were swarmed by medium-sized reddish-brown ants. Ant behavior was closely monitored on a number of fruits during each field year, and voucher specimens of ants observed removing seeds from *A. tobuschii* fruits at all three metapopulation sites were collected into kill jars charged with ethyl acetate. After transport to the laboratory in Austin, ants from each collection were placed along with collection labels into separate vials containing 90% ethyl alcohol for preservation until species identification could be made.

To better monitor the activities of fruit-swarming ants, one near-mature fruit was removed from each of several randomly chosen cacti within several different colonies at each site. Fruits were placed in plastic petri dish bases which had small holes (i.e., smaller than *A. tobuschii* seeds) drilled in the bottom to allow drainage of rain water and condensation. Petri dish bases were secured to the ground with wire stakes in areas near the plants from which the fruits were collected. Each petri dish base was then shaded with a white plastic plate "awning" supported several inches above the ground by wire stakes to protect the contents of the petri dish from scatter due to heavy precipitation, and to discourage birds from feeding on the fruits.

The number of plates set up in this manner was as follows: 1992 — six plates at BWM and five plates at DSH ; 1993 — five plates at BWM; 1994 — two plates at KPC. In 1992, one unsplit fruit and one fruit which was split open with a knife (to simulate natural dehiscence) were placed into each dish; because unsplit fruits in all dishes remained intact throughout the trial, only one "split" fruit was placed into each dish for all trials conducted in subsequent years. Dish contents were observed within one-half to one hour of placement, again the next day (if possible), and once more during the next site visit one to two weeks following fruit placement in dishes. While the plate-covered design did not necessarily prevent access to dishes by other insects or small animals, no other animals were observed visiting the dishes during

the trials, and ants so quickly swarmed the split fruits following placement that their presence may have deterred other potential visitors.

Fruit-swarming ants were collected from several dishes at each site for voucher specimens. Collection and preparation of ant vouchers were as described above. Dish contents were collected into individual labeled envelopes during the one to two week follow-up visit, and transported to the laboratory in Austin for later examination. This material was examined to determine the average number of seeds remaining in plates at each site during each year.

In order to investigate the possibility that small mammals were involved in frugivory for this species, trapping was conducted during two nights each in May, 1992 and May, 1993 at BWM and DSH. During each trapping night, nine — 23.0 cm X 7.5 cm X 9.0 cm Sherman traps were placed alongside prospective rodent trails in the vicinity of reproductive-size plants at various locales within populations at each of the two metapopulation sites. Each trap was baited with one newly-collected near ripe but undehisced fruit from a nearby Tobusch fishhook cactus, and left overnight. Contents of the traps were inspected the next morning, and the traps were collected.

### Greenhouse Assessment of Seed Germination

In order to ascertain germinability of field-collected seeds, naturally-produced ripe fruits were collected from BWM and DSH each year from 1991 through 1994, and from KPC during 1993 and 1994. To minimize the impact to study groups, the number of fruits collected during any one year was limited to no more than 20 % of the annual flower production for each site. Quantitative information on annual fruit and seed production is presented in Chapter 5, which provides detailed demographic features of the study metapopulations.

Upon maturation in late April or early May of each year, fruits were collected into individual labeled envelopes and transported to the laboratory in Austin for further processing. In the laboratory, fruits were carefully split open and allowed to air-dry at room temperature (ca. 22°C) for a period of one to two months. Seeds were then removed from each dried fruit and were counted, treated with a commercial fungicide (Fertilome with benomyl), and dry-stored in individual labeled, capped bottles in refrigeration (ca. 8°C) until performance of the germinability assessment.

Germinability of each year's seeds was assessed in a growth chamber. The growth chamber germination trial of field-collected seeds was begun during July of each year, except for 1991 seed germination which was begun in March, 1992. Seeds were removed from refrigeration and sown into a 2:2:1 mixture of commercial potting soil:sharp sand:perlite in compartmentalized seedling flats, one seed/compartment. Twenty seeds from each fruit were utilized for this test except when a fruit yielded less than twenty seeds, in which case all of the seeds from that fruit were used. Unused seeds from each fruit were placed back into refrigeration for possible later use. Flats were kept covered with clear plastic lids in the climate-controlled growth chamber at 30°C, 100% relative humidity "daytime" (13 hrs.), and 21°C 100% relative humidity "nighttime" (11 hrs.). Daytime artificial light intensity within the growth chamber was measured with a hand-held digital light meter (Extech Instruments Model L246348), and averaged ca.  $200 \pm 10 \times 10^2$  Lux. Darkness constituted the nighttime lighting conditions. Trays were thoroughly watered ca. every 2-3 days. Trays were monitored for germination of seeds weekly for the first 2 months of the trial, then monthly thereafter. Germinability was determined at the maternal plant level (i.e., percentage germination of seeds from each fruit), and at the metapopulation level (i.e., percentage germination of all seeds produced within the metapopulation site) based on the collected subsamples.

Seed germinability data were square root transformed to normalize residuals, then were analyzed using the two-way analysis of variance procedure included in SYSTAT version 5.0.3 (SYSTAT, Inc., 1990) to compare average seed germinability between metapopulation sites for each year, and for each metapopulation site between years. Two separate runs of this procedure were necessary because the different monitoring periods for sites (i.e., BWM and DSH — four years; KPC — two years) resulted in empty matrix cells. The first two-way ANOVA was run to test for significant differences in mean per fruit seed germinability between sites and between years for BWM and DSH during the four year period 1991 through 1994. The second two-way ANOVA was run to test this for all three sites during 1993 and 1994.

#### Assessment of Seed Germination Within Field Enclosures

Because earlier field observations had shown that seeds of *A. tobuschii* are readily collected by ants, it became apparent that any attempt to investigate field germination of seeds would require use of enclosures to preclude ant activity. During Summer, 1993, germination enclosures were constructed and sown with previously field-collected seeds in several locations at each of the three study metapopulation sites, to allow some determination of the timing and environmental conditions

associated with *A. tobuschii* seed germination in habitat. Two earlier field trials at BWM and DSH that were started during Summer, 1992, met with catastrophic failure associated with disturbance from heavy rains. The enclosure design was modified for the third trial, and is described below.

During July, 1993, germination enclosures were set up as follows: BWM and DSH (each) — five enclosures containing 1993 field-collected seeds and three enclosures containing 1992 field-collected seeds; KPC — two enclosures containing 1993 field-collected seeds. Enclosures were placed in several different locales throughout each metapopulation site. Criteria for enclosure placement sites included: 1) little or no slope, and 2) occurrence within the boundaries of a monitored Tobusch fishhook cactus colony, but sufficiently far from known reproductive-sized plants to minimize the likelihood of naturally-occurring *A. tobuschii* seeds occurring in or on the soil at that spot.

Each enclosure consisted of one — twelve inch diameter X eight inch long ring of aluminum stovepipe flashing, spray-painted gray to decrease its apparency among the rocky limestone substrate at each population site. Each ring of flashing was secured in place with wire stakes driven into the ground; rocks and soil were built up around the base of its outer periphery to deter crawling insects from entering

and to prevent seeds from easily washing out. Exclosures were not trenched into the ground as in the first two unsuccessful attempts however, as this apparently prevented sufficient outflow of rainwater from the exclosure. Once in place, the outer surface of each flashing ring was coated with insect tanglefoot to further deter ants or other crawling insects from gaining entrance to the exclosure.

Seeds were from lots ("seed lot" = seeds from one fruit) which had either already been assessed with respect to germinability (1992 seeds), or for which germinability was in the process of being assessed (1993 seeds) at the time field exclosures were prepared. Seed lots which had the highest number of remaining seeds (following removal of a subset of seeds from each lot for greenhouse germinability assessment) were chosen for this investigation. Seeds from each lot were evenly divided among the number of replicates ("exclosure groups") chosen for that metapopulation site and seed year, plus one back-up group. Each exclosure group consisted of twenty-one seeds. No more than three seeds from each lot were included in each exclosure group.

In the field, the twenty-one seeds comprising each exclosure group were individually placed into separate spots characteristic of one of three microhabitat-types identified within each exclosure (i.e., seven seeds per microhabitat type per

exclosure; twenty-one total seeds per exclosure). Upon placement, the location of each seed was marked with a color-headed pin, with different colors used to indicate each of the three different microhabitat types within each exclosure. The three microhabitat types utilized for seed placement include 1) along the edge of and slightly beneath a rock or amongst several large pieces of gravel; 2) within a mass of spikemoss (*Selaginella* sp.), nostoc (*Nostoc* sp.), true moss or lichen; 3) within a clump of bunchgrass. Use of an "open, unprotected" test group for seed placement was ruled out because of the high potential for weather-related disturbance, as made evident during the first two failed trials of this investigation.

As seeds were being placed within the first exclosure at KPC (the initial placement site of this third trial), medium-sized ants appeared and began to carry off the seeds. Ants were similar in appearance to those observed removing seeds from fruits at this and other sites, as described in "Fruit Maturation, Frugivory, and Seed Dispersal" above. The decision was made to spray-treat the interior and outer periphery of this and all other exclosures at all sites with Diazinon insecticide just prior to seed placement. A back-up lot of KPC seeds was then utilized to replace those taken by ants within this first exclosure. With the Diazinon pretreatment, no further problems with ants were encountered at other exclosures.

Seed germination within field exclosures was monitored periodically throughout the 1993-1994 field season. Because 1992 and 1993 seed germination appears comparable, and because "within exclosure" germination in general for each site appears comparable, these variables were not considered during statistical analysis. A multi-way contingency table was constructed and then analyzed by log-linear models (Sokal and Rohlf, 1981) using SYSTAT version 5.0.3 (SYSTAT, Inc., 1990) to examine differences in one-year seed germination by site and microhabitat.

#### Soil Seed Reserve

This investigation was conducted to determine if the Tobusch fishhook cactus maintains a reserve of seeds in the soil and, if it does, to determine the density and spatial distribution of this seed reserve. The survey of the soil seed reserve was accomplished by collecting soil samples at various locations at BWM and DSH in 1992 through 1994 and at KPC in 1993 and 1994. Several preliminary samples were also collected at BWM in 1991. Sampling was performed in late March or April of each year. This time period immediately precedes the onset of annual fruit maturation and seed set, and so assured that any seeds collected from the soil during sampling were at least ca. one year old. All samples were collected using a soil core sampler (Oakfield model KB) with an inner tip diameter of ca. 20 mm, to a depth of

ca. 40 mm. Upon collection, samples were placed in individual plastic bags, and labeled with their point of origin.

Observations made earlier in this study indicated that the majority of *A. tobuschii* seeds may be removed from the maternal plant by ants or other animal vectors. Those relatively few seeds which are not so removed remain within the basal portion of the fruit, which is still loosely attached to the plant or is lying amongst the spines and tubercles near the plant apex. As the fruit remnants dry and decay, the seeds fall out among the tubercles near the plant apex. As the plant grows and produces new apical tubercles, the seeds may fall or be washed onto the ground by rainwater. Unless further dispersed by, e.g., rainwater or ants, seeds probably remain relatively close to the maternal plant, especially if the plant is growing in an approximately flat situation. Data obtained during the first field season (i.e., 1991) indicated that an average reproductive-sized *A. tobuschii* produces ca. 112 seeds/year.

Taking into account the above observations and associated informed speculation on seed dispersal and fate, the probability of encountering Tobusch fishhook cactus seeds during soil sampling at a distance of more than several decimeters from the maternal parent plant is likely to be low, especially in diffusely-spaced colonies. Because the three study sites differed greatly in plant density (see

Chapter 1), several different sampling strategies were employed during various points of this field investigation. Colonies at BWM consist of diffusely-spaced individuals or small groups. A sampling strategy that was biased toward plants of reproductive size (i.e., ca.  $\geq 2.0$  cm. stem diameter) was therefore employed at this population during 1992-1994. Each sample obtained using this method consisted of 3 soil cores, one each taken along a short transect line at ca. 10 cm, 20 cm and 30 cm on the downslope side of a plant known from censuses to have produced at least one fruit which had not been collected during the previous season. Sampling was restricted to just one transect/plant and three soil cores/transect to limit damage to the plant root system. To further limit impact to each plant, different plants were sampled during consecutive years. Eight plants were sampled in this manner at BWM in 1992, twelve plants in 1993, and thirteen in 1994.

Within two more densely-spaced colonies at DSH, where higher seed production from a greater number of reproductive-sized individuals could result in a more substantial and spatially widespread soil seed reserve, a random approach to sampling within colonies was employed in 1992 using a technique presented in Bigwood and Inouye (1988) and modified by Emmett (1989). Three soil cores were taken surrounding each of twenty-five randomly selected points within a 1 m X 1 m quadrat which was centered within each colony. The two quadrats contained five and

eleven *A. tobuschii* plants of reproductive size, with numerous other reproductive size individuals within several meters of the outer quadrat boundaries. Because no seeds were detected within either colony using this method, the biased sampling method used at BWM was also employed at DSH in 1993 and 1994. Nineteen samples were collected using biased sampling at DSH in 1993, and twenty-one in 1994.

While relatively small in areal coverage, the Tobusch fishhook cactus study populations at KPC are more dense than populations at the other two sites. Because of this small but dense nature, soil sampling was conducted at regular intervals along several transects (following, e.g., Antfinger, 1989) through the southern KPC study population in 1993, to investigate the extent of the seed reserve. In each of two separate areas within the southern KPC population, soil sampling was conducted along two — eight meter long transects which were aligned ca. 90° from each other. Each sample was composed of three soil cores collected around a point along the transect. Samples were taken at 0.5 m intervals along the transect when possible, but the prevalence of limestone rock and cobble at this population site limited the total number of samples able to be collected. A total of twenty samples were collected at KPC in 1993 using this method. Because no seeds were obtained using this method, the biased sampling strategy described for BWM above was also employed at KPC in 1994. Ten biased soil samples were collected at KPC in 1994.

Following completion of field sampling each year, samples were transported to the laboratory in Austin for processing. Material from each sample was washed with tap water through several sieves of different mesh sizes to separate seed-size from nonseed-size material. Seed-size material was air-dried and viewed under a dissecting microscope to allow identification and removal of seeds. This "elutriation" sample processing method was used because seeds of this cactus are easily recognizable from other seeds and debris in samples and, once removed from each sample, seeds could be easily dry-stored for later germination assessment (see Gross, 1990). All seeds which were recovered in this manner were stored and tested for germinability as described in "Greenhouse Assessment of Seed Germination" above.

Data obtained from soil sampling and germinability assessment were used to calculate the density of germinable seeds in the soil seed reserve (seeds/m<sup>2</sup>) for each year. Because several different sampling strategies were employed during the course of this investigation, and because so few seeds were actually detected at all, only summary statistics are provided.

#### 4.4 RESULTS

##### Frugivory, Seed Predation, and Seed Dispersal

Each of the "unsplit" fruits which were placed into petri dish bases (along with the "split" fruits) in 1992 was found intact and apparently undisturbed during the follow-up field visit one to two weeks after placement. Because ants were observed to swarm the split fruits within the first half-hour to hour following placement into the dish, and because unsplit fruits — which could still be attractive to other small animals — were found to be undisturbed in all dishes, it appears that ants are the primary (if not only) vector effecting seed removal from the petri dishes in this trial.

The ants which were observed and collected while carrying Tobusch fishhook cactus seeds at all three sites during the course of this field study were all the same species: *Forelius foetidus* (= *F. foetida*, = *F. maccooki* (Shattuck, 1994)) (Dolichoderinae). These small ants were observed to be at least equally intent on gathering and removing seeds, fruit pulp, and the fleshy funiculi which are typical of many cactus species (Mauseth, 1984). While seeds of another cactus have reportedly been largely ignored by ants which swarmed dehiscing fruits (Emmett,

1989), seeds of this species were observed being transported back to the ant mound along with the funiculi and fruit pulp.

Table 4.1 presents the average number of seeds remaining in petri dish bases for each year and site, along with the average seeds/fruit production for each site and year for general comparison. From these data, it is apparent that most seeds were removed from each petri dish, although it is noteworthy that a few seeds remained in several dishes after one to two weeks. Observations associated with these trials indicated that ants were the most likely vector of most if not all seed removal from petri dish bases.

Table 4.1. Average number of seeds remaining within petri dish bases after ca. one to two weeks during each of several years at each site. The average number of seeds/fruit for each year is included for evaluative purposes.

YEAR	BWM		DSH		KPC	
	Avg. # Seeds Remaining/Dish (n=# trials)	Avg. # Seeds/Fruit (n=# fruits)	Avg. # Seeds Remaining/Dish (n=# trials)	Avg. # Seeds/Frt. (Meta) (n=# fruits)	Avg. # Seeds Remaining/Dish (n=# trials)	Avg. # Seeds/Frt. (Meta) (n=# fruits)
1992	0.2 n=6	40.2 n=17	0.6 n=5	36.0 n=20	—	—
1993	4.0 n=5	33.0 n=24	—	37.2 n=29	—	46.0 n=9
1994	—	32.6 n=10	—	28.7 n=10	0.0 n=2	30.6 n=8

For recently-dehisced fruits which were still attached to a Tobusch fishhook cactus, ants were observed to be generally very effective at removing the majority of each fruit and its seeds to their mound. All ant mounds of this species which were observed during the course of this investigation occurred beneath very large partially buried rocks, which is typical for this species (Wheeler and Wheeler, 1986).

Ants were observed occasionally to drop and eventually abandon a seed during transport to the mound, however. Similar to the situation noted in the petri dish trials above, there were occasionally a few seeds which remained uncollected from some fruits each year, and these seeds were usually tightly held within the basal remnant of a fruit. Such basal portions were often retained on the plant among the tubercles and tangle of spines near the plant apex for many months after fruits had matured and ant seed collecting activity had ceased. Removal and examination of these fruit bases often yielded one to several apparently normal seeds of varying germinability. Such seed-bearing fruit remnants were observed on ca. 5% to 10% of the plants at each site each year.

Similar to the situation noted in another report (Marshall, 1952), seedlings were observed at the base of many plants at each site, including around the spiny remnants of plant carcasses, providing further evidence that some seeds from many

plants are unavailable to or are overlooked or dropped by ants on or near the maternal plant. Twenty-two *A. tobuschii* carcasses from naturally-occurring reproductive-sized plants which died in 1992 or 1993 due to various causes were collected and examined in the laboratory. Seven of these carcasses (ca. 32%) were found to contain seeds among the spines and decaying tubercles. The number of seeds collected from these carcasses ranged from one to eighty-eight (mean = 27), and the average germinability of these seeds was assessed at ca. 10%.

No small mammals were collected within Sherman traps during the thirty-six "trap nights" (i.e., two nights x two sites x nine traps) each in 1992 and 1993. None of the traps, nor any of the *A. tobuschii* fruit "bait" contained within, appeared to have been disturbed during this effort. Strong evidence of frugivory by larger animals such as birds or small mammals was observed on several plants during the course of this field study, although direct observation of frugivory "in progress" by birds or mammals was not observed at any site during the course of the field study. This evidence includes the discovery of torn/shredded fruit remains found a short distance from the plant which had produced them, and the rapid disappearance of all or most predehiscent fruits from several larger plants. Additional circumstantial evidence for noninsect frugivory includes: several isolated plants discovered growing around an old pole anchored into the ground near the very top of a large hill at the

BWM site, which suggests that a bird may have landed on the pole some time after having ingested an *A. tobuschii* fruit and defecated or regurgitated the seeds to the ground; and, the occurrence of several *A. tobuschii* plants at all sites growing directly adjacent to large partially-emergent limestone rocks which, as high points in an open field, could be used as a perch for avian or mammalian potential frugivores. Based on the infrequency with which such evidence of vertebrate frugivory was witnessed during this study (i.e., no more than once or twice per site per year), avian or mammalian frugivory probably involved no greater than ca. 5% of the annual fruit production at each study site. Based on all of the data and other observations on seed fate for this species, it is likely that myrmecochory accounted for approximately 80% to 85% of the seed removal from fruit-bearing Tobusch fishhook cacti observed during the course of this study.

#### Greenhouse Assessment of Seed Germination

During all four years, the onset of seed germination in the growth chambers was noted within seven to ten days from the time seed flats were first watered. In general, little additional germination was noted after four or five months from the start of the assessment.

Average per fruit germinability of naturally-produced Tobusch fishhook cactus seeds ranged widely during the course of this investigation, from a high of ca. 67% for KPC in 1993, to a low of ca. 1% for BWM and KPC in 1994 (Table 4.2). The average seed germinability for all sites over all field years was 38.7% (n=188). In general, 1991 and 1993 appear to have been years of relatively high seed germinability for all monitored sites, while seed germinability was more modest in 1992 and extremely low in 1994. The two-way ANOVA procedures showed that significant differences in germinability of naturally-produced seeds occurred between years for each site, while no significant differences were detected between sites within each of the years (Tables 4.3 and 4.4). Statistically significant interactive effects were also detected between BWM and DSH between different years during the period 1991 through 1994 (Table 4.3). For the four-year, two-site comparison, "between years" differences in mean germinability were all significant with the exception of between 1991 and 1993 ( $\alpha < 0.05$ , Tukey's multiple comparison test). In addition to many statistically significant "between years" pairings identified for the interactive effect, analysis of the interaction of site and year also detected a significant difference between BWM and DSH for 1991 seed germination ( $\alpha < 0.05$ , Tukey's multiple comparison test) (Table 4.3).

Table 4.2. Greenhouse-assessed germinability of naturally-produced field-collected seeds of *A. tobuschii* at each site for each field season, reported as percentage germination of seeds per fruit  $\pm$  standard error of the mean. The number of plants (n) from which seed germination was assessed is also provided.

YEAR	MEAN GERMINATION OF SEEDS/FRUIT		
	BWM	DSH	KPC
1991	62.7 $\pm$ 5.1 n=35	34.2 $\pm$ 6.1 n=20	—
1992	23.5 $\pm$ 5.8 n=19	25.4 $\pm$ 4.8 n=20	—
1993	46.5 $\pm$ 5.8 n=24	52.2 $\pm$ 5.1 n=30	67.1 $\pm$ 6.7 n=9
1994	1.0 $\pm$ 1.0 n=10	7.3 $\pm$ 4.2 n=11	1.3 $\pm$ 1.3 n=8

#### Assessment of Seed Germination Within Field Enclosures

Germination within field enclosures was fully assessed in early February, 1994, and again in late May, 1994, and the results are somewhat mixed. Of the total germination noted within enclosures at each site, the majority took place between February and May, 1994, for both BWM (62%) and DSH (89%). At the KPC site, where overall enclosure germination was extremely low, no additional seed germination was noted during this same period.

Over all, approximately 20% of the seeds placed in enclosures had germinated after nearly one year, although this varied from 7% at KPC to 27% at DSH (Table

Table 4.3. Two-way analysis of variance on the effect of year and site on seed germinability for BWM and DSH only, for 1991, 1992, 1993, and 1994. Results of a Tukey multiple comparisons test for the interactive effects (i.e., Year \* Site) are also provided. Groups not sharing a letter showed a significant difference between group mean germinabilities. Tukey multiple comparison test results for the "year" effects are discussed in the text.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Year	560.5	3	186.85	25.06	< 0.001
Site	0.5	1	0.50	0.06	0.794
Year * Site	92.5	3	30.85	4.13	0.007
Error	1215.2	163	7.45		

1991	BWM	a
1991	DSH	b
1992	BWM	b, c
1992	DSH	b, c, d
1993	BWM	a, b, c, d, e
1993	DSH	a, b, d, e
1994	BWM	f
1994	DSH	c, d, f

4.5). The results of G-tests indicate that seed germination differences between sites were not statistically significant, however, nor were interactive effects of site and microhabitat type. Statistical significance was detected between microhabitat types when data from all three sites were pooled (Table 4.5) which indicates that there were significant differences in germination between the three types of microhabitat. The "rock" microhabitat had the highest germination percentage at BWM and KPC,

Table 4.4. Two-way analysis of variance on the effect of year and site on seed germinability for all three study sites (i.e., BWM, DSH, and KPC) for 1993 and 1994.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Year	683.9	1	683.90	110.23	< 0.001
Site	19.3	2	9.66	1.55	0.217
Year * Site	19.2	2	9.62	1.55	0.218
Error	533.5	86	6.20		

while the "selaginella" category was highest at DSH. For all sites combined, the "rock" microhabitat produced the highest germination (22%), followed by "selaginella" (20%) and "grass" (17%).

#### Soil Seed Reserve

Few seeds were detected during the seed reserve survey at all sites, and those seeds which were obtained were from soil samples collected in relatively close proximity to a reproductive-sized plant using the biased sampling strategy. None of the nonbiased soil core samples collected at DSH and KPC (i.e., quadrat- and transect-based, respectively) yielded any Tobusch fishhook cactus seeds. Table 4.6 provides a summary of the number and germinability of seeds collected during sampling at each site for each year, as well as an estimation of the number of

Table 4.5. A three-way contingency table which shows site and microhabitat differences in ant-excluded field seed germination percentage. Results from G-tests are also provided.

SITE	MICROHABITAT	% GERM	% NO GERM
BWM	Rock	20	80
	Selaginella	14	86
	Grass	13	87
	Subtotal	15	85
DSH	Rock	27	73
	Selaginella	30	70
	Grass	23	77
	Subtotal	27	73
KPC	Rock	14	86
	Selaginella	0	100
	Grass	7	93
	Subtotal	7	93
<b>TOTAL</b>		<b>19.6%</b>	<b>80.4%</b>

Site * Seed Fate	$\chi^2=4.82$	P=0.964
Microhabitat * Seed Fate	$\chi^2=116.78$	P= < 0.001
Site * Seed Fate + Microhabitat * Seed Fate	$\chi^2=3.56$	P=0.894

germinable seeds per square meter based on these data. Soil core samples were of very small areal coverage, so the latter estimation is only very approximate, and only pertains to the area immediately surrounding reproductive age *Tobusch* fishhook cacti. These data indicate that, while of modest size and generally limited spatial distribution, *A. tobuschii* did maintain a reserve of viable seeds in the soil at BWM and DSH during at least a portion of this four-year investigation.

Table 4.6. Summary of data from the soil seed reserve investigation at each site for each year, including the total number of soil samples collected, the total number of seeds from samples, the greenhouse-assessed germination percentage of seeds, and the estimated density of germinable seeds in the soil, based on these data. All soil samples were collected using the "biased" method described in the text, with the exception of DSH 1992 (quadrat) and KPC 1993 (transect). Pooled data are from biased sampling only.

YEAR	BWM				DSH				KPC			
	# Samples	# Seeds	Germ %	# Germ SDS/M <sup>2</sup>	# Samples	# Seeds	Germ %	# Germ SDS/M <sup>2</sup>	# Samples	# Seeds	Germ %	# Germ SDS/M <sup>2</sup>
1991	3	0	—	0	—	—	—	—	—	—	—	—
1992	8	1	100	132.6	50	0	—	0	—	—	—	—
1993	12	0	—	0	21	4	25	50.5	20	0	—	0
1994	13	0	—	0	21	2	50	50.5	10	0	—	0
Pooled Data	36	1	100%	29.5	42	6	33%	50	10	0	—	0

#### 4.5 DISCUSSION

Seed dispersal in cactus species may be effected passively by gravity and rainwater (Anderson, 1969; Emmett, 1989), or actively by such animals as ants, birds, and various mammals (Steenbergh and Lowe, 1977; Wendelken and Martin, 1988). Ants appear to be the dispersal agent impacting the majority of the annual Tobusch fishhook cactus seed production. The seeds are relatively small in size and from a relatively small plant, which are two characteristics typical of some other plant species for which myrmecochory has been noted (Westoby et al., 1990). Tobusch fishhook cactus seeds do not appear to have an elaiosome or caruncle, however, and so are unlike many other types of seeds adapted to ant-dispersal (e.g., Bullock, 1989; Hughes and Westoby, 1990). Also, the fleshy, spineless berry fruit type of this cactus is more typical of fruits adapted for vertebrate dispersal (e.g., Kaufmann et al., 1991). Still, based on the findings of this investigation, it is apparent that the immediate fate of the majority of the annual Tobusch fishhook cactus seed production at the three study sites involves direct removal from fruits by ants, primarily *Forelius foetidus*, for transport into their mound. Fruit and seed predation by pyralid moths (*Yosemitia* spp.) has been reported for other North American cacti (Heinrich, 1956; Johnson, 1992), but this was not noted for *A. tobuschii* at any of the three study sites during the course of this study.

The rate and thoroughness of seed collection by ants varies widely with plant density, ant species, and climatic conditions (Davidson, 1977a, 1977b; Smith et al., 1989). There were no obvious differences in the rate of seed removal from petri dishes or from newly dehisced fruits on plants between any of the sites utilized for this study, even though colonies and populations were quite different with respect to plant density.

A high percentage of seed consumption is typical of arid areas, and ants are often heavily involved in this activity (Gutterman, 1994). The fate of *A. tobuschii* seeds once in the ant mound is not yet understood, however, so it can not be assumed that all of such seeds have been permanently removed from the realm of eventual germination. It has been reported that removal of seeds into mounds by some ant species may ultimately prevent more seed loss than it causes, by providing seeds with a refuge from small mammal herbivory (Bullock, 1989) or unusually severe fires (Hughes and Westoby, 1992). Occasionally, germinable seeds are removed from ant mounds along with refuse, although some species of ants bury their refuse underground, while other species move refuse to surface piles which may then provide suitable sites for seed germination (Bullock, 1989; Levey and Byrne, 1993).

Results of the petri plate trials, along with observations of seed-bearing fruit remnants on plants, germinable seeds collected from many plant carcasses, detection of a modest seed reserve, and evidence of occasional vertebrate frugivory; all indicate that a portion of the annual seed production — perhaps up to 15% to 20% — is at least initially overlooked or lost by, or is somehow unavailable to the ants. Ants and small rodents can also be of considerable importance in post-dispersal seed movement and predation; however (Kaufmann et al., 1991; Levey and Byrne, 1993; Hulme, 1994). Although this facet of the seed ecology of *A. tobuschii* has not been fully investigated, evidence for secondary dispersal by ants was observed while setting up field seed exclosures, and indicates that those seeds which are initially unavailable or lost by seed vectors are not necessarily exempt from additional movement and predation.

Several studies have identified invertebrate seed predation as contributing to the decline of populations of rare species (Menges et al., 1986; Hegazy and Eesa, 1991) and, if the role of ants were solely a destructive one with respect to *A. tobuschii* seeds, this could be the case for this cactus also. The limitation of seed dispersal away from parent plants has also been shown to be detrimental to successful reproduction within plant populations, however (Chapman and Chapman, 1995). If germination and establishment of those relatively few seeds which are dropped by

ants during transport or which are removed from the mound with refuse is sufficient to compensate for plant mortality within the colony, however, ant dispersal of seeds away from parent plants could be a worthwhile strategy for this cactus. Such situations have been reported for other plant species with both ant (Levey and Byrne, 1993) and rodent seed vectors (Wada and Uemura, 1994).

Birds and larger mammals such as, e.g., rabbits, can play a substantial role in seed dispersal of some plant species (e.g., Izhaki and Safriel, 1990; Sargent, 1990; Zedler and Black, 1992), and may be of great importance to the establishment or reestablishment of plant species into an area (Primack and Miao, 1992). The role of vertebrates in the latter regard can even be facilitated by artificially increasing the attractiveness of desired establishment areas to potential frugivores (McClanahan and Wolfe, 1993). The occurrence of frugivory by birds or other vertebrates, while apparently of limited frequency for this species, may provide for occasional longer distance dispersal of *A. tobuschii* seeds, perhaps to the point of allowing establishment of new populations or colonies.

Based on the results of this investigation, seed germinability in the Tobusch fishhook cactus appears to be highly variable between years, and reasons for this are not readily apparent. Menges (1991) noted a positive correlation between percentage

seed germination and population size for another rare species, and he attributed this relationship to either increased geitonogamy or general inbreeding depression in smaller populations. Variation in *A. tobuschii* seed germinability was generally noted to affect each of the study populations similarly during concurrent years, without regard to population size. Possible causes for the observed year to year variation in Tobusch fishhook cactus seed germination are as yet unclear. Other facets of reproduction, namely flower production, fruit set, and seed set, did not vary as widely during the period of this investigation (see Chapter 5). Reports for other cacti show that seed germination percentage can be quite high, e.g., 88 percent germination for the organ pipe cactus (Parker, 1987), and 50-60 percent for the saguaro (Alcorn and Kurtz, 1959). Similar to the situation observed for the Tobusch fishhook cactus during this study, however, a wide range in seed germinability (ca. 1% to ca. 51%) has also been reported for the black lace cactus (Emmett, 1989).

The greenhouse germinability assessment appears to indicate that no prolonged period of dormancy is required before seeds of this cactus are able to germinate, so it appears that environmental constraints such as precipitation and/or temperature may dictate the period of germination in habitat. The period of highest germination noted within enclosures at two of the three study sites — i.e., from February through May — encompasses the months of typically highest rainfall for this part of the state

(Bomar, 1983), although 1993 and 1994 local climatic records specific to period of the field enclosure trials have not yet been assessed.

Safe sites are especially important for the successful germination and establishment of arid land plants because of the typically harsh climatic conditions and large amounts of granivory and herbivory associated with these areas (Guterman, 1994; McAuliffe, 1984, 1986; De Jong and Klinkhamer, 1988; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991). Germination of *A. tobuschii* seeds within enclosures was approximately similar for each of the three microhabitat types. This indicates that, in the absence of ants or other potential secondary seed dispersers which may have been excluded from enclosures, the type of microsite does not appear to be especially important for enabling seeds of this cactus to germinate. The survival of seedlings in each of these microsites past initial germination and early establishment, and the relative protective quality of these different sites when ants are present are not yet known, however.

While a great deal of the earlier study of soil seed reserves focused on seeds of weedy species in arable soils (e.g., see Roberts, 1981), more recent work has investigated the seed reserves of different and more natural habitat settings (e.g., Johnson, 1975; McMillan and Soong, 1989; Brown, 1992; Kinucan and Smeins,

1992; also see Leck et al., 1989). Seed reserves have been identified as often important features of different arid-land systems (Gutterman, 1994), and studies in North American deserts have shown an average community-wide seed reserve density of between 8,000 and 30,000 seeds/m<sup>2</sup> (Kemp, 1989). Based on the findings of the current investigation, the Tobusch fishhook cactus appears not only to maintain a relatively modest reserve of viable seeds in the soil but, to a limited extent, amongst the tubercles and spines of reproductive-sized plants as well.

Within arid-land systems, the seed reserve may be distributed in an extremely patchy manner, with soils in most areas nearly devoid of seeds, but with occasional areas of substantial numbers of seeds (Reichman, 1984). While the soil sampling effort for this study was of limited scope in order to minimize disturbance to the study plants, hence limiting the accuracy of the actual estimate presented, germinable seeds were detected in the soil at two of the three sites, and the distribution of these seeds appears to be patchy and biased toward reproductive-sized adults. A study of the soil seed reserve of another rare Texas cactus also noted substantial patchiness in seed distribution that was heavily skewed toward reproductive adults, and an average density of seeds that is comparable to the estimates presented in this investigation (Emmett, 1989). The modest soil seed reserve maintained by *A. tobuschii* may afford this species some recuperative ability against the catastrophic disappearance of

individuals and, depending on the duration of persistence of seed reserve seeds, against loss of genetic diversity.

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CHAPTER 5.0 ANNUAL MORTALITY, REPRODUCTIVE EFFORT,  
AND CHANGES IN PLANT SIZE IN THREE NATURALLY-OCCURRING  
POPULATIONS OF THE TOBUSCH FISHHOOK CACTUS  
(*ANCISTROCACTUS TOBUSCHII*) IN CENTRAL TEXAS

5.1 ABSTRACT

Mortality, reproduction, and changes in plant size were monitored at two population sites of Tobusch fishhook cactus for four consecutive years (BWM and DSH), and at one additional site during two consecutive years (KPC). Individual plant diameter varied significantly between years, occasionally resulting in an average decrease between annual censusing periods. Its value as a measure of annual growth is therefore somewhat limited, but plant diameter does appear to have useful predictive value concerning the onset of sexual reproduction, reproductive output and, to an extent, of impending senescence. Plant diameter may therefore be useful in delineating different life stages for demographic analysis of populations.

Annual mortality was high during all years at BWM and DSH, but was more modest at KPC. Of the plants monitored in 1991, 55% at BWM and 69% at DSH had died by the end of March, 1994. Grub infestation accounted for the majority of

attributable mortality at all sites during all years, and was probably responsible for a large percentage of mortality for which a cause was not discernable. Grubs of two cactus-specialist coleopteran species were identified as causing such mortality: *Moneilema armata* LeConte and, especially, *Gerstaeckaria nobilis* LeConte. Herbivory by larger mammals accounted for a small but constant portion of the annual attributable mortality, although such activity was not always immediately fatal because many plants (especially at DSH) produced branches following mammal-associated damage to the main stem.

For reasons which are not yet apparent, annual flower, fruit, and seed production per plant decreased consistently and significantly at all populations during each year of this study. Annual fruit set (fruits/flower) was generally constant at near 70% throughout the course of this investigation, while average seed germinability varied widely between years, from populational annual averages of ca. 65% to ca. 1%.

## 5.2 INTRODUCTION

The Tobusch fishhook cactus (*Ancistrocactus tobuschii* W.T. Marshall ex Backeberg) is a small, tuberculate member of the Cactaceae which is endemic to the

south central and western portions of the Edward's Plateau region of Texas. Individuals comprising several naturally occurring populations of *A. tobuschii* at three locales — the Buck Wildlife Management Area (BWM), Kimble County, Tx.; the Devil's Sinkhole State Natural Area (DSH), Edwards County, Tx.; and Kickapoo Caverns State Natural Area (KPC), Kinney and Edwards Counties, Tx. — were censused repeatedly over a period of four consecutive years (two consecutive years for KPC). Censusing was conducted to gather information about the size structure of each population, and the annual reproductive effort, mortality, and changes in size of constituent individuals.

For studies of plants especially, the size of an individual can be much more informative than age with regard to its reproductive potential and chances for future survival within the population (Werner, 1975; Gross, 1981; Fiedler, 1987; Piper, 1992). For long-lived perennial species, plant size and some knowledge of annual changes in plant size can be used to estimate the age of a plant or cohort of plants (e.g., Shreve, 1910) which, in conjunction with (e.g.) local climatological records from the estimated period of seed germination and seedling establishment, could be useful in assessing sets of conditions necessary for successful plant establishment.

Knowledge of the average rate of plant size change may also provide some insight as to the amount of time necessary for a plant to reach the onset of reproduction. There has been some speculation that *A. tobuschii* reaches reproductive maturity in the field in as little as three years, and that the average lifespan for this cactus may be as short as ca. 13 years, but the rate of growth and timing of the onset of reproduction has never been closely investigated (TPWD, 1984).

Growth, reproduction, and mortality in plants tends to vary with both time and place (e.g., Piper, 1992), but many studies present data related to these features which were obtained from a one-time or one-population survey as being representative of typical conditions (e.g., Parker, 1987; Hegazy and Eesa, 1992). Censusing of different populations over regular time intervals is important in allowing for more accurate assessment of both typical conditions, and of the type and degree of environmental variation which populations may experience (Hutchings, 1991). With this in mind, censusing of plants for the current investigation was conducted several times each year during 1991 through 1994 to investigate plant size distribution and annual changes in plant size; annual flower, fruit, and seed production and seed germinability; and annual mortality and the factors associated with plant mortality.

### 5.3 MATERIALS AND METHODS

#### Yearly Field Censusing

Detailed descriptions of each of the study sites are provided in Chapter 1, along with the methodology used during the initial search for and marking of study plants at each site. The number of plants at each site which were included in censuses at some point during the course of the field study is as follows: 162 plants at BWM; 504 plants at DSH; and 116 plants at KPC. In addition to the regularly censused study plants, plants in several separate colonies or populations at DSH and KPC were also utilized for certain other aspects associated with this study, but were not included in the annual censusing.

To assess mortality, reproductive effort, and changes in plant size, populations were thoroughly censused several times each year. Plants at BWM and DSH were monitored each of four consecutive years from 1991 through 1994, while plants at KPC were monitored during the two consecutive years of 1993 and 1994. The initial annual census of all plants at each site was conducted during February or March. During this early census each year, information was gathered from each plant regarding whether the plant was living or dead; the cause of death (if dead) or the

apparent general health (if living); and the number of flowers or flower buds borne on the plant.

Also during the initial annual census, the stem diameter of each living individual was measured to the nearest millimeter, and recorded. Diameter measurements were taken during February-March of each year because this period was noted to immediately precede the onset of new growth for this cactus. During 1991, diameter measurements were made using a hand-held ruler, while a dial caliper was used to obtain diameter measurements during 1992 through 1994. The recorded diameter for each plant for each year consisted of the average of two separate measurements made across the center of the plant stem apex from tubercle tip to tubercle tip, with the position of the second measurement rotated approximately 90° from the position of the first measurement. Plant stem diameter can fluctuate substantially with (e.g.) changes in soil water potential, especially for plants with a large amount of cortical water storage tissue within the stem like xerophytic cacti (Nobel, 1977; Mauseth, 1984), but other possible measures by which to judge plant size and size change in *A.tobuschii* such as plant height were noted to fluctuate to an even greater extent with changes in moisture availability. Also, accurate measures of plant height were not always obtainable due to the existence of obstructions such as rocks or other plants around the cactus. In an attempt to minimize variation in

factors which could cause wide changes in plant diameter, annual measurements were taken during the same period each year, although no attempts were made to time field measurement to a specific set of environmental conditions such as (e.g.) weather or soil moisture conditions.

In late April or early May of each year, plants were recensused to determine fruit production on those plants which had produced flowers earlier that year. A subset of naturally-occurring fruits was collected at this time to allow evaluation of annual seed production and seed germinability; fruit collection and processing protocol are discussed in detail below. Mortality and general health were also assessed on all plants during the April/May censuses. During 1991 through 1993, censuses of all plants were also conducted during the month of August to evaluate mortality and general plant appearance.

For plants which were found dead at the time of a census or during other project-related activities, carcasses were examined and the cause of death recorded, if determinable. In many cases, grubs (larval Coleoptera) were found within the plant remains, and voucher specimens were collected at each site during all years to allow later species identification. Vouchers were collected by either directly placing the larva into 90% EtOH, or by collecting entire plant carcasses back to the

laboratory in Austin, where they were planted in pots to allow maturation of the insects to the adult phase. Upon emergence, adult beetles were placed in a kill-jar charged with EtAc. After several days, specimens were removed from the kill-jar, pinned, labeled, and stored in an insect box for later species determination.

### Fruit and Seed Production

To allow estimation of the average annual seed production, one naturally-produced near-mature fruit (i.e., of ripe appearance but which was not yet split open) was collected from each of a randomly chosen subset of plants within each population during field visits from late April through May of each year. In order to minimize the impact on the study population, collection of fruits was limited to no more than ca.20% of the total number of flowers produced at each site for a given year. When available, fruits were collected from nearby unmonitored plants to minimize further the impact on the study population.

Fruits were transported to the laboratory in Austin, where they were carefully split open and allowed to air-dry at room temperature for a period of 1 to 2 months. After fruits were dry, seeds were removed from the fruit, counted, treated with a commercial fungicide (Ferti-lome with benomyl), and dry-stored in individual

labeled, capped bottles in refrigeration (ca. 8°C) until used in germination trials. Germinability assessment protocol and results are presented in Chapter 4.

#### Survey for Naturally-Occurring Seedlings

Relatively few naturally-occurring *A. tobuschii* seedlings (i.e., stem diameter < 11 mm) were encountered during routine population censusing and performance of other field tasks. Of the few seedlings which were discovered during 1991 and 1992, the overwhelming majority occurred within several centimeters of a monitored study plant of reproductive size. While the almost exclusive discovery of seedlings which were associated with larger plants was due at least in part to the greater focus of attention given to the area immediately surrounding larger study plants, the small size and extremely inconspicuous nature of Tobusch fishhook cactus seedlings also contributed to their infrequent discovery. Several sampling strategies were therefore utilized to locate additional seedlings at each site in order to obtain a larger sample from which to monitor size changes and mortality in this smallest size category.

It was decided that the survey for seedlings should be performed biased to reproductive-size plants at BWM, where *A. tobuschii* plants are relatively few in number and generally occur as diffusely-spaced individual plants or small groups,

because it was felt that sampling throughout the various colonies would probably prove fruitless. In March, 1993, the area within a one-meter radius centered around each reproductive-sized plant at BWM was surveyed for additional seedling and juvenile-sized plants.

A sampling strategy which was not biased to reproductive-sized plants was performed within several sites at the more densely-grouped DSH and KPC populations. In March, 1993, three transects were established within the largest monitored colony at DSH, and two transects were established within each of five other monitored colonies at DSH, and within the two monitored colony sites at KPC. Two of the three transects at the largest DSH colony were aligned parallel to the slope of the hill on which the majority of known plants were growing, and one transect was placed perpendicular to the first two transects. The two transects at all other sites were placed perpendicular to each other, with one parallel and one perpendicular to the slope at the colony site or, when the site was approximately level, the transects were aligned perpendicular to each other along the major compass directions. Depending on the areal coverage of a colony, transects ranged from six to sixteen meters in length; sampling was conducted at one-meter intervals along the transects, within a 0.15 meter radius circular quadrat centered around each sampling

point. When seedlings were located, they were tagged, mapped and monitored as for all plants.

### Statistical Analysis

The majority of statistical analyses of data collected during this portion of the investigation were performed using SYSTAT version 5.0.3 statistical software for IBM PC-compatible computers (SYSTAT, Inc., 1990), although some of the summary statistics were generated using the Q&A version 3.0 database management program for IBM PC-compatible computers (Symantec, Inc., 1988).

The annual change in plant diameter was determined for individual plants which were alive and measured during the early annual census of consecutive years (e.g., February/March 1991 and February/March 1992). Annual diameter changes were then compared for each site between years, and between sites over all years, using a two-way analysis of variance (for BWM and DSH during the period 1991 through 1994), or a one-way analysis of variance (for all three sites for the 1993-1994 diameter change only). When appropriate, significant differences from ANOVAs were further determined using Tukey multiple comparison tests. One and two-way ANOVAs of annual diameter changes for individual plants were used instead

of repeated measures ANOVAs of annual plant diameter values for the entire monitoring period because high mortality limited the number of plants which were able to be measured during each year of the entire field censusing effort, and because many plants were added to census populations after the initial year.

Annual mortality was determined as the percentage of plants which were known to have been alive after the end of one early census period, but which had died by the end of the next early census period (e.g., alive on or after 1 April 1991, but dead on or before 31 March, 1992). Contingency tables were constructed to allow comparison of "between site" and "between years" differences in annual mortality. A three-way log-linear analysis and G-test were used to detect statistically significant differences in annual mortality for BWM and DSH during the period 1991 through 1994. A two-way log-linear analysis and G-test were used to compare differences for all three study populations for the one-year period 1993-1994. Log-linear models were chosen for these analyses because the dependent variable (plant condition — alive or dead) is an attribute, and not a measurement variable (Sokal and Rohlf, 1981).

With few exceptions, flower, fruit, and seed production in the Tobusch fishhook cactus was limited to those plants which had attained a stem diameter of

greater than 20 mm (see Appendix A, B, and C for data summary tables). Annual datasets for these reproductive features which were subjected to statistical analysis were therefore limited to only those plants which were 21 mm or larger during the year for which data was recorded. Annual data for flower production is reported as the number of flowers per reproductive-sized plant ("flowers/plant"); fruit production is reported as both the number of fruits per plant which actually produced flowers that year ("fruits/flowering plant"), and as the percentage of flowers which resulted in a fruit ("fruit-set"); seed production is reported as the number of seeds per fruit; and seed germinability is reported as the percentage germination of seeds per plant (usually from one fruit), as assessed in the campus growth chamber. Kruskal-Wallis tests were used to analyze flowers/plant, fruits/flowering plant, and fruit-set data, to test for statistically significant differences between sites within years, and between years for each site. Nonparametric tests were employed because dependent variables in each of the above datasets were not continuous (flowers/plant, fruits/flowering plant), or residuals were not normally distributed, even following transformation (fruit-set) (Sokal and Rohlf, 1981). Data for seed production and seed germinability (square root transformed) did meet the assumptions of analysis of variance, so two-way ANOVAs were performed to test for statistically significant effects of site and year on both of these variables. Two-way ANOVAs were run to test for significant differences in annual seed production and germinability between sites and years for

BWM and DSH during each year from 1991 through 1994, while another set of two-way ANOVAs was run to test the same features for all three sites during 1993 and 1994.

Finally, one-year changes in flower and fruit production for individual plants were also analyzed for significant differences between sites and between years. Annual flower and fruit change data were gathered from reproductive-size plants which were censused during any two consecutive years (i.e., 1991-1992, 1992-1993, and 1993-1994). Such plants were placed into one of three categories: a) produced one less or fewer flowers/fruits during the second year than the first; b) produced the same number of flowers/fruits both years; and, c) produced one more or greater flowers/fruits during the second year than the first. Contingency tables were constructed for these data, and three-way log-linear models employed to test for significant site and year differences for BWM and DSH during each of the three one-year periods. Two-way log-linear models were used to test for significant differences in flower-change and fruit-change between all three sites during the one year period 1993-1994.

## 5.4 RESULTS

### Plant Diameter

Census data collected at each site shows average annual changes in individual plant diameter of from near one to several millimeters per year (Tables 5.1, 5.2, and 5.3). Perhaps the most noteworthy feature of these data is the negative average diameter change recorded for BWM and DSH during 1992-1993 (and for those plants censused during both 1991 and 1994 at BWM), which indicates that plants actually decreased in diameter between these two censuses. During all other years, plants showed a slight to modest average increase in diameter.

The two-way analysis of variance of annual diameter change differences for BWM and DSH from 1991 through 1994 indicates that differences between the two sites for each set of years were significant ( $P < 0.001$ ), and that differences within sites between sets of years were also significant ( $P < 0.001$ ) (Table 5.4). A Tukey multiple comparison test indicated that all differences between sets of years were statistically significant. Diameter change differences between all three study sites during 1993-1994 were judged not significant by the one-way ANOVA (Table 5.5).

Table 5.1. Summary of plant diameter and average plant diameter change for census plants at BWM. Plant diameter is in millimeters. "Number of Plants" includes those which were alive and censused during February/March of the year listed, and those which were newly discovered after March but before the end of August of that year ("Diameter Undetermined"). "Diameter Change" is the mean change in diameter (mm) for plants which were measured during both of the years listed in the column heading (and the number of plants the average is based upon), categorized by the plant diameter measured during the first year of the column heading. The  $\pm$  standard error of the mean is provided for the overall average annual diameter change. Note that the final column covers a three-year increment.

Plant Diameter		Number of Plants				Diameter Change			
		1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10		1	2	40	18	—	0.0 (1)	+1.1 (18)	—
11-20		8	15	19	14	+2.9 (7)	-1.0 (14)	+2.7 (14)	+5.0 (6)
21-30		15	26	22	22	+0.6 (13)	-1.7 (18)	+1.3 (19)	+1.8 (5)
31-40		21	25	19	18	+1.7 (14)	-2.9 (20)	-0.2 (17)	-0.5 (10)
41-50		10	9	8	5	+0.1 (7)	-5.8 (8)	-1.6 (5)	-5.8 (4)
51-60		11	8	2	1	+3.1 (7)	-8.1 (7)	+2.0 (1)	-3.4 (5)
61-70		2	2	2	2	-1.0 (2)	-1.5 (2)	0.0 (2)	0.0 (1)
Diameter Undetermined		18	0	1	3	—	—	—	—
Pups	# of Branches	2	3	3	2	—	—	—	—
	# of Plants	1	2	2	1	—	—	—	—
TOTAL		87	89	115	84	+1.5 ( $\pm 0.6$ ) (50)	-3.0 ( $\pm 0.4$ ) (70)	+0.9 ( $\pm 0.3$ ) (80)	-0.2 ( $\pm 1.2$ ) (31)

Table 5.2. Summary of plant diameter and average plant diameter change for census plants at DSH. Plant diameter is in millimeters. "Number of Plants" includes those which were alive and censused during February/March of the year listed, and those which were newly discovered after March but before the end of August of that year ("Diameter Undetermined"). "Diameter Change" is the mean change in diameter (mm) for plants which were measured during both of the years listed in the column heading (and the number of plants the average is based upon), categorized by the plant diameter measured during the first year of the column heading. The  $\pm$  standard error of the mean is provided for the overall average annual diameter change. Note that the final column covers a three-year increment.

Plant Diameter		Number of Plants				Diameter Change			
		1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10		8	36	57	26	+3.4 (7)	+0.5 (24)	+1.6 (27)	+0.9 (3)
11-20		56	63	71	49	+4.7 (45)	-0.5 (46)	+2.6 (51)	+7.3 (26)
21-30		49	70	68	46	+3.7 (34)	-0.5 (59)	+1.9 (49)	+2.7 (21)
31-40		47	40	41	32	+2.3 (33)	-2.3 (31)	+0.8 (22)	+1.4 (15)
41-50		15	32	21	16	+1.2 (9)	-2.9 (22)	-1.5 (12)	-5.4 (5)
51-60		10	5	4	2	-6.0 (4)	-0.4 (5)	-4.0 (4)	-6.5 (2)
61-70		—	—	—	—	—	—	—	—
Diameter Undetermined		62	30	7	9	—	—	—	—
Pups	# of Branches	59	78	73	47	—	—	—	—
	# of Plants	34	43	38	25	—	—	—	—
Total		281	319	307	205	+3.2 ( $\pm 0.4$ ) (132)	-0.9 ( $\pm 0.3$ ) (187)	+1.5 ( $\pm 0.3$ ) (165)	+3.5 ( $\pm 1.0$ ) (72)

Table 5.3. Summary of plant diameter and average plant diameter change for census plants at KPC. Plant diameter is in millimeters. "Number of Plants" includes those which were alive and censused during February/March of the year listed, and those which were newly discovered after March but before the end of August of that year ("Diameter Undetermined"). "Diameter Change" is the mean change in diameter (mm) for plants which were measured during both of the years listed in the column heading (and the number of plants the average is based upon), categorized by the plant diameter measured during the first year of the column heading. The  $\pm$  standard error of the mean is provided for the overall average annual diameter change. Note that the final column covers a three-year increment.

Plant Diameter		Number of Plants				Diameter Change			
		1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10		—	—	40	29	—	—	+0.7 (29)	—
11-20		—	—	26	22	—	—	+0.9 (21)	—
21-30		—	—	24	20	—	—	+2.4 (20)	—
31-40		—	—	9	13	—	—	+1.4 (7)	—
41-50		—	—	10	8	—	—	-2.9 (8)	—
51-60		—	—	6	5	—	—	+1.3 (5)	—
61-70		—	—	—	1	—	—	—	—
Diameter Undetermined		—	—	0	6	—	—	—	—
Pups	# of Branches	—	—	1	1	—	—	—	—
	# of Plants	—	—	1	1	—	—	—	—
Total		—	—	115	98	—	—	+0.8 ( $\pm 0.4$ ) (98)	—

Table 5.4. Two-way analysis of variance on the effect of year and site on plant diameter change for BWM and DSH during the one-year periods 1991-1992, 1992-1993, and 1993-1994. Significant differences are discussed in the text.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Year	18.169	2	9.085	63.121	< 0.001
Site	2.972	1	2.972	20.652	< 0.001
Year * Site	0.604	2	0.302	2.097	0.124
Error	97.580	678	0.144		

Table 5.5. One-way analysis of variance on the effect of site on plant diameter change for all three study sites during the one-year period 1993-1994.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Site	0.372	2	0.186	1.487	0.228
Error	42.516	340	0.125		

### Mortality

Annual mortality was greater than 20% at BWM and DSH during each of the three one-year monitoring periods, while mortality was a more modest 9% at KPC during 1993-1994 (Tables 5.6, 5.7, and 5.8). No statistically significant differences in annual mortality were detected between BWM and DSH during 1991 through 1994, or between years for either of these two sites (Table 5.9), but differences

Table 5.6. Summary of mortality for BWM. Plant diameter is in millimeters. Columns provide the number of plants which died from April of the first year through March of the second year in each column heading, due to U = undetermined cause, M = mammal activity, or G = grub infestation. % and Total % indicate the mortality percentage of the total number of plants which were known to have been alive at some point between April and March of the years in each column heading. Note that the final column covers a three-year increment.

Plant Diameter		1991-1992			1992-1993			1993-1994			1991-1994		
		U	M	G	U	M	G	U	M	G	U	M	G
01-10		1	0	0	1	0	0	17	1	0	1	0	0
11-20		0	1	0	1	0	0	3	2	0	0	2	0
21-30		0	0	3	1	0	8	0	0	2	1	2	7
31-40		3	2	2	1	1	4	0	0	2	3	2	6
41-50		2	1	0	0	0	2	0	0	1	3	1	2
51-60		4	1	0	1	0	0	0	1	0	4	2	0
61-70		0	0	0	0	0	0	0	0	0	0	0	1
Diameter Undetermined		5	1	4	0	0	0	1	0	0	5	1	5
Pups	# of Branches	0	0	0	0	0	0	0	1	0	0	0	0
	# of Plants	0	0	0	0	0	0	0	1	0	0	0	0
Subtotal		15	6	9	5	1	14	21	5	5	17	10	21
%		17.2	6.9	10.3	5.6	1.1	15.7	18.3	4.3	4.3	19.5	11.5	24.1
Total%		34.5			22.5			27.3			55.2		

between all three sites during the 1993-1994 one-year period were significant ( $P < 0.001$ ) (Table 5.10).

Table 5.7. Summary of mortality for DSH. Plant diameter is in millimeters. Columns provide the number of plants which died from April of the first year through March of the second year in each column heading, due to U = undetermined cause, M = mammal activity, or G = grub infestation. % and Total % indicate the mortality percentage of the total number of plants which were known to have been alive at some point between April and March of the years in each column heading. Note that the final column covers a three-year increment.

Plant Diameter		1991-1992			1992-1993			1993-1994			1991-1994		
		U	M	G	U	M	G	U	M	G	U	M	G
01-10		1	0	0	8	0	1	21	2	2	3	0	2
11-20		10	0	0	5	1	10	5	2	10	17	2	11
21-30		15	0	0	4	0	8	5	3	10	21	3	8
31-40		12	0	3	0	1	8	7	3	9	15	5	15
41-50		2	1	3	2	1	6	2	3	4	6	1	4
51-60		3	1	1	1	0	0	0	0	0	3	2	3
61-70		—	—	—	—	—	—	—	—	—	—	—	—
Diameter Undetermined		21	0	2	4	0	2	0	0	1	29	4	17
Pups	# of Branches	1	2	0	4	4	5	6	4	18	11	12	14
	# of Plants	1	2	0	2	2	4	4	4	9	7	8	7
Subtotal		65	4	9	25	5	39	44	17	45	101	25	67
%		23.1	1.4	3.2	7.8	1.6	12.2	14.3	5.5	14.7	35.9	8.9	23.8
Total%		27.8			21.6			34.5			68.7		

By far, the most common discernable factor associated with *A. tobuschii* mortality at all three sites during 1991 through 1994 was grub infestation. It is probable the grubs were also responsible for a substantial portion of the undetermined

Table 5.8. Summary of mortality for KPC. Plant diameter is in millimeters. Columns provide the number of plants which died from April of the first year through March of the second year in each column heading; due to U = undetermined cause, M = mammal activity, or G = grub infestation. % and Total % indicate the mortality percentage of the total number of plants which were known to have been alive at some point between April and March of the years in each column heading. Note that plants in this population were only censused during 1993 and 1994.

Plant Diameter		1991-1992			1992-1993			1993-1994			1991-1994		
		U	M	G	U	M	G	U	M	G	U	M	G
01-10		—	—	—	—	—	—	4	0	0	—	—	—
11-20		—	—	—	—	—	—	0	0	2	—	—	—
21-30		—	—	—	—	—	—	1	1	1	—	—	—
31-40		—	—	—	—	—	—	1	0	1	—	—	—
41-50		—	—	—	—	—	—	0	0	0	—	—	—
51-60		—	—	—	—	—	—	0	0	0	—	—	—
61-70		—	—	—	—	—	—	—	—	—	—	—	—
Diameter Undetermined		—	—	—	—	—	—	0	0	0	—	—	—
Pups	# of Branches	—	—	—	—	—	—	0	0	0	—	—	—
	# of Plants	—	—	—	—	—	—	0	0	0	—	—	—
Subtotal		—	—	—	—	—	—	6	1	4	—	—	—
%		—	—	—	—	—	—	5.2	0.9	3.5	—	—	—
Total %		—			—			9.6			—		

plant deaths, but carcasses of many plants thus classified were found which had been destroyed or had decayed to a point which prevented identification of the cause of death. There were also instances when no plant remnants were found, and this was especially true for plants in the smallest diameter category in 1993-1994. It is quite

Table 5.9. Contingency table constructed for a three-way log-linear analysis of differences in annual mortality between the study sites BWM and DSH during the one-year periods 1991-1992, 1992-1993, and 1993-1994. Plant condition was assessed during February - March censuses of the latter year in each annual couplet for plants known to have been alive at some point during April through March of that one-year period. Results of a G-test are also provided.

SITE	YEAR	NUMBER OF PLANTS (% OF TOTAL)	
		ALIVE	DEAD
BWM	1991-1992	57 (65.5%)	30 (34.5%)
	1992-1993	69 (77.5%)	20 (22.5%)
	1993-1994	84 (73.0%)	31 (27.0%)
DSH	1991-1992	203 (72.2%)	78 (27.8%)
	1992-1993	250 (78.4%)	78 (27.8%)
	1993-1994	203 (65.5%)	104 (34.5%)

$\chi^2 = 6.8$   
 $P = 0.149$

likely that many of these "seedlings" succumbed to extreme desiccation during the rain-free months of July and August of 1993. Mammalian activities generally accounted for only a small percentage of the total annual mortality at each site, although a portion of the mortality for which the cause was not determinable may have also been caused by mammals. Activities by which mammals caused the death of Tobusch fishhook cactus plants included not only direct herbivory of plants, but also incidental destruction of plants during (e.g.) animal foraging. Damage by mammals was not always immediately fatal to plants, as many plants which had sustained obvious mammalian damage to the above-ground portion of the stem were observed to later produce one or more "pups" (branches) from the below ground

portion of the stem. No Tobusch fishhook cacti were observed to survive obvious grub infestation, however.

Table 5.10. Contingency table used for a two-way log-linear analysis of differences in annual mortality between all three study sites during the one-year period 1993-1994. Plant condition was assessed during the 1994 February - March census for plants known to have been alive at some point during that one-year period (i.e., April - March, 1993-1994). Results of a G-test are also provided.

SITE	NUMBER OF PLANTS (% OF TOTAL)	
	ALIVE	DEAD
BWM	84 (73.0%)	31 (27.0%)
DSH	203 (65.5%)	104 (34.5%)
KPC	104 (90.4%)	11 (9.6%)

$\chi^2 = 28.73$   
 $P < 0.001$

At least two species of beetles (Coleoptera) were identified from adult specimens which had been collected in the larval stage within dead or senescent *A. tobuschii*, and allowed to mature in the laboratory. Positive identification to species could not be made for the larval voucher specimens. By far, the most common beetle species collected from the Tobusch fishhook cactus during the course of the field investigation was *Gerstaeckaria nobilis* (LeConte) (Curculionidae), a cactus-specialist weevil. As many as four grubs of this species were collected from individual *A. tobuschii* plants, although one or two grubs per cactus was more typical. Numerous curculionid grub specimens were collected at BWM and DSH (but

not KPC) during each of the four years which these populations were studied, and all specimens which were allowed to mature to the adult stage in the laboratory have been identified as *G. nobilis*. Curculionid specimens which were preserved in the larval stage probably also belong to this same genus and species (E. Riley, Tx. A&M Entomology Dept., pers. comm., 1995). *Gerstaeckaria nobilis* accounted for at least 85% of the grub-related mortality observed at BWM and KPC during the course of this study. Another cactus-specialist beetle, *Monellema crassum* LeConte (Cerambycidae), was collected as a larva within *A. tobuschii* from a fourth site (Dolan Creek Ranch, Val Verde County) and matured to the adult stage in the laboratory. Cerambycid grubs which were similar in appearance to the *M. crassum* specimen were also collected from Tobusch fishhook cactus at KPC and BWM (but not DSH), and are probably also this same species (E. Riley, pers. comm., 1995). If this is the case, *M. crassum* accounted for the remaining grub-related mortality at BWM and KPC.

### Reproduction

For plants of reproductive size (i.e., > 20 mm diameter), average flower and fruit production showed a general year-to-year decline during the course of this study, with the exception of flower production at KPC. Flower and fruit production

dropped by ca. one-half of the 1991 average by 1994 at BWM and DSH (Table 5.11). The average decrease in annual flower and fruit production was noted for all plant diameter categories (See Appendices A and B). Statistically significant differences in flower production between sites for individual years were detected only during 1994 (Kruskal-Wallis (K-W) test;  $P < 0.05$ ), while between years significant differences were detected for BWM (K-W test;  $P < 0.001$ ) and DSH (K-W test;  $P < 0.001$ ) but not KPC. Significant differences in fruit production were detected between sites during 1993 (K-W test;  $P < 0.05$ ) and between years at BWM (K-W test;  $P < 0.001$ ) and DSH (K-W test;  $P < 0.001$ ).

Data for one-year changes in flower and fruit production for individual plants also indicates that a general decline in these features occurred during the course of this field investigation (Tables 5.12 and 5.13). No significant differences were detected between populations and between years for the percentages of individuals in the three flower- or fruit-change categories.

The percentage fruit-set varied somewhat between years and sites, but was generally around 70-75% of the flower production (Table 5.11). Statistically significant differences in fruit-set were detected between BWM and DSH during 1992 (K-W test;  $P < 0.05$ ), between all three sites in 1993 (K-W test;  $P < 0.001$ ), and

Table 5.11. Summary of reproductive effort at each study site during each monitoring year. This table contains data from only those plants which were of reproductive size (i.e., > 2.0 cm stem diameter) during the February - March census of the monitoring year, which were not included in manipulative field pollination trials, and which were not "pupped" plants. Statistically significant differences have been assessed at the following levels: 1) for each site between years, and 2) between sites within each year. ANOVA tables for "Seeds/Fruit" and "Seed Germinability" are provided in Appendix D.

		Flowers/Plant <sup>a</sup>		Fruits/Flowering Plant <sup>a</sup>		Percent Fruit-Set <sup>a</sup>		Seeds/Fruit <sup>b</sup>		Seed Germinability <sup>b</sup>	
		1	2	1	2	1	2	1	2	1	2
1991	BWM	3.1 (±0.3)	*** ns	2.6 (±0.3)	** ns	76.6% (±5.7)	** ns	54.2 (±4.3)	** ns	65.6%	*** ns
	DSH	2.7 (±0.2)	***	2.6 (±0.2)	***	77.7% (±5.0)	ns	48.3 (±5.2)	**	34.2% (±6.1)	***
1992	BWM	2.3 (±0.3)	ns	1.6 (±0.3)	ns	55.4% (±6.8)	*	42.9 (±6.6)	ns	23.9% (±7.1)	ns
	DSH	1.7 (±0.2)		2.0 (±0.3)		77.1% (±6.2)		36.5 (±4.4)		25.5% (±5.1)	
1993	BWM	1.9 (±0.2)		1.3 (±0.2)		52.1% (±6.5)		33.5 (±6.3)		46.2% (±6.0)	
	DSH	1.5 (±0.1)	ns	1.6 (±0.1)	*	76.0% (±3.9)	***	38.0 (±3.8)	ns	53.8% (±5.4)	ns
	KPC	1.6 (±0.2)	ns	2.1 (±0.3)	ns	91.7% (±4.3)	*	46.0 (±7.0)	ns	67.1% (±6.7)	***
1994	BWM	1.6 (±0.2)		1.3 (±0.2)		72.3% (±6.7)		31.9 (±10.9)		1.1% (±1.1)	
	DSH	1.1 (±0.2)	*	1.5 (±0.2)	ns	69.6% (±6.8)	ns	29.8 (±5.9)	ns	8.9% (±5.0)	ns
	KPC	1.7 (±0.2)		1.6 (±0.3)		67.5% (±7.1)		30.6 (±8.2)		1.3% (±1.3)	

\* P < 0.05

\*\* P < 0.01

\*\*\* P < 0.001

ns = not significant

<sup>a</sup> Data analyzed using Kruskal-Wallis tests.

<sup>b</sup> Data analyzed using two-way analysis of variance procedures.

Table 5.12. Contingency table constructed for three-way log-linear analyses of one-year changes in flower and fruit production for individual plants (i.e., monitored both years of the couplet) for three consecutive years at BWM and DSH. Results of G-tests are also provided.

SITE	YEARS		NUMBER OF PLANTS (% OF TOTAL)		
			-1 or Fewer	No Change	+1 or Greater
BWM	1991-1992	Flowers	12 (55%)	5 (23%)	5 (23%)
		Fruits	5 (42%)	4 (33%)	3 (25%)
	1992-1993	Flowers	24 (62%)	12 (31%)	3 (8%)
		Fruits	14 (48%)	11 (38%)	4 (14%)
	1993-1994	Flowers	22 (48%)	18 (39%)	6 (13%)
		Fruits	11 (34%)	11 (34%)	10 (31%)
DSH	1991-1992	Flowers	17 (68%)	5 (20%)	3 (12%)
		Fruits	12 (36%)	8 (24%)	13 (39%)
	1992-1993	Flowers	37 (43%)	28 (33%)	21 (24%)
		Fruits	13 (57%)	7 (30%)	3 (13%)
	1993-1994	Flowers	26 (37%)	31 (44%)	14 (20%)
		Fruits	12 (36%)	8 (24%)	13 (39%)

Flower change:  $\chi^2 = 9.40$        $P = 0.152$

Fruit change:  $\chi^2 = 8.97$        $P = 0.175$

within sites between monitoring years for BWM (K-W test;  $P < 0.01$ ) and KPC (K-W test;  $P < 0.05$ ).

Seed production also showed a general decline during the course of the field investigation, from ca. 50 seeds per fruit for both BWM and DSH in 1991, to ca. 30 seeds per fruit for all three populations in 1994 (Table 5.11). Two-way ANOVAs detected no significant differences between sites during any one year, but significant

Table 5.13. Contingency table constructed for two-way log-linear analyses of 1993-1994 changes in flower and fruit production for individual plants (i.e., monitored during both years) at all three study sites. Results of G-tests are also provided.

SITE		NUMBER OF PLANTS (% OF TOTAL)		
		-1 or Fewer	No Change	+1 or Greater
BWM	Flowers	22 (48%)	18 (39%)	6 (13%)
	Fruits	11 (34%)	11 (34%)	10 (31%)
DSH	Flowers	26 (37%)	31 (44%)	14 (20%)
	Fruits	12 (36%)	8 (24%)	13 (39%)
KPC	Flowers	12 (27%)	17 (39%)	15 (34%)
	Fruits	17 (61%)	5 (18%)	6 (21%)

Flower change:  $\chi^2 = 7.43$       P = 0.115

Fruit change:  $\chi^2 = 6.01$       P = 0.199

"within site" differences were detected for BWM and DSH between 1991 and each of 1993 (Tukey MCT;  $\alpha < 0.01$ ) and 1994 (Tukey MCT;  $\alpha < 0.05$ ) (Appendix D).

Average per fruit germinability of naturally-produced Tobusch fishhook cactus seeds ranged widely during the course of this investigation, from a high of ca. 67% for KPC in 1993, to a low of ca. 1% for BWM and KPC in 1994 (Table 5.11). In general, 1991 and 1993 appear to have been years of relatively high seed germinability for all monitored sites, while seed germinability was more modest in 1992 and extremely low in 1994. The two-way ANOVA procedures showed that significant differences in germinability of naturally-produced seeds occurred between years for each site, while no significant differences were detected between sites

within each of the years (Appendix D). Statistically significant interactive effects were also detected between BWM and DSH during the period 1991 through 1994. For the four year, two site comparison, "between years" differences in mean germinability were all significant (Tukey MCT;  $\alpha < 0.05$ ), with the exception of between 1991 and 1993 (Appendix D).

## 5.5 DISCUSSION

Stem size has been used to estimate growth in other cacti (e.g., Steenbergh and Lowe, 1983), but such studies often measure stem height rather than diameter. Field observations of the Tobusch fishhook cactus by others (B.L. Westlund, pers. comm., 1990) as well as those made early in this study indicated that plant height was much more variable than plant diameter in response to (e.g.) changes in moisture availability. Plant diameter was therefore chosen as the measure of plant size to be used in this investigation, and may prove useful for similar studies of other globose or hemispherical types of cacti as well.

Because of the ability of succulent stem tissue to shrink and swell with changes in moisture availability, plant diameter is not an entirely accurate measure of plant growth rate for the Tobusch fishhook cactus. Plant diameter showed annual

changes of only several millimeters, and occasionally showed a substantial decrease between years. The average three-year change in plant diameter for individual plants which were monitored during 1991 and 1994 was also only several millimeters and, again, a decrease in size was noted at one site (BWM) even over this three-year period.

While desiccation due to lower moisture availability between census years probably explains at least a portion of the diameter size decrease noted for some plants, plant senescence may have also contributed to this. Data records for plants which eventually died due to (e.g.) grub infestation often show a decrease in diameter during at least the most recent census conducted prior to plant death, and in this way the measurement of plant diameter is of some predictive utility.

Plant size is a good predictor of the onset of reproduction in many types of plants, with the general exception of annuals (Lacey, 1986). Studies of cacti have shown plant size (Parker, 1987) and plant volume (Johnson, 1992) to be adequate measures of the onset of reproduction. During the course of this investigation, plant diameter proved to be a somewhat accurate indicator of the onset of sexual reproduction in the Tobusch fishhook cactus, as very little reproductive output was noted for plants below ca. 21 mm. Diameter may also have useful predictive value

for plant reproductive effort in general. Further investigation into the relationship of plant diameter as a possible indicator of the degree of reproductive output (i.e., flower, fruit, and seed production) could prove this measurement useful as a marker of life stage boundaries for demographic analysis.

Although not a highly accurate measurement for exact quantification of plant growth, repeated censusing of the stem diameter of individuals over four consecutive years during the same period each year does provide some insight into plant growth rate. There has been speculation that Tobusch fishhook cacti are relatively fast-growing and short-lived, attaining reproductive size by about the third year following seed germination, and not living past thirteen years (TPWD, 1984). Based on yearly diameter change measurement data collected during this study, however, it appears that this previous report may have greatly overestimated the rate of growth of this cactus. Using the highest three-year average diameter change for plants under 21 mm observed during this study (i.e., +7.3 mm for plants 11-20 mm diameter at DSH from 1991-1994; ca. +2.4 mm per year), plants would still require nearly nine years to attain a diameter at which the onset of reproduction typically occurs. Similarly, using the highest overall three-year average for plants of all sizes (i.e., +3.5 mm at DSH from 1991-1994; ca. +1.2 mm per year), twenty-five years would be required for a plant to attain an even modest size of 30 mm diameter. The stem diameter of

many plants at all three sites was measured at 40 mm to over 60 mm and, based on the above average diameter increase, the largest individuals could be over fifty years old. Such calculations of diameter increase do not take into account the potential occurrence of occasional years when "ideal" environmental conditions for growth exist, however, and it may be that increases in plant size occur which are much greater during such periods than those recorded during the four years encompassed by this study.

Annual mortality was very high during all years for BWM and DSH, while mortality was significantly lower at KPC during the one-year period in which this site was monitored. Grub infestation was by far the most common verifiable factor associated with mortality at all three sites and, because many of the plant deaths for which the cause was undeterminable were probably also associated with grub infestation, it was likely the most common factor overall. Certain types of moth larvae (*Yosemitia* sp.) have also been implicated in *A. tobuschii* mortality (A. Zimmerman, pers. comm., 1992), such has been reported for other small, rare cacti (Donnell, 1986), but no evidence of moth-related mortality was witnessed at any of the three study sites during the course of this investigation.

One species of weevil, *Gerstaeckaria nobilis* (Curculionidae), appears to have been responsible for approximately 85% of the grub-related mortality at BWM and DSH, but this species may be less common at KPC. Previous reports indicate that the western-most collection record for this species is from Uvalde County, so *G. nobilis* appears may be near the edge of its distributional range around the vicinity of the study sites monitored during this study (Mann, 1969). While this species is a cactus-specialist, it has been described in the past as occurring only on various species of cholla and prickly-pear cactus (*Opuntia* spp.) (O'Brien, 1970). *Gerstaeckaria nobilis* weevils were seen and collected during different time periods throughout each year, and Mann (1969) states that this species probably produces two to three generations annually.

Another species of cactus-specialist beetle, *Moneilema armata*, appears to have been responsible for the remaining portion of overall grub-related mortality. This species, or grubs which are likely to be this species, were collected at BWM, KPC, and from an unmonitored population in Val Verde County. Although specimens were not collected at DSH during 1991 through 1994, this site is located between BWM and KPC, so it is certainly possible that *M. armata* could occur at DSH as well. This species has been recorded from Fort Stockton southward through Brownsville, and is generally found within 100 miles of the Rio Grande (Mann,

1969). If the BWM specimens are in fact *M. armata*, they could represent the northeastern extent of the known range of this species. As with *G. nobilis*, previous reports indicate that *M. armata* has been collected only on *Opuntia* spp., and that this species probably undergoes more than one generational cycle per year (Mann, 1969). The congener *M. gigas* LeConte is reportedly associated with mortality of the rare acuna cactus (*Echinomastus erectocentrus* (Coulter) B. & R. var. *acunensis* (Marshall) Bravo) in southern Arizona (Johnson, 1992).

Mortality that was obviously attributable to mammalian activity was only about 5% per year, although the unattributable complete disappearance of smaller plants could have been due at least in part to mammalian herbivory. Evidence of mammalian herbivory of larger plants (i.e., > 10 mm diameter) included the occasional complete removal of the above-ground stem of plants, often in association with the occurrence of naked spine clusters scattered within several decimeters of the plant. Herbivory was not always immediately fatal to the cactus, however, as many plants were observed to produce one or more branches from the below-ground portion of the stem following such damage. Branches produced in this manner probably do not effect substantial asexual reproduction similar to "pup" branches formed by other cacti (e.g., Anderson, 1969; Parker and Hamrick, 1992). While such herbivory was never observed in progress, mammals which are known to occur

within the study sites which could be responsible for this include jackrabbits and porcupines. In addition to herbivory, a small portion of mortality associated with mammals occurred following obvious foraging-related disturbance in the direct vicinity of some plants, such as when rocks were flipped over onto several plants. Armadillos were fairly common at all sites, and may have been responsible for many of these occurrences.

Reproduction varied substantially during the course of this investigation and, with few exceptions, statistical analysis has shown the majority of significant variation occurred between years rather than between sites for the same year. In general, the three study populations showed a year to year decrease in flower, fruit, and seed production, ultimately resulting in an ca. 50% decrease in each of these features at BWM and DSH from 1991 to 1994. Reasons for this steady, substantial decrease in reproduction are at present unclear. Occasional year-to-year variation in percent fruit set was noted but, in general, usually remained near 70% for all sites, and never dropped below 50%. In this respect, *Ancistrocactus tobuschii* is an above-average plant, as fruit set is usually not much more than ca. 25% in normally outcrossing plant species (Sutherland, 1986).

If the trends observed during this investigation continue, the high mortality, decreasing reproductive effort and success, and apparently low seedling recruitment could lead to the rapid extinction of the study populations, especially at the BWM and DSH sites. While more information concerning the autecology of this cactus should be acquired prior to any attempts at development of a long-range management strategy, it may be necessary to employ stop-gap measures in the mean time, and control of the grub-related mortality seems like an obvious starting point.

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## **APPENDIX A: FLOWER PRODUCTION**

Table A1. Average flower production for BWM. Plant diameter is in millimeters. Average change in the number of flowers/plant is for plants which were censused during both years shown in the column heading, and is categorized by plant diameter at the earlier of the two years. The  $\pm$  standard error of the mean is provided for each annual overall average. The number in parentheses is the sample size (i.e., number of censused plants). Note that the last column covers a three-year increment.

Plant Diameter	Mean # Flowers/Plant				Mean Change # Fl/Pl			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	0.0 (1)	0.0 (2)	0.0 (40)	0.0 (18)	—	0.0 (1)	0.0 (20)	—
11-20	0.3 (8)	0.1 (15)	0.1 (19)	0.1 (14)	+0.3 (7)	-0.1 (14)	+0.2 (14)	+0.2 (6)
21-30	1.6 (15)	1.0 (26)	0.9 (23)	0.8 (22)	-0.3 (13)	-0.6 (18)	-0.2 (19)	-0.2 (5)
31-40	2.8 (21)	2.4 (25)	1.8 (20)	1.6 (18)	-0.7 (14)	-1.3 (20)	-0.4 (17)	-1.2 (10)
41-50	3.7 (10)	2.9 (9)	2.9 (8)	2.4 (5)	-0.3 (7)	+0.1 (7)	-1.3 (7)	-0.3 (4)
51-60	6.0 (11)	5.1 (9)	4.5 (2)	4.0 (1)	-0.1 (7)	-2.1 (7)	-2.0 (1)	-2.6 (5)
61-70	3.5 (2)	9.0 (2)	8.0 (2)	7.0 (2)	+4.0 (2)	-1.0 (2)	-1.0 (2)	+3.0 (1)
Overall Average	2.9 ( $\pm 0.3$ ) (68)	2.1 ( $\pm 0.2$ ) (88)	0.9 ( $\pm 0.1$ ) (114)	1.0 ( $\pm 0.2$ ) (80)	-0.1 (50)	-0.8 (69)	-0.3 (80)	-0.7 (31)

Table A2. Average flower production for DSH. Plant diameter is in millimeters. Average change in the number of flowers/plant is for plants which were censused during both years shown in the column heading, and is categorized by plant diameter at the earlier of the two years. The  $\pm$  standard error of the mean is provided for each annual overall average. The number in parentheses is the sample size (i.e., number of censused plants). Note that the last column covers a three-year increment.

Plant Diameter	Mean # Flowers/Plant				Mean Change # Fl/Pl			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	0.0 (2)	0.0 (36)	0.0 (58)	0.0 (26)	0.0 (2)	0.0 (24)	0.0 (27)	0.0 (1)
11-20	0.4 (32)	0.1 (57)	0.1 (71)	0.1 (49)	0.0 (23)	0.0 (42)	+0.1 (51)	0.0 (11)
21-30	1.9 (33)	1.0 (66)	0.8 (68)	0.6 (46)	-0.9 (20)	0.0 (54)	0.0 (49)	-1.4 (10)
31-40	2.9 (24)	1.9 (35)	2.0 (41)	1.4 (32)	-0.8 (13)	-0.3 (28)	-0.3 (22)	-1.0 (5)
41-50	4.2 (5)	3.0 (29)	2.5 (21)	2.4 (16)	-1.5 (2)	-0.9 (22)	-0.8 (12)	-3.0 (1)
51-60	6.0 (5)	5.4 (5)	4.3 (4)	4.5 (2)	-3.0 (2)	-2.2 (5)	-1.5 (4)	-2.0 (1)
61-70	—	—	—	—	—	—	—	—
Overall Average	2.0 ( $\pm 0.2$ ) (101)	1.1 ( $\pm 0.1$ ) (228)	0.8 ( $\pm 0.1$ ) (263)	0.7 ( $\pm 0.1$ ) (171)	-0.6 (62)	-0.2 (175)	-0.1 (165)	-0.8 (29)

Table A3. Average flower production for KPC. Plant diameter is in millimeters. Average change in the number of flowers/plant is for plants which were censused during both years shown in the column heading, and is categorized by plant diameter at the earlier of the two years. The  $\pm$  standard error of the mean is provided for each annual overall average. The number in parentheses is the sample size (i.e., number of censused plants). Note that plants in this population were only censused during 1993 and 1994.

Plant Diameter	Mean # Flowers/Plant				Mean Change in the Number of FI/PI			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	---	---	0.0 (40)	0.0 (29)	---	---	0.0 (33)	---
11-20	---	---	0.0 (26)	0.1 (22)	---	---	+0.1 (21)	---
21-30	---	---	0.7 (24)	0.8 (20)	---	---	+0.3 (21)	---
31-40	---	---	1.4 (9)	1.5 (13)	---	---	+0.1 (7)	---
41-50	---	---	2.1 (10)	2.5 (8)	---	---	0.0 (10)	---
51-60	---	---	4.3 (6)	3.6 (5)	---	---	0.0 (6)	---
61-70	---	---	---	8.0 (1)	---	---	---	---
Overall Average	---	---	0.7 ( $\pm 0.1$ ) (115)	0.9 ( $\pm 0.1$ ) (98)	---	---	+0.1 (98)	---

**APPENDIX B: FRUIT PRODUCTION**

Table B1. Fruit production for BWM. Plant diameter is in millimeters. "Mean Fruits/Flowering Plant" represents the mean number of fruits produced by only those plants which produced flowers. "Mean Change in the Number of Fruits/Plant" represents the mean change in number of fruits produced by plants which were censused and flowered during both years shown in the column heading, categorized by the plant diameter at the earlier of the two years. Data from plants which were utilized for pollination experiments are excluded. Note that the last column covers a three-year increment.

Plant Diameter	Mean Fruits/Flowering Plant				Mean Change in the Number of Fruits/Plant			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	—	—	—	—	—	—	—	—
11-20	0.0 (2)	1.0 (2)	1.0 (1)	0.5 (2)	+0.5 (2)	—	—	+1.0 (1)
21-30	1.1 (14)	0.6 (14)	0.5 (18)	0.8 (14)	-0.8 (4)	0.0 (12)	0.0 (8)	-0.8 (4)
31-40	2.2 (18)	1.8 (14)	1.0 (17)	1.5 (13)	-0.3 (3)	-1.4 (8)	+0.4 (14)	-1.1 (8)
41-50	3.3 (9)	2.6 (5)	2.6 (7)	1.4 (5)	-1.3 (3)	-2.3 (4)	-1.5 (6)	-1.3 (3)
51-60	5.5 (6)	2.9 (7)	3.5 (2)	2.0 (1)	-6.0 (1)	-0.3 (4)	-2.0 (1)	-1.5 (2)
61-70	4.0 (1)	0.0 (1)	3.5 (2)	4.0 (2)	+3.0 (1)	+1.0 (1)	+0.5 (2)	—
Overall Average	2.5 (±0.3) (50)	1.6 (±0.3) (43)	1.3 (±0.2) (47)	1.3 (±0.2) (37)	-0.7 (14)	-0.7 (29)	-0.2 (31)	-1.0 (18)

Table B2. Fruit production for DSH. Plant diameter is in millimeters. "Mean Fruits/Flowering Plant" represents the mean number of fruits produced by only those plants which produced flowers. "Mean Change in the Number of Fruits/Plant" represents the mean change in number of fruits produced by plants which were censused and flowered during both years shown in the column heading, categorized by the plant diameter at the earlier of the two years. Data from plants which were utilized for pollination experiments are excluded. Note that the last column covers a three-year increment.

Plant Diameter	Mean Fruits/Flowering Plant				Mean Change in the Number of Fruits/Plant			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	—	—	—	—	—	—	—	—
11-20	0.2 (10)	0.5 (2)	0.8 (8)	1.5 (2)	+0.6 (11)	0.0 (2)	+0.5 (2)	+1.1 (7)
21-30	1.5 (32)	1.0 (18)	1.0 (35)	1.0 (16)	+0.2 (13)	-0.5 (10)	+0.7 (17)	+0.6 (8)
31-40	2.4 (22)	2.2 (12)	1.5 (38)	1.3 (14)	+0.3 (15)	-1.0 (7)	+0.3 (6)	-1.0 (6)
41-50	4.2 (5)	2.6 (7)	2.1 (21)	2.4 (10)	-0.3 (3)	-1.4 (5)	0.0 (7)	-4.0 (1)
51-60	6.0 (5)	11.0 (1)	5.7 (3)	3.0 (2)	-5.0 (1)	-3.0 (1)	-4.5 (2)	-3.0 (1)
61-70	—	—	—	—	—	—	—	—
Overall Average	2.1 (±0.2) (74)	1.9 (±0.2) (40)	1.5 (±0.1) (105)	1.5 (±0.2) (44)	+0.1 (43)	-0.9 (25)	+0.2 (34)	0.0 (23)

Table B3. Fruit production for KPC. Plant diameter is in millimeters. "Mean Fruits/Flowering Plant" represents the mean number of fruits produced by only those plants which produced flowers. "Mean Change in the Number of Fruits/Plant" represents the mean change in number of fruits produced by plants which were censused and flowered during both years shown in the column heading, categorized by the plant diameter at the earlier of the two years. Data from plants which were utilized for pollination experiments are excluded. Note that plants in this population were only censused during 1993 and 1994.

Plant Diameter	Mean Fruits/Flowering Plant				Mean Change in the Number of Fruits/Plant			
	1991	1992	1993	1994	91-92	92-93	93-94	91-94
01-10	---	---	---	---	---	---	---	---
11-20	---	---	---	0.0 (1)	---	---	---	---
21-30	---	---	1.2 (13)	0.6 (14)	---	---	-0.8 (9)	---
31-40	---	---	1.7 (7)	1.2 (10)	---	---	+0.2 (5)	---
41-50	---	---	2.4 (8)	2.3 (8)	---	---	-0.6 (8)	---
51-60	---	---	4.0 (6)	2.8 (5)	---	---	-0.3 (6)	---
61-70	---	---	---	8.0 (1)	---	---	---	---
Overall Average	---	---	2.1 ( $\pm 0.3$ ) (34)	1.5 ( $\pm 0.3$ ) (39)	---	---	-0.5 (28)	---

**APPENDIX C: SEED PRODUCTION AND GERMINABILITY**

Table C). Average seed production and germinability data for BWM. The  $\pm$  standard error of the mean is provided for annual overall averages. Plant diameter is in millimeters.

Plant Diameter	Seeds/Fruit				Germination %			
	1991	1992	1993	1994	1991	1992	1993	1994
01-10	—	—	—	—	—	—	—	—
11-20	—	20.5 (2)	22.0 (1)	39.0 (1)	—	10	55	0
21-30	31.0 (7)	26.2 (6)	8.5 (6)	37.5 (2)	75	16	35	0
31-40	54.4 (11)	26.0 (2)	28.9 (8)	17.7 (3)	64	13	61	0
41-50	68.0 (7)	51.8 (4)	46.8 (5)	20.5 (2)	61	49	38	0
51-60	65.5 (6)	75.7 (3)	73.5 (2)	5.0 (1)	58	15	63	0
61-70	50.0 (1)	—	54.0 (2)	113.0 (1)	100	—	23	10
Overall Average	54.2 ( $\pm 4.3$ ) (32)	40.2 ( $\pm 6.2$ ) (17)	33.0 ( $\pm 6.1$ ) (24)	32.6 ( $\pm 9.8$ ) (10)	65.6 ( $\pm 5.2$ )	22.2 ( $\pm 6.3$ )	46.5 ( $\pm 5.8$ )	1.0 ( $\pm 1.0$ )

Table C2. Average seed production and germinability data for DSH. The  $\pm$  standard error of the mean is provided for annual overall averages. Plant diameter is in millimeters.

Plant Diameter	Seeds/Fruit				Germination %			
	1991	1992	1993	1994	1991	1992	1993	1994
01-10	—	—	—	—	—	—	—	—
11-20	—	26.0 (1)	13.0 (1)	19.0 (1)	—	10	23	0
21-30	29.7 (3)	23.2 (6)	22.4 (7)	27.3 (4)	23	26	47	6
31-40	46.8 (10)	40.8 (6)	48.7 (9)	24.0 (2)	20	17	63	2
41-50	74.0 (2)	38.3 (6)	40.4 (10)	21.5 (2)	65	34	49	3
51-60	52.2 (5)	80.0 (1)	32.8 (2)	68.0 (1)	57	20	65	45
61-70	—	—	—	—	—	—	—	—
Overall Average	48.3 ( $\pm 4.8$ ) (20)	36.0 ( $\pm 4.4$ ) (20)	37.2 ( $\pm 3.8$ ) (29)	28.7 ( $\pm 4.5$ ) (10)	34 ( $\pm 5.4$ )	24.8 ( $\pm 4.8$ )	52.7 ( $\pm 5.3$ )	10.4 ( $\pm 4.1$ )

Table C3. Average seed production and germinability data for KPC. The  $\pm$  standard error of the mean is provided for annual overall averages. Plant diameter is in millimeters. Note that plants in this population were only censused during 1993 and 1994.

Plant Diameter	Seeds/Fruit				Germination %			
	1991	1992	1993	1994	1991	1992	1993	1994
01-10	---	---	---	---	---	---	---	---
11-20	---	---	---	---	---	---	---	---
21-30	---	---	28.7(3)	---	---	---	80	---
31-40	---	---	62.0 (1)	11.0 (2)	---	---	50	0
41-50	---	---	47.3 (3)	27.8 (4)	---	---	75	0
51-60	---	---	62.0 (2)	35.0 (1)	---	---	45	0
61-70	---	---	---	77.0 (1)	---	---	---	10
Overall Average	---	---	46.0 ( $\pm 7.0$ ) (9)	30.6 ( $\pm 8.0$ ) (8)	---	---	67.1 ( $\pm 6.7$ )	2.5 ( $\pm 1.3$ )

**APPENDIX D: ANALYSIS OF VARIANCE TABLES FOR  
SEED PRODUCTION AND SEED GERMINABILITY**

Table D1. Two-way analysis of variance on the effect of site and year on the number of seeds per fruit for BWM and DSH during each year from 1991 through 1994. Significant differences are discussed in the text.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Site	193.005	1	193.005	0.329	0.567
Year	8,463.978	3	2,821.326	4.802	0.003
Site * Year	876.650	3	292.217	0.497	0.685
Error	86,363.970	147	587.510		

Table D2. Two-way analysis of variance on the effect of site and year on the number of seeds per fruit for all three study sites during 1993 and 1994.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Site	339.419	2	169.709	0.274	0.761
Year	1,185.911	1	1,185.911	1.914	0.170
Site * Year	489.050	2	244.525	0.395	0.675
Error	49,564.300	807	619.544		

Table D3. Two-way analysis of variance on the effect of site and year on seed germination for BWM and DSH during each year from 1991 through 1994. Data were first square-root transformed to normalize residuals. Significant differences are discussed in the text.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Site	2.025	1	2.025	0.262	0.609
Year	485.294	3	161.765	20.941	0.001
Site * Year	111.260	3	37.087	4.801	0.003
Error	1,120.068	145	7.725		

Table D4. Two-way analysis of variance on the effect of site and year on seed germination for all three study populations during 1993 and 1994. Data were first square-root transformed to normalize residuals. Significant differences are discussed in the text.

ANALYSIS OF VARIANCE					
Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
Site	23.777	2	11.889	1.879	0.160
Year	613.033	1	613.033	96.888	0.001
Site * Year	21.463	2	10.732	1.696	0.190
Error	493.527	78	6.327		

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