DISTRIBUTION, GROWTH, AND REPRODUCTION OF PIMA PINEAPPLE CACTUS (Coryphantha scheeri Kuntz var. robustispina Schott)

by

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A Thesis Submitted to the Faculty of the
SCHOOL OF RENEWABLE NATURAL RESOURCES
In Partial Fulfillment of the Requirements For the Degree of
MASTER OF SCIENCE WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE
In the Graduate College
THE UNIVERSITY OF ARIZONA

1996
DEDICATION

This thesis research is dedicated to my grandmother, Mildred L. Howard, a humble woman and teacher of endless strength and determination. She taught me to walk forward and learn.
ACKNOWLEDGMENTS

Everyday, over a time period of 790 days, an absolutely certain event took place which was directly related to this ontological research. A student researcher wondered when, where, how and mostly why. Thanks to the patience, knowledge and firm commitment given to that student, from her advisor, Bill Halvorson and committee members, Steve McLaughlin and Guy McPherson, she found her own patience, knowledge and commitment. This adventure called research has not given us all the answers, but perhaps some reliable conclusions.

My family, David, Linda and Dayton Roller, taught me to work hard, gave me the tools and strength I needed to do this project. Their support helped me build the bridge.

I thank the US Fish and Wildlife Service, especially Rees Madsen and staff of the Buenos Aires National Wildlife Refuge with Sue Rutman and staff of the AZ State Ecological Services Office for planting the Pina pineapple cactus. All of the people, (Joan Ford, Mary Greene, Eugene Maughan, Ceci Schwalbe and Coop Students) from the National Biological Service were essential to the development and culmination of this research. Other people and organizations: (Abed Anouti, Damian Ravetta) Arid Lands Bioresource Research Facility, (Dan Robins) Natural Resource Conservation Service, (Jim Maerder) Arizona Department of Agriculture, (Bill McClosey) UA Plant Sciences Department, (Margaret Livingstone) SRNR, (Peter Warren) The Nature Conservancy, and (Mina Fál) Coronado National Forest.

I am very grateful to have gained so many friends and experiences through this research. I will miss you all: Bruce Andrea, Rena Ann & Bob Abol, Keith Snyder, Jake Wertzin, Mark Kahl, Jenn Duran, Rob Dudley, Leslie Ruiz, Don Swann, Clarise Hedland, Laurie Abbott, Ronny & Jardynn Mac, John Fleming, Cid Schlesinger and Tom Ashbeck.

Somehow we all made it, even after we searched for Pina pineapple cactus, counted oak seedlings and tree rings, or measured MIFI bushes till we cried, sometimes in the dark, usually after-hours, somewhere down a long dusty road, on our way to the Sea of Cortez.
ABSTRACT

Pima pineapple cactus (Coryphantha scheri var. robustispina) (PPC) is listed as endangered by the US Fish and Wildlife Service. This taxon occurs south of Tucson, Arizona and Sonora, Mexico. Knowledge of this plant's distribution, growth, and reproduction is important for management. Research has documented reduced plant vigor and lack of reproduction within Lehmann lovegrass stands. PPC density and seedling presence were described at five sites in two different vegetation types. Field observations of 72 plants at five sites were monitored from fall 1993 through summer of 1995 and shadehouse studies were conducted. This research resulted in five conclusions: 1) fire-induced mortality of PPC may be related to Lehmann lovegrass, 2) PPC grows vegetatively in the spring, 3) flower buds are initiated in May and open after a few summer rains, 4) seed germination follows several summer rains, and 5) cross-pollination produces significantly more PPC seeds than self-pollination.

INTRODUCTION

Pima pineapple cactus (Coryphantha scheri Kuntze var. robustispina Schott) (hereafter, PPC) is a low growing hemispherical cactus with finger-like projections called tubercles extending outward from the stem (Fig. 1). At the tip of each tubercle is a rosette of 10-15 straw-colored spines with 1 central, hooked spine. Older, more mature spines fade to black or gray. Tubercles are 2-3 cm long and grooved along upper surfaces on adult plants (Benson 1969). Plants can be either single- or multiple-stemmed and they produce brilliant yellow flowers (Fig. 2).

Populations are known to occur in southern Arizona, south of Tucson in the Altar and Santa Cruz valleys and adjacent northern Sonora, Mexico, at elevations ranging from 720 to 1440 m (Phillips et al. 1981, Ecosphere Environmental Services, Inc. 1992) (Fig. 3). PPC are found in open patches within the semi-desert grasslands and Sonoran desert scrub plant communities (Brown 1982). They occupy the flat (<10%) alluvial bajadas that are primarily comprised of granitic parent material. Soil descriptions are quite variable, however most reports characterize them as sandy, silty loams with gravel and little rock or clay components (Benson 1969, Phillips et al. 1981, Mills 1991, Ecosphere Environmental Services, Inc. 1992, Tolley 1992, U.S. Department of Interior 1993). PPC appear to be most abundant within the ecotonal boundary between the grassland and desert scrub regions (Roller and Halverson in press).
Fig. 1. Pima pineapple cactus *Coryphantha scheeri* var. *robustispina*, X 1.2, except as indicated. 1. Plant in flower, X 1. 2, 3, 4, 5 Tubercles with areoles; rosette of spines and central hooked spine, Flower in longitudinal section, Fruit. Fruit in longitudinal section X 1.1 7, Seed, X 13.2 (Benson 1982)

Fig. 2. Pima pineapple cactus (*Coryphantha scheeri* var. *robustispina*) as it blooms a group of bright yellow flowers. This photo was taken at Buenos Aires National Wildlife Refuge in southern Arizona (P. Roller)
In October 1993, PPC was listed as a federally endangered plant (U.S. Department of Interior 1993). The reasons listed in the federal register for its endangered status were urbanization, fire, grazing and illegal collection. However, knowledge of this taxon was limited to plant taxonomy and general distribution. Basic life history and ecological information on PPC was minimal and consisted of anecdotal observations. The objective of this study was to gain perspective of PPC basic life history and current distribution. I studied three general topics: basic distribution, growth, and reproduction, and used information from these studies to hypothesize ecological relationships and recommend future research and management activities. For the conservation of PPC it is important to evaluate ecological and applied questions with substantial reliability. Descriptive life history patterns and then developing hypotheses applicable to distribution should be used to initiate future research and management.

Pima pineapple cactus is found on lands where the management of particular populations may be affected by fire and human activities. For example, extensive residential development in Green Valley, Arizona is fragmenting PPC habitat. On these private lands, 473 plants have been relocated from their native environments into ex-situ conservation facilities and over 174 hectares of habitat has been lost in the past two years. Section 7 of the endangered species act (ESA) does not authorize federal action to regulate activity effecting plants or habitat located on private land unless the land owner receives federal funding, permitting, or consultation for land management practices (US Department of Interior 1994). Arizona Native Plant Law, Arizona Revised Statutes...
Chapter 7 does not prohibit development on private lands if the landowner attempts to salvage and replant or re-locate highly safeguarded plant species for educational or scientific purposes.

To sustain human demands in the Sonoran desert, the Bureau of Reclamation is planning to extend the Central Arizona Project by creating a 6070.5 hectare-foot reservoir, called Tucson Aqueduct Reservoir Site (TARSi). It will serve as a storage facility and as a source for recharging depleted ground water or a source to directly supply city water users. Land adjacent to the reservoir site is zoned for residential and recreational use (USFWS 1994).

The TARSi project is, however, a federal action and section 7 consultation of the ESA will recommend the salvage and relocation of individual plants to a suitable habitat purchased through mitigation by the Bureau of Reclamation (BOR) for refugium purposes (USFWS 1994). Here again, habitat will be divided and reduced, and some individual plants may die during salvage and re-location activities. Considering dramatic changes associated with urbanization on private lands within portions of PPC habitat, managers of federally regulated lands have an even greater responsibility towards PPC conservation.

Fire is used as a tool by many state and federal land management agencies to reduce fuel loading. Other objectives are to restore native grasses and forbs and reduce woody shrubs and exotic grasses. Information regarding fire associations with historical vegetation change and its effectiveness in meeting these state and federal objectives has been documented primarily in grasslands by: Cable (1971, 1973), Bahre (1985, 1991), Sumrall et al. (1991), Anable et al. (1992), Bogh and Bock (1992), McClarren and Van Devender (1995) and McPherson (1995). Agencies responsible for fire management are also responsible for the management of this rare and endangered plant.

Given the above, PPC in-situ conservation may rely upon managing fire and urbanization effects within an ecotonal boundary between the Sonoran desert scrub and semi-desert grasslands. Research conducted by Roller and Halvorson (in press) demonstrated patterns of vegetation, fire history and PPC health at five sites located throughout the plant’s range. They described two community types: 1) a patchy community codominated by Lehmann lovegrass, snakeweed (Gutierrezia microcephala) and tall herbs—(Lehmann lovegrass Grassland); 2) a mid-sized (Ht < 2.5 m) mesquite shrubland community with Prosopis velutina, bush muhly grass (Muhlenbergia porteri), desert zinnia (Zinnia acerosa) with scattered creosote (Larrea tridentata) and succulents—(Mid-sized Mesquite Shrubland). Generally, PPC vigor was found to decrease in the first community type characterized by higher fire frequencies, and with continuous stands of Lehmann lovegrass. For purposes of creating reliable hypotheses to guide future research, my first objective was to document PPC’s distribution within these two plant communities.

The effects of fire in semi-desert grasslands characterized as continuous stands of Lehmann lovegrass (Eragrostis lehmanniana) has been documented. The introduction and spread of non-native Lehmann lovegrass has the potential to alter historical fire regimes (Ruhl et al. 1988, Cox et al. 1990, Sumrall et al. 1991, Anable et al. 1992,
Lehman lovegrass was introduced in 1922 to revegetate areas with resistant species to drought and grazing, and which would control erosion (Cable 1971). This grass has increased its abundance to cover nearly 200,000 ha (Cox and Ruylo 1986). Work has also been done on the effects of fire in Sonoran desert scrub (Bunting et al. 1980, McLaughlin and Bowers 1982, Rogers 1985, Thomas and Goodson 1992). McLaughlin and Bowers (1982) found Sonoran desert communities to burn when there was a build-up of substantial amounts of surface fuels. Adequate fuels were produced by a couple of seasons of above-average precipitation followed by a year of below-average precipitation.

A general study on the effects of fire on cacti illuminated two mechanisms by which various Sonoran Desert cactus species survive: occupying refugial habitats or resprouting (Thomas and Goodson 1992). McLaughlin and Bowers (1982) also found that fire-related mortality of saguaros (Carnegiea gigantea) decreased, and seed viability and production increased, with increasing plant height and biomass. If apical meristematic tissue is destroyed in saguaros or barrel cactus (Ferocactus wislizenii) they have no mechanism to recover from fire (Steenberg and Lowe 1977, Bunting et al. 1980, Rogers 1981, Johnson et al. 1993). Death of cacti may not occur for 2-4 years after a burn. During such periods cacti apparently live on stored reserves (Bunting et al. 1980).

Lower-growing species were found to survive by occupying refugial areas, apical resprouting, or producing basal offsets when burned in dense grasslands or under volatile shrubs (Thomas and Goodson 1992). Apical resprouting decreases on plants in areas with greater woody biomass near the stem apex after a burn. Some cactus species survive fire by producing basal offsets when the apical meristematic tissue at the stem apex is destroyed (Thomas and Goodson 1992). As a grassland/desert scrub associated cactus, PPC may have evolved mechanisms to tolerate fire by resprouting or avoiding fires by occupying refugial areas where biomass or fuel loading are less.

Consequently, specific information regarding size, growth rates, and phenology of PPC are important. The second objective was to document changes in plant shape and growth rates on two temporal scales, seasonal and annual. Two types of plant growth related to basic life history stages were documented, seedling and adult. Understanding basic growth changes over time may help define how PPC functions within its microhabitat.

The third objective was to describe patterns of reproductive biology. Reproductive growth rates and phenological patterns were studied across five different sites and many plant sizes, changes in reproductive growth rates and phenological patterns. I described the relationship between plant size and productivity. Evaluating demographical information of plant size with reproductive output within a population can be inferred from this type of correlation and mechanistic explanations may help define the relationships. Rates of recruitment and population stability may be further understood using this information.

Phenological patterns of six life stages which are components of reproduction were described and biological processes influencing reproductive success were determined. The
Literature involving other Sonoran Desert cacti has documented certain life history stages as being coincident with abundant summer precipitation events (Parker 1977, Steenbergh and Lowe 1977, Jordan and Nobel 1981). Saguaro and organ pipe (Lemaireocereus thurberi) bloom in the early, dry period of summer, seed dispersal and germination immediately follow in response to summer rain events. Dispersal is a function of both biotic organisms consuming, scarring, and depositing seeds, and abiotic movement of overland water flow across the soil surface. The Mojave fishhook cactus (Sclerocactus polyacanthus), a cylindrical, low-growing species, blooms, sets fruit, disperses seed, and germinates in the Mojave desert during late winter/early spring rain events (May 1994).

Substantial soil moisture for seed imbibition has been determined to be a critical element for seed germination in these and other cactus species (Parker 1977, Steenbergh and Lowe 1977, Jordan and Nobel 1981, May 1994). Certain levels of light and temperature have also been attributed to saguaro and barrel cactus germination. Alcorn and Kurtz (1969) found saguaro germination increased with a 72-hour imbibition period. Saguaro seed germination responded to multiple exposures of red light or day light (6550 Å) and decreased with far red (7350 Å), night light. Optimal temperature ranged from 20-35°C. Greater saguaro germination occurred when temperatures were decreased at night to mimic natural diurnal fluctuations. Neither species germinates with temperatures below 20°C, nor has germination been observed during winter rainy seasons in the Sonoran Desert.
Individual losses due to seedling mortality can be reduced if seeds germinate only when the environment is most suitable. A protective cap structure which covers the hilum on some species of the Mohave fishhook cactus prevents premature seed germination when rainfall is early or inadequate (May 1994). Jordan and Nobel (1981) estimate that in recent times, barrel cactus seeds have germinated only eight out every 18 years, the years with abundant precipitation.

**GENERAL METHODS**

Field Study sites.

Five sites were established to conduct field studies across the range of PPC distribution (Fig. 3). Two sites were located on Buenos Aires National Wildlife Refuge (BANWR) (Balaosa, Batour), one at Green Valley (GV) which is located on both private land and the Santa Rita Experimental Range (SERR), one in Vail (Vail) and one at King Anvil Ranch (KAR). Sites varied in size from 2 to 648 ha. The two sites at Buenos Aires National Wildlife Refuge (BANWR) are characterized by Brown (1982) as Sonoran semi-desert grasslands, with moderately deep, alluvial soils at elevations of 1143 m and mean annual precipitation of 41.0 cm (U.S. Dept. of Agriculture 1974, Sellers et al. 1985, McLaughlin 1992). KAR receives an average of 28.7 cm of annual precipitation and is characterized as Sonoran desert scrub (Brown 1982) at 994 m in elevation. However, this site was observed to be an ecotone between semi-desert grassland and Sonoran desert scrub. Green Valley and Vail are in Sonoran desert scrub (Brown 1982) at 884 and 975 m elevation and mean annual precipitation of 26.9 cm and 32.0 cm, respectively (Sellers et al. 1985). Vail, GV and KAR soils are characterized as deep, well drained, alluvial sandy loams (U.S. Dept. of Agriculture 1974, 1978). The field studies took place between August 1993 and August 1995.

Not all five of the established study sites (Fig. 3) were used for every field study related to distribution, growth or reproduction. However, all of the individual plants...
the 76 individuals salvaged, many vegetative offsets were potted separately from adult plants. Following transplanting there was a total of 116 plants available for shadehouse investigations.

Experimental work using mature cacti was conducted using these transplanted cacti. Individuals were supplied supplemental water, weekly or biweekly during seasons with inadequate precipitation and annual fertilizer applications (10-25-10). They were grown under a reduced light intensity by using shadecloth.

Sections

This thesis is separated into three sections, each with its own methods, results and discussion. The first section describes PPC distribution across five sites. The second section is on vegetative growth. The third is on reproductive biology.

Shadehouse Site

A total of 76 plants were salvaged from private land undergoing development. These plants were transplanted into a controlled shadehouse and used for descriptive and experimental investigations. The shadehouse was located at the University of Arizona’s Agrilands Bioresource Research Facility (BRF) in Tucson, Arizona. To transplant these plants, roots were trimmed within 3.0 cm of the tap root, hardened off for two weeks and rootone hormone was applied prior to transplanting into pots with a 1:1:1 mixture of sand, peat, and surface. This soil mixture was the standard used in all shadehouse studies.
DISTRIBUTION

Survey Methods

A general survey for locating individual PPC within each study site was conducted prior to field investigations. To survey for PPC a specific area was delineated using 7.5 min. U.S.G.S. topographical maps. Belt transects which were 8 m in width, were oriented in an east to west direction from a baseline (Riechenthaler 1990). The Batour site was surveyed by the BANWR staff a year prior to this particular study in 1992 and four plants incorporated into the GV study site were found on the Santa Rita Experimental Range without using a survey. Previous surveys documented PPC as not occupying drainage bottoms or steep slopes (Phillips et al. 1981, Mills 1991, Ecotope Environmental Services Inc. 1992, Rees Madsen 1993 (BANWR pers. comm.)).

Upon finding an individual cactus a search of the local area was done to find additional plants. Plants were then marked by using t-posts or re-bar 9 m south of each individual. At each site, using the number of individuals found and the site area, an entire site density was calculated. Selected plants which were surveyed at these sites were used for biological data collection.

A random sample of 41 plants from all surveyed individuals at each of five sites (Balaosia, Batour, Vail, GV, KAR) was selected to thoroughly search, at close proximity by people crawling on their hands and knees, a 50 m² quadrat encompassing adult plants for seedlings. One hundred and twenty PPC seedlings were randomly selected for germination and grown in 10-cm³ pots for a 22-month period under shadehouse conditions, to develop a search image for detecting seedlings and young individuals in the field. For purposes of this documentation, individual seedlings were considered to be if they were unable to reproduce and had no cleft development along upper surfaces of tubercles. Within the 41 seedling quadrats I monitored the season of germination.

A more extensive survey was conducted for a salvage project involving the relocation of PPC from a private land development project to the BRF for studies involving controlled shadehouse conditions. This particular salvage project was permitted through the Arizona Department of Agriculture and located in Green Valley, Arizona. It was our objective to completely remove all PPC from the land area. Repeated coverages were run from varied directions to search at different light angles. We repeated the coverages seven times, until no new individuals were found.

Survey Results

Patterns relative to PPC health and reproduction were associated with plant communities at five sites (Fig. 3). These were characterized as being dominated by Lehmann lovegrass or a mixture of species representing an ecotonal boundary, or a mid-sized mesquite shrubland community (Roller and Halvorson in press). I found PPC density to be higher and seedlings present within the mid-sized mesquite shrubland community which occurred at GV, KAR and at two smaller sites, Balaosia on BANWR and Vail. One site on BANWR, Batour, had the lowest density of living adult PPC and no seedlings present.
In general PPC distribution appeared to be patchy, and plants were widely-dispersed and varied in density through its range. As of 1995 a total of 4895 ha was surveyed across five sites and different PPC densities were observed (Table 1). At GV 397 plants were located on 1038 ha of private land; at KAR 334 plants were found on 3459 ha; at Vail 5 plants were found on 5 ha, on BANWR, 25 plants were located on 386 ha at Batour, and nine on 7 ha at Balsa. I found no small or young individuals in the thoroughly-searched, 50-m² quadrats located at the Batour site and the adults were generally ranked as being in poor condition. The vegetation at the Batour site was the only site characterized as being dominated by Lehmann lovegrass (Roller and Halvorson in press). All quadrats located on the four other sites were not dominated by Lehmann lovegrass as the grass was generally absent or rarely present.

Table 1. Pima pineapple cactus densities as of January 1994 at five sites in southern Arizona which were characterized as either 1) mid-sized mesquite shrublands or 2) Lehmann lovegrass grasslands.

<table>
<thead>
<tr>
<th>Site</th>
<th>Community</th>
<th>#Acti</th>
<th>#Acre</th>
<th>#Hectare</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsa</td>
<td>Mid-sized Mesquite Shrubland</td>
<td>9</td>
<td>3.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Vail</td>
<td>Mid-sized Mesquite Shrubland</td>
<td>5</td>
<td>3.00</td>
<td>1.00</td>
</tr>
<tr>
<td>GV</td>
<td>Mid-sized Mesquite Shrubland</td>
<td>397</td>
<td>1.00</td>
<td>0.33</td>
</tr>
<tr>
<td>KAR</td>
<td>Mid-sized Mesquite Shrubland</td>
<td>334</td>
<td>0.25</td>
<td>0.10</td>
</tr>
<tr>
<td>Batour</td>
<td>Lehmann Lovegrass Grassland</td>
<td>53</td>
<td>0.17</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Only 9 seedlings were found within the 41 quadrats and they were found at 4 of the 5 sites not dominated by Lehmann lovegrass. Five were located in a ring within 1 cm of each other at Balsa. Two were found in separate plots at a distance > 100 m at GV, and single seedlings were found at KAR and Vail. The seedlings varied in size from 1.5-3.0 cm in diameter, 1.0-2.5 cm in height and were similar in dimensions to 12-month-old seedlings grown in the shadehouse. Generally seedlings were found to occur at the edge of half stub or mesquite canopies or in relatively open patches. These areas show evidence of both overland water flow and rodent activity, factors which might be considered in hypothesizing dispersal mechanisms.

The repeated-searching methodology used for the salvage project delineated substantially more PPC than found using a single pass over an area. After the third pass we were still finding up to 100% as many plants as we found initially. No individual PPC were found on the seventh coverage.

**Distribution Discussion**

Lower PPC densities occupied a community dominated by Lehmann lovegrass when compared to those counted in mid-sized mesquite shrubland vegetation. No young individuals were found in quadrats where the lovegrass exists, but seedlings were found in quadrats at the four mid-sized mesquite shrubland sites. PPC vigor was measured in previous research at all five sites by estimating percent living tissue of individuals and ranking them into four classes. Individual vigor was found to be lower within Lehmann
lovegrass grasslands than in the mid-sized mesquite shrublands (Roller and Halverson in press).

The cause and effect relationship between compositional differences of the plant community and the distribution and recruitment of PPC could not be discerned from our data. However, three components of PPC population stability: density, individual vigor, and reproduction, appeared to have a negative association with some factor present at one of the five sites. Here again, the single site was typified as a Lehmann lovegrass, grassland with a high fire frequency (Roller and Halverson in press). These patterns suggest a testable hypothesis that Lehmann lovegrass influences PPC distributions, and several other hypotheses which possibly explain processes underlying these vegetation patterns associated with varied PPC distribution.

One specific explanation hypothesized by Roller and Halverson (in press) was that fire intensities achieved with greater herbaceous biomass destroy apical meristematic tissue at the stem apex and limit apical resprouting. Increased Lehmann lovegrass densities have increased fuel loading and possibly fire frequencies (Anable et al. 1992) due to the fact that the grass is enhanced by the more open environment which fire creates in semi-desert grasslands of southern Arizona (Ruyie et al. 1988, Sunrall et al. 1991). Stands dominated by this grass produce up to four times the above ground biomass than native bunch grasses (Cox et al. 1990), and produce continuous spatial distributions of fuel. Fire intensity increases with increasing biomass and continuity of fuels which allow for thorough burns.

Increases in the fire return interval were documented by Thomas and Goodson (1992) to show increases in mortality of several Sonoran cacti species. Therefore, a second explanation suggests that higher fire frequencies within Lehmann lovegrass vegetation increase fire-induced mortality of individual PPC. These hypotheses would account for the decreased density and vigor of cactus on sites dominated by Lehmann lovegrass.

A third possible explanation is that lovegrass limits recruitment, particularly in the germination or establishment stage of PPC life history. Depending upon the season of germination or seedling growth, fire within these Lehmann lovegrass stands may not limit PPC distribution at this life history stage. A cactus seedling could be short enough during dormant, drought seasons when fire is present. Lehmann lovegrass may, instead, limit a resource required for PPC germination or establishment.

From these results and findings from other research, future research which tests the pattern that Lehmann lovegrass limits PPC distribution, and the three other process-oriented hypotheses, is strongly recommended.
GROWTH

Seeding Methods

To document the immediate growth and structural change of PPC seedling development, size measurements were collected and daily growth rates were calculated. Daily growth rates were defined as the changes in height and diameter over a 20-day interval for 200 days from Dec. 23, 1993 through July 9, 1994. Data were collected daily for the first week and twice-weekly for the following 4 weeks. By week six they were moved to the BRF shadehouse and measured every 20 days.

To determine annual seedling growth, PPC seedlings were monitored for a 12-month period, from December of 1993 to 1994. Annual growth was determined from size measurements collected after one year's growth following germination in December of 1993.

Seedlings were grown in a laboratory where light and water were controlled for their first 5 weeks and then transferred to the BRF shadehouse facility. They were grown in 10-cm³ pots in the standard BRF soil mixture and provided supplemental water when seasonal precipitation was limited. A sample of 160 field collected PPC seeds was germinated and seedlings were used to collect size measurements and observe structural changes. The height and diameter measurements collected from seedling cacti included spines. A narrow ruler and a superpolymid holometer caliper were used to measure seedlings.

Adult Methods

Adult growth was quantified seasonally and annually by measuring the size of 14 plants and pooling the recorded data from all known individuals at two field sites (Batour, Balaos). Seasonal data were collected from post-monsoon (August 31, 1993) through pre-monsoon (June 19, 1994). Seasonal size variation was documented and daily growth rates were calculated by measuring the difference in size between seasons divided by the number of days between data collections. The number of days between data collection varied with the weather events of 1993 and 1994.

Two growing seasons (1994, 1995) of annual growth were recorded on 16 plants. The annual growth of 1995 recorded from August 4, 1994 to September 20, 1995 and was used as a conservative representative for extrapolating plant longevity in years. All sites in southern Arizona sustained below-average winter and summer precipitation during this year (NOAA 1995). The average size of larger individuals, those with an entire cactus diameter > 10 cm, was calculated to determine an estimate of PPC life span in years.

Five variables were measured: basal offsets (stem #), apical tubercles, diameter of the large central stem (adult diameter), largest diameter of entire plant (largest diameter), and height. For the purposes of this research, basal offsets are described as the number of stems. Height and diameter measurements were taken from the same aspect of every sampled individual. Growth was evaluated from measurements of plants that survived the entire study period.
Seedling Results

Establishment success at the end of the first year of growth was 47% of the 160 seeds planted. A total of 51% germinated initially and 6 individuals died within the year. By the end of the first year, seedlings were an average 0.8 cm tall, 1.1 cm in diameter and had rosettes of sharp hardened spines at the tips of nodule-like tubercles. At month 5, premonsoon spines were thin and pliable. The cleft found on adult tubercles was not present, nor was the central hooked spine. The average number of spines per tubercle was six. The average number of tubercles per seedling was 8. Premonsoon tubercles ranged between 2 and 4 and post monsoon numbers rose to 8.

Initial seedling growth in height occurs through the first 5 weeks, and by month 5 (May 29, 1993) diameter increased substantially, as the seedling contracted nearer to the soil surface (Fig. 4a). Although height growth rates fluctuated across seasons, diameter steadily increased, even during the premonsoon season when height decreased (Fig. 4b).

The decrease in height at month four may be attributed to increased summer temperatures and decreased water availability during the summer months through June 19 and the slight increase at month seven may be due to some set of factors associated with monsoon climate.

Fig. 4a. PPC seedling size variation across 200 days from winter 1993 through monsoon season 1994 after germination under shadehouse conditions.

Fig. 4b. PPC seedling daily growth rate across 200 days from winter 1993 through monsoon season 1994 after germination under shadehouse conditions.
One year following germination in December, mean height decreased and mean diameter increased by .5 cm. Water treatments were reduced and temperatures decreased during the winter months. When seedlings were subject to colder temperatures in the shadehouse during both winter seasons, I observed a pigment change from green to red. This change in coloration may suggest that seedlings undergo a form of winter dormancy. The only period of seasonal height increase in seedlings was during monsoon rainy seasons. During the premonsoon drought and colder winter seasons seedlings shrink becoming nearly flush with the soil surface and thus allowing less surface area exposure to unsuitable conditions. These phenomena were also observed in the field at the seeding location at Bajaosa site.

Growth change and establishment success documented in this investigation could be used as a proxy for growth under the most optimal conditions.

**Adult Results**

Adult PPC exhibited seasonal size variation from post monsoon (August 31, 1993) to premonsoon season (June 19, 1994) (Fig. 5). Three variables: height, largest diameter, and adult diameter all vary similarly across seasons, however stem height did not follow this pattern. The number of new apical tubercles were not used to illustrate size variation.

PPC produces vegetative clones (basal offsets). During the transplanting project 27 of 34 offsets (stems) had to be physically separated from the adult stem at the base of

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**Fig. 5.** Mean seasonal size variation of 34 plants beginning post monsoon season (August 31, 1993) through monsoon season (July 24, 1994). Size was recorded from two combined field sites on the Buenos Aires National Wildlife Refuge in southern Arizona.
Tubercles along the upper surface. Stem # exhibited minimal growth increases or size variation during the fall and spring seasons (Fig. 5, 6).

Adult PPC are largest during the post monsoon season, as illustrated by three of four variables (Fig. 5). Although size varied most during the post monsoon season, growth increased substantially in the spring following winter precipitation (Fig. 6). Similarly to PPC seedlings after their first four months of germination, adults also contracted and growth rates declined during the fall and winter seasons. Adult exerts grew at a slower rate than did seedlings.

Each year an adult plant greater than 10 cm in height produces an average of 9 new tubercles (SD = 6.5). Apical growth occurred both years in mid-March and the average number of new tubercles found in the field varied with plant size \((r = .44, p < .001)\) from 4 to 25 on the adult stems. The number of new tubercles decreased by 17 from the 1994 to 1995 growing season, which may be a function of below-average precipitation in 1995. The number of new tubercles increased during the spring only. New tubercles were produced at the apex of each stem in mid-March. New tubercles appeared on offsets, however, they were not counted. This growth can be recognized by a rosette of pliable, crimson spines at the tip of each tubercle.

The greatest annual average growth for 1994, of the five variables measured, was PPC adult stem diameter. Adults increased annually (mean ± SD): stem # (0.22 ± 0.09).

Fig. 6. Mean daily growth rate of 34 plants across seasons beginning post monsoon season (August 31, 1993) through monsoon season (July 24, 1994) at two combined field sites on the Buenos Aires National Wildlife Refuge in southern Arizona.
ight (1.04 ± 3.3 cm), largest diameter of the entire PPC (1.54 ± 3.2 cm), and adult 
38  diameter (1.72 ± 4.9 cm).

The average diameter of larger PPC was 19.3 cm (± 1.54). The size variable that 
39  exhibited the least variation in annual growth and may be the most accurate measurement
r  for quantifying PPC growth was the largest diameter of the entire cactus. Using these 
39  measures, I calculated an estimate PPC life of < 30 years. This value was derived using only
39  of PPC sampled from the two field sites located on BANWR and was extrapolated
39  to an unusual drought year.

Growth Discussion

Under optimal conditions the establishment of seedling PPC was less than 50%
39  establishment was 30% lower than seed germination. Seedlings have the fewest number
39  of protective spines which are also shorter, soft and pliable. Pima pineapple cactus appear
39  to be more limited from reaching reproductive maturity during the establishment rather
39  than germination life history stages. Similarly, Steenbergh and Lowe (1983) found that
39  establishment seedlings had higher mortalities than older plants of saguaro. Biotic and
39  biotic factors contributed to seedling declines. Seedling mortality was greatest during the
39  dry fall and early summer seasons following germination. During these seasons
39  , desiccation, and freezing, as well as rodent and insect herbivory, were established as
39  primary factors responsible for these losses. Protective spine formation and root-system
39  development are not complete until the seedlings' first year of growth. Survival of 1-2

year old Coryphantha robbinsorum seedlings was found to be lower than all other life
39  history stages (Schmaizel et al. 1995).

Seedlings had the highest growth rates immediately germination and they
39  elongated under low light environments. Other cacti exhibit similar growth patterns
39  between seedlings and adults as those recorded here (May 1994, Schmaizel et al. 1995). I
39  suspect that following initial germination the increases in seedling height will occur mostly
39  during summer rainy seasons. This means that PPC seedlings would be actively growing
39  in height during the season that the likelihood of fire is reduced due to substantial
39  precipitation.

PPC exhibit seasonal growth rate differences. Adults and seedlings show declines
39  in aboveground biomass and changes in pigment from green to red during winter when
39  temperatures are relatively lower, sometimes below freezing, and in late spring and early
39  summer, when precipitation is low and temperatures are relatively high. Seedlings
39  contract until spines are nearly flush with the soil surface during the winter and
39  premonsoon months. This morphological condition could, moderate environmental
39  extremes associated with arid lands, including the passage of fire, and make them difficult
39  to locate during surveys. One adult plant decreased 3 cm in height during the premonsoon

Other species of Sonoran Desert cacti, particularly low growing cacti that occupy
39  higher elevations, shrink and undergo pigment changes with freezing temperatures. These
39  changes associated with the colder season represent a dormancy condition exhibited by
Cacti, known as cold hardening. Spring and pre-monsoon season changes may exhibit a similar dormancy, only associated with drought and high temperature conditions.

Regardless of conditions, cold or hot, the object of dormancy is to limit respiration across epidermal tissue to the plant. Certain low growing species of cacti retain a higher osmotic potential by reducing respiration during dormancy (Nobel 1982, Moore and Clark 1995).

*Coryphantha robbinsorum* seedling growth was positively correlated with winter precipitation, however both seedlings and adults exhibited winter cold hardening by shrinking. Although, aboveground biomass appears to undergo a cold hardening process while the winter rains are occurring, the belowground root system could be using winter rains and stored reserves. These plants could then use the stored reserves from the root system and base of the plant for apical vegetative growth in the spring (Nobel 1982, Moore and Clark 1995).

For future studies of growth I recommend annual data collection during the post-monsoon season when plants are largest. Our findings show substantial variation in PPC size. Acquiring these annual measurements, consistently, would demonstrate growth rates representing the greatest annual change. Secondly, I recommend taking measurements from the same location and aspect. Cacti grow at such a slow rate that accuracy is very important for illustrating size changes.

I calculated annual growth for a single year with below-average precipitation. This single event does not establish a reliable representation of the wide variety of interannual fluctuations which influence PPC growth in the field. If growth is a function of precipitation, which it probably is, than my estimate of PPC life span of < 30 years is relatively conservative.
REPRODUCTIVE BIOLOGY

Reproductive Production Methods

Reproductive potential of PPC was characterized at four sites, Balaosa, Batour, GV, and KAR (Fig. 3), in summer and fall of 1994 by measuring the number of flowers and fruits of several plants. A total of 39 plants was measured: four at Balaosa, 12 at Batour, 4 at GV and 19 at KAR. The average value of each variable was calculated for each site and used to evaluate reproductive potential accounted for in each separate reproductive stage across and between sites. The two variables were multiplied to quantify the combined reproductive potential and a univariate analysis of variance was used to identify significant differences between sites. Plant density was calculated for each site. A regression analysis was performed to characterize the relationships between flower and fruit productivity and plant density at the five sites. In both analyses, productivity was measured from a population of the total adult plants surveyed at each site, which were used to calculate the density figures.

Fruit and flower productivity relative to PPC size classes was evaluated by describing relationships between the number of flowers per individual in both the BRF shadehouse on 110 plants and in the field at 2 combined sites using 21 plants and four size variables. The number of flowers was then related to size variables: height, number of stems, adult diameter and largest diameter of entire cactus, using Pearson product-moment correlation coefficients. A fifth variable was measured in the field which was the total number of new tubercles produced at the apex of the largest stem. Growth was evaluated from size measurements of plants which survived the entire 2-year study.

The growth of three reproductive structures forming the PPC flower bud and fruit was quantified. For the purposes of this research, two parts of the entire flower will be referenced, the inferior ovary and perianth (flower bud) (Fig. 1). The flower bud and ovary as it develops into a fruit structure after pollination were measured at the BRF shadehouse on 10 plants. Data were collected during the 1994 growing seasons from June 6, 1994, when flower buds were apparent on all individuals, through August 9, 1994 when cross-pollinated individuals set fruit. Three size measurements were taken every other day during the initial growing season for 20 days and otherwise taken monthly. All measurements were taken with a very thin ruler to gain access to the buds found below the protective spines. Flower bud height was measured from the base of the ovary which exists below the white, pubescent hairs to its highest point. Flower bud diameter was measured across its widest dimension until flowering took place and the ovary was measured through fruit maturation.

Reproductive phenology was monitored across four study sites for a two-year period from September 1993 to August 1995 (Fig. 3). Balaosa, Batour, KAR, and GV. Seven morphological variables pertaining to PPC reproduction were counted on 91 individuals and related to season or timing at four sites and between two growing seasons (1994 & 95). Variables measured were: 1) number of new flower buds, 2) daily growth of flower buds in height, 3) diameter, 4) percent of plants in flower (anthesis %), 5)
presence of mature fruits, 6) absence of fruits and 7) presence of new seedlings. Again, the number of flowers counted at the KAR was taken from a larger sample size of 35 versus 14 for all other variables. Sampling periods varied with reproductive events. These sites were monitored monthly until the growing season when they were visited at least weekly, and occasionally daily. Daily precipitation for 1994 and 1995 was recorded from NOAA weather stations located within 1.7 km of each site.

A pollination experiment was conducted to determine if PPC could self pollinate. Two treatments were applied to a random sample from a population of blooming plants, a self-cross and a pair-cross pollener transfer. I evaluated differences in fruit production or seed set by using Chi-square statistical tests between treatments (Kearns and Inouye 1993). A random sample from a population of blooming plants was chosen for each treatment group. Eighty individuals from a population of flowering plants were cross-pollinated and 42 self-pollinated.

Self pollinations were isolated from outside pollinators within the BRF shadehouse and an additional screened cage. Pollen transfers were made using a small paint brush which was dipped in alcohol following every pollination. Successful pollinations were counted one week following the treatment which enabled sufficient time for fruit set to be evident.

Seed Biology Methods

Seeds for all germination investigations were collected across widely scattered portions of the taxon’s known distribution at four sites (Balboa, Batour, Vai, and GY).

Half of the fruit from every other plant contacted was gathered and seeds were air dried after being extracted from the soft, fleshy fruit (Rutman, pers. comm. 1993). PPC seeds were drawn for each of the germination investigations from a mixture collected from the four sites. Germination was counted if either a radical or two cotyledons protruded from the seed coat.

Field Germination Methods

To establish with greater accuracy the optimal season for germination, we monitored PPC seed germination in the field while measuring diurnal temperature extremes, and changes associated with rain events. These were used to detect varied patterns of temperature change with water and germination in the field. Germination was monitored during the summer rainy seasons of 1994 at Balboa where seedlings were located within 5 m of each germination location. Three replicates of 40 seeds were held in cheesecloth bags and buried at 1 cm depth (Abbott et al. 1995). Bags were buried 1 m apart to uniformly sample seedling micro-habitat for germination.

Soil temperature, number of rain events and total seasonal precipitation were measured. Light was withheld, as seeds were all planted below soil surfaces. To measure soil temperatures, three copper-constantan thermocouples were buried at 1 cm depth at each seed bag location. Sixty-minute averages were recorded by using a Campbell CR-10 micrologger. Each seed bag was checked for germination at 10-day and 30-day intervals until germination occurred. Summer precipitation was recorded by Buenos Aires NFR.
staff using a 12" rain gauge. The rain gauge was located 30 m from the Balsas seed germination plot.

Seed Viability Methods

In November 1994, seed viability, longevity, and dormancy across four sites (Batour, Balsas, GV, Vail) were monitored through various germination trials. PPC seeds were germinated to determine if mature plants were producing viable seeds in the field. Seed dormancy and seed longevity over time were determined to establish the time period from fruit maturation in which seeds had the innate, botic potential for germination. A series of germination trials was conducted monthly for 22 months.

Percent germination was measured to evaluate seed viability, longevity, and dormancy from a set of 3 replications of 20 randomly selected seeds in 10-cm petri dishes on 9-cm filter paper, with 15 ml of distilled water. To minimize water loss due to evaporation, cellophane was wrapped around each dish. All trials took place at the same location, a south facing window, at room temperature. The first trial was conducted immediately after ripened fruits were collected in mid-October. Trials were repeated, once monthly for 20 months to establish the short-term seed viability.

A univariate analysis of variance was used to evaluate differences in germination between months (Milton 1992). To ensure seed source viability for further investigations where light, temperature and water treatments were applied, percent germination measurements were taken from these monthly trials to serve as reference points.

Laboratory Methods

Light requirements for seed germination was tested with two trials in November 1993 by measuring percent germination of three replicates containing 20 seeds each with light and dark treatments. Again, 10 cm petri dishes with Whatman 9 cm filter paper and 15 ml of water were wrapped in plastic cellophane and placed under a 75-Watt artificial light source which sustained a temperature range of 29-31°C. Aluminum foil was wrapped around dark treated dishes to limit light penetration. A paired t-test with two treatments was used to distinguish differences between light and dark treatment groups (Milton 1992).

Germination depth within the soil was determined by planting seeds at 3 depths: surface, 5-1.0 cm, 1.0-2.0 cm in 189 liter stock tanks. This study was conducted in a relatively controlled shadehouse environment. Soil was gathered from the KAR field sites and placed in the tanks with holes drilled in the bottom to allow water drainage. Seeds placed at the soil surface received light and buried seeds did not. The soil surface was not allowed to dry between water applications. These results were used to document surface germination of seeds which were tested for a germination light requirement in the previous study, as well as to establish appropriate soil depths for planting seeds in field germination studies.

To gain a general perspective on the period of time and amount of "seed available water" to allow inhibition of PPC seeds, two watering frequencies and amounts were applied to 160 seeds in separate 4" pots. A soil mix consisting of 1/3 peat moss, 1/3
sand, 1/3 surphix was the medium used. Temperatures and light were held at a range of 29-31°C under the 75 Watt artificial light. To minimize evaporative water losses within the germination room, a humidifier was used to keep relative humidity at a measured range of 70-80%.

Treatment #1 received twice the amount of water at twice the rate of treatment #2. A 20-ml application was sprayed on Treatment #1 every 24 hours. The soil surface did not appear to dry between the 24-hour applications. In treatment #2, a 20-ml application was applied every 48 hours which allowed the soil surface to dry between applications. Seeds were planted 0.5 cm below the soil surface. Chi-square test of independence was used to test for differences between 24-hour and 48-hour treatment groups (Little and Hills 1978).

Temperature thresholds for germination were determined by measuring percent germination across a temperature gradient while holding light and water constant. Two trials of five replicates at each temperature contained 20 seeds. Millipore petri dishes which were 49 mm by 9 mm in size and blotter germination paper was used. Four ml of water was initially added to each dish and 2 ml was added every 48 hours to the dishes that dried due to evaporation. Each trial was run separately. In the first, percent germination was measured across 18 temperatures ranging from 14-39°C. The second was similar except 10 temperatures were evaluated in the range of 17-45°C. Germination took 3-5 days. To ensure complete germination measurements were taken after 16 days for trial #1 and 14 days for #2. Seeds which did not successfully germinate at a specified temperature were retested within optimal temperature ranges for germination after the study was completed to be certain they were viable.

**Reproduction Results**

Density at each site was different (Table 1). No significant differences in reproductive potential, measured as the quantity of flowers and (flowers X fruits), were found between any of the five sites (P>0.01) (Fig. 7). Across all sites an average of seven flowers and five fruits are produced on each cactus. The proportion of flowers that achieve fruit set through pollination in the field which included all sites was at 71% with a range of 41-82%.
Plant size may have varied between sites and I found in other investigations that reproductive productivity varies with PPC size. I did not measure PPC during the summer and fall growing season except for plant size at only 2 of the 4 sites shown in Figures 10 and 11. I did not have data at all four sites to evaluate the relationship between plant size, plant density and reproductive potential.

Merristematic tissue and protective pubescence were found at the base of the tubercle eleft. PPC as small as 3.0 cm in height and 7 cm in diameter produced a flower, typically 1 or 2 a season. Reproductive growth was initiated at the base of new tubercles on the apex of the stem (Fig. 1). Flower buds emerged in groups or cohorts which ranged in size from 1 to 23. A cohort of emerged flower buds appeared within 1-3 days of each other. A second and occasionally third cohort emerged in consecutive periods of 10-14 days and ceased by mid-July. The average size and standard deviation of all three structures, found on 10 plants across the growing season is illustrated in Figure 8, and their growth rates in Figure 9. The greatest growth was represented by flower bud height as the average reached 7.5 cm above protective apical spines prior to anthesis. The size change in height and variance depicts how flower buds grew to 2.5 cm, and delayed growth for a period of time until the cohort illustrated a substantial increase in growth rates immediately prior to anthesis. Following anthesis the corolla of the flower desiccated, however the inferior ovary at the flower base swelled in fruit development. The flower bud diameter did not increase in size or growth until three to four days prior to anthesis.
when it expanded to 2.0 cm. The ovary diameter remained relatively stable at 5 cm until
one week following pollination when it widened to 2.0 cm during fruit development.

Fig. 8. Average size change and variability during 1992's reproductive growing season (June-
August) of 22 flower buds on 10 plants observed at the shadehouse in 1994.
No differences in reproductive potential were found between the two sites evaluated in this investigation (Fig. 7a, b). Generally, in the field at BANWR larger PPC measured during the 1994 were correlated with flower production ($p < 0.001$) except as measured by stem number (Figs. 10, 11). Of the five variables measured, the greatest diameter of entire PPC plants and the total number of tubercles produced showed the strongest correlation's (Figs. 10, 11). A regression of the number of flowers produced as a function of the number of tubercles and greatest diameter showed a correlation ($p < 0.001$), with flower number increasing with increasing tubercle number ($r^2 = 0.555, 0.10$) and greatest diameter ($r^2 = 0.815, p < 0.001$).

No, correlation's between PPC sizes with reproductive potential were found in the shadehouse. Flower and (flower $X$ fruit) numbers with size relationships evaluated from variables measured under the BRF shadehouse conditions did not show significant associations between the two. These results may have been influenced by the fertilizer treatment applied to these plants in May prior to anthesis and data collection.

Occasionally flower buds were initiated on a plant and desiccate prior to anthesis. These buds obviously were not available for pollination. This occurrence was rare, only being seen on 9 out of 110 plants observed at BRF.
Fig. 10. Reproductive potential in terms of PPC flower production related to plant height and adult diameter at two sites combined (Balcon, Balawa) on BANWR during the 1994 monsoon season. 

Fig. 11. Reproductive potential in terms of PPC flower production related to number of new tubercles and largest diameter of the entire cactus at two sites combined (Balcon, Balawa) on BANWR during the 1994 monsoon season.
Flower buds were initiated at sites and between the two study years at nearly the same time on May 16, 17, and 18 and apparently varied with an environmental cue which was constant between them. An average of 2 flower buds on each of the 93 plants would appear during the initial establishment of buds. New tubercles began appearing in the shadehouse and in the four field sites in mid-March (16-20). Flower buds continued to appear in groups through late July and persisted into the later stages of summer monsoon seasons and mid-August in the BFR shadehouse. Plants had up to three cohorts, however, generally they had 1 or 2. Again, I found flower bud initiation was synchronous across the 4 sites and between years.

Photoperiod appears to be the only variable constant across all four sites and between years, suggesting that flower bud initiation is stimulated by photoperiod. Since the cumulative hours of daylight, available from mid-May through late-July does not fall below a certain threshold, it appears that PPC is a long day/short night plant which responds to red far red wavelengths for flower bud initiation (Moore and Clark 1995).

Fig. 12. Synchronous anthesis of 73 PPC plants at four sites during the 1994 reproductive season in southern Arizona. Measured from flower bud initiation (May 11, 1994) through last anthesis event (August 4, 1994).
After synchronous initiation of a cohort of flower buds and a period of minimal growth, they extended high above protective spines and provided pollinator access as they bloomed. Flowers buds bloomed in synchrony within a single plant, site and occasionally between sites (Fig. 12). Percent anthesis across four sites during the 1994 season occurred earlier at lower elevations (GV & KAR) and later, at higher elevation sites (Batour & Balsaos). More sites shared anthesis events later in the monsoon season.

Anthesis between years (Fig. 13) was not always shared, however, occasionally it was similar. Two types of anthesis events took place in both 1994 and 1995 seasons. The first event occurred at two of four sites following a late spring rain with fewer individual flowers (1-2) per plant and less percent blooming plants. A second larger anthesis event took place across all four sites at the height of monsoon season, showing 100% at 2 of the four sites (Fig. 12). No flowers appeared to bloom before the actual monsoon rains during 1995 nor was there late spring precipitation at any site.

Sites that shared anthesis events during 1994 shared a rain event 5 to 7 days prior (Fig. 14). Anthesis occurred at KAR with minimal, single rains yielding 8 cm and GV with 4 cm of precipitation. Batour and Balsaos at higher elevations shared events later into the season following 6 rains yielding 123 cm and 288 cm precipitation, respectively.

During the 1995 summer season, anthesis occurred later at GV and KAR which were lower in elevation and rainfall events came later.

Fig. 13. Percent FPC anthesis in 1994 & 1995 at four field sites starting from flower bud initiation (FB) on May 15, 16, and 17, 1994 through the mid-summer season in southern Arizona.
Only the four plants located on the SRER bloomed during this first anthesis event which occurred as late as July 17, 1995. The other 20 plants did not bloom at the same time.

Before the 1995 flowering data collection, the 20 individuals on private land in the GV sample were transplanted onto the SRER to measure the effects of transplanting. These plants were stunted and appeared to be dehydrated. They flowered in synchrony within their sample but, later than all other plants at other sites including the 4 SRER plants which were within the site but not transplanted. Although the KAR flowering event took place with a minimal amount of precipitation the GV sample did not flower until 4 rain events had fallen and 4.0 cm of precipitation had been received. Here again, flower buds were initiated on these plants as early as May 18, 1995. However, they did not bloom their first cohort until August 16, 1995.

Any cohort of PPC flowers bloomed only for a single day during mid-day when temperatures were high and bees were active. Pollination events were observed to generally take place from 10:30 a.m. to 4:00 p.m. Both native and European honey bees were observed visiting 93 plants during mid-afternoon. Synchronous flowering and pollinator observations suggested PPC required cross-pollinations for seed production.

**Pollination Results**

The stigma was observed to be sticky, the anthers extended and flowers were fully open between 12:30 and 3:00 p.m. Plants set fruit a week after native and European honey bees were observed pollinating the flowers in the field as early as 12:30 p.m. and as late as 4:00 p.m. Seed production was significantly reduced through self-pollination.
Significant differences between self and cross pollination treatment groups were found using Chi-square tests of independence (p<0.001) (Table 2).

Table 2. Compared results between cross & self pollinations conducted during the summer season of 1994 under controlled shadehouse conditions in southern Arizona.

<table>
<thead>
<tr>
<th>Treatment</th>
<th># Fruit</th>
<th>% Fruit</th>
<th>Avg. Seed Pr.</th>
<th>Max. Seed</th>
<th>Min. Seed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross</td>
<td>55</td>
<td>86</td>
<td>73</td>
<td>106</td>
<td>16</td>
</tr>
<tr>
<td>Self</td>
<td>2</td>
<td>5</td>
<td>18</td>
<td>33</td>
<td>2</td>
</tr>
</tbody>
</table>

Fruit development started immediately after pollination and within a week, success could be distinguished by observing the swelling at the base of each flower.

Pollinations which were successful resulted in ovaries which became plump and avoid and those which were not appeared dried and withered.

Mean number of seeds per fruit found in a pooled sample from all 5 sites was 89 with a range of 24 to 131. Fruits were generally completely dispersed by December following pollination in August. Half of all the fruits produced in 1994 were still present in mid-October. Roadrunners were observed collecting and eating the fruit. Rodent and lagonochep tooth and activity were often associated with individual PPC’s during the fruiting season.

Germination of new seedlings in the field was observed in both 1994 and 1995 during the middle portion of the monsoon season. These observations took place at Balaosa on BANWR.

Seed Biology Results

In 1993 combined and mixed seed from all five sites showed viability which was relatively high with an average percent germination of 89% and a standard error of 4%.

No separate site germinations were conducted to test for site differences. Mean seed germination over 21 months ranged from 80 to 95% (SE = 6%) with no significant differences between months (p=0.12) (Fig. 15). Therefore, there appears to be no seed dormancy period and based on the result of no reduction in viability, seed longevity appears to last beyond 21 months.

Mean germination between all light and dark treatment groups ranged from 82% to 88%. No differences between groups were found in trial #1 (p=0.294) and trial #2 (p=0.422). Seeds planted at the soil surface in the controlled shadehouse study did not germinate. Seeds planted <1 cm below the soil surface showed 85% germination, while those planted deeper exhibited no success. Light does not limit PPC seed germination.

Watering treatments administered 48 hours apart were dry in appearance between applications. Thus, not allowing continuous periods of available water for seed imbibition. 51% of seeds germinated under 24-hour watering intervals, as compared to 5% under 48-hours. Chi-square test of independence did establish 24-hour watering treatments to be significantly more successful in germination success than 48-hour periods at a confidence level of 99%. PPC seed imbibition requires at least 96 hours of constant, relatively high soil saturation level of water, however exact soil potentials are unknown.
Temperature limitations for seed germination in both trials showed a threshold temperature limitation of 18 to 19°C along the cooler range of the gradient. Substantial decreases were found at 38°C in both trials with 16% to 28% success at higher temperatures (Fig. 16). Replicates treated in trial #1 at temperatures greater than 26°C did occasionally dry out for periods less than eight hours (Fig. 16) due to evaporative losses. Greater numbers of dry periods were present in replicates at temperatures >38°C, due to extremely high temperatures. An optimal temperature range for inhibition was detected when petri-dishes were kept consistently moist, as shown in trial #2 (Fig. 16) between 25 and 33°C. Within this optimal range mean seed germination varied between 61% and 77%.

Due to the late monsoon season of 1995, no rain events occurred during the temperature monitoring period. Thus, I was unable to document soil temperatures at 1 cm depth with PPC germination in the field. However, I was able to observe pre-germination temperatures in the field (Fig. 17) and they were substantially higher the optimum range found for PPC germination in the laboratory (Fig. 16). Without rain events, maximum temperatures reached into the high 50° and mid 60° C range which are far from the 20-38° C optimal temperature range found in the laboratory.

Fig. 15. The average germination and standard deviation of field-collected PPC seeds from five sites in southern Arizona. Germinations were conducted monthly across a 21 month period.
Fig. 16. Average percent germination and standard error run at 18 temperatures ranging from 0 to 58.5 degrees C for trial #1 and 10 temperatures ranging 0 to 45 degrees C for trial #2 in a laboratory investigation conducted in 1994.

Fig. 17. Ten diurnal soil temperatures at 1 cm depth below the soil surface at PFC germination locations taken prior to summer monsoon rains in southern Arizona.
Following late monsoon season rains, when soil temperatures may have decreased, with precipitation and cloud cover, on September 20, 1993 PPC germination had taken place some time between then and July 31 with a mean of 88% for the three replicates. In 1995 the monsoon rains occurred late in the season at the Balossa site where 88% germination was observed with a substantial number of rain events (16) which yielded 16.5 cm of precipitation.

Reproduction Discussion

Reproductive growth began with the initiation of flower buds, probably in response to photoperiod or, possibly, the number of days above a certain temperature in mid-May. Flower development responds to another set of environmental conditions associated with the summer monsoon season. Increased transpiration rates may be an explanation for this pattern of increased flower development to bloom in synchrony during the summer rainy season (Moore and Clark 1995). This phenological relationship regulates synchronous flowering within populations which is critically important for producing significantly more seeds with cross-pollination, at least within a population.

Three periods of reproductive phenology were investigated in this research. If PPC are subjected to similar periods of light and temperature in the near future we can be relatively certain flower buds will be produced. However, development of buds into flowers may be limited by climatic (i.e., water and light) variation, which may limit the number of cohorts per season and opportunities for cross-pollination. PPC pollination will be limited by pollinator access and attraction to flowering individuals.

This third consideration relates to the spatial distribution of PPC within a population. Not to assume that cross-pollination between individuals from widely separated populations would generally be recommended for long-term conservation of diversity within this taxon. PPC distribution was observed as being patchy and widely dispersed across its range and there is no information describing the genetic variability present between the patches of PPC throughout its range (Miller and Libby 1991).

In general, larger PPC produce more flowers which has also been observed with other similar species. Coryphantha robbinsorum showed increased reproductive potential as flower and fruit productivity increased with plant diameter (Schnittele et al. 1995). No differences in flower and fruit production were found between PPC sites, even though spatial distribution may be important for achieving cross-pollination. The actual distance between plants may be a more reliable measure of how distribution relates to productivity than population density.

Basically PPC germination occurs with adequate moisture availability, and so allows for at least a 72-hour imbibition period and temperature must be above 19°C and below 50°C. These results found that germination can occur at constant temperatures of 38°C with adequate moisture, however it is not optimal. To consider temperature and precipitation limitations on PPC germination during the summer monsoon field or laboratory investigations should represent actual field patterns.
Across PPC distribution, winter minimum temperatures fall to 0°C (Sellers et al., 1985). Such low temperatures would not seem adequate for germination, which requires breaking down the hardened testa at the hilum which is made of hard protein fibers and lipids (Gibson & Nobel 1985). Winter germination was not observed to take place during this two-year investigation and these results suggest the event unlikely to occur.

Seed viability which represents a combination of five sites spread across the taxon’s range is relatively high with minimal variability over a 21-month period. A dormancy period was not shown to exist in this study. Hence, seeds may germinate at any time following fruit maturation. Seeds are able to germinate immediately after fruit maturation which is 1-2 weeks following pollination. Therefore germination could occur within the same monsoon season from which they were produced and since seed longevity lasts for at least 21 months, they could germinate the subsequent summer, also.

The average number of seeds produced per fruit is 89. Seeds are available in mature fruits within 2 weeks following pollination. Seeds which are not lost to predation or destroyed by other means are then available to germinate under appropriate conditions.

An investigation which measured soil temperatures near a PPC seedling location was conducted by Roundy et al. (1992) during a summer rainy season at the KAR site. Thirty-minute mean soil temperatures of 5 locations were measured over a period of five days. Dry-sunny conditions had diurnal temperatures at 1 cm depth which ranged from 24-62°C, wet-sunny range was 20-51°C, and wet-cloudy range was 21-37°C.

Measurements were taken from areas where mature PPC plants occur and are similar in habitat description to seedling locations on the KAR site. Therefore, wet, cloudy conditions can potentially decrease high temperature extremes as much as 25°C. Roundy et al. (1992a) documented maximum 37°C soil temperatures influenced by rain events at soil depths of 1 cm in similar habitat and near to PPC seedling locations. Maximum soil temperatures and plant available moisture (AWS) varied diurnally and with rain events. Our data (Fig. 17) are similar in temperature ranges found under sunny-dry conditions to Roundy et al. (1992a). Water availability and temperature probably interact to influence germination for PPC.

Pima pineapple cactus germination was observed during monsoon seasons of both years. Seed germination occurred during the 1995 monsoon season only after substantial precipitation, 16.5 cm after 16 rain events. The period of seed imbibition shown in all studies using transparent petri dishes varied between 72 and 120 hours. Although 1995 was considered a drought year, germination was observed at a single location occupying the higher elevations with greater summer precipitation. Minimum temperatures of 19°C were found to stop germination completely and maximum temperatures of 38°C decreased germination substantially. Both of these extremes were present for a short duration of each diurnal period. Similarly to barrel and saguaro cacti, germination can not occur at temperatures lower than 15°C.
CONCLUSIONS

Using the single, pass survey method to locate PPC may cover 100% an area, however, the potential of locating above 50% of the individuals is low. PPC are well camouflaged within their microhabitat. To increase the probability of effectively finding all PPC within a given area, we recommend repeated passes using this survey technique, coupled with smaller intensive searches within the potential PPC habitat. With our current knowledge, the vegetation described as mid-sized mesquite shrublands by Roller and Halverson (in press) could be used to recognize PPC habitat. Resources or competition for those resources which limit PPC abundance and distribution were not experimentally discerned in this research, however they were described.

PPC grow vegetatively from the apex following the winter rainy season and reproductive growth occurs during the summer rainy season. No clear phenological pattern between basal offsets (stem number) was detected, they may be related to some other factor. PPC shrink and exhibit a dormant stage during the summer drought and winter cold seasons. Winter rainfall patterns have been strongly correlated with vegetative growth and productivity of many plant species in arid ecosystems (Noy-Meir 1973).

Flower buds appear in mid-May, at the same time throughout PPC range and appears to be responding to photoperiod. Flowering occurs 5 to 7 days after the first summer rains of over 3 mm. Pollination of a cohort of flowers takes place in a single day. Fruits develop within 2 weeks after pollination. Therefore, fruit or seed dispersal can occur 2 weeks after the first summer rains through the winter and following pre-monsoon season.

A relatively small proportion of 35 seeds were produced through self-crosses in the pollination experiment. These self-crossed seeds could have been tested against outcrossed seeds for differences in seedling establishment to further investigate how self-crosses may limit reproduction within populations.

Thus far, we know germination appears to occur during summer monsoons. PPC germination may be coincident with abundant moisture to sustain some level of relatively consistent available soil moisture for imbibition at summer monsoon temperatures. If rains in late May instigate early flowering then the seed produced from a single pollination may have two opportunities for germination.

Seedlings were similar to adults that they were found in the open or along the drip line of taller shrub canopies where higher levels of light occur. However, PPC did not have a light requirement for germination, they germinate below the soil surface.

We have focused a great deal of attention on PPC germination and now have a basic understanding of its phenology and abiotic constraints. Seed production across the five field sites is strong in terms of seed viability. Therefore, pollination in 1993 appears to be producing seeds successfully in the field. Seeds planted in the field can germinate at a relatively high 88%. However, very few established seedlings were located. Other research has identified the seedling establishment periods as crucial for individuals to survive to reproductive maturity in many cactus species (Steenbergh and Lowe 1977,
1983, Johnson et al. 1993, Schmalzel et al. 1995). Stembergh and Lowe (1977) observed the pre-establishment stage of saguaro development as being most vulnerable to predation and mortality related to climate. Having only found 9 established seedlings at half of the sites searched, it may be the establishment life history stage which is currently limiting. I suggest seeding establishment be a priority for future conservation research.

Laboratory investigations which maintain constant temperature do not effectively answer questions relative to field conditions. The duration at which a seed is influenced by the treatment should be reproduced in the laboratory. Preliminary field measurements using thermocouples and microloggers could be conducted to measure diurnal temperature patterns associated with germination in the field. These conditions could then be used in laboratory growth chambers.

Reduced PPC recruitment within Lehmann lovegrass vegetation suggests an ecological hypothesis involving competition of resources. PPC does not have a light requirement and inhibition requires 72 hours of water availability for germination. PPC germinates when lovegrass is actively growing during the summer monsoon season. Therefore, I suggest another hypothesis which suggests that Lehmann lovegrass limits the water availability required for PPC germination.

Conservation of Pima pineapple cactus requires consideration of long term population dynamics. Based on my research, I recommend the following research:

1) determine limitations of seed germination and seedling establishment limitations in continuous dense stands of Lehmann lovegrass; 2) determine the effects of different

Lehmann lovegrass densities on PPC mortality with fire, and 3) determine spatial distribution constraints on PPC seed production.

To address the issue involving fire on state and federal lands two inferences can be made to make a management recommendation. PPC seedlings through their first couple of years are unlikely to be negatively affected by fire. Germination does not occur during the fire season and seeds do not appear to germinate in heavily fueled areas. The fire intensity and residence time may not be adequate to directly effect PPC seedlings.

However, occupation of heavy fuels following seeding establishment may be a concern. Larger adult cacti do not shrunk level with the soil surface during the fire season, as seedlings do. These results and the previous study conducted by Roller and Halverson (in press) found a possible negative interaction between adult PPC and Lehmann lovegrass with fire.

I suggest groups of PPC plants found within the mid-sized mesquite shrubland to be managed in the context of the entire community. First, by controlling the invasion of Lehmann lovegrass into the local area or community; and secondly, by managing fire with a fire line around the local area of PPC plants and vegetation. Thus, PPC can be sustained as patches within, and enrich the diversity of southern Arizona's arid desert grasslands.

Presently in Southern Arizona, lands are undergoing degradation. There is a public interest in conserving endangered plants and species diversity within these landscapes for the sake of humanity. The land area available for conservation of species diversity exists within a complex ecosystem involving dynamic land uses. It is important to incorporate
species conservation within these ecosystems by managing lands with an understanding of species population requirements and dynamics.

LITERATURE CITED


