FINAL REPORT

A MONITORING PROGRAM FOR THE ENDANGERED *Pediocactus bradyi* L. BENSON, LEE'S FERRY, GLEN CANYON NATIONAL RECREATION AREA

John R. Spence

Resource Management

Glen Canyon National Recreation Area

23 November 1992

1. INTRODUCTION

Pedicactus bradyi L. Benson is a federally listed endangered species distributed locally along the Colorado River in Marble Canyon, northern Arizona. Most known populations are on Bureau of Land Management and Navajo Nation lands along the Colorado River. A small population, of unknown extent, exists near Lee's Ferry on land under jurisdiction of Glen Canyon N.R.A. (NRA). The status of this population needs to be documented, because of its proximity to heavily used roads, park recreational areas, and livestock, grazing and mineral exploration activities.

This report documents a biological monitoring program for the Lee's Ferry population of P. bradyi, and is organized into six parts; a preliminary literature review, site description, methodology, results, discussion, and recommendations.

2. LITERATURE REVIEW

The genus Pediocactus consists of eight species, distributed primarily on the Colorado Plateau. Of these, seven are listed endangered or threatened, or under consideration for listing. Only P. simpsonii is common and widespread. The genus is very poorly known, with little work done on it other than basic taxonomy.

L. Benson (1961; 1962a,b,c; 1982) described the genus, defining it primarily by the unique capsule dehiscence. At one time species in the genus were scattered among Echinocactus, Mammillaria, Navajoa, Pilocanthus, Toumeya, and Utahia. More recently, Arp (1972) suggested that Pediocactus and Sclerocactus be combined, but Heil et al. (1981), in the most recent revision, maintained the two genera. However, they excluded a ninth species, P. papyracanthus, from the genus.

Plants of Pediocactus are mostly small, ranging from a few mm in diameter

up to 10-15 cm in P. sileri. Flowers are very showy, varying in color from pink, to purple, white, yellow or bronze. Some species are spiny while others lack spines. The capsule dehisces by a single vertical slit on one side of the capsule wall. The species are insect-pollinated, principally by native bees. Very little is known about the reproductive and population biology of the genus. Butterwick (1987) found that P. peeblesianus exhibited a high population depletion, with most individuals surviving less than 5 years. However, Olwell et al. (1987) found high survival rates in natural and transplanted populations of P. knowltonii over a one year period. Work is currently underway on the breeding biology of both P. bradyi and P. sileri by Dr. Vince Tepedino and his associates at the Utah State University Bee Biology and Systematics Lab, but results have not yet been published. However, they have discovered that caged plants of P. bradyi did not set seed, suggesting individuals are self-incompatible (V. Tepedino, pers. communication, 1992).

3. SITE DESCRIPTION

The population of P. bradyi is located south of Lee's Ferry on flat open terrain above and west of the Colorado River (Figure 1). Elevation is ca. 1020 m. The climate is hot and dry, with average annual spring and summer temperatures in the 25-35° C range. Precipitation is low, generally below 25 cm/year. P. bradyi appears to have very specific soil requirements. It is found exclusively in sites covered with white limestone chips of the Kaibab Formation, and underlain by Moenkopi shale and sandstone. Common associates at the site include shadscale (Atriplex confertifolia), mormon tea (Ephedra viridis), desert trumpet (Eriogonum inflatum), and galleta grass (Hilaria jamesii).

Specific, anthropogenic, threats to the Lee's Ferry population include livestock trespass, off road vehicle use, and illegal collecting. Of the three,

at present ORV traffic seems the most immediate threat, since the population grows within a few hundred meters of the Lee's Ferry road, and as fresh vehicle tracks were seen near plants. Natural factors affecting the population include climate and herbivory. Pediocactus is easily affected by root rot (Heil et al. 1981), which could occur following unusually cool temperatures and heavy precipitation in winter and spring. Butterwick (1987) notes that mammal grazing, probably by either rodents or lagomorphs, appears to have been causing losses in a population of the endangered P. peeblesianus.

4. METHODOLOGY

A preliminary reconaissance of the site was conducted on 29 March, 1992. The population was in full flower at this date. Return visits to the site were made on April 2, 3, and 7, at which times a monitoring program was established and preliminary observations on pollination ecology were made.

The population of P. bradyi was growing as widely scattered individuals or small groups. Because of the low density, traditional line or belt transects would have contacted relatively few individuals. The chosen design consisted of a fixed circular plot, with a radius of 10 meters. A permanent stake was placed at the circle center, then distance and bearing to plants or clumps was measured. Clumps of two or more indivudals were mapped to reduce the number of bearing-distance coordinates. The following data were taken from each mapped plant:

1. Plant long axis diameter in millimeters (mm),
2. Number of flowers per plant,
3. Number of fruits per plant,
4. Estimated seed set per plant,
5. Substrate slope,
6. Nearest flowering P. bradyi individual,

7. Distance to nearest flowering individual in centimeters (cm),
8. Nearest perennial species other than P bradyi,
9. Distance to nearest perennial species in cm,
10. Signs of herbivory (scored as percentage of flower, fruit, or vegetative body damaged/missing; ie, F50 = 50% of flowers removed)
11. Evidence of damage to plant from other kinds of disturbance.

Four plots were established in relatively dense patches of P. bradyi individuals. All located plants within 10 m of the center point were mapped and measured. Mapped areas comprised 314 m^2 per site. Pediocactus plants are hard to locate, as they barely project above ground level and are small and gray-green. Future censuses will probably locate additional individuals in the plots.

Observations were made on insect visitors during site visits. Potential pollinators were observed entering flowers, then captured as they left, and checked for Pediocactus pollen. Pollination efficiency was examined by observing the movements of pollinators within flowers. Each flower visitor was scored for the following behavior; contacted the anthers only, stigma surface only, both, or petals only. Times within the flower, starting from the first point of contact, were recorded for visitor species. For four plants, observations were made on motile stamen behavior (see results for explanation) under controlled conditions. Stamen movement was triggered by probing the flower with forceps, then the flower was covered with a net to prevent insects from entering. The time taken for the stamens to curve down and contact the base of the style, and to return to an upright, open, position, were recorded. For one flower, the same procedure was done, but instead of forceps a single insect visitor was allowed to visit the flower and trigger the stamens.

Data were analysed by parametric multiple linear regression and Pearson's

product-moment correlation coefficient. Variables were examined for departures from normality using the Shapiro-Francia statistic.

5. RESULTS

Demographic data are located in the DBASE III+ file PBRADYI.DBF. Plot sketches are found in the appendix. In the four circular plots (see Figure 1 for location) 181 individuals of P. bradyi were located, mapped and measured. Density of plants was very low (0.14 individuals/m^2), and the plants tended to be clumped (see sketches in appendix). Although the extent of the population along the river is unknown, an estimated 1000 plants occur in the study area itself (delineated in Figure 1), based on counts of individuals on walking surveys.

Morphology and Reproduction

Morphological and reproductive data are summarized in Table 1. Stem diameters ranged from 7-56 mm, with a mean of 29.47. The smallest flowering stems located were 19 mm. No stem below this diameter flowered. The size frequency distributions of the two populations, flowering and non-flowering individuals, are graphed in Figure 2-3. Table 2 presents Person's product-moment correlations between all possible combinations of the five variables stem diameter, flower number, nearest P. bradyi plant, nearest individual of other perennial species, and slope in degrees. The only strong correlation evident is that between flower number and stem diameter.

Flower number on reproductive individuals ranged from 1-5, with a mean of 1.18 per stem. In the population 61 of 181 recorded individuals (33%) did not flower. A significant relationship exists between flower number and stem diameter, with larger stems more likely to produce more flowers. This relationship is described by the linear equation

$$\text{Flower number} = -1.2405 + 0.0822 * \text{stem diameter in mm}$$

The slope of this equation is significantly different from zero (Table 3; Figure 4), and the regression has an adjusted correlation coefficent of 0.5785.

Fruit maturation and seed set could not be measured in the population in 1992. Because of time constraints, a return visit to the site was not conducted until May 20, by which time the fruits had dehisced and seeds had dispersed. Hopefully, these data can be collected in the 1993 season.

Phenology of the population was not studied in detail because of the limited number of visits. However, a suggested phenological cycle for 1992 would be as follows; first flowering ca. 20 March, with flowering going through ca. April 10, fruit maturation finished and dispersal of seed in late April and early May, followed by retraction and shrinking of plants back to ground level (characteristic of Pediocactus) by end of May and through June, and dormancy the remainder of the season.

Microhabitat

Average distance between plants was 27.6 cm, and is left-skewed (Table 1), indicating a degree of clumping. Average slope of the substrate was 5.0 degrees, and ranged from 1-15 degrees. Average distance to the nearest perennial species other than P. bradyi was 39.9 cm. Species recorded as nearest neighbors to each P. bradyi are listed in Table 4. The most common species recorded were Atriplex confertifolia and Eriogonum inflatum. In all, 10 species were recorded as nearest neighbors.

Threats to the population

Very little sign of herbivory was noted on P. bradyi individuals. No feeding sign was observed on the stems, and only three flowers were damaged, showing obvious feeding sign. However, herbivory is highly dynamic temporally (Dirzo 1984), and considerable damage could have occurred to individuals after

fieldwork was completed. The herbivore feeding on the flowers is not known, but was likely to have been either rodents, lagomorphs, or larger insects such as grasshoppers.

No damage by ORV use was noted in the population. However, fresh ORV tracks were seen near the population during the April and May visits, suggesting that occasional ORV activity occurs in the area.

The area is not currently grazed by cattle, and no sign of livestock activity was seen in the area.

Pollination ecology

Pediocactus bradyi flowers opened at the site between 0900-1000 hours, at least during warm sunny days, and closed in the evening. They open for four or five days. Flowers are herkogamous, as the anthers and stigma do not come in contact at anthesis. Motile stamen behavior (see below) was present in most of the flowers observed. Numbers of insect visitors over 4 hours of observation on April 3-4 and 7, 1992, are presented in Table 5. Three potential pollinators were seen visiting flowers of P. bradyi. Feral honeybees were only observed on the morning of April 4, and were absent on April 7. Two members of the Halictidae were observed and captured on P. bradyi. Both the Apagostemon and Dialictus species (identification to species must wait study by bee experts) were found on all dates, with the former much rarer than the latter. All three species were observed to collect pollen from the stamens of P. bradyi on their hind tibia. Individuals of all species were also observed to move to other flowers following pollen collection visits. Also listed in Table 5 are the different parts of the flowers each species and individual contacted. Pollination efficiency was determined as the number of times flower visitors would contact both the stamens and stigmatic surface during a visit. Honeybees were the most efficient potential

pollinators (100%), followed by the Apagostemon (44%) and Dialictus (23%).

Data on the first 30 visitors to a single flower that had just opened (data independent of that in Table 5) and lengths of each visit are listed in Table 6. The flower had not been open at any time prior to the start of the experiment. The first visitor, an individual of Apagostemon, stayed 215 seconds in the flower and was actively collecting pollen the entire period. Subsequent visits declined in length substantially following this first visit. Of the first 30 visitors, 93% were by Dialictus.

Many cactus genera exhibit a phenomenon known as motile stamen behavior. The stamen filaments bend over to the base of the ovary after tactile disturbance, such as when an insect visits the flower. A chamber is formed when all the flower's stamens react, trapping a visiting insect near the base of the flower. In other genera this has been suggested as a mechanism to effect pollination, as it forces the insect to travel a specific path up the ovary and style onto the stigma as it exits the flower, at which time it would presumably come in contact with the stigmatic surface and deposit pollen (B. Simpson, pers. comm. 1992).

Four flowers were selected on April 7 to examine the motile stamen phenomenon. One of these had first opened on the day of the experiments, while the other three were 2-3 days old. The results for each of the flowers can be found in Tables 7-8. For the three older flowers, the motile stamen movement gradually ceased, and usually stopped after 4-5 tests. No attempt was made to determine the behavior of the stamens at a later date. For the younger flower, even after three hours and repeated tests, the anthers were still actively contracting and straightening. One interesting find was that the stamen response was faster when it was triggered by insects, compared to forceps. Since insects

were frequently visiting P. bradyi flowers, stamens tend to remain in the contracted position in most flowers.

6. DISCUSSION

The demographic data was collected in this study primarily to establish a monitoring program for P. bradyi. In order to be effective, a census of the population will be required for the next 2-3 years. With the data gathered on mortality rates, age to reproduction, fruit and seed set estimates, and population size, minimum viability analysis and predictions on population persistence can be performed using stage-structured Leslie matrices (cf. Menges 1986).

Few threats currently exist for the population at Lee's Ferry. Illegal cactus collecting has been a threat for many rare species, but no unequivocal sign of such activities was observed at the study site. Livestock do not, or only rarely tresspass in, the area. The principal threat to the population at present appears to be potential ORV acitivty. Some activity has occurred in the vicinity of the four study plots. The presence of an access road under the power line extending from Marble Canyon to Lee's Ferry, and the open terrain, may encourage ORV activity. Monitoring of the area is probably required to minimize such activity.

P. bradyi appears to be typical for the family in its breeding biology. Many southwestern cacti are self-incompatible and insect pollinated. Preliminary caging experiments suggest the species is self-incompatible, although this should be interpreted with care as complex variation from selfing to complete incompatibility is known in species of Opuntia (Simpson and Neff 1987). Little nectar is present in P. bradyi flowers, and the primary reward for pollinators is pollen. The majority of cactus species studied, except for night blooming

species which are moth and bat pollinated, appear to be pollinated by an array of generalist and specialist bees in the families Andrenidae, Halictidae, and Megachilidae (Simpson and Neff 1987; Osborn et al. 1988). In the case of P. bradyi, generalist halictids in the genera Apagostemon and Dialictus appear to be the principle native pollinators. These same taxa are apparently also the principal pollinators in other populations of P. bradyi (V. Tepedino, pers. comm. 1992). These are solitary, small bees, generally averaging only a few mm in length.

Of the natives bees, the Dialictus was abundant, while the Apagostemon was rare. Both species were observed actively collecting pollen. The smaller Dialictus appeared to be little hampered by activity of the motile stamens, but the larger Apagostemon was observed to only exit the flower by climbing the style onto the stigma. The introduced honeybee was common at the site during the first day of observations, and was observed actively collecting pollen. Honeybees are much larger than the native bees, and generally collected pollen while on top of the cage formed by the stamens, in contrast to the other two species which generally spent most of their time collecting pollen from within and below the cage. Despite its large size, the honeybee was probably the most successful species at transferring pollen between flowers, and had a potential pollination efficiency rating of 100%. However, honeybees had abandoned the site by April 7, presumably because pollen resources had become deleted below some threshold.

7. RECOMMENDATIONS AND MANAGEMENT OBJECTIVES

Future monitoring and research

At least two more years of monitoring will be required to establish demographic transition states. In addition, more data on pollination, and seed germination and seedling establishment, should be collected, to determine basic

requirements for seedling ecology. A suggested time schedule is:

Visit 1: preliminary visit in late March to determine status of population	1 day
Visit 2: collect demographic data	2 days
Visit 3: collect pollination and flowering data	2 days
Visit 4: record fruiting data and establish seed germination plots	2 days
Office: data analysis and write up	5-7 days

Training of personnel would be minimal, as the plants are readily identified, and the demographic data are easy to collect. In future work it may be useful to add extra study plots in other areas where Pediocactus occurs. The current distribution of plots is adequate for that part of the population on the map, but future surveys will probably find individuals elsehwere on the Kaibab limestone to the south of the known population along the river, to the south of Cathedral Wash.

Another useful addition to future monitoring is permanent location of the plot centers using Global Positioning System technology. In the event that the markers currently in place are lost or removed, permanent GPS location data would be invaluable in relocating the plot centers.

Management

Based on this report, it is recommended that the park discourage ORV activity in the Lee's Ferry district. More signs placed along the road, requesting people to stay on the paved road, may help. A barrier could be erected to prevent access to the road along the transmission line.

Informal discussions with Lee's Ferry personel indicated that, although they were aware of P. bradyi, the exact locations and appearance of the plants

were not known. Furthermore, they were unaware of the legal status of the species. A visit to the site with the district personnel, discussing and showing the plant, and it's legal status and protection under the Endangered Species Act, would be very useful.

8. LITERATURE CITED

Arp, G. 1972. A revision of Pediocactus. Cactus & Succ. J. 44: 218-222.

Benson, L. 1961. A revision and amplification of Pediocactus I. Cactus & Succ. J. 33: 49-54.

Benson, L. 1962a. A revision and amplification of Pediocactus II. Cactus & Succ. J. 34: 17-19.

Benson, L. 1962b. A revision and amplification of Pediocactus III. Cactus & Succ. J. 34: 57-61.

Benson, L. 1962c. A revision and amplification of Pediocactus IV. Cactus & Succ. J. Amer. 34: 163-168.

Benson, L. 1982. The cacti ofthe United States and Canada. Stanford U. Press, Stanford.

Butterwick, M. 1987. Bureau of Land Management's efforts to conserve Pediocactus peeblesianus var. peeblesianus (Cactaceae). pp. 257-262 in Elias, T.S. (ed.). Conservation and management of rare and endangered plants. California Native Plant Society, Sacremento.

Dirzo, R. 1984. Herbivory: a phytocentric overview. Ch. 7 In Dirzo, R. and J. Sarukhan (eds.). Perspectives in plant population ecology. Sinauer Assoc. Inc., Sunderland.

Heil, K.D., B. Armstrong & D. Schleser. 1981. A review of the genus Pediocactus. Cactus & Succ. J. Amer. 53: 17-39.

Menges, E.S. 1986. Predicting the future of rare plant populations: demographic monitoring and modeling. Natural Areas J. 6: 13-25.

Olwell, P., A. Cully, P. Knight & S. Brack. 1987. Pediocactus knowltonii recovery efforts. pp. 519-522 in Elias, T.S. (ed.). Conservation and management of rare and endangered plants. California Native Plant Society, Sacremento.

Osborn, M.M., P.G. Kevan & M.A. Lane. 1988. Pollination biology of Opuntia polyacantha and Opuntia phaeacantha (Cactaceae) in southern Colorado. Plant Syst. Evol. 159: 85-94.

Phillips, B.G., A.M. Phillips & M. Butterwick. 1984. Peebles Navajo cactus Pediocactus peeblesianus (Croizat) L. Benson var. peeblesianus recovery plan. U.S.D.A. Fish & Wildlife Service, Albuquerque, New Mexico. 58 p.

Phillips, B.G., A.M. Phillips & M. Butterwick. 1985. Recovery plan for the Brady pincushion cactus, Pediocactus bradyi L. Benson. U.S.D.A. Fish & Wildlife Service, Albuquerque, New Mexico. 58 p.

Simpson, B.B. & J.L. Neff. 1987. Pollination ecology in the arid southwest. Aliso 11: 417-440.

9. TABLES

Table 1. Summary statistics for selected morphological and habitat variables, based on the 181 individuals in the four plots. Stem diameter is in millimeters, distance between P. bradyi plants and distance to nearest other perennial species are in centimeters, and slope is degrees from horizontal. Skewness, kurtosis, and the Wilk-Shapiro statistic analyse the shape of the distribution curve for each variable. A normal distribution has a skewness of 0, kurtosis of 1.0, and Wilk-Shapiro of 1.0.

	Stem Diameter	Flower Number	Distance	Slope	Nearest Perennial
MEAN	29.47	1.18	27.55	5.02	39.93
1 S.D.	9.99	1.08	40.20	3.66	27.08
N	181	181	156	181	174
MEDIAN	30	1	7	4	37
MINIMUM	7	0	1	1	1
MAXIMUM	56	5	185	15	110
SKEWNESS	0.004	0.065	2.003	0.966	0.696
KURTOSIS	-0.046	+0.006	3.876	-0.214	-0.154
WILK-SHAPIRO	0.992	0.862	0.706	0.866	0.932

Table 2. Matrix of Pearson's product-moment correlation coefficients between all possible pairwise combinations of the five variables listed.

	Diameter	Flownumb	Distance	Slope	Nearest
Diameter	1.000				
Flownumb	0.753	1.000			
Distance	0.106	0.026	1.000		
Slope	0.020	-0.035	0.066	1.000	
Nearest	0.021	0.015	-0.240	-0.234	1.000

Table 3. Results of a simple linear regression of flower number against the predictor variable stem diameter.

VARIABLE	COEFFICIENT	STD ERROR	STUDENT'S T	P
Constant	-1.2405	0.1624	-7.64	<0.0001
Stem diameter	0.0822	0.0052	+15.75	<0.0001
N		181		
Degrees of Freedom		179		
Overall F		248.1		
Adjusted R^2		0.5785		
R^2		0.5809		
Residual Mean Square		-0.0489		

Table 4. Nearest neighbor summary for each of the 181 individuals of P. bradyi. For each individual, the nearest perennial individual of a species other than P. bradyi was measured to the nearest centimeter. Individuals under the canopy or touching other plants were arbitrarily assigned a distance of 1 cm. Individuals of the two smaller species of Opuntia were not identified in the field.

Species	Number	% of total
Atriplex confertifolia	95	55.0
Eriogonum inflatum	30	18.0
Ephedra viridis	11	6.0
Opuntia erinacea	11	6.0
Hilaria jamesii	9	5.0
Opuntia phaeacantha/polyacantha	9	5.0
Echinocereus triglochidiatus	3	2.0
Erioneuron pulchellum	1	1.0
Hymenopappus filifolius	1	1.0
Tiquila latior	1	1.0

Table 5. Flower visitation numbers and efficiency (determined as flower parts contacted by body of insect) in three potential pollinators of *P. bradyi*. No data were collected on time in flower for *Apis*. Symbols are A=androecium, G=gynoecium, PO=petals only, Ef=efficiency (number of times A&G/total visits), average time in seconds in flower, and sample size for the times.

Pollinator	A	G	PO	A&G	Ef	time	N
Apis mellifera	0	0	0	16	100%	-	16
Apagostemon sp.	9	0	0	7	44%	47.0	16
Dialictus sp.	23	0	7	9	23%	26.8	46

Table 6. Insect visitation schedule for a single, recently opened (first day) flower of P. bradyi. The total observation time was one hr. Symbols are A = androecium, G = gynoecium, PO = petals only, Ap = Apagostemon sp., Di = Dialictus sp., X = contacted by insect. Time In is amount of time in flower in seconds.

Sequence	A	G	PO	Time In	Species
1	X	X	-	215	Ap
2	X	-	-	120	Di
3	X	X	-	35	Di
4	X	-	-	24	Di
5	-	-	X	1	Di
6	-	-	X	10	Di
7	-	-	X	69	Di
8	X	X	-	45	Di
9	X	-	-	24	Di
10	X	-	-	23	Di
11	X	-	-	20	Di
12	X	-	-	10	Di
13	X	X	-	15	Di
14	X	-	-	1	Di
15	-	-	X	1	Di
16	-	-	X	58[a]	Di
17	X	X	-	18[a]	Di
18	X	-	-	46[b]	Di
19	X	-	-	35[b]	Di

20	X	X	-	7	Di
21	X	-	-	7	Ap
22	X	-	-	10	Di
23	X	-	-	19	Di
24	X	-	-	9	Di
25	X	-	-	30	Di
26	X	-	-	110	Di
27	X	-	-	3	Di
28	X	-	-	16	Di
29	X	X	-	24	Di
30	X	-	-	7	Di

---

[a]visitors 15/16 overlapped

[b]visitors 17/18 overlapped

Table 7. Motile stamen experiments on flowers one through three. Reaction time after being touched by forceps, and time to regain original position, are noted.

Test No.	Closing Time (seconds)	Opening Time (minutes)
	FLOWER 1 (open 2-3 days)	
1	10	8
2	10	10
3	not responding well	>15 (not responding well)
4	8	9
5	no response	no response
	FLOWER 2 (open 2-3 days)	
1	12	7
2	9	13
3	9	not responding well
4	no response	no response
	FLOWER 3 (open 2-3 days)	
1	18	7
2	15	8
3	25	>15 (not responding well)
4	23	8
5	22	>15 (not responding well)
6	15	no response

Table 8. Motile stamen experiment on flower four. The first seven tests were done with forceps, while the last six were done by introducing a single insect visitor to the flower at the start of each test. The flower had opened the morning of the experiment. Time is the start of each test. * indicates no observations made.

Test No.	Closing Time (seconds)	Time	Opening Time (minutes)
	MECAHNICAL MANIPULATION		
1	10	1036	22
2	27	1103	7
3	15	1112	14
4	20	1130	8
5	25	1141	7
6	51	1159	10
7	40	1215	*
	INSECT MANIPULATION		
8	9	1227	10
9	12	1238	9
10	16	1251	12
11	11	1304	11
12	9	1316	8
13	9	1324	12

10. FIGURES

Figure 1. The Lee's Ferry location and study plots (numbered 1-4).

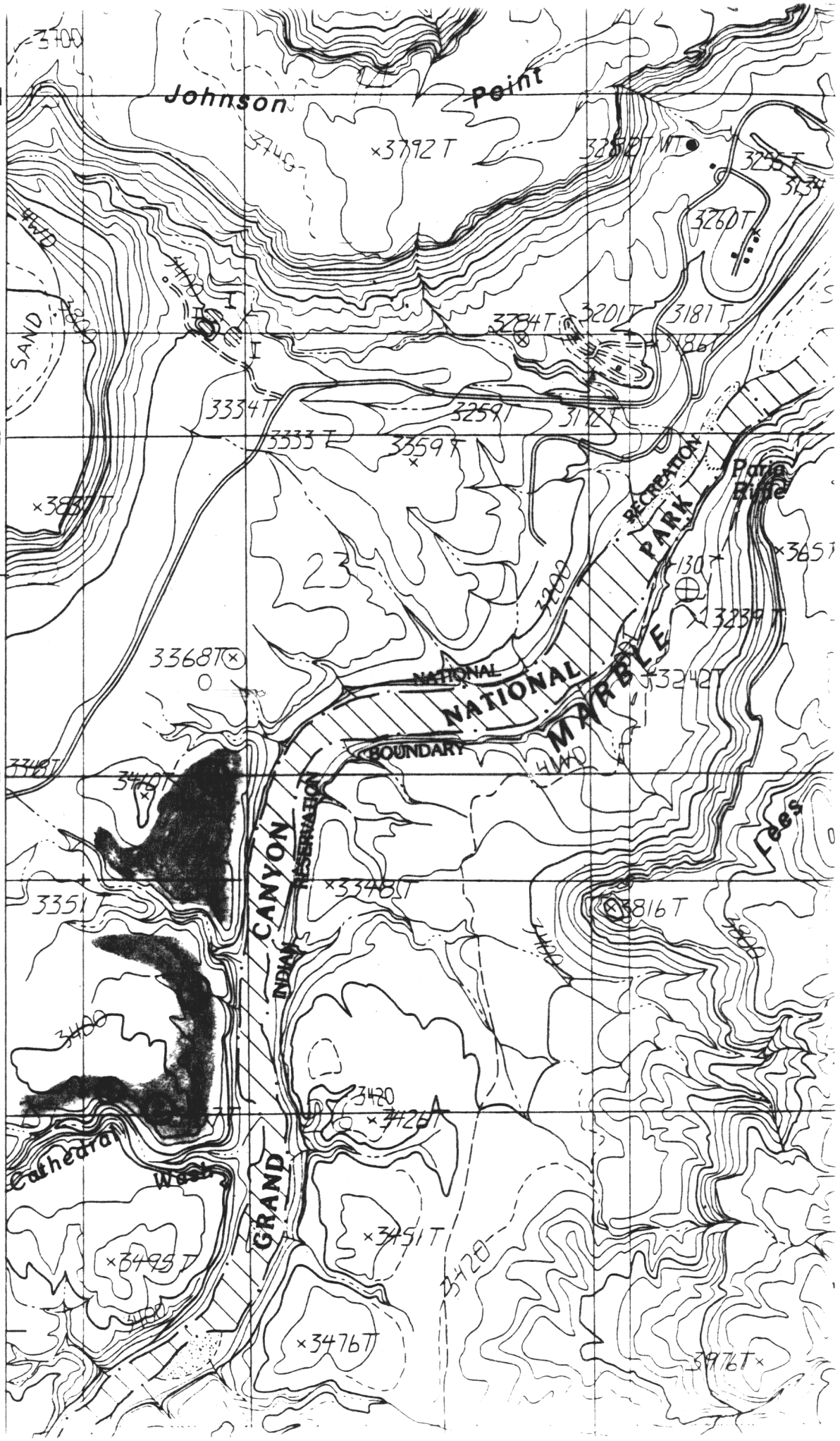
Figure 2. Size-frequency distribution for the entire population, with number of plants on the Y axis and stem diameter in mm on the X axis.

Figure 3. Size-frequency distribution for flowering and vegetative (non-flowering) individuals, with number of plants on the Y axis and stem diameter in mm on the X axis.

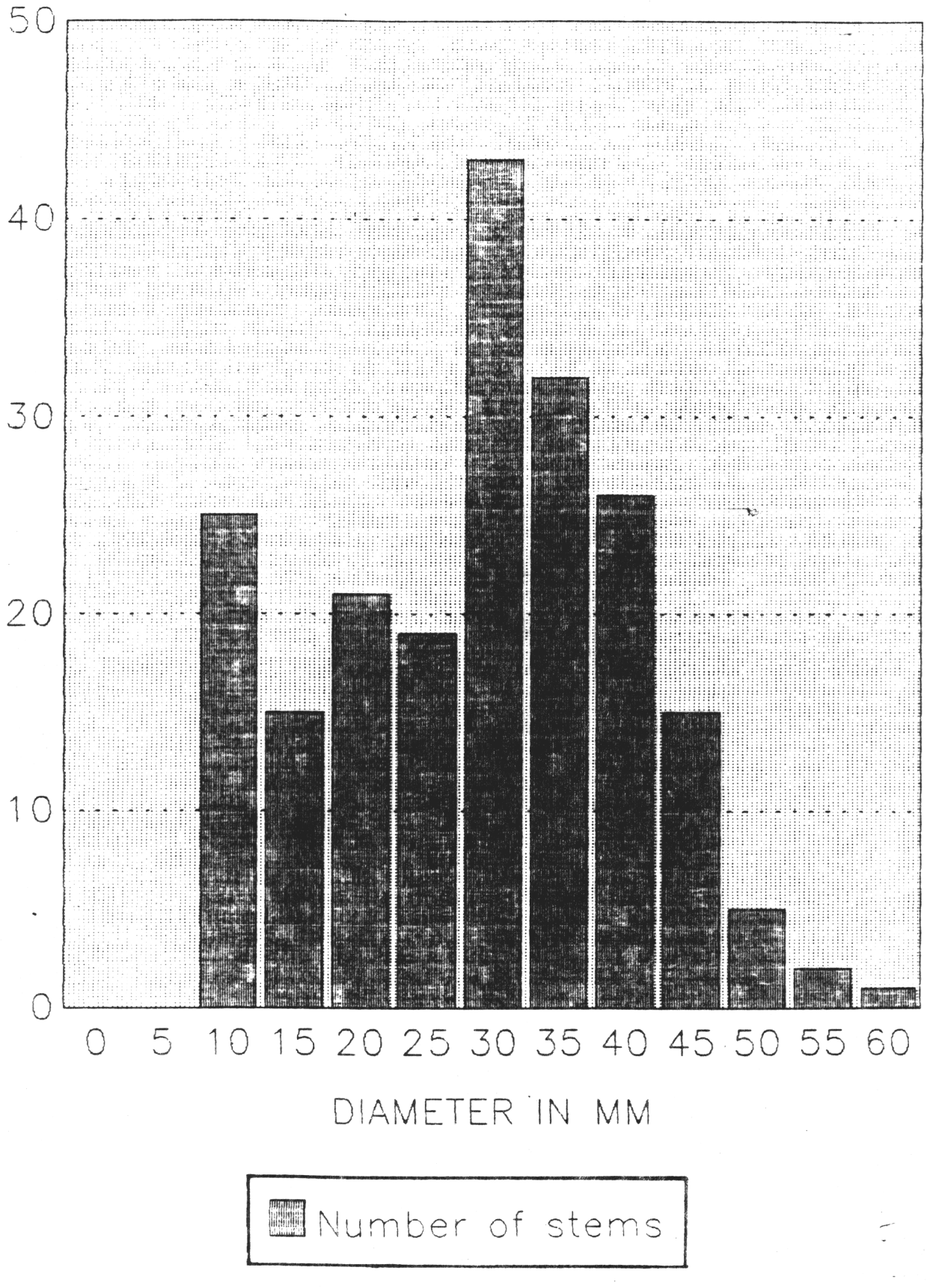
Figure 4. Plot of predicted number of flowers per plant against stem diameter in mm. The equation obtained from a least-squares linear regression is shown.

Figure 1

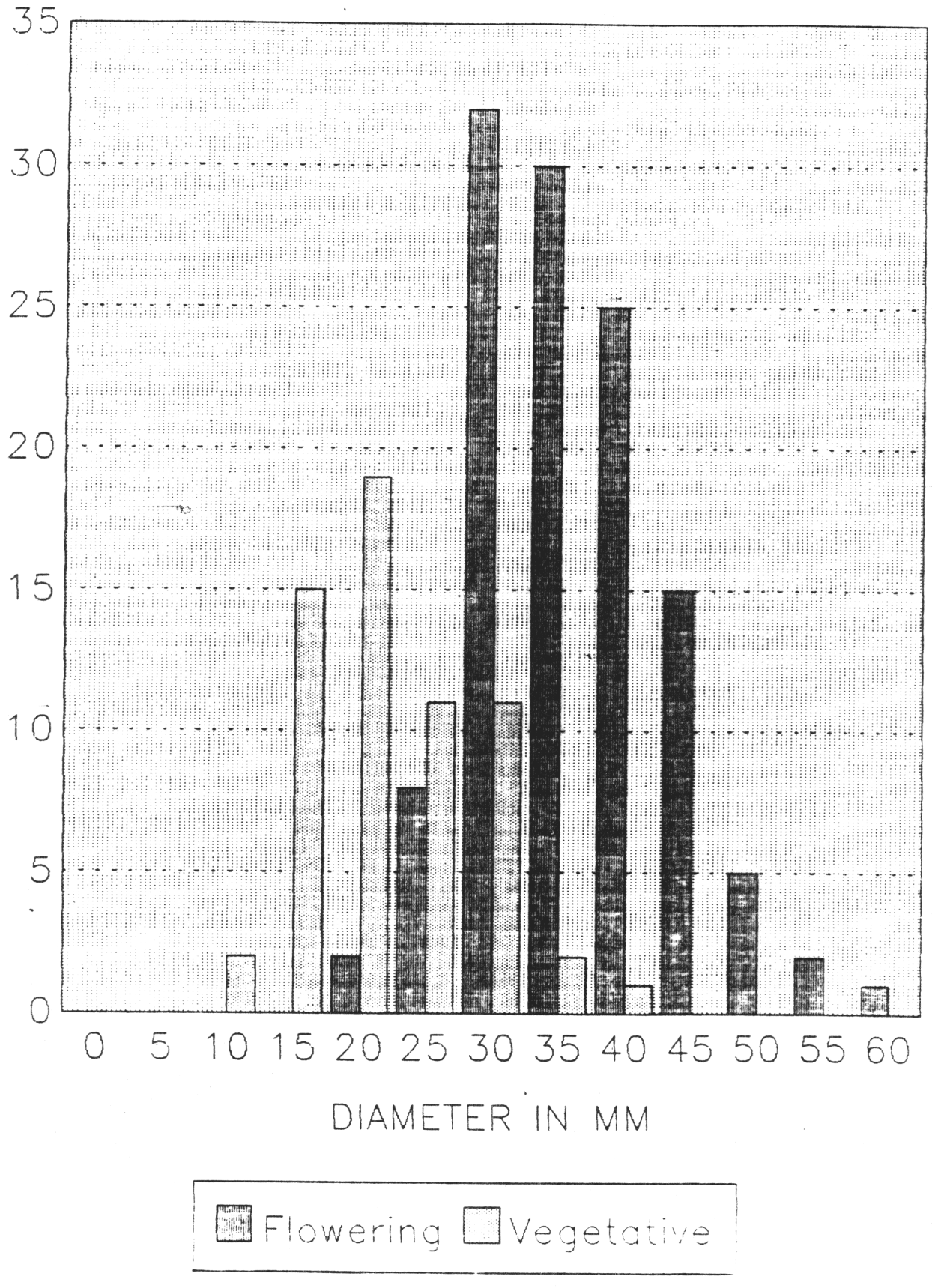
Study location and plots



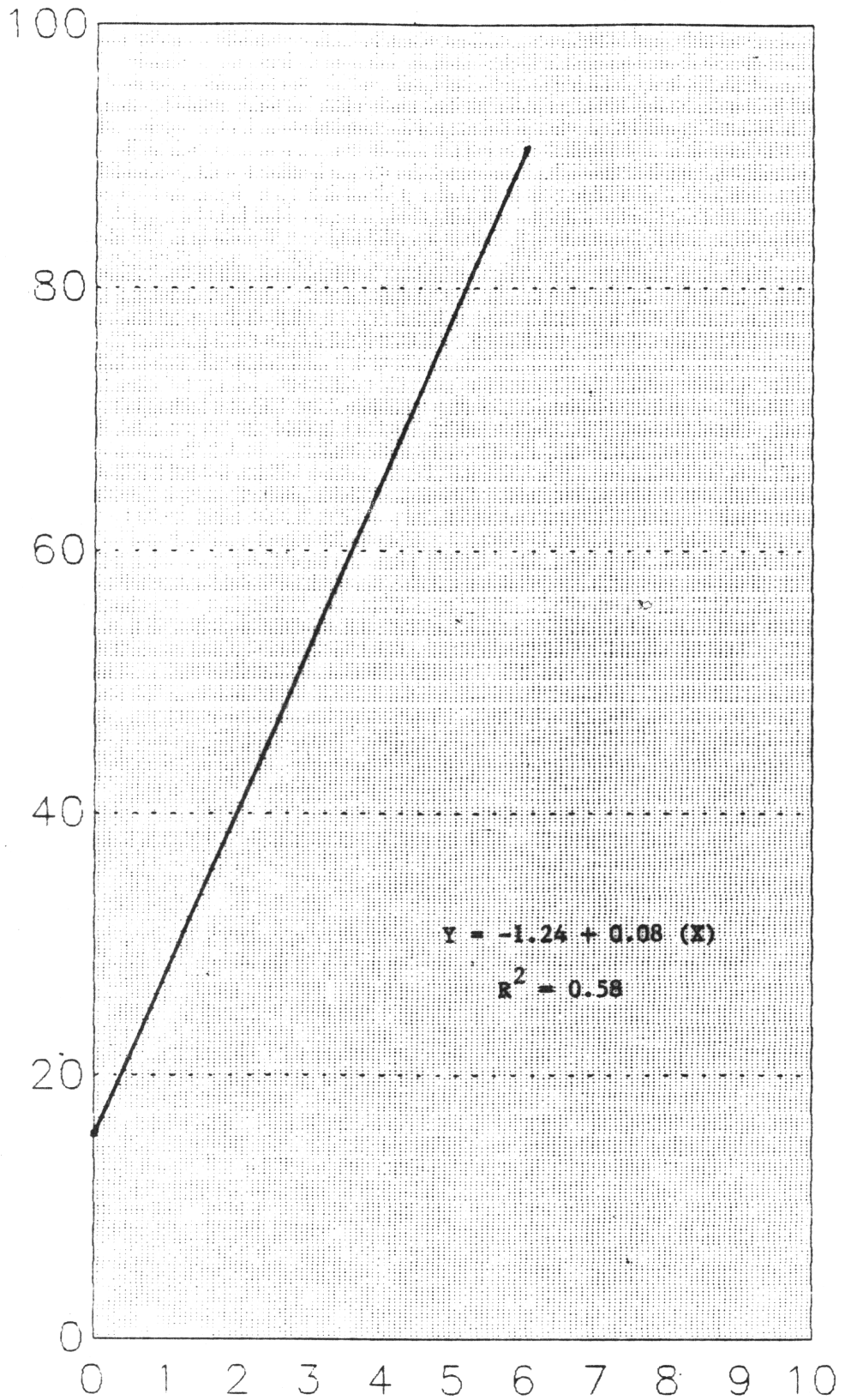
SIZE–FREQUENCY DISTRIBUTION



SIZE–FREQUENCY DISTRIBUTION



FLOWER NUMBER (X) vs DIAMETER (Y)

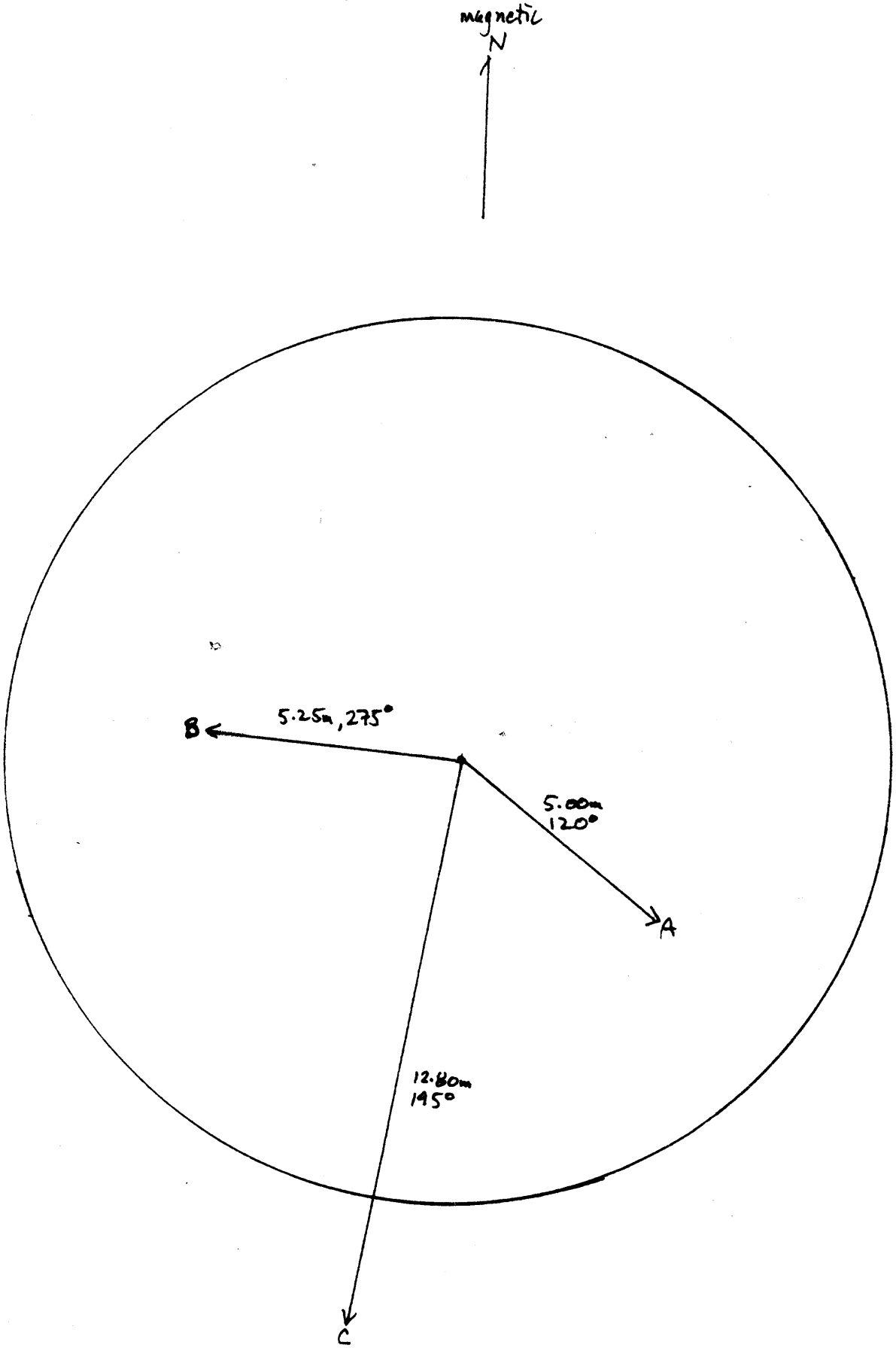


11. APPENDIX

The positions of individual plants or groups of plants are found on the accompanying sketches. For each plant or group, distance from the center stake and bearing in degrees (magnetic) is shown on the circular plot. Maps of plants in alphabetical groups are also shown (not to scale) on the quadrat/study plot maps of individuals. For all maps, magnetic north is at the top of the sketch. For the quadrats of groups of plants, the distance to the stake is at the center of the sketch, unless otherwise indicated. If no quadrat sketch is shown for a particular letter-distance combination, this indicates that a single plant is represented by the letter. In a few cases letters were skipped during field work.

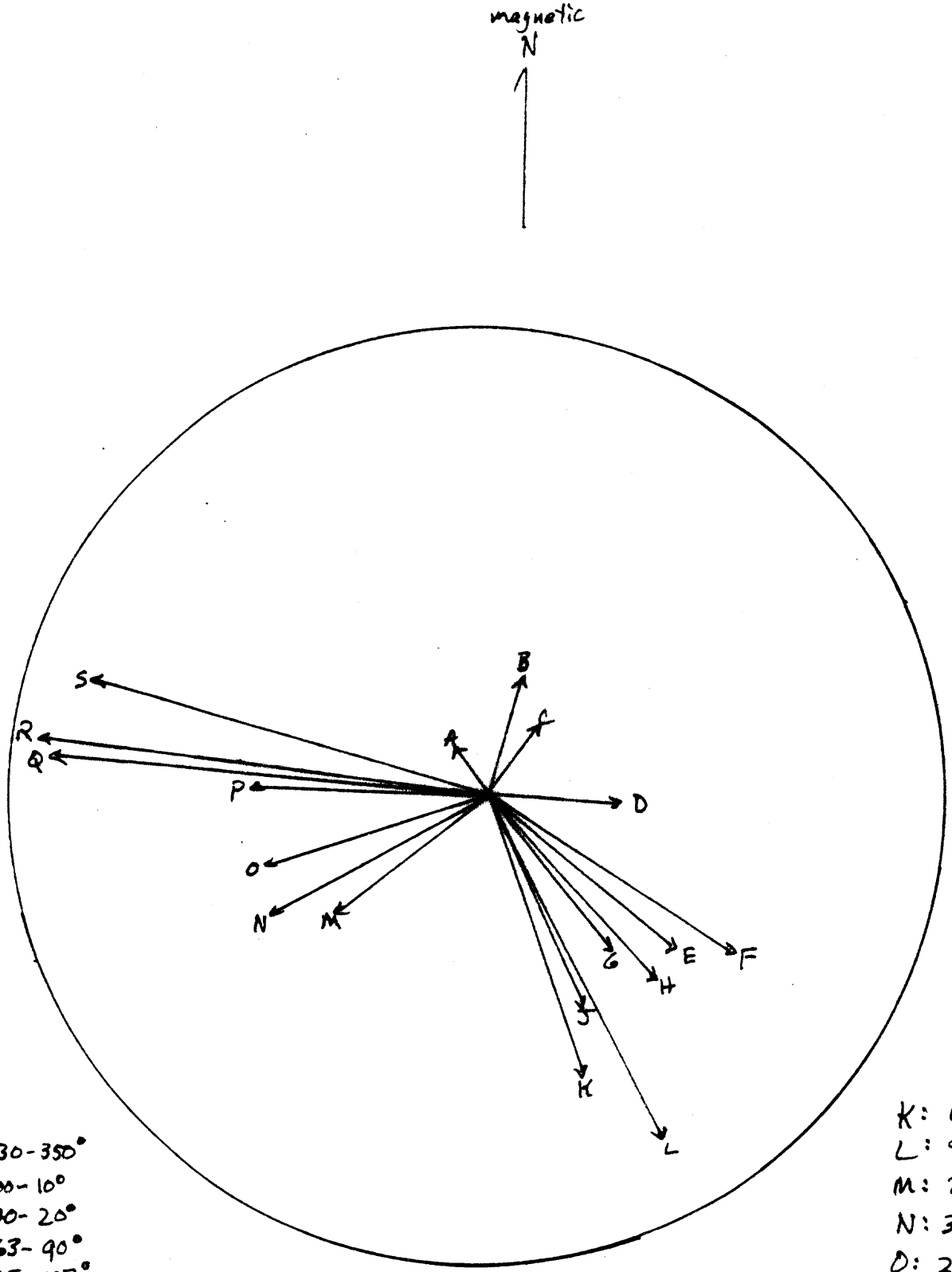
Species: Ferocactus wislizeni

Location: Lee's Ferry - GLCA Site No: Plot 1



Species: Pediocactus bradyi

Location: Lee's Ferry – GLCA Site No: Plot 2

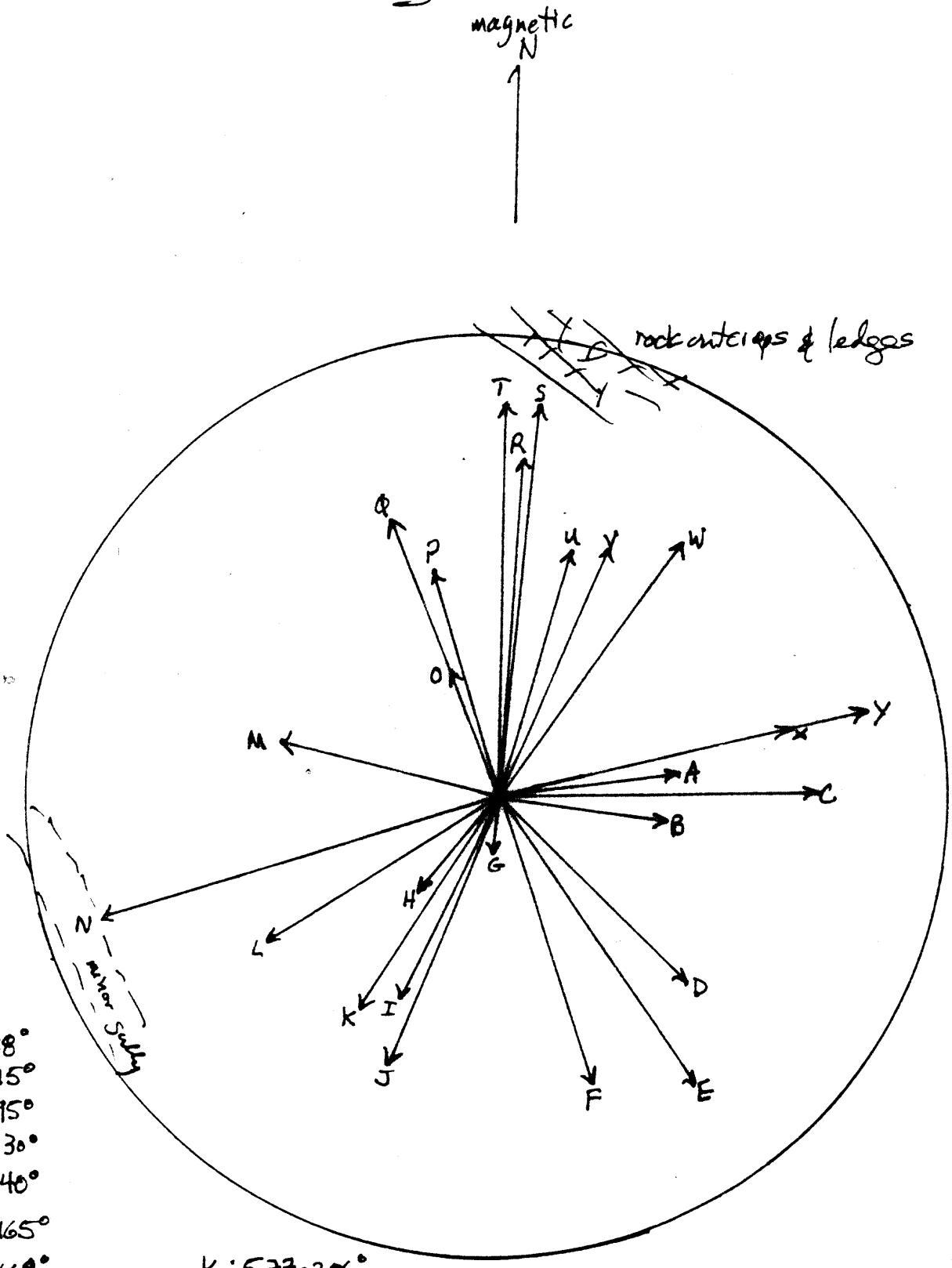


A: 0.30-350°
B: 3.00-10°
C: 2.70-20°
D: 2.63-90°
E: 6.35-107°
F: 7.32-105°
G: 4.72-120°
H: 5.25-115°
J: 6.52-127°

K: 6.40-130°
L: 8.25-120°
M: 2.85-224°
N: 3.42-230°
O: 2.60-246°
P: 2.81-288°
Q: 8.68-292°
R: 9.76-295°
S: 8.25-305°

Species: Leucocrinus gracilis

Location: Lees Ferry - GLCA Site No: Plot 3



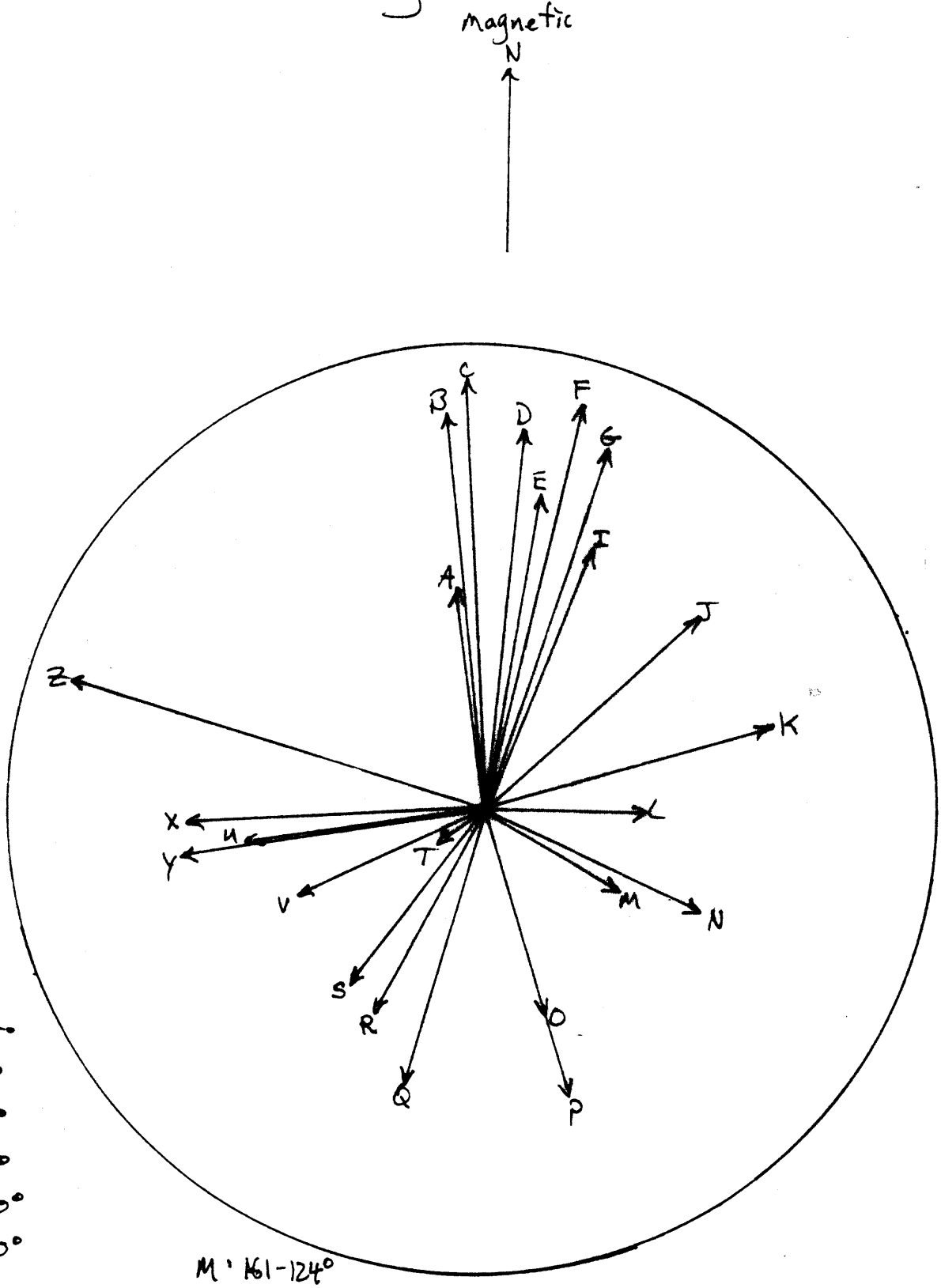
A: 2.40-88°
B: 2.10-115°
C: 7.36-95°
D: 6.60-130°
E: 8.40-140°
F: 6.50-165°
G: 0.90-168°
H: 1.45-210°
I: 3.00-195°
J: 4.88-189°

K: 5.77-206°
L: 5.24-230°
M: 3.95-285°
N: 8.60-255°

O: 1.75-345
P: 4.70-348
Q: 5.80-345°
R: 5.97-12°
S: 8.40-14°
T: 9.15-11°
U: 5.15-25°
V: 5.93-35°
W: 6.50-45°
X: 6.12-80°
Y: 7.10-80°

Species: Feathered Dalea

Location: Lee's Ferry - GLCA Site No: Plot 4



A: 3.30-355°
B: 7.80-355°
C: 9.63-0°
D: 8.48-10°
E: 5.36-15°
F: 8.90-20°
G: 9.33-30°
H: —
I: 5.15-38°
J: 7.68-58°
K: 6.15-70°
L: 1.90-88°

M: 161-124°
N: 2.47-115°
O: 3.05-155°
P: 5.42-155°
Q: 7.50-200°

R: 6.30-20
S: —
T: 0.30-20
U: 5.00-25
V: 3.63-23
W: —
X: 5.50-26
Y: 6.30-25
Z: 9.00-29