Demography of Endemic Psammophytes, Eureka Valley, California

II

Survivorship, Seed Bank Dynamics and Frequency of Establishment

by

Bruce M. Pavlik
Department of Biology
Mills College
Oakland, California 94613

and

Michael G. Barbour
Department of Botany
University of California
Davis, California 95616

for

State of California
Department of Fish and Game
Endangered Plant Program
Sacramento, California

funded by

U. S. Fish and Wildlife Service
Contract EP85 IV-1
December 1986

Preface

The management recovery plant for the Eureka Dunegrass (Swallenia alexandrae Soderstrom and Decker) and the Eureka Evening Primrose (Oenothera avita ssp. eurekensis W. Klein) specified the need for a monitoring program that could provide long-term, quantitative data on these species populations (DeDecker 1981). These data could indicate the "post-preservation" status of Swallenia and Oenothera, suggest management guidelines for the dune endemics and lead to a general design for monitoring programs that could be used with other rare and endangered taxa.

In part I of the present series of studies on the demography of the Eureka Dune endemics, Pavlik and Barbour (1985) reported on the results of field and laboratory work conducted during the period of February to August 1985. The main topics of that research were seed production, dispersal and the effects of herbivores on the species populations, including the rare Astragalus lentiginosus var. micans Barneby (also endemic to Eureka Dunes). Recommendations were made for further investigations regarding other aspects of these species. The specific objectives of the present proposal were developed from those recommendations. The objectives include; 1) a continuation of the demographic monitoring of seedlings and juveniles (from a late summer 1984 germination event) that was begun last year (1985) in permanent census plots, 2) continuation of the demographic monitoring of mature and senescent individuals that was begun last year in those same census plots, 3) an analysis of macroclimatic records in an effort to characterize the conditions of summer and fall 1984 that led to a rare mass germination of all three species and to determine the frequency of those conditions over longer periods of time, 4) an analysis of seed bank composition to determine the number of viable progeny stored within the substrate, and 5) a laboratory experiment that will give some indications of long-term seed viability under optimal conditions. Objectives 1 and 2 are incorporated into Chapter 1, 4 and 5 in Chapter 2 and objective 3 in Chapter 3 of this report. In addition, Appendix A provides more data on seed production and seed rain and Appendix B is a copy of the paper presented at the CNPS conference on the conservation and mangement of rare plants in California[1]. Appendix B is included to provide a summary paper that combines results from the 1985 and 1986 studies.

Acknowledgements

We gratefully acknowledge the field assistance of Lauren Krieger and Eileen Manning, students of biology at Mills College. Lauren also conducted many of the studies on seed biology, including such aspects as germination and viability, seed bank composition and seed predation <u>in situ</u>. Finally, the support of Susan Cochrane of California Fish and Game, Office of Endangered Species, is especially appreciated.

---

[1] Rare and Endangered Plants: A California Conference on Their Conservation and Management. November 1986, Sacramento CA. California Native Plant Society.

Chapter 1:

Survivorship

Introduction

Demographic studies of plants indicate that each species population can possess unique attributes that ultimately determine local abundance and/or persistence through time (Harper 1977). A thorough analysis of these attributes is of primary importance in the management of endangered populations simply because abundance and persistence are at the center of all recovery efforts. Such efforts are usually undertaken once the threat of human disturbance has been minimized (by various land-use restrictions) so that management requires a knowledge of the population's status (whether it is declining, stable or growing) under the most "natural" of conditions. This determination can be made by selecting a few, relevant and related population attributes and conducting a demographic monitoring program (Pavlik 1987). The purpose of this paper is to illustrate the use of survivorship, seed production, seed bank and temporal establishment data for addressing the status of three endemic populations at Eureka Dunes, Inyo County, California. The Eureka Valley populations comprise the entire known distribution of <u>Swallenia</u> <u>alexandrae</u> (Soderstrom and Decker), <u>Oenothera</u> <u>avita</u> ssp. <u>eurekensis</u> W. Klein and <u>Astragalus</u> <u>lentiginosis</u> var. <u>micans</u> Barneby, all of which are suffrutescent perennials restricted to deep, windblown accumulations of sand (Pavlik 1979a,b).

Methods and Materials

<u>Establishment of the demographic plots.</u> In February 1985 three sites were established on the northwest flank of the main dune (Figure 1) in an area that has been extensively studied in the past (Henry 1976, Pavlik 1979a, 1979b, 1980, Pavlik and Barbour 1985). The sites were chosen so that each represented one of

the study species according to the following criteria; 1) the species population was composed of at least 150 individuals from all age/size classes, 2) the population was located in a dune habitat typical of the species (e.g. steeper, less stable slopes for Swallenia and lower, more stabilized slopes for Oenothera and Astragalus (DeDecker 1976, Pavlik 1979a)), 3) germinule and seedling densities were similar to those observed in other parts of the dune system and 4) the site was a considerable distance from footpaths used by dune visitors.

At each site a large plot was randomly positioned with its lower boundary oriented along a 60^0 compass bearing. Plot size varied among the three species (Figure 2) and reflected differences in the size and density of individual plants (Mueller-Dombois and Ellenberg 1974). The corners of the plots were marked with 0.5 cm diameter stainless steel rods that were threaded over their entire length and had a 8 cm diameter hook on one end. These rods could be screwed into the sand for a distance of about 30 cm leaving the hooked end exposed. They were used to attach sampling tapes during subsequent visits and insure that the relocation of subplots could be accurately achieved. The markers were left in place after the 1986 field season.

Swallenia - The upper plot contained the Swallenia subpopulation and was 50 m X 50 m (2500 m^{-2}). Its western half was dominated by a large, gently contoured valley whose longitudinal axis had a bearing of 340^0 and an average slope of 8%. The eastern half was bisected by a broad sand ridge that paralleled the adjacent valley. Sand in the valley was rather loosely aggregated, whereas that on the ridge tended tobe tightly packed in the most exposed locations. The subterranean distance to moist layers of sand appeared to be uniform throughout the plot and varied between 10 and 50 cm over the course of 1985. Dicoria canescens ssp. clarkae was the only other plant commonly found in the Swallenia plot and numerous seedlings were observed in the springs of 1985 and 1986. Relatively few of these, however, lived to bear fruit during the fall. The plot also was the site of considerable animal activity, with ample evidence of jackrabbits, kangaroo rats, kit fox, lizards, ants and beetles.

Oenothera - This plot was placed approximately 100 m downslope (north) from the Swallenia plot on a gentle (< 5%) northwest-facing slope. It was 50m X 10m (500 m^{-2}) with the long axis oriented along a 60^0 bearing. Sand packing in the plot was uniformly loose. In the western two-thirds of the plot exposed bands of moist sand were found throughout the year, indicating that dune water was in close proximity to this Oenothera subpopulation. Swallenia, Astragalus, Cleome sparsifolia, Dicoria canescens ssp. clarkae and Oryzopsis hymenoides were also found here, as were many signs of animal activity.

Astragalus - Approximately 10 m north of the Oenothera plot was the stand of Astragalus. The plot was 30m X 25 m (750 m^{-2}) with its longitudinal axis along a 60^0 bearing. There was almost no slope to the plot and the sand was uniformly loose throughout. The distance to moist sand was greater than in the other two plots and seldom closer than 40 cm from the dune surface. Also found in this plot were Swallenia, Oenothera, Tiquilia plicata, Psorothamnus polyadenia and Oryzopsis hymenoides. Only a few signs of animals were observed here.

Demographic sampling. On five occasions during 1985 (2/15-16, 3/21-22, 4/26, 5/31-6/1 and 8/11-12) and three during 1986 (3/22-23, 5/29 and 10/4-5) the demographic plots were sampled for the number of live individuals and notes were made regarding their vigor, growth, life history stage and phenological state. Life history stages for the study plants are given in Table 1 and were developed from observations made on laboratory and field-grown plants (Pavlik 1979b). These stages included established plants (mature (M) or senescent (St)) and recruits (germinule (G), seedling (S), juvenile (J) or in the case of *Swallenia*, hummock-forming juvenile (Ⓙ)). Phenological observations followed the conventions used by Pavlik (1979a).

Swallenia - The plot was subsampled using 10 strip sub-plots, each 50 m X 1m (50 m^{-2}) that extended upslope from the baseline (Figure 2). These were randomly located in February 1985, but from then on they became the permanent subplots. The centers of subplots were located 4, 9, 15, 19, 24, 28, 36, 38, 43, and 48 m from the NE corner of the plot. Subplots 4, 9, and 15 were on the east-facing slope of the sand ridge, 19, 24, and 28 were on crest of the ridge itself and subplots 36, 38, 43 and 48 were in the broad valley. Each time the census was taken, a scaled map of each subplot was generated by marking the location of live and dead individuals rooted within the subplot. A plant was considered dead if it possessed no green tissue during the March-November growing period or if it could not be found in its previous location. Certain large individuals were staked as reference points and the locations of other landmarks (e.g. distinctive clusters of *Dicoria* seedlings) were noted. This allowed the fates of individual plants to be accurately monitored throughout the study. Attempts were made to tag all plants in addition to mapping, but this effort was defeated when wind storms (or possibly vandals) removed the 30 cm wire stakes that held the tags.

Oenothera - The plot was subsampled using 15 subplots, each 10m X 1m (10 m^{-2}) and oriented with the long axis upslope from the baseline. These were randomly located in February 1985, but from then on they became the permanent subplots. The centers of subplots were located 5, 8, 10, 12, 13, 16, 20, 23, 24, 26, 29, 32, 35, 39, 42 and 48 m from the NE corner of the plot. Subplots 29-48 were closest to the exposed bands of water-bearing sand. Each time a census was taken a map of each subplot was generated by marking the location of live and dead individuals rooted within the subplot. A plant was considered dead if it possessed no green tissue during the year or if it was not found in its previous location. Certain large individuals were staked as reference points and photographed repeatedly during the study period. This allowed the fates of individual plants to be accurately monitored. Attempts were made to tag plants in addition to mapping, but this effort was defeated when wind storms removed the 30 cm wire stakes that held the tags.

Astragalus - Unlike the previous plots, that of Astragalus was not subdivided into subplots. It was completely surveyed because the density of plants was not very high and each individual was conspicuous. It was possible to accurately map every individual in the plot, including germinules and seedlings. Landmarks were also used here, including some distinctive clumps of Psorothamnus and Oryzopsis. A plant was considered dead if it possessed no green tissue during the year or if it could not be located in its previous location. Attempts were made to tag plants in addition to mapping, but this effort was defeated when wind storms removed the 30 cm wire stakes that held the tags.

Data analyses. Plots of time (days since the February 1985 census) versus the number of living individuals were made using the 1985-86 census data. These plots represented true survivorship curves for young plants (recruits) of Swallenia, Oenothera and Astragalus (germinules, seedlings and juveniles) that were established as a single cohort after the fall 1984 germination event. Plots for older, established plants (mostly mature and senescent individuals) of the three species represented population depletion curves because these individuals may have been from different cohorts of various ages (Harper 1977). It was then possible to calculate half-lives (the time in which a population decreases by 50%) and persistence (the time in which a population decreases by 100%) for whole populations or for subpopulations at different life history stages (Harper 1977, Hutchings 1986). It should be emphasized that calculations of population persistence are most tenuous for long-lived perennials because of excessive extrapolation beyond the limits of the data. Persistence will only be used, therefore, as a rough guess at the time required for a population to go extinct in the absence of recruitment.

Results and Discussion

Changes in the total Swallenia population (□ , Figure 3) were largely the result of mortality experienced by the fall 1984 cohort of germinules, seedlings and juveniles (■). Field observations indicated that the most common cause of death was uprooting and mechanical damage associated with the windstorms of March and April 1985. Sand abrasion did not appear to be a major factor because seedling tissues remained intact and unscarred after death. This may be due to the unusual degree of anatomical sclerification noted by Pavlik (1979a). After nearly two years, 24 percent of the 1984 cohort had survived and grown into hummock-forming juveniles. During this time the cohort was dominated by seedlings (S) in the late winter of 1984-85, juveniles (J) for the next 400 days and finally hummock-forming juveniles (Ⓙ) 600 days after establishment of the study plot. One mature hummock was judged as entering the senescent stage and four hummocks died so that 92 percent of the mature and senescent plants (▲) were still alive at the end of the study. The total population was more than twice its original size two years after the fall germination event.

Oenothera produced cohorts of seedlings in both years of the study (Figure 4). Only 4% of the winter 1984-85 cohort survived until the next year (thus, the truely perennial population was very small). There was no obvious cause of mortality in the cohort except that germinules and seedlings were susceptible to burial by moving sand. The clumped nature of young plants (usually localized around dead adults from the previous year) may have contributed to density-dependent mortality factors, but data are lacking. Despite high mortality, nearly 75 percent of the cohort had produced large amounts of seed during 1985 (see Pavlik and Barbour 1985). Under laboratory conditions it has been observed that *Oenothera* can flower 3 months after germination (Pavlik 1979b), thus confirming the precocious nature of this taxon. The winter 1985-86 cohort had higher survivorship (41 percent) a lower percentage of reproductive individuals (48) and was comprised of smaller mature plants (mean canopy volume (Vc) = 12 dm^3) than the 1984-85 cohort (mean Vc = 60 dm^3).

The establishment/survivorship pattern observed for *Astragalus* (Figure 5) was similar to that of *Oenothera*, except that none of the winter 84-85 cohort survived or reproduced. This population crash occurred 145 days after plot establishment and probably resulted from severe wind storms in March and April and the onset of high temperatures during May. Seedling survivorship was much higher in 1986 (54%) but none of these had reproduced within the year. Like *Swallenia*, survivorship of mature *Astragalus* plants was high (69 percent) thereby making a large population of perennial individuals. If even half of the 1986 cohort survived another year (likely in that they already survived the first summer), then the established Astragalus population would more than double in size.

Survivorship data are re-interpreted in Figure 6 as the mean mortality (1985 and 1986) experienced by each life history stage. Mortality was generally low (< 25 percent) and constant for Swallenia, although data from the germinule stage are lacking. This stage was still present in February 1985 but only represented by a total of 12 individuals. In contrast, mortality was high (25-80 percent) and increasing with age for Oenothera. High mortality in the mature and senescent stages lead to a small carry-over of established individuals from year to year (although this does not preclude perennation by rootstocks or branchling formation, see below). Astragalus germinules were produced in enough numbers to allow calculation of mortality at that stage. Mortality was extremely variable (15-95 percent) and perhaps declined with age for the locoweed.

Half-lives for recruits, established (adult) plants and the total population were derived from survivorship data (Table 2). The values for Oenothera and Astragalus were similar and about half those of Swallenia. Swallenia half-lives compare favorably with those of non-endangered perennial grasses from arid environments (0.5-4.5 years, Table 3). Those of Oenothera and Astragalus, however, are on the low end of the spectrum for non-endangered herbaceous perennials (0.5- >50 years, Table 3). Extrapolating until the time of population extinction (potentially erroneous but nevertheless valuable for comparative purposes), established Swallenia populations might persist for as long as 88 years in the absence of recruitment while Oenothera and Astragalus might persist from 3 to 16 years. Indeed, individual Swallenia hummocks have been directly observed for as long as 12 years with little indication of senescence (M.A. Henry, personal communication) whereas Oenothera and Astragalus individuals have only been directly observed for 6 years prior to death (personal field notes).

Table 2. Half-lives and persistence (both given in years) of the endemic populations at Eureka Dunes. The total population has been subdivided into life history stages for further analysis. See text for explanation of symbols.

	Recruit (G + S + J)		Established (Ⓙ + M + St)		Total population (G + S + J + Ⓙ + M + St)	
	1/2 LF	P	1/2 LF	P	1/2 LF	P
Swallenia	0.5	6.4	15.9	88.4	0.8	9.2
Oenothera	0.3	2.4	*	*	0.4	3.2
Astragalus	0.3	2.4	2.7	15.8	0.4	5.5

* = insufficient data (too few established individuals)

The contribution of branchling formation to the population dynamics of Oenothera is shown in Figure 7. Branchlings were formed in the late spring and early summer of 1985 and 1986 and increased the size of the total population by an average of 82% at those times. The effect of branchlings on the total population half-life was small (0.45 years vs. 0.4 years, Table 2) owing to the late timing of their production. The effect on persistence of the total population, however, was much more substantial and resulted in an increase of nearly a year (4.1 vs 3.2 years, Table 2).

Table 3. Half-lives (given in years) of non-endangered plants that may be comparable to the Eureka Dune endemics.

Arid-land perennial grasses		
Stipa variabilus	0.5	(Williams 1970)
Bouteloua filiformis	0.8	(Canfield 1957)
Enteropogon acicularis	4.5	(Williams 1970)
Mesic-meadow herbaceous perennials		
Polygonum viviparum	0.5	(Linkola 1935)
Geum rivale	2.0	" "
Filipendula vulgaris	18.4	(Tamm 1956)
Sanicula europaea	>50.0	" "

Conclusions and Management Recommendations

1) From the standpoint of population dynamics, Oenothera appears to be the most endangered of the three Eureka Dune endemics. Recruits and adults experience the highest mortality rates and have very short half-lives when compared to Astragalus and Swallenia or to other non-endangered herbaceous perennials. In the absence of evidence for other compensating demographic factors, the observation of high mortality rates and short half-lives would mandate intensive efforts to enhance the primrose population by increasing survivorship and reproductive output. It is clear, however, that there are compensating factors that enable Oenothera populations to persist despite an apparently high turnover of individuals.

These factors include; 1) the ability to produce branchlings (by vegetative segmentation) that spread the risk of genet mortality between potentially numerous ramets (thus increasing survivorship and population half-life), 2) precocious and copious seed production (Pavlik and Barbour 1985, Appendix A this volume), 3) low post-dispersal seed mortality due to predators (Chapter 2 this volume), and 4) long-lived seeds (Chapter 2 this volume). Species populations like those of Oenothera are in a continual state of fluctuation but are capable of replenishment by vegetative segmentation, seed production and maintaining seed bank "assets". For such dynamic populations we simply cannot document growth or stability over a two year period. It can be said, however, that the present studies of Oenothera did not reveal any intrinsic obstacles to population replenishment and subsequent growth or stability. Intensive management and efforts to enhance the Oenothera population by experimental manipulation, therefore, seem unwarranted at present. This conclusion assumes that extrinisic endangerment factors will remain under strict control. Of primary concern here are the status of Oenothera pollinators (Pavlik and Barbour 1985), the watershed management practices affecting dune hydrology (Pavlik and Barbour 1985) and human disturbance (Pavlik 1979b). The latter two can by minimized by regional planning, management and enforcement, but adequate protection from human disturbance must be maintained if populations of Oenothera avita ssp. eurekensis are to be regarded as secure. Occasional monitoring in the future is necessary in order to verify these conclusions and the techniques upon which they are based.

2) The characteristics of the Astragalus population are somewhat similar to those of the Oenothera population. Mortality can be high, especially in the younger life history stages, and the population is relatively short-lived

when compared to non-endangered taxa. But again, there appear to be compensating demographic factors. Astragalus individuals produce large numbers of seeds and can do so in successive years. These seeds are long-lived and can disperse in order to minimize post-dispersal predation (Pavlik and Barbour 1985). Germination is in response to late fall or winter precipitation, an event that can occur quite often in the northern Mojave desert. During this study, germination was observed in both years and the population of established plants doubled as the result of the 1985 germination event. Once established (juvenile stage and beyond), individuals may live for three to sixteen years (4-6 years has been directly observed) and flower nearly every year. Therefore, we conclude that because the Astragalus population grew during the study and because no intrinsic obstacles to population growth were observed, intensive mangement of the population is not warranted if human disturbance continues to be minimized. It should be noted, however, that of the three Eureka endemics, Astragalus is geographically the most restricted. Although populations have recently been observed at the Saline Spur locality (Mark Bagley, Bishop, CA, personal communication 1986), none occur at the Marble Canyon dunes where populations of Swallenia and Oenothera are large (personal observation 1985). This makes protection of the Eureka and Saline Spur populations even more critical for the preservation of Astragalus.

3) Swallenia experiences the lowest mortality and has the longest half-life of all three endemics. Its half-life compares favorably with other non-endangered perennial grasses from arid habitats. The established population doubled during this study as the result of the 1984 germination event. This result, in and of itself, suggests that the Eureka Dune populations of Swallenia are capable of growth if protected from human

disturbance. Despite rather low seed production per individual (Pavlik and Barbour 1985, Appendix A this volume), moderate rates of post-dispersal seed predation (Chapter 2 this volume) and rather infrequent germination and establishment (Chapter 3 this volume), mature individuals are long-lived and can apparently set seed every year. Those seeds escaping predation can also be long-lived and form part of a "quiescent" seed bank (Chapter 2 this volume). Therefore, the Swallenia population is growing and appears capable of maintaining itself in the future. Additional monitoring is necessary to verify these conclusions and the techniques upon which they are based.

Table 1. Characteristics of *Swallenia*, *Oenothera* and *Astragalus* plants at six demographic substages.

	germinule	seedling	branchling	juvenile	mature	senescent
general	from seed, w/ 1-2 seed leaves. surficial & unbranched root system	from seed, w/ 4-many leaves. root system deep and branched	from a stolon, rhizome or rootstock of an established plant. shoot but very little root of its own	not flowering. well branched, leafy shoots or rosette	flowering, well branched leafy shoots	large plants, few-flowered, chlorotic shoots w/ much non-psn biomass
Swallenia	w/ 1 seed leaf & up to 4 leaves. caryopsis attached, roots unbranched. 0-4 weeks old	unbranched shoot. caryopsis absent (usually). 1-12 months old	found very close to parental clone.	no fertile culms. many vigorous shoots, some branching >1 year old	fertile culms, many vigorous branched shoots.	many old culms exposed, growth is not vigorous (culm length)
Oenothera	w/ 2 attached seed leaves, 2-4 leaves. roots unbranched. 0-3 weeks old	4-16 leaves in a small rosette (< 6 cm diam.). unbranched. 1-3 months old	rosette from a branched rootstock. 4-16 leaves.	16-many leaves in a large rosette, perhaps 2-several rosettes/rootstock. > 3 months old	bolted rosette, long stems, rosettes found on apex of fl. stems	
Astragalus	w/ 2 attached seed leaves, trifoliate leaves present. 0-4 weeks old	5-7 leaflets per leaf. branching very rare. 1-3 months old	--	9-13 leaflets/ leaf. branched		

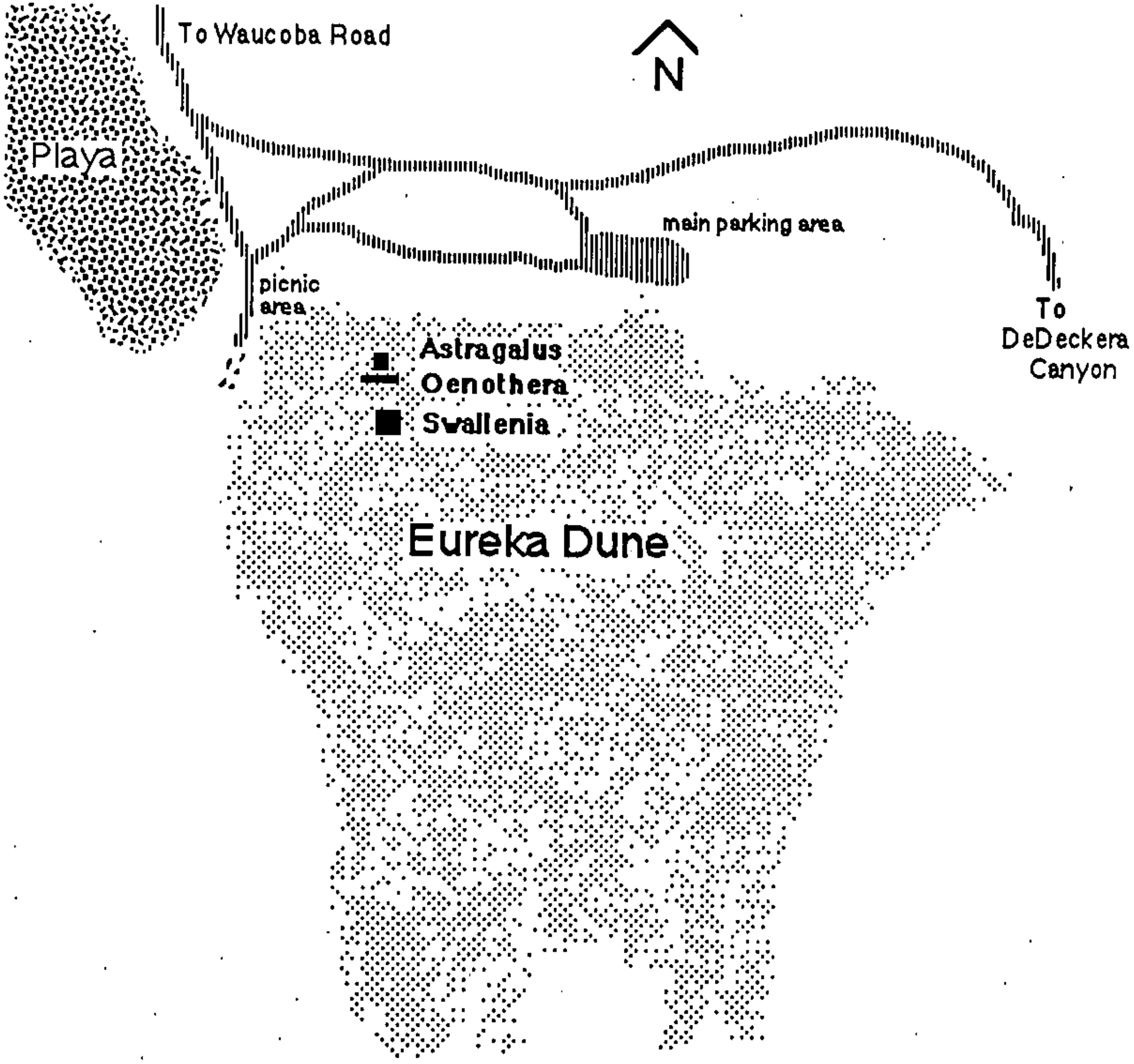


Figure 1. Location of the demographic study plots for Swallenia, Oenothera and Astragalus at Eureka Dune, 1985-86.

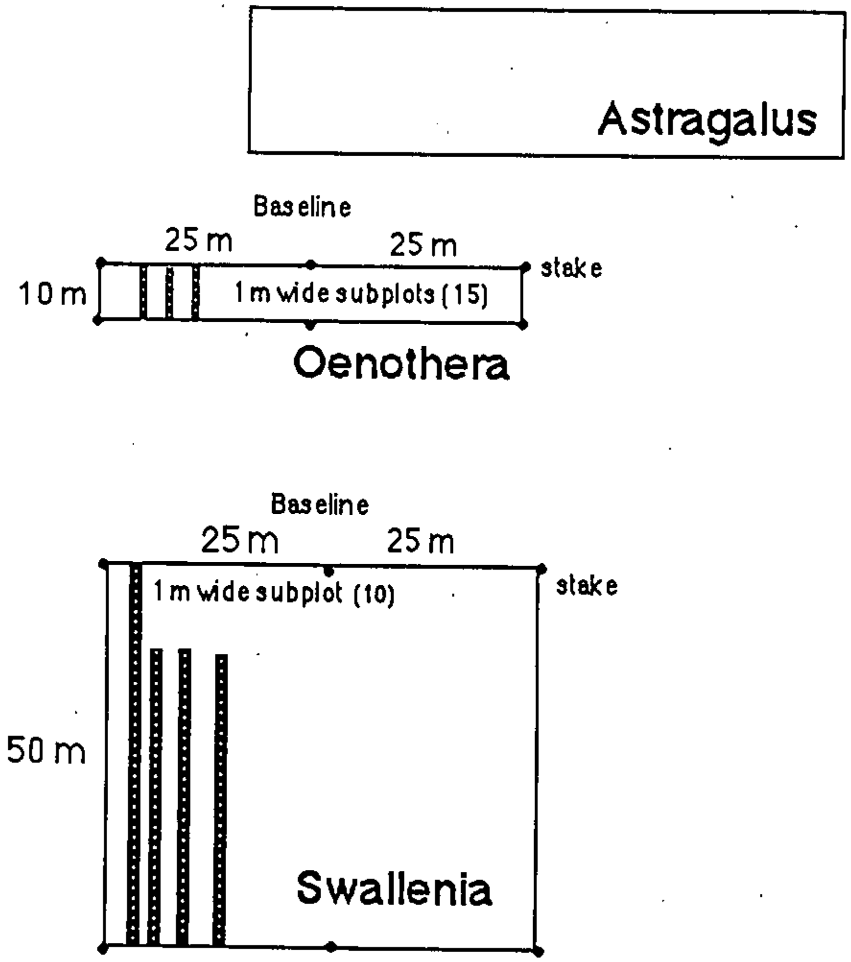


Figure 2. Configuration of the demographic study plots.

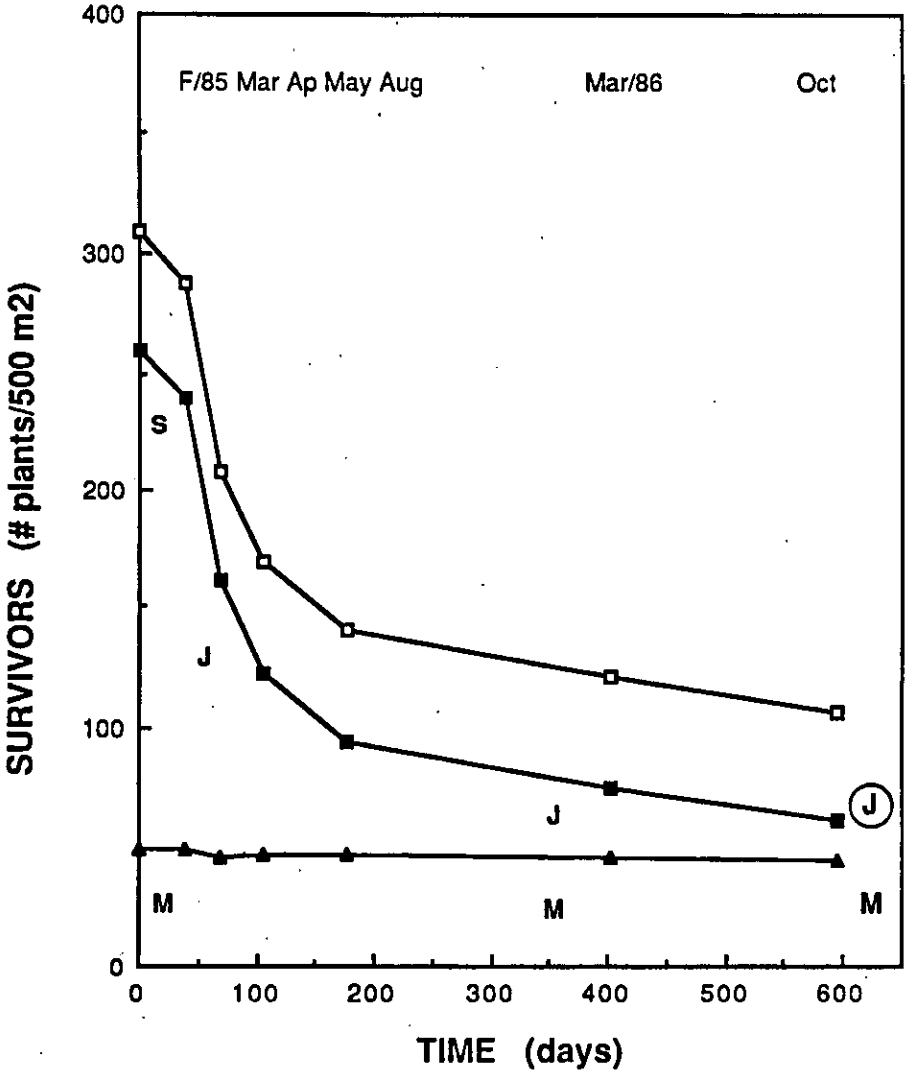


Figure 3. Survivorship and depletion curves for *Swallenia*, 1985-86. Total population (□), the summer 1985 cohort of seedlings (S), juveniles (J) and hummock-forming juveniles (Ⓙ) is shown (■), as is the established population of mature (M) and senescent (St) individuals (▲). Letters indicate the predominate life history stage for each curve at the time of sampling.

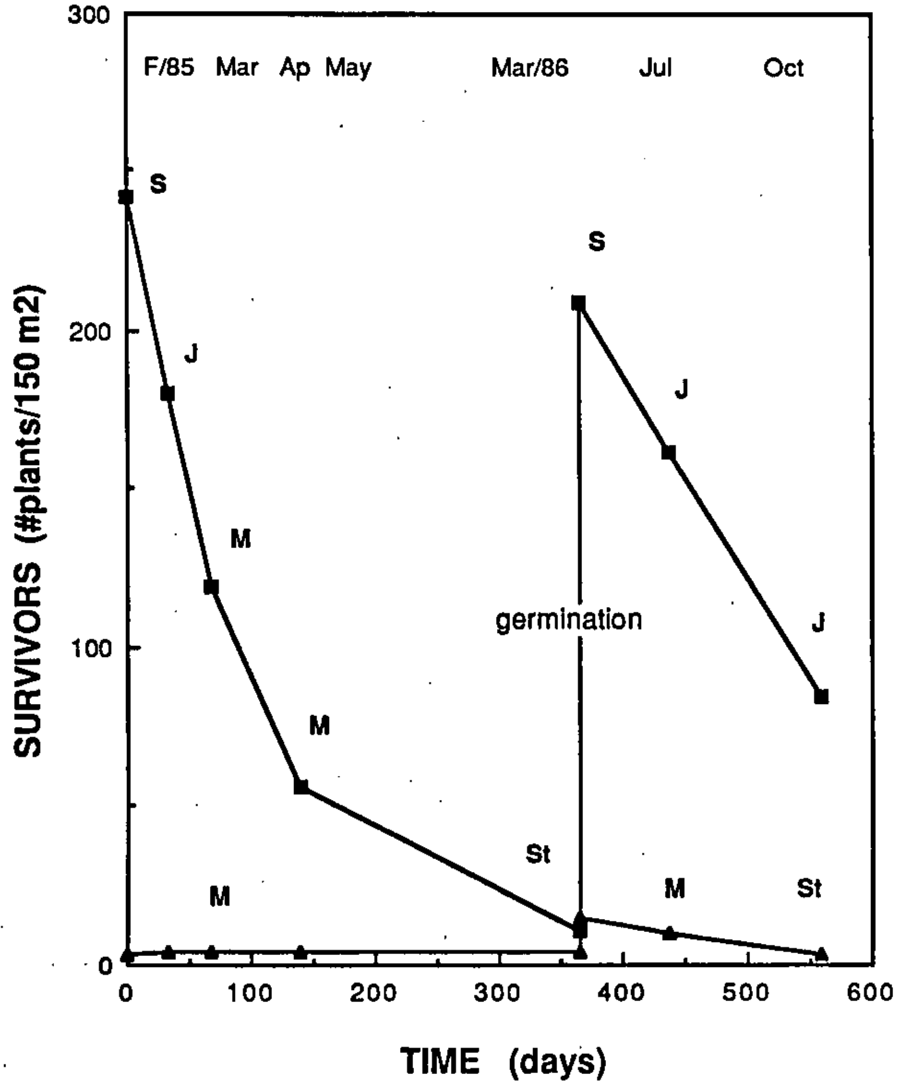


Figure 4. Survivorship and depletion curves for Oenothera, 1985-86. Symbols as in Figure 3.

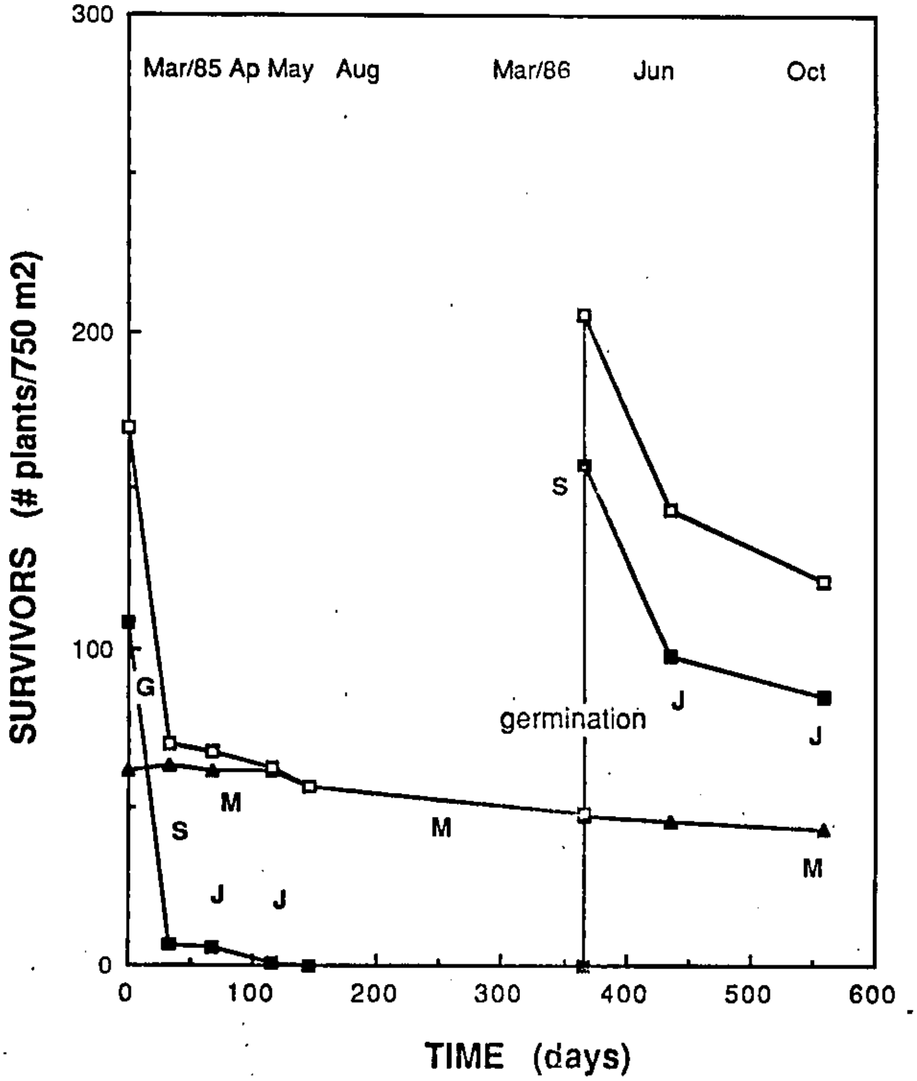
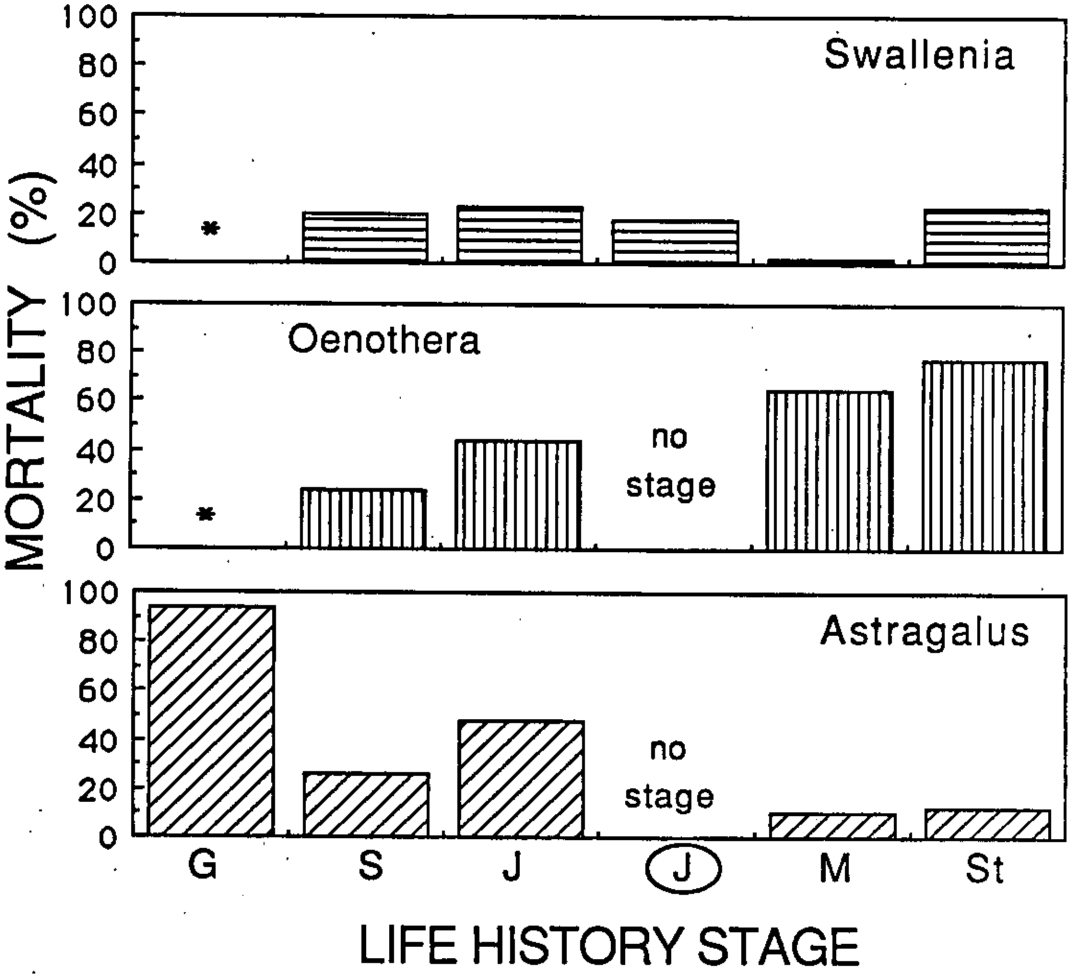


Figure 5. Survivorship and depletion curves for Astragalus, 1985-86. Symbols as in Figure 3, except G = germinule.



* insufficient data

Figure 6. Mortality at each life history stage, averaged for the years 1985 and 1986.

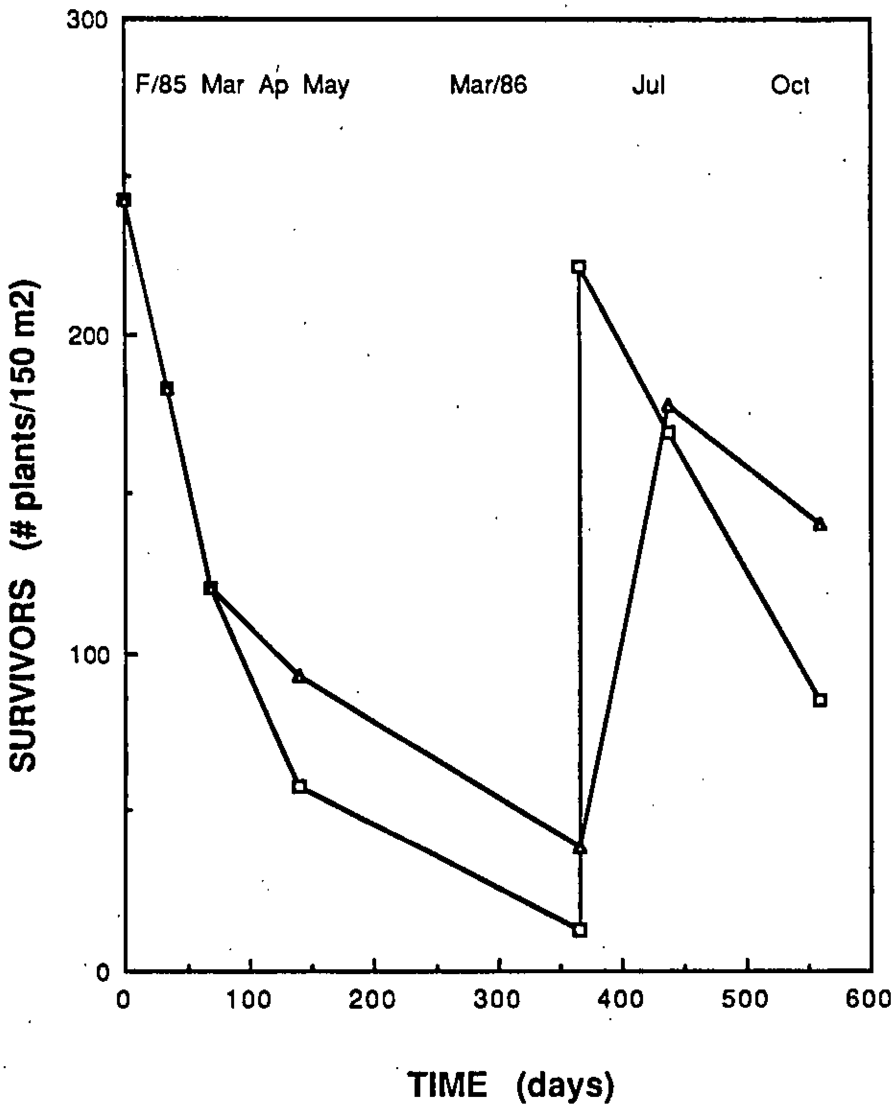


Figure 7. Effect of branchling production on survivorship curve of the summer 1986 cohort of Oenothera. Indicated are the total population without branchlings (□) and the total population including branchlings (△).

Chapter 2:

Seed Bank Dynamics

Introduction

Demographic studies of plants cannot ignore the fates of seeds because the highest rates of mortality often occur during this stage of the life cycle (Sharitiz and McCormick 1972, Leverich and Levin 1979). Life table analyses that do not include estimates of mortality in the seed stage will, therefore, greatly overestimate the net reproductive rate (R_0) of individuals and lead to erroneous conclusions about the stability of the population. For example, if R_0 is calculated for Oenothera avita ssp. eurekensis using mortality and seed production data for the post-germination part of the life cycle during 1985, each individual could replace itself with 12,914 other plants! This rate of population growth would soon cover all of the available dune habitat with a thick sward of primroses.

Despite the obvious importance of the seed stage in life table analyses, it is often difficult to obtain the relevant data . This is because of the potentially long period of time that seeds can exist in a cryptic, soil-borne state. A truely demographic analysis (one that follows the fates of individuals) is too laborious, time consuming, and uncertain to be of any practical significance in rare plant research. Instead, we may have to infer the relative importance of seed mortality factors from a series of parallel studies that examine each of several possible fates. One such series is suggested in Figure 8 and was adopted from the discussion presented by Harper (1977). After dispersal, propagules become incorporated into the soil seed bank where they can remain quiescent for relatively long periods of time. If favorable conditions for germination are infrequent, the seeds from several successive years can accumulate and enlarge the seed bank considerably more than a single year's seed rain. Predation, decay and (in habitats such as unstabilized sand dunes) secondary dispersal can deplete the viable seed bank within a stand (Harper 1977). Germination can also deplete the seed bank, especially if establishment of the seedlings (and subsequent reproduction) does not occur. The purpose of this study is to examine the seed bank dynamics of _Swallenia_ _alexandrae_, _Oenothera_ _avita_ ssp. _eurekensis_ and _Astragalus_ _lentiginosus_ var. _micans_ and to try and explain those dynamics by examining seed longevity, predation, germination and secondary dispersal (including burial and movement out of the seed bank).

Methods and Materials

Seed bank dynamics. In March, May and October of 1986, estimates of the seed bank within survivorship plots of _Swallenia_, _Oenothera_ and _Astragalus_ were made by pressing 1 liter plastic containers a maximum of 15 cm into the dune and trapping the sand in the container with a plastic lid. These containers sampled 0.178 m^2 of dune surface near and between mature plants. Their placement was random but spread throughout 100 m^2 of each plot. Owing to the patchy vegetation cover found in the _Swallenia_ stand, 50 of these samples were required, whereas 8 were used for _Oenothera_ and _Astragalus_ stands on each date. Seeds of _Swallenia_ and _Astragalus_ could be separated from the sand with medium-coarse soil sieves. _Oenothera_ samples, however, required sieving with fine-mesh screens and immersion of the throughfall (very fine sand + seeds) in tubs containing a saturated salt (NaCl) solution. The small seeds floated on the salt solution more than 90% of the time as determined by spiking studies. After separation from the sand, seed quality was subjectively assessed from general appearance (size, shape, surface features and color) when compared to new seeds. High quality seeds were presumed to be fully viable while low quality seeds probably had impaired germination. The sizes of the total seed bank (high + low quality) and viable seed bank (high quality only) were calculated by dividing the appropriate number of seeds found in all samples by the total area of dune surface sampled by the plastic containers.

Seed longevity. Seed longevity was tested by germinating seeds from the 1978 and 1985 crops. These had been stored dry and at room temperature in sealed plastic zip-lock bags. They were germinated in the dark under optimal temperature and moisture conditions according to the results of Pavlik (1979a). Three replicate petri dishes of 50 seeds each were used for Swallenia and Oenothera and 25 scarified seeds for Astragalus. Each dish contained a thin layer of sand covered by a filter paper disk to hold moisture. The closed dishes were placed in a temperature-controlled dark room and checked daily for 20 days. Germinated seeds (those with protruding radicles) were tallied and immediately removed. Tetrazolium tests were run on all ungerminated seeds at the end of the trials to determine if they were viable and dormant or simply dead.

Longevity may also be decreased if seeds are exposed to high temperatures, such as those found near the dune surface (Pavlik 1979a), or if sand deposition brings seeds in contact with warm, subsurface dune moisture. In order to test the effects of heat and moisture on seeds of Swallenia, Oenothera and Astragalus, 3 replicate dishes of 1985 seeds were treated with heat (58 C) or moisture + heat (58 C) for 10 days. These dishes were then placed under the same optimal temperature and moisture conditions as untreated control seeds and monitored for 20 days. This experiment sought to determine if; 1) seeds on the hot sand surface could loose viability during the summer and 2) buried seeds, in contact with moisture stored in the warm dune sand were capable of germination.

Predation. On two nights in October 1986, seed and fruit selection experiments were run at Eureka Dunes by placing 10 naked *Swallenia* seeds, 10 *Swallenia* seeds in their floral bracts, 10 *Oenothera* seeds, 1 ripe *Oenothera* capsule (containing numerous seeds), 10 *Astragalus* seeds and 10 *Astragalus* pods(with seeds) in a shallow glass or plastic dish. A total of 27 dishes were sunken below the sand surface (9 in each species plot). Some were placed next to the canopies of established plants and others either 1 or 3 m away. Seeds could not be easily blown from the dishes (the two nights were perfectly still anyway) and footprints in the surrounding sand revealed if seeds were missing due to nocturnal, mammalian predators. Foraging ants, however, could not escape from the dishes once they had fallen in. This allowed some assessment of ant vs. mammal seed predation. Also on each night 40 live mammal traps (Sherman type) were scattered around the plots and baited with balls of peanut butter and oatmeal. The traps were checked early the next morning for captured foragers. Attempts to quantify seed predation were made on other nights but these were not successful. No predation was detected on nights with full or partial moons or if the dishes were put out after 0200 hours.

Germination in the field. Survivorship plots were monitored during 1986 and the presence of germinules recorded as part of the demographic monitoring program (Chapter 1 this volume).

Secondary dispersal. No attempt was made to quantify the vertical or horizontal migration of buried seeds. Instead, observations were made regarding the amount of sand deposited of removed from the survivorship plots during the study. If large amounts of either occurred, it was inferred that deposition had the potential to bury seeds deeper in the dune and deflation had the potential to uncover and disperse seeds.

Results and Discussion

Seed bank dynamics. The densities of Swallenia and Astragalus seeds in the seed bank corresponded with the magnitude and timing of seed rain during 1986 (Figure 9 and Appendix A this volume). The differences between the total and viable seed banks were very small for these taxa and probably not significant. Increases in total and viable seed density were on the order of 8 to 35 fold as seed output and dispersal peaked during the April-May period. In general, the ranges for Swallenia (2 to 24 seeds/m^2) and Astragalus (7 to 200 seeds/m^2) were extremely low when compared to the seed banks from other community types. Undisturbed native prairie, dominated by perennial grasses, has a range of 300-800 seeds/m^2 and up to 20,000 seeds/m^2 (mostly Sporobolus) if disturbed (Lippert and Hopkins 1950). Other arid or semi-arid grasslands have a range of 4,000 to 15,000 seeds/m^2 (Budd et al. 1954, Major and Pyott 1966). The small seed banks of Swallenia and Astragalus undoubtedly result from the low populations densities on the dune as a whole and, in the case of Swallenia, low seed production per plant (Pavlik and Barbour 1985, Appendix A this volume). At Eureka Dunes the modest spring increases in Swallenia and Astragalus seed banks reflect the modest seed rain produced by these populations.

The seed bank of Oenothera, however, did not peak during the period of maximum seed production, but declined from March to May (Figure 9b). Differences between the total and viable seed bank appear large as judged from the appearance of the seeds. There are at least two factors contributing to this pattern; 1) the large 1985 and small 1986 seed rains (i.e. the dune sand contained a large number of 1985 seeds and was not significantly enriched during 1986, Appendix A this volume) and 2) dispersal of the extremely mobile seeds during spring wind storms. Regarding the latter, Pavlik and Barbour (1985) compared the small, lightweight Oenothera seeds to those of Swallenia and Astragalus and found they were the fastest dispersers at any wind velocity (and, therefore, most likely to leave the habitat). This dispersal ability allows Oenothera to maintain the largest geographic range of all three dune endemics. Dispersal of 1985 seeds may have contributed to the modest seed density increases of Swallenia and Astragalus, but to a lesser degree. This is because the discrepancy between 1986 seed rain and seed density in the bank was not great for these taxa.

All three endemics had much smaller seed banks in October. In unstable sand dune habitats there are four possible fates of these seeds; 1) aging, death and decay, 2) predation, 3) germination, and 4) secondary dispersal either by burial (i.e. vertical migration) or by deflation (horizontal migration) as substrate is moved by high wind.

Seed longevity. Table 4 shows that seeds of all three taxa remained viable and germinated after 8 years when stored under laboratory conditions. Although the aging of Swallenia seeds did not affect viability, it did decrease the germination response to a greater degree than in the other taxa (Figures 10-12). Presumably these seeds, if properly induced, could germinate in years that were temporally distant from the year of production and dispersal. It seems unlikely, therefore, that seeds in situ would age, die and decay after five months and contribute to the observed decline in seed density over the summer.

Seeds of all three species remained viable and could germinate after being exposed to a temperature representative of the dune surface during the summer (Figures 13-15). The heat treatment reduced final germination by less than 15% in the three taxa, although treated seeds did respond more slowly to favorable conditions than did the controls. The addition of moisture to the heat treatment, however, resulted in a complete loss of germination and viability (the seeds were attacked by fungi after being placed under optimal conditions). Therefore, buried seeds exposed to moist layers in the sand during the late summer and fall are likely to die and not form a part of the buried seed bank. Buried seeds that do not come in contact with moisture might be less subject to predation, however.

Predation. Predation, however, must significantly contribute to decreasing the seed reserves of Swallenia and Astragalus. Over a single night period, 14 percent of all naked Swallenia seeds and 9 percent of all naked Astragalus seeds were collected (principly by the kangaroo rat Dipodomys, as judged from tracks and Peromyscus maniculatus as judged by a single trapped individual). These results confirm earlier observations of seed predation by nocturnal mammals (Pavlik and Barbour 1985). Swallenia disseminules were taken to a lesser extent (6 percent of those caryopses that had attached floral bracts), but those of Astragalus were

Table 4. Laboratory germination and viability of Swallenia, Oenothera and Astragalus seeds from the 1978 and 1985 crops. Viability determined with tetrazolium tests. Differences between 1978 and 1985 germination are significant (ANOVA, P<0.01) for Swallenia and Oenothera.

	1978		1985	
	germination (%)	viability (%)	germination (%)	viability (%)
Swallenia	5.0 ± 5.0	100	81.2 ± 5.4	100
Oenothera	40.8 ± 15.0	60	74.9 ± 2.9	80
Astragalus	76.6 ± 15.0	60	100.0 ± 0.0	100

In three dishes there were several ants observed (and photographed) carrying Swallenia seeds, suggesting that if they could leave the dish they would take the seeds with them. Indeed, ants liberated from the dishes carried the Swallenia seeds to their burrows, confirming earlier observations (Pavlik and Barbour 1985). Of all seeds and disseminules removed, those of Swallenia were more likely to be selected by rodents and ants (Table 5). There was no evidence that Oenothera seeds or fruits experienced any predation by nocturnal rodents or ants.

Seed predation rates of 10-15% per night give an estimated half-life of between 4 and 7 days if all seeds are assumed to be eaten. In contrast, recruits and established plants have half-lives measured in months or years. This suggests that at Eureka Dunes, the seeds do experience high mortality when in the seed bank. It is unlikely, however, that these mortality rates are sustained for long periods of time because of 1) dispersal and the patchy distribution of disseminules in vivo, 2) seasonal variability in predator activity (including the lunar cycle), and 3) secondary dispersal of seeds to deeper soil horizons (see below). It is also unknown if, in the absence of the larger Swallenia and Astragalus seeds, rodents and ants would begin to harvest the smaller Oenothera seeds or any seeds still contained in the fruit or floral bracts.

Germination. Germinule emergence was not observed during the May to October period and so it seems unlikely that seed bank decline was the result of aseasonal germination. The possibility of subsurface germination and death is remote owing to the fact that 1) the upper 15 cm of dune sand was dry and significant rain did not occur over the summer and early fall, 2) dead germinules were never found in

Table 5. Relative seed and fruit predation by rodents and ants at Eureka Dunes, October 1986. Mean values from nine dishes per taxon. Differences in seed predation between species are statistically significant (ANOVA, P<0.025).

	seeds removed (%)	disseminules removed (%)
Swallenia[1]	74.0 ± 13.0	100.0 ± 0.0 (+ bracts)
Oenothera	0.0 ± 0.0	0.0 ± 0.0 (capsules)
Astragalus	26.0 ± 13.0	0.0 ± 0.0 (legumes)

[1] seed = caryopsis

seed bank samples and 3) summer sand temperatures (35-60 C) have been shown to inhibit germination of the three taxa completely, even if supplied with ample moisture (Pavlik 1979a).

Secondary dispersal. Observations made in all three survivorship plots indicated that less than 10 cm (mostly less than 4 cm) of sand accumulated over the summer. In this case the seed bank samples would not have been greatly affected by the deposition of small amounts of seedless substrate (the most biasing case). Sand accumulation can vary greatly with position on the dune and time of the year (Pavlik 1979a) and it is entirely possible that many seeds become buried for long periods of time. If the seeds remain dry and relatively cool they could remain viable. If, however, they come in contact with moist, warm layers of sand, they might germinate too deeply and die or simply loose viablity as previously discussed. The size and dynamics of this "quiescent" seed bank remain unknown.

The last possible fate of seeds in the dune seed bank is horizontal migration resulting from sand deflation. This cannot be excluded for any of the taxa since all three are capable dispersers (Pavlik and Barbour 1985). It should be noted that very little, if any sand deflation occurred during the summer to fall period, in marked contrast to the spring. Nevertheless, the possibility of secondary horizontal dispersal cannot be ignored. Dispersal, along with predation both contribute to the summer-fall decline of Swallenia and Astragalus seed banks but only dispersal affects the Oenothera seed bank. It could be argued that since seeds might be transported in as well as out of the seed bank by substrate movement, only predation is significant. This argument is extreme and does not recognize the very patchy and sparse cover by endemics on the dune and the great volume of lifeless, shifting sand.

Conclusions and Management Recommendations

1) The seed banks of Swallenia, Oenothera and Astragalus at Eureka Dune are small when compared to other plant communities. This reflects the low population densities of these taxa on the dune as a whole and, in the case of Swallenia, low seed output per individual plant. Within the upper 15 cm of sand, the seed bank showed considerable seasonal variability, with the lowest seed densities occurring in early spring and fall. It is not possible to conclude that a large buffer of germinable seeds occurs at Eureka Dunes, especially since the shallow seed bank is depleted during the summer and fall when precipitation critical for germination and establishment is likely to occur. Every year of seed output, therefore, may be

essential for positioning new propagules within the shallow seed bank as if to "hopefully anticipate" the unpredictable summer and fall rains.

2) Seed predation and secondary dispersal are the factors most responsible for the observed patterns of seasonal variation in the seed banks. Swallenia and Astragalus seeds are actively gathered by rodents and ants, with 9-14% of the naked seeds gathered per night. If all the seeds are assumed to have been eaten, mortality would be extremely high when compared to other phases of the life cycle. High seed mortality rates are probably not sustained throughout the year, however. This may be due in part to secondary dispersal, which can move seeds into habitats not frequented by predators (horizontal migration) or result in burial and "escape" (vertical migration). Seeds which move into deeper layers of the soil may be less obvious to predators, but they may also die as the result of coming into contact with high soil temperatures and moisture or by germinating too deeply for emergence to occur (not directly observed in this study). The available data indicate that predation and secondary dispersal depletes the seed banks of Swallenia and Astragalus but only the latter affects Oenothera.

3) It is possible that a large, quiescent seed bank exists for all three taxa at a depth greater than 15 cm below the dune surface. Buried seeds, if they do not contact moisture, will experience a moderated soil temperature environment and remain viable for over 8 years. When unearthed by deflation, these seeds may become positioned for germination and successful establishment. The importance of this

deep seed bank to the demography of the endemics is unknown.

4) With respect to the overall life history of these taxa, the death of non-emergent germinules and seedlings may be a significant source of mortality and the principle constraint on net reproductive rate. This conclusion is reached by process of elimination: If, for example, each emergent Oenothera plant could replace itself with 12,914 seeds (as stated in the introduction), those seeds must experience a considerable rate of mortality (given our observations of little change in the size of the population). Seed bank studies have shown that mortality from predation, summer germination and short seed life are negliglible. Death during fall or winter germination (particularly for deeply buried seeds) must, therefore, account for the fates of many of the 12,914 seeds, but this has not been directly observed or tested.

5) There are no obvious or convenient manipulations of the seed bank possible that could significantly enhance these populations. This is because there are no known manipulations that can enhance seed rain (specifically seed output per plant, (Pavlik and Barbour 1985)) or control seed predation by rodents and ants. Therefore, the natural integrity of these seed banks must be maintained by preventing widespread disturbance of the dune surface and the uppermost layers of sand. This disturbance can be the result of foot or vehicle traffic, but mostly the latter. Additional consequences of these activities at Eureka Dunes are discussed in Pavlik (1979a, 1979b).

[illegible] ?

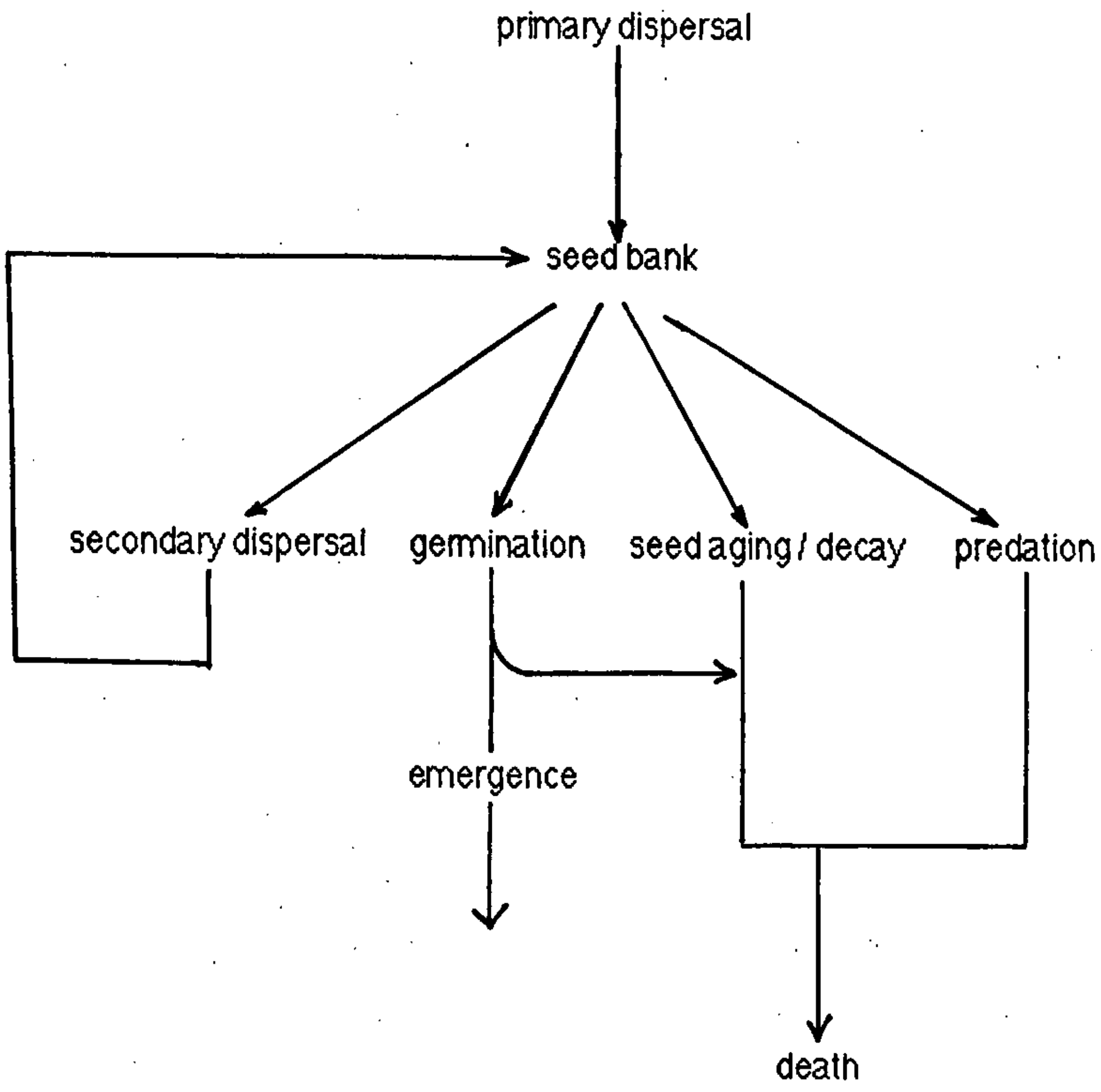


Figure 8. The post-production fates of seeds. Not all of the possible pathways are shown. Modified from Harper (1977).

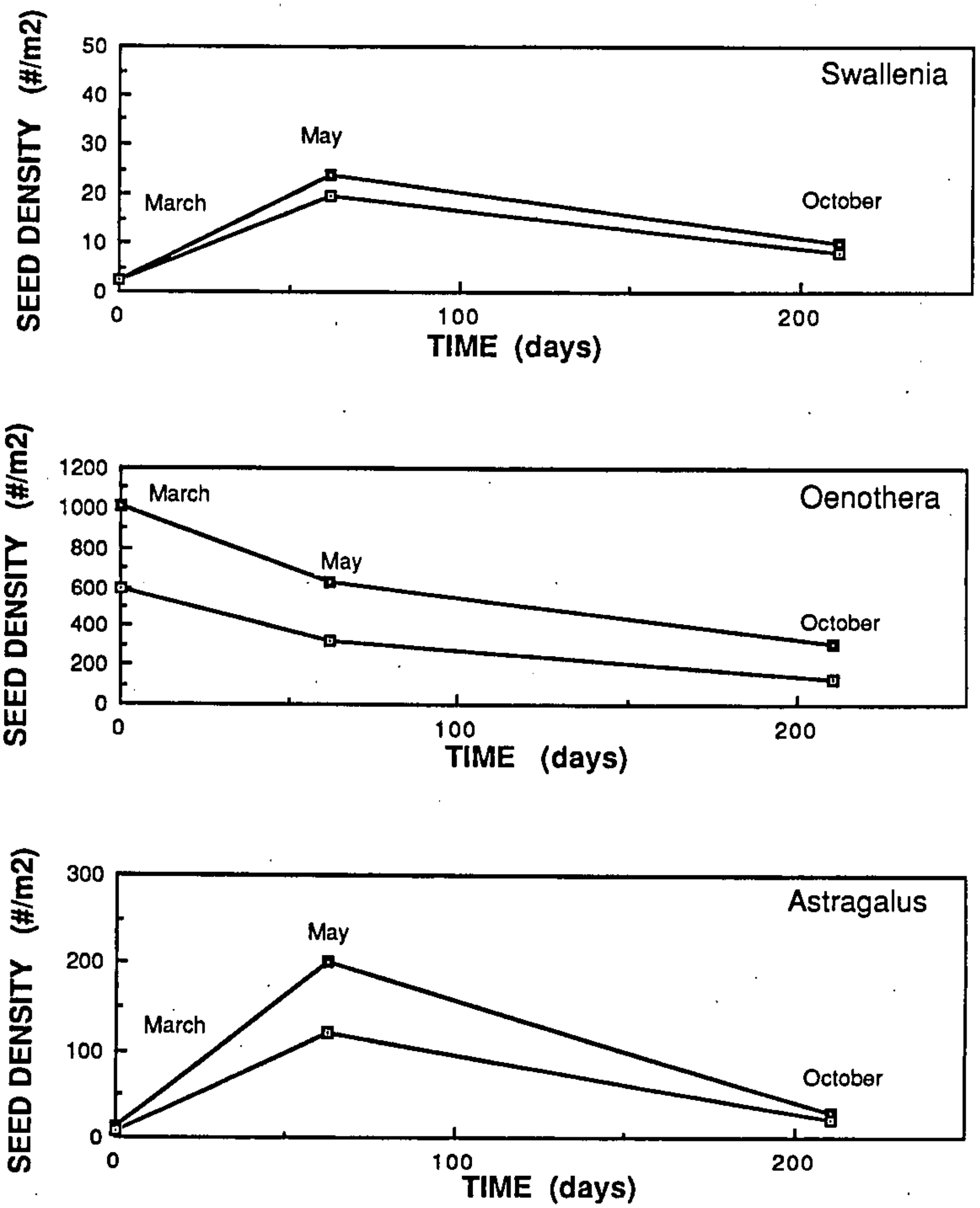


Figure 9. Seed density in the seed banks at Eureka Dunes, 1986. Total seed density of all seeds (■) and of high quality seeds (□) shown. Note different scales on the y-axes.

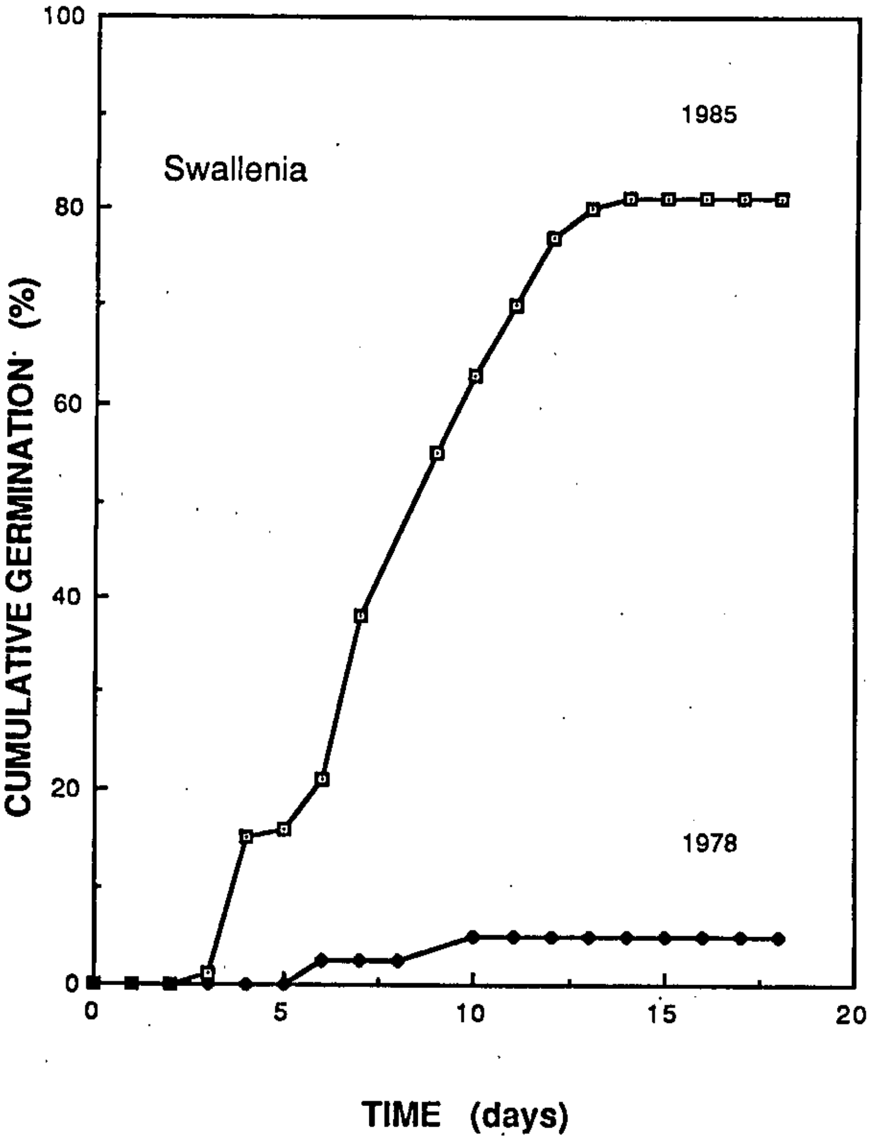


Figure 10. Effect of seed age on germination of Swallenia caryopses.

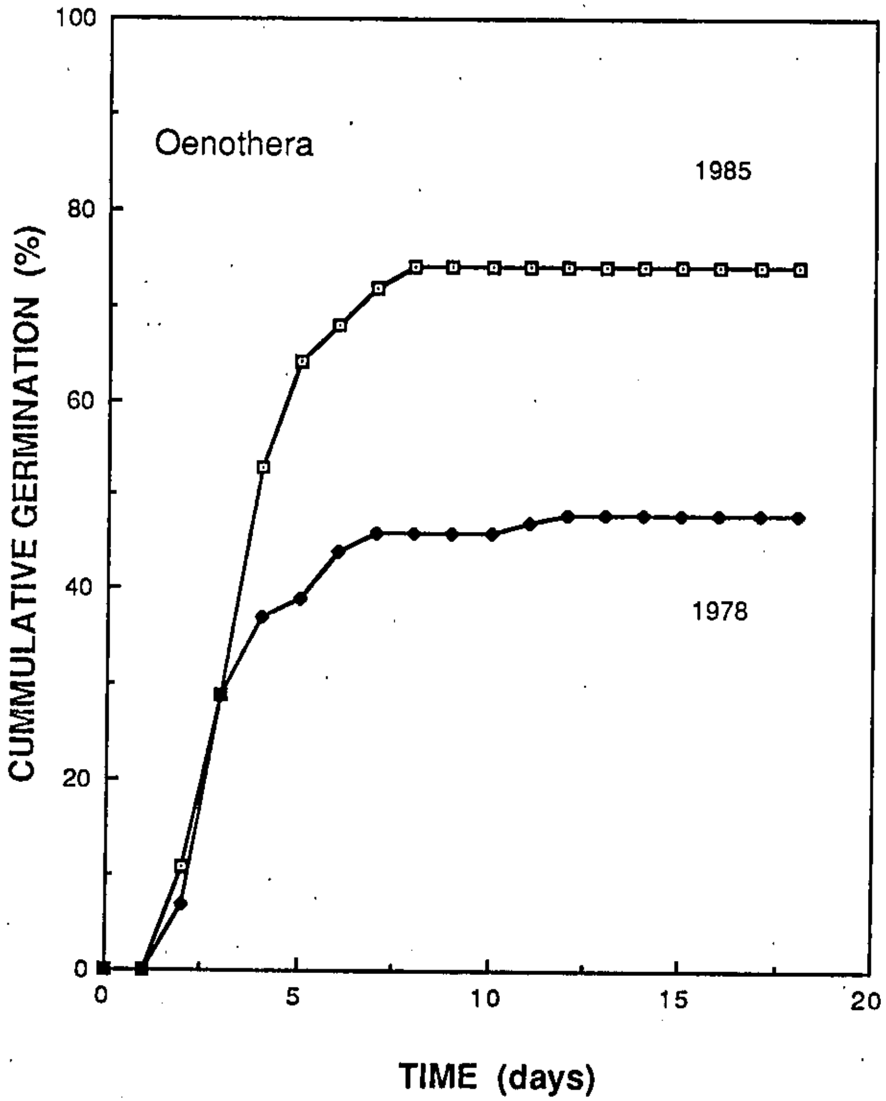


Figure 11. Effect of seed age on germination of Oenothera.

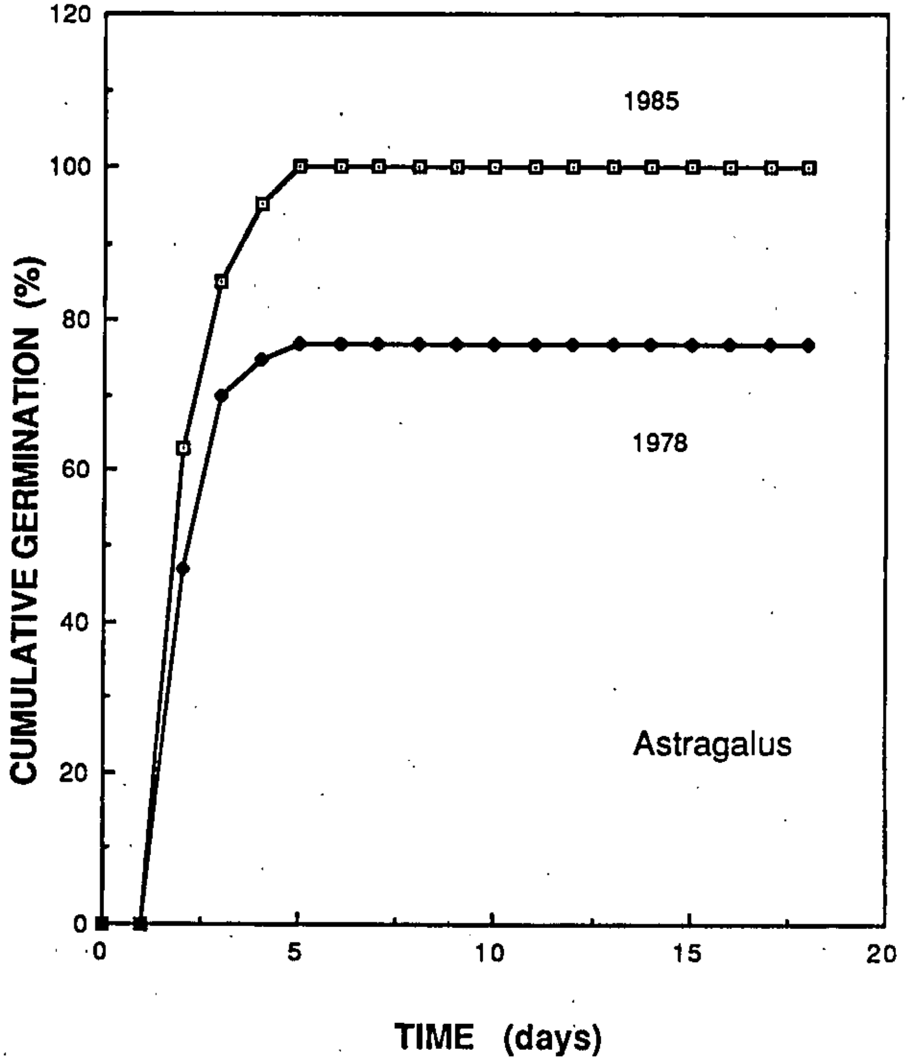


Figure 12. Effect of seed age on germination of _Astragalus_.

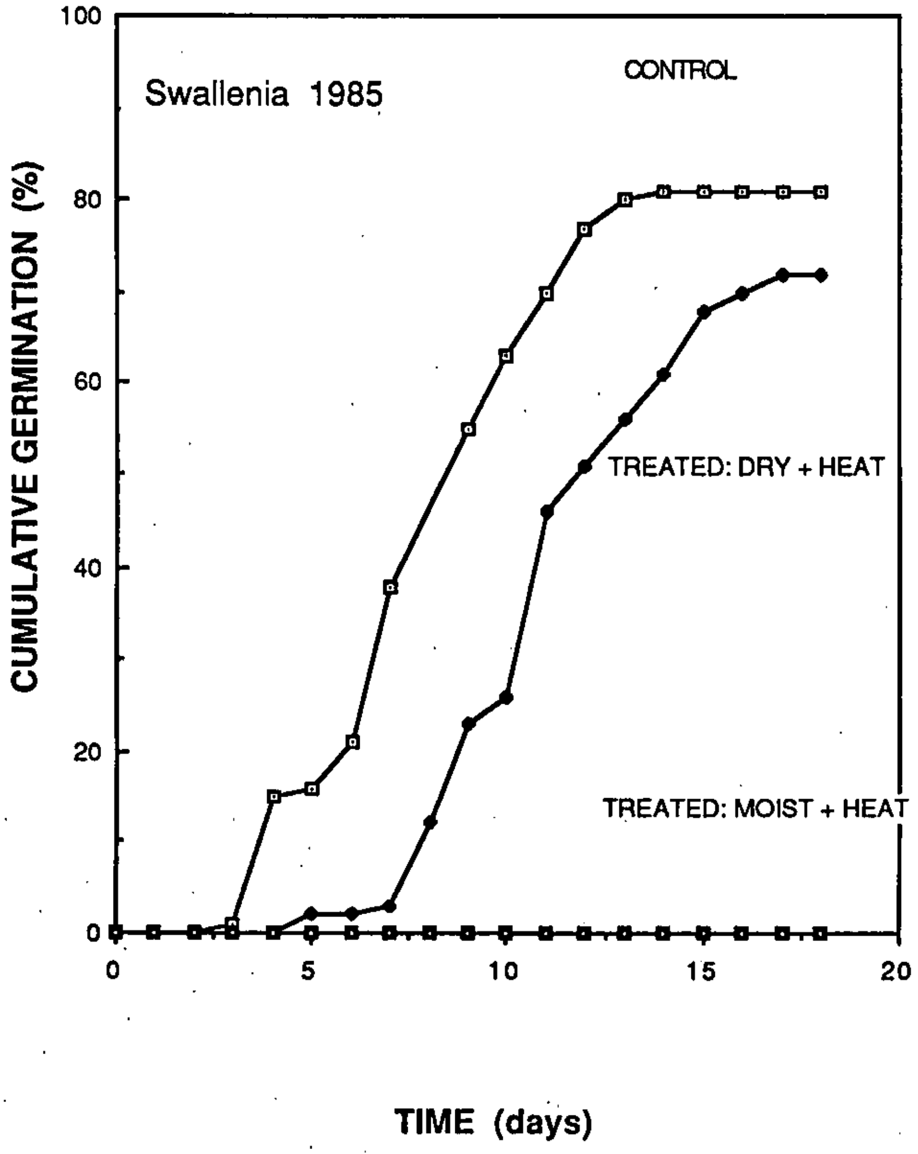


Figure 13. Effect of dry heat and moist hear treatments on the germination of Swallenia caryopses.

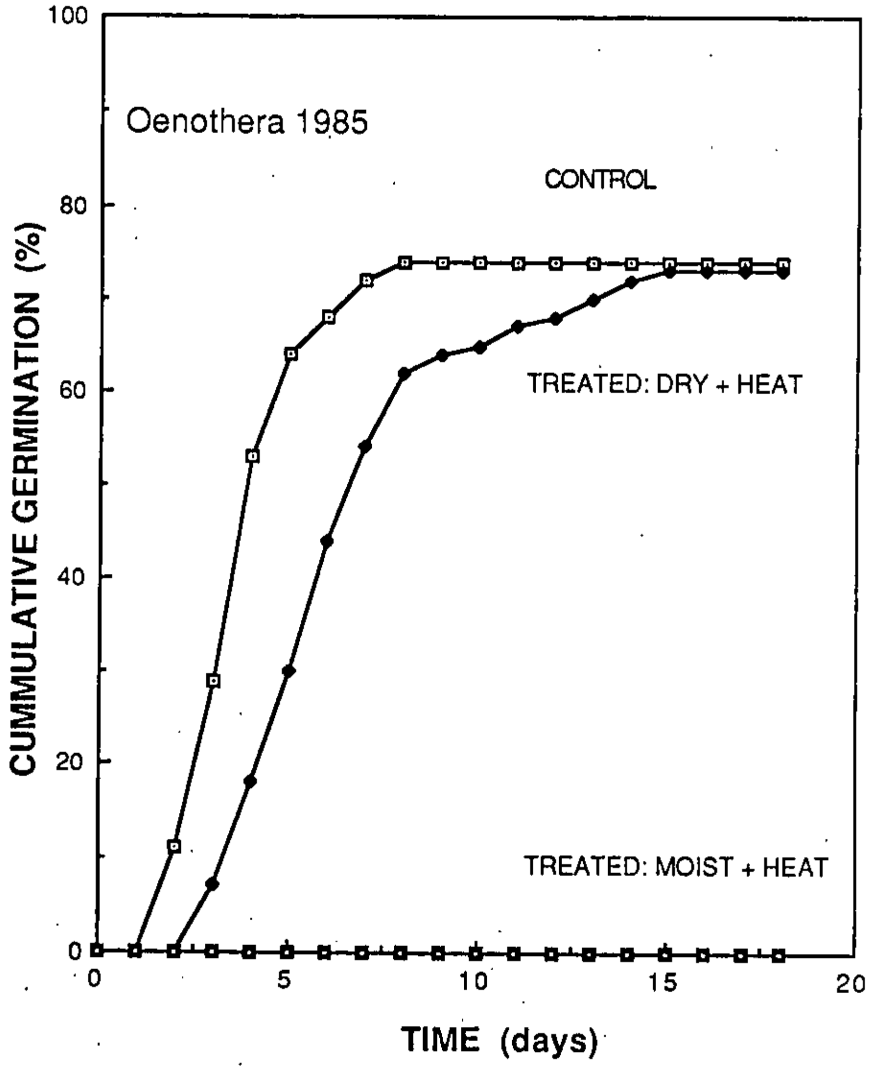


Figure 14. Effect of dry heat and moist heat treatments on the germination of *Oenothera* seeds.

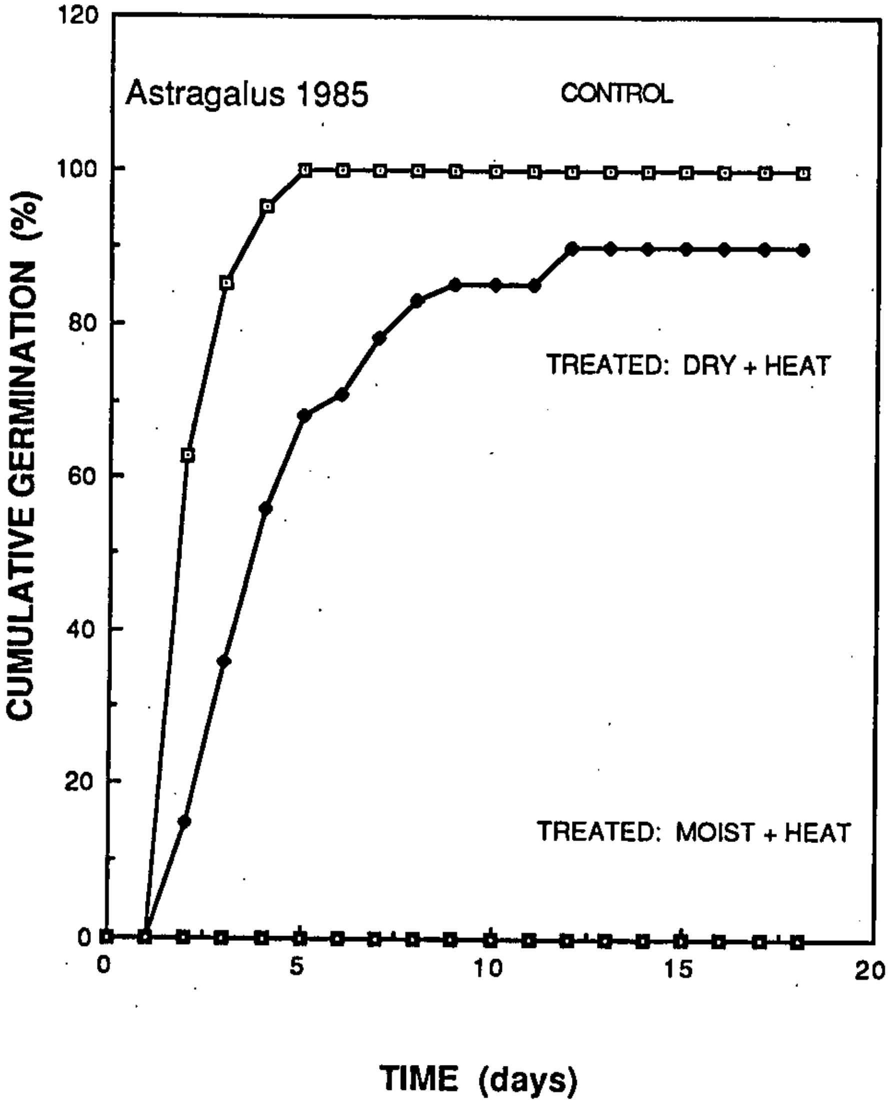


Figure 15. Effect of dry heat and moist heat treatments on the germination of Astragalus.

Chapter 3:

Frequency of Establishment

Introduction

Desert ecosystems are controlled by the amount and temporal pattern of precipitation (Shreve 1942, Noy-Meir 1973). Beatley (1974) concluded that mass germination and establishment of Mojave Desert annuals depends upon the occurrence of at least 25 mm of rain during the September to December period. Sudden, unusually strong storms that drop large amounts of precipitation may also be of importance as trigger factors in the episodic germination of perennial species (Barbour 1968). Went and Westergaard (1949) noted that after a vigorous October rain in Death Valley, thousands of Larrea seedlings were observed where there had been none for years. Sporadic precipitation has also been linked to the establishment of Carnegia gigantea and Ferocactus acanthoides (Brum 1973, Jordan and Nobel 1981). These kinds of climatic events could also control germination and recruitment of rare plants and, therefore, would be of concern in a demographic study of an endangered species.

Whereas germination of Oenothera and Astragalus can occur in nearly every year to some extent (see Chapter 1), Swallenia germination appears to be very sporadic. Successful Swallenia establishment may be even rarer than germination. Analyses of survivorship curves has shown that in the absence of successful establishment the population would go extinct in as little as 16 years or as much as 88 years (Table 2, page 12). A population must, therefore, experience successful germination and recruitment at least once within a span of 16 to 88 years. The purpose of this study is to determine 1) if Swallenia germination is linked to a particular kind of climate event (e.g. unusual amounts of precipitation) and 2) the long-term frequency of that climatic event.

Methods and Materials

Estimates of live germinule/seedling density of Swallenia were available for the years between 1974 and 1986 (Henry 1976, Pavlik 1979b). These measurements were obtained by different methods at different sites along the northwest slope of the main dune and may not, therefore, be strictly comparable in terms of absolute magnitude. Henry (1976) used seven permanent transects spaced 18 meters apart to obtain the 1974-75 estimates. Four of these transects were 3.6 X 300 m and three were 3.6 X 200 m, running from the Psorothamnus zone on the lower edge of the dune to the upper edge of the Swallenia zone on the north side of the main dune. Pavlik (unpublished data) used four 10 X 10 m quadrats in the Swallenia zone to monitor seedlings on the northwest flank of the main dune during the years between 1976 and 1984. This same area was intensively sampled during 1985-86 using the demographic study plot described in Chapter One of this report. For the most part they represent the seedling density during the late fall/winter/early spring period after summer and fall precipitation would have occurred. Swallenia germination has never been observed in the spring or early summer (Henry 1976, 1979, Pavlik 1979a). It is also unlikely that germination takes place during the late fall-winter period when vegetative plants are dormant.

In order to determine if yearly variations in Swallenia seedling density are correlated with precipitation events in eastern California, four U.S. Weather Bureau stations were chosen for analyses of their climatic records (NOAA 1974-1984). The stations (Bishop WSO AP, Death Valley, Deep Springs and Independence) circle Eureka Valley (Figure 16) with an average radius of 60 km (36 miles) and occur at comparable elevations (-59 to1593 m, the dune being at 930 m).

Actual monthly precipitation (M) and the departure from normal monthly precipitation (N+, based on 26 to 90+ years of record depending on the station) were obtained for the months of July, August, September, October, November and December of the years 1974 to 1984. Total annual precipitation (A) was also noted for each year. A regional value of monthly precipitation (Mr) for each month of each year (e.g. July 1974, July 1975, October 1978) was obtained by averaging the monthly precipitation of the climate stations for that month. A regional value for the positive (+) departure of that month's precipitation from the norm (Nr+) was also obtained in this manner. These regional values are assumed to represent the monthly precipitation or + departure of that month's precipitation for the vicinity of Eureka Dunes. The latter would tend to emphasize unusual precipitation events in subsequent correlation analyses.

An initial search for correlations between A, Mr or Nr+ and <u>Swallenia</u> seedling density was performed by calculating Kendall's rank correlation coefficient (τ). This nonparametric test was used to identify potential correlations without the assumption of linearity (Sokal and Rohlf 1973). A $P<0.05$ level of significance was adopted, but correlations with a $P<0.10$ level were also noted. Once correlated parameters (e.g. <u>Swallenia</u> seedling density and July Nr+) were identified, linear correlation coefficients were calculated in order to reveal the presence of robust relationships. Owing to the small data set available for <u>Swallenia</u> density, it is possible that curvilinear relationships, rather than linear relationships, may better describe certain climate-germination phenomena. This possibility remains untested by the present study.

Long-term climate analyses for the southeastern desert area in California were obtained for the years 1895 to 1984 by referring to the atlas compiled by Karl (1985). These maps utilize monthly Palmer moisture anomaly indices to plot, on a large scale, the occurrence of six precipitation scalars (extreme wetness, severe wetness, mild to moderate wetness, near normal, mild to moderate drought, severe drought and extreme drought) for each month in the record period. Data for these indices were derived from NOAA records for regional climatic units within the state. The unit which includes Eureka Valley is the southeast desert unit, extending from the southern border of the state to the northern Owens valley aand from the Sierran/peninsular mountain chain to the eastern border of the state. If Swallenia seedlings can be linked to certain precipitation events, then it should be possible to estimate the frequency of those events over the 90 year period using the Palmer indices.

Results and Discussion

During the 1974 to 1984 period, several years had strong germination events occurring in two temporal "clusters" (Figure 17). The first cluster was composed of the years 1974, 75 and 76 (5-15 seedlings/100 m^2) while the second cluster was composed only of 1984 (52/100 m^2). Very few seedlings ($\leq$ 1/100 m^2) were observed in 1977, 78 and 79 and none between 1980 and 1984 or in 85-86. These data indicate that mass germination (and perhaps establishment) may occur once every 8-10 years.

The results of nonparametric tests for correlations between Swallenia seedling density and total monthly precipitation are shown in Table 6. Significantly correlated with seedling density were the regional monthly precipitation (Mr) for the solitary summer months of July and August and the Mr values for the following combinations of months; 1) mid-summer through mid-fall (Jul+Aug, Jul+Aug+Sep, Jul+Aug+Sep+Oct) and 2) late summer through mid-fall (Aug+Sep+Oct). Note that removing July Mr from the precipitation variable reduces the significance of correlations between seedling density and late summer/ fall precipitation and removing August eliminates all significant correlations related to fall/early winter precipitation only (September to December). No correlations were found between seedling density and total annual precipitation ($\tau = -.139$, P = n.s.). Precipitation must occur, therefore, during the months of July or August in order to affect significant Swallenia germination.

Similar patterns were obtained when only the + departure of monthly precipitation from the norm was considered for the region (Nr+). If unusual amounts of precipitation occurred in either July or August, the response of germination was significantly correlated with the magnitude of the departure (Table 6). This was also true for the following combinations of mid-summer to early winter months; Jul+Aug+Sep, Jul+Aug+Sep+Oct, Jul+Aug+Sep+Oct+Nov, and Jul+Aug+Sep+Oct+Sep+Oct+Nov+Dec. Note that if July and August departures are eliminated, the significance of fall precipitation becomes nil. No correlation was found between Swallenia seedling density and the departure of the total annual precipitation from normal ($\tau = -.258$, P = n.s.). These results indicate that unusual amounts of precipitation during July and August lead to mass germination of Swallenia.

Tests for linear correlation (Table 7) indicate that its is the monthly departure from normal (Nr+) during July that controls Swallenia germination rather than the August departure or monthly total during July and August. Significant correlations were also observed for all combinations of mid-summer to early winter months (July to December). If the July departure was removed from the combination, no correlation was found for any sum of late summer, fall and early winter precipitation (August to December). These results strongly suggest that summer precipitation is the trigger for Swallenia germination and that the earlier the better (July > August > early September). Perhaps the newly emerged C_4 germinules perform best (i.e. have maximum CO_2 fixation rates) when exposed to warm, late summer/early fall air temperatures (30-35 C) and are able, therefore, to establish an adequate root system prior to late fall dormancy. Otherwise, germinules emerging in the fall might not become anchored well enough to endure winter and early spring wind storms (a major cause of mortality during this period, Chapter 1). It is interesting to note, however, that optimal <u>Swallenia</u> germination occurs at moderate temperatures (25-30 C depending on thermoperiod) rather than the warm to hot summer temperatures of the upper sand layers (Pavlik 1979a).

In general, the two clusters of high <u>Swallenia</u> seedling density were correlated with the occurrence of extremely wet conditions (EW, Palmer index $\geq$ 4.0) during the months of July, August or September. The peak density (15 seedlings/100 m^2) during the mid-seventies cluster was associated with EW conditions during September 1976 and the mid-eighties peak (52 /100 m^2) with EW conditions during July 1984 (Figure 18). EW conditions during August of 1977 and 1983, however, were not correlated with any significant germination events. This suggests that seedling production may be limited by low seed production and/or low seed density in the seed bank, as noted in Chapter 1 of this report. Nevertheless, the frequency of summer EW conditions appears to be correlated with the frequency of summer precipitation events in the Inyo desert region and would represent, therefore, the maximum potential frequency of <u>Swallenia</u> germination. No correlations were observed between <u>Swallenia</u> seedling density and the occurrence of moderate wetness (MW, Palmer index $\geq$ 1.5) conditions during the summer or fall months between 1974 and 1984. Severe wetness conditions (SW, Palmer index $\geq$ 3.0) did not occur during that time, so no conclusion can be reached regarding their importance to <u>Swallenia</u> germination. It is reasonable, therefore, to examine the frequency of both EW and SW conditions keeping in mind that the latter are less effective with respect to germination than the former.

The probability of a significant (i.e. producing extreme or severe wetness conditions) mid-summer/early fall precipitation event in the desert regions of southeastern California is 0.17 as judged from records of the 1895-1984 period

(Table 8). Extremely wet conditions for the months of July, August and September occurred 11 times within the 90 year period, an average of 8.2 years apart. Severe wetness occurred 4 times during the July to September months of this period.

These 15 events would not be equivocal with respect to their effects on the germination of Swallenia. The most important event, EW in July, appears to be particularly rare. The July 1984 precipitation that produced a very high density of Swallenia seedlings (52/100 m^2), contributed to EW conditions that occurred only once in 90 years. Less effective EW conditions during August and September (as judged by data in Tables 6 and 7) occurred 2 and 8 times during the same period, respectively, and thus occurred 45 and 11 years apart on the average. SW conditions only occurred during July for some unknown reason, so that even though less precipitation was received, it came when the potential effect was greatest.

In order to summarize the probability of germination-inducing climatic events within the context of their relative effectiveness, three classes of events were constructed (Table 9). A primary (I^0) climate event is defined as the occurrence of EW conditions during the month of July and would be the most effective with respect to stimulating Swallenia germination (Tables 6 and 7). This event occurs only once every 90 years (P = 0.01), as it did in 1984. A secondary (II^0) event is the occurrence of SW conditions in July or EW conditions in August. II^0 events occur once every 15 years on the average (P = 0.07). A tertiary (III^0) event is the occurrence of SW conditions in August or EW conditions in September. III^0 events occur once every 11 years (P = 0.12). Therefore, the probability of a particular climatic event occurring is inversely related to its expected effectiveness with respect to Swallenia germination. II^0 and III^0 events have a frequency that is just within the population half-life of 16 years and well within the persistence period of 88 years for Swallenia. These events do not result in the massive germination event observed in 1984 but they might provide small numbers of new individuals to stock the population over short spans of time. I^0 events are quite rare but have a large impact on the structure of the population if mass germination is followed by mass establishment.

Conclusions and Management Recommendations

1) Studies of the 1974-1984 period show that the fall/winter density of Swallenia seedlings is correlated with the amount of precipitation above normal during the summer months of July and August. Parametric and non-parametric analyses suggest that 1) the greater the departure of the precipitation amount from the monthly norm, the greater the response of germination and 2) precipitation is most effective if it occurs earlier (e.g. July) rather than later (e.g. September) in the summer season. It is tempting to speculate that these characteristics of Swallenia are indicative of its sub-tropical ancestry - a throwback to the summer-wet Miocene grasslands of which the dune grass is undoubtedly a remnant.

2) The climatic conditions that led to mass germination and establishment of Swallenia seedlings in 1984-85 have occurred only once in the last 90 years. This frequency coincides with the best available estimate of the time until population extinction at Eureka Dune (88 years, Table 2 of Chapter 1). Other, less effective, climatic events must also supply new individuals to the established population. These occur once every 11 or 15 years, the latter being more effective (rain during August) than the former (rain during September) and both provide a small number of new individuals to counteract the slow mortality of established hummocks (half-life of

16 years, Table 2). Each climatic event, regardless of its frequency, may not result in germination and establishment, however. Limitations on the effectivity are imposed by factors related to seed production and the fates of seeds in the seed bank (Chapter 2).

3) These considerations lead to the conclusion that events controlling the perpetuation of the *Swallenia* population occur infrequently at best and rarely at worst. Of all the possible demographic attributes that threaten the survival of this species (e.g. low seed production, seed and seedling mortality, competition with other dune plants), the time interval between successful establishment may be the most important. It is also the one over which we could exert the least control in the form of management or manipulation. As a paleoendemic occupying an anomalous desert habitat, *Swallenia* has persisted along an arete of existence for hundreds of thousands and perhaps millions of years. On one precipitous side lies the possibility of extinction due to the passage of decades with summer drought and, therefore, a lack of suitable climatic conditions for establishment. On the other, equally precipitous side is the possibility that Swallenia's sand dune habitat might be lost to erosion or stabilization as the frequency and intensity of summer rainfall (i.e. conditions for good germination) increase during wetter intervals of a long-term climate cycle. *Swallenia* has persisted and thrived in the absence of human disturbance despite the uncertainties associated with the dynamics of arid-land climate. Demographic studies have found no significant restriction on its ability to do so in the future.

Table 6. Correlations between *Swallenia* seedling density and regional precipitation parameters (Mr and Nr+) during the 1974-84 period. τ is Kendall's rank coefficient and P the level of significance (n.s. = not significant). n = 11 for all comparisons.

Swallenia density vs. Mr			*Swallenia* density vs. Nr+		
Mr	τ	P	Nr+	τ	P
solitary months					
Jul	.921	<0.01	Jul	.751	<0.01
Aug	.590	<0.05	Aug	.590	<0.05
Sep	.404	n.s.	Sep	.348	n.s.
Oct	.378	n.s.	Oct	.289	n.s.
Nov	.329	n.s.	Nov	.278	n.s.
Dec	.303	n.s.	Dec	.396	n.s.
mid-summer to early winter					
J+A	.575	<0.05	J+A	.484	<0.10
J+A+S	.547	<0.05	J+A+S	.542	<0.05
J+A+S+O	.537	<0.05	J+A+S+O	.537	<0.05
J+A+S+O+N	.378	n.s.	J+A+S+O+N	.577	<0.05
J+A+S+O+N+D	.418	<0.10	J+A+S+O+N+D	.537	<0.05
late summer to early winter					
A+S	.466	<0.10	A+S	.461	<0.10
A+S+O	.497	<0.05	A+S+O	.457	<0.10
A+S+O+N	.421	<0.10	A+S+O+N	.338	n.s.
A+S+O+N+D	.179	n.s.	A+S+O+N+D	.258	n.s.
early fall to early winter					
S+O	.381	n.s.	S+O	.298	n.s.
S+O+N	.298	n.s.	S+O+N	.341	n.s.
S+O+N+D	.219	n.s.	S+O+N+D	.378	n.s.
mid-fall to early winter					
O+N	.286	n.s.	O+N	.242	n.s.
O+N+D	-.021	n.s.	O+N+D	.063	n.s.
late fall to early winter					
N+D	-.022	n.s.	N+D	.110	n.s.

Table 7. Linear correlations between _Swallenia_ seedling density (y variable) and the significantly correlated (P<0.05) precipitation events (x variable) as indicated in Table 6. r is the correlation coefficient and df1/df2 = 1/9 for all comparisons of total monthly (Mr) or monthly + departure (Nr+) in the Eureka Valley region.

Swallenia density vs. Mr			_Swallenia_ density vs. Nr+		
Mr	r	P	Nr+	r	P
solitary months					
Jul	.552	n.s.	Jul	.959	<0.01
Aug	.291	n.s.	Aug	.295	n.s.
mid-summer to early winter					
J+A	.578	n.s.	J+A	.858	<0.01
J+A+S	.412	n.s.	J+A+S	.796	<0.01
J+A+S+O	.393	n.s.	J+A+S+O	.783	<0.01
J+A+S+O+N		n.s.	J+A+S+O+N	.766	<0.01
J+A+S+O+N+D	.218	n.s.	J+A+S+O+N+D	.692	<0.05
late summer to early winter					
A+S	.293	n.s.	A+S	.305	n.s.
A+S+O	.270	n.s.	A+S+O	.261	n.s.
A+S+O+N	.506	n.s.	A+S+O+N	.602	n.s.
A+S+O+N+D	.	n.s.	A+S+O+N+D	.547	n.s.

Table 8. Years of occurrence and frequency of extreme wetness (EW), severe wetness (SW) and moderate wetness (MW) conditions during July, August and September in the California desert region as determined by Palmer moisture anomaly indices for the period 1895-1984. Data from Karl (1985a, b).

July			August			September		
EW	SW	MW	EW	SW	MW	EW	SW	MW
84	38,44	11,13	45, 83		01, 04	04,12		96, 16
	68,69	14,15			09, 13	18,19		25,67
		16, 22			31, 35	23, 39		83
		32, 33			41, 42	63, 76		
		36, 41			51, 61			
		46, 52			79			
		67, 79						
		80						

$f\ (EW_{july}) = 1/90$ years $(P=0.01)$

$f\ (EW_{aug}) = 2/90$ years $(P=0.02)$

$f\ (EW_{sept}) = 8/90$ years $(P=0.08)$

$f\ (EW_{july + aug}) = 3/90$ years $(P=0.03)$

$f\ (EW_{july + aug + sept}) = 11/90$ $(P = 0.12)$

$f\ (EW + SW_{july + aug + sept}) = 15/90$ $(P = 0.17)$

Table 9. Frequency of climatic conditions for the 1895-1984 period in the deserts of California grouped according to relative effectiveness with respect to *Swallenia* germination. Data from Table 8 and Karl (1985a, b).

I° events	II° events	III° events
EW_{july}	$SW_{july} + EW_{aug}$	$SW_{aug} + EW_{sept}$
1/90 years	(4 + 2)/90 years	(0 + 8)/90 years
= ≥90 years apart	= 15 years apart	= 11 years apart

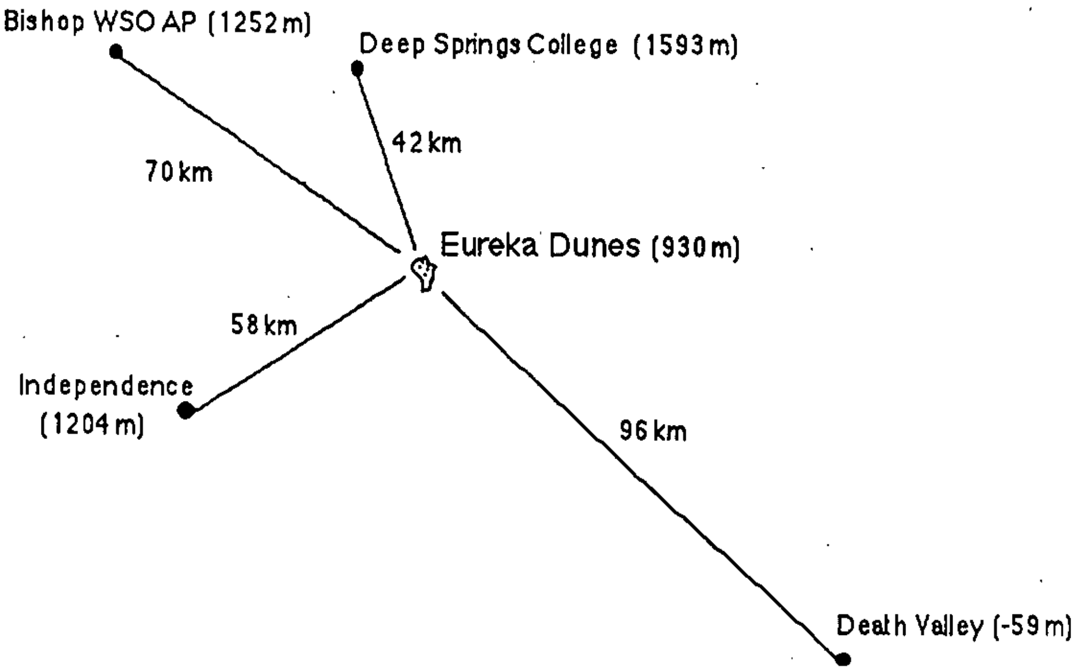


Figure 16. Relation of U.S. Weather Bureau stations to Eureka Dunes. Distance of the station from the dunes and its elevation are shown.

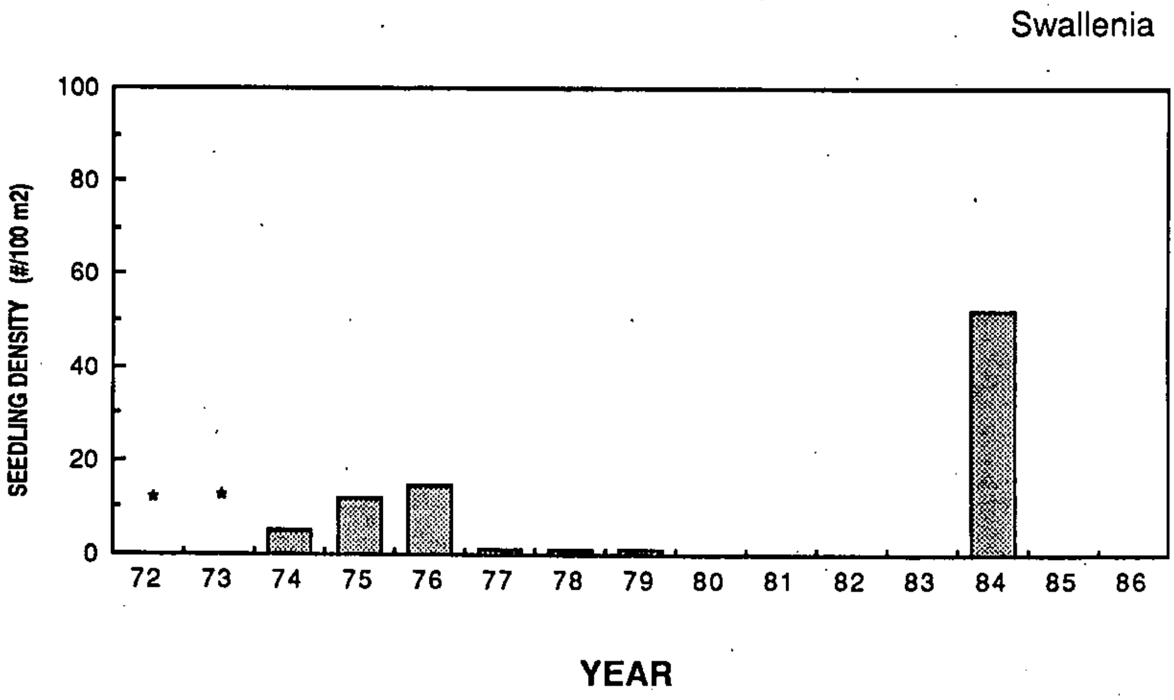


Figure 17. Seedling density of Swallenia on the northwest flank of the main dune, 1974-1986. Astericks indicate no available data.

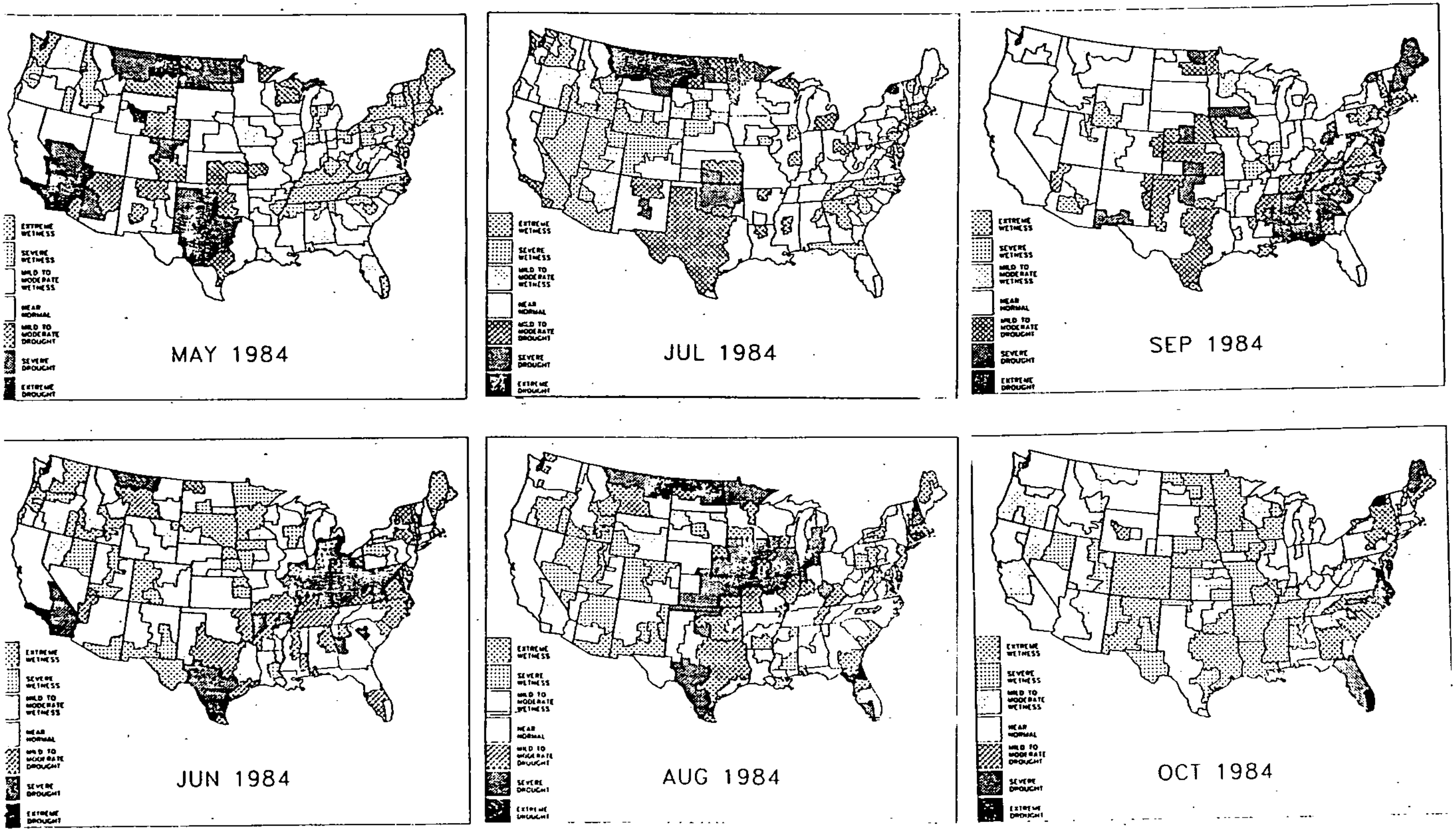


Figure 18. Monthly Palmer moisture indices for the summer and fall of 1984. July 1984 map shows the rare occurrence of extreme wetness conditions in southeastern California that led to the mass establishment of seedlings monitored in this study. From Karl (1985).

Appendix A:

Seed Production and Seed Rain, 1985-1986

Appendix A

Seed Production and Seed Rain, 1985-1986

Additional seed production data were collected during the 1986 field season. The purpose was to 1) examine year-to-year variability in seed output per plant for each of the endemic species, and 2) provide estimates of seed rain to compare with estimates of seed density in the 1986 seed bank. The methods for making these measurements are found in Pavlik and Barbour (1985).

Results and Discussion

The relationship between canopy volume and seed output per individiual during 1985 and 1986 is shown in Figures a, b and c. Swallenia seed production was a linear function of canopy volume ($r > 0.85$) and varied significantly between 1985 and 1986. The equation for the 1985 relationship (seed output = 4.226 (canopy volume, dm^3) - 31.348, $r = 0.92$) had a slope that was four times as great as that of the 1986 relationship (seed output = 0.889 (canopy volume) + 125.292, $r = 0.85$). The principle difference between Swallenia reproduction in 1985 and 1986 was a decrease in the number of inflorescences per individual during 1986. It is not known if this decrease was the result of environmental stress or part of an intrinsic reproductive fluctuation. As previously indicated (Pavlik and Barbour 1985), the output for an averaged sized Swallenia was low (1000-3100 seeds/plant/year, $V_c = 750\ dm^3$) compared to non-endangered perennial grasses from arid environments.

Annual seed production by Oenothera and Astragalus was a logarithmic function of canopy volume ($r > 0.85$) and fairly constant from year to year (Figures b and c). Average sized individuals of Oenothera ($Vc = 60\ dm^3$) produced 36,000 seeds in 1985 while those in 1986 ($Vc = 12\ dm^3$) nearly 7,000. (Note that although the relationship between canopy volume and seed output did not vary from year to year, the average size of primrose individuals did.) Average sized individuals of Astragalus ($200\ dm^3$) produced 10,000 seeds in 1985 while those in 1986 ($Vc = 190\ dm^3$) produced nearly 12,000. These estimates of annual seed output per plant compare favorably with whose presented for other non-endangered members of the genera Oenothera and Astragalus (Pavlik and Barbour 1985).

Considerable variation in the seed rain was observed during the two years of ths study (Table a), but the cause of the variation differed for each taxon. Swallenia seed rain was more than halved during 1986 due to the decline in seed output per plant (Figure a). Oenothera seed rain declined by more than 75 percent because each plant was on the average 80 percent smaller during 1986 (see above). Most of the 30 percent decrease in Astragalus seed rain was due to the death of mature plants after 1985, resulting in a lower density of reproductive individuals. These estimates of seed rain correspond in magnitude to the estimates of seed density in the seed bank during 1986 (Chapter 2 this volume and Table b).

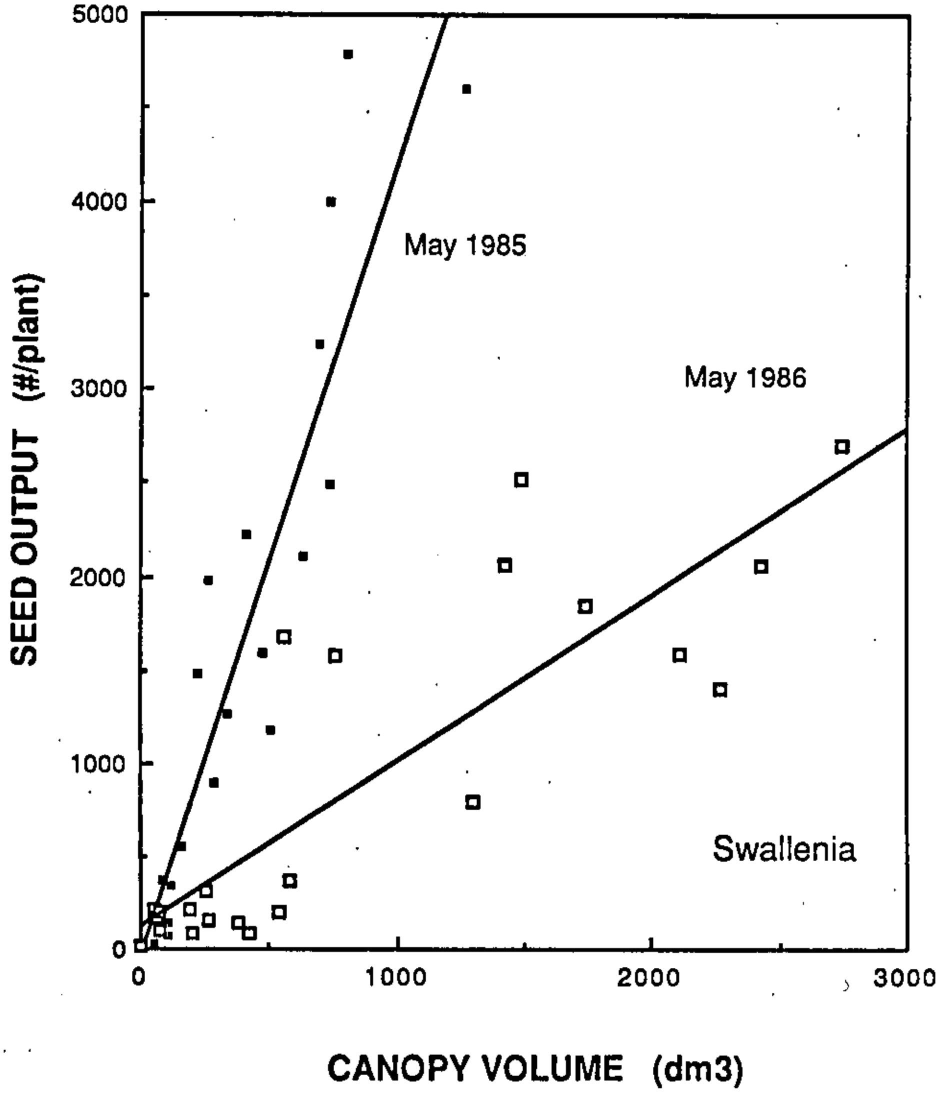


Figure a. Seed production of Swallenia individuals as a function of canopy volume, 1985 and 1986. Closed symbols represent 1985, open represent 1986.

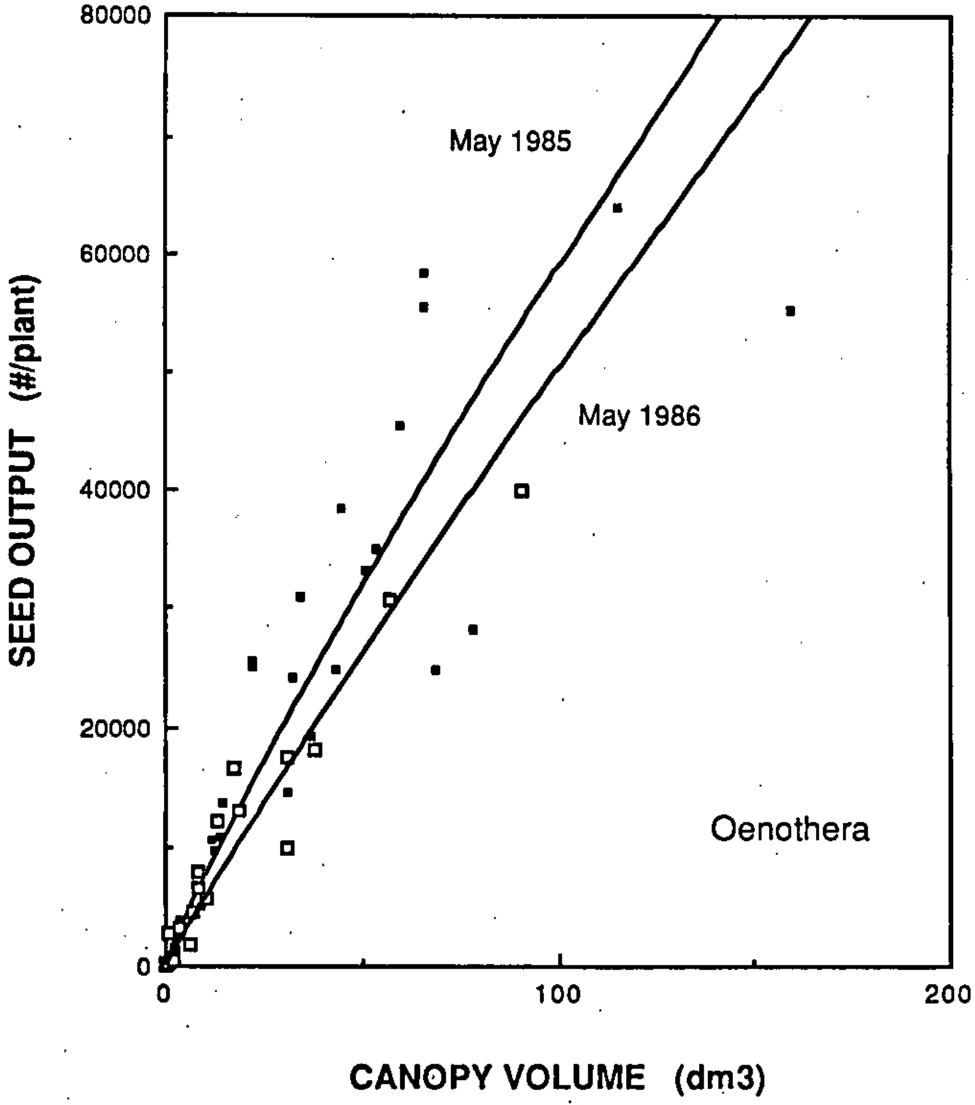


Figure b. Seed production of Oenothera individuals as a function of canopy volume, 1985 and 1986.

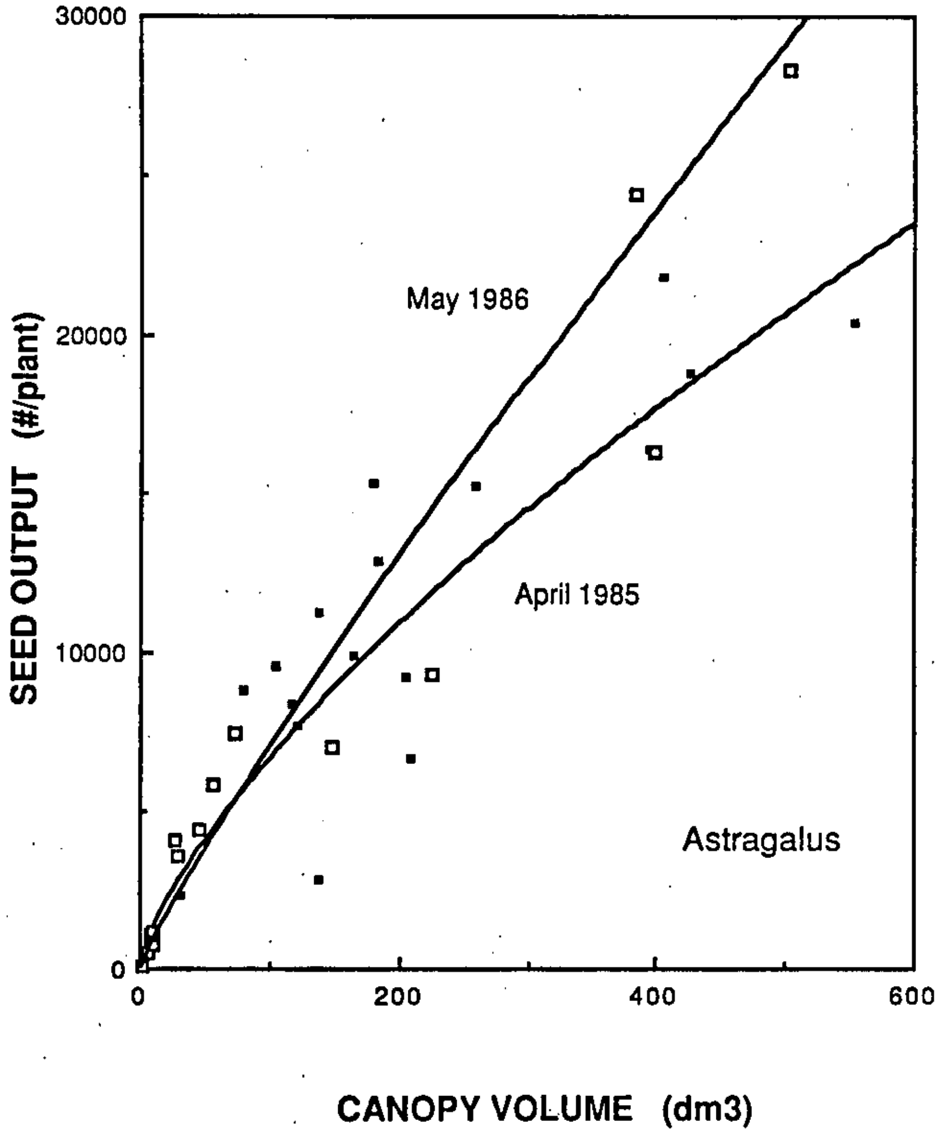


Figure c. Seed production of <u>Astragalus</u> individuals as a function of canopy volume, 1985 and 1986.

Table a.

PLANT DENSITY AND SEED RAIN FOR POPULATIONS AT EUREKA DUNE

	1985		1986	
	plant density (# / m2)	seed rain (# / m2 / yr)	plant density (# / m2)	seed rain (# / m2/yr)
Swallenia	0.084	63	0.082	25
Oenothera	0.600	21,317	0.510	3568
Astragalus	0.081	693	0.063	491

Appendix B:

Population Attributes and Their Management Implications

Appendix B

Population Attributes and Their Management Implications[1]

Abstract: Plant survivorship, seed production, seed bank dynamics and frequency of establishment can be used to determine if endangered plant populations are declining (thus requiring intensive monitoring and recovery efforts) or stable and/or growing when protected from human disturbance. A two year study of the perennial endemics Swallenia alexandrae, Oenothera avita ssp. eurekensis and Astragalus lentiginosus var. micans was conducted at Eureka Dunes, Inyo County, California. Based on analyses of survivorship it was concluded that the populations are at least stable (even short-lived Oenothera cohorts survive long enough to reproduce) or growing (the number of established Swallenia and Astragalus plants doubled during the study). The high mortality and short life span of Oenothera and Astragalus populations were offset by copious seed production, long-lived seeds, low to moderate seed predation, and frequent establishment. The low and variable seed production, high seed predation and infrequent establishment of Swallenia populations were counterbalanced by a low mortality of recruits and established plants, a long reproductive life and long-lived seeds. It is possible, therefore, to conclude that the factors endangering these endemic populations are mostly extrinsic. No additional manipulations are warranted if adequate protection from human disturbance is maintained. Occasional monitoring in the future is necessary in order to verify these conclusions.

---

[1] Paper presented at "Rare and Endangered Plants: A California Conference on their Conservation and Management" November 5-8, 1986 Sacramento, CA.

INTRODUCTION

Demographic studies of plants indicate that each species population can possess unique attributes that ultimately determine local abundance and/or persistence through time (Harper 1977). A thorough analysis of these attributes is of primary importance in the management of endangered populations simply because abundance and persistence are at the center of all recovery efforts. Such efforts are usually undertaken once the threat of human disturbance has been minimized (preservation by land-use restriction). This is because preserve management requires a knowledge of the population's status (whether it is declining, stable or growing) under the most "natural" of conditions. This determination can be made by selecting a few, relevant population attributes and conducting a demographic monitoring program (Pavlik 1987). The purpose of this paper is to illustrate the use of survivorship, seed production, seed bank and temporal establishment data for determining the post-preservation status of the endemic populations at Eureka Dunes, Inyo County, California. The Eureka populations comprise the entire known distribution of *Swallenia alexandrae*[2] (Soderstrom and Decker), *Oenothera avita* ssp. *eurekensis* W. Klein and *Astragalus lentiginosis* var. *micans* Barneby. All three taxa are perennial, suffrutescent herbs restricted to deep, windblown accumulations of sand (Pavlik 1979a).

---

[2] All three endemic taxa are herein referred to by their generic epithet.

METHODS AND MATERIALS

Plant Survivorship

In February 1985 three sites were established on the northwest flank of the main dune in an area that has been extensively studied in the past (Henry 1976, Pavlik 1979a, 1979b, 1980, Pavlik and Barbour 1985). The sites were chosen so that each represented one of the study species according to the following criteria; 1) the species population was composed of at least 150 individuals from all age/size classes, 2) the population was located in a dune habitat typical of the species (e.g. steeper, less stable slopes for Swallenia and lower, more stabilized slopes for Oenothera and Astragalus (DeDecker 1976, Pavlik 1979a)), 3) germinule and seedling densities were similar to those observed in other parts of the dune system and 4) the site was a great distance from footpaths taken by dune visitors.

At each site a large plot was randomly located with its lower boundary oriented along a 60^0 compass bearing. Plot size varied among the three species and reflected differences in the size and density of individual plants. The upper plot contained the Swallenia subpopulation and was 50 m X 50 m (2500 m^{-2}). The Oenothera plot was placed approximately 100 m downslope (north) from the Swallenia plot and was 50m X 10m (500 m^{-2}). Approximately 10 m north of the Oenothera plot was the 30 X 25 m (750 m^{-2}) Astragalus plot. The corners of the plots were marked with 5 cm diameter stainless steel rods that were threaded over their entire length and had a 8 cm diameter hook on one end. These rods could be screwed into the sand for a distance of about 30 cm leaving the hooked end exposed. They were used to attach sampling tapes during subsequent visits and insure that the relocation of sub-plots could be accurately achieved. The markers remained in place after the 1986 field season.

On five occasions during 1985 (2/15-16, 3/21-22, 4/26, 5/31-6/1 and 8/11-12) and three during 1986 (3/22-23, 5/29 and 10/4-5) the demographic plots were sampled for the number of live individuals and notes were made regarding their vigor, growth, life history stage and phenological state. Life history stages (see below) for the study plants were developed from observations made on laboratory and field-grown plants (Pavlik 1979b, Pavlik and Barbour 1985). Swallenia and Oenothera plots were subsampled using 10 or 15 randomly-placed subplots, respectively. The Astragalus plot was sampled in its entirety. Each time the census was taken, a scaled map of each subplot was generated by marking the location of live and dead individuals rooted within the subplot. This allowed the fates of individual plants to be accurately monitored throughout the study. Attempts were made to tag all plants in addition to mapping, but this effort was defeated when wind storms removed the 28 cm wire stakes that held the tags.

Plots of time (days since the Feb 1985 census) versus the number of living individuals were made using the 1985-86 census data. These plots represented true survivorship curves for young plants of Swallenia, Oenothera and Astragalus (germinules, seedlings and juveniles) that were established as a single cohort after the fall 1984 germination event. Plots for older, established plants of the three species represented population depletion curves because these individuals may have been from different cohorts of various ages (Harper 1977). It was then possible to calculate mortality and half-lives (the time in which a population decreases by 50%) for the population as a whole or for subpopulations at different life history stages (Harper 1977, Hutchings 1986). These stages included established plants (mature (M) or senescent (St)) and recruits (germinule (G), seedling (S), juvenile (J) or in the case of Swallenia, hummock-forming juvenile (

Ⓙ)). Details of these methods may be found in Pavlik and Barbour (1986).

Seed Production

At least 15 individuals of each taxon were selected prior to flowering for making estimates of seed production during the springs of 1985 and 1986. All individuals were located very near or in the survivorship plots of their respective species. Plants varied in terms of canopy volume (Vc) as calculated from measurements of plant length, width and height.

An enumeration model was used for each species in order to estimate the actual seed output per plant having a given Vc at the time of maximum flower and fruit production (March-April for *Astragalus*, May-June for *Swallenia* and *Oenothera*). During March, April, May and July these plants were surveyed for Vc, the number of inflorescences per plant and the number of developed fruits, aborted fruits, flowers and flower buds per infrutescence (from a subsample of 5 infrutescences). During peak fruit production, 20-44 infrutescences per taxon were examined in the laboratory to determine the mean number of seed-containing fruits per infrutescence. In the case of *Swallenia* it was possible to estimate the mean number of caryopses (herein referred to as seeds) per infrutescence directly since each caryopsis contains one seed.) This mean value compared favorably with field estimates of the same parameter and so it was used to calculate the mean number of seed-containing fruits per individual from other field measurements mentioned above. This was converted to the mean number of filled, undamaged seeds per individual of *Oenothera* and *Astragalus* by counting the number of filled seeds in 30 fruits of each taxon and determining the mean. Details of this method are found in Pavlik and Barbour (1985).

In order to estimate the seed rain (seed output of a stand of plants on a habitat area basis) the survivorship data (number of live, mature plants per square meter of the stand of size Vc) were combined with regressions of seed production on plant size for each taxon. This method takes into account differences in mortality and reproductive output among individuals in the population and, therefore, represents a partial life table analysis (Hutchings 1986).

Seed Bank Dynamics

In March, May and October of 1986, estimates of the seed bank within survivorship plots of Swallenia, Oenothera and Astragalus were made by pressing 1 liter plastic containers into the dune and trapping the sand in the container with a plastic lid. These containers sampled 0.178 m^2 of dune surface near and between mature plants. Their placement was random but spread throughout 100 m^2 of each plot. Owing to the patchy vegetation cover found in the Swallenia stand, 50 of these samples were required, whereas 8 were used for Oenothera and Astragalus stands on each date. Seeds of Swallenia and Astragalus could be separated from the sand with medium coarse soil sieves. Oenothera samples, however, required sieving with fine-mesh screens and immersion of the throughfall (very fine sand + seeds) in tubs containing a saturated salt solution. The small seeds floated on the salt solution more than 90% of the time as determined by spiking studies.

Seed longevity was tested by germinating seeds from the 1978 and 1985 crops. These had been stored dry and at room temperature. They were germinated under optimal light, temperature and moisture conditions according to the results of Pavlik (1979a). Three replicate dishes of 50 seeds each were used for Swallenia and Oenothera and 25 scarified seeds for Astragalus. In addition, tetrazolium tests were run on all ungerminated seeds at the end of the 10 trials to determine if they were dormant or dead.

On two nights in October 1986, seed selection experiments were run at Eureka Dunes by placing 10 naked Swallenia seeds, 10 Swallenia seeds in their floral bracts, 10 Oenothera seeds, 1 ripe Oenothera capsule (containing numerous seeds), 10 Astragalus seeds and 10 Astragalus pods(with seeds) in a shallow glass or plastic dish. A total of 27 dishes were sunken below the sand surface (9 in each species plot). Some were placed next to the canopies of established plants and some up to 3 m away. Seeds could not be easily blown from the dishes (the two nights were perfectly still anyway) and footprints in the surrounding sand revealed if seeds were missing due to nocturnal, mammalian predators. Foraging ants, however, could not escape from the dishes once they had fallen in. This allowed some assessment of ant vs. mammal seed predation.

Frequency of Establishment

Estimates of fall seedling density of Swallenia were available for most years between 1972 and 1986 (Henry 1976, Pavlik 1979, Pavlik and Barbour 1986). The records for Oenothera and Astragalus were not as long-term or complete and came only from the author's field notes. These could, however, provide information on the frequency of germination over the same time period.

RESULTS AND DISCUSSION

Survivorship

Survivorship and depletion curves for the three endemic taxa are shown in Figures 3-5 (pages 20-22 of this report). Changes in the total Swallenia population (□) were the result of mortality in the fall 1984 cohort of germinules, seedlings and juveniles (■). After nearly two years 24 percent of this cohort had survived and grown into hummock- forming juveniles whereas 97 percent of the mature and senescent plants (▲) were still alive. The total population was more than twice its original size two years after cohort emergence. This contrasts with Oenothera which produced cohorts of seedlings in both years. Only 4% of the winter 1984-85 cohort survived until the next year (thus, the truely perennial population was very small), but nearly 75 percent had produced seed during that time. The winter 1985-86 cohort had higher survivorship (41 percent) a lower percentage of reproductive individuals (48) and was comprised of smaller mature plants (mean Vc = 12 dm^3) than the 1984-85 cohort (mean Vc = 60 dm^3). This pattern was also observed for Astragalus, except that none of the winter 84-85 cohort survived or reproduced. Seedling survivorship was much higher in 1986 (54%) but none of these had reproduced within the year. Like Swallenia, survivorship of mature Astragalus plants was high (69 percent) thereby making a rather large population of perennial plants. If even half of the 1986 cohort survives another year (likely in that they already survived the first summer), then the established Astragalus population will more than double in size.

Survivorship data are re-interpreted in Figure 6 (pg. 23) as the mean mortality (1985-86) experienced by each life history stage. Mortality was generally low (< 25 percent) and constant for Swallenia, high (25-80 percent) and increasing with age for Oenothera and extremely variable (15-95 percent) and perhaps declining with age for Astragalus.

Half-lives for recruits, established (adult) plants and the total population were derived from survivorship data (Table 2, pg. 12). The values for Oenothera and Astragalus were similar and about half those of Swallenia. Swallenia half-lives compare favorably with those of non-endangered perennial grasses from arid environments (0.5-4.5 years, Williams 1970, West et al. 1979). Those of Oenthera and Astragalus, however, are on the low end of the spectrum for non-endangered herbaceous perennials (0.5- >50 years, Harper 1977). Extrapolating until the time of population extinction (potentially erroneous but nevertheless valuable for comparative purposes), established Swallenia populations might persist for as long as 88 years in the absence of recruitment while Oenothera and Astragalus might persist from 3 to 16 years. Based on survivorship data alone, Oenothera is the most endangered of the three taxa (high mortality and short half-life of recruits and adults), Astragalus the next (high mortality and short half-life of recruits but high adult survivorship) and Swallenia the least (lowest mortality, longest half-life of all stages).

Seed Production

The relationship between canopy volume and seed output during 1985 and 1986 is shown in Figures a, b, and c (Appendix A). Swallenia seed production was a linear function of canopy volume ($r > 0.90$) and varied significantly between 1985 and 1986. The output for an averaged sized Swallenia was low (3,100 seeds/plant/year, $Vc = 750\ dm^3$) compared to non-endangered perennial grasses from arid environments (16,000-200,000 seeds/plant/year, Stevens 1932, Huiskes 1979, Davy 1980). Annual seed production by Oenothera and Astragalus was a logarithmic function of canopy volume ($r > 0.85$) and fairly constant from year to year. Average size individuals of Oenothera (60 dm^3) produced 36,000 seeds in 1985 and those in 1986 (12 dm^3) produced 7000. Average size individuals of Astragalus (200 dm^3) produced 10,000 seeds in 1985 and those in 1986 (190 dm^3) nearly 12,000). These estimates of annual seed output per plant compare favorably with those presented for other non-endangered members of the genera Oenothera and Astragalus (Stevens 1932). Based on seed production data alone, it would appear that Swallenia is the most endangered of the three taxa and Oenothera the least. When the survivorship data are taken into consideration, however, it is obvious that the high mortality and short half-life observed in the Oenothera population are to some extent ameliorated by copious and consistent seed production from year to year. On the other hand, Swallenia is a poor seed producer but its recruits and adults experience lower mortality and greater longevity.

Considerable variation in the seed rain was observed during the two years of study (Table a, Appendix A), but the cause of the variation differed for each taxon. Swallenia seed rain was more than halved due to an intrinsic decline of seed output per plant (Figure a): Oenothera seed rain declined by more than 75 percent because each plant was on the average 80 percent smaller (see above). Most of the 30 percent decline in Astragalus seed rain was due to the death of mature plants after 1985, resulting in a lower density of reproductive individuals.

Seed Bank Dynamics

The densities of Swallenia and Astragalus seeds in the seed bank corresponded with the magnitude and timing of seed rain during 1986 (Figure 9 pg 39 and Table a, Appendix A). Increases in seed density were on the order of 8 to 35 fold as seed output and dispersal peaked during the April-May period. The seed bank of Oenothera, however, did not peak during the period of maximum seed production, but declined from March to May. There are at least two factors contributing to this pattern; 1) the large 1985 and small 1986 seed rains (i.e. the dune sand contained a large number of 1985 seeds and was not enriched during 1986) and 2) dispersal of the extremely mobile seeds during spring wind storms. Regarding the latter, Pavlik and Barbour (1985) compared the small, lightweight Oenothera seeds to those of Swallenia and Astragalus and found they were the fastest dispersers at any wind velocity (and, therefore, most likely to leave the habitat). This dispersal ability allows Oenothera to maintain the largest geographic range of all three dune endemics.

All three taxa had much smaller seed banks in October. In unstable sand dune habitats there are five possible fates of these seeds; 1) aging, death and decay, 2) predation, 3) germination, 4) deep burial by moving substrate, and 5) dispersal out of the stand as substrate is moved by high wind.

Table 4 (pg. 32) shows that seeds of all three taxa remained viable and germinated after 8 years. It seems unlikely that seeds in situ would age, die and decay after five months.

Seed predation, however, must significantly contribute to decreasing the seed reserves of Swallenia and Astragalus. Over a single night period, 14 percent of all naked Swallenia seeds and 9 percent of all naked Astragalus seeds were collected (principly by the kangaroo rat Dipodomys, as judged from tracks). Swallenia disseminules were also taken (6 percent). In three dishes there were several ants observed carrying Swallenia seeds, suggesting that if they could leave the dish they would take the seeds with them. Of all seeds and disseminules removed, those of Swallenia were more likely to be selected by rodents and ants (Table 5, pg. 34). There was no evidence that Oenothera seeds or fruits experienced any predation by nocturnal rodents or ants.

Germinule emergence was not observed during the May to October period and so it seems unlikely that seed bank decline is a result of germination. The possibility of subsurface germination and death is remote owing to the fact that 1) the upper 30 cm of dune sand was dry and significant rain did not occur over the summer and early fall, 2) dead germinules were never found in seed bank samples and 3) summer sand temperatures (35-55 C) completely inhibit germination of the three taxa even if supplied with ample moisture (Pavlik 1979a).

Casual observations made in all three populations indicate that less than 10 cm (mostly less than 4 cm) of sand accumulated in portions of the study plots over the summer. In this case the seed bank samples would not have been greatly affected by the deposition of small amounts of seedless substrate (the most biasing case). Sand accumulation can vary greatly with position on the dune and time of the year (Pavlik 1979a) and it is entirely possible that many seeds become deeply buried for long periods of time. The size and dynamics of this "quiescent" seed bank remain unknown.

The last possible fate of seeds in the dune seed bank is dispersal out of the stand. This cannot be excluded for any of the taxa since all three are capable dispersers (Pavlik and Barbour 1985). Dispersal and predation both contribute to the summer-fall decline of Swallenia and Astragalus seed banks but only dispersal affects the Oenothera seed bank. It could be argued that since seeds might be transported in as well as out of the seed bank by substrate movement, only predation significantly affects these seed banks. This argument is extreme and does not recognize the very patchy and sparse cover by endemics on the dune and the great volume of lifeless, shifting sand.

Frequency of Establishment

Finally, the available evidence suggests that significant germination and establishment of Swallenia many occur infrequently, perhaps once every 8-10 years (Figure 17). Apparently this phenomenon is associated with sporadic occurrences of unusually large amounts of summer-early fall precipitation. This agrees with other studies of desert perennials (Brum 1973, Jordan and Nobel 1981). If the population of mature Swallenia individuals can persist for 16 years (its half-life, a conservative estimate) to 90 years (the time of population extinction, a very rough approximation), then 2-9 establishment events could occur. Oenothera and Astragalus can germinate more frequently (perhaps annually as in figures 2 and 3), although successful establishment and reproduction may be less common (every 2-4 years according to field notes).

CONCLUSIONS

The data clearly indicate that the endemic populations of Swallenia, Oenothera and Astragalus at Eureka Dunes are not declining. Based on analyses of survivorship they are at least stable (even short-lived Oenothera cohorts survive long enough to reproduce) or growing (the number of established Swallenia and Astragalus plants more than doubled during the study period). As might be predicted from the r-K selection hypothesis, the high mortality and short life of

Oenothera and Astragalus populations were offset by copious seed production, long-lived seeds, low to moderate seed predation, and frequent establishment. Oenothera even has the ability to clone in order to increase population half-life (data not included). The low and variable seed production, high seed predation and infrequent establishment observed in Swallenia populations is counterbalanced by a low mortality of recruits and established plants, a long reproductive life and long-lived seeds. At this time it seems possible to conclude that the factors endangering the endemic populations at Eureka Dunes are mostly extrinsic. These extrinsic factors include the status of Oenothera and Astragalus pollinators (Pavlik and Barbour 1985), the watershed management practices affecting dune hydrology (Pavlik and Barbour 1986), and human disturbance (Pavlik 1979b). The latter two can be minimized by regional planning, management and enforcement. No additional manipulations of the Eureka Dune populations are warranted **if adequate protection from human disturbance is maintained**. Occasional monitoring in the future is necessary in order to verify these conclusions. Although we can never turn our backs on endangered but stable populations, we can for the moment turn our attention to other, more critically threatened taxa.

ACKNOWLEDGEMENTS

I gratefully acknowledge the field assistance of Lauren Krieger, Eileen Manning, Monty Knudsen, Bob Pavlik, Lynn Suer and Derham Giuliani. This research was made possible by grants from California Department of Fish and Game, Endangered Species Office, the University of California at Davis, and Mills College. The support of Susan Cochrane of California Fish and Game, Office of Endangered Species is especially appreciated.

Literature Cited

Barbour, M.G. 1968. Germination requirements of the desert shrub Larrea divaricata. Ecology 49, 915-923.

Beatley, J. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55, 856-863.

Brum, G.D. 1973. Ecology of the Saquaro (Carnegia gigantea) : phenology and establishment in marginal populations. Madrono 22, 195-204.

Budd, A.C., W.S. Chepil and J.L. Doughty. 1954. Germination of weed seeds. III. The influence of crops and fallow on the weed seed population of the soil. Can. J. Agric. Sci. 34, 18-27.

Canfield, R.H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. J. Range Man. 10, 199-203.

DeDecker, M. 1981. Recovery plant for the Eureka Dunegrass and the Eureka Evening Primrose. U.S.F.W.S. contract report, Sacramento, Ca.

Harper, J. 1977. Population Biology of Plants. Academic Press, London.

Henry, M.A. 1976. A living fossil, Swallenia alexandrae (Eureka Dune Grass). Paper presented at Southern California Academy of Science Meeting, May 8, 1976, Santa Barbara, CA.

——— 1979. A rare grass on the Eureka Dunes. Fremontia 7, 3-6.

Hutchings, M.J. 1986. Plant population biology. In: Moore, P.D. and S. B. Chapman (eds.) Methods in Plant Ecology. Blackwell Scientific Publications, Oxford.

Jordan, P.W. and P.S. Nobel. 1981. Seedling establishment of Ferocactus acanthodes in relation to drought. Ecology 62, 901-906.

Karl, T. 1985. Atlas of monthly Palmer moisture anomaly indices for the contagous United States. Volume I (1895-1930) and Volume II (1931-1984). Historical Climatology Series 3-8 and 3-9. National Climatic Data Center, Asheville, N.C.

Leverich, W.J. and D. A. Levin. 1979. Age-specific survivorship and reproduction in Phlox drummondii. Amer. Nat. 113, 881-903.

Linkola, K. Uber die Dauer und Jahresklassenverhaltnisse des Jungenstadiums bei einigen Wiesenstauden. Acta Forest. Fenn. 42, 1-56.

Lippert, R. D. and H. H. Hopkins. 1950. Study of viable seeds in various habitats in mixed prairies. Trans. Kansas Acad. Sci. 53, 355-364.

Major, J. and W. T. Pyott. 1966. Buried viable seeds in California bunchgrass sites and their bearing on the definition of a flora. Vegetatio Acta Geobotanica 13, 253-282.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. J. Wiley and Sons, New York.

National Oceanic and Atmospheric Adminstration (NOAA). 1974-1984. Climatological Data - California.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst. 4, 25-51.

Pavlik, B.M. 1979a. A synthetic approach to the plant ecology of desert sand dunes, Eureka Valley, California. M.S. thesis, Univ. Ca. Davis.

——— 1979b. The biology of endemic psammophytes, Eureka Valley California, and its relation to off-road vehicle impact. California Desert Plan, BLM contract no. CA-060-CT8-000049.

——— 1980. Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. Oecologia 46, 147-154.

——— 1987. Populations attributes and their management implications. Rare and Endangered Plants: A California Conference on Their Conservation and Management. Proceedings published by the California Native Plant Society.

Pavlik, B.M. and M.G. Barbour. 1985. Demography of plants endemic to desert sand dunes, Eureka Valley, California. I. Seed production, dispersal and the effects of herbivores. Research report submitted to U.S.F.W.S. Endangered Plant Program, Sacramento, Ca.

Sharitiz, R.R. and J.F. McCormick. 1973. Population dynamics of two competing annual plant species. Ecology 54, 723-740.

Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. 8, 195-246.

Sokal, R.R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman Co., San Francisco, CA.

Tamm, C. O. 1956. Further observations on the reproduction and survival of some perennial herbs. Oikos 7, 274-292.

Went, F. W. and W. Westergaard. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. Ecology 30, 26-38.

Williams, O. B. 1970. Population dynamics of two perennial grasses in Australian semi-arid grassland. J. Ecol. 58, 869-875.