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EUREKA CALLEY, CALIFORNIA, AND ITS RELATION
TO OFF-ROAD VEHICLE IMPACT

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THE BIOLOGY OF ENDEMIC PSAMMOPHYTES

EUREKA VALLEY, CALIFORNIA, AND ITS RELATION TO

OFF-ROAD VEHICLE IMPACT

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DEPARTMENT OF BOTANY

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INTRODUCTION

The vegetation ecology of desert lands in California has only begun to emerge, as quantitative descriptions of the different floristic and structural units appear in recent literature. Similarly, the physiological ecology of arid-land species--the manner in which they assemble themselves and future generations--now supplements and somewhat clarifies our knowledge about the distribution, interaction and survival of desert plants.

However, considerable gaps exist in the understanding of these species, population and communities. For example, Vasek and Barbour (1977) pointed out that no quantitative data seemed available on the ecology of plants adapted to the desert sand dune habitat in California. Such gaps do not allow for the development of responsible management plans for public lands being exposed to ever-increasing recreational demands. Paramount among these demands is that of the off-road vehicle (ORV) enthusiast, whose activities may conflict with the fragile existence of desert life (Stebbins, 1974). Several studies have been made on the effects of construction disturbance on Mojave Desert vegetation (Johnson et al. 1975, Vasek et al. 1975a, 1975b) and at least one has dealt specifically with ORV effects (Davidson and Fox 1974). Unfortunately, little quantitative data are available on the effects of ORV activity on the inhabitants of desert sand dunes (see Kuhn 1974). This reflects our lack of knowledge about the biology of these organisms and the inherent difficulty of such studies. The effects of ORV impact on the physical environment of the desert has been more fully explored (see

Wilshire and Nakata 1976, Wilshire et al. 1977).

Eureka Dunes, located in the southeastern corner of Eureka Valley, Inyo County, California, are a unique desert habitat. Owing to their geographic location, age, large size and complex structure, these dunes support a rich assemblage of organisms. Among these organisms, three plant taxa have been considered endemic to the dune complexes of Eureka Valley. The rarity of these plants and the potential for their extinction has qualified them for listing on various rosters of rare and endangered plants. The plant taxa endemic to Eureka Dunes and their status are as follows:

	Federal	Ca. State	CNPS*
<u>Swallenia alexandrae</u>	endangered	very rare & rare & endan- gered	3-2-1-3
<u>Oenothera avita</u> ssp. <u>eurekensis</u>	endangered	very rare & rare & endan- gered	3-2-2-3
<u>Astragalus lentiginosus</u> var. <u>micans</u>	threatened	very rare & rare & endan- gered	3-2-1-3

*California Native Plant Society

Until recently, the dunes were subject to heavy disturbance by ORVs and this resulted in apparent damage to the vegetation and the disruption of other biological activities (BLM 1976, DeDecker 1976). However, too little is known about the life histories of the endemic plants and the effects of ORV activity to properly assess their critical interaction.

OBJECTIVES OF THE STUDY

- 1) To obtain biological data on the rare, threatened and endangered plants of the Eureka Dunes from field observation, laboratory study and library research, emphasizing the ecological aspects of their life histories.
- 2) To obtain data on the relevant features of the sand dune physical environment.
- 3) To obtain experimental data and make observations on the effects of off-road vehicles on the rare, threatened and endangered plants of the Eureka Dunes.

ACKNOWLEDGEMENTS

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THE STUDY SITE

Location

The Eureka Dunes are located in the southeastern portion of Eureka Valley, Inyo County, California, approximately 71 aerial km southeast of Bishop (Figure 1). They are reached from Bishop by U.S. 395 south to California Route 168, proceeding east until the Waucoba Road diverges to the southeast and remaining on it until encountering the South Eureka Valley Road. This is a total distance of 90 km. The main dune lies 18.5 km to the south of this intersection and is clearly visible from most points within the valley. Essential map coverage is given by the Last Chance Range 15' topographic quadrangle.

Eureka Valley is divided from Deep Springs and Fish Lake valleys to the north by the Inyo Mountains, whose southerly extension and coalescence with the Saline Range forms the western and southern boundaries. To the east rise the Last Chance Mountains which abruptly separate Eureka Valley from northern Death and Saline valleys. The lowest elevation of 878 m is at the playa adjacent to the base of the dune (Figure 2).

The dune itself measures 2.4 x 5.4 km with the long axis oriented north to south. Its summit is relatively stable in its position and height, latitude $37^{\circ} 06' N$ and longitude $117^{\circ} 40' W$, elevation 1087 m. Eureka Dunes appear to be the tallest in California, towering at least 203 m above the playa (Berkstresser 1974, Dean 1978).

Geology and Geomorphology

Little has been written on the local geology of Eureka Valley. Knopf (1918) extensively described the stratigraphy and mineral resources

Figure 1. Location of Eureka Valley, California.

Figure 2. Topographic features of Eureka Dunes and vicinity, from the U.S.G.S. Last Chance Range quadrangle.

of the Inyo Range but did not venture beyond the western portion of Saline Valley. Later work by Nelson (1962) and Stewart (1965) concentrated on the major Paleozoic rock units of the Inyo and Mono regions. Detailed geologic mapping by the United States Geological Survey (U.S.G.S.) was not begun until the early 1960's and the Last Chance Range quadrangle (which includes the dune area) remains unpublished. A U.S.G.S. generalized map (1967) and a similar map given by Berkstresser (1974) do, however, include the portions of the Last Chance Mountains which lie adjacent to the main dune.

Unlike other major dune systems in California, Eureka Dunes have not received adequate geomorphic description. Gattung et al. (1978) presented a limited data base for the Eureka, Saline, and Panamint Valley dunes which included sand stratigraphy, mineralogy and grain size distributions. Dean (1978) surveyed these and other dunes in California and gave preliminary information on physiography, dune form and grain assortment. Dune classification and terminology herein follows the framework of Bagnold (1941) with modifications borrowed from Melton (1940) and Hack (1941).

Eureka Valley

Eureka Valley is a down-faulted desert basin primarily delineated by fault-block mountains. Large portions of the Inyo and Last Chance Mountains are composed of metamorphosed Cambrian sediments. These include the sandstones, quartzites, siltstones, limestones, and dolomites of the Bonanza King, Saline Valley, Harkless and Poleta Formations (Stewart 1965, Nelson 1971). These units are invaded by plutons of

Mesozoic granites, quartz monzonite and hornblende, resulting in a complex assemblage of rocks contacting along several major thrust faults and many splinter faults. However, the Last Chance Mountains adjacent to the dune are dominated by Paleozoic carbonate rocks and are largely devoid of the acidic plutons. Tertiary volcanic deposits overlay the older strata in the Inyo-Saline Ranges and are composed of basaltic and rhyolitic flows. Degradation of these rocks resulted in debris of finer and finer textures. This debris was and is subject to transportation and aggradation within the Eureka Valley basin where (owing to internal drainage) it has accumulated to a depth of hundreds or thousands of feet (Quaternary valley fill). The coalescence of alluvial distributaries resulted in the gently sloping bajadas presently comprising the majority of the valley's surface area. Finer particles and evaporite minerals continue to be transported to the lowest point in the basin where they form a cemented and saline playa surface. The playa is an ephemeral remnant of a larger Pleistocene lake, the shores of which are still visible in the vicinity of the dune (Plate 1).

Hydrologic work in the valley has not been very detailed. Old well-drilling records indicate that a perched water table exists at approximately 90 to 150 m depth (BLM 1976). It has been suggested that subterranean water flow into the valley is blocked by an impermeable batholith. Indeed, only a single spring is found in Eureka Valley. It is located in the Last Chance Mountains southeast of the dune where it is of no importance to plant life in the valley. Runoff from the surrounding mountains can be substantial during intense storms resulting in overland sheetwash, channeled flash floods, and occasional standing water in the playa.

Eureka Dunes

Gattung et al. (1978) presented the only detailed mineralogical data available for the dune substrate from samples of unknown position and depth. They described a sand dominated by quartz (silicon dioxide) grains of three types which vary in their color, angularity and clarity. (These characteristics are often used to infer the age and activity of dunes.) The diverse origin of these grains does not allow their assignment to any single, local rock unit although parental sources are abundant in the region. Dark, heavy materials present as smaller grains were largely magnetite (an iron oxide commonly derived from igneous rocks), hornblende or augite (both are complex silicates of magnesium, iron, calcium, and aluminum found in metamorphic and igneous rocks) and olivine (a magnesium and iron silicate of igneous origin). A rough correlation between dune mineral distribution and the position of adjacent rock units was also noted, with higher carbonate concentrations on the northern and higher igneous mineral concentrations on the southern portions of the dune. R. Henry (1978) reported a 3-4% magnetic fraction and a 3-5% acid (1.2 N HCl) soluble fraction in samples from the northern main dune. The mean grain size of 0.30 mm is considerably larger than that of Saline Valley Dunes (0.16 mm), Panamint Valley Dunes (0.23 mm) and Death Valley Dunes (0.12 mm) as reported by Dean (1978). Unlike most California sand dunes this high proportion of coarse grains resulted in a particle size distribution that was significantly skewed to the right. Grain size is determined by the differential weathering of minerals with varying structural or chemical resistivities. Easily degraded minerals such as olivine will be found as smaller grains while the stable quartz

minerals will be present as the larger grains in a sand population.

The formation of dunes requires a sand source, effective wind vectors, and a depositional site. Local topography, rock lithology, sand reservoir size, and wind patterns as well as moisture and vegetation will determine the type of dune formed. The nature of sand physics and desert dunes has been described in detail by Melton (1940), Bagnold (1941), McKee (1966), and McKee et al. (1971). With reference to Eureka Dunes, the sand and its sources have been given in the text above. Accumulations of the fine-grained materials in the northern portion of the valley are removed by deflation as a function of particle diameter and wind speed. This results in a well-sorted eolian sand and residual materials of larger size that form the scoured desert pavement. Sand deposition occurs in the southern portion of the valley as transporting winds lose velocity and eddy in response to mountainous barriers and surficial irregularities (i.e. ancient lake terraces, exposed rocks and plants). It has even been suggested that the Eureka Dunes surround a large bedrock core (Norris and Webb 1976), although such a core would represent a geologic anomaly in this particular basin. The form, structure, growth, and movement of the new accumulations are precisely controlled by a network of ever-changing and poorly understood factors.

Melton would have classified Eureka Dunes as complex; that is, formed by the action of multiple and variable wind patterns and the coalescence of many simple dune forms. Bagnold's widely accepted work would further resolve that the northern portions are a classic seif or longitudinal dune (Plate 2). Such a dune is formed independent of major topographical features with its long axis parallel to the prevailing effective winds.

The sensitivity of dune features to wind vectors permits their use in local wind pattern analyses and so one would predict a strong northern wind by the north-south trending seif. Gattung et al. (1978) specifically described the Eureka longitudinal dune form and noted that the southern area was a series of transverse dunes. They postulated a complex wind pattern to account for the origin and evolution of these features. It included a major north-northwestern depositional wind possessing western and eastern vectors. A wind from the south of unknown origin was suggested, which would "express itself only by the form the dune takes whereas the dominant northern wind determines dune location." Dean (1978) classified Eureka Dunes as a complex (sensu Melton 1940) sand mountain which "appears to require unlimited sand, high velocity and multi-directional winds."

The structure of dunes is a function of wind orientation, grain sorting, differential deposition and transport, and avalanching. Gattung et al. included data on lamination as well as particle sorting along north-south and vertical transects. The laminae on the northern low dunes appeared to be of varying thickness, striking $N40^{\circ}E$ and dipping $22^{\circ}SE$. Sand grains tended to be coarse and poorly sorted on the low northern and southern toes of the dune (slightly coarser on the former) but became finer and well sorted with elevation (Table 6). R. Henry (pers. comm.) also found that the northern dune sands were composed of coarser particles (59% greater than 0.42 mm) than those from the south (39% greater than 0.42 mm). Both Henry and Gattung et al. found the southern sand textures enriched in intermediate size grains (0.15 to 0.42 mm) but similar to the north in the finer components (less than 0.15 mm).

Sand movement is a major feature of aeolian environments and

results in dune growth and migration. Relative to a fixed level such as a stake or plant stem, sand will be accumulated or removed during wind storms. Shoot burial, root exposure and mechanical abrasion are therefore important factors in the psammophyte habitat (Warming 1909). Long-term measurement of sand movement at Eureka Dunes is lacking. M. A. Henry (pers. comm) tagged Swallenia stems in various locations on the lower dune flanks and monitored sand level fluxuation for a one year period. She found that 10 cm of sand accumulation or removal in a one month period was common. Net sand movement was variable but could be quite significant. Major wind storms apparently occurred between March and late May and from August to November. My own measurements were made from late August 1978 to March 1979. At all six stakes located within Swallenia hummocks on the lower dune there was a net accumulation of 3 to 6 cm of sand. Upper slopes of greater incline and exposure and smaller grain diameters would be considerably more active. An excellent long-term study at Kelso Dunes, California by Sharp (1966) provides an unsurpassed record of desert dune dynamics. Ten permanent transects consisting of 8-12 poles each were monitored for up to 12 years. Sharp observed net accumulations of 11 to 40 $\text{cm}\cdot\text{yr}^{-1}$ and net losses of 7 to 41 $\text{cm}\cdot\text{yr}^{-1}$ with extremes exceeding 50 $\text{cm}\cdot\text{yr}^{-1}$ and 123 $\text{cm}\cdot\text{yr}^{-1}$, respectively. Either process could occur on any exposure (windward, crest or lee) but that accumulation exceeded removal on upper slopes while the opposite was true for the lower slopes. Average rates of sand level fluxuation for the 12 year period varied between $-2.3 \text{ mm}\cdot\text{day}^{-1}$ and $+7.0 \text{ mm}\cdot\text{day}^{-1}$. During one thirty day period he recorded an accretion of 117 cm of sand. It seems likely that these conditions approximate those found on the higher

slopes of Eureka Dunes, although these two dune systems may differ in the degree they are stabilized by moisture and vegetation.

The age of Eureka Dunes is unknown. Dumont and Kelso Dunes are thought to have formed in the last 10,000 to 20,000 years (MacDonald 1970, Sharp 1966). It is possible, however, that these dunes may represent ancient mobile habitats which have only occupied their present sites as of recent times. Even mountain barriers cannot stop mobile dunes. Evans (1962) described the nature of falling and climbing dunes in the Cronese Mountains of San Bernadino County, California and noted that sand bodies can surmount ridges over 270 meters high. Such dunes are also active in the western portion of Eureka Valley near Marble Canyon where they are apparently traversing a summit of comparable height.

Although much is known about the hydrology of subterranean sand aquifers, very few studies have been concerned with the dynamics of water within dunes. It has been noted by Sharp (1966) at Kelso Dunes and Norris and Norris (1961) at Algodones Dunes that subsurface dune sands may be moist well into the summer months. This is also the case at Eureka Dunes. Moisture accumulates within the large dune volume by the rapid infiltration of precipitation and dew through the porous substrate. Baver (1956) notes that the percolation rate of water through a quartz sand with grains larger than 0.42 mm in diameter is nearly twice that of a sand with grains between 0.42 and 0.25 mm and almost ten times that of certain sandy clay loams. Masch and Denny (1966) noted that water permeability increases with increasing sand particle diameter and increasing degrees of sorting. Thus, the sand grain distribution and structure of the dune may significantly affect the distribution of stored moisture. Frank

(1968) found that an Oregon dune area was capable of storing 80% of the annual precipitation. Runoff water from the Last Chance Mountains may also constitute an important water input along the eastern flanks of the dune. Dry, reflective surface layers and a low dune surface area to volume ratio serve to minimize evaporative losses. The resultant "water table" is of unknown subsurface form and detailed hydrologic studies are needed. In March 1979, the sand was "homogenously moist" to depths of over 1 m. Capillary rise in sands is less than 50 cm and perhaps as low as 10 cm (Baver 1956). The movement of water in response to temperature gradients (Stark and Love 1969, Syvertsen et al. 1975) has yet to be demonstrated in North American desert dunes but may occur to a limited extent. These factors undoubtedly contribute to a complex distribution of water within the dune.

One accessory point may be added here. Owing to the dryness of the climate, grain architecture, sand lamination, and factors as of yet not understood, slippages of sand at Eureka Dunes may produce a distinct, low-frequency sound audible up to several hundred meters away. Thus it is one of the few "booming dunes" in the continental United States (Schad, 1979).

Climate

In his review of California climate, Major (1977) pointed out the paucity of recording stations and recent data summaries as well as the hazards of climate extrapolation into remote areas. This is especially true in the hot deserts of eastern California where stations are well dispersed, variable in altitude and inconsistent with regard to the type of observations recorded. Localized studies are rare in the vicinity of

Eureka Valley but include those of Hunt (1966) in Death Valley and Randall (1972) in Saline Valley, the latter being particularly useful here. In this analysis, regional data from the U. S. Weather Bureau (1964) and the National Oceanic and Atmospheric Administration (1969 to 1978) are applied to Eureka Valley using environmental lapse rates. Microclimatological data collected at the dune site during 1977 and 1978 are also included and further details may be found in Pavlik (1979).

Regional Climate

Five U. S. Weather Bureau stations within reasonable distance to Eureka Valley were chosen on the basis of altitude, duration of record and consistency of measurement (Table 1). Considerable variation occurs in their altitudes with respect to the 930 m elevation chosen to represent the low dune area of Eureka Valley. However, all stations are located in either hot or cold desert vegetation types. Randall (1972) analyzed two additional stations of interest, those at Beatty, Nevada (elev. 1010 m) and Haiwee, California (elev. 1166). All exhibit continental desert climates typified by high mean annual temperatures (T) and considerable annual ranges of temperatures (A). These are reflected in the low indices of equability (M) and warmth (W) (Baily 1960, Axelrod and Bailey 1976). Winter frosts are common to all of these stations except at Death Valley (Greenland Ranch) where it is rare. Annual rainfall is low and unevenly distributed in time and space. Potential evapotranspiration (PotE) may commonly exceed 1000 mm while actual evapotranspiration (ActE) is low and assumed equivalent to the annual precipitation (Major, 1977).

In his analysis of climate for Saline Valley, Randall derived a

Table 1. Data for climate stations within the region of the study site. T=mean annual temperature, A = mean annual range of temperature, M = equability index, W = warmth index, ppt = precipitation (Bailey 1960). Data from U.S. Weather Bureau (1964) and the National Oceanic and Atmospheric Administration (1976).

station	elev. (m)	re- cord (yrs)	aerial dist. to site (km)	T (°C)	A (°C)	M	W	mean annual ppt. (mm)
Bishop WSO AP	1252	40	70.8	12.8	21.1	51	57	147
Death Valley (Greenland Ranch)	-59	49	96.6	24.4	27.8	38	61	41
Deep Springs College	1593	12	41.9	11.3	25.7	46	56	142
Independence	1204	69	58.0	14.6	21.7	51	58	127
Wildrose RS	1250	11	99.8	13.6	20.0	53	57	157

Table 2. Station data extrapolated for the 930 m elevation level using the annual lapse rate of Randall (1972). T^{930} = mean annual temperature, A^{930} = mean annual range of temperature, M^{930} = equability index, W^{930} = warmth index, ppt = precipitation, all at the 930 m level. Mean represents Eureka Valley at 930 m elevation.

station	T^{930} (°C)	A^{930} (°C)	M^{930}	W^{930}	mean annual ppt ⁹³⁰ (mm)
Bishop WSO AP	15.3	21.1	50	58	126
Death Valley (Greenland Ranch)	16.6	27.8	44	58	104
Deep Springs College	16.5	25.7	46	58	100
Independence	15.8	21.7	49	59	109
Wildrose RS	16.1	20.0	52	58	136
mean (Eureka Valley)	16.3	23.3	48	58	115

Table 3. Mean monthly temperatures, mean annual temperature (T), and mean annual range of temperature (A) for Bishop WSO AP and Death Valley (GR) stations compared to those calculated for the 930 m elevation of Eureka Valley using Randall's (1972) summer and winter lapse rates.

station	Mean Monthly Temperature ($^{\circ}\text{C}$)												($^{\circ}\text{C}$)	
	J	F	M	Ap	M	J	J	Au	S	O	N	D	T	A
Bishop WSO AP	2.7	5.3	7.9	12.2	15.8	20.2	23.8	22.3	18.9	13.3	7.3	3.6	12.8	21.1
Eureka Valley	4.9	8.0	11.6	15.0	19.2	24.0	28.0	26.5	22.3	17.0	9.9	5.6	16.0	23.1
Death Valley (GR)	10.9	14.4	19.2	24.4	29.1	34.4	38.7	37.2	32.2	24.4	16.3	11.4	24.4	27.8

temperature lapse rate of $-0.93^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ using 23 pairs of summer minima recorded in a single season. Hunt (1966) reported $-0.91^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ for Furnace Creek while Major (1977) noted $-1.10^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ for the western Colorado Desert. Using both maximum/minimum and thermistor-type ("Telethermometer," Yellow Springs Instrument Company) thermometers, maximum air temperatures were measured at four points along a 1200 m elevation gradient on the western slope of Eureka Valley on June 11 and July 20, 1978. Regressions made with this very limited data gave lapse rates of $-1.08^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ and $-1.15^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ respectively ($r = -.99$ and $-.97$). However, transformation of the station data in Table 1 to an elevation of 930 m employed Randall's yearly temperature lapse rate of $-0.79^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ and a precipitation lapse rate of $+6.4\text{ mm}\cdot 100\text{ m}^{-1}$ (Hunt 1966, Major 1977). The results are presented in Table 2 and averaged as an estimation of the temperature, precipitation and growth regime of Eureka Valley. Derivation of the mean monthly temperatures used Randall's summer (April to September) and winter (October to March) lapse rates ($-0.57^{\circ}\text{C}\cdot 100\text{ m}^{-1}$ and $-0.97^{\circ}\text{C}\cdot 100\text{ m}^{-1}$, respectively) applied to data for the Bishop and Death Valley Stations (Table 3). Note that T and A calculated in this manner are only slightly different from the values given in Table 2. Thus it seems likely that the climate of Eureka Valley is similar to that found in Owens Valley and Death Valley at similar elevations, a conclusion reached by Randall for Saline Valley.

Field Data

Microclimatological data were collected on ten occasions at the study site since August of 1977, ending in November of 1978.

Radiation regime - Pavlik (1979) measured solar irradiance and photosynthetic photon flux density at the dune site in July, 1978. He found that the high albedo of the white sand created an intense energy regime with a maximum irradiance at solar noon of 1338 W.m^{-2} . Lewis and Nobel (1977) reported a July maximum of 1038 W.m^{-2} at 300 m elevation in the western Colorado Desert.

Air and soil temperatures - The daily and season courses of air temperature were monitored using a maximum/minimum and a thermistor-type thermometer previously described. The former was placed within plant canopies on the dune, approximately 20 cm above the shaded sand surface while the probe of the latter was positioned slightly higher. Both remained out of the direct path of the sun all day. A thermistor soil probe was used to measure soil surface and subsurface temperatures in fully exposed and undisturbed sands. The temperature-sensitive thermistor circuitry required a zero-adjustment prior to each reading.

Table 4 summarizes the data obtained for the dune site. Values given by the max/min thermometer generally agreed with the thermistor readings or fell within $\pm 2^{\circ} \text{ C}$. Air temperatures frequently exceeded 40° C in the summer months, with July seemingly the hottest and most rapid to heat early in the day. The daily maxima were almost always reached between 1400 and 1600 hours solar time, although windless mornings could be quite warm. Minimum summer night temperatures were moderate and this resulted in daily air thermoperiods exceeding 25° C on several occasions. Sub-zero temperatures are common at night from November to February and radiation frosts may form on the dune surface. Sand surface temperatures did get quite warm (58° C) but never approached

Table 4. Air and soil temperature data ($^{\circ}\text{C}$) for dune study site, 1977 and 1978.

date	maximum daily air temperature	minimum daily air temperature	daily air thermoperiod	maximum daily sand surface temperature	minimum daily sand surface temperature	daily sand surface thermoperiod	maximum daily sand 15 cm depth temperature	minimum daily sand 15 cm depth temperature	daily sand 15 cm depth thermoperiod	remarks
8-10-77	45.0	19.5	25.5							sunny, few clouds
11-11-77	22.5	1.0	21.5							sunny, heavy clouds after 2 pm
3-24-78	29.5	5.0	24.5	37.5	5.5	32.5	21.0	8.2	12.8	sunny, windy, clouds to the east
5-20-78	36.5	5.0	31.5	50.0	12.0	38.0	28.5	23.0	5.5	sunny, light high clouds
6-11-78	34.5	15.0	19.5							sunny, clear
7-02-78	37.2	8.5	28.7	48.0	10.0	38.0	33.5	27.2	6.3	sunny, clear, wind light
7-20-78	43.0			58.0			36.0	32.5	3.5	sunny, clear
8-24-78	34.0	8.0	26.0							sunny, clear
9-16-78	31.5	10.0	21.5	40.6	10.0	30.6	25.0	17.8	7.2	sunny, clear, wind strong at times
11-22-78	9.0	-4.0	13.0							heavy cloud cover in day

the maximum range of 73° to 82° reported by Hunt (1966) for soils near sea level in Death Valley. This may be attributed to the lower air temperatures and the higher albedo, the heat capacity and thermal conductivity of dune sand, especially when moist (Nobel 1974, Hadas 1977). These factors also influence the rate at which temperature is attenuated with depth and therefore influence seasonal changes in soil thermoperiod and heat flux (Geiger 1965).

Relative humidity - Relative humidity was measured with a sling psychrometer in March and July of 1978. Daily minima occurred between 1400 and 1600 hours and were frequently below 12%. Calculations based on the assumption that leaf temperatures equal air temperatures showed that the midday vapor pressure deficits in July could be three times those of March. This would have profound effects on transpiration rates, leaf water potential, and stomatal conductances (Pavlik 1979).

Precipitation - On March 24, 1978 a rain gauge was installed on the lower flanks of the dune with its opening about 60 cm above the ground. The gauge emptied by tygon tubing into a sealed and insulated underground bottle. An oil film was used inside the bottle to minimize evaporative losses. The system was checked, emptied, cleaned and re-oiled on six occasions ending March 19, 1979.

The rain gauge measured a total of 68 mm of precipitation at the dune site. This probably represents an underestimation because of its inability to collect water in the form of snow or frost, the partial obstruction of the tubing by sand and insects, and the evaporation of moisture from upper gauge surfaces. Precise dates of water input were

not always available but could be inferred from precipitation patterns of other eastern California locations. Major storms occurred in late April/early May, early September, and late October/early November. From mid-May to late August little or no rain fell.

Recent climate records (National Oceanic and Atmospheric Administration 1977-78) show that precipitation was abnormally high for 1978 at both the Bishop WSO AP and Death Valley stations (Tables 1 and 5). In 1977, the last year of a three year drought, Bishop had received slightly less than normal amounts of precipitation while Death Valley somewhat more. Seasonal analysis shows that 80 to 90% of the rain in 1978 fell in the colder months while the months of April to October received below or near normal amounts (Table 5).

The uncertainties regarding the measurement of precipitation at the dune do not prevent the conclusion that water inputs for 1978 were typically low but perhaps greater than those of 1977. Late spring and summer were quite dry and hardly interrupted by the passing of convectional storms. The poor spring wildflower display and short flowering season in 1978 confirmed that the amount and timing of precipitation was less than optimal.

Table 5. Annual precipitation and its seasonal pattern. Data from the National Oceanic and Atmospheric Administration (1977-1978) and field measurement at the study site.

precipitation (mm)						
station	1977	1978	normal Jan-Mar+ Nov-Dec	actual Jan-Mar+ Nov-Dec 1978	normal Apr-Oct	actual Apr-Oct 1978
Bishop WSO AP	122	244	112	220	35	24
Death Valley	71	102	24	80	17	22
Eureka Dunes	--	68*	--	--	--	30

*March 1978 to March 1979

Soils

The constant activity of unstabilized desert dunes does not allow for the development of a true soil. The correct designation for these substrates would be psamment Entisols (Steila 1976). Other than the characteristic sand laminations, dunes lack pedogenic horizons. Their youth is maintained by constant surficial growth and disturbance, the resistance of quartz to weathering, and the sparsity of rainfall and vegetation. In contrast, the substrates of the surrounding area may possess weathering profiles with clay accumulations and be classified as argillic Aridisols.

The mineral composition and sand particle characteristics of the Eureka Dune substrate have been described above. Pavlik (1979) assessed additional properties, those best categorized as of the "soil." He sampled substrates from dune and non-dune sites at a depth of 25 cm and his findings are summarized as follows:

- 1) Sand was the dominant particle size class at all sites, although the non-dune substrates possessed greater amounts of gravel, silt and clay and somewhat distinct pedogenic horizons.
- 2) The moisture release properties of samples from the 25 cm depth did not significantly differ because of inherent errors in pressure-plate techniques at low soil moisture contents. However, the saturation percentages of soils from the dune and non-dune sites were 18% and 23% respectively, indicating that differences in moisture retention did exist.

- 3) The seasonal course of soil moisture showed that greatest depletion occurred from spring to fall and dune levels may fall below 1%. The 1% moisture level (dry weight basis) corresponded to rapid decreases in soil water potential in July at 25 cm depth. Small amounts of precipitation have a great effect on dune moisture content and soil water potential.
- 4) Both dune and non-dune substrates were slightly alkali (pH of 8.1 and 8.4 respectively) and similar to Larrea dominated sites in the Mojave Desert region (Barbour 1967). The pH of the dune substrate increased with elevation to a maximum of 9.3 on the highest slopes (R. Henry pers. comm.). This probably reflects alkali inputs carried from the surrounding playa and adjacent carbonate rocks.
- 5) The concentration of total dissolved salts (and individual levels of P, K, Mg, and Ca) were low, reflecting the low cation exchange capacity and well leached nature of sandy dune substrates. Both dune and non-dune soils would be regarded as non-saline and non-sodic.
- 6) Total nitrogen in these soils was extremely low (less than 0.06 ppm). The question of nitrogen economy in desert dune systems has not been explored. Astragalus lentiginosus var. micans was observed to possess root nodules possibly active in N₂ fixation (Plate 9). Swallenia alexandrae appears to have rhizosheaths similar to those of Oryzopsis hymenoides, which have been suggested as sites of symbiotic fixation (Wullstein 1977). Also of great interest is the

inorganic production of ammonia by desert sands as demonstrated by G. N. Schrauzer at Imperial Dunes (Anonymous 1978). Soil binding algal/fungal crusts may be insignificant contributors of nitrogen at Eureka Dunes owing to surficial disturbance and severe moisture deficits to which they are highly susceptible (Rychert and Skujins 1974).

Habitat Classification

In order to summarize the preceeding information, a classification of Eureka Valley habitats is presented in Table 6. The sole use of physical characteristics is convenient at this point and certainly open to modification and refinement. Later it will be seen that classification does have biological foundation and application with reference to the distribution, abundance and activity of plant taxa. The dune study site is hence located in the low dune habitat and the non-dune study site in the ecotone. I would like to emphasize the importance of recognizing two distinct dune habitats.

Flora and Vegetation

The first botanical reconnaissance of Eureka Valley was made by the Wheeler Expedition in July of 1871. It is uncertain whether or not the dune area was investigated, although the report describes the problems encountered by man and mule when crossing an extensive sand area. Unfortunately, the specimens were lost enroute to the Smithsonian Institution (M. A. Henry 1976). Significant collections were not made in the dune area until May of 1949 when Louise Kellogg and Anne Alexander

Table 6. A classification of Eureka Valley habitats and summary of their physical characteristics.

habitat	slope & stability	relative exposure to wind & sun	relative sand movement	substrate characteristics physical	chemical	relative moisture retention	comments
high dune	20° to 34° mostly unstable	medium to high, variable with slope & aspect	greatest	deep, finer-grained, well sorted sand	pH 9.0 to 9.3, low nutrients	medium to low	
low dune	(0°) 5° to 25° , mostly stable	low to high, variable with slope & aspect	intermediate	deep, medium to coarse-grained, poorly sorted sand	pH 8.1 to ~ 9.1 , low nutrients, non-saline	medium to high	fastest water infiltration?, dune study site location
ecotone	0° to 10° , stable	low to medium, variable with location	lowest	shallow sand or sandy loams with gravel	pH ≈ 8.4 , low nutrients non-saline	medium to low	cold air drainage, non-dune study site location
playa	0° , stable	low to medium	lowest	fine silts & clays, cemented	pH ≥ 9.0 , saline	low	cold air drainage, low soil O_2
bajada	1° to 5° , stable	low	lowest	gravelly or rocky soils, pavement	(?), probability slightly alkaline	low	
mountain inside	low to nearly vertical	low to high	lowest	rock or gravel with soil pockets	(?), much calcareous & volcanic	(?)	

gathered material of the yet undescribed Swallenia. Philip Munz and John Roos visited the area in summer of 1954, obtaining type specimens of Oenothera avita ssp. eurekensis and Stanleya pinnata ssp. inyoensis and discovering Astragalus lentiginosus var. micans.

However, the most extensive collecting in the area has been the work of Mary (Foster) DeDecker. The taxa presented in Table 7 are largely compiled from her checklists and herbarium except for several additions and modifications. The listing is complete only for the dune habitat and many peripheral taxa may have been excluded. Of particular interest I note: 1) the three Eureka Dune endemics Swallenia alexandrae, Oenothera avita ssp. eurekensis, and Astragalus lentiginosus var. micans, 2) the geographically widespread but sand-restricted Dicoria canescens ssp. clarkae, Cleome sparsifolia and Coldenia plicata, 3) the occurrence of Stanleya pinnata ssp. inyoensis, 4) the southernmost population of Chaetodelphia wheeleri (DeDecker 1976), 5) the northernmost Mojavean population of Asclepias erosa (DeDecker 1978), and 6) the introduced population of Corispermum hyossifolium. Approximately 20 taxa occur on the dune itself (see below) with many more occurring in the dune/non-dune ecotone. The dune flora is distinctly Mojavean in its affinities although some essential elements may be found in the Sonoran regions (i.e. Dicoria canescens ssp. clarkae, Oenothera avita, Coldenia plicata). Salsola paulsenii is the only introduced plant commonly found on the dune. The region as a whole is characterized by a high degree of endemism (Raven 1977). Within a 12 km radius centered at Eureka Dunes, two monotypic genera endemic to the eastern Inyo region (Dedeckera, Swallenia), two monotypic genera of very restricted distribution in

Table 7. Flora and its distribution, Eureka Dunes and vicinity. Nomenclature follows Munz (1974). X = major occurrence within the habitat.

	high dune	low dune	ecotone	playa	bajada
<i>Dicoria canescens</i> ssp. <i>clarkae</i>	X	X			
<i>Swallenia alexandrae</i>	X	X			
<i>Oenothera avita</i> ssp. <i>eurekaensis</i>		X	X		
<i>Stephanomeria pauciflora</i>		X			
<i>Astragalus lentiginosus</i> var. <i>micans</i>		X	X		
<i>Coldenia plicata</i>		X	X		
<i>Oryzopsis hymenoides</i>		X	X		
<i>Cleome sparsifolia</i>		X	X		
<i>Stanleya pinnata</i> ssp. <i>inyoensis</i>		X	X		
<i>Salsola paulsenii</i>		X	X		
<i>Camissonia claviformis</i> ssp. <i>funerea</i>		X	X		
<i>Abronia turbinata</i>		X	X		
<i>Lupinus shockleyi</i>		X	X		
<i>Cryptantha micrantha</i> ssp. <i>micrantha</i>		X	X		
<i>Euphorbia ocellata</i> var. <i>arenicola</i>		X	X		
<i>E. micromera</i>		X	X		
<i>Chaetadelphia wheeleri</i>		X	X		
<i>Sphaeralcea ambigua</i>		X	X		
<i>Dalea polyadenia</i>		X	X		
<i>Hymenoclea salsola</i>		X	X		
<i>Baileya pleniradiata</i>			X		
<i>Pectis papposa</i>			X		
<i>Palafoxia linearis</i>			X		
<i>Astragalus sabulonum</i>			X		
<i>Nama demissum</i>			X		
<i>Corispermum hyssopifolium</i>			X		
<i>Oenothera primiveris</i> ssp. <i>bufonis</i>			X		
<i>Eriogonum insigne</i>			X		
<i>E. reniforme</i>			X		
<i>Antirrhinum kingii</i>			X		
<i>Bouteloua barbata</i>			X		
<i>Asclepias erosa</i>			X		
<i>Atriplex confertifolia</i>			X	X	X
<i>A. canescens</i>			X	X	X
<i>A. polycarpa</i>			X	X	
<i>A. truncata</i>			X	X	
<i>Suaeda torreyana</i>				X	
<i>Conyza coulteri</i>				X	
<i>Kochia americana</i>				X	
<i>Tamarix ramosissima</i>				X	
<i>Larrea tridentata</i>			X		X
<i>Tidestromia oblongifolia</i>			X		X
<i>Ambrosia dumosa</i>			X		X
<i>Eriogonum inflatum</i>					X
<i>Dalea fremontii</i>					X
- <i>Opuntia basilaris</i>					X
- <i>O. echinocarpa</i>					X
- <i>Echinocactus polycephalus</i>					X
<i>Erioneuron pulchellum</i>					X
<i>Langloisia setosissima</i>					X
<i>Atrichoseris platyphylla</i>					X
<i>Chaenactis carphoclinia</i>					X
<i>Allonia incarnata</i>					X
<i>Eriogonum inflatum</i>					X

California (Hecastocleis, Scopulophila), and an array of other rare or endemic taxa (Oenothera avita ssp. eurekensis, Astragalus Lentiginosus var. micans, Stanleya pinnata ssp. inyoensis, Mimulus rupicola, Buddleja utahensis, Enceliopsis nudicaulis) may be found.

Employing the habitat classification it can be seen that only two species are commonly found on the steepest, least stable slopes of the high dune (Plate 3). In fact, Dicoria more often exceeds Swallenia in elevation on the dune and both may occur within 50 m of the bare seif crest. On the eastern dune margins Swallenia occurs on deep sands with little or no slope. Other psammophytes (Oenothera avita ssp. eurekensis, Astragalus lentiginosus var. micans, Coldenia plicata, Cleome sparsifolia, and Abronia turbinata) tend to be found in the low dune or ecotone habitats. Stanleya pinnata ssp. inyoensis rarely occurs on the low dune although the presence of a few such individuals allowed for dune/non-dune comparisons within a single taxon. Dalea polyadenia may also be found on the lowest aprons of the dune and ecotone. Although it dominates the bajada, Larrea tridentata approaches the dune with a few individuals scattered widely through the ecotone. More detailed accounts of Eureka Dunes plant taxa are found in BLM (1976) and Pavlik (1979).

The quantitative basis for the vegetation classification given in Table 8 and mapped in Figure 3 is incomplete and not included here. The units were resolved by the use of oblique and high-angle photographs, aerial survey, field mapping, and quadrat, transect or relevé data. The maximum species richness (MSF), as calculated from Table 7, is the greatest possible number of species which occur in a particular association.

Küchler (1977) mapped the region as primarily desert saltbush and

Mojave creosote bush scrub types which would correspond to associations of the playa and bajada, respectively. Vasek and Barbour (1977) also account for these major units and further divide the playa type into xerophytic and halophytic phases. It should be emphasized that the vegetation of Eureka Valley's playa and bajadas is considerably more complex than presented here, consisting of intergrading mosaics which differ in floristic and structural composition. Several additional associations occur in the dune and ecotone habitats. The recognition of two dune associations is substantiated by Table 6 and by my own investigations at other desert dune sites in California and Nevada. The high dune vegetation appears to be unique to Eureka Valley. This may be contributed in part to the presence of the endemic Swallenia which grows on and partly stabilizes the uppermost slopes (Plate 3). It is interesting to note that the high dune habitats of other desert dunes (when present) are barren and potential colonizers (such as Dicoria) are restricted to the low dune slopes and hollows. MSR increases from the high dune to the ecotone, decreases towards the playa and increases again towards the bajada. It must be noted that because Table 7 is incomplete in regards to the bajada and some portions of the ecotone, the MSR for these associations is underestimated. Absolute cover increases along the same dune to bajada transect. The associations of the ecotone tend to be extensive in area and typically ill-defined at their margins. These ecotonal types, which are composed of many short-lived perennials, may be seral to creosote bush scrub as alluviation continues to fill the playa basin and improve soil and microclimatic conditions for the growth of Larrea.

Table 8. Major vegetation units in the vicinity of Eureka Dunes. Habitats as in Table 6, MSR = maximum species richness from taxa in Table 7, NEU = no equivalent unit and -- or ? signify no data or designation.

habitat	association(s)	MSR	% abs. cover	dominant life forms	Barbour & Major (1977)
dune, high	1 Dicoria - Swallenia	8	t - 3	summer annuals, hummock forming perennial grass	NEU
low	2 Swallenia - Dicoria - Coldenia	26	t - 5	annuals, short-lived perennials	NEU
ecotone	3 Atriplex canescens - Dalea polyadenia - Sphaeralcea	39	10 - 35	long and short-lived perennial shrubs	NEU
	4 A. polycarpa - Oryzopsis	--	--	perennial shrubs and grasses	NEU
	5 Oryzopsis - Cleome	--	--	perennial grasses, some herbs	NEU
	6 Oryzopsis	--	--	perennial grasses, some herbs	NEU
playa	7 A. confertifolia - A. canescens	14	--	perennial shrubs	xerophytic saltbush scrub
	8 Suaeda - Atriplex	8	--	perennial shrubs	halophytic saltbush scrub
bajada	9 Larrea - Dalea fremontii - A. confertifolia	18	10 - 30	long-lived perennial shrubs	creosote bush scrub
mountain inside	?	--	--	?	NEU

Figure 3. Vegetation map of Eureka Dunes and vicinity superimposed on major contour lines and roads (see Figure 2). Numbers in key refer to the associations given in Table 8. From Pavlik (1979).

KEY

DUNE

1 & 2

ECOTONE

3

4

5

6

PLAYA

7

8

BAJADA

9

BARE

737

Q10

Q11

Q12

Q13

Q14

THE STUDY SPECIES

Taxonomy and Distribution

Swallenia alexandrae Soderstrom and Decker (Poaceae)
 = Ectosperma alexandrae Swallen

The type specimens of Eureka Dunegrass were collected by Louis Kellogg and Annie Alexander on May 24, 1949 while on a rather adventure-some exploration of eastern Inyo County. Plant material was sent to Herbert L. Mason at U. C. Berkeley who referred it to agrostologist Jason R. Swallen at the U. S. National Herbarium. Swallen (1950) thought it so unique as to represent an undescribed genus and gave it the name Ectosperma ("free from seed," describing the readily falling caryopsis) alexandrae (after Annie Alexander). It was later renamed Swallenia by Soderstrom and Decker (1963) because the former generic designation was used in 1803 for a group of green algae.

Since its first description, the taxonomic affinities of Swallenia remain obscure. Swallen had assigned it to the classical tribe Festuceae as did Pilger (1954). The principle criteria used was that of conventional morphology, but as the taxonomic structure of the Gramineae changed in response to the "new systematics" it became evident that such a placement did not agree with other lines of evidence. Metcalf (1960) had sectioned type material of the dunegrass in his survey of monocotyledon anatomy and noted the leaf structure to be festucoid but with some "panicoid tendencies." Stebbins and Crampton (1961) allied Eureka Dunegrass with Distichlis, Vaseyochloa, Monanthochloe, Jouvea and Aeluropus in the tribe Aeluropodeae, subfamily Eragrostoideae. Anatomical studies of the Festuceae sensu lato by Decker (1964) support such a

treatment. The basic chromosome number in the Aeluropodeae, $x = 10$, is consistent within the aforementioned genera, with Swallenia being $2n = 20$ (Anderson 1964). Recent surveys of the grasses with respect to carbon isotopic ratio and carbon fixation pathway (Smith and Brown 1973) strengthens the concept of the tribe and the placement of Swallenia (see page 46). Gould (1974), however, points out that Swallenia is "an extremely odd and interesting endemic of uncertain affinities" and "does not fit well into this group (Aeluropodeae) and its placement here is only tentative."

Swallenia alexandrae is composed entirely of four known discontinuous populations found in the southern portion of Eureka Valley which probably represent the remnants of a once more widespread distribution. The most disjunct of the populations are separated by 14.5 km of bajada and playa. Reproductive isolation is improbable because of the intermediate positions of the other two populations. At all localities the substrate is sand of varying depths. The western and northern-most population is found at the mouth of Marble Canyon between 1000 and 1100 m of elevation and is approximately 0.65 km^2 in extent. Common associates at this site may be Oenothera avita ssp. eurekensis, Astragalus lentiginosus var. micans, Dicoria canescens ssp. clarkae and Coldenia plicata, although the first two taxa were not found upon inspection in May 1979 (M. Knudsen pers. comm.). Immediately south of Marble Canyon is a previously unknown population which was spotted from helicopter on July 23, 1978. It occurs in a narrow sand-filled valley which drains to the southeast. Here Swallenia reaches its highest elevations, from about 1220 to 1320 m. The stand covers less than 0.52 km^2 and has yet

to be visited on foot. Five kilometers to the east of the new Swallenia site is a geographically ill-defined population found on shallow sands at the base of the Saline Range adjacent to Eureka Valley. The site was visited in the 1960's by Philip A. Munz and Mary DeDecker who noted the presence of other dune taxa. Like the two previous populations, the number of individuals at this site is relatively low and may therefore be susceptible to small amounts of perturbation. The last population, that of the Eureka Dune massif, has received the greatest attention in this and other studies. Swallenia clumps may be found from the gently sloping ecotone habitat (elevation 900 m) to the steep sides of the highest seif to within 50 m of the bare crest. Generally, the steeper the slope the higher the extensions of the grass. Only Dicoria extends above Swallenia on these unstable sands. The Eureka Dunegrass is well distributed on the main dune with the more extensive stands to be found on its northern and western slopes and to a lesser degree on the east. The low topography of the southern transverse dunes supports the least dense stands. Common associates are given in Table 7.

Oenothera avita ssp. eurekensis W. Klein (Onagraceae)
 = Oe. californica ssp. eurekensis W. Klein
 = Oe. deltoides ssp. eurekensis Munz and Roos

The original material collected from the main dune area was assigned to the Oenothera deltoides complex as subspecies eurekensis (Munz and Roos, 1955). Its distinguishing features within this taxon were its perennial, suffrutescent habit and the densely villous herbage. Later, Klein had allied the subspecies with Oe. californica on the basis of its tendency to perenniate from underground rootstocks and its non-woody fruit capsules. Eventually this same author (1962) placed the

Eureka Primrose in a new species complex, Oe. avita of eastern California and western Arizona. This most current treatment is supported by karyological data (Oe. avita with $n=7$, Oe. avita ssp. eurekensis with $n=7$, whereas Oe. californica is $n=14$) but one cannot help wondering about the relation to Oe. deltoides ($n=7$). Members of the Oe. deltoides complex range east and north into Arizona, Nevada and Utah (i.e. ssp. deltoides, ssp. piperi, ssp. ambigua) and several are sand dune dwellers (ssp. deltoides, ssp. howellii). Oe. avita ssp. eurekensis is the only exclusive sand dune plant within the avita complex. Klein (1970) reasoned that perennial ancestors of Oe. avita gave rise to Oe. deltoides (all annuals except ssp. howellii) on the basis of morphologic, cytogenetic and biosystematic lines of evidence. Oe. a. ssp. eurekensis was found to be self-incompatible (confirmed by crosses I attempted in Davis) but would freely cross with Oe. a. ssp. avita (93% stainable pollen) and Oe. deltoides ssp. howellii (49% stainable pollen). In nature the vespertine flowers of the Eureka Evening Primrose are primarily pollinated by hawkmoths (Sphingidae) of the genus Celerio (Gregory 1963).

Populations of Oe. a. ssp. eurekensis have been found at Marble Canyon (although not seen in a 1979 survey) and the sands at the base of the Saline Range adjacent to Eureka Valley, but mostly on the massive southern dune system. Here individuals may be found on most exposures but are particularly common on the north and east sides. The primrose is commonly associated with the species listed for Swallenia and additionally Dalea polyadenia, Cleome sparsifolia and Stanleya pinnata ssp. inyoensis. It is never found on the steep unstable slopes where Swallenia and Dicoria predominate. On the eastern side of the dune the

primrose occupies the lower, gentle slopes and flats where it inter-fingers with an extensive stand of Oryzopsis hymenoides. It is in this area that the population is most concentrated, although in years of low rainfall it may seem quite scarce.

Astragalus lentiginosus var. micans Barneby (Fabaceae)

This member of the vast lentiginosus complex was first "discovered" by P. A. Munz and J. C. Roos on September 18, 1954 at Eureka Dunes. Specimens collected in the spring of 1955 were sent to R. C. Barneby who accommodated the unique population by proposing a new variety (Barneby 1956). He stated that "var. micans represents an independent offshoot of the Coulteri-variabilis complex which has acquired a few distinctive qualities in its isolated dune-habitat in the sink of Eureka Valley. . .". Chromosome counts are not available for var. micans although other members of the complex so far surveyed (vars. fremontii, palans, and variabilis) are $2n = 22$ (Ledingham 1960, Ledingham and Fahselt 1964).

Beatley (1976) reported collecting Astragalus lentiginosus var. micans from Big Dune, Nye County, Nevada. She reported that the plants reach their best development on the dune but that populations could be widespread on the sandy Larrea-Ambrosia bajada. These plants are not consistently perennial and may be biennial or annual in habit. This is in marked contrast to the distribution and habit of var. micans at its type locality and suggests that the Big Dune population may constitute yet another distinct taxon. Plants similar to those at the Nevada locality have recently been collected by myself at Dumont Dunes, al-

though adequate reproductive material was not obtained.

This distribution of var. micans in Eureka Valley is similar to that of Oenothera avita ssp. eurekensis. Two minor populations may occur at the Marble Canyon Dunes and the Saline Range sandfields. The largest population is found at the main dune where it is restricted to its lower flanks. The stands of Eureka Locoweed are best developed on the northern and eastern portions of the dune although recent elimination of off-road vehicle activity has allowed some establishment on the northwest corner.

Other taxa

Dicoria canescens (T. & B.) ssp. clarkae (Kenn.) Keck is a member of the Asteraceae widely distributed in the Mojave and Colorado Deserts. It is primarily found on sandy substrates and dunes where it may be the most abundant summer annual. At Eureka Dunes it is restricted to the upper and lower dune habitats and may rival or exceed Swallenia in colonization of the steepest upper slopes.

Stanleya pinnata (Pursh) Britton ssp. inyoensis Munz and Roos of the Brassicaceae was first described from Eureka Dunes by Munz and Roos (1955) from collections made on the northern sandy flats. It is a shrubby perennial commonly found in the ecotone habitat but a few individuals do grow on the lowest flanks of the dune. Stanleya pinnata ssp. inyoensis is widespread through the Inyo region, overlapping and intergrading with var. pinnata and S. elata. It is distinguished primarily by its thickish leaves and woody habit.

The biology and distribution of Larrea tridentata (Sesse & Moc. ex DC.) Cov. has received extensive review elsewhere (Barbour et al.

1977, Vasek and Barbour 1977}. This long-lived shrub is found primarily in the bajada and ecotone habitats and does not occur on the main dune.

Selected Morphological, Anatomical and Physiological Features

Morphological details of the study taxa may be found in their respective publications (see Taxonomy and Distribution) or in standard manuals (Barneby 1964, Munz 1974). The purpose of this section is to indicate adaptive "macro-characters" as they relate to the desert dune habitat.

Previous anatomical studies of Eureka Dune plants are understandably rare. Metcalf (1960) sectioned type material of Swallenia (then Ectosperma) in his survey of monocot anatomy. Anderson (1964) further detailed the epidermal features of the dunegrass. However, anatomical observations linked to ecological or physiological data for a species are very rare in the literature (Carlquist 1975). For this study, fresh material for the plants in question was collected and immediately fixed in FAA. Cross-sections were prepared and mounted by Sonia Cook and Chris Laning (Department of Botany, UCD). Measurements were made from several slides, averaged, and a "linear stomatal index" (LSI, in # of stomates $\cdot \text{mm}^{-1}$) was determined by counting the number of stomates along a leaf margin seen in cross-section. The count was divided by the length of the margin examined to obtain the relative index. Pavlik (1979) also detailed important structural and functional adaptations of Dicoria canescens ssp. clarkae and Stanleya pinnata ssp. inyoensis. The reader is now referred to Plates 4 through 9 which illustrate aspects of the

habit, morphology and anatomy of the dune endemics.

Morphology

Swallenia alexandrae - This perennial hummock-forming grass possesses stout, glabrous leaves born on erect sterile culms (Plate 4). Upon burial the culms may serve as rhizomes and produce adventitious roots or shoots but no distinct, leafless rhizomes are formed. New shoots may be produced from the axils of previously active leaves, thus promoting hummock building and dune stabilization. The net effect is an elevation of the growing points which is essential to survival on the mobile substrate. An indeterminate mode of reproduction is of obvious advantage and Swallenia flowers are born on short-lived fertile culms. The root system is fibrous and fine with main rootlets seldom over 1 mm in diameter (excluding the rhizosheath). Upon excavation a lateral system was noted 20-30 cm below the surface, but many feeder roots were observed to extend below 60 cm.

Oenothera avita ssp. eurekaensis - By virtue of its ability to form new vegetative rosettes at the ends of buried branches (Plate 6), the Eureka Primrose is uniquely adapted among California members of the genus to its sand dune habitat. This implimentation of elongated fruiting shoots serves to elevate the growing points and to retain seed within the vicinity of the parent plant. The low rosette form may also be suited for minimizing sand blast damage. Creeping horizontal stems are also observed as little as 6 cm below the sand surface which may give rise to leafy rosettes. Roots have been observed to depths of over 40 cm.

Astragalus lentiginosus var. micans - One of the striking features of this locoweed variety is the dense vesture of white-silky hairs which cover the herbage. Leaflets produced in summer and fall are visibly more pubescent than those of the winter and spring. Mooney et al. (1977) and Ehleringer and Bjorkman (1978) have shown that pubescence modifies leaf absorptance, thereby reducing heat load and leaf temperature. Pinnate leaves, as possessed by Astragalus, have also been shown to be effective in convective heat dissipation (Balding and Cunningham 1976). The ecological significance of these morphological features lies in the improved water-use efficiency (carbon gain to water lost) resulting from reduced transpiration. Astragalus also has the ability to activate buds high on the leafless stems which result in a new flush of growth high above the sand surface. This type of perennation appears unique to A. l. var. micans among related members of the section Diphysi (Barneby 1964). Roots are nodulated and have been observed to extend below 40 cm.

Anatomy

Swallenia alexandrae - Leaves of the dunegrass were found to be deeply furrowed with longitudinal grooves, possessing silica bodies, microhairs, and a relatively thin cuticle (Plate 7). Stomata were rather infrequent and restricted to the internal surfaces of the furrows. Although observed on both sides of the leaf, the stomata were much more common abaxially (Table 9). Guard cells were dumbell-shaped, as is typical of many grasses (Esau 1965). Internally the leaf exhibited Kranz-type anatomy, possessing well developed bundle sheaths (with numerous large chloroplasts) and a reduced radiate chlorenchyma. The bulk of the leaf was composed of dense aggregations of fibers surrounding the vascular

bundles and filling the prominent ridges. Little intercellular air space was observed. Vascular bundles were noted to be of two distinct types. Type I possessed the largest diameter vessels of all the taxa surveyed, surrounded by a ring of thick-walled fibers and then the bundle sheath cells. Type II bundles lacked conducting elements entirely or possessed a few vessels whose average diameter was the smallest of all taxa measured ($8.9\ \mu$). Thick-walled fibers were absent so the vascular tissue was immediately surrounded by large bundle sheath cells containing numerous chloroplasts. The ratio of Type I to Type II bundles was commonly 1 to 4. Culms of this grass were noted to be solid, cutinized, possessing stomata and a single ring of large vessels within a cylinder of fibers. Roots also had wide vessels surrounded by a ring of fibers and heavily cutinized epidermis.

Most structural features of Swallenia are rather xeromorphic in nature (fibrous and sclerified construction, stomata located in furrows, lack of intercellular air space) but several mesomorphic characteristics are observed. These include a thin cuticle and the presence of vessels with large diameters. Carlquist (1975) noted that $29\ \mu$ is a vessel diameter typical of stems from desert shrubs. That large vessels are unable to withstand extreme hydrostatic tensions but are capable of high conduction rates is generally excepted (Carlquist 1975, Rundel and Stecker 1977). This suggests that Swallenia is structurally ill-equipped to deal with water stress but may at times exploit large volumes of soil water and sacrifice transpiratory losses for the assimilation of carbon. The Kranz-type anatomy indicates the potential for the C₄ fixation pathway. It is also reasonable to speculate that the abundance of sclerenchyma may serve to reduce water loss, impart strength to newly buried stems or,

Table 9. Quantitative anatomical characteristics of the study taxa. LSI = linear stomatal index.

	leaf		LSI (stomates · mm ⁻¹)		stem		root	
	cuticle thickness (μ)	leaf thickness (μ)	adaxial	abaxial	max. vessel diam. (μ)	max. vessel diam. (μ)	max. vessel diam. (μ)	
Swallenia alexandrae	4.6	435	1.9	4.2	26.5	75.2	89.3	
Oenothera avita ssp. eurekensis	6.4	343	4.2	1.6	10.0	--	113.4	
Astragalus lentiginosus var. micans	6.9	329	2.2	1.8	12.8	--	85.9	
Dicoria canescens ssp. clarkae	5.8	266	4.0	2.6	16.2	--	85.9	
Stanleya pinnata ssp. inyoensis	17.4	1003	1.2	1.8	23.7	--	--	

as suggested by Warming (1909), guard against abrasion by wind and sand.

Oenothera avita ssp. eurekaensis - In contrast to the sclerophylls of Swallenia, primrose leaves were thinner, softer, densely covered by trichomes and tended to have a thicker cuticle (Plate 8). Stomata were concentrated on the adaxial leaf surface but were present on both sides. The mesophyll was faintly differentiated into a two or three tiered palisade layer and a well-branched spongy layer. Intercellular air space comprised a significant portion of the leaf volume. Vessels were small in diameter but numerous within the scattered vascular bundles. The roots possessed large vessels, ample storage parenchyma, and a thin, exfoliating cork layer.

The leaves of Oenothera are remarkably mesomorphic for a desert perennial. The well-developed palisade may have significant effects on the Ames/A ratio (the ratio of mesophyll surface area to leaf surface area) and thereby reduce internal resistances to CO₂ fixation (Smith and Nobel 1977, 1978).

Astragalus lentiginosus var. micans - The leaflets of this taxon were similar to Oenothera in thickness and degree of cutinization (Plate 8). Stomates were found on both surfaces with near-equal frequency beneath a dense canopy of terete trichomes. The mesophyll appeared largely undifferentiated and isolateral with irregular palisade cells. Fibers were very infrequent and vessels small but numerous. Cross-sections through roots revealed their non-woody nature and the presence of numerous fibers. When sections through a presumptive root nodule were made the cells appeared large and deeply stained and seemed to have bacteroid-like inclusions (Plate 9).

The leaflets of Astragalus in many ways resemble those of Oenothera except for the lack of a strongly differentiated palisade layer and the lower stomatal frequency. The observation of "bacteroid-like inclusions" provides further support that the root nodules are capable of nitrogen fixation but further studies are needed to substantiate this.

Physiology

The results of carbon isotope analysis confirm that Swallenia possesses the C_4 pathway of photosynthesis (Pavlik 1979). At least five of the taxa listed in Table 7 as occurring in high and low dune habitats (Swallenia, Salsola, Euphorbia ssp., Pectis) are known to be C_4 (Downton 1975, Mulroy and Rundel 1977, Smith and Turner 1975). With the exception of the dunegrass, all are summer annuals of low or prostrate form which contribute very little to the vegetal cover on the dune. Cover and biomass of C_4 plants increases away from the dune owing to the dominance of Atriplex spp. and Suaeda torreyana in the ecotone and playa habitats.

Phenology

The phenological record for February 1978 to January 1979 is presented in Figure 4 using notation similar to that of Sauer and Uresk (1976). Table 10 details the major events which are summarized below.

Germination - New Swallenia seedlings were first noted at the study site in mid-September. Of the seven originally mapped, three were alive in March 1979. Oenothera and Astragalus seedlings were noted in the winter

Figure 4. Plant phenology, Eureka Dunes and vicinity, 1978. "D" signifies dune habitats, "E" ecotone habitats of observation. From Pavlik (1979).

Table 10. Phenological details of plants in the vicinity of Eureka Dunes, 1978-1979. Dune habitat is denoted by "(D)", ecotone habitat by "(E)".

	Feb-78	Mar	Apr	May	Jun	Jul
<i>Swallenia alexandrae</i> (D)	growth of new shoots begins	new shoots 4-5 cm long; 1-4 leaves per apex		growth accelerates; shoots are 15-25 cm long; flowers present on fertile culms; seed immature	shoot growth continues; seed matures and is dispersed	shoot growth continues; seeds mostly dispersed; a few shoots senescent
<i>Oenothera avita</i> <i>ssp. eurekaensis</i> (D)	plants in rosette stage	plants in rosette stage, many 10-12 cm in diameter		plants have bolted; many in flower, some with fruit	shoot growth continues as does flowering; some capsules open, seed released	some individuals veg. and reprod. vigorous, others senesce or persist as rosettes
<i>Astragalus lentiginosus</i> var. <i>micans</i> (D)	shoot growth, floral initiation	leaves dense on shoots, flowers are profuse		plants have bolted so foliage appears less dense; fruit and seed immature	fruit and seed mature and dispersed; foliage begins to senesce	some plants die back, others produce new leafy shoots; fruits buried by moving sand
<i>Dicoria canescens</i> <i>ssp. clarkae</i> (D)	seed germination (?)	seedlings in cotyledon stage		plants about 12 cm tall, bearing 6-12 leaves	some plants reach 30 cm tall, well branched	many plants 30-40 cm tall, getting quite woody at base

Table 10 (cont.)

	Aug	Sep	Oct	Nov	Dec	Jan-79
<i>Swallenia alexandreae</i> (D)	shoots green and growing	shoots growing, first seedlings seen		shoots stop growing, enter dormancy; seedlings with 2-4 leaves	older plants dormant	older plants dormant
<i>Oenothera avita</i> <i>ssp. eurekaensis</i> (D)	only rosettes seen; caps. buried	rosettes; one individual with flowers on east side of dune		rosettes	rosettes; germination sparse	rosettes; seedlings
<i>Astragalus lentiginosus</i> <i>var. micans</i> (D)	vigorous growth; foliage ample	growth continues		growth continues; one individual seen flowering on west side of dune	growth continues	growth continues; germination
<i>Dicoria canescens</i> <i>ssp. clarkae</i> (D)	rapid growth	rapid growth, many plants over 60 cm tall; flowers initiated; some new seedlings and plantlets seen		growth slows and stops; fruit and seed set; death of the plants	seed dispersal	

Table 10 (cont.).

	Feb-78	Mar	Apr	May	Jun	Jul
<i>Stanleya pinnata</i> ssp. <i>inyoensis</i> (D)	vegetative growth	some shoots 12-15 cm long		growth continues; flowers profuse, some fruit	flowering and fruiting continues	flowering and fruiting
(E)	vegetative growth	shoot growth		peak of flowering, fruiting	a few per- sistent flowers, mostly in fruit	leaf drop; no flowers; seeds dispersed
<i>Dalea polyadenia</i> (D)		new foliage present		in full foliage; flowers initiated and open	flowering; fruits formed	foliage and flowers persist; much fruit
(E)		new foliate present		in full foliage; flowers initiated and open	foliage and flowers begin to abscise; fruit formed	most individuals lack foliage and flowers
<i>Larrea tridentata</i> (E)		new shoot growth well underway		peak of flowering; some fruit is set	fruit is dispersed	some growth continues (?)

Table 10 (cont.).

	Aug	Sep	Oct	Nov	Dec	Jan -79
<i>Stanleya pinnata</i> ssp. <i>inyoensis</i> (D)	bearing ample foliage and many flowers	bearing ample foliage and a few flowers		with foliage and fruit; flowers mostly gone	slow growth	
(E)	dormant	small surge of new foliage and flowers		with sparse foliage only	slow growth	
<i>Dalea polyadenia</i> (D)	ample foliage and a few flowers	foliage and flowers begin to abscise		dormant	dormant	dormant
(E)	dormant	dormant		dormant	dormant	dormant
<i>Larrea tridentata</i> (E)	leaves persist; slow growth?	small surge of new foliage and flowers in a few individuals		leaves persist		

months although it was difficult to be precise as to the time of germination. Dicoria seedlings were observed in great numbers in March, but germination continued throughout the summer months.

Vegetative activity - The perennial Swallenia and the annual Dicoria were primarily summer-active, the shoots of the former becoming dormant in November while individuals of the latter died. This correlated with the onset of freezing night temperatures (Table 4). Oenothera spent most of the year as a small rosette, but stem growth was quite rapid when the plants bolted in early May (Plate 5). Rosettes were formed at the tips of flowering stems, old leaves dropped, and burial returned the plants to an inconspicuous form. Astragalus bore ample foliage all year, set flower and fruit, and then lost this "winter set" of leaves by late June. However, most individuals were able to activate new buds on these barren stems (Plate 6) and by mid-July they displayed a "summer set" of foliage. Continued growth of these shoots during the summer and fall adds new leaves which will become the next winter foliage. Beatley (1970) noted a similar perennation response of the annual Astragalus lentiginosus var. fremontii to rainfall. However, var. micans is capable of this response for at least several years and in the absence of rainfall if growing on the dune. The favorable water status of the Eureka Dune substrate is probably responsible. Also it is important to note the prolonged vegetative activity of Stanleya and Dalea individuals growing on the dune compared to those residing in the nearby ecotone habitat.

Reproductive activity - Floral initiation of A. l. var. micans probably began sometime in February, as profuse flowering was noted in March

(Plate 4). In contrast, Dicoria did not begin until late August and September. All other taxa exhibited peak floral displays in late April and May. Stanleya and Dalea individuals growing on the dune had protracted flowering compared to plants of the ecotone. All of the perennial taxa in Figure 4 except Swallenia responding to the rains of early September with aseasonal flowering (Table 10). It is important to note that floral activity on the dune can take place from March to at least October--about 75% of the entire year.

The subsequent formation of seed and fruit and their dispersal follows a pattern similar to the one described above. However, there is a significant difference between the dune-restricted perennials (Swallenia, Oenothera, and Astragalus) and the typically non-dune perennials (Stanleya and Dalea). Whereas the latter, when found on the dune, had protracted reproductive activity, the former tended to be concise in this regard. The dune-restricted perennials seemed to truncate the reproductive mode by early summer and return to a state of vegetative activity. This may represent an adaptive change in allocation patterns as a response to shifting sand and the burial of vegetative shoot apices. Years with additional summer and fall rain may allow for greater aseasonal flowering in Oenothera and Astragalus but not without rapid stem elongation and the resultant elevation of growing points. Aseasonal flowering has never been observed in Swallenia, which may reflect the higher necessary investment of producing entire fertile culms instead of simply floral buds. If this is true, it suggests a very conservative "strategy" on the part of the dunegrass with respect to resource partitioning between vegetative and reproductive modes.

Water Relations and Photosynthesis

Pavlik (1979) reported on the water relations and photosynthetic characteristics of Swallenia alexandrae, Oenothera avita ssp. eurekensis, Astragalus lentiginosus var. micans, Dicoria canescens ssp. clarkae, Stanleya pinnata ssp. inyoensis, and Larrea tridentata. The study was conducted over a one year period and included the field assessment of water status on a daily and seasonal basis using pressure bomb techniques (Scholander et al. 1965), field photosynthesis by $^{14}\text{CO}_2$ exposure (Tieszen et al. 1972), and laboratory gas exchange measurements. Several major results may be summarized as follows:

- 1) Plants which grew on the dune exhibited significantly less negative xylem water potentials than plants of the adjacent ecotone habitat. Swallenia seldom experienced potentials less than -1.5 MPa during the summer months, compared to Larrea of the ecotone at -4.5 MPa.
- 2) Plants growing on the dune had smaller changes in predawn water potentials from March to September than plants growing off the dune, indicating a slow rate of substrate moisture depletion in the rooting zone of the dune.
- 3) Plants growing on the dune exhibited dampened seasonal amplitudes of water potential compared to the large fluxuations experienced by non-dune plants.
- 4) Dune endemics (Swallenia, Oenothera, and Astragalus) maintained higher water potentials than nonendemics which also grew on the dune (Dicoria, Stanleya). The perennial endemics (perhaps incapable of

osmotic regulation) regulate their internal water status by stomatal closure at relatively high water potentials in order to maintain a high longterm water-use efficiency. Therefore, substrate moisture depletion is minimized and lethal water potentials in the root zones of the perennials are not reached. The annual Dicoria exploits large amounts of soil moisture which it transpires freely, but experiences more negative water potentials than the endemics.

- 5) Three of the taxa surveyed were found to possess high photosynthetic capacities which were realized under field conditions. Swallenia had the attributes of other C_4 plants, such as high CO_2 fixation rates and water-use efficiency by virtue of its ability to utilize low intercellular CO_2 concentrations. The C_3 Oenothera also exhibited high photosynthetic rates during September 1978 which were near those reported for some C_4 plants. This was due in part to a relatively high mesophyll conductance as demonstrated in laboratory grown material. Dicoria, the C_3 summer annual, was found to have the greatest photosynthetic productivity, with rates measured in the field well exceeding those of Swallenia throughout the summer and early fall. Astragalus had rates comparable to those reported for most C_3 taxa. Laboratory studies further confirmed the high photosynthetic capacities of Swallenia, Oenothera, and Dicoria.
- 6) Laboratory grown Swallenia was three times more water-use efficient than Oenothera as the result of low leaf conductances to water vapor and a very high mesophyll conductance. However, in the absence of physiological adaptations which promote water-use efficiency, the C_3

Oenothera and Astragalus may reduce the total amount of water transpired from the root zone by reductions of shoot surface area in early summer (see phenological data).

These data led to the proposal of a model which focused on the differences in adaptive syndromes observed between perennial and annual psammophytes at Eureka Dunes. Perennial psammophytes must deal with long-term sand accumulation and/or removal. The exaggerated growth of shoots (later to function as rhizomes) and the elevation of perenniating buds serve to minimize the probability of carbohydrate depletion by buried foliage, mechanical resistance to growth, the loss of a holdfast during severe deflation and the burial of immature reproductive structures. Such growth requires photosynthate not only for the generation of new tissues but also for the maintenance of the old but functional. This requirement may be met by assimilation systems of high capacitance coupled with the favorable dune moisture conditions that allow for sustained gas exchange. Structural, phenological and physiological adaptations optimize water-use efficiency such that growth is maintained and dessication avoided. An annual psammophyte, such as Dicoria may only have to deal with shifting sand on a short term basis or may occupy sites of greater stability. High photosynthetic capacity, sustained gas exchange, and the tolerance of water potentials lower than those maintained by the perennial psammophytes result in a great assimilation of carbon. A considerable portion of this carbon is allocated to a root system which continually exploits soil water reserves. Although burial may eliminate portions of the shoot, a prolific formation of seed completes the life cycle and progeny and parent are scattered by the wind.

Growth in the Field

A quantitative comparison of growth and productivity of Swallenia and Dicoria was made by Pavlik (1979). He found that shoot extension of the dunegrass could approach a rate of $1 \text{ cm} \cdot \text{day}^{-1}$ during June and July and that the total length of culms produced in a single year could be near 1 m. Dry matter accumulation rates per culm reached a maximum of $0.19 \text{ g} \cdot \text{day}^{-1}$ and total above-ground productivity could potentially be $1500 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Pavlik also speculated that Swallenia allocates less carbon to roots than shoots based on observations of the root system and the lack of specialized rhizomes. Dicoria, however, did not seem to emphasize the longitudinal growth of shoots, although seasonal productivity per plant was exceedingly high. Maximum rates of above-ground biomass accumulation were near $5 \text{ g} \cdot \text{day}^{-1}$ but even more impressive was the apparent investment of carbon in a woody taproot. A 75 cm length of an unbranched primary root weighed 96 g and was $2\frac{1}{2}$ cm in diameter at the sand surface.

The bolting stems of Oenothera avita ssp. eurekensis have been observed to exceed 1 m in length when favorable moisture and temperature conditions were sustained.

Burk and Dick-Peddie (1973) reported that maximum seasonal stem elongation of Larrea tridentata was slightly greater than 5 cm. Maximum seasonal additions of dry weight were less than $0.30 \text{ g} \cdot \text{shoot}^{-1}$ even though the site averaged nearly twice the annual precipitation predicted for Eureka Valley. Such patterns of allocation and assimilation would necessarily exclude species like Larrea from unstable dune habitats where sand accumulation would exceed the growth of shoots. The exaggerated

shoot elongation observed in Swallenia would serve to elevate growing points even on the uppermost slopes where the frequency of sand avalanching can be high. Another factor which must be assessed is the loss of shoots to wind damage and predation by jackrabbits (Lepus californicus deserticola). Severe harvesting by the hares during the summer, presumably to obtain moisture from the succulent stems has been observed. Although Dicoria does exhibit considerable above-ground growth, the well developed woody tap root system indicates that high water-use and soil moisture depletion are more critical factors than sand burial for this annual plant. The perennial Swallenia in contrast, may maintain a fine, deep root system and higher water-use efficiency such that shoot extension and perennation are of prime importance.

Pavlik also monitored seasonal changes in specific leaf area for several dune taxa and discussed its significance in relation to leaf temperature, photosynthetic capacity, and water-use efficiency.

Germination

Seeds of Swallenia alexandrae, Oenothera avita ssp. eurekensis and Astragalus lentiginosus var. micans were collected in June 1978 in order to question the relationship between the sand dune habitat and germination in these highly restricted taxa. The seeds were separated from fruit or chaff and stored at room temperature in a dessicator until tests were begun in November 1978. At this time, unfilled seeds were discarded and tetrazolium tests were made on the remaining "high quality" seed using the procedure outlined by Copeland (1976). A thin layer of sterile sand was placed in the bottom of a small glass petri dish, covered

with a sheet of filter paper and wet until saturated. These dishes were only 5 cm in diameter and had ground-flush bottoms to insure minimal thermal heterogeneity. Fifty "high quality" Swallenia and Oenothera seeds and 25 Astragalus seeds were placed in each dish and usually two dishes (replicates) were used per treatment. The effects of various constant temperatures, thermoperiodic regimes, light, seed coat scarification, and ripening time were observed using a temperature gradient bar (Sankary and Barbour 1972) which could be supplied with florescent and incandescent light fixtures. Additional details of the experimental design and the presentation of data may be found in Pavlik (1979).

All taxa tested from the 1978 crop appeared to have a high percentage of viable seeds (Table 11). When compared to seed collected in 1977 there was little variation in size and weight. Oenothera seeds were observed to secrete a mucilage upon imbibition which caused them to adhere to the substrate. A cursory inspection of Astragalus seeds revealed that they may be of two forms, small and large, so only the latter were used in the experiments. Supplies of this seed were limited by a heavy natural infestation of olethreutid moth larvae.

The meager response (2%) of Swallenia to constant temperatures did not delineate an "optimum" although germination was confined to the 20° C treatment. Oenothera exhibited a rather narrow optimum at 20° C but with only 49% germination after 12 days. Astragalus had an optimum at 25° C but was capable of germination at temperatures as low as 10° C. No seeds of these taxa were observed to germinate at constant temperatures of 30° C or higher.

Constant light was completely inhibitory to these seeds under all

Table 11. Seed characteristics of three Eureka Dune psammophytes. Viability determined by tetrazolium tests on filled seed. Average seed size determined from a 100 seed sample, range from a 10 seed sample.

	l	seed size (mm)	w	seed weight (g)		% viable	comments
				average	range		
<i>Swallenia alexandrae</i>	6/77	3.0	1.5	0.0050	0.0031-0.0070	--	a reddish-brown caryopsis with copious white endosperm
	6/78	3.5	2.3	0.0057	0.0043-0.0072	100	
<i>Oenothera avita</i> ssp. <i>eurekaensis</i>	5/77	2.5	1.0	0.0008	0.0006-0.0009	--	lt. brown with black spots, secretes mucilage upon imbibition
	6/78	2.5	1.0	0.0007	0.0005-0.0008	90	
<i>Astragalus lentiginosus</i> var. <i>micans</i>	6/78	4.0	2.5	0.0088	0.0069-0.0101	90	large series only (polymorphic ?), lt. green or tan with hard seed coat

constant temperature regimes and no seeds responded after 12 days. When constant darkness was imposed, seeds of Oenothera and Astragalus germinated within six days.

Thermoperiodic alterations greatly stimulated germination in both Oenothera and Swallenia, appearing to be obligate in the latter. A 5° C alteration at the 25/20° C and 30/25° C regimes proved optimal for Swallenia, with 35% and 24% germination, respectively. Overall, this was low considering the apparent high viability of the seed. Peak germination of Oenothera occurred with both 5° C and 10° C alterations and was 32% greater than at the optimum constant temperature. Pavlik also presented additional data which suggested that it was necessary to alternate a low temperature, such as 15° C or 20° C with a higher temperature of longer duration in order to achieve a high percentage germination event in Oenothera.

When experiments on the effects of thermoperiod on Astragalus seeds were being conducted, it became apparent that other factors were of overriding importance. Prior to this time, germination had been occurring in unscarified seeds but slowly declined and became zero for the duration of these trials. Scarification, however, allowed for immediate swelling and ample germination a few days later. Scarification of Swallenia caryopses had a minor positive effect on germination but also made them very susceptible to fungal attack.

An analysis of the kinetics of germination indicated that the overall temperature regime and the fluctuation of temperatures within this critical regime partition the seed population's response between continuous and simultaneous modes (as defined by Pemadasa and Lovell 1975).

Additionally, 25 seeds of Swallenia and Oenothera from the 1977 crop were treated with darkness and a 25/20⁰ C thermoperiod. After nine days 28% and 48% of the seeds germinated, respectively.

The seeds of desert plants must accommodate the great uncertainty associated with the fleeting optimal conditions for establishment. In sands and dunes where the soil water potentials wildly fluctuate as the result of summer thunderstorms, subsurface storage, sand deflation, and subsequent drying, this may be especially true. Seeds which lie dormant only for lack of water might germinate under these ephemeral conditions and meet with rapid dessication or thermal havoc. Clearly, other mechanisms exist which insure the soil seed reserves and optimize for successful completion of the life cycle. Pavlik (1979) discussed the observed germination responses of Swallenia, Oenothera, and Astragalus in relation to the sand dune habitat and presented a model of desert seed germination which incorporated the variables of moisture, mechanical limitation, light, temperature regime, and thermoperiod. He stated that "only the optimal coincidence of at least three independent variables (burial, moisture, and critical temperature regime) and at least one dependent variable (sand thermoperiod) will trigger the rare simultaneous germination event." At this time the probability for establishment and survival would be greatest in an environment of harsh extremes and unrelenting change.

Growth in the Laboratory

Seeds which germinated on the temperature gradient bar were placed on filter paper discs in glass petri dishes. The discs were supported

by a layer of sand in the bottom of the dish which kept the seeds supplied with water and nutrient solution (1% Hoagland's) while avoiding excess wetting. The dishes were then placed in a growth chamber with $30^{\circ}/10^{\circ}$ C, 16 hr/8 hr temperature and light cycle. Maximum light intensity at seedling height was $0.6 \text{ nmol} \cdot \text{m}^{-2} \cdot \text{sec}$. Root and shoot growth as well as phenology were observed and measured under these conditions. Seedlings were transplanted to 15 cm pots filled with sterile sand 6 days after germination and supplied with full strength Hoagland's solution.

Root Growth

Swailenia alexandrae - After the elongation of the coleorhiza, the radicle emerged in 1 or 2 days following germination and exhibited a strong geotropic response. The roots were of uniform diameter along their length, possessed small and inconspicuous root hairs and did not form laterals during the 6 days of observation. Growth rates were slow, ranging from $3.0 \text{ mm} \cdot \text{day}^{-1}$ to $5.5 \text{ mm} \cdot \text{day}^{-1}$ as observed from 13 seedlings. In case that growth of roots was inhibited by light, 7 additional seedlings were cultured in constant darkness. Growth was still slow and ranged from $3.4 \text{ mm} \cdot \text{day}^{-1}$ to $9.3 \text{ mm} \cdot \text{day}^{-1}$. The caryopses remained firmly attached to the seedlings and persisted for months.

Oenothera avita ssp. eurekensis - Following protrusion of the radicle through the testa, root growth rates increased steadily until the sixth day after germination. Average rates were not very high for the 10 seedlings monitored but individual rates were as high as $17.0 \text{ mm} \cdot \text{day}^{-1}$.

These results compare favorably with those reported by Barbour (1967) for Larrea tridentata and Rost et al. (1977) for Simmondsia chinensis (maximum rates of $16.0 \text{ mm} \cdot \text{day}^{-1}$ and $15.0 \text{ mm} \cdot \text{day}^{-1}$ respectively). The resultant roots may have possessed abundant apical root hairs, root hairs along the entire root axis, or no root hairs at all. Lateral roots frequently formed during the observation period.

Astragalus lentiginosus var. micans - Maximum root growth rates of the locoweed were observed within 2 or 3 days following germination (up to $10.0 \text{ mm} \cdot \text{day}^{-1}$) which then declined rapidly. Root hairs were profuse in a zone 6 to 10 mm from the root apex and a distinctive swelling usually marked the root-hypocotyl transition.

Shoot growth

Swallenia alexandrae - After the seedling became established, mature shoots in the growth chamber elongated at an average rate of $4.0 \text{ mm} \cdot \text{day}^{-1}$. Although this is less than half the maximum rate observed for plants in the field (during June and July), it corresponds to the field rate observed during August and September of $4.4 \text{ mm} \cdot \text{day}^{-1}$. The low light intensity of the growth chamber (less than 1/3 full sun) probably contributed to a sub-optimum elongation ability. Numerous leaves were produced along the shoot axis which remained green for at least a month prior to senescence. Leaves were never observed to "re-green," but instead, branching occurred by the activation of axillary buds along the culm. A strong branching response was obtained if the tip of the main shoot was removed, but these new shoots did not elongate rapidly. After 9 months, individual plants could possess as many as 30-40 culms

of various lengths. The production of fertile shoots and flowers was never observed under laboratory conditions.

Oenothera avita ssp eurekensis - Two or three days following germination the cotyledons emerged from the seed coat and began expansion. Initially they are greenish, puberulent, ovate to oblong, 1.0-1.5 mm long by about 1.0 mm wide and adnate to a very short hypocotyl. During the fifth or sixth day after germination the hypocotyl extended, the blades of the cotyledons expanded to about 3 mm long, and the petioles subsequently elongated. At this stage the epicotyl/shoot apex was barely visible but the first true foliage leaves could be present. Seedlings grown completely in the dark developed hypocotyls which were very long (2.4-3.5 cm) and straight and with partly expanded cotyledons.

Approximately 10 to 11 days after germination the cotyledons and petioles attained lengths of 10 to 15 mm and up to 4 foliage leaves were conspicuous. At this stage additional growth of the hypocotyl was imperceptible so that total plant height was less than 10 mm above the surface of the substrate. The activity of the shoot apex was entirely devoted to production of new foliage leaves and unbranched stems with very short internodes. The resultant growth form was a low rosette which after 2 months of growth was 8 to 13 cm in diameter and composed of 20 to 40 mature leaves. A single plant could subsequently be composed of several to many rosettes all united to a common stem or rootstock. Growth and proliferation of these rosettes was quite rapid and as many as 20 were produced by a single individual in less than 5 months post-germination.

The transition from the vegetative rosette state to the bolted, reproductive state occurred in as little as 3 months after germination. Branch buds were formed inside the rosette and began growth concurrently with rapid internode elongation of the main rosette axis. This release from dormancy was not stimulated by progressive changes in photoperiod or temperature. Stem elongation (at rates as high as $8.0 \text{ mm} \cdot \text{day}^{-1}$) resulted in a profusion of leafy shoots. Some of these shoots exceeded a meter in length within a 2 or 3 month period, thus substantiating observations made in the field. Many new rosettes were visible in the axils of leaves along the stems. Interestingly, these new rosettes became larger in diameter as one proceeded along the main shoot towards the apex, indicating a lack or reversal of normal apical dominance patterns. This could tend to promote development of the most elevated rosettes as an adaptation to sand burial.

During stem bolting, lateral flower buds were produced and released from dormancy independent of progressive changes in photoperiod and temperature. Prior to anthesis there was a sudden lengthening of the "ovary-pedicel" so that flowers were displayed well beyond the foliage. Anthesis occurred within 2 days of bud display and flowers remained functional (petals turgid, stigma lobes and anthers erect) for about 5 days total. Under growth chamber conditions the flowers did not demonstrate the vespertine habit as seen in the field but remained open well after darkness and throughout the "day." Within a week, a single rosette could display as many as 12 flowers and flowering could last for weeks. Attempts at crossing flowers on the same individual and flowers of different individuals were not successful so that seed was never

produced in the laboratory.

Plants grown under growth chamber conditions since March of 1978 remained leafy and vigorous to the date this was written (June 1979) and are to be transferred into permanent culture at Davis.

Astragalus lentiginosus var. micans - The cotyledons of the locoweed began to emerge from the testa 3 days after germination. They were ovate, light green and quite fleshy. Hypocotyl elongation was observed within 6 days and the trifoliate primary leaves could be seen. Leaflet number increased with each new leaf produced (i.e., 3, 5, 7, 9, etc.). Apparently the growth of these plants was not promoted by the growth chamber conditions and only 4 total individuals became established. Additional time is required before an adequate laboratory description of Astragalus can be made.

Notes on Population Biology

Swallenia alexandrae - Observations made by myself and others suggest that vegetative reproduction in the dunegrass is not a common event. Each hummock tends to grow "up" rather than "out," although expansion is a necessary consequence of culm burial. Fragmentation of hummocks must occur but its effects on the population structure remain unknown. It is very difficult to define an individual Swallenia plant and to ascertain the biology of a hummock.

The monoclinous dunegrass can produce large amounts of seed as observed in the field. Measurements made on five individual hummocks of various sizes showed that a hummock with an average canopy volume

of 0.43 m^3 produced an average of 68 inflorescences. Each inflorescence may bear numerous florets so that the potential seed production per hummock may be very high.

In rare years when all conditions for germination are optimal, numerous seedlings will appear in the fall. M. A. Henry (1976) observed densities of $0.05 \text{ seedlings} \cdot \text{m}^2$ and $0.12 \text{ seedlings} \cdot \text{m}^{-2}$ in the fall of 1974 and 1975, respectively. The 1975 seedlings followed a heavy rain which came in September. An unusually heavy storm in September of 1976 produced stands which I observed to have densities of 1 to 2 $\text{seedlings} \cdot \text{m}^{-2}$. Henry also noted that mortality of seedlings which germinated in fall of 1975 was as high as 89% by March of 1976, although vehicle impact may have accounted for part of this loss. However, seedlings from the ample 1976 crop (established after closure of the dunes to vehicles) had experienced up to 100% mortality as of June 1978 by my observation.

Oenothera avita ssp. eurekensis - Very little data on vegetative reproduction of the primrose were gathered. Rosettes may be produced on the elongated flowering axis or from the creeping underground rootstocks. The relative contributions of these modes to the total population is not known although the potential of either appears high.

Calculations based on five individuals measured in June 1978 showed that an Oenothera plant with an average canopy volume of 0.12 m^3 possessed an average of 264 flowers and flower buds and 121 mature fruits. Assuming that each flower and bud successfully develops seed and that 50 seeds are produced per fruit (an underestimation), an average plant

(at this point in time) will produce 19,250 seeds.

Despite this copious seed production, true seedlings of the primrose have not been seen in abundance. The reasons for this remain obscure and detailed studies and observations are necessary before any understanding of the population biology of this plant is achieved.

Astragalus lentiginosus var. micans - Vegetative reproduction in this taxon does not occur. Individuals are probably short-lived.

Each plant may produce large amounts of seed. Seeds remain in the legume during dispersal and tend to be buried in large groups within microtopographic depressions of the low dune and ecotone habitats.

Seedlings may be relatively common compared to the primrose, but data on survivorship and population growth are not available.

OFF-ROAD VEHICLE IMPACT STUDIES

Recent concern over the effects of vehicle disturbance on desert ecosystems has generated the need for detailed studies of habitat and organismal responses to impact. Davidson and Fox (1974) Wilshire and Nakata (1976) and Wilshire et al. (1977) have reported on off-road vehicle (ORV) damage to various geomorphic surfaces in the California desert. Papers by Berry (1973), Rauth (1973), Davidson and Fox (1974), Kuhn (1974), Stebbens (1974), and Vasek et al. (1975a, 1975b) have addressed the problem of biological responses to impact in a variety of arid habitats. The reader is hereby referred to these studies for an overview of the topic in areas other than the Eureka Dunes study site.

The Eureka Dunes Environmental Analysis (BLM 1976) attempted to summarize specific aspects of ORV impact at Eureka Dunes. The study suffered from an inadequate data base pertaining to the biology of specific dune-restricted organisms, the physical nature of the dune habitat, and the specific responses of these organisms and dunes to ORV use. In general, the study concluded that any level of ORV activity would result in a deterioration of the flora, fauna, physical habitat, and dune ecosystem. Sustained vehicular use in dune areas with concentrations of the endemic plants would ultimately result in their extinction (see pages 58, 59, 64, and 69 of the BLM study). A program of photographic site evaluation by the BLM had been in progress at the dune site but was not continued after the closure of the area in November 1976.

A two year study conducted by M. A. Henry (1976) monitored the responses of Swallenia hummocks to continuing ORV activity and discussed some details of vehicle effects as they might relate to growth and survival of the dunegrass. She reported a 30% decline in the number of hummocks and a net decrease in the size of the total population from transects located on the north side of the main dune. Unfortunately, a reasonable control plot was not available with which to compare these changes. The study is being continued in order to assess post-closure hummock mortality (M. A. Henry, pers. comm.).

All of the studies listed above have used a descriptive approach to the problem of assessing the aftermath of ORV activity rather than employing an experimental design. This is quite understandable because an experimental approach would require 1) the possible expenditure of the organism, regardless of its rarity, survival status or inherent value (which would not have otherwise occurred), 2) ample data on the biology of the organism whose response to vehicle impact is in question, 3) an adequate experimental design which included control organisms and significant sample sizes, 4) an indepth understanding of the physical nature of ORV impact and the complexity of its effects, and 5) some provision for multiple impact treatments and long-term observations. Many of these criteria are mutually exclusive; for example, can liberal use of a rare or endangered plant population in such experiments be justified by the statistical significance of impact data? The conscience of the investigator and federal law would say no. Our scant understanding of even the most widespread forms of desert life is also a major constraint on such studies. It may also be difficult

when using either the descriptive or experimental approach, to attribute certain organismal responses as direct consequences of vehicle impact rather than biological or environmental heterogeneity.

The purpose of the present study was to evaluate ORV impact on the Eureka Dune endemic plants in a manner which would reflect the present understanding of their biology and would minimize ambiguous interpretation of data obtained from a small sample size. The experimental approach employed here dictates that results must be extrapolated but avoids an after-the-fact assessment in which the conclusions may come too late to prevent irreversible trends.

Mechanical Impact

In order to assess the immediate effects of ORV impact on mature (reproductive) plants of the Eureka Dunes, four plants each of Swallenia alexandrae and Astragalus lentiginosus var. micans and five plants of Oenothera avita ssp. eurekensis were subjected to direct contact with a single four-wheel drive vehicle (a Willys Jeep). The vehicle, equipped with sand tires, passed without hesitation over the plants at a speed of 10-15 mph. One or two tires would make contact with the individual. One plant of each taxon was submitted to 2 or 3 seconds of rear tire spinning as might occur when vehicles start or accelerate. The initial degree of impact was subjectively assessed by the amount of disturbance to the plant and its immediate surroundings. However, a quantitative record of damage was made by counting the number of shoots (stems or culms) and shoot apices severed from the plant as indices of vegetative depletion. Reproductive (sexual)

depletion of Oenothera was determined by counting the number of flowers and floral buds which were found on the severed shoots. These results were expressed as a percentage of the total shoots, apices, or flowers found on the plant prior to impact. Damage to foliage and underground parts was subjectively assessed when possible but the plants were not disturbed any further.

Results

The results of the mechanical impact trial of June 12, 1978 are presented in Table 12 and illustrated in Plates 10, 13, and 14.

Small vegetative plants (10 to 35 culms each) of Swallenia experienced an average of a 33% loss of shoots from light to moderate levels of vehicle impact. Rear tire spinning completely uprooted the individual, severing underground connections which resulted in a 100% loss of living shoots. In the case of the dunegrass, loss of potential branching apices could not be accurately determined because perenniating buds may be present in the axil of each leaf. Considering the fact that each culm may possess 20 to 50 leaves, this loss could be substantial. Damage to the stout leaves was not readily apparent at this time.

The rosette-stage individual of Oenothera sustained very little damage after initial impact. The leaves of the primrose, although ruffled, were probably cushioned and supported by the sand as the wheels made contact. Caulescent individuals, however, were highly susceptible to mechanical disturbance and experienced a 33% to 56% loss of shoots, an 11% to 75% loss of apices, and up to a 69% loss of flowers

Table 12. Impact of a four wheel drive vehicle on sand dune endemics, Eureka Valley, as assessed by immediate mechanical damage June 12, 1978. Numbers in species column refer to specific individuals, "--" denotes lack of reproductive material, and "?" indicates no data available.

						% of total						
						phenological stage	impact	shoots severed	apices removed	flowers removed	foliage loss or damage	damage to underground parts
<i>Swallenia alexandrae</i>	74	small	vegetative plant	light, w/both tires	30	?	--	?	some damage			
	79	"	"	mod-heavy, w/both tires	33	?	--	?	light			
	72	"	"	mod-heavy w/both tires	36	?	--	?	some damage			
	62	"	"	heavy, spun on w/rear tire for 2-3 seconds	100	?	--	?	some damage			roots and rhizome severed
<i>Oenothera avita</i> ssp. <i>eurekaensis</i>	72	unbolted	rosette with fruit	light, w/both tires	0	0	0	0	some damage			?
	77	bolted, w/flowers and fruit		mod-heavy w/both tires	56	75	69		heavy			?
	45	"	"	light, front tire only	33	11	7		light			?
	48	"	"	moderate, w/both tires	50	50	0		light			?
	10	bolted, no flowers		heavy, spun on w/rear tire for 2-3 seconds	100	100	--		heavy			root severed

Table 12 (cont'd).

	phenological stage	impact	shoots severed	% of total			foliage loss or damage	damage to underground parts
				apices removed	flowers removed			
<i>Astragalus lentiginosus var. micans</i>	56 bearing fruit	light-moderate, one tire only	50	50	--		heavy	?
	71 " "	mod-heavy, w/ both tires	90	90	--		heavy	?
	54 bearing fruit	moderate, one tire only	66	66	--		heavy	?
	15 fruit dispersed	heavy, spun on w/rear tire for 2-3 sec- onds	100	100	--		heavy	root severed

and floral buds. The loss of apices may signify the loss of an equal number of individual rosettes (Plate 6). Oenothera is a prolific seeder and a 69% reduction in sexual reproductive potential would have significant, detrimental effects on the population dynamics of this geographically restricted taxon. As in the case of Swallenia, tire spinning was completely destructive to Oenothera and the test individual was uprooted and shredded beyond possible recovery.

Astragalus lost 50% to 90% of its shoots upon light to moderate or heavy levels of vehicle impact. This loss of stems, if sustained earlier in the year, would also represent the destruction of inflorescences and/or immature fruits. Perennation and growing point elevation would also be severely retarded. Impacted plants shed their leaves immediately as the result of mechanical disturbance, indicating a structurally weak nodal anatomy (a lack of foliar sclerenchyma was noted in the anatomy section of this report). Tire spinning, again in this case, was completely disruptive.

Summary

All three Eureka Dunes taxa sustained moderate to heavy damage from the single passing of an off-road vehicle. Swallenia and rosettes of Oenothera were slightly more resistant than caulescent Oenothera and Astragalus individuals. The fragile structure of the seedlings of these plants cannot withstand even the lightest disturbance by foot traffic, much less the passing of vehicles. The reduction of vegetative and sexual reproductive potential by the loss of apices and/or floral structures would have profound impact on the population dynamics of these

taxa. Severed or damaged stems, foliage and roots would constitute a considerable loss of energy from the budgets of these plants. The reduction in photosynthetic surface area and the investment of non-productive carbon in impacted tissues are roughly analogous to severe levels of herbivore predation in their effects on plant survival. Coupled with the mechanical disruption of xylem and phloem conduction, these factors would inhibit plant recovery from relatively small levels of initial impact. Several seasons of such extravagant losses would deplete carbon reserves and retard the growth and development so necessary for successful completion of the life cycle in this habitat.

Post-Impact Survival

After the vehicle impact of June 12, 1978, test plants and controls were tagged and their positions carefully mapped. Their condition and survival was monitored over the summer and early fall of 1978. In some cases the impacted plants could not be located upon subsequent inspections, although the metal tag was frequently recovered. This was interpreted as the death of the individual if excavation did not reveal the presence of underground, perenniating organs. Adjacent controls were nearly always located, but they too suffered mortality.

Results

Tables 13, 14, and 15 follow the survival of impacted plants until August 1978 and Table 16 compares the mortality of non-impacted controls and impacted experimental plants in September 1978. Plates 11, 12, and 15 provide illustration.

Table 13. Status of impacted plants on July 1, 1978. The comment "plant missing" denotes probable death.

species		impact	comments
Swallenia	74	light, w/both tires	one additional branch lost, the others appear healthy.
"	79	mod-heavy, w/both tires	one additional branch lost, others appear healthy although unburied and prostrate (plate 11)
"	72	mod-heavy, w/both tires	six additional branches lost.
"	62	heavy, spun on w/rear tire 2-3 seconds	replanted branches dead and mostly uncovered by the wind
Oenothera	72	light, w/both tires	plant missing
"	77	mod-heavy, w/both tires	plant missing
"	45	light, front tire only	remaining stems persist with two floral buds: no additional flowers or fruit.
"	48	moderate, w/both tires	two partially severed branches with some green foliage, one flower, and one flower bud, 5 fruits (control w/16 buds + 31 fruits on 4 branches)
"	10	heavy, spun on w/rear tire 2-3 seconds	plant missing

Table 13 (cont'd).

species		impact	comments
Astragalus	56	light-moderate, one tire only	no additional damage: some partially severed branches bear healthy foliage
"	71	mod-heavy both tires	one branch remaining with chlorotic foliage (plate 15)
"	54	moderate, one tire only	many green leaves remain: natural senescence
"	15	heavy, spun on w/rear tire 2-3 seconds	plant missing

Table 14. Status of impacted plants on July 20, 1978. The comment "plant missing" denotes probable death.

species	impact	comments
Swallenia	74	light, w/both tires appears healthy, although probably not growing
"	79	mod-heavy, w/both tires gaining erect form again
"	72	mod-heavy w/both tires additional stems lost, only 21% of original stems appear healthy: some signs of hare predation
"	62	heavy, spun on w/rear tire 2-3 seconds plant missing
Oenothera	72	light, w/both tires plant found dead, tag recovered
"	77	mod-heavy, w/both tires plant missing
"	45	light, front tire only plant missing
"	48	moderate, w/both tires plant completely destroyed by hares, tag recovered
"	10	heavy, spun on w/rear tire 2-3 seconds plant missing

Table 14 (cont'd).

species		impact	comments
Astragalus	56	light-moderate, one tire only	ample new foliage being produced
"	71	mod-heavy, both tires	appears dead above ground, rootstock partially exposed
"	54	moderate, one tire only	some new foliage appearing
"	15	heavy, spun on w/rear tire 2-3 seconds	plant missing

Table 15. Status of impacted plants on August 25, 1978. The comment "plant missing" denotes probable death.

species	impact	comments
Swallenia	74	light, w/both tires tips of several shoots green, foliage appears stunted
	79	mod-heavy, w/both tires five shoot tips green (a bit chlorotic), one new shoot observed and and two other shoots grazed by hares (Plate 11)
	72	mod-heavy, w/both tires all but two shoots are completely lacking chlorophyll, the individual is no longer growing (Plate 12)
	62	heavy, spun on w/rear tire 2-3 seconds plant missing
controls	none	shoots remain green primarily at their apices and younger leaves, although some older leaves are still alive.
Oenothera	72	light, w/both tires plant missing
	77	mod-heavy, w/both tires plant missing
	45	light, front tire only plant missing
	48	moderate, w/both tires plant missing
	10	heavy, spun on w/rear tire plant missing
controls	none	most plants have formed rosettes and are alive

Table 15 (cont'd).

species		impact	comments
Astragalus	56	light-moderate one tire only	perennation occurring similar to controls
	71	mod-heavy, both tires	plant dead (Plate 15)
	54	moderate, one tire only	some new foliage is present, but much less vigorous than controls
	15	heavy, spun on w/rear tire 2-3 seconds	plant missing
controls		none	plants appear quite leafy, green and erect with some shoot growth.

Half of the impacted Swallenia individuals had died by September and displayed no green or growing shoots. Control plants remained active but showed signs of fall senescence. The other plants retained their chlorophyll and one new shoot was observed.

None of the impacted Oenothera plants survived in September, however one was probably destroyed by hare predation. It was apparent that impacted plants soon dessicated and were then scattered by the wind. One of the four control plants had also died during this period.

Two of the four Astragalus plants impacted in June were still alive in September, compared to all of the controls. These plants were capable of producing new shoots and foliage on the unbroken stems which remained after initial impact.

Table 16 . Mortality (# dead plants/total plants x 100) of non-impacted control plants and impacted experimental plants, September 17, 1978, at Eureka Dunes.

	% mortality	
	control	experimental
<u>Swallenia alexandrae</u>	0	50
<u>Oenothera avita</u> ssp. <u>eurekensis</u>	25	100
<u>Astragalus lentiginosus</u> var. <u>micans</u>	0	50

Summary

Individuals of the taxa tested in this experiment were less likely to survive the summer months after contact with a single off-road vehicle than were non-impacted individuals. Mortality was highest in Oenothera, with Swallenia and Astragalus exhibiting greater resilience. However, long-term survival and the effects of multiple impact treatments were not examined in this study. It is important to realize that the simple type of impact employed here resulted in lowered survival and abnormal phenological activity.

THE CRITICAL INTERACTION: A DISCUSSION AND SUMMARY

- 1) The lack of detailed geological and hydrological data on Eureka Dunes does not allow for an understanding of the processes which gave rise to its pristine form. Heavy vehicle activity may disturb dune structure such that an accurate assessment of its natural state would be difficult, if not impossible. The relationship between subtleties in dune structure and biological activity on the dunes would remain obscure.
- 2) Although off-road vehicles do not have significant effects on sand compaction and bulk density, a loss of sand strength has been shown to result in greater wind erosion and subsequent sand transport (Wilshire and Nakata 1976). Increasing sand movement would impose additional burial, deflation and abrasion problems on plants of the dune habitat. No quantitative studies are available on this important factor, nor are data on the burial tolerances of Swallenia alexandrae, Oenothera avita ssp. eurekensis and Astragalus lentiginosus var. micans. These plants possess structural, physiological, and phenological adaptations to shifting sand. However, they are not equally competent to deal with it, as suggested by their distributions on the dune. It is likely that the abilities of these taxa to cope with sand movement could be exceeded if wind erosion was increased by ORV activity.
- 3) Critical vegetative and reproductive activities of the Eureka Dune endemic plants may occur throughout the entire year. Germination and seedling establishment are during the fall and winter. Flowering extends

from February to June and may even be significant in the fall of certain years. Spring and summer vegetative growth is essential for perennation of the endemics in this unstable habitat. Therefore, there is no portion of the year when vehicle impact could occur without disrupting the life cycle of at least one of these taxa.

4) The germination requirements of Swallenia, Oenothera, and Astragalus seeds would seldom be met under conditions of ORV disturbance. Sand churning would uncover seeds as well as bury them. Exposure to light, drying, and a disruptive and/or unfavorable temperature regime and thermoperiod would inhibit germination as shown by laboratory studies. Field experiments would be decisive in assessing the importance of vehicular germination inhibition with respect to the population dynamics of these taxa.

5) The establishment of Swallenia, Oenothera and Astragalus in nature from seed may be infrequent except during a few, fleeting and unpredictable occasions. A rare coincidence of factors is required to accomodate the relatively slow growth of young roots, to allow for shoot emergence and growth ahead of shifting sand, and to minimize the probability of predation. Natural seedling mortality imposes great restrictions on the population sizes of these plants. Therefore, it is not possible that establishment of the endemics would be positively stimulated by ORV activity. It has been observed that in the absence of heavy ORV traffic at the northwest corner of the dune (a barren area well used by ORV's in the past), numerous Astragalus seedlings and plants recently became established. However, Oenothera has yet to

invade (re-invade?) this site.

6) Laboratory propagation of the endemic taxa from seed had mixed results. Oenothera proved to be readily cultured, but Swallenia and Astragalus less so. Only the primrose flowered under laboratory and greenhouse conditions, but no viable seed was produced despite numerous attempts at artificial pollen transfer. Only the natural populations insure the seed production and genetic reserves of these taxa.

7) The population biology of these taxa remains virtually unknown. Critical limits on population sizes cannot be determined from the existing data base. The Eureka Dune populations of Swallenia, Oenothera, and Astragalus are the strongholds of these plants. The latter two taxa were not observed at the Marble Canyon Dunes in a May 1979 survey (M. Knudsen, pers. comm.).

8) All of the endemic Eureka Dune taxa experienced moderate to heavy damage as the result of contact with an ORV. The losses would constitute significant vegetative and reproductive depletions within these populations if continued over several years. Impacted plants showed varying degrees of post-impact survival but always less than non-impacted controls.

9) The effect of ORV impact on the trophic ecology of the dune - the transfer of energy from producers to consumers - has not been assessed. Such consideration must be made in order to understand the relation of impact to plant and animal interdependence within the ecosystem.

Plate 1. Aerial view of Eureka Dunes and vicinity, July 1978. Note the relic lakeshore to the left, the mudflow at the base of the Last Chance Mountains, and the Eureka-Saline corridor. Photo by Mary DeDecker.

Plate 2. A) Looking north along the seif crest of Eureka Dunes. Note the transverse dunes to the right and the "hidden valley" marked with the arrow. B) Presumably an old portion of the ancient lakebed now surrounded by dunes in "hidden valley".

Plate 3. A) Vegetation of the high dune habitat which is unique to Eureka Dunes and composed mainly of Swallenia and Dicoria. B) Ecotone along the eastern margin of the main dune.

Plate 4. A) Habit of Swallenia alexandrae in June 1978. Also note Coldenia plicata. B) Habit of Astragalus lentiginosus var. micans when flowering in March 1978. Note 15 cm scale.

A

B

C

Plate 5. A) Rosette habit of Oenothera avita ssp. eurekaensis
B) Bolted form of Oe. a. eurekaensis. Note 15 cm scale
C) Flower of Oe. a. eurekaensis, 5 cm in diameter.

A

B

C

Plate 6. Elevation of perennating buds in A) Swallenia alexandrae, B) Oenothera avita ssp. eurekensis (note new rosettes on the old fertile shoot w/ open capsules), and C) Astragalus lentiginosus var. micans. A & C 1x, B $\frac{1}{2}$ x in scale.

Plate 7. A) Leaf X-section of Swallenia, showing furrowed surfaces, fibrous ridges, conspicuous bundle sheaths, and a 1 to 4 ratio of Type I and Type II vascular bundles (144x). B) Stem X-section of Swallenia (144x).

A

B

Plate 8. Leaf and leaflet X-sections of A) Oenothera avita ssp. eurekaensis and B) Astragalus lentiginosus var. micans, both 144x.

Plate 9. X-section through root nodule of Astragalus lentiginosus var. micans showing nodular tissue towards the right and possible bacteroids in this region (287x).

Plate 10. Swallenia # 79 immediately A) before and B) after impact by a single test vehicle, June 1978. Note 15 cm scale.

A

B

Plate 11. Swallenia # 79 in A) July and B) August 1978 after the June 1978 impact. Note 15 cm scale.

Plate 12. Swallenia # 72 A) immediately after the June 1978 impact of the test vehicle and B) in August 1978. Note the 15 cm scale.

Plate 13. Oenothera # 77 immediately after impact of the test vehicle in June 1978, showing severe loss of stems and foliage. The plant was not found on subsequent visits and had presumably died.

Plate 14. Astragalus # 71 immediately A) before and B) after impact by a single test vehicle, June 1978. Note 15 cm scale.

A

B

Plate 15. Astragalus # 71 in A) July and B) August 1978, after the June 1978 impact. Note 15 cm scale.

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