A PRELIMINARY SURVEY OF THE OENOTHERA ORGANENSIS POPULATION

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HABITAT AND DISTRIBUTION

ENOTHERA ORGANENSIS is known solely from the one range of mountains from which it takes its name. The Organ Mountains of southern New Mexico form part of a long chain lying east of and parallel to the Rio Grande. They differ from the San Andres Mountains on the north and the Franklin Mountains on the south by their greater altitude and in their volcanic origin. There has recently been published a Geology of the Organ Mountains (DUNHAM 1935) from which the accompanying map (figure 1) has been taken. The Organ Mountains occupy an area approximately eighteen miles long (north and south) and varying from three to eight miles in width, lying about fifteen miles east of Las Cruces, New Mexico. The mountains rise from a plain of four to five thousand feet elevation to a height of 9108 feet at Organ Peak. Of the area occupied by the mountains, approximately thirty-three square miles are above the 6000 feet level and less than ten square miles above the 7000 feet level. Oenotheras have been found only at elevations above 6000 feet and only in canyons which drain relatively large areas of higher land.

The canyons in which the oenotheras are found have been carved out of the solid igneous rock, rhyolite, which makes up the greater part of the mountains. Both the side walls and the floors of the canyons are for the most part very steep, so that the runoff of water after rains is extremely rapid. The rainfall in the mountains has not been measured but is perhaps not much greater than at State College, near Las Cruces, where the mean annual precipitation in a period of over seventy years is approximately eight and one-half inches. The largest amount of precipitation occurs in the summer months and generally as local thunder showers. A large part of the mountains is definitely arid, and with the exception of Filmore Canyon, which has a permanent stream, all the water courses are dry most of the time. While the canyons were being formed, however, basins were eroded in the canyon floors. These have become filled with rock and gravel and it is in these natural reservoirs that the oenotheras are found. Growing with the oenotheras in these pockets is an Aquilegia, whereas the immediate environs are occupied by such xerophytes as Yucca, Agave, Opuntia, etc. These conditions are illustrated in the photographs in figure 2.

Oenothera organensis, unlike the other oenotheras with angled seeds (that is, the onagras), is strictly perennial. The central axis never elongates,



FIGURE 1.—Topographical map of the Organ Mountains—after DUNHAM (1935) in the Bulletin of the New Mexico School of Mines. The original is one inch to the mile and shows the geological formations.

but all stems are lateral branches arising from the axils of the rosette leaves, or from adventitious buds produced on the roots. Instead of a single tap root there are numerous "fibrous" roots varying from one-eighth

to three-quarters of an inch in diameter and usually attaining a length of about two feet in the first season. The plants are capable of withstanding severe drought, but under such conditions there is little growth and no flowering. In fact, under our conditions of culture, the water requirements



FIGURE 2.—Upper left: rhyolite cliffs at Dripping Springs, the East Fork runs slightly to the right of the center of the photograph, the North Fork is at right angles and only the base is included in this photograph; upper right: portion of a group of twenty-two plants of *Oenothera organensis* in the upper part of the North Fork; right center: the same group from the opposite side showing yuccas and cacti in the near background; lower left: water-course in the East Fork with one oenothera shown; lower right: higher in the same canyon, the oenothera in the foreground has been flattened by a recent runoff of water. Upper right photograph by D. G. CATCHESIDE.

for flowering in this species are very much greater than in other oenotheras. An instance of the failure of plants growing in their normal habitat to flower because of drought was observed in a small canyon on the north slope of the mountains (number 4 in figure 1). A population of about 20 plants was found there in September, 1937. All plants showed the effects of drought in their burned leaves and arrested growth, and only one had flowered that season whereas six still bore seed capsules from the previous year.

The foregoing is an account of the conditions to which *Oenothera organ*ensis is adapted. I have not searched other mountain ranges in the region for this species, but it has never been reported outside of this one range, and the lesser altitudes and the sedimentary origins of the near-by mountains make it seem improbable that they support populations of this species.

Within the Organ Mountains, Oenothera organensis has been found in four localities. The largest stand (114 plants) so far discovered is at Dripping Springs, the type locality. The first collections were made in 1881 by VASEY, 1894 to 1899 by WOOTON, 1898 by COCKERELL, 1906 by STANDLEY, as reported by WOOTON and STANDLEY (1913) under the name Oe. macrosiphon, and a later collection was made by PROFESSOR P. A. MUNZ in 1935. DOCTOR D. G. CATCHESIDE and I visited this locality in June, 1937, collecting seeds and cuttings, and I returned in September of that year for further collections. The oenotheras occur in two forks of the canyon (numbers 1 and 2 in figure 1). In the East Fork there were 43 plants growing in ten locations having respectively 1, 4, 4, 1, 2, 9, 1, 9, 5 and 7 plants and spread over about 800 feet of the water course. This fork is the source of the material collected by MUNZ (Emerson 1938). In the North Fork, 71 plants occur in seven locations having respectively 4, 2, 3, 22, 9, 19 and 12 plants each, and spread over about 400 feet of the water course. The populations in the two forks are over 600 feet apart and separated by a ridge 300 to 400 feet high. Two smaller forks of the canyon, extending to the southeast and southwest respectively, were devoid of oenotheras. In September the plants had been severely beaten by the runoff of a recent rain, but as near as could be judged, 47 of the plants at Dripping Springs had flowered and set seed, 38 others had apparently flowered but no capsules were found, and the remaining 29 (mostly young plants) had evidently not flowered that season. All but 19 of the plants then at Dripping Springs are now represented in the garden at Pasadena, either as plants grown from cuttings from the original plants or by the progenies from open-pollinated capsules.

Modoc Waterfall (number 3 in figure 1) is about a mile from Dripping Springs from which it is separated by high land, though it is possible that

the upper extreme of the North Fork of the canyon at Dripping Springs is narrowly separated from the upper part of Filmore Canyon. A previous collection from this locality had been made by DR. E. W. ERLANSON and DR. A. E. ARCHER in 1928 (EMERSON 1938). In June, 1937, there were about 20 plants growing on the cliff on the north side of the waterfall where they were watered by the mist from the fall. Cuttings were made from 14 of these plants (all that could be reached without ropes) and are now growing in Pasadena. DOCTOR CATCHESIDE and I explored Filmore Canyon for about half a mile above Modoc Waterfall and found only one straggling plant growing about five hundred vards above the falls. The canyon above the falls has a fairly level floor, running water and very much more vegetation than other canyons visited. It is possible that the oenotheras can not compete with other plants in the moister habitat, but it is also possible that oenotheras once grew here but have been destroyed by cattle which now graze this canyon. Filmore Canyon penetrates deeply into the mountains and may support oenothera colonies in the upper portions.

The oenotheras in McAllister Canyon (number 4 in figure 1) are about three miles distant from the localities reviewed above, from which they are separated by the highest part of the range. About 20 plants were found scattered along a very steep and rocky water course in one branch of the canyon. Seeds were collected in September, 1937, from the six plants on which capsules remained from the previous year.

McAllister Canyon was selected as the most promising region in which to find oenotheras on the northern slope after driving around the northern half of the mountains (Dripping Springs to Beasley Ranch in figure 1). The entire northern spur and the east slope from Texas Canyon to Beasley Ranch appeared much too dry to support oenotheras. The vegetation at the mouth of McAllister Canyon indicated a greater runoff of water than at other points, which suggested it as a favorable locality. It is probable that stands of *Oenothera organensis* are to be found in other branches of McAllister Canyon and presumably in the canyon on the west of Sugar Loaf Peak and in some of the canyons extending from Soledad Canyon back towards Organ Peak. On the basis of this preliminary survey, it is estimated that the entire population of this species consists of less than one thousand plants and very likely less than five hundred.

IDENTIFICATION OF SELF-STERILITY ALLELOMORPHS

The cuttings from Dripping Springs and from Modoc were rooted by the indole-acetic acid technique (COOPER 1936). The resulting plants were kept in the greenhouse over winter and treated with extra hours of illumination. Those which flowered were tested for sterility allelomorphs

and later the whole collection was transferred to the field, where they suffered a severe set-back and few additional plants flowered during the summer. Cultures were grown from seed collected at Dripping Springs and McAllister Canyon, and these flowered more freely.

The method used to identify self-sterility allelomorphs has been described in an earlier paper (EMERSON 1938). Following appropriate pollinations, the growth of pollen tubes in the stylar tissue is observed. Pollen carrying a particular allelomorph produces extremely short tubes in styles also carrying that allelomorph, but produces normally growing tubes in any style not carrying that allelomorph. Plants of known constitutions had been retained from previous years and were used as testers. New testers were established as rapidly as additional allelomorphs were found.

The raw data showing the results of these tests are too cumbersome to publish as they involve other 3000 crosses between approximately 100 different genotypes.¹ The data presented at this time show the distribution of genotypes in the progenies of open-pollinated capsules collected in the wild (table 1) and the distribution of the different self-sterility allelomorphs in the four localities from which collections were made (table 2). The additional observations reported at this time are in agreement with the genetic results previously reported (EMERSON 1938). All self-sterility genes so far determined, and there are now 37, are apparently different mutations at a single locus, that is they are strictly allelomorphic. In testing individual plants, pollen carrying many different allelomorphs was used, and in each instance pollen carrying two and only two allelomorphs failed to produce normally developing pollen tubes in the styles of the plant tested. In the cultures derived from open pollinated capsules it is apparent that two and only two allelomorphs were derived from the maternal parent. No allelomorph has been found which permits normal pollen tube growth following self-pollination.

The purpose of growing seeds from open pollinated capsules was in part to determine the allelomorphs carried by plants from which no cuttings were rooted and in part to determine the number of kinds of pollen taking part in the pollination of single flowers. To insure the identification of allelomorphs carried by the seed parent, seeds from more than one capsule from each plant were sown, since if a single capsule resulted from pollination by a single pollen parent there could be no more than four allelomorphs represented in the progeny and it would be impossible to tell which were of maternal and which of paternal origin. One culture (listed under #100 in table 1) illustrates this point. Plants in this culture carried four

¹ I am indebted to MR. GEORGE T. RUDKIN for the preparation of most of the styles used in these tests. By improving the dissection technique, he was able to make as many as 45 completed preparations in an hour, which was twice the previous rate and greatly accelerated the tests.

TABLE I

Frequencies of genotypes in progenies from open-pollinated capsules. The italicized numerals refer to specific self-sterility allelomorphs, x and y to incompletely identified allelomorphs which, however, are distinct from all other allelomorphs recorded in the same progeny.

McAllister Canyon:

<i>u</i> ,	SEEDS FROM	SEEDS N	IXED FROM	ſ
#1	I CAPSULE	5 CA		
₽∕♂	26 31 x y	6 16	29 x	y
2	— I I I	I I		_
25	3		II	I
#2	I CAPSULE	1 C/	AP. I CA	PSULE
₽\d ⁷ 2	14 19 29 33	x 2	35 14	34 x
9 — 31 2	4 I — I — I I 3	I I	2 I — —	3 — 2 I
#3	I CAP.	5 CAPSU	LES	
	♀ \ _{0⁷} x y	7 13 2	28 30	
	27 I —	— I	I —	
	31 — 1	I	— I	
#4	I CAPSU	LE	3 CAPS.	
\$\	3 11 12 25 37	7 x y	9 34	
19	I I I I	I	— I	
31	I I I 3	I I	I —	
	#5 5 C	APSULES		
	₽∖♂ <u>1</u> 3	x y		
	37 2	I I		
	38 2			
	#6 7 0	APSULES		
	₽ d ⁷ 12	34 x y	-	
	<i>I</i> 3 I	ı — —		
	37	— <u>1</u> 1		
al. Dainning Souis				

East Fork, Dripping Springs:

ings: #100	10	AP.	I CAP.	
			<u> </u>	
₽∖♂	12	20	5	
II	2	5	I	
19	2	3		

OENOTHERA ORGANENSIS POPULATION

TABLE I—(Continued)

#104	10	AP.	I CAPSULE				
₽∕♂₹	7	x	4	12	18	21	31
26	I	_	I	I	I	I	
35		I	I		_		2

#105		10	APSU	JLE		I CAPSULE			
₽∖♂	3	12	21	37	x	3	39	x	у
7				I	_	I	I	I	I
24	I	I			I	—	1	—	

#10 6		IC	AP.	І САР.		
	0\-7					
	¥ ∕o.	3		13		
	7	2	I	-	2	
	24	r	4	3		

North Fork, Dripping Springs:

#215	I CAP.	10	1 CAPSUL			
₽∖♂	36	7	13	x		
9 29		1 	 I	1		

#261		I CAI	SUL	Ξ	I CAP	
₽∖♂	7	17	x	у	x	
22	I	I	_	_	I	
29	-	—	I	τ		

#267			I CAPSULE						I CAPSULE			
	₽∕♂	15	19	22	30	36	x	у	3	7	33	x
	20					_	_	_	_		I	I
	29	I	I	2	I	2	I	I	I	I	3	—

#269	I CAP.	I CAP.		
₽∕3	29 x	35		
3	2 1	r		
20	I			

TABLE 2

Gene frequencies of 34 self-sterility allelomorphs in four localities in the Organ Mountains.

					1	ORIPPINO	SPRIN	GS					
ALLELO-	МСА	LLIST	ER CN	E	AST FO	ORK	NC	RTH I	ORK	MODOC	TOT	TALS	
MORPHS	çφ	୰୰	TOTAL	çç	ਹ ੈ ਹੈ	TOTAL	φç	୰ୖ୰	TOTAL	φç	çç	ਰ ¹ ਰੋ ¹	TOTAL
2 3 4	т 	2	(3)	I	 2 1	(3) (1)	3		(3)		1 4 4	2 2 1	(3) (6) (5)
5 6 7		 I I	(1) (1)	1 2	2 I	(3) (3)			(3)		I 2	2 : 5	(3) (1) (7)
9 11 12	I 	1 1 2	(2) (1) (2)	2 I		(2) (4)	2 2 1		(2) (2) (1)		3 4 2	1 1 5	(4) (5) (7)
13 14 15	I 	2 2 	(3) (2)	2	і —	(1) (2)	1 	I I	(2) (4)	3	2 5 3	4 2 1	(6) (7) (4)
16 17 18		1 	(1)	3 1 5	 	(3) (1) (6)			(1)	 	3 1 5	I I I	(4) (2) (6)
19 20 21	т 	т —	(2)	I 	 I 2	(1) (1) (2)	1 5 3	т —	(2) (5) (3)		3 5 3	2 I 2	(5) (6) (5)
22 24 25	 	 I	(2)	 	I I	(1) (2) (1)	3	1	(4)	1 1 1	3 2 1	2 2	(5) (2) (3)
26 27 28	I	1 	(1) (1)	т —		(1)					1 1	1 1	(2) (1) (1)
29 30 31		2 I I	(2) (1) (4)	I 	 	(I) (I)	3	1 1 	(4) (1)		4 3	3 2 2	(7) (2) (5)
33 34 35		1 3 1	(1) (3) (1)	 I		(1)	 	1 1	(1) (2)		2	2 3 2	(2) (3) (4)
36 37 38	2 I		(3) (1)		 I 	(1)	3	2	(5)		3 2 1	2 2 	(5) (4) (1)
<i>39</i>	_			_	I	(1)				_	_	I	(1)

combinations of four allelomorphs: II/I2, II/20, I2/I9 and $Ig/20.^2$ This distribution of allelomorphs is characteristic of the progeny of a cross between two plants, one carrying allelomorphs II/I9, the other I2/20, but which was the maternal and which the paternal parent can not be determined from this distribution alone. Another capsule from the same seed-parent produced a plant of the constitution 5/II. In this plant allelomorph II is the only one that could have been derived from the maternal parent which must consequently be II/I9. Table I is arranged to show which allelomorphs were derived from the maternal and which from the paternal parents in each instance.

In table 2, under the heading Q Q, are listed the number of plants carrying particular allelomorphs as determined directly from the cuttings or by progeny tests. The number of capsules in which a particular allelomorph was contributed by the pollen parent are listed under the heading $\sigma \sigma$. It is realized that the number of pollinations in which a particular allelomorph takes part should not correspond exactly to the frequency in the population of plants carrying that allelomorph, but it may give a fairly good approximation. It should also be noted that the pollen sampled from McAllister Canyon was produced in 1936, that from Dripping Springs in 1937.

DISTRIBUTION OF ALLELOMORPHS BETWEEN CANYONS

The distributions shown in table 2 seem to indicate that the samples collected in different canyons represent parts of a single interbreeding population. The data from the three localities best sampled are summarized in the following table. Allelomorphs obtained from the 1935 collection have already been reported (EMERSON 1938).

	1937 COLLECTION	INCLUDING COLLECTION OF 1935
McAllister only	6	5
East Fork only	5	7
North Fork only	2	2
McAllister and East Fork only	6	7
McAllister and North Fork only	3	2
East Fork and North Fork only	5	5
All three localities	7	8
Totals	34	36

² Self-sterility allelomorphs are customarily designated by the symbols S_1 , S_2 , S_{11} , etc., but it has been found that the small subscripts do not adequately distinguish the different allelomorphs. For this reason the numeral subscripts alone are being used in this paper and are italicized to distinguish them from other numerals used to designate frequencies, etc. The symbol S_{11} becomes simply II, the fractional form II/I2 represents a plant carrying S_{11} and S_{12} .

Thirteen allelomorphs (or 14 if the 1935 collection is included) have each been recovered from but one locality, 13 (or 15) are common to Mc-Allister Canyon and the East Fork of Dripping Springs, 10 are common to McAllister Canyon and the North Fork of Dripping Springs, and 12 (or 13) are common to the east and North Forks of Dripping Springs. The similarities between the three canyons are apparently equally strong and are as great as would be expected in samples of such sizes from a uniform population.

The sample reported from Modoc Waterfall is still very small. Allelomorph 4 is common to Modoc and the East Fork of Dripping Springs and allelomorph 14 is common to Modoc, McAllister and the East Fork of Dripping Springs. One plant from Modoc is known to carry either 15 or 22, both of which are known from the North Fork of Dripping Springs, so that Modoc has allelomorphs in common with each of the other localities sampled. The collection made at Modoc in 1928 (EMERSON 1938) contained allelomorphs 1, 2, 3 and 4. The first has not turned up again, but allelomorph 2 was found in McAllister Canyon, 3 in both forks of Dripping Springs, and 4 is present in the East Fork of Dripping Springs and is apparently the commonest allelomorph still at Modoc.

DISTRIBUTION OF ALLELOMORPHS IN SMALL LOCAL REGIONS

The group of plants growing highest in the East Fork of Dripping Springs contains seven plants, of which five have been completely identified. These have the following constitutions: 14/18, 16/17, 16/18, 14/18 and 14/18. These constitutions suggest that the entire group was derived from a single seed parent, perhaps 14/16 or 17/18. A group of plants lower in the same canyon contains allelomorphs 3, 5, 11, 12, 18 and 29, no one of which has so far been found in more than a single plant in this locality, indicating a more diverse origin than that of the group higher in the canyon.

The group highest in the North Fork is composed of 12 plants of which only three have been completely determined. These have the constitutions 22/29, 20/29 and 3/20, again suggesting a close ancestral relationship. A group of 22 plants lower in the same canyon has given the following constitutions: 11/36, 11/36, 9/29, 15/22, 3/22, 15/x, 9/35 and 12/13, indicating a certain degree of ancestral relationship, but also considerable diversity.

Five plants of the population of about 20 growing at Modoc Waterfall have been incompletely identified. These have the constitutions 4/14, 4/x, 4/y, 14/z and 4/14, suggesting a very close ancestral relationship. It should be remembered that allelomorph 4 was known to be present in this immediate locality nine years earlier.

The one branch of McAllister Canyon visited had about 20 plants which were fairly well scattered, but which were also well isolated from other stands. The six plants identified from this locality have the following constitutions: 2/25, 9/3I, 27/3I, 19/3I, 37/38 and 13/37. All but one of these plants had either allelomorph 31 or 37.

The data so far obtained seem to indicate that seed dispersal is brought about principally by water and accordingly takes place in a down-stream direction for the most part. Plants growing at the tops of canyons or in otherwise isolated groups would often be descended from plants previously occupying the same location and should show close relationships.

The transfer of allelomorphs from one canyon to another is likely accomplished through the pollen, though some transfer of seeds is to be expected. There were apparently but six plants in one branch of McAllister Canyon that flowered in 1936 and these plants carried only nine allelomorphs. The pollen functioning on them carried 13 additional allelomorphs that presumably originated in other localities. Seeds are probably carried by birds, but the likelihood of their falling in favorable spots is less than when carried by water.

TYPES OF POLLINATIONS

Oenothera organensis, like other members of the genus, is presumably insect pollinated, but the particular insect effective in this instance is not known. The flowers are open and receptive to pollination from early dusk till a few hours after sunrise. The conditions suggest that some strongflying, nocturnal insect, such as a sphinx moth, is a likely agent. Against this supposition is the observation that sphinx moths regularly visit other species of oenothera in the garden at Pasadena but do not bring about the pollination of Oe. organensis. It is estimated that less than 50 open-pollinated capsules have set on the 500 or more plants of this species that have flowered in the garden during the last two seasons. In the Organ Mountains, on the other hand, there is an abundant set of capsules, even on isolated plants. Since the hypanthium in this species is so long, averaging six inches or longer, a sphinx moth with a tongue of suitable length was sought in the Organ Mountains, but none of this sort was attracted to our light on the two evenings on which attempts were made. The difficulties of descending after dark from the relatively inaccesible locations of freely flowering groups of oenotheras discouraged us from making direct observations on the pollinating agents, but such observations will probably be necessary to settle the point.

The data presented in table I tell something of the manner in which pollinations take place even though the means by which they occur is unknown. It was to be expected that most of the pollen deposited on a

stigma would come from the flower previously visited by the pollinating agent. The pollen should often come from another flower on the same plant, resulting in self-pollination from which no seeds would set. In case the pollen came from a plant of different genetic constitution, only two allelomorphs should be carried by the pollen. Cultures from four openpollinated capsules (one capsule listed under each of $\#_2$ and $\#_{100}$ and both capsules under $\#_{100}$ in table 1) indicate that this type of pollination does occur. It should be noted that each of the plants from which these capsules were collected was growing at some distance from other plants then in flower. Most of the other tests indicate that more than two allelomorphs are usually present in the pollen deposited on any one stigma. Thirteen plants tested from one capsule (see #4, table 1) showed six allelomorphs present in the functioning pollen, and nine plants tested from another capsule (see #267) showed seven allelomorphs in the functioning pollen. It is expected that further tests will show that a large number of allelomorphs are usually present in the pollen functioning on any one stigma. Two means are suggested by which this result could be accomplished: either the pollinating insect brings a mixture of pollen from many flowers, or the flowers must be visited repeatedly, with pollen from more than one visit functioning.

FREQUENCIES OF ALLELOMORPHS

The sample of allelomorphs so far identified is too small to show the relative frequencies of different allelomorphs in the native population. There is still little agreement between the frequencies of allelomorphs recovered through the pollen and of those carried by the plants so far sampled. The data now available are shown in table 2.

ACKNOWLEDGMENTS

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SUMMARY

Oenothera organensis has been recorded only from the Organ Mountains of southern New Mexico. The particular type of habitat in which it is found and the water requirements for normal flowering are such that it

seems unlikely that the species occurs in other mountains in that region. The entire population is believed to consist of very few plants, perhaps not more than 500.

The samples so far analyzed show that the oenotheras growing in different canyons form part of a single, freely interbreeding population. The indications are that seed dispersal is brought about principally by water and is chiefly in a down-hill direction. The interchange of self-sterility allelomorphs between canyons is believed to be accomplished chiefly through the pollen. The means by which the pollen is carried has not been determined, but individual flowers have been shown to be pollinated by a mixture of pollen coming from many plants. The sample so far analyzed is insufficient to indicate the relative frequencies of different self-sterility allelomorphs.

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