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S. A. Cook

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POPULATION REGULATION OF *ESCHSCHOLZIA CALIFORNICA* BY COMPETITION AND EDAPHIC CONDITIONS

By S. A. COOK

Department of Biology, University of Oregon, Eugene, Oregon

INTRODUCTION

Eschscholzia californica Cham., the California poppy, occurs naturally in western North America from the Columbia River south to Baja California and from the coast of California eastward into the Great Basin. Within this extensive region it grows in open sites, frequently associated with grasses. Both the poppy and the grasses require ample light for optimal development and begin growth contemporaneously after the advent of winter rains. In dry years, when grass develops poorly, poppies apparently do well; in wet years the reverse is true.

The poppy grows on well-drained soils of dunes, alluvial fans, river terraces, steep banks, and rocky places. These soils may be derived from a wide range of parent materials, including serpentine. It has also been observed to colonize burned-over areas and endure on them for a number of years (Bowerman 1944). The poppy has behaved as a benign weed under conditions created by man. Small populations arise atop gravel piles, in gravelly ballast of railroads, or on road cuts and other areas where the established vegetation has been destroyed by excavation. Occasionally poppies may be seen in grain fields, where their growth is apparently favoured by mowing the overtopping grain. Although the plants themselves are cut back, new shoots emerge from ground level and flower from mid-summer to autumn.

These observations suggested the following hypotheses: (1) Genetic adaptation to specific soil type is involved in the poppy's adaptation to a broad range of soil types. Such response has been reported for other herbaceous species (Kruckeberg 1951; Jowett 1958, 1959; Bradshaw & Snaydon 1959; Bradshaw 1960). (2) Growth of associated grass is antagonistic to *Eschscholzia*. (3) *Eschscholzia* cannot tolerate soils with high water content but can become established on porous soils high above the water table. These hypotheses were tested experimentally at the Botanical Garden of the University of California at Berkeley during 1959 and 1960.

METHODS AND RESULTS

Genetic adaptation to soil type

Poppy seeds produced on given soil types were grown on the soils of their origin and on foreign soils in redwood boxes 36 in. (91 cm) long by 14 in. (36 cm) wide by 24 in. (61 cm) high (inside dimensions). The boxes, large enough to allow good taproot development and coated inside with black asphaltum paint, were placed outdoors. Beach sand was obtained from a dune at the northern end of Half Moon Bay, San Mateo County; serpentine soil from the east side of Crystal Springs Lake, San Mateo County; calcareous soil from a hillside at the north end of Rockaway Beach, San Mateo County; and soil derived from shale from the Berkeley Hills, Alameda County. Seeds were either sown directly or first germinated on filter paper with distilled water and then planted. All watering was with distilled water.

In the first experiment three boxes were filled respectively with beach sand, serpentine, and calcareous soils. A vertical board separated each box into two sections; in one a control population native to the soil type was grown and in the other, a test population, number 886, which was native to a coarse, shaley soil from near the coast (Table 1). Seeds were sown in May and germination was excellent, except on sand. This may have been due to the low water-holding capacity of the sand. No attempt was made, however, to assess the effect of soil on germination itself. The plants, thinned to thirteen per section, grew well and flowered until early October. Collections of capsules were made at intervals to obtain a record of total fruit production (Table 2), which was assumed to indicate vigour. Capsules were removed only after maturation in order that pruning might not encourage production of additional flowers.

Table 1. *Provenance of plant populations used in experiments on genetic adaptation to soil type*

Collection no.	Site	Elevation (ft (m))	County	Habitat
400	Rockaway Beach	50(15)	San Mateo	West-facing hill on shore; calcareous soil
851	Coyote	300(91)	San Mateo	Disturbed undifferentiated serpentine
852	McClure's Beach	80(24)	Marin	Roadside; sandy loam
886	Pt. San Pedro	300(91)	San Mateo	Road cut; loose shale

Table 2. *Mean total capsule production per individual in four populations of* Eschscholzia

Population	Soil of origin	Soil type on which grown: Beach sand	Calcareous	Serpentine
886	Shale	16·7	19·1	16·5
852	Sand	0·1		
400	Calcareous		27·7	
851	Serpentine			45·7

Table 3. *Results of* 1960 *experiment comparing the growth of serpentine population* 851 *on several soils*

Soil	No. of plants	Mean dry wt (g)	2 S.E.	Mean no. of flowers	2 S.E.
Serpentine	10	8·03*	2·4	46·3*	16·6
Calcareous	10	7·52*	1·4	33·1*	6·3
Shale	10	5·90*	2·1	37·0*	16·5

* Do not differ significantly at the 5% level as determined by simple analysis of variance.

In 1960 a population of poppies native to serpentine, number 851, was grown on serpentine, calcareous, and shale soils. Seedling progeny of a single individual were set out in January, after having been germinated on filter paper. Ten plants were grown in each box. Flowering began in mid-April and the plants were harvested in June. Flowers were counted and dry weights determined from aerial parts and the top 5 cm of roots which had been dried in a forced-draft oven at 90° C for 48 h (Table 3).

Effect of competition with Avena *and distance to water table*

The hypotheses that grass is antagonistic to *Eschscholzia* and that *Eschscholzia* can not tolerate soils with a high water content but can become established on porous soils well above the water table, were tested concurrently in the manner described below.

Plants were grown on a slope at varying heights above a stable water table (Phot. 1). Two separate experiments were conducted in consecutive years. In the first, poppies and oats were grown in pure and mixed culture. In the second experiment two mixed plantings were made with oats and poppies in different proportions.

A flat concrete basin was formed 9 ft (2·75 m) square and 6 in. (15 cm) deep. On the north border a 6 ft high (1·83 m) wall was erected; sides were constructed from this back wall sloping down to the southern border at the front. This prism-shaped space was divided into three parts by building two internal partitions parallel to the sides. Water was introduced at the back through a perforated pipe which ran from side to side. This pipe lay 8 in. (20 cm) off the floor of the basin. In the front an outlet was provided 3 in. (8 cm) above the floor. Manometers were installed at four places along the sides to permit gauging the level of water table after the space was filled (Phot. 1). Soil was taken from an alluvial fan issuing from Arroyo Mocho, Livermore Valley, Alameda Co., California. It was chosen because it is a soil on which the poppy grows naturally and because it is characteristic of the coarse gravelly material on which the plant often occurs. The soil was dug from a bank, thoroughly mixed, and sterilized with methyl bromide (Baker 1957) before being shovelled into the basin. The height of slope was made 3 ft 7 in. (1·09 m) in 1959 and 5 ft 7 in. (1·70 m) in 1960 (Phot. 2). The slope was sown by scattering the seeds evenly by hand. The surface was then lightly raked. During the early stages of growth the whole slope was covered with chicken wire to keep out birds and other animals. In 1959 it was necessary to sprinkle with water for 2 weeks to initiate germination. In 1960

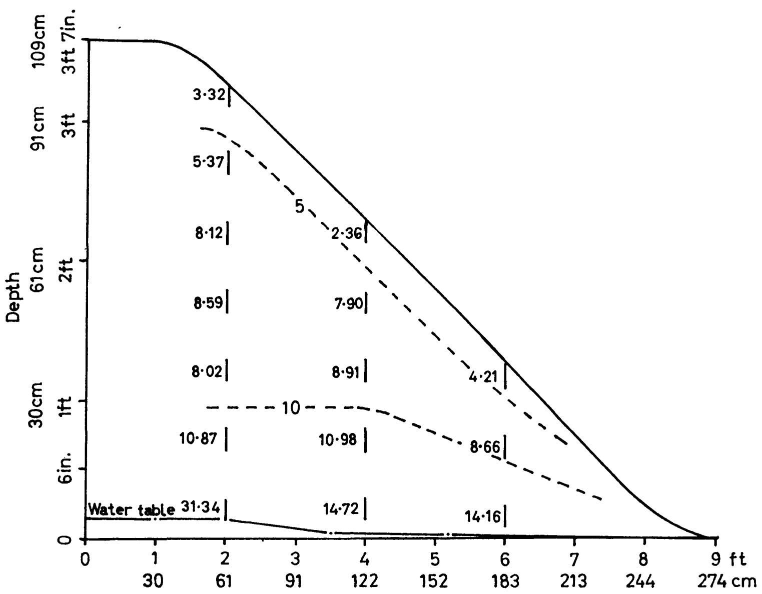


Fig. 1. Profile of water content in slope at end of 1959 experiment. Values inside the soil profile represent water content as percentage of the fine fraction of the soil. The dotted lines are interpolated 5 and 10% levels.

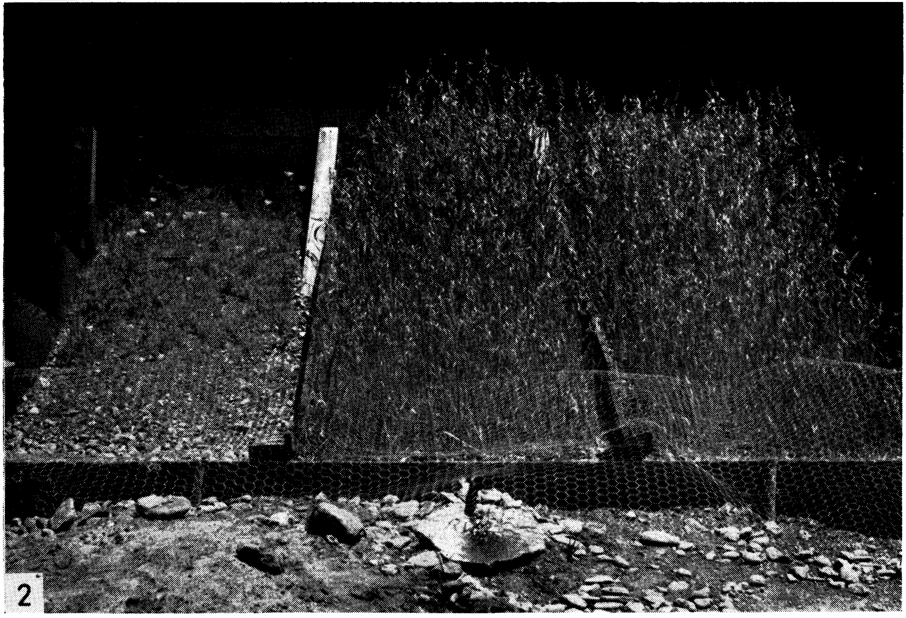
sowing was completed before winter rains began, so no supplemental water was needed. Once begun, the only water available was from precipitation and capillary rise from the basin.

The profile of water content in the soil was determined at the end of the first experiment on a foggy afternoon, 25 October 1959. The soil water was considered to be in its normal state for dry periods, as it had not rained for over a month prior to the date of excavation. Soil samples were taken in duplicate from representative levels at three places on the slope. These samples were placed immediately in plastic bags and weighed as soon as possible. They were then dried at 90° C for 48 h, weighed, sifted through a 2 mm sieve with round holes, and the fine fraction was weighed again. The water content was expressed as a percentage of the dried fine fraction using the mean of two values (Fig. 1). This mode of expression was chosen because it is the material which passes the 2 mm sieve which is the principal water reservoir of the soil.

The first experiment was begun on 10 April 1959, with the sowing of 14 400 poppy seeds on the western section, 6350 oat grains on the eastern section, and a mixture of 14 400 poppy seeds and 6350 oat grains in the centre section (Phot. 2). The *Eschscholzia* seed had been gathered from plants of a perennial race growing wild in the Botanical Garden, and the oats were the Kanota variety of *Avena fatua* obtained from a commercial source. By 25 April, seedlings were abundant from top to bottom of the three sections. Their density was least at the top, for the seeds bounced down the incline somewhat at sowing. Differences in size and shape of the seeds may have caused differential movement downhill. Also, there were several small places on the slope where the soil surface was smooth, so that seeds would slide over such places. The best germination of *Eschscholzia* was around rocks and pebbles, a phenomenon related probably to their need for darkness for germination and the catching ability of the rocks. The *Avena* germinated anywhere, exposed or covered.

Thriftiness of the species was measured in terms of the number of individuals at termination of the experiment (in mid-October) and their reproductive capacity. For sampling purposes, the slope was divided into areas formed by the projection onto it of an imaginary horizontal grid of square feet. Each 3 ft wide (91 cm) section was thus divided into nine tiers of three rectangles. Only the middle rectangles in each section were sampled so as to reduce effects at the margins. It was possible to count individual *Eschscholzia* plants but not those of *Avena* (which had died and could not be dug up). Therefore, the number of culms of *Avena* was counted. Fruit production was measured by counting numbers of receptacles on the one hand and glume pairs on the other. An average number of glumes per culm was obtained from the number of glumes on twenty-five culms. This average is less than the true figure, since some of the glumes had fallen off the withered inflorescences. The mean values of receptacles per poppy plants were computed from the entire number of individuals present (Table 4).

For the second experiment (1960) the height of the slope was increased from 3 ft 7 in. (1·09 m) to 5 ft 7 in. (1·70 m) in order to increase the vertical distance to the water table. The western section was sown with 2050 poppy seeds and 10 300 oat grains, and the eastern section with 10 300 poppy seeds and 2050 *Avena* grains. The poppies were from the same source as in the previous experiment, while the oats had been collected the previous summer in vacant lots in Berkeley. Planting took place on 18 December 1959 with procedures similar to those of the first experiment. Germination was good, except that there appeared to be a degree of dormancy in the wild oats, which caused germination to be less extensive than in the cultivated variety. The plants reached maturity and



Phot. 1. The prism-shaped container of the artificial slope.

Phot. 2. The artificial slope as it appeared in 1959. Pure *Eschscholzia* on the left (west), mixed *Eschscholzia* and *Avena*, centre, and pure *Avena*, right (east).

Table 4. *Results of slope experiment*, 1959

		West section			Centre section						East section		
Soil depth (cm)	Dist. from back (ft)	No. of poppy plants (A)	Total capsules (B)	B/A	No. of poppy plants (C)	Total capsules (D)	D/C	No. of *Avena* culms (E)	Total spikelets (F)	F/E	No. of *Avena* culms (G)	Total spikelets (H)	H/G
109	0–1	92	55	0·60	6	4	0·67	174	974	5·6	315	1575	5·0
107	1–2	123	56	0·46	7	0	0·00	108	637	5·9	183	970	5·3
93	2–3	126	47	0·37	10	10	1·00	102	612	6·0	251	1355	5·4
78	3–4	192	59	0·31	17	19	1·12	354			303	1242	4·1
62	4–5	333	31	0·09	75	0	0·00	558	2399	4·3	327	1472	4·5
46	5–6	387	13	0·03	114	0	0·00	411	1233	3·0	474	1612	3·4
29	6–7	291	0	0·00	243	0	0·00	393	1297	3·3	474	995	2·1
14	7–8	168	3	0·02	20	0	0·00	453	1359	3·0	395		
4	8–9	1	0	0·00	1	0	0·00	103	278	2·7	62		
Total		1713	264		493	33		2656			2779		
Seed sown		Poppy 14 400, *Avena* 0			Poppy 14 400, *Avena* 6350						Poppy 0, *Avena* 6350		

were harvested in late May. By harvesting at this time it was possible to extract whole oat plants and also to observe the roots of both species. There was, however, the disadvantage that the poppy plants would have gone on to produce more flowers. It is not admissible, for this reason, to compare the absolute values from 1960 with those of 1959. Data were gathered as in the first experiment (Table 5). Regardless of the plants' position on the slope, the roots of both species grew down to completely saturated soil, then turned horizontally. At this level, roughly that of the water table in Fig. 1, anoxic conditions began. This was evident from a change in soil colour from red to blue. The poppy plants of these experiments had unbranched tap roots, whereas those dug up in the wild are usually found to have one or two lateral branch roots. The *Avena* had a fibrous root system.

Table 5. *Results of slope experiment*, 1960

		Poppy				*Avena*		
Soil depth (cm)	Distance from back (ft)	No. of plants	Total capsules	Mean no. of capsules per plant	Mean height (cm)	No. of plants	Mean no. of spikelets per culm	Mean height (cm)
West section								
162	0–1	6	18	3·0	37·5	336	4·4	47·1
143	1–2	66	40	0·6	18·1	393	2·1	30·4
125	2–3	108	65	0·6	24·7	546	2·1	30·6
107	3–4	150	15	0·1	15·6	753	1·4	22·8
85	4–5	120	6	0·05	15·0	990	1·1	21·8
65	5–6	75	0	0·0	8·6	1212	1·5	30·1
46	6–7	91	0	0·0	5·5	837	1·5	25·1
27	7–8	39	0	0·0	5·8	570	1·2	24·0
6	8–9	3	0	0·0	(4·0)*	480	1·3	23·4
Total		658	144			6117		
Seed sown			Poppy, 2050				*Avena*, 10 300	
East section								
162	0–1	57	220	3·9	25·0	0		
143	1–2	90	270	3·0	35·3	3	(9·0)	(78)
125	2–3	78	100	1·3	26·9	3	(9·0)	(80)
107	3–4	399	40	0·1	10·9	6	6·4	44·5
85	4–5	375	150	0·4	20·4	3	16·0	(72)
65	5–6	384	0	0·0	6·1	24	4·9	51·9
46	6–7	69	0	0·0	5·6	57	5·4	48·0
27	7–8	120	0	0·0	4·4	93	4·2	36·0
6	8–9	21	2	0·1	12·1	84	2·4	30·1
Total		1593	782			273		
Seed sown			Poppy, 10 300				*Avena*, 2050	

* Figures in parentheses are maxima rather than means.

DISCUSSION

Genetic adaptation to soil type

The data in Tables 2 and 3 suffer from a basic inadequacy in design of the experiments. A randomized experiment in which each population was tested against each soil type would have given more meaningful results; however, this was impossible with the available resources. If less importance had been attached to taproot development, more extensive testing would have been possible, for the plants could have been grown in pots.

In spite of this limitation, it is clear that a non-serpentine population (886) and a serpentine population (851) can mature and reproduce on serpentine and other soils. These populations are thus *bodenvag*, i.e. indifferent to soil type. That they are not totally indifferent is hinted at, although not proven, by the experiments.

In the 1959 experiment (Table 2), test population 886, native to shale, did not reproduce as well on calcareous and serpentine soils as plants native to those soils (there was no opportunity to run a control experiment). No particular significance can be attributed to the fact that 886 did better than the sand population (852) on sand. The low result for 852 on its native soil was probably due to its being a slow-growing coastal race. It remained vegetative during 1959 and only bloomed appreciably after April 1960.

The serpentine race (851) grown in 1960 produced more dry weight and flowers when grown on its native soil than when grown on calcareous and shale soils. A simple analysis of variance shows, however, that the differences are not significant at the 5% level. That the serpentine race did best on its native soil, together with the facts that in the previous experiment the non-serpentine test race did best on a non-serpentine soil and the control populations out-performed the test on their respective soils, suggests there is a degree of genetic adaptation to soil type.

Effect of distance to water table

Vastly more seeds were sown than produced plants on the artificial slope (Tables 4 and 5). *Eschscholzia* germinated and began development at all levels; however, even when grown alone, very few individuals survived below a height of 6 cm above the water table. A large number of individuals were established at heights below 65 cm when grown alone or in competition with *Avena*, but they remained stunted (below 10 cm high) and produced almost no flowers. Above 65 cm the number of poppy plants again diminished in pure and mixed culture, but they increased in size and reproductive vigour. These results may be explained in several ways. First, the seeds rolled down the slope at planting time, increasing their concentration at lower levels. Second, the higher water content of the surface layers at the bottom of the incline favoured a higher rate of germination than above. The seedlings were not able to live appreciably below 6 cm elevation above water table, probably because damping off or anoxia killed them. Between about 10 and 65 cm height above water table seeds germinated in large numbers and seedlings also survived. Above that level there were either fewer seeds, or germination and survival were rendered more difficult by increasing aridity.

Progressive depauperation of *Eschscholzia* plants with decreasing distance to water table, when grown in pure or mixed stands, might on first consideration be taken as evidence in favour of the hypothesis that the species cannot tolerate soils with high water contents. But, in fact, the experiment does not show this. It is more easily attributed to progressive diminution of above-water-table soil volume available to each plant. This statistic was computed on a relative basis by dividing the mean depth of soil under the area sampled by the number of plants growing in that area. This was plotted against mean number of receptacles (an index to vigour) formed by the pertinent plants. The resulting curve (Fig. 2) shows that vigour is a function of available space. Usable soil space is reduced as the water table is approached. Also it is further reduced by the increase in numbers of individuals germinating and surviving closer to the water table.

If fewer seeds had been sown, it is conceivable that plants would have been able to mature even close to the water table. This is attested to by the fact that in the centre section, which was not planted in December 1959, a single poppy growing alone could mature and bloom near the bottom of the slope the following spring. Also, since performing these experiments, the author has seen plants growing on sand bars of streams where they were only a few inches above water level. Thus, water content itself does not appear to inhibit the poppy except where completely water-logged conditions prevail. The experiments do show that the species can germinate on porous soils and develop deep taproots which penetrate to saturated soil at the water table.

Perennial races of *Eschscholzia californica* are normally found in sites where ground water is available throughout the year. Obligate annual races occupy arid regions by developing shallow root systems which exploit surface water during the rainy season, and survive the dry season as seeds (Cook 1962). It is likely that annuals reach maturity on smaller soil volumes than perennials, but this possibility has not been tested.

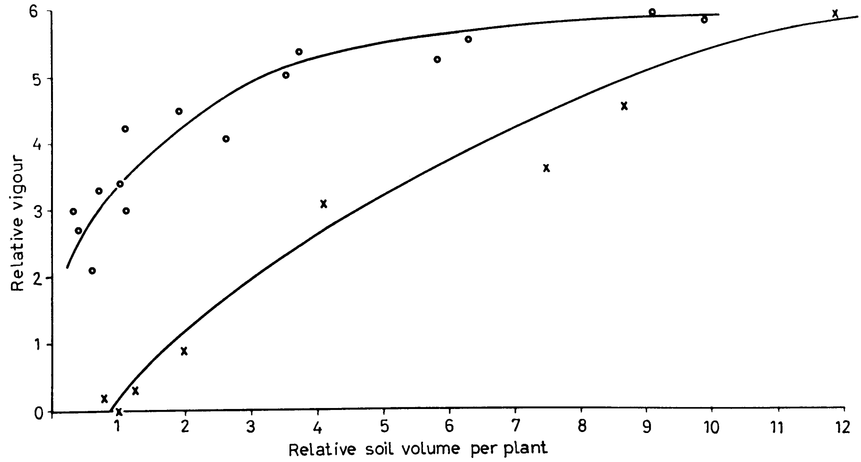


FIG. 2. Dependence of vigour, as measured by mean number of fruit produced, on soil volume available to each plant. Relative soil volume available was obtained by dividing the mid depth of soil to water table under each sample area by the number of plants growing on it. ×, *Eschscholzia*; ○, *Avena*.

The data of Tables 4 and 5 show that *Avena* was more successful than *Eschscholzia* in completing its life cycle in wet soil, although the development of individual plants improved toward the top of the slope. Also, the number of plants per unit area was at a maximum from around 30 to 65 cm above water table. When reproductive vigour, as measured by seed set, is plotted against relative volume of soil available to each plant (Fig. 2), it is seen that *Avena* can succeed in reproducing on a smaller volume than is needed by the poppy. The curve for *Avena* has levelled off whereas that for *Eschscholzia* is still rising under the conditions of the experiment. This reflects the fact that the poppy is more flexible in its development. When given optimal conditions, California poppies can become very large plants, producing many more flowers than were produced under the conditions of this experiment.

Height and seed set are reduced in both *Avena* and *Eschscholzia* as volume of soil available above water table is diminished. This effect has long been appreciated in agriculture (Weaver 1926) where, for instance, it is known that raising the water table in a cotton field causes die-back. When it is lowered the plants revive. A similar relation has been observed in silviculture (Ford 1954). Daubenmire (1959) has put it this way: 'Plants that can neither tolerate poor aeration nor develop a shallow root system are unable to grow where the water table is high'. *Avena* has a deeply penetrating root system (to around 2·14 m) and also a highly proliferated, spreading, shallow system (15–20 cm deep) (Weaver 1926). Its better success in wetter soils and in lesser volumes of usable soil may be due to this root configuration. The simple root system of *Eschscholzia* is not adapted to rapid, efficient use of the surface layers. When it grows in wet places it is not able to survive in competition with other, better adapted species. When, however, other conditions are unfavourable for competing species, poppies may grow even where the water table is high—for instance, on sand and gravel bars of streams, where conditions may be unfavourable for the germination of grasses.

Competition between oats and poppies

Avena was chosen as competitor in the slope experiment because it frequently grows with or near *Eschscholzia.* Examination of Table 4 shows that competition with the poppy (under the density of the 1959 experiment) only slightly reduced the total number of culms of *Avena*. This reduction was most marked at the top of the slope. The total number of spikelets is also slightly reduced; for those samples which can be paired, the total produced in absence of competition was 7979 and in presence of competition, 7152.

The effect of oats on poppy was, on the other hand, very strong; fewer poppy plants reached maturity (493 as against 1713) and none was able to flower below a height of *c.* 78 cm above the water table. A total of 264 capsules were formed without competition and only thirty-three under competition. The repetition of the experiment in 1960 with different proportions of seeds served to show again that *Avena* restricts the range over which poppies can mature to heights above about 78 cm. When the ratio of poppy to oat seeds was 0·2:1 (west section), the ratio of mature poppy plants to oat culms was 0·11:1. When the seed ratio was 5:1 (east section), that of mature plants and culms was 5·8:1. Thus, at the latter ratio and density, *Avena* has diminished ability to suppress the numbers of poppies. Also, the relative fertility of individual poppies increased from 0·2 to 0·5 receptacles per plant as the seed ratio changed from 0·2:1 to 5:1, *Eschscholzia* to *Avena*.

The poppies are not able to grow as close to the water table when competing with *Avena* as when growing alone. This displacement by competition was observed by Ellenberg (1954) in growth of mixed cultures of grasses over a gradient in depth to water table. It is an example on a local scale of the generally accepted idea that biotic competition may restrict geographical range. Ellenberg (1954) also recognized that in the sort of experiment described here many factors vary with approach to water table and that what is explained in terms of a certain factor may in fact be explicable in terms of others.

The ability of oats to suppress poppies may be due to the rapid upward growth of its leaves, which, in turn, may be due to its having larger seeds. The poppy is soon overtopped and robbed of light. This is similar to the behaviour of wheat relative to *Agrostemma* (Harper & Gajic 1961). Yet for effective suppression, the oats must become established in much larger numbers and form a continuous cover. Therefore, events at the time of dissemination and germination assume great importance. For instance, if at the top of a slope the density of seeds of both species is reduced and that of the grass is reduced below the amount necessary for suppression, a single poppy would be able to germinate and grow into a large plant producing many flowers by virtue of its open system of growth (plasticity).

When large numbers of individuals of one genetic type germinate over a sublimital volume, all become stunted and may not reproduce. This is a case of 'scramble' in Nicholson's terminology (Nicholson 1954). In what Nicholson calls 'contest' some individuals outgrow others and mortality results. This leaves for the survivors sufficient requisites to complete their life cycles. Harper & Gajic (1961) called this the mortality response. Between scramble and contest there is the plastic response of Harper & Gajic (1961), in which individual size and seed output are inversely proportional to density.

Eschscholzia is capable of a plastic response until a certain density is reached. When this density is exceeded scramble results.

Intraspecific competition appears mainly characterized by plastic response and scramble, while interspecific competition is mainly characterized by contest.

CONCLUSION

The range and abundance of a species is a resultant of numerous factors acting on it. Evidence has been presented which indicates that individuals of given *Eschscholzia* populations can tolerate a wide range of soils, including serpentine, although there is apparently a certain degree of genetic specialization to soil type amongst the populations. During early stages of development a long taproot and a low rosette of leaves are produced. This taproot permits the plant to survive subsequent drought at the soil surface and to grow in soils of low water holding capacity. These observations help to explain how the species can grow in what appear to be inhospitable sites. They do not answer the question of why it does not occur in greater abundance on deeper, moister, chemically more favourable soils. The answer to this is found in competition.

Avena germinates abundantly in situations with favourable moisture conditions. It can reproduce on smaller soil volumes per individual than the poppy, probably because its more highly proliferated surface root system permits it to exploit surface layers more effectively. Oat seedlings grow rapidly upward and, where germination has been dense enough, overtop the poppies. Hence oats may suppress poppies both by reducing available soil volume and by over-topping and shading. Reduction of available soil volume appears to be most important in the present experiments at depths to the water table of 78 cm or less. This may be one reason why poppies are seldom found naturally in wet sites. They live in habitats unfavourable to high densities of oats; for instance, in the gravelly alluvium at the top of the artificial slope, on steep hillsides, rocky, porous, sterile and toxic soils such as sand or serpentine. Possibly their occasional occurrence after fires may be a result of the temporary release of competition.

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SUMMARY

Eschscholzia californica occurs on a wide variety of soils, frequently associated with grass. Usually it grows on well-drained soils of dunes, alluvial fans, river terraces, steep banks, and rocky places. It may be found on serpentine soils and is sometimes adventive after fires. To explain these observations the following experiments were undertaken.

Populations were grown on soils on which they do and do not occur naturally. The results suggest that in general the species is insensitive to soil type but that a certain degree of genetic specialization exists.

An artificial slope was constructed with constant water table. *Eschscholzia californica* and *Avena fatua* were grown singly and together on it in different proportions. When grown alone, poppies survive in greater numbers and flower closer to the bottom of the slope (i.e. nearer water table) than when grown competing with *Avena*. They respond more plasticly to intraspecific than to interspecific competition, in which mortality is higher. The results indicate, but do not demonstrate, that there is a certain minimum density of oats above which poppies are fully suppressed and cannot reproduce. Poppies grow principally where the oats can not exist in densities above this minimum: rocky or steep places, in porous, sterile or toxic soils such as serpentine. The poppy is adapted to these conditions through its deep taproot and inherently wide physiological tolerance to soil type.

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