

DYNAMICS OF CLONAL MICROSPECIES IN CHOLLA CACTUS

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Microspecies have been redefined recently, following long usage, as plant populations which reproduce mainly if not exclusively by uniparental methods, are morphologically uniform, occupy a definite geographical or microgeographical area, are differentiated morphologically—often slightly—from related species and microspecies, and frequently possess a hybrid constitution (see Grant, 1971, chap. 4, for discussion). Different kinds of microspecies can be recognized according to the mode of uniparental reproduction. Clonal microspecies are those that reproduce by various means of vegetative propagation.

In theory, the development of a clonal hybrid microspecies entails the simple multiplication of hybrid individuals by vegetative means, and the dispersal and establishment of the daughter individuals throughout some suitable territory. The increase in population size presumably passes through the continuous and successive stages of small clone, endemic microspecies, and geographically widespread microspecies (Grant, 1971). In practice we have very little factual information about these population units and their modes of population growth; no good studies are available of clonal hybrid microspecies in plants.

A sterile species hybrid in plants can reproduce and spread asexually by agamospermous seed formation as well as by vegetative propagation. Many cases are known in *Crepis*, *Taraxacum*, *Rubus* and other groups in which sterile interspecific hybrids have spread widely by agamospermy (Gustafsson, 1946–1947; Stebbins,

1950; Grant, 1971). But the vegetative multiplication of a sterile hybrid has been recorded in only a few instances, such as *Elymus triticoides* × *condensatus* (Stebbins, 1959), and has never been investigated or documented in any detail so far as we are aware. The purpose of this paper is to describe a case of clonal hybrid microspecies in the cholla cacti.

We initially selected the genus *Opuntia* as a potentially good group in which to study vegetative multiplication of hybrids, since these cacti are known to hybridize naturally and to propagate freely from their stem joints. The *O. phaeacantha* group in the subgenus *Platyopuntia* is currently being studied taxonomically and biosystematically by Drs. Lyman Benson, D. L. Walkington, Donald Pinkava, and their students (see Benson, 1969a, 1969b). We have concentrated our attention on the other main subdivision of *Opuntia*, the subgenus *Cylindropuntia* or cholla cacti.

The point of departure for our study was provided by an early report of natural hybridization between the cholla species, *O. spinosior* and *O. fulgida*, along the Gila River in central Arizona (Kearney and Peebles, 1942). Kearney and Peebles stated (1942, p. 616): "An apparent hybrid between *O. spinosior* and *O. fulgida* is rather abundant in the bed of the Gila River between Florence and Casa Blanca, Pinal County. The hybrid plants propagate freely by means of fallen joints." This report was confirmed and repeated by the same and other authors. Kearney and Peebles later (1964) added that the hybrid plants produce very little seed. And Benson (1940, 1969a) noted that they are intermediate between the putative

¹The work reported here was carried out at the Boyce Thompson Arboretum, University of Arizona, Superior, Arizona.

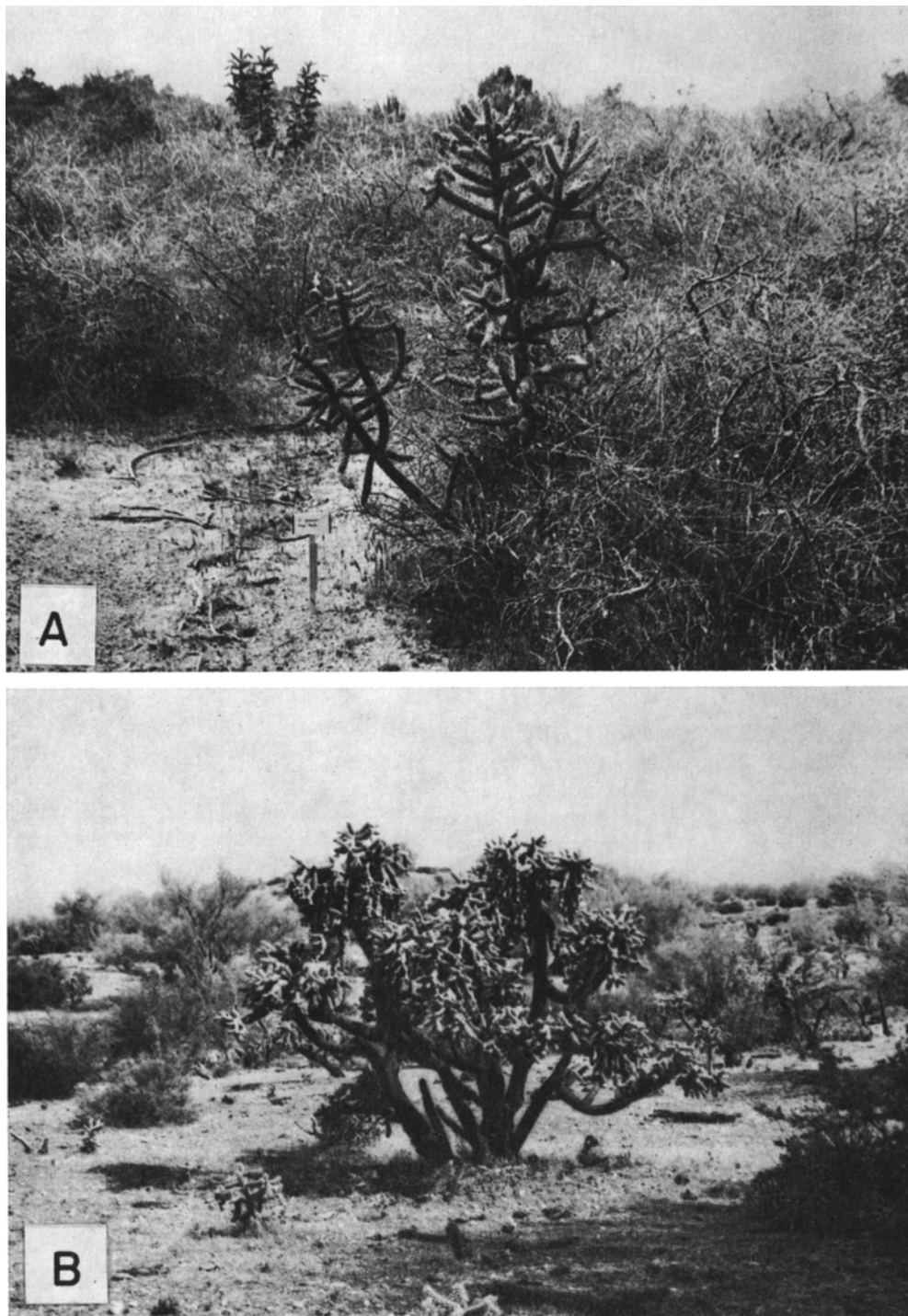


FIG. 1. *Opuntia spinosior* and *O. fulgida*. (A) *O. spinosior*, Pinal Ranch, between Superior and Globe. (B) *O. fulgida*, Superior.

parental species in several characters of the joints and fruits.

We relocated the hybrid colony on the flood-plain of the Gila River near the present Indian town of Sacaton in the low desert plains of central Arizona. We discovered another larger hybrid population in desert mountains near Kelvin 45 miles east of Sacaton. This paper describes the microgeographical, the morphological, and the fertility relationships of these hybrids and their later-generation derivatives. On the basis of this evidence we can then go on to outline the clonal micro-species derived as hybrid products of *O. spinosior* and *O. fulgida*.

THE PARENTAL SPECIES

The parental species are *O. fulgida*, the chain-fruit cholla, and *O. spinosior*, the cane cholla. *O. fulgida* is tree-like with stout trunks topped by thick branches. Its green pear-shaped fruits hang in long branched chains from the tips of the branches (Fig. 1). *O. spinosior* forms shrubs with long slender branches bearing terminal yellow tuberculate fruits (Fig. 1). The character differences between these species used in the present study are listed in Table 1. There is considerable racial variation within both species. For additional details the reader is referred to Benson (1969a).

Vegetative reproduction is very common in *O. fulgida*. The spiny terminal stem joints detach readily from the parent plant and fall to the ground. They may take root near the parent plant, or they may be carried to considerable distances by water or animals before rooting in their final resting place. The fruits of *O. fulgida* also possess buds which are capable of forming new adventitious roots and shoots (Johnson, 1918). Vegetative reproduction by stem joints is occasional in *O. spinosior*.

O. spinosior is a good seed producer and appears to reproduce mainly by seeds. The fruits of *O. fulgida*, on the other

hand, contain variable numbers of sound seeds, often few or none, and such good seeds as are formed frequently fail to germinate (Johnson, 1918). The breeding system of *O. fulgida* requires further study.

O. fulgida and *O. spinosior* are both widespread in central and southern Arizona and extend to northern Mexico. We are particularly concerned with the two species as they occur in the study area shown in Figure 2.

The eastern half of this area is mountainous and the western half consists of low plains and valleys. On the east the pine-covered Pinal Mts. (south of Globe) and Santa Catalina Mts. (northeast of Tucson) rise to heights of 7800 and 9100 feet, respectively. More extensive mountainous areas lie at lower elevations (3500 to 6500 feet) in the chaparral, woodland, and grassland zones. Farther west the mountains descend into the desert foothills (as at Superior and Hayden) and outwash plains (as near Florence) in the elevational range from 2800 feet to 1500 feet. Still farther west are low valleys (as at Sacaton) at 1200 to 1400 feet (see Fig. 2).

O. fulgida forms extensive populations throughout the desert plains and foothills in the creosote-bush and paloverde-saguaro communities up to 2700 feet elevation. *O. spinosior* characteristically occurs at higher elevations in the mountains, growing in chaparral, desert grassland, and pinyon-juniper woodland up to 6500 feet elevation; but it also extends out onto the desert plains. The lowland colonies of *O. spinosior* are small and spotty in the western part of our study area, as near Florence and Picacho (see Fig. 2); farther south *O. spinosior* becomes common in the desert plains.

The ecogeographical relationships between *O. fulgida* and *O. spinosior* differ markedly in different physiographic regions within the study area. In the southwestern part of this area the two species form extensive mixed stands. Here the lowland race of *O. spinosior* is biotically

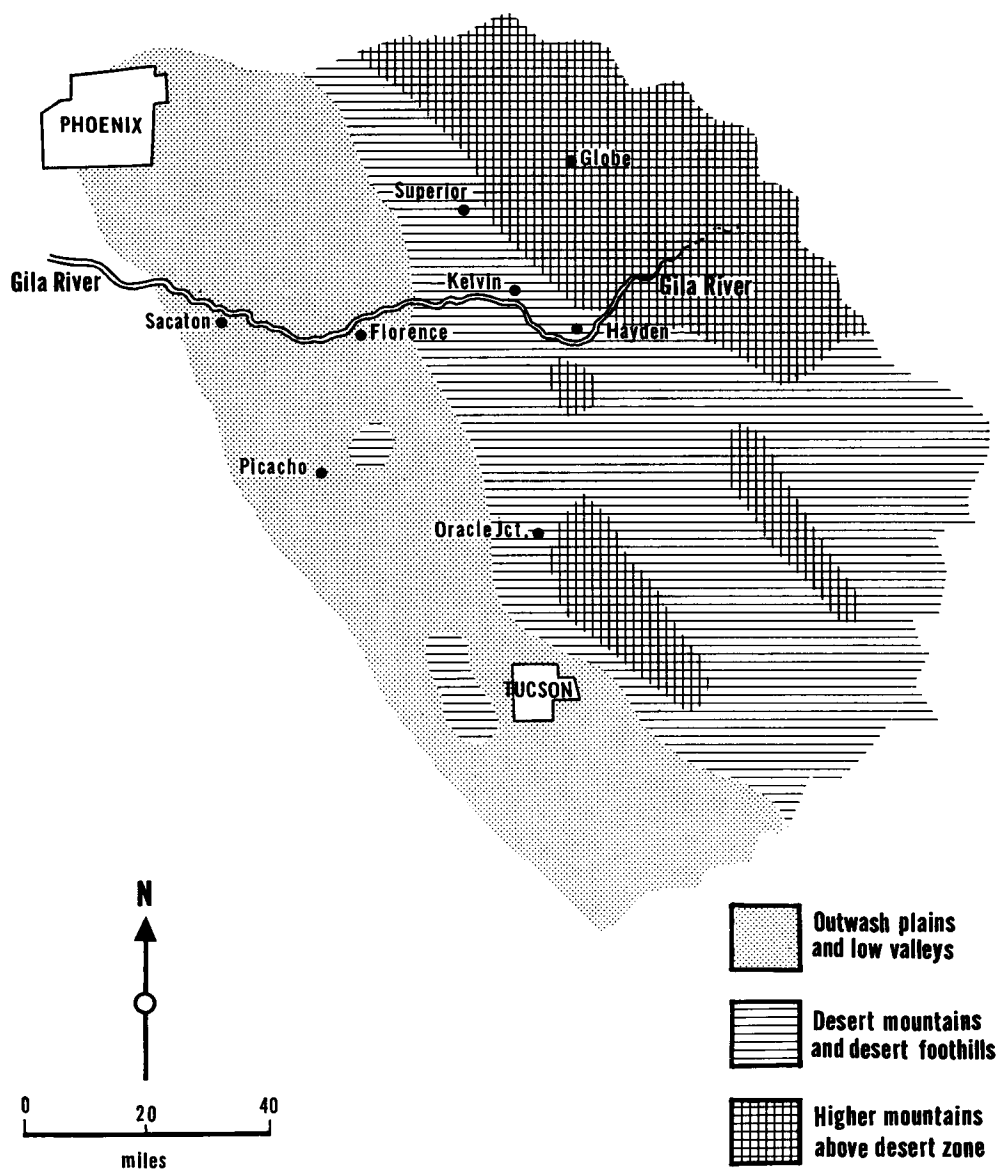


FIG. 2. Map of study area in south-central Arizona showing main physiographic features and key localities.

sympatric with *O. fulgida* over a large area. Biotically sympatric contacts between the two species are occasional and local in the low desert area farther north, as around Picacho and Florence.

In the mountainous area to the north-

east, by contrast, *O. fulgida* and *O. spinosior* are generally allopatric but nearly contiguous. Here *O. spinosior* ranges down to 4000 feet or sometimes 3500 feet and is therefore separated by an elevational gap from *O. fulgida* in the foothill zone

up to 2700 feet. This elevational gap is accompanied by a microgeographical gap of varying extent. We have found two places—one near Superior and one north-east of Hayden—where populations of the two species occur less than five miles apart. There may well be biotically sympatric contacts between *O. spinosior* and *O. fulgida* in the foothill zone, at least occasional ones, which we have not observed.

Seasonal isolation is the first and perhaps most important mode of reproductive isolation between *O. fulgida* and *O. spinosior* in nature. The two species differ in flowering time. *Opuntia spinosior* blooms in late spring from late April to June, whereas *O. fulgida* blooms in the summer from June to September. Furthermore, the flowers of *O. fulgida* are vespertine and short-lived, while those of *O. spinosior* are diurnal and remain open for days.

In the lowland areas of biotic sympatry between *O. spinosior* and *O. fulgida*, the former species is well past its peak of flowering before the latter begins to bloom, and the seasonal isolation is therefore essentially complete. In the mountains *O. spinosior* blooms somewhat later than it does in the lowlands. Sympatric contacts have not been found in the north-eastern mountainous part of our study area, as noted earlier, but could and probably do occur occasionally, and in such instances the seasonal isolation would be expected to break down partially.

It will be recalled that *O. spinosior* is a good seed producer whereas *O. fulgida* produces seeds sparsely and irregularly and then retains them for years in persistent fruit chains on the mother plant. The chances of hybrid seeds forming and germinating where *O. fulgida* is the maternal parent are consequently very slight as compared with the chances of effective hybridization occurring in the opposite direction. Hybrid formation would appear to have the best chance of succeeding where *O. spinosior* serves as the seed parent and *O. fulgida* as the pollen parent.

THE HYBRIDS

Hybrids between *O. fulgida* and *O. spinosior* are now known from two localities. The oldest known locality is Sacaton, as mentioned previously, while the best stand of hybrid plants is in the vicinity of Kelvin (see Fig. 2). The hybrid plants are intermixed with *O. fulgida* at both Sacaton and Kelvin. *O. spinosior* occurs with both *O. fulgida* and the hybrids in one locality 15 miles southwest of Kelvin; the nearest known plants of *O. spinosior* in the Sacaton area are 13 miles away from the hybrid colony. We have looked for hybrids of this combination in other parts of the study area, including the southern region of extensive biotic sympatry between the parental species, but have not found any indisputable cases, though these may of course turn up with further search.

The morphological features of the hybrids are shown in Table 1 and Figures 3 and 5. From the total array of character differences between *O. fulgida* and *O. spinosior* we selected five vegetative and four fruit characters which could be scored reliably in the field or laboratory, as listed in Table 1. Local populations of *O. fulgida* from Kelvin and *O. spinosior* from Pinal Ranch (between Superior and Globe) will serve as standards of reference for the two parental species. These are compared with hybrids from Kelvin of the type designated *K* and hybrids from Sacaton of type *R* in Table 1. Other hybrid types will be introduced later.

The table shows that hybrid plants of type *K* at Kelvin are intermediate between geographically neighboring races of the parental species in growth habit, joint characteristics, fruit shape, and fruit surface. These hybrids resemble *O. fulgida* in fruit color and *O. spinosior* in fruit attachment. The table also indicates that type *R* hybrids at Sacaton are very similar but not identical to type *K* hybrids at Kelvin. Some of the characters listed in the table are shown in Figure 3.

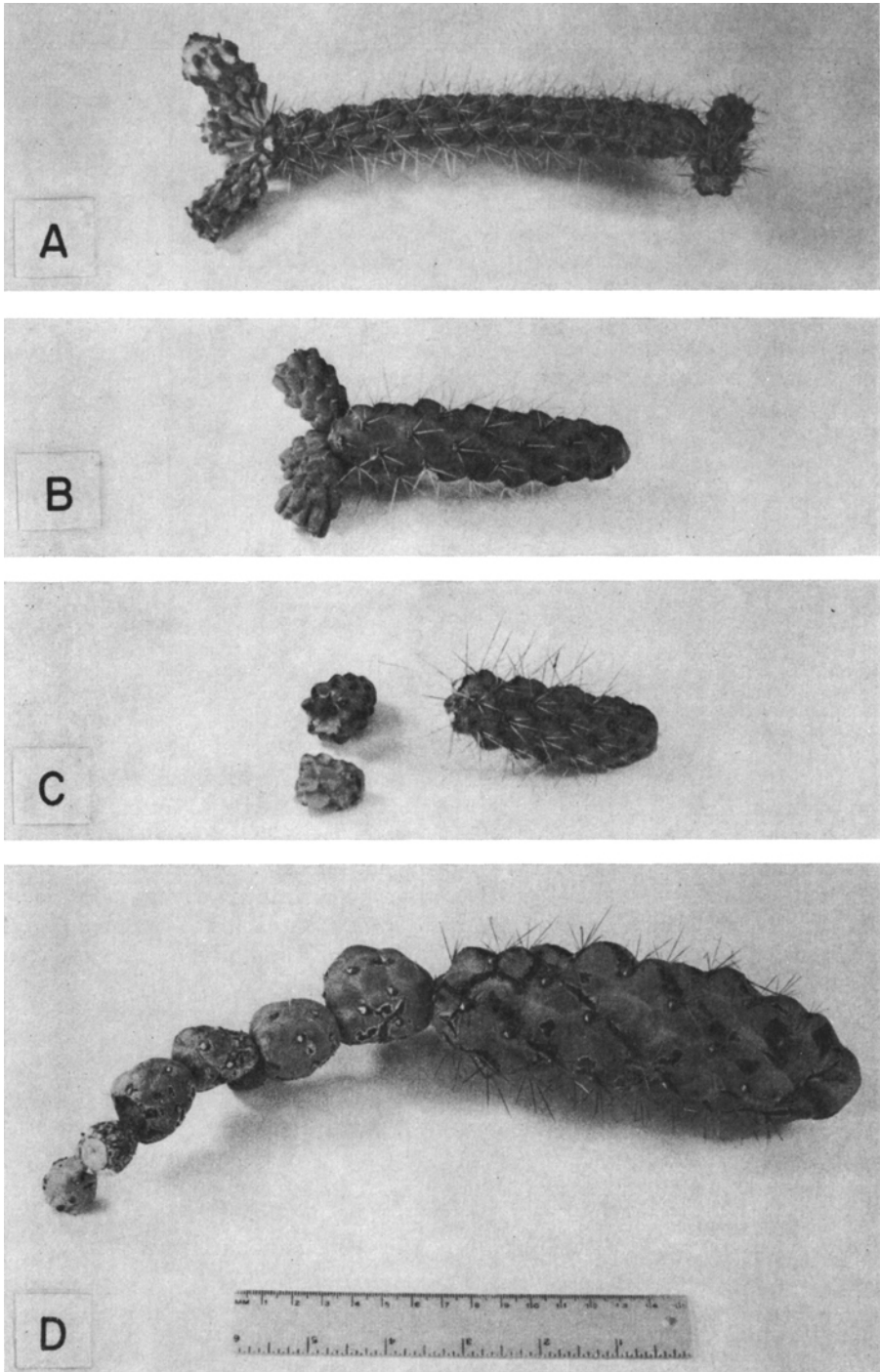


FIG. 3. Terminal stem joints and fruits of *Opuntia spinosior*, *O. fulgida*, and natural hybrids. (A) *O. spinosior*, Pinal Ranch. (B) Hybrid type R, Sacaton. (C) Hybrid type K, Kelvin. (D) *O. fulgida*, Superior. All to same scale.

TABLE 1. *Vegetative and fruit characters in Opuntia fulgida, O. spinosior, and their hybrids.*

Character	<i>O. fulgida</i> , Kelvin	Hybrid <i>K</i> , Kelvin	Hybrid <i>R</i> , Sacaton	<i>O. spinosior</i> , Pinal Ranch
Growth habit	large, tree-like, irregular branching with drooping branches	intermediate	intermediate	medium-sized, shrubby, branches in whorls
Terminal joint diameter	4.1 cm	2.6 cm	2.6 cm	2.0 cm
Terminal joint detachment	drop off freely	detach fairly easily	detach fairly easily	cling on
Tubercles, width at base	1.4 cm	0.9 cm	0.8 cm	0.4 cm
Spines, length of longest	2.4 cm	2.4 cm	2.1 cm	1.4 cm
Fruit shape	pear-shaped	olive-shaped	olive-shaped	cone-shaped to oblong
Fruit surface	smooth	moderately tuberculate	moderately tuberculate	strongly tuberculate
Fruit attachment	forms chains of 3 or more fruits, chains usually long and branched	single	single, or sometimes in short chains of 2 fruits	single or in whorls, but not in chains
Fruit color	green	green	green	yellow

The hybrid populations at Kelvin and Sacaton contain some other variants in addition to the types *K* and *R*. These have been labelled types *C*, *V* and *W* in the Kelvin area and types *S* and *T* in the Sacaton population. They are very similar morphologically to types *K* and *R*, and consequently are likewise intermediate between *O. fulgida* and *O. spinosior*, but they also differ somewhat from standard types *K* and *R*. The differences will be described briefly here.

In the Sacaton hybrid population, plants of type *S* are larger shrubs than type *R*, they have stouter main trunks, and bear longer chains of bigger fruits. There are four individuals of type *T* in the Sacaton population. These differ from *R* in having a reddish hue on the stem joints and fruits, in flowering early, and in lacking any tendency to form short chains of fruits. Type *S* differs from *R* in the direction of the *O. fulgida* parent and type *T* differs in the direction of *O. spinosior*.

In the Kelvin area, where type *K* plants preponderate, type *C* forms a small uniform colony. Type *C* differs from type *K* in having more irregular and compact branching, smaller flowers, and a tendency to form short chains of two or three fruits. These are variations in the direction of *O. fulgida*. Type *V* in this area is represented by a single known individual growing with type *K* hybrids downstream from Hayden. The *V* plant differs from type *K* in having a more loose open habit of branching, more slender stem joints, strongly tuberculate fruits, and yellow fruits. In these features it approaches *O. spinosior*.

Type *W* is abundant in the desert hills west and southwest of Kelvin. It differs from type *K* in growth habit, being smaller of stature, and in its fruits, which are cone-shaped and quite tuberculate. In these features it approaches the condition found in *O. spinosior*.

Five populations of *O. spinosior* rang-

ing from mountain to desert habitats were examined for pollen fertility and/or seed fertility. All populations had normal fertility, with 90% or more well-formed pollen grains and abundant sound seeds. Plants of *O. fulgida* from Superior showed 88 to 98% good pollen. Most fruits contain numerous fully plump or half plump seeds. Johnson (1918) has previously shown that some seeds in both size classes have abortive embryos. *O. fulgida* seems to be highly fertile as to pollen and semi-fertile as to seeds.

Four individual plants of hybrid type *K* from Kelvin and two individuals of hybrid type *R* from Sacaton were examined for pollen and seed fertility. The Kelvin plants had 5%, 7%, 12%, and 13% well-formed and well-stained pollen grains; and the Sacaton *R* plants had 8% and 18% well-formed pollen grains. Forty fruits from Kelvin *K* plants all had numerous abortive ovules in the central cavity; most of these fruits had no plump seeds; an occasional fruit had one plump seed. Among six fruits from Sacaton *R* plants, five had no plump seeds, and one fruit had one plump seed. Thus, both the Kelvin *K* plants and the Sacaton *R* plants are highly but not completely sterile.

In general, the other hybrid types are highly sterile but are somewhat more fertile as to pollen or seeds than types *R* and *K*. Thus the *C* plants at Kelvin have 21–22% well-formed pollen and 0–2 plump seeds per fruit. Plants of type *W* exhibited from 28 to 49% good pollen. In the Sacaton colony type *T* has 13–14% well-formed pollen and 0–8 plump seeds per fruit.

The interspecific hybrid constitution of the various types of plants at Kelvin and Sacaton described above is demonstrated by their morphological intermediacy and sterility considered jointly. The morphological intermediacy falls in the middle range and the sterility is greatest in types *K* and *R*, suggesting strongly that these types may well be F_1 hybrids. The plants belonging to types *C*, *V*, *W*, *S*, and *T*

deviate from *K* and *R* in the direction of one parental species or the other with respect to particular morphological characters. And, though fairly sterile, these other hybrid types are slightly more fertile than the putative F_1 types *K* and *R*. This suggests that these other types are later-generation segregation products derived from the original F_1 hybrids.

THE CLONAL MICROSPECIES

At Sacaton the type *R* hybrids are dispersed throughout an area one-quarter mile square. We counted 24 individual plants of type *R*; there may be a few more which we missed. Type *T* is represented by four identical individuals, standing 15–35 feet apart and forming a small clonal group on one edge of the quarter-mile square area.

Hybrid plants of type *K* are numerous and widespread over a fairly long distance along the Gila River in the vicinity of Kelvin. One subpopulation on a flat ridge near Kelvin proper is three miles long by one-half to one mile wide and includes an estimated 600 individual plants. On one transect through this subpopulation 100 individuals were inspected and observed to be essentially identical. A second subpopulation of *K* plants is strung out in the Gila River valley upstream from Kelvin for a distance of ten miles. A third subpopulation occurs downstream from Kelvin.

The *C* type hybrid plants occur in a disjunct and discrete colony on the Gila River a half-mile downstream from Kelvin. The colony numbers about 100 individuals. These are all alike.

The largest population is that composed of type *W* plants in the Tortilla Mts. west and south of Kelvin. The *W* plants are abundant over an area 20 miles long and 26 miles wide in these desert hills. There must be hundreds of thousands of type *W* individuals in this area.

There is a high degree of individual-to-individual uniformity within a given type of hybrid in both the Sacaton and Kelvin

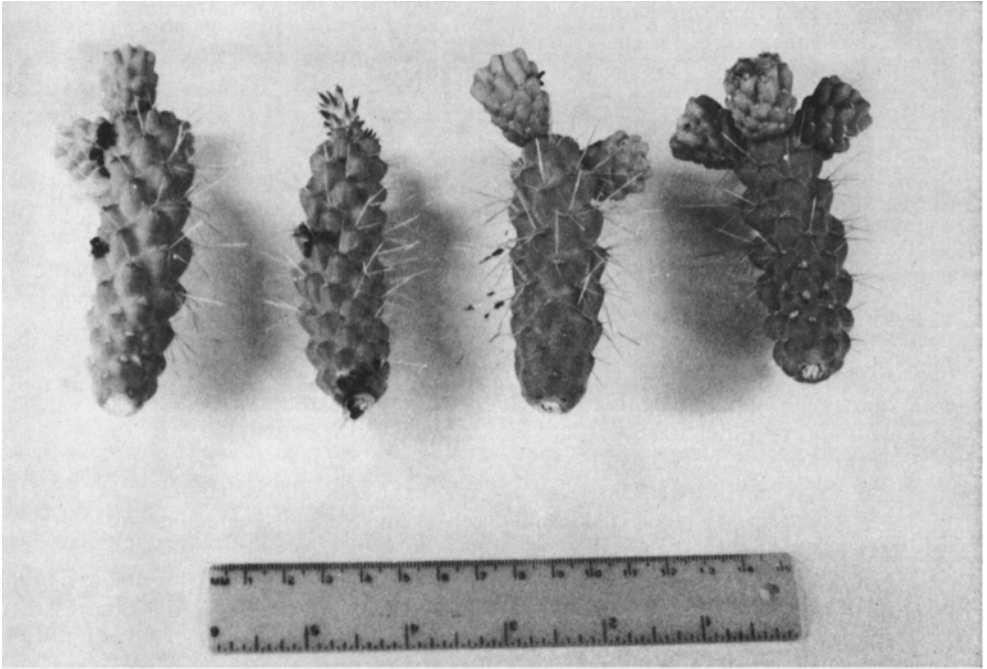


FIG. 4. Terminal stem joints and fruits from four sister individuals of hybrid type *R* at Sacaton.

areas (see Fig. 4). This indicates that these hybrid individuals have arisen not by sexual but by asexual means of reproduction. Vegetative propagation from stem joints is the obvious candidate in view of the known reproductive biology of the parental species. The Sacaton hybrids are all old plants and consequently do not furnish direct evidence for this mode of origin. However, direct evidence of vegetative propagation is available for the *K*, *C* and *W* types in the Kelvin area. Young plants of these hybrid types can be seen to be attached laterally at the soil surface to fallen stem joints or the remnants of decayed stem joints.

Some of the expected stages of population growth are well exemplified by the various hybrid types. We have a small clone consisting of four neighboring individuals in the case of hybrid type *T* at Sacaton. The type *R* hybrids at Sacaton and *C* hybrids at Kelvin are medium-sized clones. The type *K* hybrids, on the other hand comprise an endemic clonal micro-

species extending along the Gila River over a linear distance some 20 miles long. And the type *W* plants form a rather widespread clonal microspecies occupying an area of several hundred square miles in the Tortilla Mts.

DISCUSSION

A clonal complex is a hybrid complex, a taxonomically critical group of basic species and their hybrid derivatives, in which the hybrids reproduce mainly by vegetative means (Grant, 1953). As compared with other types of hybrid complexes—agamic, polyploid, etc.—clonal complexes are rather poorly known. Clonal complexes have been tentatively identified as such in the *O. phaeacantha* and *O. spinosior* groups (Grant, 1953, 1971). In no case, however, has a clonal complex been subjected to a thorough biosystematic and phylogenetic analysis. It is desirable to carry out this task in one or more plant groups in order to round out our picture of the patterns of plant evolution.

The taxonomic studies of Benson (1969a, 1969b, and in press) on western American cacti provide a good foundation on which to build in this direction. Pinkava (unpubl.) is currently investigating the complex *O. phaeacantha* group from the biosystematic standpoint.

The essential first step in the phylogenetic analysis of a clonal complex is to establish the hybrid constitution and parentage of at least one clonal microspecies. The work reported in the present paper accomplishes this first step. The clonal microspecies designated as Kelvin *K* consists of sterile, intermediate, vegetatively reproducing hybrids of *O. spinosior* and *O. fulgida*.

The *K* and *R* hybrids are highly but not completely sterile, retaining the capacity of producing some apparently good pollen and seeds. Evidently some sexual reproduction does take place in the F_1 hybrids so as to engender new later-generation segregates.

The plants belonging to types *C*, *V*, *W*, *S*, and *T* are probably later-generation segregation products derived from the original F_1 hybrids, for they approach one parental species or the other in particular morphological characters, and are slightly more fertile than the putative F_1 types *K* and *R*. The discrete clonal population *C* in the Kelvin area provides a concrete case of a later generation of hybrid derivatives which has apparently originated by segregation from the Kelvin *K* population, and which has multiplied vegetatively in a small local area. Clone *T* at Sacaton and microspecies *W* in the Tortilla Mts. have probably arisen independently by parallel processes of hybrid reproduction.

In the southern part of the Tortilla Mts., where *O. fulgida* and *O. spinosior* overlap in range, microspecies *W* is biotically sympatric with both parental species. In one locality in this area we found a hybrid swarm consisting of type *W* plants and their segregates and apparent backcrosses to *O. spinosior*. The sexual mode

of reproduction is going on here and is engendering a varied array of new hybrid types.

These cholla cacti exhibit an alternation of sexual and asexual processes in hybrid reproduction similar to the alternation which has long been recognized in agamosperous groups and in agamic complexes. This cycle of sexual and asexual reproduction is evidently a successful way of producing and then multiplying new adaptive hybrid types.

The next step in the analysis of a clonal complex will be to refine the analysis by the application of cytotaxonomic and chemotaxonomic methods. The subsequent steps are to extend the investigation to other related parental species and their hybrid products. *O. spinosior* apparently hybridizes with *O. versicolor* and *O. imbricata* (Benson, 1969a). Does this hybridization yield any clonal microspecies? *O. fulgida* exhibits some seed sterility and reproduces mainly by vegetative propagation. Is it a hybrid derivative of some preexisting species? The answers to these and numerous other specific questions will add up to an understanding of the clonal complex as a whole.

SUMMARY

This paper describes a case of vegetative multiplication of sterile interspecific hybrids in the cholla cacti. The parental species are *O. fulgida* and *O. spinosior* in south-central Arizona. Several types of hybrid products are found at two localities in this area.

Two of these types, which are morphologically intermediate in the middle range between the parental species, and highly but not completely sterile as to pollen and seeds, are identified as probable F_1 hybrids. The other hybrid types are identified on morphology and fertility as later-generation segregation products.

Direct evidence was obtained for the vegetative propagation of these hybrid types by means of the fallen stem-joints. One hybrid type has formed a clone of

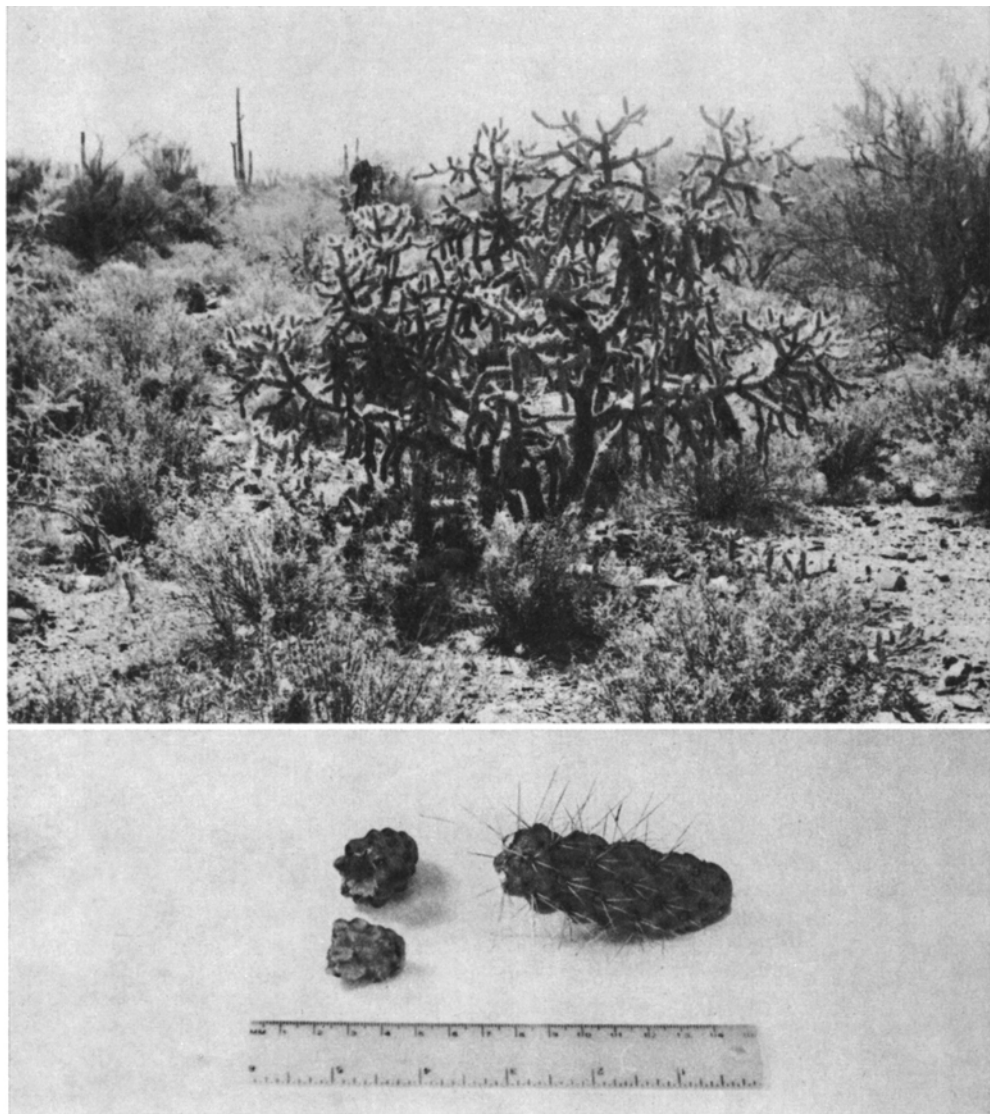


FIG. 5. *Opuntia kelvinensis*. A plant of type *K* from a low desert ridge above the Gila River near Kelvin, Arizona. Above, plant body; below, terminal stem joint and two fruits.

four identical individuals; another a clone of about 100 identical individuals; still another forms an endemic clonal microspecies; and one other clonal microspecies occurs in large numbers throughout an area of several hundred square miles.

The observed series of clones and microspecies exemplifies the expected but hitherto undocumented stages of growth

of clonal hybrid microspecies. Their development involves a cyclical alternation of sexual and asexual processes, as has been found previously in agamospermous microspecies, the only known difference being the method of asexual reproduction.

The results reported here have implications for formal taxonomy, which are taken up in the appendix.

APPENDIX: DESCRIPTION OF *Opuntia*
kelvinensis SP. NOV.

The needs and the categories of formal taxonomy are different from those of population biology. The minor phenomena of population biology do not necessarily warrant formal taxonomic recognition, but microspecies which form a distinctive element in the local flora, on the other hand, may warrant recognition as a taxonomic species. Where to draw the line is of course a matter of taxonomic judgment based on the premise that a taxonomic species is or should be a practically useful category.

The hybrid plants discussed in this paper do form a definite and recognizable element in the cactus flora of Arizona, and therefore we have concluded that it will serve a useful purpose in both southwestern floristics and cactus systematics to describe these plants as a taxonomic species. The description which follows is drawn up so as to include the various clones and clonal microspecies mentioned in this paper in one collective taxonomic entity. It is appropriate to describe the new taxonomic species here in conjunction with the publication of the biological details.

Opuntia kelvinensis, sp. nov. (Fig. 5)

Shrubs, 4-6 feet (1.2-1.8 meters) tall, 1-3 stems from base, much branched above. Terminal stem joints 6-10 cm long, 2.5-3.5 cm in diameter. Tubercles on terminal joints rounded and medium high, 1.2-1.8 cm long, 5-9 mm high, 6-10 mm wide at base, 4-5 rows of tubercles visible from one side of stem. Spines 4-8 in a group, with one long spine 1.7-2.5 cm long, one medium-long spine, and several short spines. Spines pale pinkish with deciduous sheaths. Flowers with bright pink or wine-colored perianth, yellow anthers, and yellow stigma. Perianth spreading, 5 cm in diameter. Flowering in May and June. Fruits ovoid to slightly cone-shaped, 2.5-3.5 cm long, green to yellowish-green, moderately tuberculate, with apical cavity present. Fruits borne singly or in whorls of 2 or 3 at tips of joints; not in chains, or occasionally in short chains of 2 or 3 fruits. Seed cavity at maturity containing numerous abortive ovules and occasionally one or a few plump seeds.

Frutex 1.2-1.8 m altus, ramis numerosis; caulis ad ultimum 6-10 cm longus 2.5-3.5 cm diametros, tuberosus; flos color puniceus 5 cm diametros; fructus ovoideus viridis tuberosus 2.5-3.5 cm longus, non in catenis; flos et fructus sterilis vel semisterilis.

Distinguishing characteristics.—Closely related to *O. spinosior* (Engelm.) Toumey and *O. fulgida* Engelm. from which derived as hybrid products. Differs from *O. spinosior* as follows: branching

irregular rather than whorled; terminal stem joints short and stout, instead of long and slender; tubercles moderately rounded, rather than sharply ridged; fruits green or greenish, rather than lemon-yellow; fruit wall moderately tuberculate rather than strongly so. Differs from *O. fulgida* as follows: small shrubs, instead of tall arborescent plants with large trunks; terminal stem joints much smaller in diameter than in *O. fulgida*; fruits not forming long chains; fruit wall moderately tuberculate instead of smooth; fruits having a prominent apical cavity instead of a shallow or no cavity.

Range.—Flat ridges and hill-tops in desert hills in the saguaro-paloverde zone at 1700-2100 feet elevation. Usually growing with *O. fulgida*, occasionally with *O. spinosior*. From Kelvin southeast to Kearney and beyond; and south and southwest of Kelvin in the desert foothills to the lower elevational limits mentioned above. A disjunct colony occurs in a low desert valley at 1270 feet elevation near Sacaton to the west of Kelvin. Pinal County, south-central Arizona.

Type.—V. Grant, collection no. 70-29, just southeast of Kelvin, Pinal County, Arizona, June 15, 1970. Herbarium, University of Texas, Austin.

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