

Flowering Phenology and Outcrossing in Tetraploid *Grindelia camporum* Greene

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Abstract

Several reproductive processes of tetraploid *Grindelia camporum* were investigated. This plant is a potential resin crop for the southwestern United States. Field observations of 100 flower heads from unopened buds through 100% achene dispersal were made. It was found that individual flower heads are available for pollination for approximately 5 days but all disc florets are open for only 1 day. On average, achenes mature in 22 days and are dispersed 53 days after flowering. Fourteen-hundred hand-pollinations were also made on plants from 6 wild populations of *G. camporum* grown in a greenhouse and shade house. Estimates of fertility and crossability of populations were made based on achene number and achene weight data from these crosses. All populations studied were interfertile and no evidence of outbreeding depression in between-population crosses was found. It is shown that tetraploid *G. camporum* is self-incompatible and requires manipulation for achene set.

Introduction

Economic Botany of *Grindelia camporum*.

Grindelia camporum Greene (Asteraceae) is a member of the widespread gumweed genus, which consists of 58 species distributed throughout western North America and much of South America. The 45 North American species range from the Pacific Coast to the Great Plains and from Alaska to Mexico (Steyermark, 1934).

Within *Grindelia* diploid ($2n=12$) and tetraploid ($2n=4x=24$) species have been found (Whitaker and Steyermark, 1935). Both ploidy levels are also found within a single species. Within *G. camporum*, ssp. *davyi* is diploid and ssp. *camporum* is tetraploid. Based on cytological analysis of interspecific hybrids, Dunford (1964) hypothesized that tetraploid *G. camporum* is an "auto-polyploid" which originated by hybridization of diploids similar to *G. procera* and *G. camporum* with subsequent chromosome doubling and diploidization. Dunford characterized this hybrid as autopolyploid because the genomes of the putative parents are nearly identical in chromosome morphology.

Tetraploid *G. camporum* is an herbaceous perennial. The vegetative phase of its life cycle is spent as a basal rosette of leaves. Figure 1A shows a *G. camporum* rosette beginning to bolt. Tetraploid *G. camporum* grown at Tucson, Arizona, bolts in its first year of growth; diploid *G. camporum* usually does not bolt until its second year. Bolting results in formation of erect, occasionally semi-woody, paniculately-branched stems, 0.5–1.5 m. tall. Figure 1B shows an experimental field plot of *G. camporum* at this stage. In the desert climate of southern Arizona where this study was conducted, flowering begins in May or June and continues through September or October. Figure 1C shows a small plant with flowers in various stages of development exemplifying the indeterminate flowering of *G. camporum*. The typical Asteraceae capitula are entomophilous. Figure 1D shows mature *G. camporum* in its reproductive stage. Once flowering is completed the stems die back and the plant overwinters as a perennial woody rootstock. In the warm days of spring, root crown buds develop and the bolting and flowering processes are repeated. The total life span of an individual is unknown.

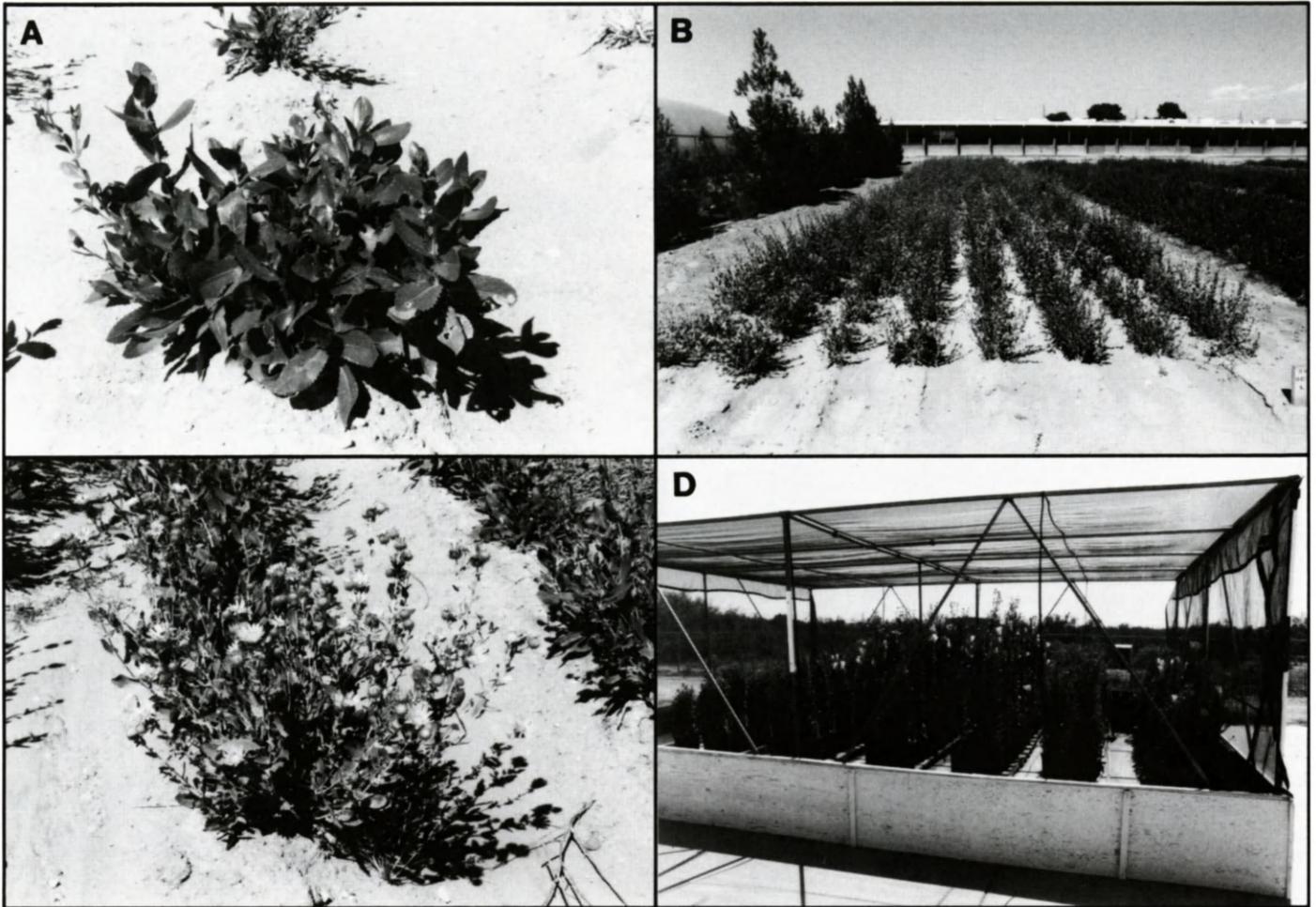


Figure 1. Growth habit of tetraploid *Grindelia camporum*. **A:** basal rosette starting to bolt; **B:** experimental field plot after bolting; **C:** small plant showing indeterminate growth habit; **D:** mature plants growing in shade house.

Throughout its life cycle *G. camporum* is covered with a layer of sticky resin. This resin arises from multicellular glands on the plant's surfaces. The highest concentration of these glands is on the involucre of the flower heads, with less on the leaves and even fewer on the stems (Hoffman and McLaughlin, 1986). *Grindelia* resin is obtained by cutting the plant above the woody base which is left to regrow. Many accessions regrow to produce 2 harvests per year. The bulk of the plant is dried and hammermilled. The resin can then be extracted with dichloromethane or other nonpolar solvents. Whole-plant crude resin yields are highest when *Grindelia* is harvested at peak flowering (Hoffman and McLaughlin, 1986).

Grindelia resin is composed of a mixture of labdane diterpene resin acids similar to those found in pine rosin. The major components of *Grindelia* resin are grindelic acid and its derivatives (Timmermann et al., 1983). These resin acids resemble abietic acid of pine rosin in both structure and physical properties. Hoffman (1983) and

Hoffman et al. (1984) suggest that *Grindelia* resin might substitute for pine rosin in the naval stores industry. Pine rosin is used in a variety of products including rubber and other chemicals, ester gums, synthetic resins, paper sizing, paints, varnishes and lacquers (Bratt, 1979). At the present time, domestic sources of high grade pine rosin are virtually nonexistent in the United States. Recovery of gum rosin (obtained by tapping living trees) is highly labor intensive and the supply of wood rosin from old pine stumps has been depleted (Hoffman and McLaughlin, 1986). For this reason, development of *Grindelia* as a resin crop would be a worthwhile endeavor.

Tetraploid *Grindelia camporum* has potential as a new crop for the arid regions of the Southwestern United States. *G. camporum* is indigenous to the drier areas of the Central Valley and foothills of the South Coast Ranges of California. Comparison of climate data for these regions to that for Tucson, Arizona (Table 1) suggests that the arid Tucson area might provide a favorable

environment for cultivation of *G. camporum*. Although Tucson is slightly warmer and gets more of its precipitation during the summer, its overall climate is comparable to that for the native habitats of *G. camporum*. Studies conducted at the University of Arizona Bioresources Research Facility (BRF) in Tucson confirm that tetraploid *G. camporum* grows well under cultivation in the deserts of the Southwest. Optimum yields of 12.5 tons ha⁻¹yr⁻¹ of biomass and 1180 kg ha⁻¹yr⁻¹ of crude resin were obtained from 2 harvests/yr with an average of only 66.7 cm of irrigation water (McLaughlin and Linker, 1987). Tetraploid *G. camporum* seems to fit the criteria for selecting new crops for arid regions as outlined by McLaughlin (1985): it grows well under arid conditions, provides a high-value chemical, and probably would not grow well in more humid regions where production costs would be lower. Hoffman and McLaughlin (1986) contend that successful development of *G. camporum* as a resin crop could bring as much as \$300 million or more into the economy of the Southwest.

The domestication of tetraploid *G. camporum* as a cash crop, however, will require improvement of resin yields through breeding. Most collections of tetraploid *G. camporum* yield approximately 10% crude resin. Under current economic conditions, *Grindelia* resin cannot compete with imported pine rosin. Hoffmann and McLaughlin (1986) estimate that breeding *G. camporum* to yield 15–20% crude resin in the aboveground biomass would lower production costs enough to make it economically competitive. Studies on mass selection and the heritabilities of characteristics contributing to resin yield have shown that an increase in resin yield of 5–10% of the aboveground dry weight is possible (McLaughlin, 1986a, 1986b).

Improvements in resin yield would most likely be made by selecting for high resin yield, good regrowth, and high biomass yield. Biomass yield is a function of both plant size and earliness since greater earliness allows for greater regrowth before a second harvest. Wild populations collected from throughout the range of tetraploid *Grindelia camporum* show highly significant variation in these and other traits (Table 2). No one population has all the desired traits so that recombination must be achieved through breeding.

Flower Morphology of *Grindelia camporum*.

Grindelia camporum capitula are typical of those found in members of the Astereae tribe. The flower head consists of many small, yellow florets surrounded by an involucre of bracts or phyllaries. The ligulate ray florets are pistillate; the tubular disc florets are hermaphroditic. The styles within the disc florets are surrounded by 5 stamens fused to form an anther column. The *G. camporum* fruit is an achene which is crowned by a pappus of 2–3 stout bristles. Figure 2 illustrates a *G. camporum* capitulum.

Objectives. Of importance to a successful breeding program for *G. camporum* is an understanding of its basic reproductive processes. This study was designed to provide insight into several of these processes. Description of the flowering phenology of *G. camporum* was undertaken to provide information which might be of use in improving pollination techniques. The intercrossability

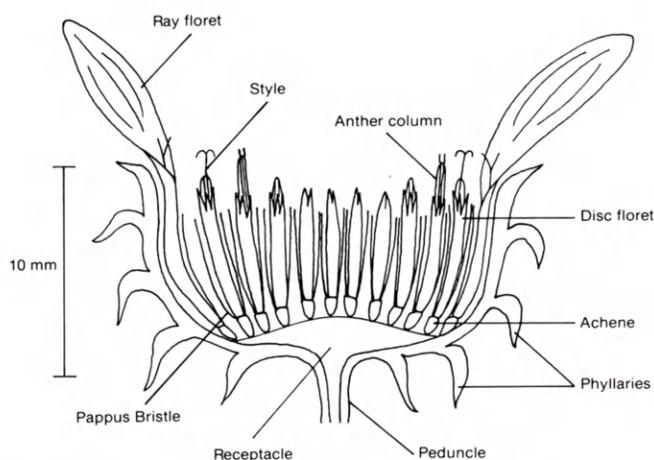


Figure 2. Flower morphology of *Grindelia camporum*.

Table 1. Climate data for selected stations within the natural and potential growing regions of *Grindelia camporum*.

Station	Mean Temperature (°C)		Precipitation (mm)		
	Jan.	July	Oct.–Mar.	Apr.–Sep.	Total
San Joaquin Valley					
Los Banos	9.5	26.6	174	32	206
Merced	7.8	26.9	232	47	279
Tracy	8.2	26.6	215	46	261
South Coast Ranges					
Paso Robles	8.9	21.9	359	43	402
Livermore	8.9	21.2	319	54	373
Sacramento Valley					
Galt	8.7	24.9	401	73	474
Colusa	7.3	25.0	346	56	402
Tucson	10.6	30.1	121	162	283

Table 2. Comparison of maturity dates, biomass yield, resin yield, and regrowth among populations of 4N *Grindelia camporum*.¹

Trait (units)	Population					
	2826	2832	2830	2831	2838	2840
Height (cm)	67.2	73.1	92.0	79.8	67.9	56.3
Peak flower date (mo./day)	8/04	8/05	8/30	8/31	8/04	8/05
Plant dry weight (gm)	275	306	430	341	289	378
Crude resin yield (%)	13.7	13.6	11.9	11.7	12.3	14.8
Post-harvest mortality (%)	28.3	19.1	15.2	20.0	6.2	60.4
Post-harvest rebolting (%)	87.9	97.6	69.2	32.4	97.8	47.7

¹Based on data given in McLaughlin (1986c).

of selected populations of *G. camporum* was also investigated to further improve breeding efficiency. Previous investigations of *G. camporum* (Dunford, 1962, 1964) suggest that it is a self-incompatible species. This study attempts to further document this self-incompatibility. The possibility of outbreeding depression occurring in *G. camporum* is also examined. Several investigators have found evidence that outbreeding depression may be expressed in crosses between isolated populations of the same species (Kruckeberg, 1957; Hughes and Vickery, 1974; Waser and Price, 1983).

Materials and Methods

Flowering Phenology. Phenological observations were made on 100 flower buds of tetraploid *Grindelia camporum* in 2 rows of an experimental field plot. Buds 5–8 mm in diameter were chosen at random and tagged.

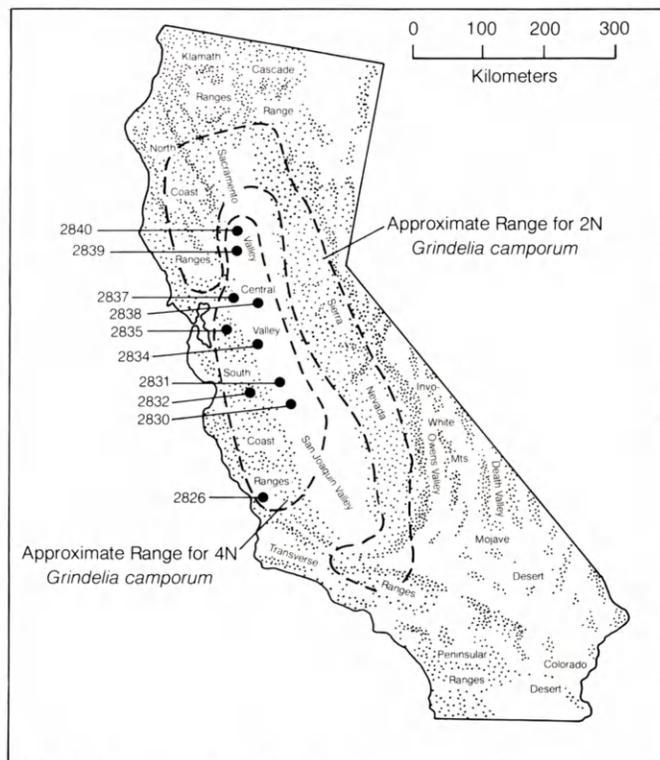


Figure 3. Locations of *Grindelia camporum* populations in California.

The experimental field plot was located at the University of Arizona's Bioresources Research Facility (BRF) in Tucson, Arizona. This plot was made up of 2 half-sib families from 2 plants of seed lot A-121. The A-121 seed lot originated from tetraploid *G. camporum* achenes collected by S. P. McLaughlin near Vernalis in San Joaquin County (2389) and just north of Firebaugh in Fresno County (2390), both San Joaquin Valley localities in California.

Description of the flowering phenology of tetraploid *G. camporum* is based on observation of the development of flowers from unopened buds to 100% achene dispersal. Flowering stages that could be easily distinguished were determined from preliminary greenhouse observations. The stages were as follows: (1) disc visible; (2) ray corollas emerging; (3) ray corollas beginning to unroll (ray corollas unroll laterally rather than uncurling from base to tip); (4) first disc florets open; (5) approximately half of disc florets open; (6) all disc florets open; (7) flowering complete; (8) involucre brown (first mature achenes); (9) 100% achene dispersal. The dates at which flower heads were first observed in a particular stage were recorded. Phenology data were collected every Monday, Wednesday and Friday morning from May through September. By late September all achenes had been dispersed.

Crossing studies. Crossing studies were conducted by hand-pollinating plants grown from the achenes of 6 wild populations of tetraploid *Grindelia camporum*. These accessions collected in California by S. P. McLaughlin, are: 2826 and 2832 (South Coast Ranges); 2380 and 2831 (San Joaquin Valley); 2838 and 2840 (Sacramento Valley). Approximate locations of these populations are shown in Figure 3. These plants were confirmed as tetraploid by cytological examination of root tip cells.

Achenes from the 6 populations were planted in flats

in the greenhouse. Five families within each population and 8 individual plants per family were selected at the seedling stage for a total of 240 plants. Seedlings were then transplanted into 5 gallon pots. Four plants in each family were grown in a shade house (Figure 4A) and the other 4 in a greenhouse (Figure 4B). The shade house consisted of a permanent metal frame covered with shade cloth that provided approximately 47% shade (Figure 4D). It was designed to keep potential insect-pollinators away from the plants. The greenhouse and shade house were also sprayed occasionally with malathion for pest control and to further protect against insect-pollinators.

Six different pollination treatments were applied to each plant in this study. One flower head per plant was bagged just prior to anthesis without pollination. A second flower head was self-pollinated by rubbing pollen from another flower head of the same plant onto it. A third flower head on each plant was pollinated using pollen from a plant in the same family (sib-pollination). A fourth flower head on each plant was pollinated with pollen from a plant within the same population but outside the family. Fifth and sixth flower heads were pollinated using flower heads from outside the population; one from within the same region (for example, 2826 X 2832 which are both from the South Coast Ranges) and one from outside the region.

Emasculation of *G. camporum* flowers is not possible. The hermaphroditic disc florets are small and are covered with a layer of sticky resin until they open. The stigmas also emerge from the anther columns already covered with pollen. The small percentage of achenes resulting from self-pollen during crossing can be deduced by comparison with self-pollinations actually made on the same plant.

All of the hand-pollinations were conducted as capitula at the right stage became available. Capitula were considered ready to use for pollinating when all or as many florets as possible had opened, and the stigmas had protruded from the anther columns. Immediately after pollination the flower heads were bagged in glassine bags labeled with cross number and date (Figure 4C). A total of approximately 1440 hand-pollinations were made and the achenes resulting from them were harvested six weeks after pollination. Achene numbers and average achene weights were determined for each pollination.

Nested analysis of variance (families nested within populations) was used to examine differences in achene numbers and achene weights produced by populations used as seed parent and pollen parent. One-way analysis of variance was used to evaluate the fertility and achene weights of different pollination and outcross types. The greenhouse and shade house served as 2 blocks in the statistical analyses.

Results and Observations

Flowering Phenology. The capitula of tetraploid *Grindelia camporum* require from 49–112 days to mature from 5–8 mm buds to 100% achene dispersal at Tucson, Arizona. The flowering process begins with the appearance of tiny flower buds at the terminal and axillary nodes after bolting. The buds enlarge slowly. A 5–8 mm bud takes an average of 16.3 days to open just enough for the disc florets to be visible within the involucre. At this point the involucre is green and spherical, and covered with a thin layer of sticky resin. The opening in the in-

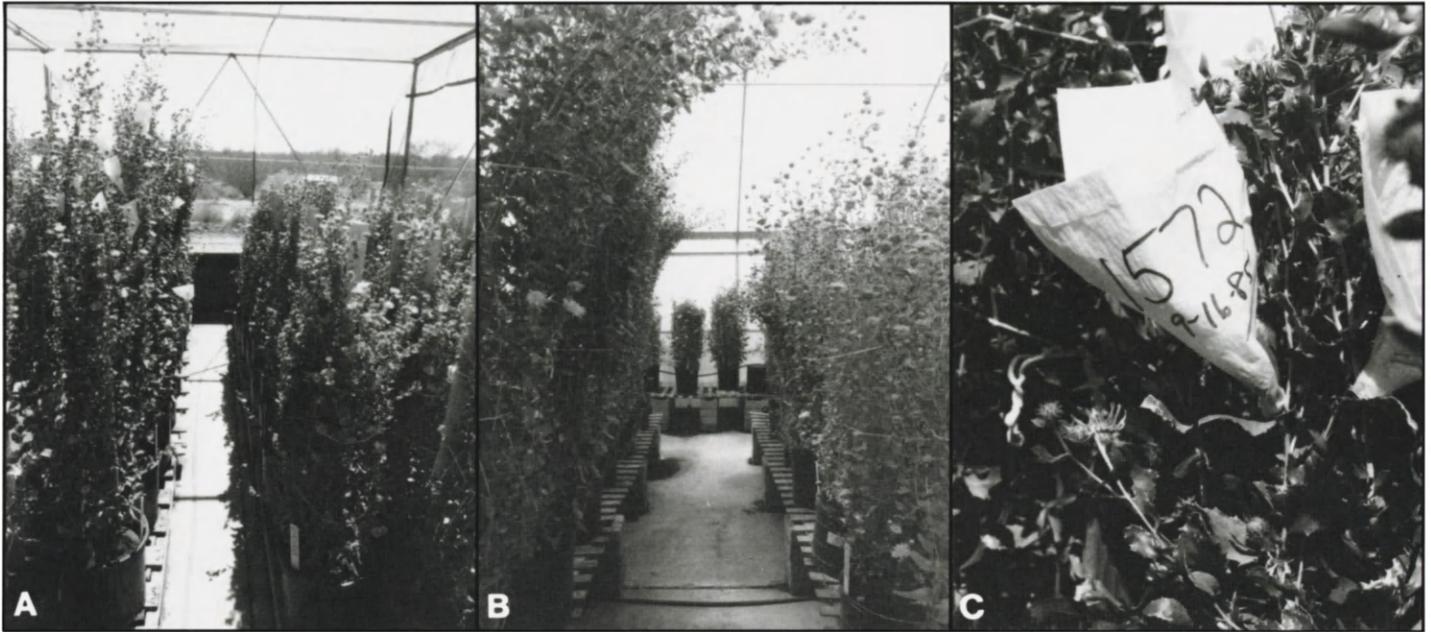


Figure 4. *Grindelia camporum* grown for hand-pollination studies. **A:** shade house plants; **B:** greenhouse plants [note the extreme height of greenhouse plants as compared to shade house plants]; **C:** bagged flower head after hand-pollination.

volucre may also be filled with a large amount of milky resin (see Figure 5A). The disc florets tend to be greenish at this point.

Once the disc is visible, flowering events occur more rapidly. The involucre continues to open revealing the spiral files of unopened disc florets. After about 3.4 days, the ray florets begin to emerge from the periphery of the receptacle. A single whorl of approximately 30 ray florets encircles the disc. The ray corolla remains tightly rolled around the ray style and is covered with a thin layer of resin (Figure 5B). By this time the disc florets have also started to turn yellow. Within approximately 1.8 days the ray corollas reach their full length and start to unroll. This lateral unrolling exposes the ray stigma and style. The inner surface of the ray corollas does not appear to be resinous.

On average, the outermost disc florets open on the same day as the ray corollas unroll, with a mean of 0.2 days between them. Only a few disc florets at a time may open or the entire outer rank or more may open the first day (Figure 5C). Opening of the disc florets nearly always begins with the outermost florets and progresses centripetally. Soon after the disc corolla opens the style surrounded by the anther column emerges from the floret. The stigmas protrude from the anther column covered dorsally with pollen. The 2 stigmatic lobes split and open to expose their receptive inner surfaces sometime later. Some never seem to split open and may require triggering by insect- or hand-pollination. After an average of 2.3 additional days approximately half of the disc florets have opened. The unopened florets may still be covered with a thin layer of resin. All of the remaining disc florets open in approximately 0.9 more days. Figure 5D shows a flower head before the last few disc florets have opened.

Flowering was considered complete when all of the styles had protruded and the ray corollas had started to wilt. This occurred in an average of 1.4 days after all the disc florets had opened or approximately 4.6 days after

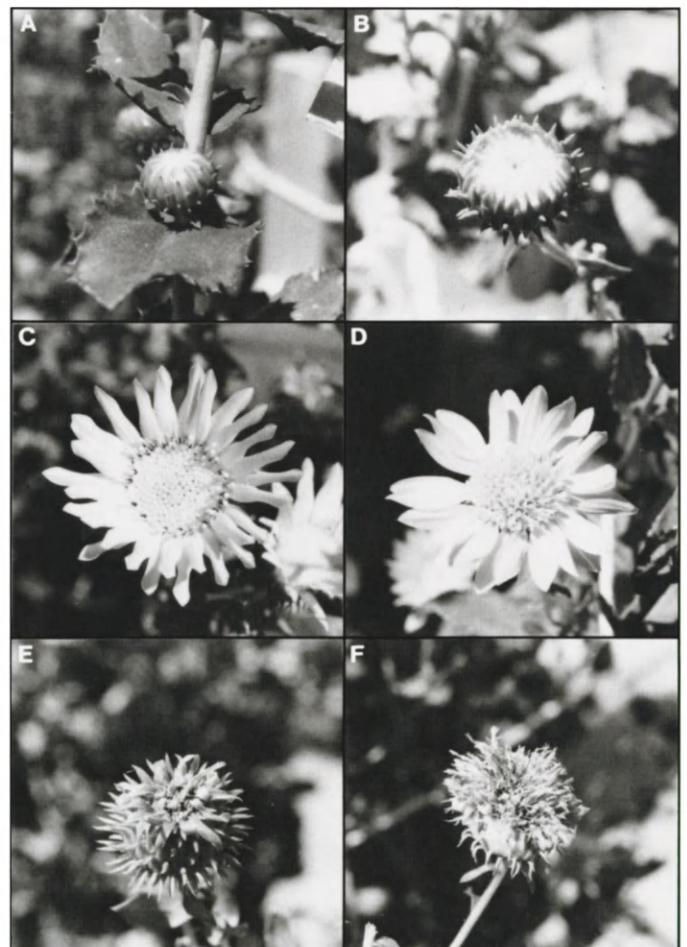


Figure 5. Flowering stages of *Grindelia camporum*. **A:** involucre opening filled with resin; **B:** ray florets beginning to emerge; **C:** first disc florets open [note resin on unopened florets]; **D:** nearly all disc florets open, stigmas covered with pollen; **E:** involucre closing around dry florets, ray corolla wilted; **F:** brown involucre starting to shatter.

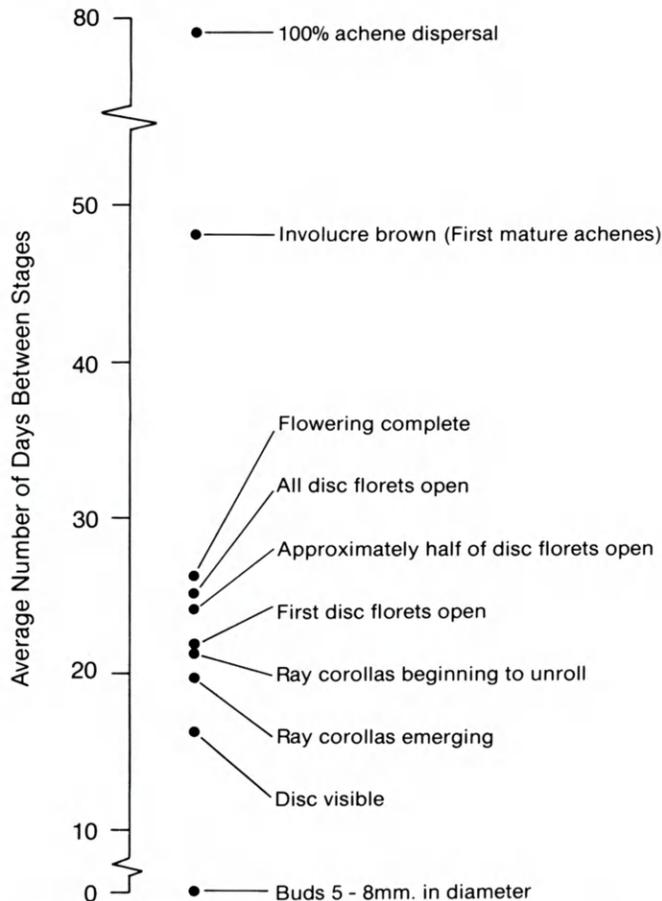


Figure 6. Average number of days between flowering stages in *Grindelia camporum*.

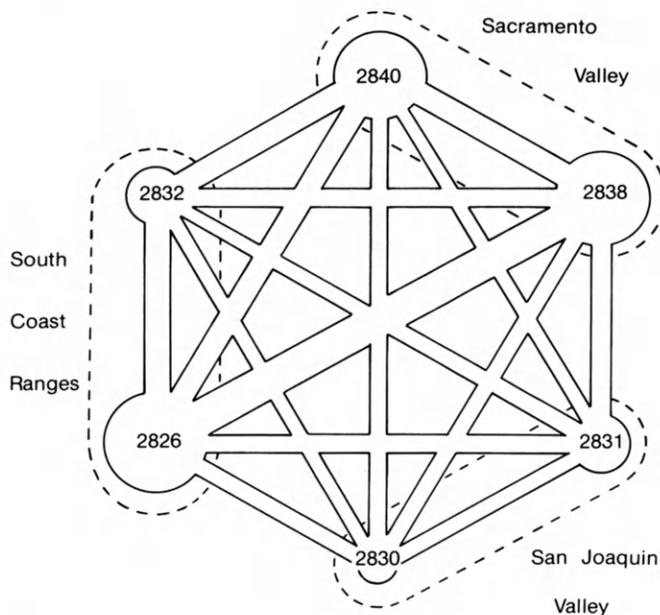


Figure 7. Crossing polygon of achene number for outcross types. Width of line is proportional to the number of achenes produced by between-population crosses; diameter of circles is proportional to number of achenes produced by within-population crosses.

anthesis. As the ray corollas wilt and turn brown the styles also dry and seem to recede back into the florets. In some plants the ray styles and outer disc styles may recede before all of the central disc florets have opened. It is probable that in at least some cases, this is due to pollination by insects. Further evidence of this is provided by the fact that in a greenhouse protected from insects, flower heads last several days with all their styles protruding.

After flowering is completed the involucre starts to close around the drying florets. The ray corollas continue to wilt and dry (Figure 5E). Eventually the involucre dries and turns brown. This takes an average of 21.9 days after flowering is complete. At this point the first achenes have matured within the involucre. The involucre does not reopen allowing achene dispersal until sometime later. The majority of achenes are dispersed by gravity because the pappus of *Grindelia*, which consists of short, usually curled, deciduous bristles, is not useful for animal or wind dispersal. The time for dispersal varies greatly with the plant and weather conditions. As might be expected, high winds and rain tend to facilitate achene dispersal. The plants in this study averaged 30.9 days from involucre browning to 100% achene dispersal. Figure 5F shows a dry involucre beginning to shatter.

A summary of the flowering process is presented in Figure 6. Approximately 80 days elapse between buds 5–8 mm in diameter and 100% achene dispersal. Individual flower heads can be pollinated for about 5 days but individual disc florets are open only for an average of 1 day. Achenes are completely dispersed an average of 53 days after flowering.

Crossing studies. Data on achene number and achene weight from pollinations on tetraploid *Grindelia camporum* were analyzed in several different ways. First, the data were grouped by 5 pollination types: none (bagged without pollination), selfed, sibs, outcrosses within a population and outcrosses between populations (includes within a region and outside the region). Table 3 gives the average achene number and weight for each pollination type. The bagged (none), selfed, sib and outcross types are all significantly different in terms of achene number. Only a few achenes are set without hand manipulation (an average of 2.5 achenes for bagged flowers). Nearly 4 times as many achenes result when plants are selfed by rubbing flowers from the same plant together. Approximately 3 times as many achenes develop in sibmatings and more than 4 times as many in outcrosses as compared with selfs. Achene numbers for crosses within a population and outside the population do not differ significantly. Mean achene weight is slightly but significantly greater for selfed plants than for all other pollination types. Analysis of variance for achene number and achene weights for pollination types showed that the block effects were significant ($p < .05$ and $p < .001$, respectively). On average, plants grown in the shade house produced more and heavier achenes than those from the greenhouse. The mean achene numbers for the shade house and greenhouse were 30.3 and 26.1, respectively. The mean achene weights for the shade house and greenhouse were 2.46 and 2.33 mg, respectively.

Analysis of achene number and achene weight were also made by grouping the data according to the popu-

Table 3. Average achene number and achene weight for pollination types. Means within a column not followed by same letter are significantly different ($p < .05$) as determined by Duncan's Multiple Range Test. Sample sizes for achene-weight data include only heads producing mature seed.

Pollination Type	Mean no. Achene/head	Sample size (no. heads)	Mean achene weight (mg)	Sample size (no. heads)
None	2.5d	235	2.42b	49
Self	9.7c	234	2.67a	164
Sib	29.6b	234	2.40b	187
Within-population	43.5a	234	2.35b	205
Between-populations	42.1a	463	2.33b	395

lation used as the seed and pollen parent in between-population crosses. The results of these analyses are given in Tables 4 and 5. The average achene number and achene weight were not significantly different for any of the populations used as seed parent (Table 4). A nested analysis of variance showed that although the blocks and populations did not differ significantly, the variation between families within populations was highly significant for both achene number and achene weight ($p < .001$).

The results of the analysis made by grouping the data by population used as pollen parent in between-population crosses is summarized in Table 5. The population used as pollen parent did not significantly affect achene number. The nested analysis of variance showed that neither blocks nor families within populations were significant for achene number. It was found, however, that the average achene weight when population 2830 was used for pollen was significantly less than that for all other populations except 2832 (Table 5). The blocks and families within populations were not significant for achene weight.

Data for achene number and achene weight were also analyzed by outcross type. For this analysis all crosses between the same two populations were grouped together. For example, crosses between 2826 and 2832 were designated as one type and crosses between 2826 and 2830 were designated as another type. Reciprocal crosses were thus placed in the same group. Within-population crosses excluding selfs and sibs were also included for a total of 21 different outcross types.

Table 6 shows that there are significant differences in the number of achenes produced by these outcross types. The crossing polygon in Figure 7 shows that in almost all cases, crosses involving 2830 and 2831 do not produce as many achenes as other crosses. Crosses of 2826 X 2838 produced the most achenes. Other combinations of 2826, 2832, 2838 and 2840 produced intermediate number of achenes except 2832 X 2838 which produced fewer achenes. Many achenes resulted from within-population outcrosses for populations 2826, 2838 and 2840. Within-population outcrosses for 2831 and 2832 resulted in fewer achenes than other populations except 2830 X 2830 which produced the fewest number of achenes. In general, the populations that produced many achenes in within-population crosses also produced many achenes in between-population crosses.

The mean achene weights for the various outcrosses are given in Table 7. There are also significant differences between the achene weights produced by certain outcrosses. In general, crosses with populations 2826, 2838 and 2840 resulted in the heaviest achenes. Crosses in-

Table 4. Average achene number and achene weight for populations as seed parent. Means within a column not followed by same letter are significantly different ($p < .05$) as determined by Duncan's Multiple Range Test. Sample sizes for achene-weight data include only heads producing mature seed.

Population	Mean no. Achenes/head	Sample size (no. heads)	Mean achene weight (mg)	Sample size (no. heads)
2826	58.9a	76	2.28a	69
2832	39.2a	78	2.08a	61
2830	25.8a	77	2.27a	66
2831	32.5a	76	2.11a	65
2838	45.4a	78	2.78a	63
2840	50.9a	78	2.49a	68

Table 5. Average achene number and achene weight for populations as pollen parent. Means within a column not followed by same letter are significantly different ($p < .05$) as determined by Duncan's Multiple Range Test. Sample sizes for achene-weight data include only heads producing mature seed.

Population	Mean no. Achenes/head	Sample size (no. heads)	Mean achene weight (mg)	Sample size (no. heads)
2826	38.4a	77	2.39a	63
2832	49.7a	78	2.30ab	69
2830	36.8a	76	2.08ba	62
2831	31.5a	76	2.42a	62
2838	53.1a	77	2.36a	69
2840	42.9a	79	2.44a	67

Table 6. Average achene number for outcross types. Means within a column not followed by same letter are significantly different ($p < .05$) as determined by Duncan's Multiple Range Test.

Outcross type	Sample size (no. heads)	Mean no. achenes/head
2826 X 2838	18	71.5a
2838 X 2838	39	62.2ab
2826 X 2826	39	61.0ab
2838 X 2840	77	52.8abc
2826 X 2832	79	51.8abc
2832 X 2840	19	49.0abc
2826 X 2840	20	47.4abcd
2840 X 2840	39	47.0abcd
2832 X 2838	20	39.9bcd
2832 X 2832	38	38.2bcd
2831 X 2838	20	37.8bcd
2826 X 2831	18	37.1bcd
2830 X 2840	20	35.5bcd
2832 X 2831	19	32.2cd
2831 X 2831	40	32.1cd
2832 X 2830	20	32.0cd
2830 X 2838	19	31.1cd
2826 X 2830	19	30.5cd
2830 X 2831	75	30.2cd
2831 X 2840	20	28.4cd
2830 X 2830	39	20.8c

Table 7. Average achene weight for outcross types. Means within a column not followed by same letter are significantly different ($p < .05$) as determined by Duncan's Multiple Range Test.

Outcross type	Sample size (no. heads)	Mean weight (mg.)
2840 X 2840	34	2.74a
2838 X 2838	35	2.71ab
2826 X 2838	17	2.69abc
2838 X 2840	69	2.66abc
2826 X 2831	15	2.58abcd
2832 X 2838	16	2.53abcde
2826 X 2840	18	2.44abcdef
2826 X 2830	16	2.43abcdef
2832 X 2831	17	2.36abcdef
2831 X 2838	14	2.36abcdef
2826 X 2826	37	2.32abcdef
2831 X 2840	16	2.26bcdef
2830 X 2838	15	2.22cdef
2830 X 2840	16	2.21cdef
2830 X 2831	65	2.14def
2832 X 2840	15	2.14def
2826 X 2832	67	2.12def
2832 X 2832	31	2.11ef
2831 X 2831	37	2.10ef
2830 X 2830	31	2.08ef
2832 X 2830	16	2.03f

cluding 2831 and 2832 produced intermediate achene weights and crosses including 2830 tended to produce the lightest achenes. Analysis of variance for outcross type showed no significant differences between blocks in achene numbers or achene weights.

Discussion

The reproductive processes of tetraploid *Grindelia camporum* enhance gene flow between individuals and populations and thus maintain variability within the species. Variability is important to the evolution of organisms because it allows the species to persist in a range of environmental conditions. It thus assures maintenance of a population in the face of changes which might wipe out a uniform, specialized population. Variability is especially important for a colonizing species such as *Grindelia*, for establishment in new environments.

Self-incompatibility is one way that variability has been maintained in *Grindelia camporum*. Dunford (1962) suggested that *Grindelia* populations including *G. camporum* are self-incompatible based on achene set of 346 flower heads bagged without pollination. Only 121 flower heads produced achenes with an average of 2.1 achenes per head in those. Results from this study (Table 3) provide substantial evidence for self-incompatibility in *G. camporum*. The fertility of self-pollinations was considerably reduced below that of cross-pollinations in 1400 pollinations. In most cases no achenes were produced without pollination or by self-pollination, but in several cases a few achenes were produced and in a few cases many achenes were produced. The latter cases may have resulted from pollination by an occasional insect that penetrated the greenhouse or shade house, or by other experimental error. The intermediate fertility of sib-matings between that of selfs and outcrosses also supports the contention that *G. camporum* is a self-incompatible species. Lewis (1979) theorizes that the advantage of self-incompatibility systems is that they protect against sib-matings which tend to reduce the heterozygosity (variability) of a population in a manner similar to selfing but at a slower rate.

Although this study was not designed to determine the genetics involved in the self-incompatibility system of *G. camporum*, certain suggestions can be made from other studies. It is most probable that a homomorphic, sporophytic self-incompatibility system is operational in *G. camporum* since all other members of the Asteraceae family studied to date exhibit this type of system. These Asteraceae self-incompatibility systems involve 1 gene with multiple alleles (Lewis, 1979). Willson (1983) notes that in general, the more alleles involved, the less effective the self-incompatibility system will be in reducing sib-matings. In *G. camporum*, there probably is a moderate number of alleles involved since sibs produced approximately 75% the achenes of outcrosses. Apparently tetraploidy does not break down self-incompatibility in sporophytic systems as it frequently does in gametophytic systems (Frankel and Galun, 1977; Lewis, 1979). This further suggests that tetraploid *G. camporum* exhibits sporophytic self-incompatibility. Since sporophytic systems with multiple alleles and hierarchical dominance

relations between alleles are complex, an extensive genetic study would be required to further characterize the self-incompatibility system in a tetraploid *G. camporum*.

Additional deductions can be made based on examination of the data in Table 3. Selfed flower heads produced significantly more achenes than unpollinated flower heads which indicates that some sort of manipulation is required for achene set. It may be that hand- or insect-pollination triggers opening of the stigmatic lobes to expose the receptive inner surfaces or that manipulation facilitates distribution of pollen on these receptive surfaces, or both. It should also be noted that even for outcrosses only an average of 42–43 achenes were set out of a potential of approximately 250 achenes. The reason for this may be that insect-pollination is much more efficient than hand-pollination because it does not damage the stigmas and because several visits are made during the receptive period of each flower head. It is also possible that achene numbers were reduced because all the stigmas on the flower head are not receptive at the same time and hand-pollinations were made only once. Or, there may be some cross-incompatibility expressed, but this is likely only if few alleles are involved in the S-gene of *G. camporum*.

Data from Table 3 also indicate that outbreeding depression is not expressed in crosses between populations of *G. camporum*. It was thought that *G. camporum* might show outbreeding depression based on findings of several investigators that outbreeding depression is often expressed in crosses between disjunct populations within a species (Kruckeberg, 1957; Hughes and Vickery, 1974; Waser and Price, 1983). This expression of outbreeding depression is often attributed to dissimilarity between mates of isolated populations due to their genetic divergence and adaptation to local environments. Kruckeberg (1957) and Waser and Price (1983) correlate the degree of genetic divergence and thus outbreeding depression with the physical distance between parents of a cross. McLaughlin (1986c) found considerable divergence between the 6 populations of *G. camporum* used in this study based on measurements of 17 phenological, physiological and morphological traits. Since these *G. camporum* populations are small, isolated, and show significant differentiation it might be expected that outbreeding depression would be expressed in between-population crosses. This was not the case, however, since there was no observed reduction in the fertility of between-population crosses as compared with within-population crosses. *G. camporum* seems to conform to the more common trend among plants of no relation between fertility and the distance between parental strains within a species (Kruckeberg, 1957).

Interpretation of the achene number and achene weights produced by crosses between different combinations of populations in *G. camporum* suggest analogy to the "general" and "specific combining ability" concepts used in development of hybrid corn. General combining ability refers to the ability of an inbred to cross with an open-pollinated variety, and gives a general measure of its performance as a parent in the production of hybrids (Briggs and Knowles, 1967). For this study, any trends in

the fertility or achene weights produced by a population in combination with all other populations may give an idea of its "general combining ability." For example, results for achene number produced by outcrosses including 2830 (see Table 6) might suggest that the "general combining ability" of 2830 is relatively poor. All of the crosses which include 2830 are in the lower half of the fertility range for outcrosses. Trends may be noted for other populations as well (Figure 7). Assessment of "general combining ability" for some populations might prove difficult since there are no clear separations in fertility for those populations. For example, population 2840 which is involved in crosses spread throughout the range of fertility. Evaluation of the fertility of specific outcrosses might be of more use to a plant breeder. This would be analogous to evaluation of inbreds for "specific combining ability" or the ability to combine in specific single, three-way or double crosses (Briggs and Knowles, 1967). For the example above, we see that even though population 2830 has poor "general combining ability," the fertility of the specific cross 2830 X 2840 is not significantly less than that for any of the outcrosses above it in Table 6, except 2826 X 2838. Population 2840 may somehow complement population 2830 to improve achene production. Similar interpretations can be made for the weight of achenes produced by different outcross combinations.

Further examination of outcross data suggests that gene flow is not restricted between geographically isolated populations of tetraploid *G. camporum*. Achenes are produced for every outcross type so all of these populations are interfertile. Dunford (1962) found no apparent structural differences in chromosomes of tetraploid *Grindelia* varieties collected from the same regions as populations in this study. He also found high fertility in tetraploid X tetraploid hybrids of *Grindelia* species and suggests that barriers to gene exchange between tetraploid varieties in nature may be geographical and ecological rather than genetic. Phenological observations of tetraploid *G. camporum* revealed that individual flower heads are only available for pollination for approximately 5 days under normal conditions. This should not hinder gene flow between populations, however, since *Grindelia* had indeterminate flowering and a long flowering season. There should be plenty of overlap in flowering of populations, even with locally-adapted seasonal variation, to allow gene exchange between populations.

Achene number and achene weight are used in this study as measures of the reproductive success of various types of crosses. It is possible that the seeds produced by these crosses vary in their viability, and that the F1 plants would vary in their fertility. Following these crosses for an additional generation might well reveal evidence of reproductive isolation between the populations examined. Seeds of several of the outcrosses are being grown out to evaluate the combining ability of the populations with regard to their economic traits (Table 2), but we lack the time and resources to grow out a complete set of plants from all the crosses made.

Variability between populations in their relative reproductive success (Tables 4, 5) is obscured by variation between families within populations. More conclusive re-

sults might have been obtained by growing out fewer populations with more families per population.

Evidence from this study and others suggest that recombination of economically important traits in tetraploid *G. camporum* is possible through breeding. The interfertility of *G. camporum* populations, lack of outbreeding depression and indeterminate flowering in *G. camporum* should facilitate gene exchange between populations. The high variability within families of *G. camporum*, in part due to self-incompatibility, provides a wide genetic base from which to select desirable traits for breeding. McLaughlin (1986a) also found highly significant heritabilities for traits contributing to resin yield in San Joaquin Valley populations which further implies that breeding for improvement of these economic traits can be achieved. Mass selection studies conducted at the University of Arizona have improved crude resin yields 0.8%/yr, but family selection probably would be more cost effective and efficient for this particular species (McLaughlin, 1986b).

This study provides practical information that will be of use in breeding tetraploid *G. camporum*. There were no significant differences between the 2 blocks (greenhouse and shade house) used in this study except in the analysis for pollination type. Though the differences between blocks were significant for pollination type they were relatively small. In all other cases there were no statistical differences between the greenhouse and shade house suggesting that both were equally effective in preventing insect-pollination and providing a suitable environment for growth of *G. camporum*. A shade house or similar structure might prove most efficient for pollination. *G. camporum* plants grown in a greenhouse tend to become very etiolated making hand-pollinations difficult (see Figure 4B). This study also suggests that mechanical harvesting of seeds 3 to 4 weeks after peak flowering would give maximum yields. However, since flowering in this plant is indeterminate, and since the flower heads shatter after reaching maturity, mechanical harvest of this plant for seed would not be particularly efficient at any time. The plant would be harvested for resin yield at peak flower stage; seed harvests would only be needed from breeding plots. Since relatively small acreages of *G. camporum* could meet the demands for rosin products (Hoffmann and McLaughlin, 1986), and since the plant is perennial, large seed-production plots would not have to be grown. Hand harvests of seed from breeding and seed-increase plots would probably be feasible.

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Arid Land Plant Resource Impact— Betterment of the Quality of Life for Desert Dwellers: Results of a 60-year Public-Private Partnership in Environmental Horticulture and Conservation in Central Arizona

**(Continued
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The Arboretum has long interdigitated with the University of Arizona. In harmony with the idea that produced the non-profit corporation act, the first administrators and scientists of the Arboretum (who were U. of A. Faculty) had to resign from their state salaries to be paid by the Arboretum directly. But although resigning as an employee of the University, the Arboretum's first Director was appointed a regent of the University and Arboretum-University cooperation actually intensified rather than diminished. In 1965, at the instigation of Wesley Goss, who served as Chairman of the Board of Regents and who happened also to be President of the Arboretum non-profit corporation, Arboretum employees were granted personnel benefits and guaranteed the procedures of the University under an agreement whereby operational funds deriving from income of the endowment were annually placed in a University account from which expenses, including salaries, were paid. The employees, rather than being adjunct members of the University community, as many had been officially recognized by unsalaried appointments, became bonafide University employees with the Arboretum recognized as a small administrative subdivision within the University. The University agreed to contribute one salary, that of the Managing Director, from its own funds. A special Arboretum fund at the University was created for receipts from Arboretum admissions, gift-shop sales and the propagated plant program, all aspects overseen by workers at the Arboretum who were now University employees. Today this fund finances many Arboretum programs.

A further aspect of public-private partnership evolved during the decade of the 1970's when Arizona State Parks was added to make a tripartite administrative organization. State Parks provides a Park Supervisor and one additional employee at this time. In doings of the two agencies, Parks employees stationed at the Arboretum function also as adjunct employees of the University and in turn University employees at the Arboretum function also as adjunct employees of State Parks. The Arboretum is officially a State Park and also an extension of the University of Arizona, although all land, buildings, and physical facilities are owned by the non-profit corporation. Agreements specify that the tripartite arrangement does not constitute a joint venture and that the three parties involved in the cooperative management remain the three separate entities as they existed before the agreement.

A fourth participant, closely interdigitated with the University of Arizona, but technically separate, is the University of Arizona Foundation, organized as a non-profit corporation. Within it is the operating unit designated as "Friends of the Arboretum" which is a membership and fund-raising organization which provides volunteer services for the Arboretum and serves as a conduit for donations from the public and from corporations. The complex organization of the Arboretum has produced a flexibility that has been very fruitful in furthering the goals of the parties involved.

Let us review a dozen of the programs and accomplishments of the Arboretum. 1) It produced the rationale, phraseology and impetus for the state's non-profit corporation act under which numerous pro-bono-publico organizations have since formed. 2) It produced a document which was adopted as the state's Native Plant Protection Act, designed to halt despoliation of the desert which was resulting from people digging cacti and other desert plants. 3) It produced the largest display garden of propagated arid land plants [not dug up in nature] in the world, in the process becoming the leader in propagation and establishment of desert plants. 4) It has made propagated desert plants available

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