CONE MORPHOLOGY IN PINUS SABINIANA [1]

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THE DIGGER PINE (*Pinus sabiniana* Dougl.) of California's foothill woodland, is unique in several ways. Few other pines can tolerate such sterile soils or xeric habitats, have such a diversity of irregularly shaped crowns, or show such impressive variation of cone forms within and between populations.

Cone morphology has been emphasized in all taxonomic accounts of *Pinus sabiniana*. After commenting on the branchy form of the crown, most authors mention the conspicuous "spurs" — as the combined umbo and apophysis of the basal cone scales will be termed here. A few authors have been impressed by extra long spurs in certain local populations. For example, Jepson (1909, p. 217) named one population on Mount Diablo having "strongly spur-hooked" scales and relatively long seed wings as variety *explicata*.

Early workers had insufficient material at their disposal to study geographical patterns in cone variation. Still, a few California botanists with wide field experience suggested some regional trends. Thus, Lemmon (1888) thought that the northern forms of the cone were less strongly spurred than the southern forms, adding that trees in the Tehachapi had large cones with strong hooks "closely approaching" *Pinus coulteri* D. Don.

The most detailed reference to cone variation in *Pinus sabiniana* was given by Stockwell (1939), who stated: ". . . the degree of variation in cone size and morphology exhibited by this pine is approached by few others." He also felt that this variation often fell into two patterns within the species as follows: "In central and northern California the cones of digger pine often resemble those of Coulter pine in size and general conformation. . . toward the southern end of its range, however, and near the coast, colonies of digger pine are known that produce an entirely different appearance. . . the general aspect of the cone is similar to that of Torrey pine. . ."

A broad study of this species was made and reported by the author in an unpublished doctoral dissertation (1962). As part of that study, cone samples from populations throughout the range of *Pinus sabiniana* were analyzed for many characters. Preliminary sampling had suggested that

[1] This paper is based on parts of a thesis submitted to the University of California in partial satisfaction of the requirements for the Ph. D. degree in botany. Portions of the study were supported by cooperative funds from the Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Berkeley, California.

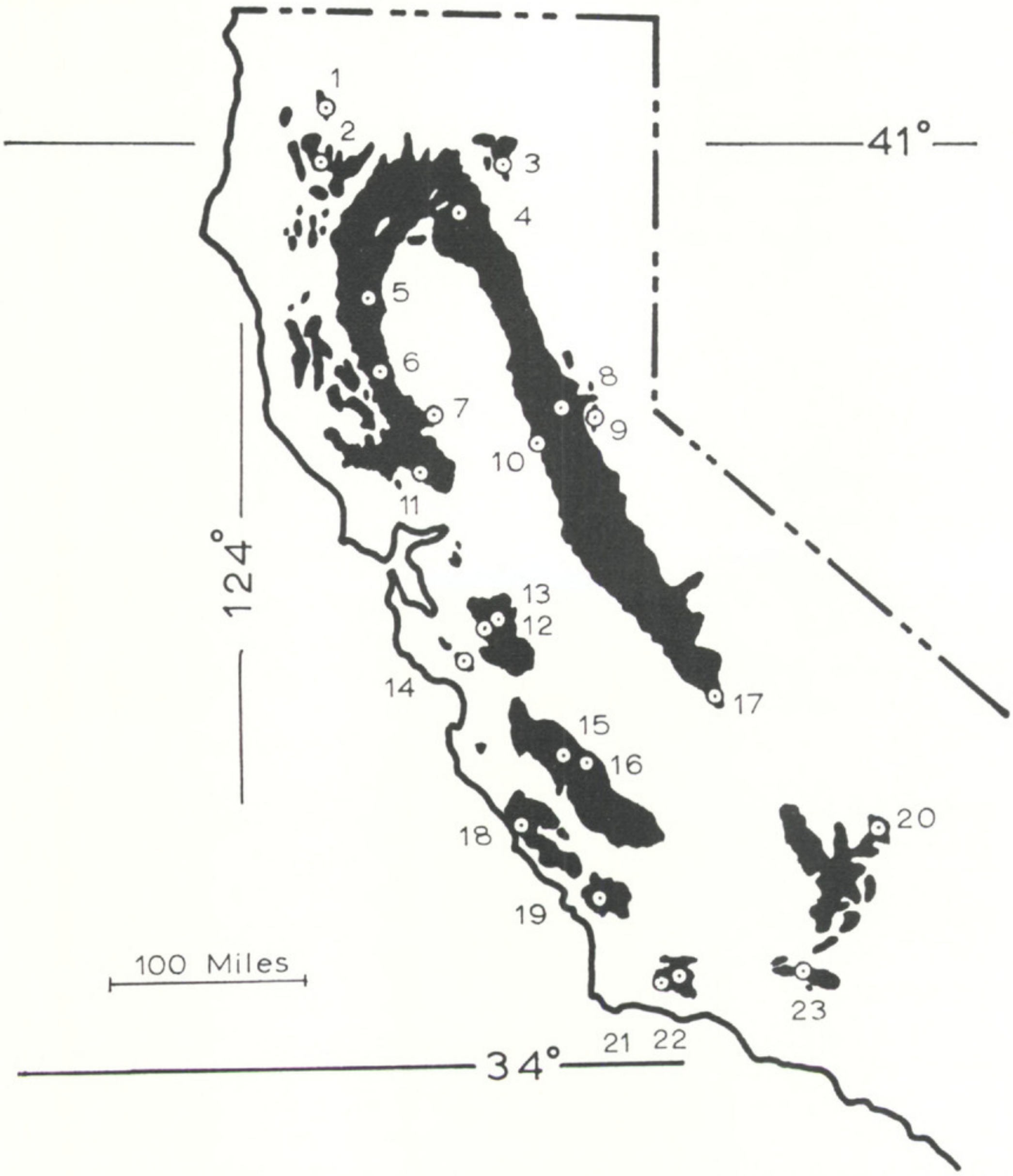

FIG. 1. Natural distribution of *Pinus sabiniana* in California. Circled dots indicate population sample locations; numbers offset from dots refer to sample descriptions in TABLE 1.

intra-tree variation in both size and form of cones was small in contrast to intra- or inter-population variation. To minimize the expected high variance within populations, trees of a "standard" size and age class were sampled. Resulting cone samples from the upper, lateral branches of standard trees were more comparable physiologically than samples from convenient ground reach would have been. Unfortunately, scarcity of standard trees in the field, as well as storage and handling problems in the laboratory, forced the major samples to be somewhat restricted — one cone from each of 20 different trees. In some localities only 10 cones were obtained. The natural distribution of the species and the relative location of samples appear in FIG. 1. In addition to population samples, the complete cone crops on two trees in one population were collected for two consecutive years in order to estimate the nature and magnitude of intra-tree variation.[2]

CONE SIZE

Stockwell (1939) suggested that a small-cone population existed on Figueroa Mountain in the southwestern corner of the range. "These examples," he emphasized, "are not of rare individual cones or of isolated trees, but of local races. . ." This note prompted Gaussen (1960) to describe forma *microcarpa*. Vague reports of other small cone populations in the Tehachapi Mountains in the southeastern corner of the range have circulated, although Lemmon alluded to large cones in the same region. Stockwell (1939) and Mason [3] had been impressed with large-cone populations in the northwestern portions of the range.

Preliminary sampling in this study suggested that a more detailed survey of cone size was desirable. Aside from the possibility of general cone size differences between populations, absolute cone size was investigated because of its influence on cone form, cone scale development, seed size, and other associated characters.

The spurs on many cones so complicated direct measurement of length or width on either open or closed cones that air-dried weight was selected as the size criterion. The results of the population survey appear in Fig. 2. No simple correlation of latitude, temperature, precipitation, or other habitat factor with cone size was apparent. The ranges of the largest and smallest samples just overlapped. Clearly, the larger and smaller samples are distinct from one another in a statistical sense, although many of the intermediate samples do not differ significantly from each other. The complete intra-tree analyses revealed that mean cone-weight per tree could vary at least 15 per cent in different years. The standard errors of the mean in Fig. 2 suggest the variable nature of many populations. Despite the high variances involved, the magnitude of difference between the more extreme samples suggests that some meaningful population differences exist.

The phenotypic differences expressed in Fig. 2 might be thought to reflect merely environmental differences — in part they must. But several factors suggest that genetic differences also are involved. One line of evidence supporting this view is found by comparing specific pairs of populations. For example, the Plummer Creek (#1) sample with the largest cones grew in a moderately unproductive "serpentine" habitat. The Applegate (#8) sample, with rather small cones, grew under a comparable precipitation regime, but on a more productive soil. General crown vigor in the two samples as measured by annual branch-length increments and

[2] Five cone subsamples from all collections are on deposit at the Institute of Forest Genetics, Placerville, California.

[3] H. L. Mason. Botany Department, University of California, Berkeley, California. Personal communication.

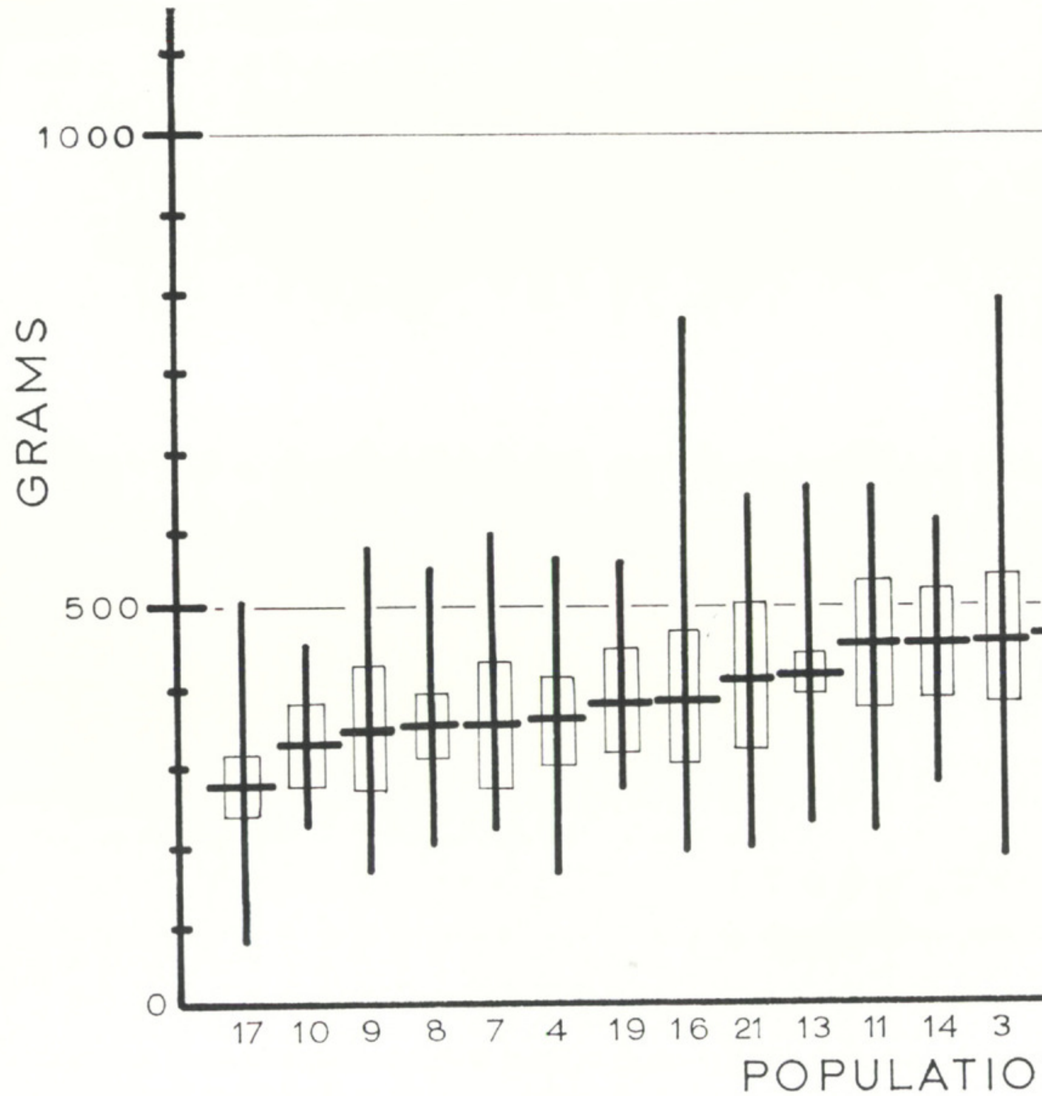

FIG. 2. Cone weight variation in *Pinus sabiniana*. Data are arranged i
bars represent sample means, vertical bars represent sample ranges, and re
mean values. Population numbers refer to descriptions in TABLE 1.

TABLE 1. **Description of population sample localities**

SAMPLE NUMBER	NO. CONES IN SAMPLE	LOCALITY	LATITUDE		LONGITUDE		ELEVATION	M.A.P.*
1	20	Plummer Creek	41°	09′	123°	13′	2,400′	45″
2	20	Big Bar	40	45	123	13	1,300	47
3	20	Murken Bench	40	50	121	26	4,500	20
4	20	Bear Creek	40	31	122	04	1,200	35
5	10	Bennett Creek	39	49	122	39	2,000	25
6	20	Summit Rock	39	09	122	44	3,500	40
7	10	Buckeye Creek	38	55	122	01	200	17
8	20	Applegate	39	00	120	59	2,000	47
9	10	Volcanville	38	58	120	48	3,200	55
10	10	Folsom Dam	38	41	121	10	250	24
11	10	Conn Dam	38	26	122	20	300	30
12	10	Mt. Hamilton-1	37	20	121	40	3,300	25
13	20	Mt. Hamilton-2	37	21	121	37	3,900	30
14	10	Uvas Creek	37	06	121	45	800	25
15	20	San Benito River	36	23	120	57	1,800	15
16	20	Clear Creek	36	23	120	44	3,800	18
17	20	Sycamore Creek	36	53	119	15	1,800	23
18	20	Redwood Gulch	35	50	121	23	1,800	40
19	10	Las Pilitas	35	21	120	29	1,500	17
20	20	Nine Mile Canyon	35	52	118	00	6,500	10
21	10	Figueroa Mt.-1	34	44	120	01	3,000	20
22	20	Figueroa Mt.-2	34	44	119	49	3,700	23
23	10	Cow Spring	34	44	118	39	3,800	18

* Mean annual precipitation, estimated for most stations.

needle-lengths was similar. Tree height growth was superior in the Applegate stand. Small cones in this case seemed not to be a function of "poor" tree-growth, and conversely, large cones were not necessarily a function of "good" tree-growth.

No evidence of unusually small cones was found in the Figueroa Mountain region (see #21 and #22 in FIG. 2). Two samples were taken in the area — one (#21) located on the most sterile site available. The cones of sample #21 were smaller than the species mean; those of sample #22 were larger than the species mean. Ironically, the heaviest individual cone of any sample was found in the general "microcarpa" area in sample #22.

CONE FORM

The shape of *Pinus sabiniana* cones varies widely, but population patterns were not clearly suggested in the samples. In large part the relationship of length to width depends upon absolute size. Many of the ovoid cones were larger than normal (FIG. 3). Although large cones have more massive individual scales, they also tend to have a greater number of scales per cone. The longer axis needed to accommodate the extra

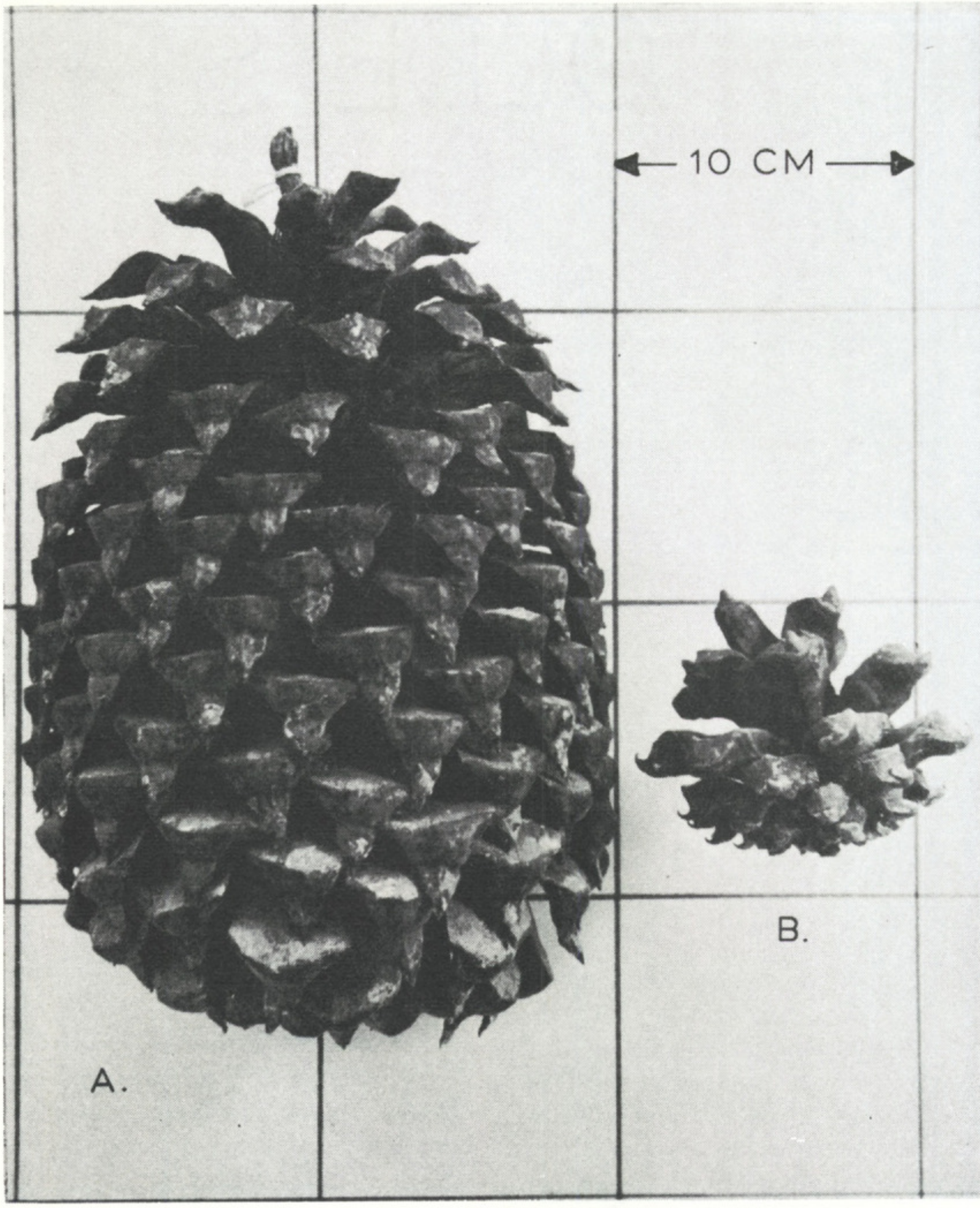

FIG. 3. Two cone form extremes in *Pinus sabiniana*. The elongated cone A has a greater number of scales than "normal," while the small spherical cone B has relatively few scales. The cones in FIG. 4 are of more usual shape.

scales of big cones makes the cones appear more cylindrical. On the trees that were intensively studied for two successive years, average cone weight decreased and average number of scales per cone decreased. The length-width ratios also shifted slightly with the decrease in cone size and scale number. In this case as cone size decreased, number of cones per tree increased.

No significant differences in phyllotaxis were noted in any of the hundreds of cones examined. The usual scale arrangement in the central portion of the cone consists of 8 obvious parastichies in one direction, and

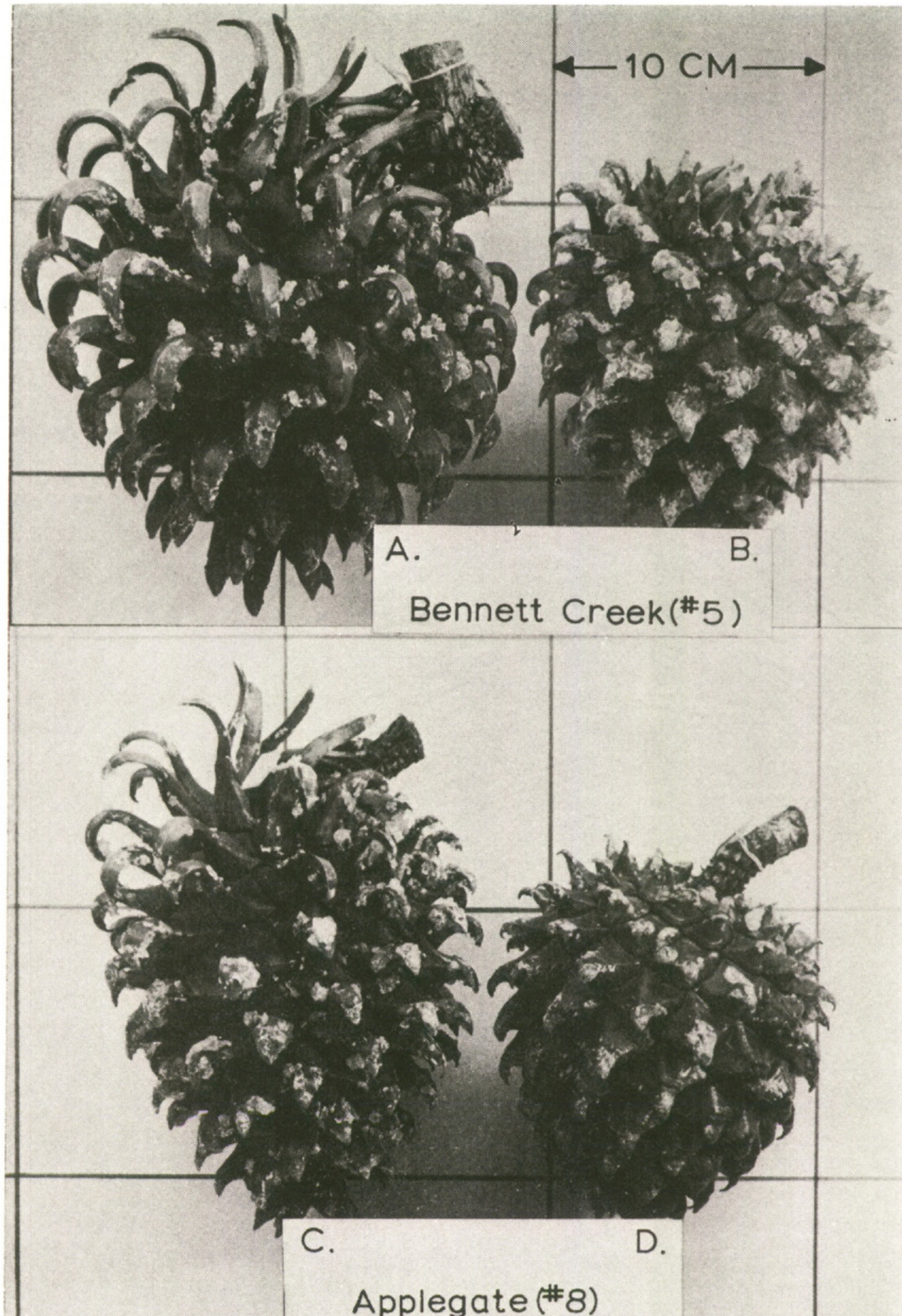

FIG. 4. Two examples of spur variation within *Pinus sabiniana* populations. The pairs of cones came from comparable trees growing a few feet apart.

13 obvious parastichies in the other direction. This arrangement is essentially the 8/21 ratio in terms of classical phyllotaxy, and it is found in the cones of many other pines. There is a tendency for the "primary

spiral" to wind in one direction, but this sometimes varies between cones from the same branch.

SPUR FORM

One of the most conspicuous features of cone variation in *Pinus sabiniana* is in relative spur length (FIG. 4). Although spur length is obvious on a given cone, the condition is rather difficult to quantify for a population. Absolute spur length is not a satisfactory measure, because it is affected by absolute cone size. In order to achieve a more independent criterion of spur development, a "spininess index" was assigned to each cone. This value was computed by measuring the length and width of one spur of constant relative position on the dorsal base of each cone. This length included both the umbo (the first year's external scale development) and the apophysis (the second year's extension growth of the cone scale). Spur length was divided into the width of the spur base. Spurs with values of 1.0 or greater were rather "blunt" (FIG. 3; FIGS. 4B, 4D). Spurs with ratios of 0.5 or less were very "spiny" in aspect (FIGS. 4A, 4C).

The differential scale-growth causing spiny cones is evident early in ontogeny. During the first season's growth of the cone, the spiny condition is obvious if it is to develop at all. The proportion of total number of scales that become spiny in a cone is variable. Occasionally all the scales are markedly affected (FIG. 5D), but more frequently only the more basal scales are affected (FIGS. 5A, 5C). No practical way to describe the proportion of spiny scales in a cone was found. Spininess values refer only to the spininess at the basal portion of the cone. One feature of cone spininess, its stability within a given tree, is quite constant. If cones on a tree were spiny, every cone on the tree was spiny to the same degree year after year.

In addition to relative length, spurs vary greatly in degree of curvature. Some spurs are strongly recurved (FIGS. 4A, 4C); others are straight except for the extreme tip of the umbo (FIG. 3A). Jepson (1910) long ago commented on such straight and recurved spur forms. Curvature seemed to be independent of spur length in many cases. In this survey each cone was assigned an arbitrary spur "curvature index." Only spurs of constant relative position on the dorsal base of the cone were used in assigning curvature values. Cones with the straightest spurs were classed "1"; cones with the most recurved spurs as "5." Intermediate values were assigned, with some difficulty, to intermediate conditions. As with spur length the degree of curvature was rather constant within all cones of a tree year after year.

The results of the spur survey are difficult to interpret. Geographic patterns in spininess or curvature are obscured by variation within a population. Very spiny cones were found infrequently in most of the populations sampled. In the area on Mount Diablo of Jepson's var. *explicata*, for example, several trees with very spiny cones were observed. Small samples in the vicinity suggested that no spiny "population" was involved.

TABLE 2. **Spininess variation of several cone samples, by populations**

POPULATION	FREQUENCY DISTRIBUTION WITHIN SPININESS INDEX CLASSES									
	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2
PLUMMER CREEK (#1)				1	2	3	5	7	1	1
FIGUEROA MT. (#22)			2	4	6	3	2	2	1	
BIG BAR (#2)	1	2	11	5	1					
APPLEGATE (#8)		9	5	3		2				

TABLE 3. **Curvature variation of several cone samples**

POPULATION	FREQUENCY DISTRIBUTION WITHIN CURVATURE INDEX CLASSES				
	1	2	3	4	5
PLUMMER CREEK (#1)	12	6	2		
FIGUEROA MT. (#22)	2	4	11	2	1
BIG BAR (#2)		4	9	2	5
APPLEGATE (#8)					

The sampling intensity was not great enough for strong quantitative conclusions, but the frequency of some combinations of spur characters does suggest population differences (TABLES 2, 3). Two of the more extreme patterns in cone morphology are compared in FIG. 6 in which weight, spininess, and curvature of all cones in two samples are plotted. A common spur situation in the species seems to be wide variation around intermediate spininess and curvature values. In FIG. 6 the Plummer Creek cones represent a skew toward straight, blunt spurs, while the Applegate data is skewed somewhat in the direction of curved, attenuated spurs. Of all the populations sampled, Plummer Creek had the most distinctive spur pattern. This population is also one of the most effectively isolated stands in the scattered Klamath Mountain populations. The blunt spurs of the Plummer Creek cones contrasted sharply with the spiny cones of the Big Bar (#2) sample 35 miles away on the other side of the Trinity Alps (see modal spininess values in TABLE 2).

One population which had an unusual display of cone size, form, and spur variation was Clear Creek (#16). Three facts about this region should be mentioned. First, the edaphic situation is extreme with an extensive area of highly serpentinized parent material occurring under a relatively low rainfall. Secondly, the mixture of pine species (*Pinus sabiniana*, *P. coulteri*, and *P. jeffreyi*) occurs nowhere else. *Pinus sabiniana* grows with *P. coulteri* in many other areas in the south and with *P. jeffreyi* in the north, but all three grow together only near Clear Creek. Thirdly, the morphological variation in these three species is quite high here.

When Zobel (1951) studied introgression between *Pinus coulteri* and *P. jeffreyi*, he found the greatest array of cone variation in his "pure"

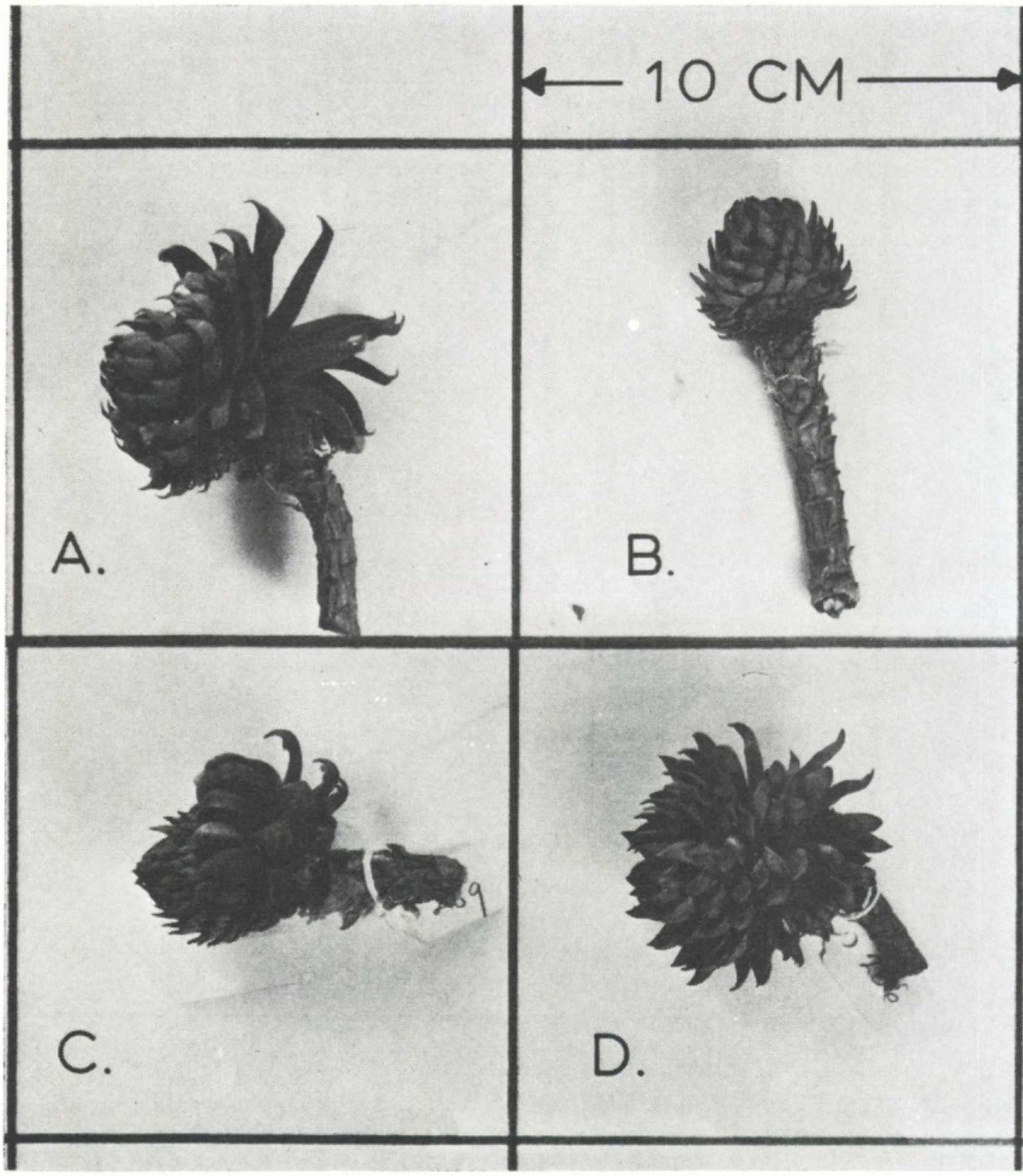

FIG. 5. Umbo variation in four normal, healthy *Pinus sabiniana* cones at end of first season's growth. Cones A and B came from trees growing a few feet apart.

Coulter and Jeffrey samples in this area. This study also showed very large morphological diversity in *Pinus sabiniana*. Zobel speculated that *Pinus sabiniana* in some way may have been involved in the great Jeffrey-Coulter variation at Clear Creek. This possibility must be seriously considered. However, the extreme nature of the habitat also may have contributed to the variation in cone form in all three species. The relative influence of the associated pines and the unique habitat on *Pinus sabiniana* variation must remain speculative.

Many authors have remarked that *Pinus sabiniana* cones occasionally resemble *P. coulteri* cones. The attenuation and curvature of the basal spurs on cones of the two species are often identical. The basic difference is that obvious spur development in *Pinus sabiniana* is often restricted to

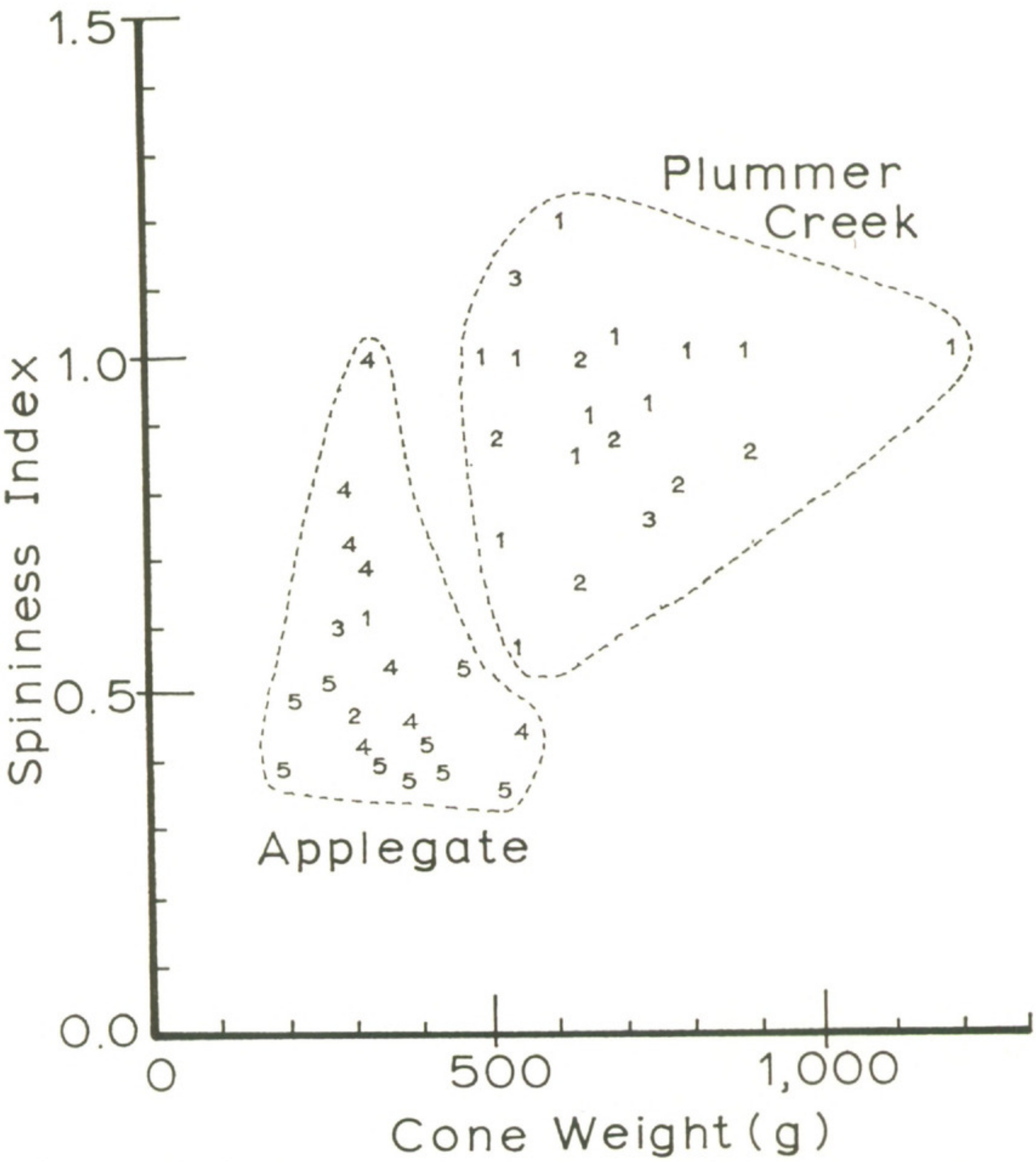

FIG. 6. Relationship of Plummer Creek (#1) and Applegate (#8) cone samples. Each plotted figure represents the curvature value for one cone of given spininess and weight.

the basal portion of the cone, while in *P. coulteri* hooked spurs commonly extend to the cone apex. No clear geographical pattern to Coulter-like cones was suggested by the limited sampling here.

A less well known aspect of *Pinus sabiniana* morphology is the occasional resemblance of cones to those of *Pinus torreyana* Parry. Stockwell's observations of Torrey-like cones were confirmed in several southern California localities. On one tree, cones with weakly developed spurs over the whole surface were essentially indistinguishable from cones of *Pinus torreyana. Pinus torreyana* has long been isolated from *P. sabiniana*, being restricted to local coastal situations in southern California. Interestingly, the particular Torrey-like cones mentioned above were from the only coastal population of *Pinus sabiniana* (Redwood Gulch, #18). One neardefinitive character that separates *Pinus sabiniana* and *P. coulteri* cones — the relative length of seed and seedwings — is not helpful in separating cones of *Pinus sabiniana* and *P. torreyana*, because the characters of seed and wing in these species overlap.

SPECIFIC GRAVITY

Since four of the samples were from stands where *Pinus sabiniana* grew with *P. coulteri*, cone specific gravities were taken to compare with the values Zobel (1951) reported for *P. coulteri*. He had found specific gravity helpful in characterizing cones of *Pinus coulteri*, and its hybrids with *P. jeffreyi*. All the *Pinus sabiniana* sample means were significantly different from Zobel's *P. coulteri* means. But the *Pinus sabiniana* values did overlap into the *P. coulteri* range. Specific gravity might be helpful in separating *Pinus sabiniana* and *P. coulteri* cones, but large samples and careful analyses would be required.

The specific gravity survey was later expanded to include all cones collected, and it was found that this physical character of the cones was loosely associated with latitude. Northern samples had lower specific gravities than southern samples (Table 4). With only minor deviations the intervening populations had intermediate values.

Although the experimental methods (by water displacement) were crude, they were reproducible. Successive annual sampling in the Applegate trees gave similar results despite changes in cone size. The two Figueroa Mountain samples had virtually identical specific gravity distributions as did the two independent samples at Mount Hamilton. Why the latitudinal trend in values was found or even why different samples from the same local area were so similar is not clear. Critchfield (1957) found specific gravity helpful in characterizing regional cone variation within *Pinus contorta*. But his specific gravity data were related to such morphological features as serotinous habit. Here, no relation to obvious morphological characters or habitat was apparent.

Table 4. **Specific gravity of cones from several samples**

Population	Mean Specific Gravity	Ranges of Specific Gravity
Northern Samples		
Murken Bench (#3)	0.70	0.59–0.79
Big Bar (#2)	0.71	0.65–0.81
Plummer Creek (#1)	0.73	0.68–0.79
Southern Samples		
Figueroa Mt. (#22)	0.82	0.71–0.88
Clear Creek (#16)	0.84	0.76–0.88
Redwood Gulch (#18)	0.85	0.77–0.96

CONE COLOR

The magnitude of cone color variation in this species has never been described adequately. Color extremes were quantified by using Munsell soil color notations (Soil Survey Staff, 1951). These standardized soil colors conveniently covered the whole range of colors encountered in mature, unweathered cones.

Modal cone color varied from reddish brown (5 YR 4/4) to dark reddish brown (5 YR 3/3). Lightest extremes were: yellow (2.5 Y 7/6) and yellowish brown (10 YR 5/4). Darkest extremes were brown (7.5 YR 5/8), and dark red (2.5 YR 3/6). Cone color within a tree was relatively constant, and color appeared to be stable on a given tree year after year. The common color is clearly a reddish brown. Color variations are stressed because of the tendency one might have to attribute occasional yellowish *Pinus sabiniana* cones to introgression from the yellow coned *Pinus coulteri*. From the limited sampling here, the striking color deviations suggested no geographic pattern. Yellowish or reddish cones appeared in low frequency in all parts of the range. Some yellowish *Pinus sabiniana* cones appeared in mixed forests containing *P. coulteri*; others appeared far removed from *P. coulteri*.

CONCLUSIONS

As a species, *Pinus sabiniana* seemed quite distinct from other "related" California pines with which it grows. No clear suggestion of introgression between this species and *Pinus coulteri* or *P. jeffreyi* was encountered in the field. Despite the wide range of habitat conditions in which the species grows, there was a general impression of uniformity in the appearance of the tree. In this context of tree similarity, the variation in cone features was impressive. The irregular pattern of this variation made it difficult to characterize the cones of local populations or to detect geographic trends within the species. A few small samples could lead to very erroneous generalities about *Pinus sabiniana* cones. With this in mind the following generalities are cautiously given:

(1) Large cones were frequently found in the North Coast-Klamath ranges; they may be elongated in form.

(2) Small cones were frequently found in the Sierra Nevada; they may be more ovoid in form.

(3) Cones with low specific gravity were frequent in the north; low specific gravity was not closely related to the larger size of northern cones.

(4) Cones with high specific gravity (overlapping into the range of *P. coulteri*) were found in the south.

(5) Spur form was quite constant within a tree but quite variable within and between population samples.

(6) Plummer Creek, a small isolated Klamath Mountain population, had a high frequency of blunt, straight spurs.

(7) Cones were occasionally quite similar in size, color, and spur form to those of either *Pinus coulteri* or *P. torreyana*.

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