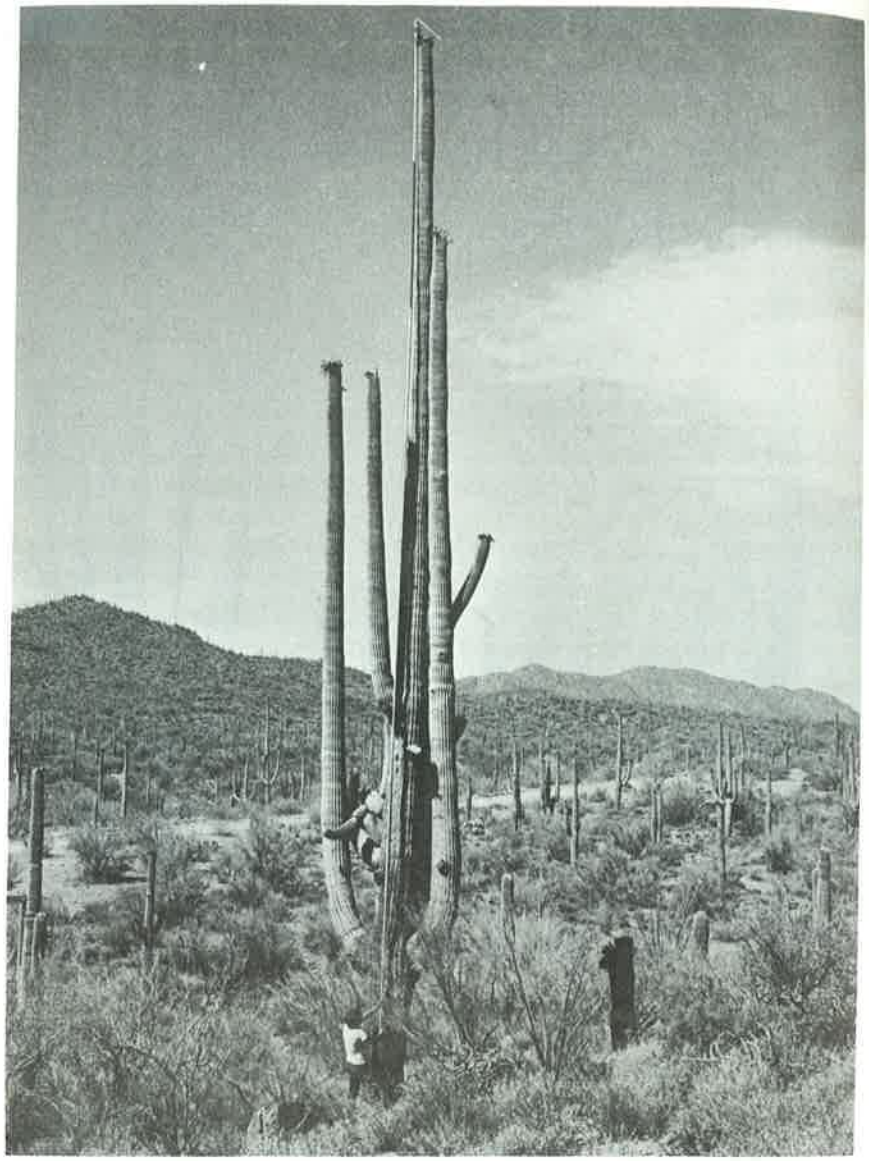

Fig. 2-11b. Tallest saguaro. The 1,600.5-cm height of this old giant is the greatest measured height ever reported for a saguaro. The location is the south-facing slope of Safford Peak in the Tucson Mountains northwest of Tucson, Arizona. The plant, broken off at the base by a windstorm, was dead two months after the photograph was taken.

The telescoping aluminum pole-caliper shown was used for periodic height measurements to determine growth increments for adult saguaros over 240 cm tall. A steel measuring tape suspended from the top of the pole permits direct measurement of height from the horizontal crossbar, which rests on the stem apex, to a

Saguaro populations growing in dissimilar climatic environments exhibit large order differences in branching characteristics. As shown in Table 2-14, the frequency of branched stems and the number of branches per stem increases across the species' distribution from west to east.

The production of branches increases with faster rates of stem growth associated with the gradient of increasing summer precipitation from west to east and greater plant-available soil moisture during the principal period of saguaro growth (Table 2-1; Fig. 2-12). Differences in the number of branches ("arms") produced by the saguaro is a function of differential growth rates; faster growing plants produce the greatest number of branches.

The ultimate function of branches on the saguaro stem is to increase the reproductive potential of the plant (Fig. 2-13). Branches increase the number of fruits, thereby increasing, by thousands to hundreds of thousands, the total number of seeds per year that are produced by the individual. Natural selection has favored those saguaro genotypes that provide greater differential reproduction and survival, i.e., the more greatly branched plants over the less productive, less branched and unbranched plants. In this case a result of selection for greater reproductive effort is, among other things, a branched columnar cactus.

Stem branching, which ultimately provides greater reproductive effort, is a function of growth rate. Selection for the branched form, which provides greater differential survival, thereby concomitantly selects for higher growth rate potential.

Growth and Climatic Factors

Precipitation and seasonal growth

Seasonal growth and response of adult saguaros to precipitation (Fig. 2-14) closely follow the pattern reported for the growth of young saguaros (Steenbergh and Lowe 1969, 1977). Periodic stem height measurements of adult saguaros growing at Saguaro National Monument (east) were made over a 15-month period from January 1970 to April 1971. Permanent benchmarks, installed adjacent to the base of the stem, and specially designed pole-calipers for stem height measurements were used as Steenbergh and Lowe described (in 1977). The growth data together with concurrently measured on-site precipitation are shown in Table 2-15.

As shown in Fig. 2-14, the principal stem growth of adult saguaros coincides with the July-September period of warm summer rains, with minor apical growth following precipitation in April and May. In these winter-cold northern environments there is water uptake, as evidenced by increased stem turgor (diameter increase), but little or no height growth in response to late fall and winter rains (October-March). It is likely, however, that some growth does occur in response to winter rains in the warmer southern portions of the species range in southern Sonora.

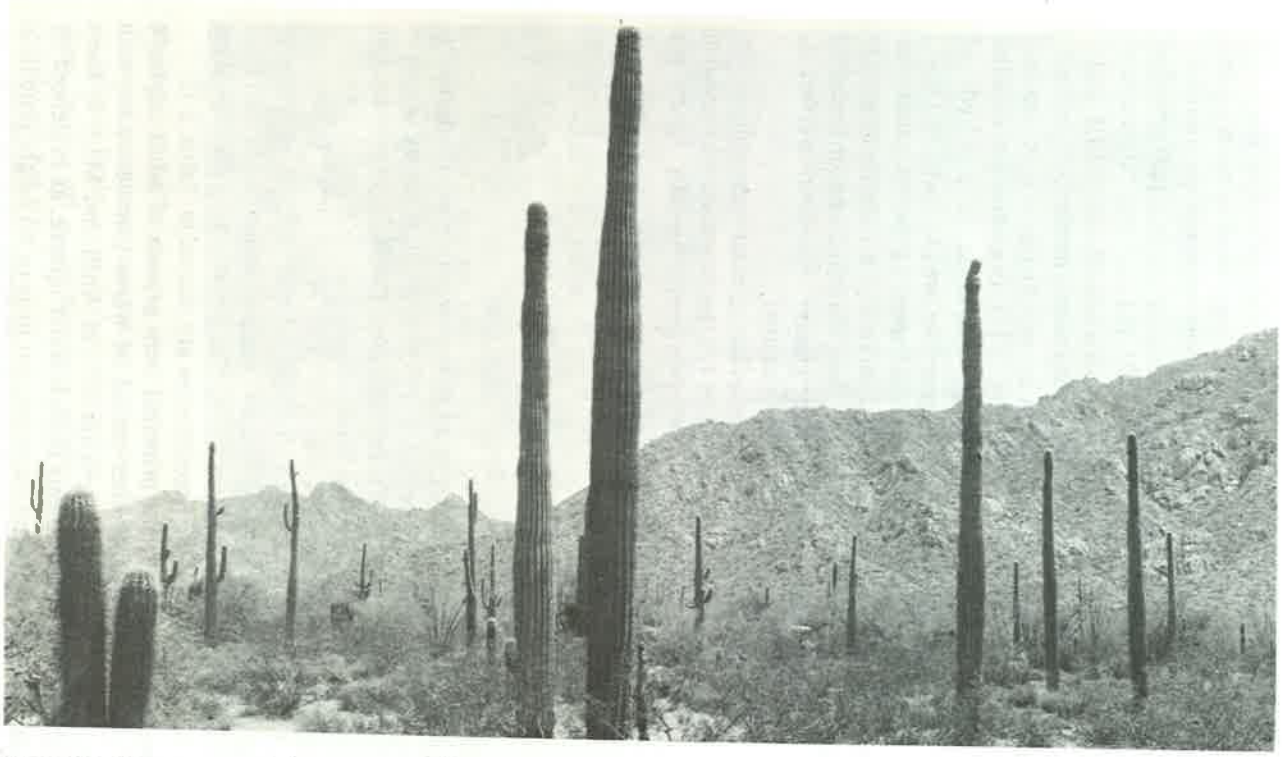

Fig. 2-12a. Saguaro population growing 16 km southwest of Sonoita, Sonora, Mexico (elevation approximately 365m). This population of slow-growing plants is situated near the moisture-limited western boundary of the species' distribution. Estimated mean annual precipiation at this location is less than 230 mm per year. Note the slender stem form and low frequency of branched individuals. Compare with Fig. 2-12b. Photographed 4 Sept. 1978.

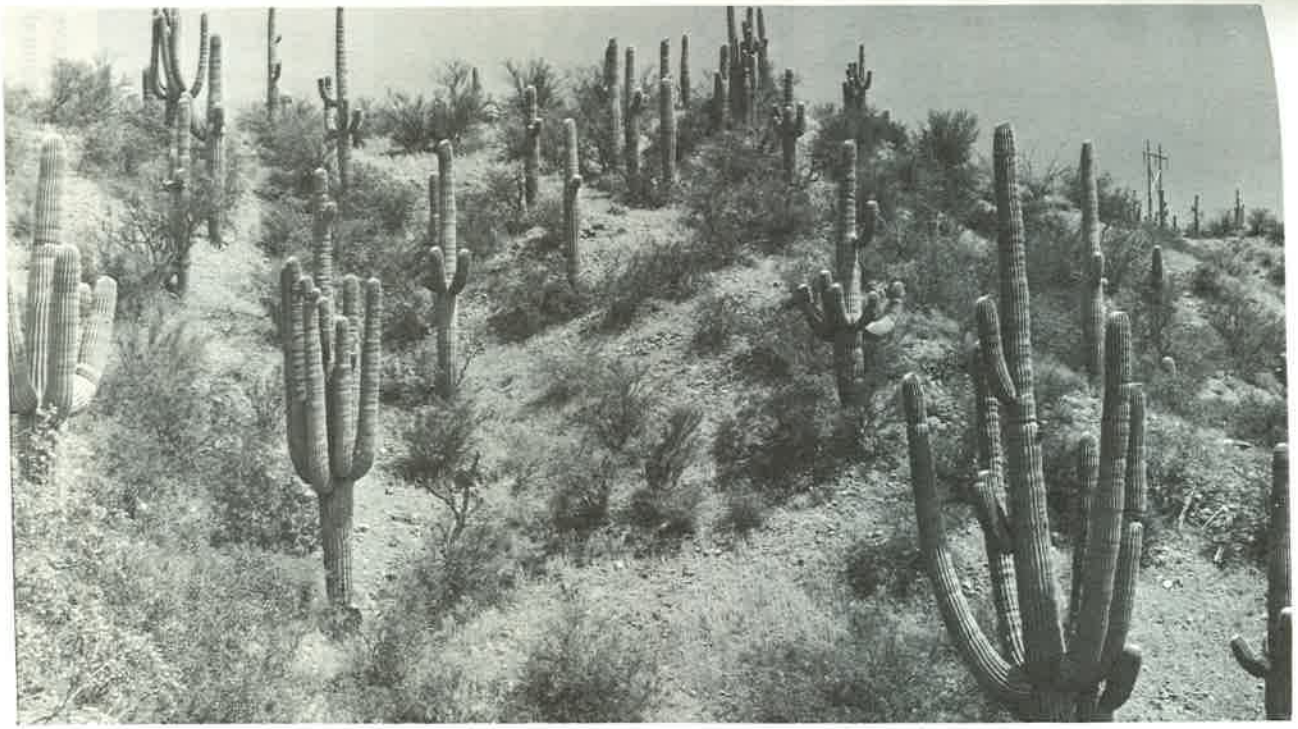

Fig. 2-12b. Saguaro population growing on a south-facing slope 29 km south of Winkleman, Arizona (elevation approximately 760 m). This population is growing near the cold-limited northeastern boundary of the species' distribution. Prolific branching and stout stems are associated with faster growth that occurs in response to relatively high annual precipitation (approximately 320 mm per year). The stout form aids resistance to freezing. The frequency of branched stems and the number of branches per stem is a function of growth rate.

Fig. 2-13a. Regeneration of branches on the 2.5-m stump of a freeze-damaged adult saguaro. The original branches and the upper stem of this plant were destroyed by the freeze of January 1971. When apical dominance is interrupted by decapitation, water and nutrients supplied by the undamaged root system are utilized for rapid generation of new branches. Photographed 23 Mar. 1979.

Fig. 2-13b. Decapitated saguaro with regenerated branches. The reproductive function of the plant has been restored by the growth of new branches. Natural selection favors those saguaro genotypes that provide greater differential reproduction, i.e., the more productive multiple-branched individuals. Photographed 23 June 1978.

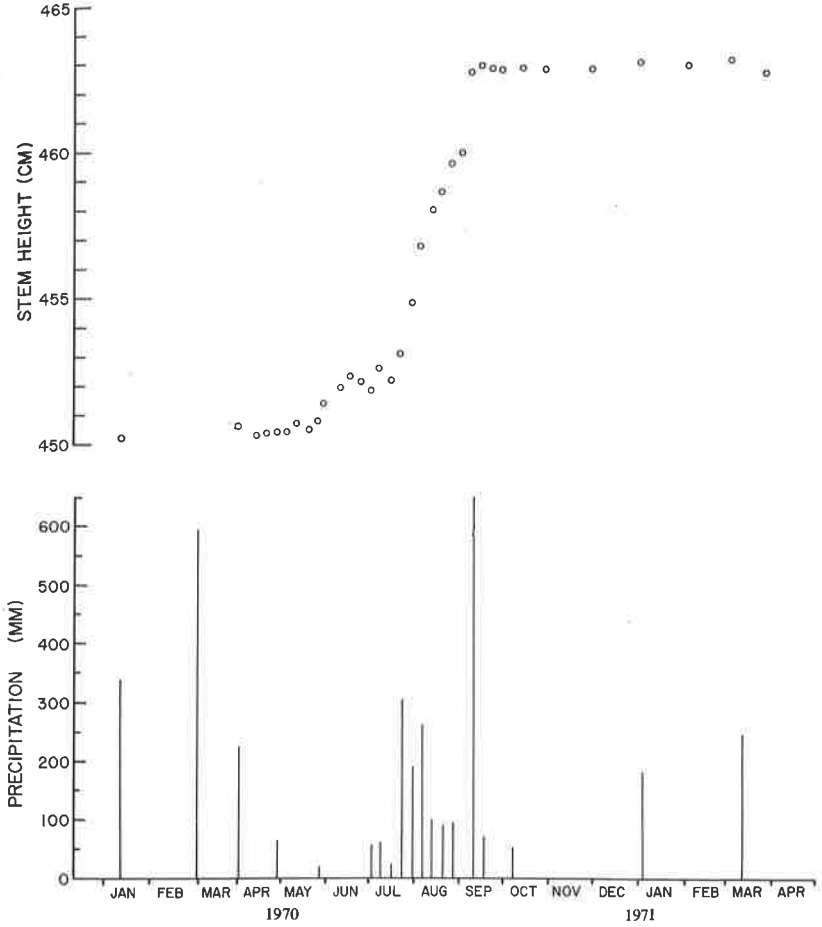

Fig. 2-14. Precipitation and seasonal stem height growth of adult saguaros (N = 2) in nonrocky habitat at Saguaro National Monument (east). Data in Table 2-15.

The principal stem growth of adult saguaros in this environment is initiated with the arrival of monsoon rains in late June or early July. Growth continues during the hot months of July, August, and September, the summer rain season, and ends during the post-summer, October-November, drought period.

TABLE 2-14. Comparison of branching characteristics of adult saguaros growing in three different climatic environments. Frequency (%) and number of branches per plant for adult saguaros 4-10 m height in bajada (nonrocky) habitats, three 2-ha plots at each location.

Location	Elevation (m)	Elevation (ft)	*N*	Branched stems No.	Branched stems %	No. branches Total	No. branches Mean
Saguaro N.M. (east)	856-878	2810-2880	94	79	84.04	317	3.37
Saguaro N.M. (west)	693-792	2275-2600	226	141	62.39	410	1.81
Organ Pipe Cactus N.M.	646-735	1970-2240	91	34	37.36	82	0.90

Freezing, vigor, and growth

Large order differences in the growth rates of saguaros growing in the same environment are associated with readily observable differences in the form of healthy and freeze-damaged plant stems (Figs. 2-15 to 2-20). As shown in Fig. 2-19, low vigor of adult saguaros is clearly evidenced by lack of turgor (flaccid, radially compressed stem and branches) and shriveled crowns on stem and branches. Such individuals also exhibit markedly reduced reproductive growth (numbers of flowers and fruits produced). Both conditions are a characteristic result of freeze-caused injury (see Steenbergh and Lowe 1976, 1977).

Height and 1-year growth increments (1975-1976) for a sample of vigorous (normal, healthy plants, $N = 11$) and nonvigorous (flaccid, $N = 7$) adult saguaros growing in the same environment at Saguaro National Monument (east) are shown in Table 2-16. The difference in the resulting means that are graphed in Fig. 2-21 is highly significant ($P<0.001$). We found that *the mean growth rate of nonvigorous (flaccid) saguaros was approximately one-half the growth rate of normal (healthy) plants growing in the same environment*—the flaccid plants are moribund. Such moribund plants, surviving mainly or entirely on diminishing water and energy reserves, have a relatively short remaining life expectancy.

Age and Growth Rates in Different Environments

The height-age curves shown in Fig. 2-4 and the growth curves for healthy saguaros shown in Figs. 2-2, 2-3, and 2-5 provide a comparison of growth rates and age in three different climatic environments that are characteristic of the major portion of the species' distribution in Arizona and northern Sonora. Comparison of the three curves for saguaros growing in similar topographic habitats clearly shows an increase in saguaro

TABLE 2-15. On-site precipitation (mm) and seasonal height growth (incr., cm) of unbranched adult saguaros ($N = 2$) at Saguaro National Monument (east), 12 January 1970 to 2 April 1971. Graphed in Fig. 2-14.

Date	Precip.[a] (mm)	Plant no. 69B Ht. (cm)	69B Incr. (cm)	69D Ht. (cm)	69D Incr. (cm)	Mean ht. (cm)
1970						
Jan. 12	34[b]	440.4		460.1		450.25
Feb. 1	0					
Mar. 5	59					
Apr. 2	224	440.7	+0.3	461.0	+0.9	450.85
Apr. 15	0	440.4	−0.3	460.3	−0.7	450.35
Apr. 22	0	440.5	+0.1	460.3	0.0	450.40
Apr. 29	6	440.5	0.0	460.4	+0.1	450.45
May 6	0	440.4	−0.1	460.5	+0.1	450.45
May 12	0	440.3	−0.1	461.2	+0.7	450.75
May 21	0	440.6	+0.3	460.5	−0.7	450.55
May 27	2	440.7	+0.1	461.0	+0.5	450.85
June 4	0	440.8	+0.1	462.1	+1.1	451.45
June 11	0	441.2	+0.4	462.7	+0.6	451.95
June 18	0	441.3	+0.1	463.4	+0.7	452.35
June 25	0	441.1	−0.2	463.2	−0.2	452.15
July 2	6	440.7	−0.4	463.0	−0.2	451.85
July 8	7	441.5	+0.8	463.7	+0.7	452.60
July 16	2	441.0	−0.5	463.4	−0.3	452.20
July 23	31	442.1	+1.1	464.2	+0.8	453.15
July 30	19	443.8	+1.7	465.9	+1.7	454.85
Aug. 6	26	445.9	+2.1	467.7	+1.8	456.80
Aug. 13	10	446.9	+1.0	469.1	+1.4	458.00
Aug. 20	9	447.6	+0.7	469.7	+0.6	458.65
Aug. 27	10	448.4	+0.8	470.8	+1.1	459.60
Sept. 3	0	449.0	+0.6	470.9	+0.1	459.95
Sept. 10	65	451.4	+2.4	474.0	+3.1	462.70
Sept. 17	7	451.6	+0.2	474.2	+0.2	462.90
Sept. 24	0	451.7	+0.1	473.9	−0.3	462.80
Oct. 1	0	451.7	0.0	473.8	−0.1	462.75
Oct. 15	5	451.8	+0.1	473.8	0.0	462.80
Oct. 30	0	451.3	−0.5	474.2	+0.4	462.75
Dec. 1	0	451.7	+0.4	473.8	−0.4	462.75
1971						
Jan. 3	18	451.9	+0.2	474.0	+0.2	462.95
Feb. 4	0	451.7	−0.2	473.9	−0.1	462.80
Mar. 11	25	452.0	+0.3	474.0	+0.1	463.00
Apr. 2	0	451.6	−0.4	473.5	−0.5	462.55

[a] Cumulative since preceding date.
[b] Cumulative, 1 Dec. 1969-12 Jan. 1970.

growth rates occurring along a gradient of increasing summer precipitation from *west to east* (Table 2-1) as reported by Steenbergh and Lowe (1977).

The greatest differential in these saguaro stem growth rates occurs in young plants. The young saguaro has a shallow, poorly developed root system that extends only a few centimeters below the soil surface, where the greatest and most rapid loss of soil moisture occurs (Fig. 2-22). Thus, the young saguaro is subject to longer and more frequent periods of low plant-available moisture (and interrupted growth) than the more deeply rooted larger plants with roots extending into a zone of stabler moisture conditions.

It should be emphasized that all of these growth data and the age estimates we present are for one topographic habitat type, "flat" (nonrocky) bajada habitats. These values are not adjusted for differences in growth rates that undoubtedly occur between "rock" habitats with shallow, rocky soils, and "flat" habitats with deeper, relatively fine-textured soils. Neither are these values adjusted for differences in growth expected for north-facing and south-facing slopes.

Freeze-caused depression of growth rates of both young and adult saguaros partially offsets the advantage of more favorable moisture conditions at Saguaro National Monument (east) and elsewhere along the cold-limited northeastern boundary of the species' distribution (Steenbergh and Lowe 1977). However, the effects of such injury (Table 2-16; Figs. 2-15 to 2-20) are not fully expressed in the growth curves shown in Figs. 2-2, 2-3, and 2-5. Data on freeze-damaged moribund plants and plants with actively growth-inhibiting, freeze-caused injury to their apical meristem were not included in the determination of growth curves for healthy saguaros provided here.

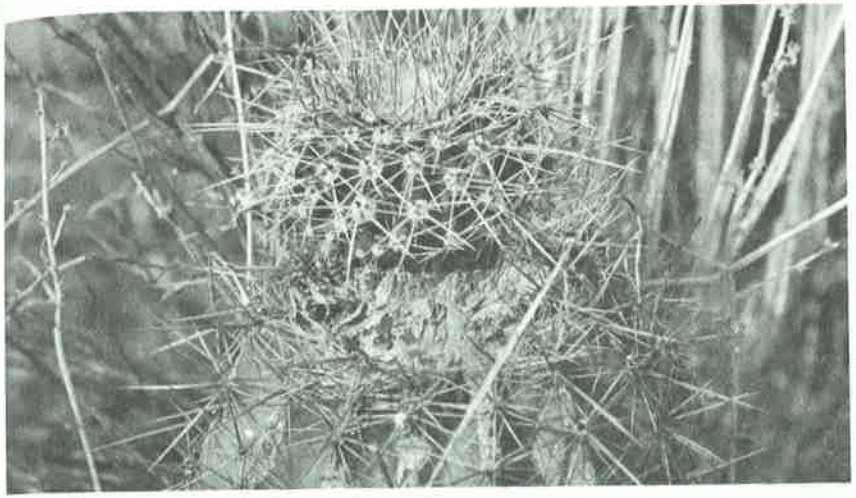

Fig. 2-15a. Regeneration by apical branching of a freeze-damaged juvenile saguaro (ht 22.5 cm) at Saguaro National Monument (west).

The ball-shaped upper stem (apical branch) of this plant is new growth produced following destruction of the original apex by freezing in January 1971. Such deforming injury increases the plant's vulnerability to subsequent freeze injury. The black coloration of the regenerated tip is the result of a second freeze that occurred in December 1975—the apical branch is dead. Photographed 25 Mar. 1975.

Fig. 2-15b. After four years, the same juvenile saguaro shown in Fig. 2-15a has grown to a height of 25.4 cm. The dead apical branch that appears in the 1975 photograph is seen on the left. The new apical branch (right) represents growth since 1975.

Stem height has increased 3.9 cm from the original 1971 height (21.5 cm), approximately 14% of normal 8-year growth (28.5 cm, Table 2-11) for a plant of this size growing in this habitat. Photographed 23 Mar. 1979.

Fig. 2-16. Freeze-caused apical branching of an adult saguaro at Saguaro National Monument (east). Fruits are borne only on the uppermost portion of stems and branches. Apical rebranching of the damaged crown restores the plant's ability to produce fruits on the central stem. Photographed 31 Jan. 1979.

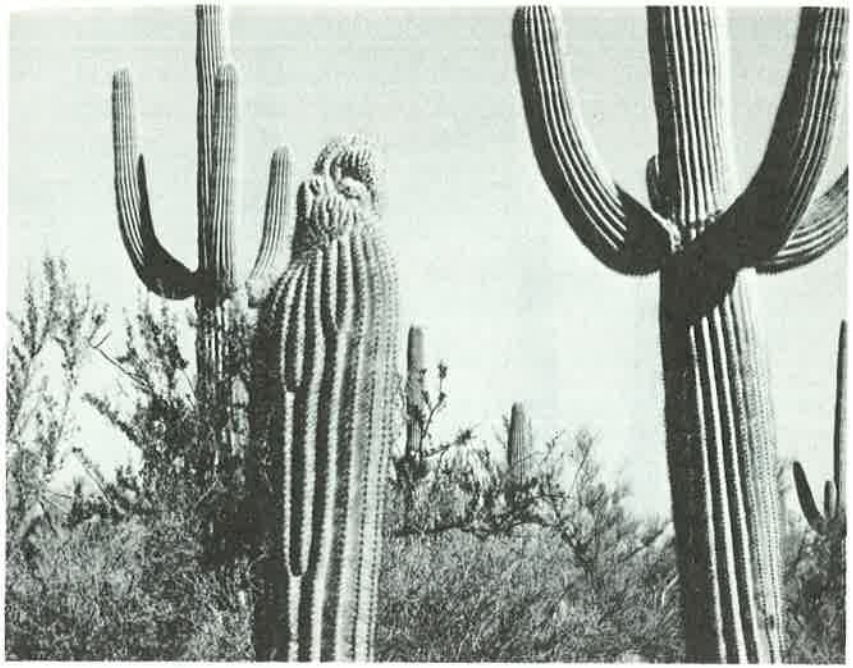

Fig. 2-17a. Developing cristate crown on a young adult saguaro (height approximately 3 m). This relatively rare form apparently results from freeze-caused or other mechanical injury to the apical meristem. It is likely that development of the cristate crown on this individual was induced by injury resulting from freeze-damage during and since January 1962. Photographed 19 Nov. 1971.

Fig. 2-17b. Adult saguaro with fully developed cristate crown at Saguaro National Monument (east). Bilateral growth from the linearly aligned apical meristem results in the development of a comblike crest. Photographed 30 June 1969.

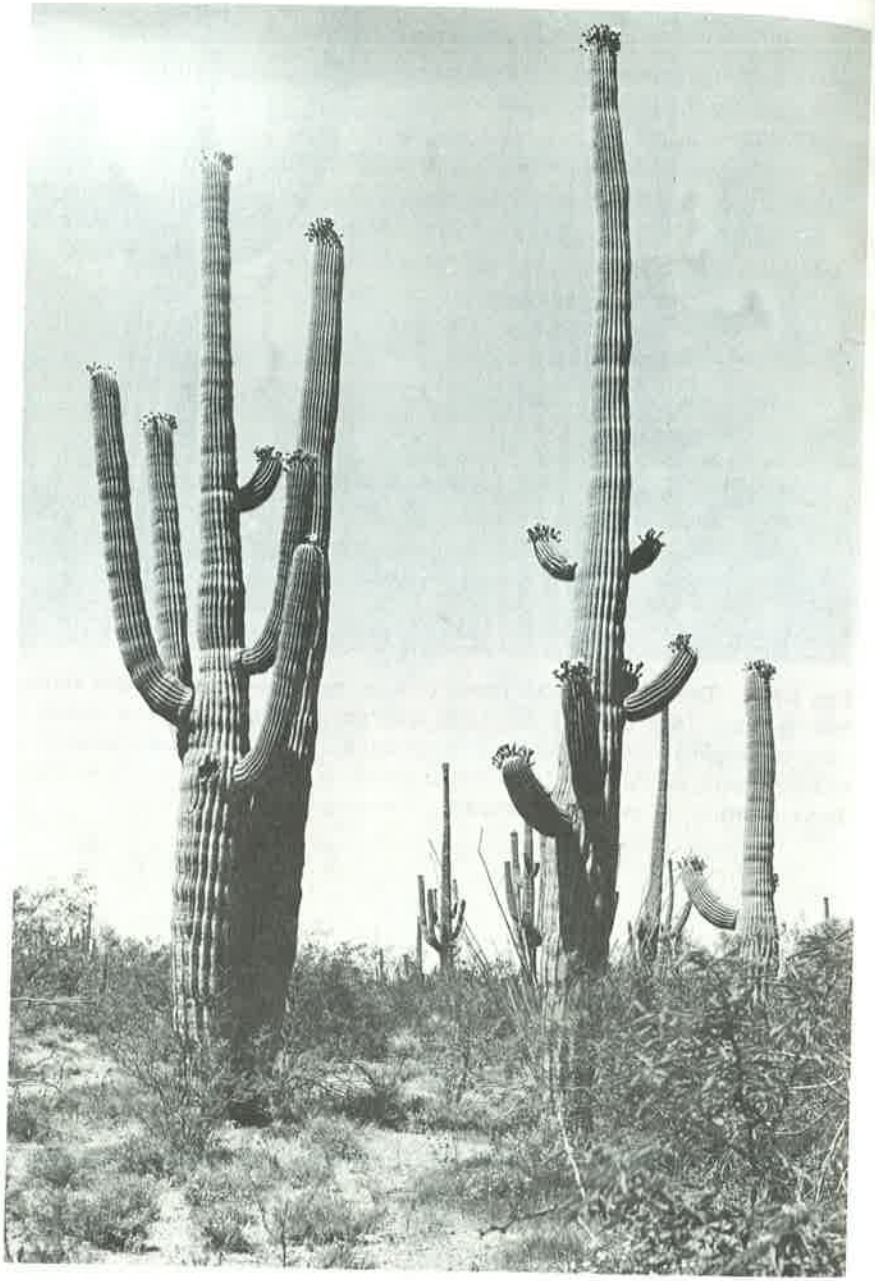

Fig. 2-18a. Nineteen forty-one photograph of saguaros at Saguaro National Monument (east, flats). Note the abnormally slender trunk and branches on the tallest saguaro (right). High surface-volume ratio increases vulnerability to freeze-caused injury. Compare with Fig. 2-18b, a photograph of the same site taken 28 years later. Photographed 12 June 1941 by Paul C. Lightle.

Fig. 2-18b. Drooping branches on the saguaro in the foreground are the result of freeze-caused injuries which occurred between 1941 and 1969. Drooping arms occur with loss of turgor which results from desiccation of freeze-damaged tissues at the base of branches. Dry rot pockets visible on the stems are further evidence of freeze-caused damage to soft tissues. Of the three foreground plants—all moribund in 1969—only the saguaro on the right was still standing in 1979. Photographed 27 May 1969.

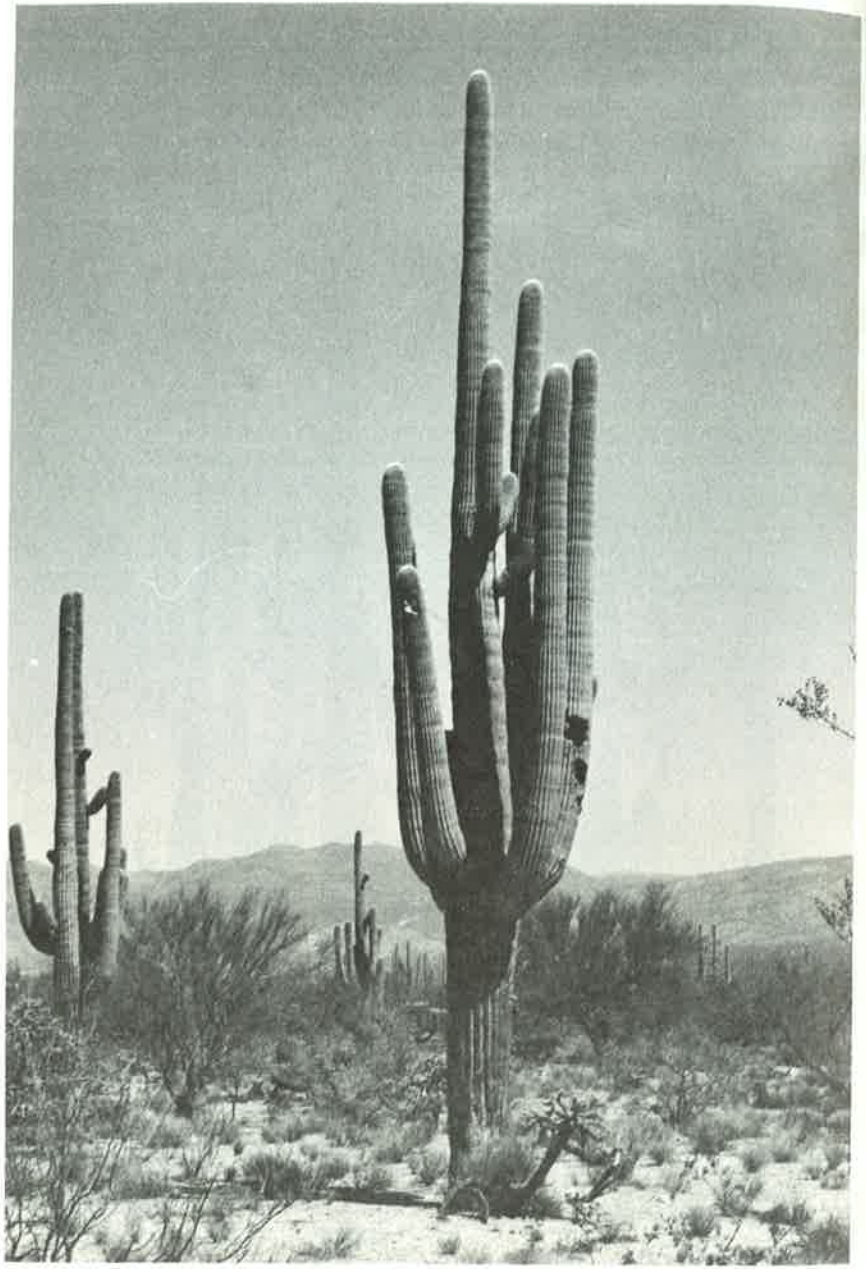

Fig. 2-19a. Vigorous adult saguaro (height 1117.1 cm) at Cactus Forest, Saguaro National Monument (east). Compare the hemispherical crown and stout form of upper stem and branches with the adjacent moribund saguaros shown in Fig. 2-19b. For this healthy saguaro, the 1-year stem height growth (April 1975 to March 1976) was 6.7 cm. Photographed 25 Mar. 1976.

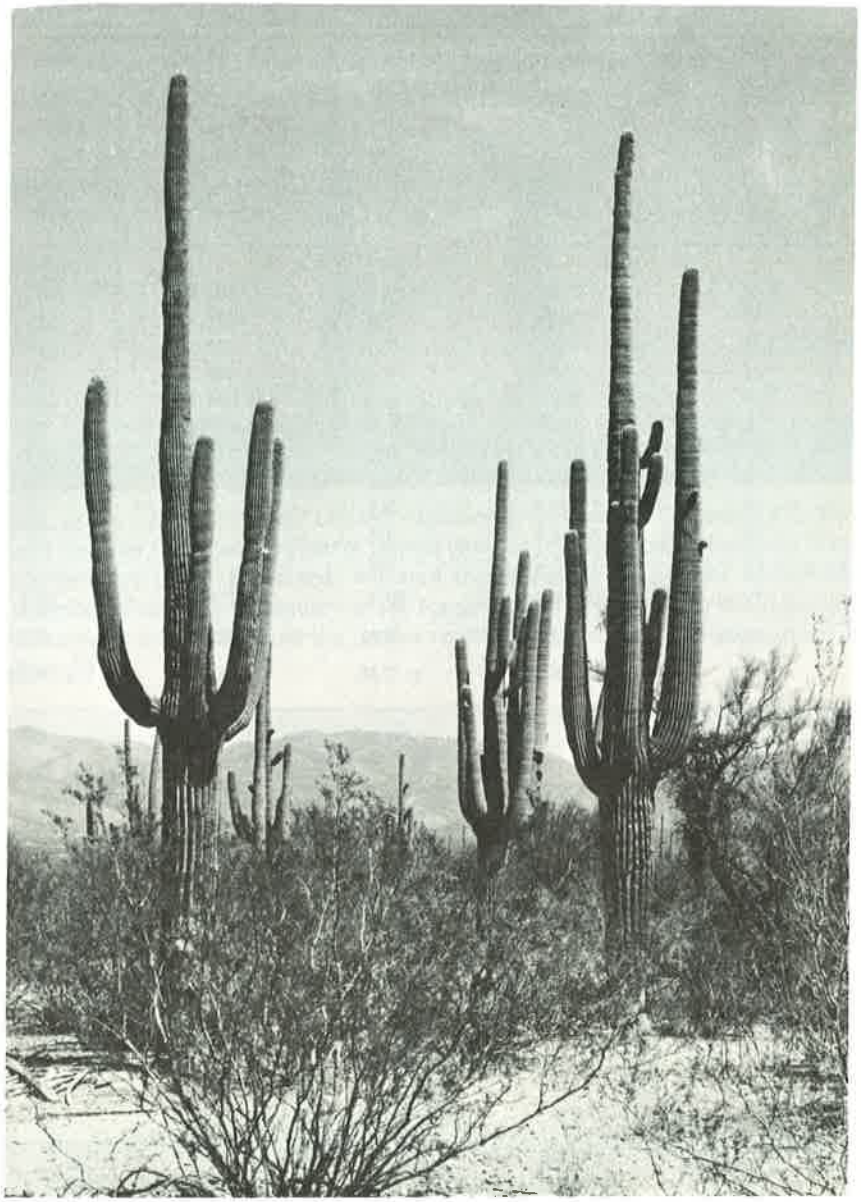

Fig. 2-19b. Freeze-damaged saguaros (foreground) showing characteristically attenuated crowns and slender, radially compressed (flaccid) stems and branches—the plants are moribund. The healthy plant visible in the center background is the same individual shown in Fig. 2-19a. One-year stem height growth (April 1975 to March 1976) of the larger of the two saguaros in the foreground (center, ht 1034.3 cm) was 3.0 cm, less than 1/2 that of the healthy saguaro growing in the same environment. Photographed 24 Mar. 1976.

TABLE 2-16. 1-year stem height growth of healthy (normal, $N = 11$) and non-vigorous (flaccid stems, $N = 7$) adult saguaros at Saguaro National Monument (east), 1975-1976 (see text). Graphed in Fig. 2-21.

No.	Normal		Flaccid	
	Height (cm)	Growth (cm)	Height (cm)	Growth (cm)
1	732.0	10.6	703.8	3.2
2	744.6	5.4	826.3	2.8
3	789.5	7.3	877.3	3.4
4	865.9	8.3	1,006.2	2.3
5	900.5	5.4	1,034.3	3.0
6	986.6	5.4	1,133.8	3.4
7	1,051.6	7.5	1,139.2	4.0
8	1,110.4	6.7		
9	1,193.5	8.4		
10	1,193.5	8.4		
11	1,276.2	7.0		
Total	10,844.3	80.4	6,720.9	22.1
Mean	985.85	7.31	960.13	3.16
S.E.	± 58.25	± 0.48	± 61.78	± 0.20

Fig. 2-20a. Initial response of adult saguaros to the freeze of January 1971. Five months after the freeze, a 3-meter branch (stub on left) has broken from the larger (7-meter ht) plant. Blackened, withered (dead) tissues are present on ball-like branches of the smaller saguaro in the foreground. The abnormally small number of fruits on both individuals is a further result of freeze-damage. Photographed 23 June 1971.

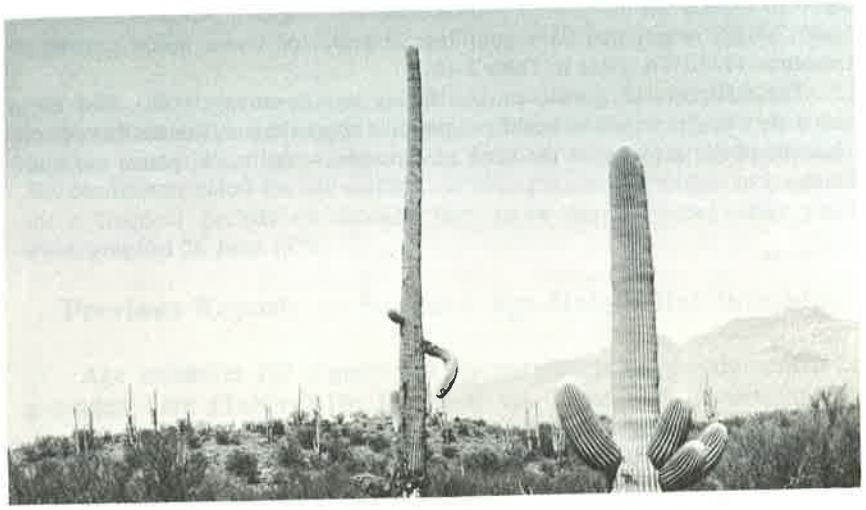

Fig. 2-20b. Eight years after the 1971 freeze, both saguaros shown in Fig. 2-20a are still standing. Injuries to the smaller saguaro have healed. The larger plant—with still-green tissues on the upper stem—is dead. All soft tissues (pith and cortex) of the lower stem have decomposed and fallen from the dead supporting woody ribs (secondary xylem). As much as 9 years or more can elapse between the date of lethal freeze-damage and the final collapse of the dead plant. Photographed 27 Feb. 1979.

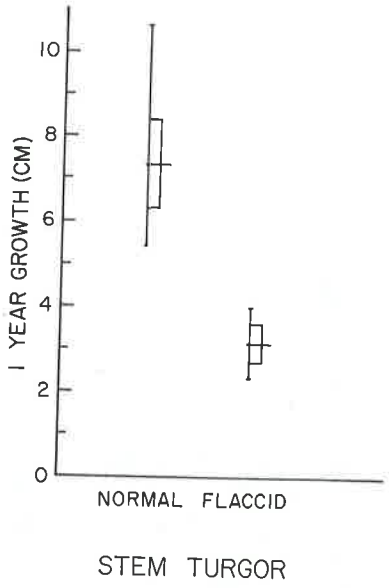

Fig. 2-21. Comparison of apical growth of healthy (normal, $N = 11$) and non-vigorous (flaccid stem, $N = 7$) adult saguaros at Saguaro National Monument (east). Mean, range, and 95% confidence interval of 1-year apical growth increments, 1975-1976. Data in Table 2-16.

The difference in growth rates is highly significant ($p < 0.001$). The mean yearly stem height growth of healthy saguaros is approximately double that of non-vigorous plants growing in the same environment—the flaccid plants are moribund.

Freeze-damaged moribund adult saguaros, growing at reduced rates, can survive up to 9 years or more after lethal injury (Steenbergh and Lowe 1977; Fig. 2-20). Thus, such individuals may be older, by several years, than healthy plants of the same height. Accordingly, age-height relationships for *healthy* adult saguaros (shown in Tables 2-10, 2-11, and 2-13, and Fig. 2-4) are conservative estimates for these populations. Furthermore, mean age-height relationships for large saguaros in any population will depend upon the proportion of moribund individuals present at any given time.

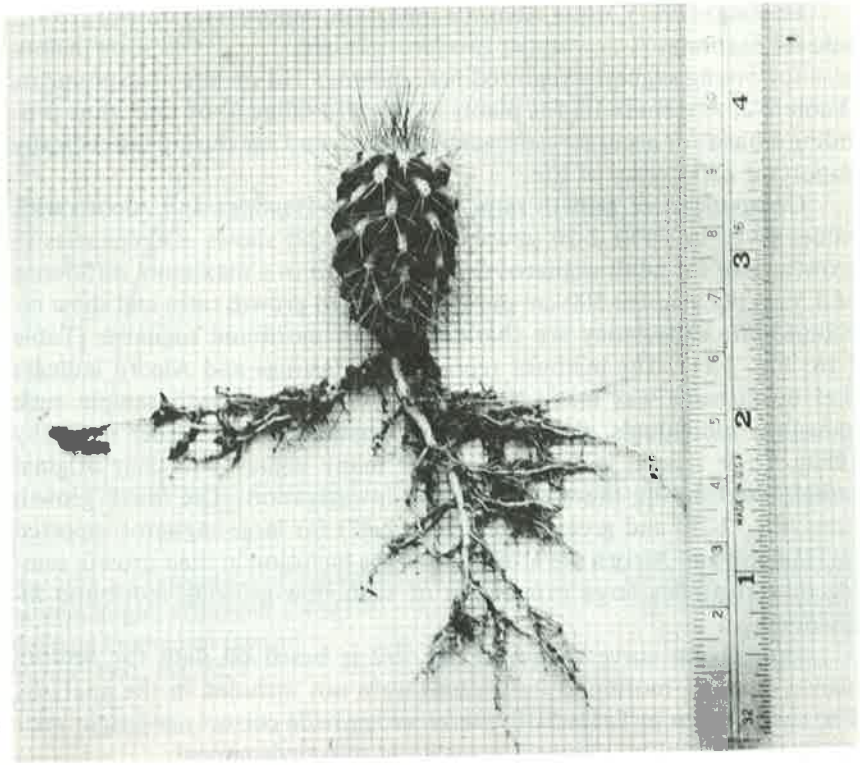

Fig. 2-22. Root system of a 4-year-old saguaro, total stem height 32 mm. The stout tap root is 50 mm in length. Shallow, wide-spreading lateral roots allow rapid uptake of water from light summer rains. Because its root system extends only a few centimeters below the soil surface, the young saguaro is subject to longer and more frequent periods of drought than more deeply rooted older plants. Photographed 26 June 1979.

Previous Reports on Saguaro Age-Height Relationships

Age estimates for saguaros at Saguaro National Monument (east) provided here (Table 2-10; Fig. 2-4) are reasonably consistent with Shreve's (1910) earlier estimates of age-height relationships for saguaros growing in the Tucson area (Table 2-17). However, as shown in Table 2-17 and Fig. 2-23, values for age and growth rates of saguaros provided by our investigations differ markedly from those reported by Hastings (1961) and Hastings and Alcorn (1961). Our values indicate slower growth (and greater age) to approximately 380 cm in height, and, for larger plants, faster growth (and lesser age) than the estimates given by Hastings and Alcorn. Discrepancies between the two estimates for saguaros growing in the same locality and habitat are attributed to important differences in data bases used as described below.