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University of Arizona, Ph.D., 1963  
Botany

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A PHYSIO-ECOLOGICAL STUDY OF JUMPING CHOLLA  
(OPUNTIA FULGIDA ENGELM.)

by  
Fred H. Tschirley

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A Dissertation Submitted to the Faculty of the  
DEPARTMENT OF WATERSHED MANAGEMENT  
In Partial Fulfillment of the Requirements  
For the Degree of  
DOCTOR OF PHILOSOPHY  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

1963

THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my  
direction by FRED H. TSCHIRLEY

entitled A Physio-Ecological Study of Jumping Cholla

(Opuntia Fulgida Engelm.)

be accepted as fulfilling the dissertation requirement of the  
degree of DOCTOR OF PHILOSOPHY

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## ABSTRACT

Tschirley, Fred H. A PHYSIO-ECOLOGICAL STUDY OF JUMPING CHOLLA (OPUNTIA FULGIDA ENGELM.). Ph.D. Dissertation, Department of Watershed Management, University of Arizona. 1963.

Jumping cholla (Opuntia fulgida Engelm.) is an arborescent cactus with cylindric joints found in Arizona and the Mexican states of Sonora and Sinaloa.

Jumping cholla has a high invasion potential, so information about its ecological limitations is important for making management decisions and for determining methods by which the species may be controlled. In addition to growth and population dynamics of this species, the factors affecting reproduction are discussed in detail.

Jumping cholla has little, if any, reproduction from seed. Germination occurs only when the seed coat is broken away at the micropyle on the radicle side of the embryo. Some seeds may germinate after they have passed through the digestive tracts of birds, rodents, or other desert animals, but a small plant that with certainty could be called a true seedling has never been found.

Optimum temperatures for germination are 25 to 30° C; no germination occurred at 20 or 50° C.

Germination inhibitors are present in the fruit pulp, and have been reported from embryos and seed coats. The presence of inhibitors

in the latter two locations was not verified, however.

Reproduction takes place predominantly by vegetative means. Root and shoot development occur readily from detached joints in contact with moist soil. Increases of more than 2000 percent in the number of rooted plants have been recorded following scattering of joints by chaining or cabling.

Root development on joints that have been brought into the greenhouse for study occurs readily throughout the year, but shoot dormancy is apparent from mid-summer to mid-winter. Both onset and the break of dormancy occur suddenly. The effects of temperature, photoperiod, light quality in the red and far-red portions of the spectrum, and injection of a wide range of chemicals were studied, but shoot dormancy was not broken by any treatment.

The life span of jumping cholla in the Desert Grassland was found to be about 40 years. A similar determination could not be made for populations in the Sonoran Desert. Mature plants of jumping cholla are larger in the Sonoran Desert than in the less arid Desert Grassland. It is not known whether the life span is longer, or whether plants simply grow larger under the more arid conditions of the Sonoran Desert.

Three population types may be defined for jumping cholla. Invasion populations are characterized by having a majority of plants in the small size classes, with a decreasing number in the progressively larger size classes. Mature populations have a large number of plants in the smallest size classes, followed by a precipitous drop in numbers

for the next two larger size classes, and then a normal, bimodal curve for the remaining size classes. Senescent populations are characterized by a normal curve in which the highest frequencies are found in the intermediate size classes.

## INTRODUCTION

Jumping cholla (Opuntia fulgida Engelm.) is an arborescent cactus found in Arizona and in the Mexican states of Sonora and Sinaloa.

Jumping cholla is an important constituent of the vegetation in the Sonoran Desert and the Desert Grassland. In many areas it is found in dense stands, making livestock management extremely difficult. Observations over many years indicate that jumping cholla can invade non-infested areas rapidly and that mature stands die out rapidly. In no case, however, have ecological studies been made that would define its invasion potential, its relationship to associated vegetation and the climatic environment, or reasons for the rapid die-off of mature stands over extensive areas.

Because of the importance of jumping cholla in the management of wild lands, and the absence of published information regarding its ecological limitations, several studies were undertaken to determine the invasion potential and the population dynamics of the species.

Jumping cholla is found growing under a relatively wide range of both precipitation and temperature. In Arizona it occurs in areas having a mean annual precipitation ranging from 5 to 20 inches. Roughly half of the annual precipitation falls during the warm season from May through October, and the remainder during the cool season from November through April.

Temperature extremes as low as 6° F and as high as 121° F have been recorded from stations within the geographic limits of jumping cholla distribution. Mean maximum and mean minimum temperatures from within the same area are 69 and 35° F, respectively, in January and 109 and 73° F, respectively, in July. High temperatures, together with high wind velocities and low humidities, account for extremely high evaporation rates. The water lost by evaporation from an open tank frequently exceeds 100 inches annually.

The vegetation associated with jumping cholla is adapted to the short and relatively uncertain rainy seasons. Most of the growth takes place in August when some rainfall can always be expected, and temperature is not limiting. Grasses, particularly, make their growth during the summer period, the topgrowth becoming dry by October and remaining so until the next summer rainy season.

Three genera, Bouteloua<sup>1/</sup>, Hilaria, and Aristida, provide most of the grass species associated with jumping cholla. Bouteloua is represented by many perennial species, but B. rothrockii, B. eriopoda, and B. curtipendula are the most abundant. In the genus Hilaria, H. mutica and H. belangeri are most common. Among the several species of Aristida, A. divaricata, A. hamulosa, A. glabrata, and A. longiseta are most common. Other grass genera characteristic of the area are Trichachne, Andropogon, Eragrostis, Heteropogon, and Leptochloa.

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<sup>1/</sup> Kearney and Peebles (1951) is the taxonomic authority for the scientific names used in this report unless specifically stated otherwise.

The woody plant growth associated with jumping cholla is extremely diversified, since representatives from the Desert Grassland and the Sonoran Desert are included. Only a relatively few genera comprise the bulk of the trees and shrubs, however. These include Prosopis, Larrea, Cercidium, Acacia, Haplopappus, Gutierrezia, Franseria, Opuntia, Carnegiea, and Lemaireocereus. Although the presence of the woody genera antedates historical record, there is a large body of information attesting to their spread over extensive areas within historical time. This is particularly true of Prosopis.

The studies discussed in this report enlarge the body of knowledge for one species, Opuntia fulgida. The reproductive potential, growth, and population dynamics of the species are discussed in view of their limiting factors.



## DESCRIPTION AND TAXONOMY

Jumping cholla is an arborescent cactus reaching a height of 3 m or more (Fig. 1). The tallest plant recorded by the author was 4.4 m high. The main trunk is woody, black for mature plants, and 10 to 20 cm in diameter at the base. Branching starts during the first few years of growth, but the lower branches drop off as the plant grows. Joints are cylindrical, break off easily, the terminal ones 3 to 5 cm in diameter, the surface bearing tubercles 8 to 20 mm long, 5 to 11 mm wide, and 5 to 8 mm deep. Areoles at the forward edge of the tubercles bear 8 to 20 sheathed, straw-colored spines 1 to 3 cm long. Petals are pink or white with lavender streaks. Fruits are obovate, strongly tuberculate when young but becoming smooth with age, usually spineless but bearing minute glochids. New flowers and fruits are formed year after year from areoles of old fruits, forming long chains of fruits that remain green and photosynthetic. Three or four fruits in a chain are common but as many as 14 generations of fruits have been observed and recorded (Johnson, 1918).

The taxonomy of the cacti has been studied by specialists of both conservative and liberal points of view. In the United States, Benson (1950) has adopted the conservative view. His treatment of the Arizona cacti includes five species in the genus Cereus; Britton and Rose (1919), using a liberal taxonomic philosophy, separated the same



Fig. 1. Top: A jumping cholla plant 3.05 m high showing the characteristic chains of fruits. Bottom: A closeup of fruit chains. The lowest chain in the foreground has 56 fruits hanging from a single parent fruit.

five species into five genera. Because of the extreme differences in taxonomic interpretation, Benson said, "The work of Britton and Rose represents nearly the height of a local 'liberalism' . . . ." But the most recent work by Backeberg (1958) is even more liberal than that of Britton and Rose. For example, Britton and Rose included all the cacti having cylindric joints in the subgenus Cylindropuntia within the genus Opuntia. Backeberg, on the other hand, classified the same group of plants in three genera: Cylindropuntia, Austrocylindropuntia, and Corynopuntia. The Opuntia fulgida of most taxonomists corresponds with Backeberg's Cylindropuntia fulgida.

The taxonomy of the Cactaceae no doubt will be passionately disputed for many years. Evidence for taxon affinities from the fields of embryogeny, cytology, genetics and other modern disciplines has not been extensively applied to the Cactaceae. After a careful study of the comparative internal morphology of cactus seeds, Martin (1946) stated that, "The proper relative position of this family is . . . . difficult to ascertain and is necessarily speculative. Also, the sequence of generic positions within the family is tentative."

The principal taxonomic treatments of the Cactaceae used today are those of Schumann (1898), Britton and Rose (1919), Berger (1929), and Backeberg (1958). The classification used by Standley (1924) and by Bravo (1937) for the Mexican species is that of Britton and Rose.

## GEOGRAPHICAL DISTRIBUTION

In the United States, jumping cholla is found only in Arizona (Benson, 1950); in Mexico, it is found in Sonora and Sinaloa (Standley, 1924; Bravo, 1937). Detailed distribution maps are not available for Mexico, but the work of Benson and collections of the author define the geographic limits concisely in Arizona (Fig. 2). Collections of the author are available in the University of Arizona Herbarium.

In Arizona, jumping cholla is found south of  $34^{\circ} 15'$  N latitude and between  $110^{\circ} 15'$  and  $114^{\circ}$  W longitude. The most northern occurrence of the species is the south side of the Bill Williams River in western Arizona. From there the distribution extends southeastward across the state. The Arizona distribution is contiguous with that of Mexico between  $111^{\circ} 30'$  and  $113^{\circ} 15'$  W longitude.

Jumping cholla has been found at a maximum elevation of 4200 ft. Since few plants are found at so high an elevation, however, the practical upper altitudinal limit may be considered as 4000 ft. The lowest elevation at which the species has been found is 800 ft.

Since reproduction of the species takes place almost entirely by vegetative means (reproduction from seed has never been observed in the field), the factors governing distribution must influence root and shoot development from severed joints. A discussion of factors affecting joint establishment is given in a later section of this report.

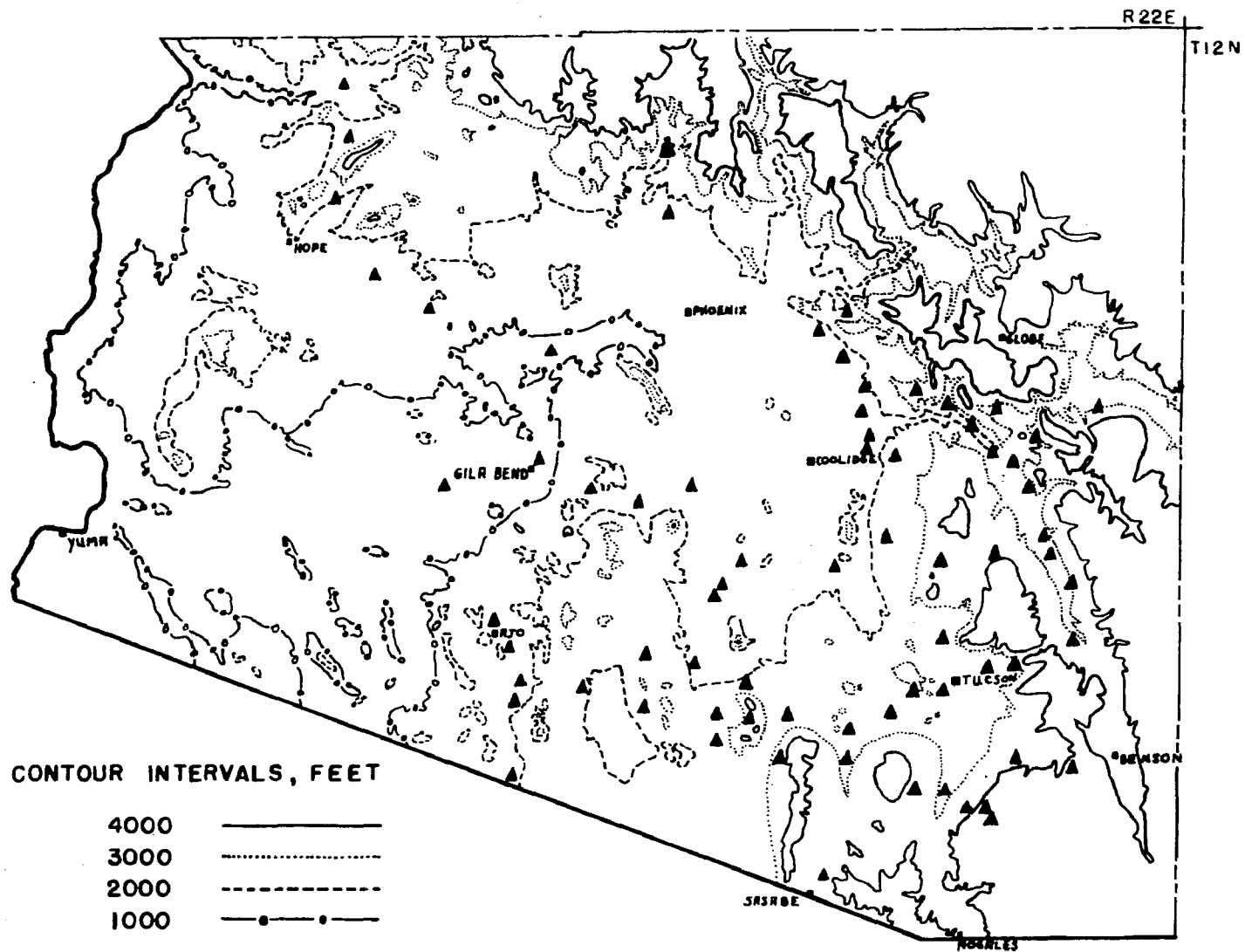


Fig. 2. Sites at which jumping cholla collections were made by the author. Collection sites are indicated by pyramids.

## SEED GERMINATION

Extensive field observations during a number of years have shown that little, if any, reproduction of jumping cholla occurs through seed germination. Despite the limited role of reproduction from seed, knowing the germination requirements is important for a number of reasons. (1) Environmental requirements may be so critical that germination occurs only in certain favorable years, (2) a knowledge of the germination requirements is necessary for defining the conditions under which germination can occur, and (3) requirements for germination may help to explain germination problems of other species.

### SEPARATION OF SEED FROM FRUIT PULP

The first problem encountered in making germination tests was the difficulty of separating seeds from fruit pulp. As mentioned previously, the fruits are persistent on the parent plant and remain green and photosynthetic. The fruit pulp, likewise, does not dry but remains mucilaginous, making the separation of the seeds from the pulp a time-consuming process. The pulp must be removed because it contains inhibitors that suppress germination (Johnson, 1918). Durbin (1956) reported that cactus seed could be separated from fruit pulp easily by soaking the seed balls<sup>2/</sup> in pectinase. His procedure was used for all

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<sup>2/</sup> Seed balls is used only in a descriptive sense to denote the mass of seeds with the associated fruit pulp.

seed separations.

Seed balls were soaked in an aqueous solution containing 3 percent pectinase, usually for 48 hours. If the seed balls were not broken down by that time, soaking was continued an additional 24 hours. At the end of the soaking period, seeds and pulp were put on window screen, and the pulp was washed away with tap water.

When the seed balls were broken down, most of the seeds settled to the bottom of the pectinase solution; the remainder floated on top. Germination percentage of submerged seeds was always higher. Consequently, floating seeds were discarded before washing with water.

#### METHODS OF SCARIFICATION

Many methods of seed treatment to promote germination were tested. In the initial tests, seeds were placed on moist filter paper in petri dishes and exposed to solar radiation in the greenhouse or put in an oven at various temperatures. Under those conditions, no seeds germinated, and there was seldom even the appearance of swelling that accompanies imbibition.

Seeds were scarified mechanically by shaving the seed coat on both radicle and cotyledon sides of the seed. When so scarified, the seeds swelled and chlorophyll developed in the cotyledons, but there was no germination.

Concentrated  $H_2SO_4$  was used to scarify seed in numerous tests, but germination occurred only once. Samples of a seed lot were soaked in concentrated  $H_2SO_4$  for 10, 20, 40, and 80 min, rinsed in distilled

water and put on three sheets of moist filter paper in petri dishes. There was no germination from the first three treatments, but soaking for 80 min in concentrated  $H_2SO_4$  resulted in 25 percent germination. Subsequently, tests were made on six different seed lots using concentrated  $H_2SO_4$  for both shorter and longer periods of time, but there was no germination from any treatment.

For effective scarification the radicle side of the seed coat must be broken away at the micropylar end of the seed so that the radicle can emerge. That portion of the seed coat breaks away quite easily, and damage to the radicle is infrequent. Radicle emergence did not take place with any other method of scarification. Photos of seed and embryo are shown in Figure 3. The method of scarification described above was developed by Dr. Rodney Cobb<sup>3/</sup> of the California Department of Agriculture.

In practice, the seeds were soaked in distilled water for about an hour and then blotted dry. Seeds were held with a fingernail while the tip of a curved forceps was placed in the hilum cup and pressed firmly outward. Each scarified seed was examined with a 3X ocular. When the radicle was damaged, the seed was discarded.

Fungus growth in petri dishes was a problem in early germination tests. At moderate temperatures, good control of fungus was obtained by soaking filter paper in 70 percent ethanol and oven-drying, and by rinsing hands and forceps in 70 percent ethanol after thorough washing

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<sup>3/</sup> Personal communication, 1960.



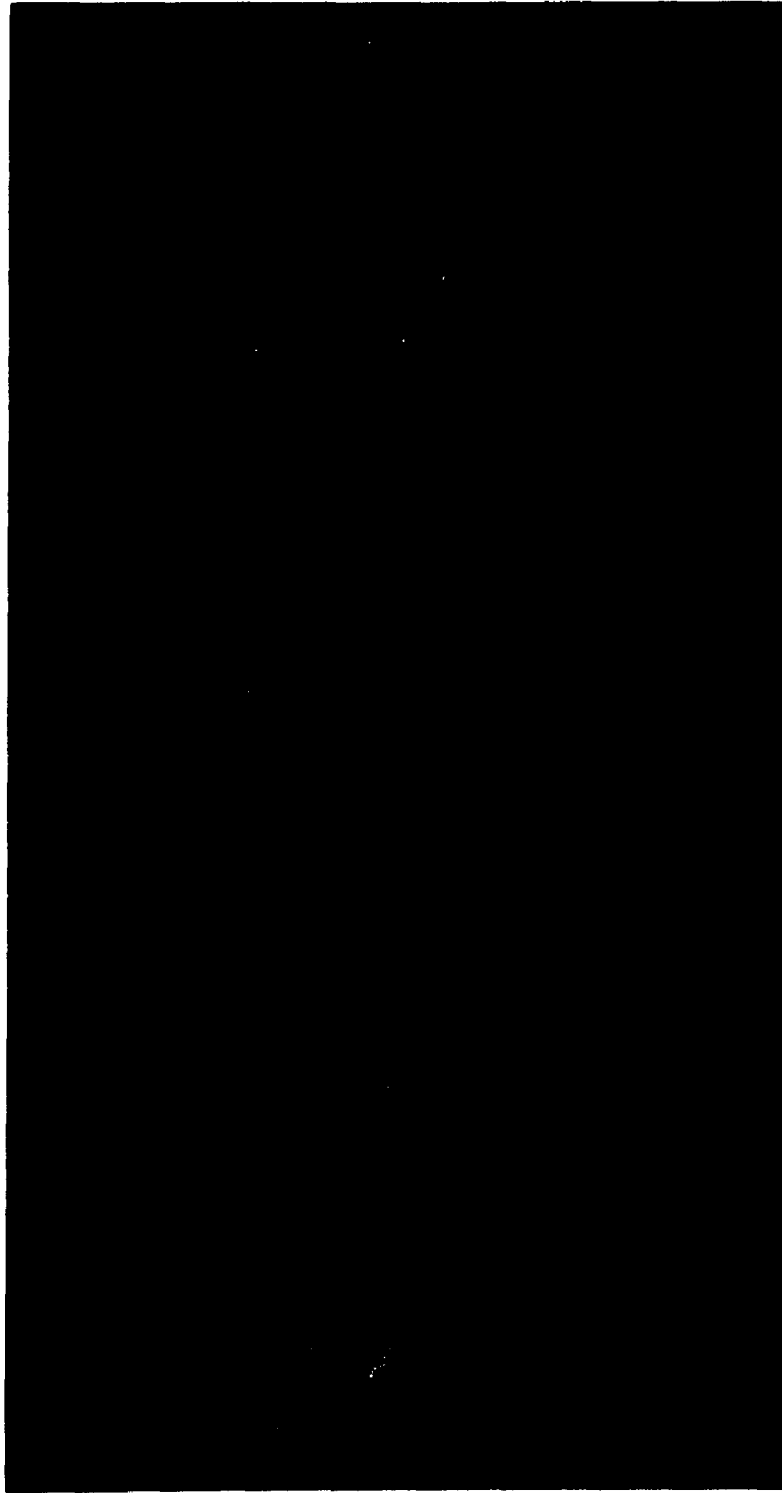


Fig. 3. Top: Seed of jumping cholla showing the micropyle at top and radicle on right. Center: Embryo with integuments intact. Bottom: Embryo with integuments removed and cotyledons visible.

with soap and water. Some fungus did develop at constant temperatures of 45 and 50° C.

#### EFFECT OF TEMPERATURE

Germination and seedling establishment are the most crucial periods in the life history of a species because newly developing tissues are more sensitive than mature tissues to environmental extremes. Of the environmental variables, temperature is one of the most important because extremely high temperatures are common in desert environments just below the soil surface and at the soil-air interface during the hot summer months.

Procedure -- Most of the temperature studies were made in a seed germinator with continuous illumination. The higher temperatures (40, 45, and 50° C) were not obtainable in the germinator. As a substitute, boxes were constructed of 3/4-in plywood with glass tops. Four strip-heaters (GE 2A425) in each box were thermostatically controlled by Minneapolis-Honeywell L4006A thermostats. Temperature in the boxes varied  $\pm$  2° C.

The four thermostatically-controlled boxes were kept in a room illuminated with fluorescent and incandescent lamps. A complete characterization of the illumination is given in the chapter on Joint Dormancy, where radiation intensity was considered more critical.

The same lot of seed was used to test germination at all temperatures. Seeds were scarified as previously described, placed on filter paper moistened with distilled water in petri dishes, and placed in the germinator or temperature-controlled box. Two replications of 100 seeds

each were used for all tests.

Seeds were checked at the end of seven days. Germination was considered to have taken place when the radicle had elongated beyond the hilum cup.

An analysis of variance and Duncan's multiple range test were used to determine the significance of differences between treatments.

Results -- Jumping cholla germinated under a reasonably wide range of temperatures as shown in Table 1. Surprisingly, there was no germination at 20° C, but maximum germination at 25° C. The highest percentage germination was obtained at constant temperatures of 25° and 30° C. Germination decreased steadily through 45° C; no germination was obtained at 50° C.

#### EFFECT OF FRUIT AGE

Cobb and Jones (1961) reported the presence of a germination inhibitor in the embryo of jumping cholla whose effect decreased with time. If this is true, it would be desirable to use fruits of known age for germination tests. Only the relative age of fruits can be determined, however, so the best alternative would be to use basal fruits because they are the oldest. In most cases only one fruit is formed each year, but sometimes four or five fruits may be formed in a single season (Johnson, 1918). The only sure method for determining fruit age would be to mark fruits when they are first formed and leave them on the parent plant until they reach the desired age.

Marking specific fruits for the purpose of determining germination percentage as a function of fruit age would require much

Table 1. Germination of jumping cholla seed at various constant temperatures.

Temperature	Germination*
°C	Percent
20	0 d
25	58 a b
30	61 a
35	51 b
40	27 c
45	20 c
50	0 d

\*Any two means having one or more subscript letters in common are not significantly different. Any two means not having subscript letters in common are significantly different at the 5 percent level.

time. A shorter, though less desirable, method is to assume that only one fruit is formed each year (the usual case) and use a large number of fruit chains as a substitute for fruits of known age. That procedure was used in an attempt to verify the conclusions of Cobb and Jones.

Procedure -- Two tests were made to determine the effect of fruit age on germination percentage. In the first test, 24 chains of three fruits each were collected. Seed was separated from pulp as described earlier and stored dry until used. Seed from each fruit was kept separate. In the second test, 30 chains of three fruits each were collected. Seed was separated in the same way and seed from each fruit was again kept separate.

Because of the size of these tests and the time required for the laborious process of individually scarifying each seed, only 50 seeds were used in each of two replications. Calculations for a number of seed lots indicated that 100 to 150 seeds were required to pick up a difference of 5 percent between means at the 5 percent level of probability. Therefore, using 100-seed samples should have permitted the detection of 5 to 10 percent differences between treatments.

Some fruits did not contain the required 100 seeds for germination tests. Consequently, seeds from two or more fruits were combined. Where it was necessary to combine seed from terminal fruits, for example, the seed from penultimate and basal fruits of the same chains were also combined. After combining, 11 lots of seed were available for the first test and 21 lots for the second. Seeds were scarified in the usual way, placed on moist filter paper, and put in the growthroom where a 14-hour

photoperiod and a diurnal temperature regime ranging from 22 to 38° C was maintained. Germination percentage was checked at the end of seven days using the same criteria for germination described previously.

Results -- Germination percentages in the first test tended to support the conclusions of Cobb and Jones, but there is cause for caution. As shown in Table 2, the pattern of germination was not consistent. Germination of seed from any fruit position may be highest or lowest for that lot. The mean values showed, however, that basal (oldest) fruits had seeds with the highest germination percentage. An analysis of variance and Duncan's multiple range test showed that the germination percentage of seed from basal fruits was significantly greater at the 5 percent level than seed from terminal or penultimate fruits. The difference between seeds from terminal and penultimate fruits was not significant.

The results of the second test did not follow the same trend as did the first. Actually, seed from basal fruits had the lowest percentage germination followed by seed from terminal and then penultimate fruits. Duncan's multiple range test showed that germination of seed from penultimate fruits was significantly greater than that of terminal and basal fruits. Germination percentage of seeds from the latter two fruit positions did not differ significantly from each other.

When the results of the two studies are combined, all three fruit positions differed at the 5 percent level in order of penultimate > basal > terminal. Actual mean percentages of germination were 28, 27, and 26, respectively.

Table 2. Germination of jumping cholla seeds from terminal, penultimate, and basal fruits.

Test No.	Lot No.	Fruit Position		
		Terminal	Penultimate	Basal
		----- Percent -----		
I	1	14	24	22
	2	24	24	24
	3	8	36	27
	4	20	21	9
	5	23	8	17
	6	8	20	21
	7	39	33	56
	8	52	37	49
	9	32	19	49
	10	18	37	21
	11	27	13	28
	Mean*	24 b	25 b	29 a
II	1	26	15	15
	2	39	33	18
	3	15	25	15
	4	35	69	52
	5	87	50	58
	6	12	6	10
	7	13	8	24
	8	11	10	7
	9	12	3	17
	10	15	28	16
	11	14	9	30
	12	41	34	14
	13	27	35	41
	14	47	39	9
	15	31	50	62
	16	11	48	22
	17	14	26	28
	18	37	27	18
	19	36	42	31
	20	34	39	11
	21	12	24	36
	Mean	27 b	30 a	26 b
	Mean for both tests	26 c	28 a	27 b

\*Any two means having one or more subscript letters in common are not significantly different. Any two means not having subscript letters in common are significantly different at the 5 percent level.

## LOCATION OF GERMINATION INHIBITORS

Only limited tests were made to determine the presence and location of germination inhibitors. The literature concerning germination inhibitors is voluminous [see Crocker and Barton (1953) and the reviews of Evenari (1949) and Toole, et al. (1956)]. For jumping cholla, Johnson (1918) found that seeds would not germinate in the fruit pulp and Cobb and Jones (1961) reported the presence of inhibitors in the embryo and seed coat.

Procedure -- Tests were made to determine the presence of inhibitors in embryos, seed coats and fruit pulp. Two replications of 50 scarified seeds each were placed on moist filter paper in petri dishes for all tests. Petri dishes were kept in the growthroom where a 14-hour photoperiod and a diurnal temperature variation of 22 to 38° C were maintained.

When fruit pulp was used as the possible inhibitor source, fresh pulp was placed on the moist filter paper. On the following day, cleaned seeds were scarified and added to the dishes containing pulp. For the other tests, embryos were dissected from seed coats and each was placed on moist filter paper in separate petri dishes. Seeds were scarified the following day and added to the dishes containing either embryos or seed coats.

Germination percentage was recorded at the end of seven days using the same criteria described previously.

Results -- Table 3 shows that germination percentage was reduced in both tests when seed was put into fruit pulp, but was not affected by either seed coats or embryos.



Table 3. Germination of jumping cholla seed subjected to the influence of possible inhibitors in fruit pulp, embryos, and seed coats. Different seed lots were used for the tests.

Treatment	Germination		
	Test No. 1	Test No. 2	Mean*
	----- Percent -----		
Control	43	60	51 b
Fruit pulp	19	20	19 a
Seed Coats	38	58	48 b
Embryos	52	72	62 b

\*Any two means having one or more subscript letters in common are not significantly different. Any two means not having subscript letters in common are significantly different at the 5 percent level.

## DISCUSSION

Definite temperature limits were found for the germination of jumping cholla seed. There was no germination at 20° C, but 25 and 30° C were optimum. Some germination still occurred at 45° C, but none at 50° C. Thus, the range at which germination can occur is wide and embraces the conditions normally found under field conditions. Temperatures higher than 45° C are commonly found at the soil-air interface during the summer months, but seeds able to withstand constant temperatures of 45° C would be expected to withstand short periods of much higher temperatures.

The results of testing the effect of fruit age on seed germination differed from those reported by Cobb and Jones (1961). Although the results of one test supported their conclusions, another larger test did not, and the results of two tests combined conflicted with those of Cobb and Jones. In these tests the mean square for lots was far greater than mean square for fruit position. Thus there was more variation between seed lots than between specific fruit positions. The conclusions of Cobb and Jones are therefore considered premature in that they were based on an insufficient number of seed lots.

Work on the location of germination inhibitors was not extensive. Germination percentage was reduced in both tests, however, when pulp was put on filter paper with scarified seed. Johnson's statement (1918) that "Even chipped seeds do not germinate 'in fruit pulp' as they do in soil or on wet filter paper, which suggests that the pulp may have an inhibitory effect on some process connected with germination", is thus verified. In addition, no germination has ever occurred when seeds have been picked from the fruit pulp without cleaning and put on moist filter

paper with additional pulp. The data suggest the presence of a water-soluble inhibitor in the fruit pulp that is removed during the cleaning process.

Cobb and Jones (1961) reported inhibitors in the embryo and seed coat. That conclusion was not supported by the author's work, but not enough work was done to disprove their conclusion. If the inhibitor is water soluble, more inhibitor would be expected in the embryo simply because there would be more contact with water by the seed coat than by the embryo during the cleaning process. Cobb and Jones did indeed find greater germination inhibition from embryos than from seed coats. Seed used by Cobb and Jones had had considerable contact with water during the cleaning procedure, so some of the inhibitor may have been dissolved from the seed coat. In order to determine the relative inhibitor concentrations in embryo and seed coat it would be necessary to clean the seeds with a solvent that does not dissolve the inhibitor.

## JOINT ESTABLISHMENT

Reproduction of jumping cholla occurs, so far as is known, entirely by vegetative means. A diligent search for true seedlings was made by the author and also by Johnson (1918), but not a single undoubted seedling was found. Usually, the remains of an old joint can be found at the base of a small jumping cholla plant. When the old joint is not present, identification of the small plant is a problem. Jumping cholla cannot be distinguished from staghorn cholla (*O. versicolor*) or cane cholla (*O. spinosior*) in the seedling stage. A number of small seedlings, tentatively identified as jumping cholla, were found to be another species after transplanting and further growth in the greenhouse.

A discussion of joint establishment would not be complete without mentioning vegetative reproduction from fruits of jumping cholla. Fruits are persistent on the mature plant, commonly forming chains of three to four fruits; sometimes as many as 12 or 14. Clusters of 20 to 30 fruits suspended from a single parent fruit are not uncommon, and as many as 100 in clusters have been observed. The fruits do not shed their seed even after falling to the ground. When fruits are dislodged from the parent plant and have undisturbed contact with the soil, they have the same potential for forming new plants as do vegetative joints. Figure 4 shows root and shoot development from a fruit of jumping cholla. Vegetative reproduction from fruits as well as from vegetative



Fig. 4. Root and shoot development from a fruit of jumping cholla.

joints further reduces the need for reproduction from seed.

The discussion of vegetative reproduction is not intended to imply that seed germination never occurs in the field. Seeds will germinate if properly scarified so germination in the field may take place after seeds have passed through the digestive tracts of rodents, birds, or other desert animals. It is clear, however, that vegetative reproduction is of primary importance in the propagation of the species.

#### POTENTIAL FOR VEGETATIVE REPRODUCTION

Jumping cholla has a tremendous potential for vegetative reproduction. When joints are brought into the greenhouse during favorable seasons of the year, roots and shoots develop from almost all joints. Mature stands are characterized by a large number of young plants, arising from old joints, that are just in the process of establishment. The density of mature stands also attests to the success of vegetative reproduction.

That tremendous increases in number of rooted plants are possible is shown by two studies in which dense stands of mature jumping cholla were chained.

#### Mt. Fagan Ranch

Located about 20 miles southeast of Tucson, the Mt. Fagan Ranch has a dense stand of jumping cholla, making livestock management extremely difficult. In January 1958, about 1000 acres were chained for the principal purpose of knocking down the cactus, but also with the hope that chaining might be an effective method of control. Permanent plots were established prior to chaining to determine the changes in

number of rooted plants.

Procedure -- Chaining was done in January 1958, using a Caterpillar D-7 and an International Harvester TD-14. An anchor chain weighing about 30 pounds per link was pulled between the two tractors travelling about 200 feet apart.

Four, 0.1-acre plots were established in the area to be chained and an additional four plots in an unchained area. Counts were made of the number of rooted cacti before chaining and annually for three years after chaining. For recording the changes, any fruit or vegetative joint that had roots in the soil was considered a rooted plant. Unfortunately, the four plots intended to serve as check plots were located in an area that was chained the following year, so no data were available for an unchained area.

Results -- The data on numbers of jumping cholla before and at yearly intervals after chaining are given in Table 4. Plots 1 and 2 were evaluated for three years following treatment; plots 3 and 4 were evaluated for only two years because the markers were pulled up and the exact plot boundaries could not be located. The data show without question that tremendous increases in numbers of rooted plants are possible. One year after chaining there was an increase of 2020 percent which then rose to a 2309 percent increase in the second year after treatment. The percentage of change could not be extended for the third year because of two missing plots. If only the first two plots are considered, there was an increase of 1107 percent the first year, rising to a 1505 percent increase during the second year, and dropping to a

Table 4. The number of rooted plants of jumping cholla on 0.1-acre plots before and 1, 2, and 3 years after chaining on the Mt. Fagan Ranch.

Plot No.	Before Chaining	Years after Chaining		
		1	2	3
		----- Number -----		
1	44	704	994	489
2	38	286	322	221
3	43	1457	1739	
4	53	1370	1281	
Mean	45	954	1084	
Percent Increase		2020	2309	



766 percent increase during the third year.

Santa Rita Experimental Range (SRER)

Additional data emphasizing the vegetative reproduction of jumping cholla were obtained from the SRER. A 20-acre area was cleared of mesquite in the 1940's. Jumping cholla increased rapidly in both size and density following the mesquite removal. This area was selected in 1961 to test methods for controlling jumping cholla.

Procedure -- Part of the experimental area was cabled in early March of 1961. Since only 10 acres was treated, one end of a cable was tied to a tree adjacent to the plots and the other end was attached to a tractor that was driven around the plots to be cabled.

Twelve, 0.1-acre plots had been established in the cabled area and an additional 12, 0.1-acre plots in an uncabled area. The number of rooted jumping cholla plants on these plots was recorded before and after cabling.

Results -- As expected, there was a large increase in number of rooted plants after cabling. The data for all plots are given in Table 5. There was a 1760 percent increase of rooted jumping cholla plants one year after cabling, dropping to a 420 percent increase in the second year.

There were also changes in the number of rooted plants on plots that had not been cabled, but the changes were minor compared to those of cabled plots.

EFFECT OF MOISTURE

The cacti as a family are distributed principally in arid and

Table 5. The number of rooted plants of jumping cholla on 0.1-acre plots before and 1 and 2 years after cabling on the Santa Rita Experimental Range.

Plot No.	Cabled			Uncabled		
	Before	+ 1 year	+ 2 year	Before	+ 1 year	+ 2 year
	----- Number -----					
1	20	745	383	59	20	36
2	72	1554	437	65	20	16
3	24	1026	299	36	14	20
4	5	348	89	20	35	72
5	37	698	199	31	27	50
6	9	427	71	41	43	38
7	37	424	57	43	42	51
8	20	203	37	61	56	88
9	21	86	19	85	63	56
10	57	690	178	98	135	62
11	13	127	28	72	52	70
12	47	370	71	40	23	38
Mean	30	558	156	54	44	60
Percent change		+1760	+420		-19	+11

semiarid regions. Established plants can survive severe drought and detached joints can become established under relatively adverse conditions. Because moisture is a severe limiting factor in desert ecology, a study of the effect of different watering regimes on cholla joint establishment was made in the greenhouse.

Procedure -- On July 25, 1961, five joints were collected from each of 40 plants so that each treatment consisted of one joint from each of 40 plants. The joints were placed on vermiculite in the greenhouse and were watered under five different watering schedules: (1) daily, (2) 2 days, (3) 4 days, (4) 8 days, and (5) 16 days. Joints were checked at 12, 19, 26, 33, and 40 days to determine the number of joints that had developed roots and shoots. Upon termination of the experiment, roots were separated from shoots, weighed, oven-dried at 70° C, and reweighed.

Results -- It should be noted (Fig. 5) that at 12 days, nine joints receiving the 16-day watering interval had developed shoots, but only five joints had rooted. Usually, root development starts before shoot development. The joints for this study were collected just before the start of new growth on plants in the field, so it must be assumed that the stimulus for shoot development was present in all joints and was expressed to a greater degree under the 16-day watering interval. Specific responses were as follows:

A. Root Response -- The rate of root response to the different watering schedules did not vary greatly although there did appear to be a slight downward trend with longer watering intervals for the first

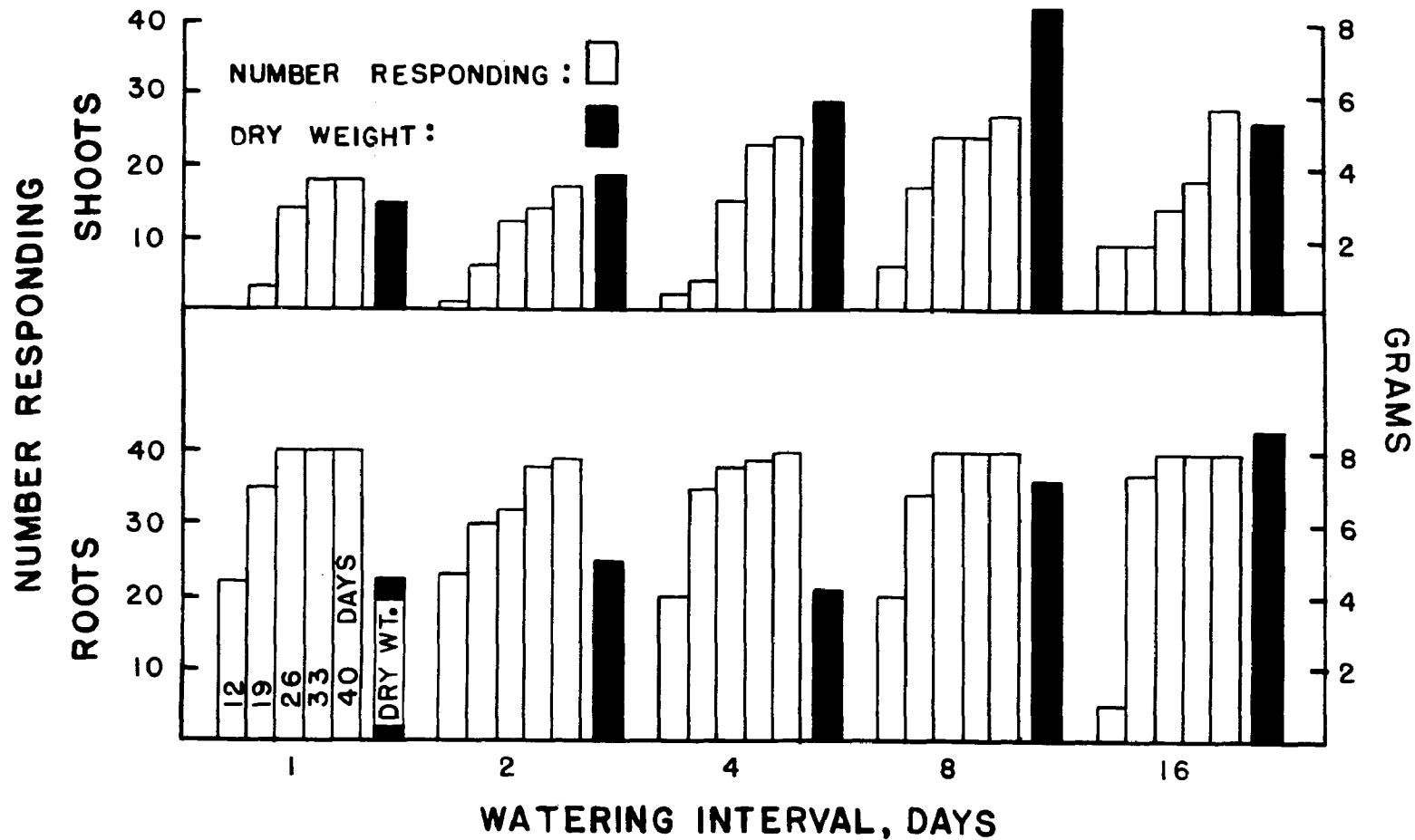


Fig. 5. Rate and degree of root and shoot response from joints of jumping cholla under five watering schedules. The number of joints developing roots and shoots was recorded first at 12 days and at weekly intervals thereafter. The dry weight of roots and shoots was determined at the end of 40 days.

observation at 12 days (Fig. 5). At the end of 19 days and thereafter, however, there was no significant difference in rate of rooting response between the five treatments.

The dry weight of roots at the end of the study was more informative than rate of root response or the total number of joints that showed a root response. Except for the 4-day watering interval, there was a gradual increase of root dry weight with longer watering intervals.

B. Shoot Response -- The rate of shoot response differed from that of the roots. At the end of 12 days a progressively greater number of joints developed shoots under the longer interval between watering. Although some variation in trend was evident from the 12-day observation to the end of the study, the last observation again showed that more joints developed shoots as the watering interval increased.

The dry weight of shoots increased progressively through the 8-day watering interval and then decreased sharply for the 16-day interval.

C. Root-Shoot Ratio -- The ratios of dry weight of roots to those of shoots were 1.50, 1.35, 0.72, 0.86, and 1.65 for the 1, 2, 4, 8, and 16-day watering intervals, respectively. The decreasing ratio for the first three watering intervals was a result of increased shoot weight as root weight remained relatively constant. For the 8-day interval root weight increased proportionately more than did shoot weight. For the 16-day watering interval root weight increased again while shoot weight decreased.

## DISCUSSION

Tremendous increases in rooted plants were recorded for both the Mt. Fagan and SRER areas after chaining or cabling, but there were differences between the two areas. On the Mt. Fagan Ranch an increase was recorded for two years after treatment, while on the SRER a decrease occurred in the second year. Also, the increase was 260 percent greater on the Mt. Fagan area than on the SRER in the first post-treatment year. The greater increase at Mt. Fagan is probably attributable to precipitation differences following the two years that chaining and cabling was done.

Climatic data following chaining or cabling were not recorded for the specific areas. Temperature data from the Tucson Weather Bureau for 1958 and 1961 were analyzed, but the temperature differences between the two years were not great enough to account for differences in the degree of joint establishment. Two rain gauges (Northwest and Desert Stations on the SRER) are located about six miles south of the Mt. Fagan area and four miles north of the SRER area. Rainfall at these stations has no bearing on the absolute amount of rainfall at the treatment areas, but it does indicate the relative precipitation during 1958 and 1961 (Table 6). Rainfall has been recorded at both stations for 36 years, so the long-term means are no longer subject to wide variation.

Table 6 shows that winter rainfall in both years was near the long-term mean. Distinct differences are apparent, however, when spring and summer rainfall for the two years are compared. In 1958 spring and summer rainfall were far above average. In 1961, spring

Table 6. Rainfall at Northwest and Desert Stations, Santa Rita Experimental Range.

Station	Year	Rainfall*		
		Winter	Spring	Summer
		----- Inches -----		
Northwest	36-year mean	2.53	1.66	5.94
	1958	2.69	4.25	9.94
	1959	1.66	6.50	4.80
	1960	4.54	0.81	5.56
	1961	2.93	0.21	6.41
	1962	5.65	1.25	3.69
Desert	36-year mean	2.80	1.83	6.38
	1958	2.80	4.04	9.08
	1959	1.76	0.46	7.48
	1960	4.77	1.20	5.19
	1961	2.92	0.28	7.25
	1962	6.03	1.41	3.70

\*Winter: October to January

Spring : February to May

Summer : June to September

rainfall was far below average and summer rainfall, though greater than the long-term mean, was considerably below that of the same period in 1958.

Because of the high spring and summer rainfall in 1958, soil moisture should have been more favorable for joint establishment than in 1961.

Considering the tremendous number of joints that developed roots after cabling or chaining, there can be no question about the effectiveness of vegetative reproduction. Many joints became established as plants even in 1961 when rainfall was below average. Barring an unforeseen influence such as disease, it is safe to assume that when the young populations on the treated areas reach maturity, plant density will be as great as before the cabling or chaining operations.

Soil moisture affects both root and shoot growth, but there is disagreement about the nature of the effect. Holch (1931) and Duncan (1941) concluded that root growth of tree seedlings is inversely proportional to the available moisture content of the soil. Salter (1954) found a proportionately greater percentage of roots of tomatoes at deeper depths when in drier soils.

On the other hand, Cannon (1911) stated that depth of root penetration of plants in the Arizona desert depends on the depth to which soil is wetted by rain. Weaver (1920) and Weaver and Crist (1922) found root penetration to be greatest in the tall-grass prairie, less in mixed prairie and least in the short-grass plains. Shively and Weaver (1939) demonstrated significant reductions of root dry weights with decreasing annual precipitation in the midwest. Stanhill (1957)



reviewed the published literature concerning soil moisture regime experiments and found that greatest yields were in most cases associated with the wettest soil moisture regimes.

Differences of opinion also exist regarding the ability of roots to grow into dry soil. Shantz (1927) wrote that the roots of certain trees of the African grasslands extend into dry soil, but that roots of ordinary crop plants do not. Magistad and Breazeale (1929), Breazeale (1930), and Breazeale and Crider (1934) found that roots of some species would penetrate into soil below the permanent wilting percentage. They believed that water absorbed in moist soil is translocated to roots in dry soil, and exuded so that soil moisture immediately around the root would be near the permanent wilting point. The results of Breazeale and his co-authors were supported by Wadsworth (1933) and by Haines (1952, 1953), but questioned by Hendrickson and Viehmeyer (1931) and Stone and Fowells (1955).

The effect of soil moisture must be assumed to be variable among species. A variable associated with soil moisture is soil aeration. Poor aeration results almost invariably in reduced growth, but many of the papers cited to demonstrate the relationship between soil moisture and growth did not discuss aeration.

Insofar as cactus is concerned, Cannon (1925) found that root growth of O. versicolor was reduced as the percentage of oxygen was reduced. The same is not true of O. fulgida, however. A test by the author showed that seedlings of jumping cholla grown in nutrient solution without aeration actually had more root growth than those grown with continuous aeration. Shoot growth of aerated seedlings exceeded that

of non-aerated seedlings, however.

Most of the literature shows that the root/shoot ratio is increased with lower soil moisture regimes (Tucker and von Seelhorst, 1898; Kiesselbach, 1910; Polle, 1910; Harris, 1914; Miller and Duley, 1925; Gordienko, 1930; Weaver, 1925; Jones, 1931; and Jones and Haskins, 1935). Williams and Shapter (1955), however, found that the immediate response of low-water treatment of barley and rye was a reduction in R/S ratio. The effect was later reversed for barley but not for rye.

Despite the decrease of the R/S ratio for the first three watering intervals, there was a decided increase in root weight with the longer watering intervals. This indicates the drought-resisting character of newly established plants and accounts for their establishment under adverse conditions. Rainfall at frequent intervals is not as necessary for the establishment of jumping cholla joints as is the case with many seedlings of both annual and perennial desert plants.

## JOINT DORMANCY

Dormancy is generally associated with the temporary suspension of visible growth, especially of buds and seeds. Admittedly, the term is not precise but its use is preferred to those of quiescence, rest, and correlated inhibition suggested by Meyer and Anderson (1952), Chandler (1925) and Chouard (1951), respectively. "Quiescence" was suggested to denote growth suspension caused by external conditions such as unfavorable temperature or water supply. "Rest" was suggested to denote growth suspension caused by internal factors that occur even when external factors are favorable. "Correlated inhibition" has been used when internal conditions of the bud, causing rest, are due to factors arising outside the organ (Samish, 1954).

Although different physiological phenomena are involved in the three suggested terms, there is sometimes not enough information available to be certain of which term to use. In too many cases a phenomenon believed to be caused by internal factors was later shown to be controlled by external factors. Thus the use of the precise terms may cause more confusion than it alleviates. The effect of photoperiod and light quality on phytochrome conversion and its influence on flowering and other plant responses is a case in point.

The concept of dormancy must be qualified to specify shoot dormancy when it is used for jumping cholla joints. Furthermore, not all

joints show dormancy. When brought into the greenhouse, all joints usually develop roots within 4 to 10 weeks regardless of the season. The same is not true for shoot development, however. Joints have been known to remain dormant with respect to shoot development for more than a year.

#### SEASONAL VARIATION

Preliminary studies indicated that the rate and degree of root and shoot development from vegetative joints of jumping cholla is not consistent throughout the year. When joints are collected and brought into the greenhouse for study, root development takes place on all joints within 4 to 10 weeks; from 6 to 40 or more weeks may be required, however, for shoot development to take place on all joints. Some joints show little or no shoot dormancy and will develop both roots and shoots quickly; others develop roots but shoot growth is suspended for long periods.

Procedure -- To study the seasonal variation of root and shoot response, terminal joints were collected at varying intervals from an area south of Tucson. The joints were brought to the greenhouse and placed on moist vermiculite on the same day that collections were made. Twenty joints from one plant constituted a sample on each date. The plant was marked to prevent the collection of sub-terminal joints at a future date. The collection area was topographically and edaphically uniform, but there were probably minor environmental differences.

On seven collection dates enough joints were collected so that seasonal response could be determined in a growthroom under controlled photoperiod and temperature as well as in the greenhouse. Illumination

in the growthroom came from eight, 200-watt, 8-foot, Power Groove fluorescent lamps (GE cool white F96PG17/CW) and 10, 60-watt, clear incandescent lamps (GE Lumiline L60). The lamps provided a light intensity of 2200 ft-c at the level of the joints. A 14-hour photoperiod was maintained starting at 5:30 AM and ending at 7:30 PM. Diurnal temperature varied from a low of 22° C at 6:00 AM to a high of 38° C at 3:00 PM.

Weekly observations were made to determine the number of joints that had initiated roots and shoots.

Results -- The number of joints developing roots and the rate at which roots were initiated was virtually the same in the greenhouse and growthroom. The longest interval needed for all joints to develop roots was 58 days; the shortest, 13 days.

Shoot development was much different than that of roots. Because of the differential response between the greenhouse and the growthroom, shoot response under the two environments will be discussed separately as follows:

A. Greenhouse -- The rate at which joints responded by initiating shoot development varied widely with season, but followed a definite pattern (Fig. 6). From late February through mid-July all joints initiated shoot development within a 6 to 7-week period. Starting with the July 31 collection, however, only a portion of the joints responded within a 7-week period. The remainder did not initiate shoots until the following April. Other samples collected before the following February showed the same response.

The data for two samples (March 12 and April 16, 1962), not included in Figure 6, gave a response similar to that shown for February 20.

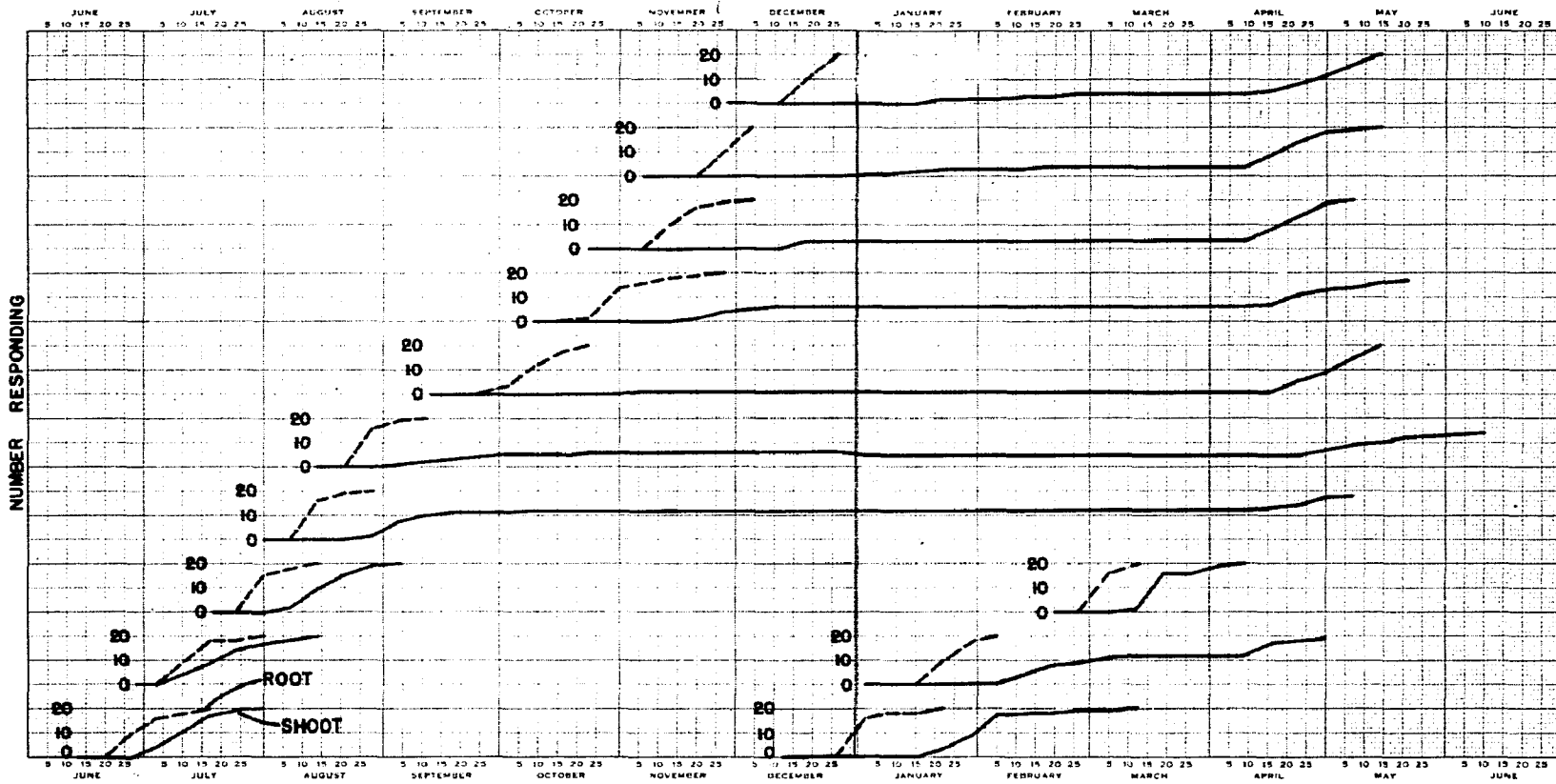


Fig. 6. The rate of root and shoot response from joints of jumping cholla in the greenhouse. The beginning of a line indicates collection and planting date.

Of eight collections that exhibited dormancy of some joints, six broke dormancy on April 9. Dormancy of the other two collections was broken on April 16 and 23.

B. Growthroom -- Data on seasonal response of joints placed in the growthroom are given in Figure 7. Except for the October 9 collection, shoot development was not characterized by a long delay as was that in the greenhouse. On the contrary, shoot response in the growthroom was about what would be expected during the non-dormant period.

Joints of the October 9 collection were the only ones exhibiting dormancy in the growthroom. These joints were moved to the greenhouse on April 16 of the next year. None of the dormant joints initiated shoot growth in April as did those that had been in the greenhouse all the time.

#### EFFECT OF ELEVATED TEMPERATURE

Elevated temperature has been effective in breaking the bud dormancy of a number of species (Samish, 1954). A series of temperatures was tested for breaking dormancy of jumping cholla buds.

Procedure -- Two treatments were made during the period of shoot dormancy, and a similar two treatments during the non-dormant period. Ten joints were used for each treatment. To reduce the possibility of genetic variation between treatments, four joints were collected from each of 10 plants; one joint from each plant being used for a treatment. Collections were made from the same plants for both non-dormant and dormant-season treatments.

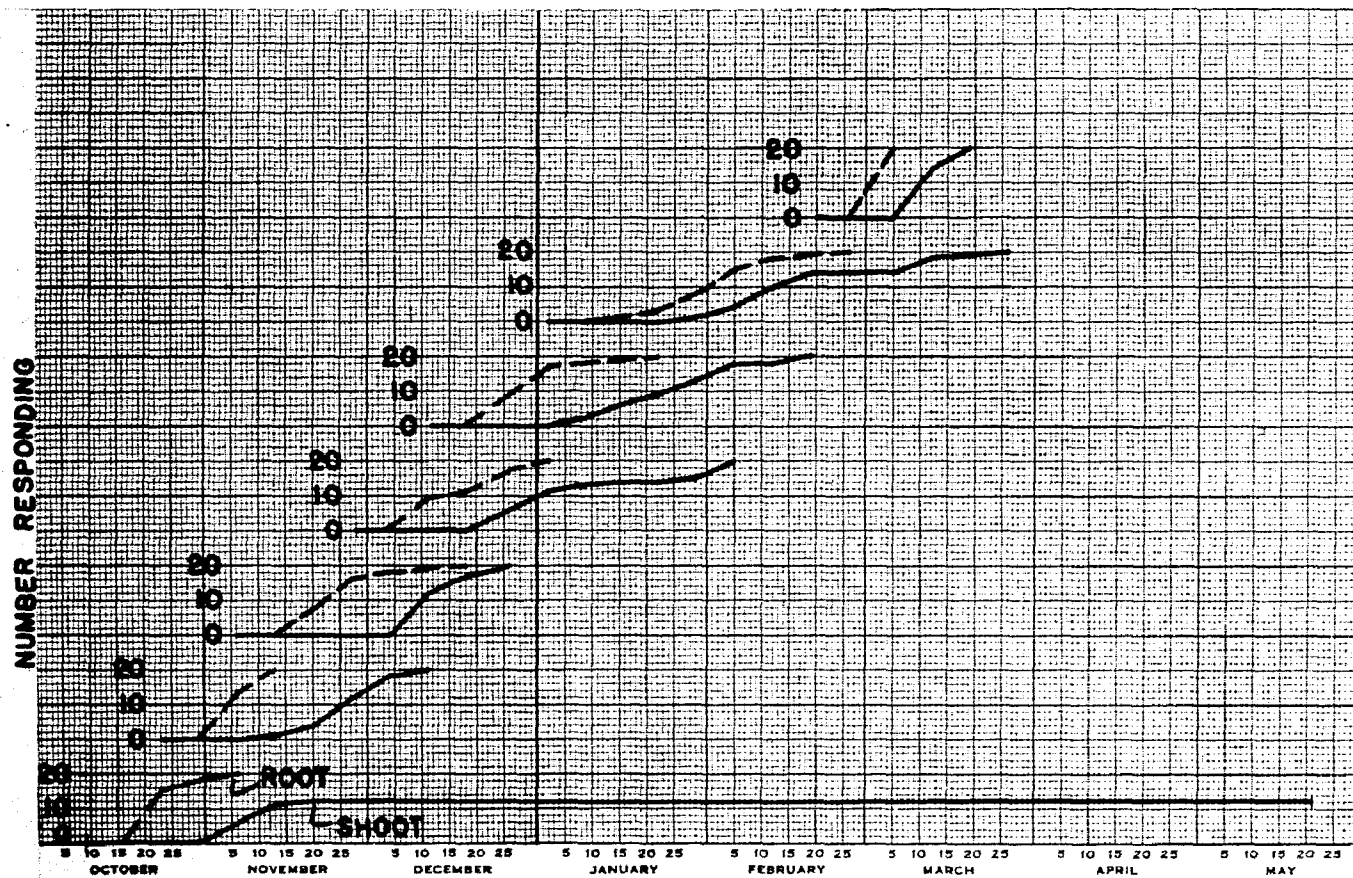


Fig. 7. The rate of root and shoot response from joints of jumping cholla in the growthroom. The beginning of a line indicates collection and planting date.



Immediately after collection, joints were placed on moist vermiculite and put in temperature-controlled boxes in the growthroom (described in the chapter on seed germination). The lowest temperature was that of the growthroom, but the flat used for that temperature was placed inside a box to obtain environmental conditions of light and photoperiod similar to the other treatments. Temperatures varied  $\pm 2^{\circ}$  C in the boxes;  $\pm 0.5^{\circ}$  C in the growthroom. Daylength was 14 hours with light intensity as described previously.

Temperatures of 25, 35, 45, and  $55^{\circ}$  C were tested during the non-dormant season; 30, 35, 40, and  $45^{\circ}$  C were tested in the dormant season. The narrower temperature range was used during the dormant season to define optimum temperature more closely.

Results -- Data for the two treatments within each season were similar, so the results were averaged (Table 7). During the non-dormant season, response was virtually the same for temperatures of 25, 35, and  $45^{\circ}$  C; both root and shoot development occurred rapidly. At  $55^{\circ}$  C, however, only one joint developed roots and none developed shoots.

During the dormant season, response to temperature was considerably different. Nine joints developed roots and five and six developed shoots at 30 and  $35^{\circ}$  C, respectively. At  $40^{\circ}$  C only three joints developed roots and none developed shoots; at  $45^{\circ}$  C there was no root or shoot development.

#### EFFECT OF PHOTOPERIOD

The onset and breaking of dormancy have been shown to depend on photoperiod in many cases (Wareing, 1956). Among species having a

Table 7. The number of joints of jumping cholla showing root and shoot response (R, S) at various temperatures during non-dormant and dormant seasons. Ten joints used for each treatment.

Days after Planting		Non-Dormant Season				Dormant Season			
		Temperature, °C				Temperature, °C			
		25	35	45	55	30	35	40	45
		----- Number -----							
10	R	0	0	1	0	1	2	0	0
	S	0	0	0	0	0	0	0	0
17	R	8	8	6	1	6	9	2	0
	S	2	4	4	0	0	1	0	0
24	R	10	9	7	1	8	9	3	0
	S	9	8	5	0	4	5	0	0
31	R	10	10	9	1	9	9	3	0
	S	10	9	9	0	8	6	0	0

demonstrated photoperiodic sensitivity, there appears to be no exception to the rule that dormancy is hastened by short days and delayed by long days. Dormancy occurs during a period of shortening days and is broken during a period of lengthening days. Furthermore, the critical photoperiod is the same in both cases; as the photoperiod falls below the critical level, dormancy ensues and as the photoperiod exceeds the same critical level, dormancy is broken.

Jumping cholla is different in that onset and breaking of shoot dormancy did not occur at the same photoperiod. Shoot dormancy began when the photoperiod was about 14.5 hours, and broke when the photoperiod was about 12 hours. In such a case, dormancy cannot be attributed to the stimulus of short days but must be regulated endogenously or by some other external stimulus. Nevertheless, a few photoperiod tests were made to determine their effect on shoot dormancy of jumping cholla.

Procedure -- Three joints were collected from each of 40 plants in June and July (the non-dormant season) to provide three treatments of 40 plants each. Joints were placed on moist vermiculite in the growth-room that was set up for a 14-hour day and a diurnal temperature variation of 22 to 38° C. Illumination was described previously. Since shoot dormancy naturally occurs at a photoperiod of about 14.5 hours, it was felt that if photoperiod were a controlling factor, shorter days would induce dormancy. Consequently, photoperiods of 10, 11.5, and 14 hours were tested.

Results -- The photoperiods tested did not induce shoot dormancy.

Results of both June and July treatments were similar. At the end of a 4-week period the mean number of joints showing shoot response was 38, 36, and 31 for the 10, 11.5, and 14-hour photoperiods, respectively. Although the data suggest greater shoot response with shorter days, a Chi-square test of independence did not demonstrate a significant difference between treatments.

#### EFFECT OF LIGHT QUALITY

In recent years the effect of light quality on various plant processes has been studied by a large number of workers. Of particular importance is the reversible pigment system called phytochrome which has absorption maxima at 660 and 730  $\mu$  according to the reaction



where  $P_r$  = phytochrome in the red-absorbing form and  $P_{fr}$  = phytochrome in the far-red-absorbing form. For convenience and by convention, red light will be used to denote radiation at 660  $\mu$ ; far-red light will be used to denote radiation at 730  $\mu$ .

A nonirradiated, dark-grown plant contains almost entirely  $P_r$  which is stable in the dark. Upon exposure to red light,  $P_r$  is converted to  $P_{fr}$  which absorbs predominantly at 730  $\mu$ .  $P_{fr}$  can be converted to  $P_r$  by exposure to far-red light or it can take place in the dark at physiologic temperatures and in the presence of oxygen. Direct knowledge of the phytochrome system has been summed up in recent papers by Butler, et al. (1959), Liverman (1960), and Butler, Siegelman, and Hendricks (1961).

Because of the sudden appearance and termination of shoot

dormancy in detached joints of jumping cholla, light quality was suspected as a possible controlling factor. Accordingly, experiments were devised to test the effect of radiation in the red and far-red portions of the spectrum.

Procedure -- Red light was obtained by using two layers of 300 PC Red Dupont cellophane under the fluorescent lights in the growthroom. Two layers of 300 PC Red and two layers of 300 MSC Dark Blue Dupont cellophane under incandescent lights in the growthroom were used to produce far-red radiation.

Joints were collected during the non-dormant season in the usual manner. Twenty joints were used for each treatment. Treatments were made on the same day as joints were collected. Treatments included: (1) exposure to usual growthroom illumination, (2) treatment with red light for 1/2, 1, and 2 hours followed by complete darkness for the duration of the study, (3) treatment with far-red light for 1/2, 1, and 2 hours followed by complete darkness for the duration of the study, and (4) complete darkness immediately after planting.

The growthroom was set up for a 14-hour photoperiod and a diurnal temperature variation of 22 to 38° C. The study was terminated at the end of four weeks.

Results -- Root and shoot development of joints having the usual growthroom illumination occurred as expected. Joints kept in complete darkness without a light treatment and those treated with red and far-red light had a reduced root response and virtually no shoot response. The number of joints having root response was 20, 12, 14, and

15 for normal light, red, far-red, and dark treatments, respectively. Shoot response in the same order of treatment was 11, 0, 1, and 1. The data given for the red and far-red treatments are averages. There was no significant difference between lengths of exposure to either red or far-red radiation.

#### EFFECT OF GROWTH-INFLUENCING CHEMICALS

Since temperature and photoperiod were not effective in breaking shoot dormancy of jumping cholla, an attempt was made to find chemicals that might initiate metabolic reactions leading to termination of dormancy.

The literature on the effects of a wide variety of chemical compounds on various aspects of plant growth is voluminous. Recent reviews of natural and synthetic auxins by Gordon (1954), van Overbeek (1959) and Fawcett (1961); gibberellins by Stuart and Cathey (1961); and kinetin and related compounds by Miller (1961) clearly attest the importance of numerous compounds in regulating various aspects of plant growth.

Although indole-3-acetic acid (IAA) has been reported in more than 30 species, incontrovertible proof of its presence by extraction and characterization has been provided only by Haagen-Smit, et al. (1946) for maize kernels and by Post (1959) in cabbage. The identification of indole compounds by chromatographic analysis (Fawcett, 1961), especially one-directional chromatography (Steward and Shantz, 1959), is questionable. For example, Dannenburg and Liverman (1957) identified indole-3-pyruvic acid (IPyA) by  $R_f$  values and Ehrlich's color reaction,

but further chromatographic and spectroscopic examination by Kaper and Veldstra (1958) showed that the compound was not IPyA. In view of the uncertainty of chromatographic identification, isolation and characterization of indole compounds is not only desirable but necessary.

The general effects of auxins on plants are initiation of root primordia and inhibition of axillary buds. Auxin either inhibits or promotes flower initiation and plays a part in the inception of leaf and bud (van Overbeek, 1952). Published reports since the review of van Overbeek support the earlier conclusions. Thus, inhibition of lateral bud development by auxin was reported by Khan and Hall (1954 a,b) for sugarcane cuttings, Brian, Hemming, and Radley (1955) and Wickson and Thimann (1958) for pea seedlings and pea stem sections, respectively, and by Skoog and Miller (1957) for tobacco stem segments. Enright (1958) reported the effectiveness of auxins for inducing rooting of Metasequoia cuttings. Many other examples of root initiation have been reported.

Gibberellins have been reported to induce or prolong dormancy of some species and break dormancy of others. Thus, Brian, Petty, and Richmond (1959 a) found that weekly applications of gibberellin to vegetative plants delayed the onset of dormancy in Acer pseudoplatanus, Betula pendula, Fraxinus excelsior, and Liriodendron tulipifera while other tree species such as Acer rubrum, Fagus sylvatica and Quercus robur were not affected. The following spring, bud break of Acer pseudoplatanus, Betula pendula, Fraxinus excelsior, and Sorbus aucuparia (Brian, et al., 1959 b) and Vitis vinifera (Weaver, 1959) was delayed

one to three weeks.

Conversely, applications of gibberellin to fully dormant Aralia cordata (Imazu and Osawa, 1958) and Hydrangea macrophylla (Stuart, 1959) promoted stem elongation and accelerated flowering. Marth, Audia, and Mitchell (1956) found that the first reaction of several species, including citrus and snapdragon, to gibberellin was elongation of main stems. When the rate of stem elongation decreased, lateral buds elongated in a bushy type of growth. Stems and terminal buds of oak and maple that had experienced a rest period, but had not yet begun to grow, were induced to elongate one to two weeks sooner than did untreated ones.

Gibberellin suppressed rooting of cuttings from pea and bean (Brian and Hemming, 1960) and citrus (Chailakhian and Nekrasova, 1958). Small dosages applied to the base of the cutting reduced rooting but did not affect stem extension. When such dosages were applied to the tip, the stems extended but rooting was not affected. Inhibition of rooting was thus entirely independent of shoot extension. Response was dependent on place of treatment. Gundersen (1958) found that repeated application of gibberellin to two species of Salix had only a slight effect on rooting. Root primordia were already present, however, so gibberellin inhibited the change of adult stems to a meristematic condition rather than inhibiting development of roots.

Recently kinetin has been recognized as a growth-promoting factor. It was isolated from aqueous slurries of deoxyribonucleic acid by Miller, et al. (1955). Shortly thereafter the structure was shown to



be 6-furfurylaminopurine and it was prepared from pure chemicals. In addition to stimulating cell division and cell enlargement, kinetin was found to greatly increase shoot initiation in Saintpaulia ionantha (Plummer and Leopold, 1957). Bud stimulation has also been reported for other species (Gorton, Skinner, and Eakin, 1957; Gorton and Eakin, 1957; Provasoli, 1958; and Mitra and Allsopp, 1959). All plants reported show some shoot formation without kinetin so the compound must be considered as a bud stimulator of plants that have an inherent tendency for bud formation.

Kinetin in the presence of casein hydrolysate and IAA increased the amount of rooting from tobacco stem callus (Skoog and Miller, 1957) at low concentrations but higher concentrations inhibited both the formation and growth of roots.

Kurz and Kummerow (1957) found that kinetin broke the rest period of winter buds of Hydrocharis. Dormancy of Lemna minor was also broken by kinetin (Deysson, 1959).

Other compounds reported to be effective in breaking bud dormancy include thiourea (Guthrie, 1940; Bokarev and Satarova, 1957; Ivanov and Satarova, 1958), thiocyanates (Ranjan and Ravindar, 1954; Bokarev and Satarova, 1957), ethylenechlorohydrin (Guthrie, 1940; Khudairi and Hamner, 1945; Ranjan and Ravindar, 1954; Thorup, 1957), xanthogenates (Ivanov and Satarova, 1958), and amino acids (LaMotte, 1960).

In view of the many reports dealing with breaking of dormancy or the initiation of root or shoot growth by chemicals, it was necessary to test a wide variety of compounds for their effectiveness in breaking

the shoot dormancy of jumping cholla joints.

Procedure -- Thirty-two compounds were tested at concentrations of 1, 20, and 400 ppmw. The compounds included 20 amino acids (tyrosine, aspartic acid, asparagine, alanine, arginine, isoleucine, methionine, phenylalanine, histidine, leucine, valine, glutamic acid, glutamine, cystine, glycine, proline, hydroxyproline, lysine, serine and threonine), five auxins or auxin precursors [tryptophan, 2,4-dichlorophenoxyacetic acid (2,4-D), IAA, indole-3-propionic acid (IPA) and indole-3-butyric acid (IBA)], and two purines (adenine sulfate and kinetin) plus potassium gibberellate, thiourea, glutathione, ammonium thiocyanate and ethylenechlorohydrin.

Ordinarily joint collections were made so that each treatment contained joints from the same plants, thereby eliminating the possibility of genetic variation. Thus, if a study required 10 joints per treatment and four treatments were planned, four joints would be collected from each of 10 plants. In this study there were 96 treatments: 32 compounds at three concentrations each. It was impossible to get that many terminal joints from a single plant, so the compounds were divided into five treatment groups. Compounds included in the treatment groups were: I. Tyrosine, aspartic acid, asparagine, alanine, arginine, isoleucine, methionine, control (distilled water) and check (no treatment). II. Phenylalanine, histidine, leucine, valine, glutamic acid, glutamine, cystine, and check. III. Glycine, proline, hydroxyproline, lysine, serine, threonine, adenine sulfate, control, and check. IV. Tryptophan, 2,4-D, IAA, IPA, IBA, potassium gibberellate and check. V. Kinetin, thiourea, ammonium thiocyanate, glutathione, ethylenechlorohydrin,

and check.

Collections and treatments for the five groups were made September 27 and 29, and October 4, 5, and 6, 1962. Joints were brought to the laboratory, treated by injecting 0.05 cc into each end of a joint, and placed on moist vermiculite. The first two groups were put into the growthroom with illumination as previously described, a 14-hour photoperiod and a diurnal temperature variation from 22 to 38° C. Lack of space in the growthroom necessitated keeping the remaining treatments in the greenhouse with the normal photoperiod for the season and less constant diurnal temperature variation.

Joints were checked at weekly intervals for a 10-week period to determine the number of joints in each treatment that had developed roots and shoots.

Results -- Since the results in the growthroom and greenhouse were not directly comparable, each will be developed separately.

A. Growthroom -- All joints of the check (no treatment) had developed roots at the end of 6 weeks; those of the control (distilled water) had all developed roots at the end of eight weeks (Fig. 8). All of the joints treated with the following amino acids had developed roots at the end of four weeks: methionine, 20 ppmw; alanine, 1 ppmw; asparagine, 1 and 20 ppmw; and glutamine, 1 ppmw. At the end of five weeks root development was completed for isoleucine, 1, 20, and 400 ppmw; arginine, 1 ppmw; alanine, 20 and 400 ppmw; aspartic acid, 1, 20, and 400 ppmw; and leucine, 20 ppmw. Rate of root development of all joints treated with the other amino acids equalled or exceeded that of the

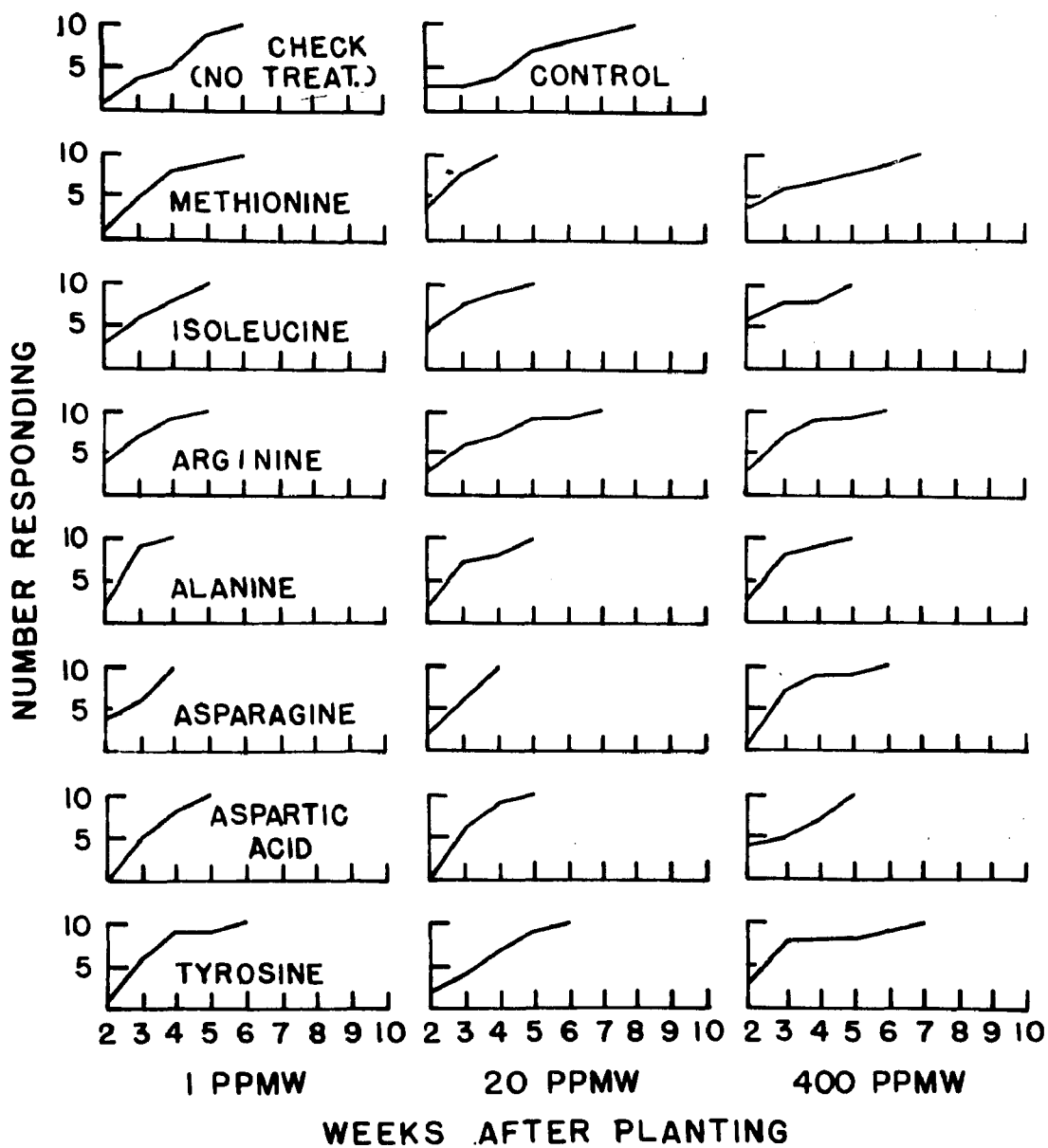


Fig. 8. Root response in the growthroom of joints injected with 0.10 cc per joint of various chemicals at concentrations of 1, 20, and 400 ppmw.

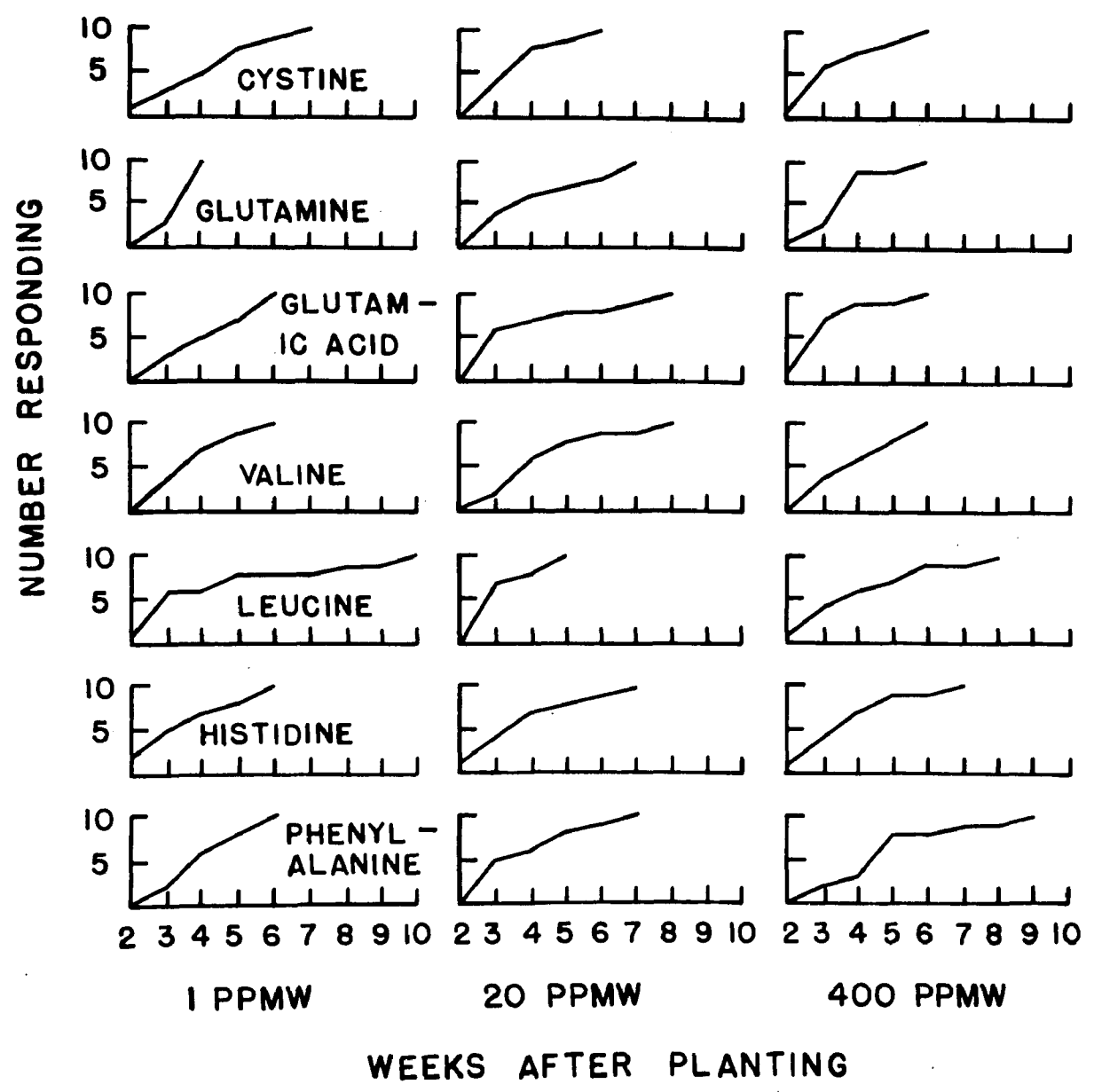


Fig. 8 (Cont'd.). Root response in the growthroom of joints injected with 0.10 cc per joint of various chemicals at concentrations of 1, 20, and 400 ppmw.

check. If the control is taken as a standard all amino acids caused an increased rate of root development except glutamic acid, 20 ppmw; valine, 20 ppmw; leucine, 1 and 400 ppmw; and phenylalanine, 400 ppmw.

Shoot development was either poor or non-existent for all treatments. The data are given in Table 8. Only three joints of the check had developed shoots at the end of the 10-week period, and only one of the control. There was no shoot response from any joints treated with five of the compounds. The others showed some response, but in no case did the response exceed that of the control.

B. Greenhouse -- At the end of nine weeks all joints treated with thiourea, ammonium thiocyanate, kinetin, and ethylenechlorohydrin at all concentrations had developed roots (Fig. 9). Joints treated with glutathione had developed roots for all concentrations at the end of 10 weeks. Root development was variable for joints treated with other compounds in the greenhouse, but none had root development on all joints at all concentrations.

Potassium gibberellate showed the most repression of root development. At the end of 10 weeks, the number of joints having root development was 5, 3, and 1 for concentrations of 1, 20, and 400 ppmw, respectively. The same downward trend of root response with increasing concentration was apparent for 2,4-D, but the repression was not so marked as was the case with potassium gibberellate.

There was no shoot response from any treatment within the 10-week period of the study.

Table 8. Shoot response of jumping cholla joints at the end of 10 weeks that had been injected with 0.10 cc per joint with various chemicals at concentrations at 1, 20, and 400 ppmw.

Compound	Conc., ppmw			Compound	Conc., ppmw		
	1	20	400		1	20	400
----- Number -----							
<u>GROWTHROOM</u>							
Tyrosine	0	0	0	Histidine	1	1	1
Aspartic Acid	0	1	0	Leucine	2	1	1
Asparagine	0	1	0	Valine	0	0	0
Alanine	0	0	0	Glutamic Acid	1	2	1
Arginine	0	0	0	Glutamine	0	0	1
Isoleucine	0	0	0	Cystine	1	0	3
Methionine	0	0	2	Control (Dist. Water)		1	
Phenylalanine	3	2	0	Check (No Treatment)		3	
<u>GREENHOUSE</u>							
Glycine	0	0	0	NH <sub>4</sub> thiocyanate	0	0	0
Proline	0	0	0	Ethylenechlorohydrin	0	0	0
Hydroxyproline	0	0	0	Tryptophan	0	0	0
Lysine	0	0	0	2,4-D	0	0	0
Serine	0	0	0	IAA	0	0	0
Threonine	0	0	0	IPA	0	0	0
Adenine sulfate	0	0	0	IBA	0	0	0
Kinetin	0	0	0	Potassium gibberellate	0	0	0
Thiourea	0	0	0	Control		0	
Glutathione	0	0	0	Check		0	

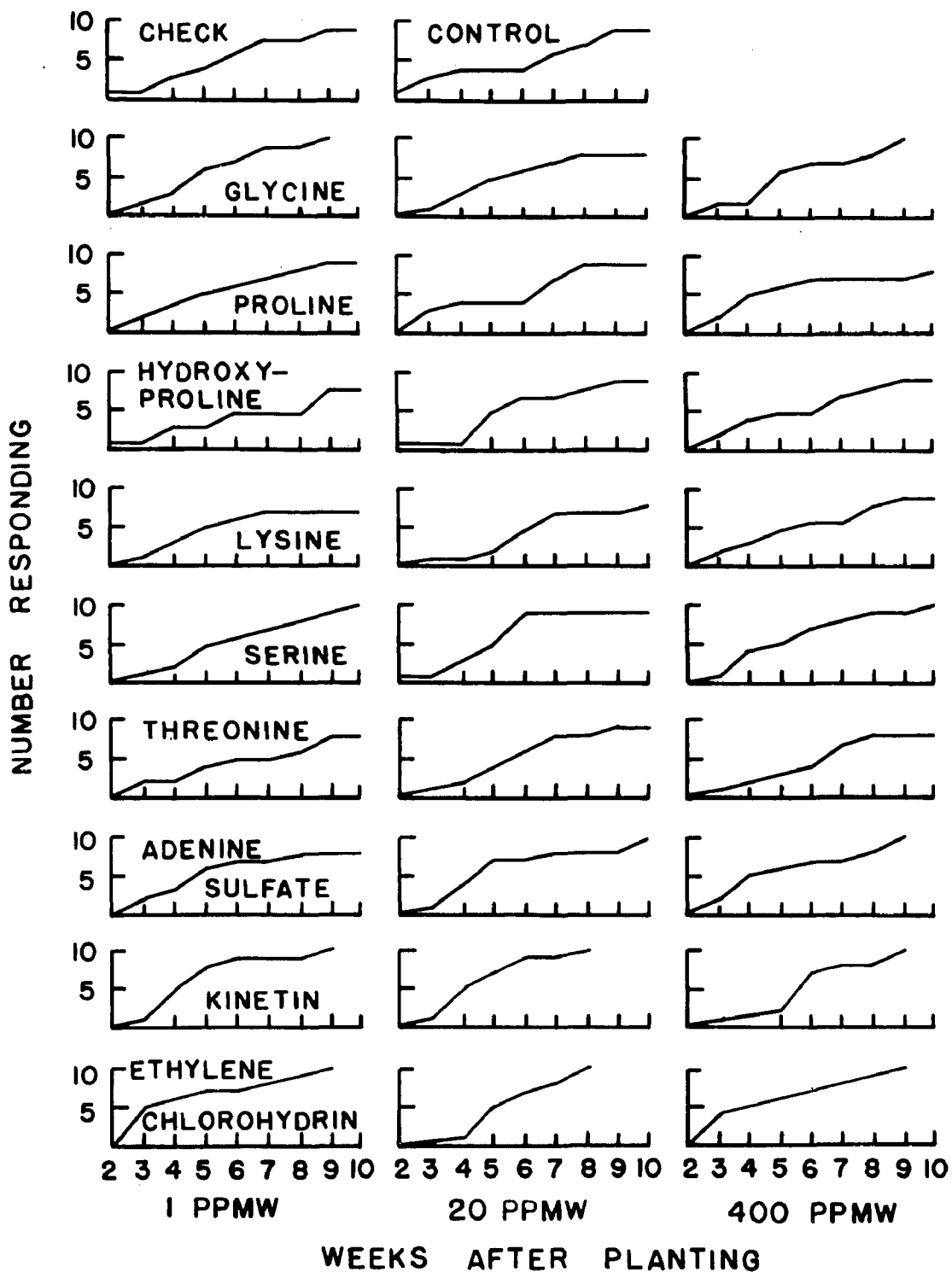


Fig. 9. Root response in the greenhouse of joints injected with 0.10 cc per joint of various chemicals at concentrations of 1, 20, and 400 ppmw.



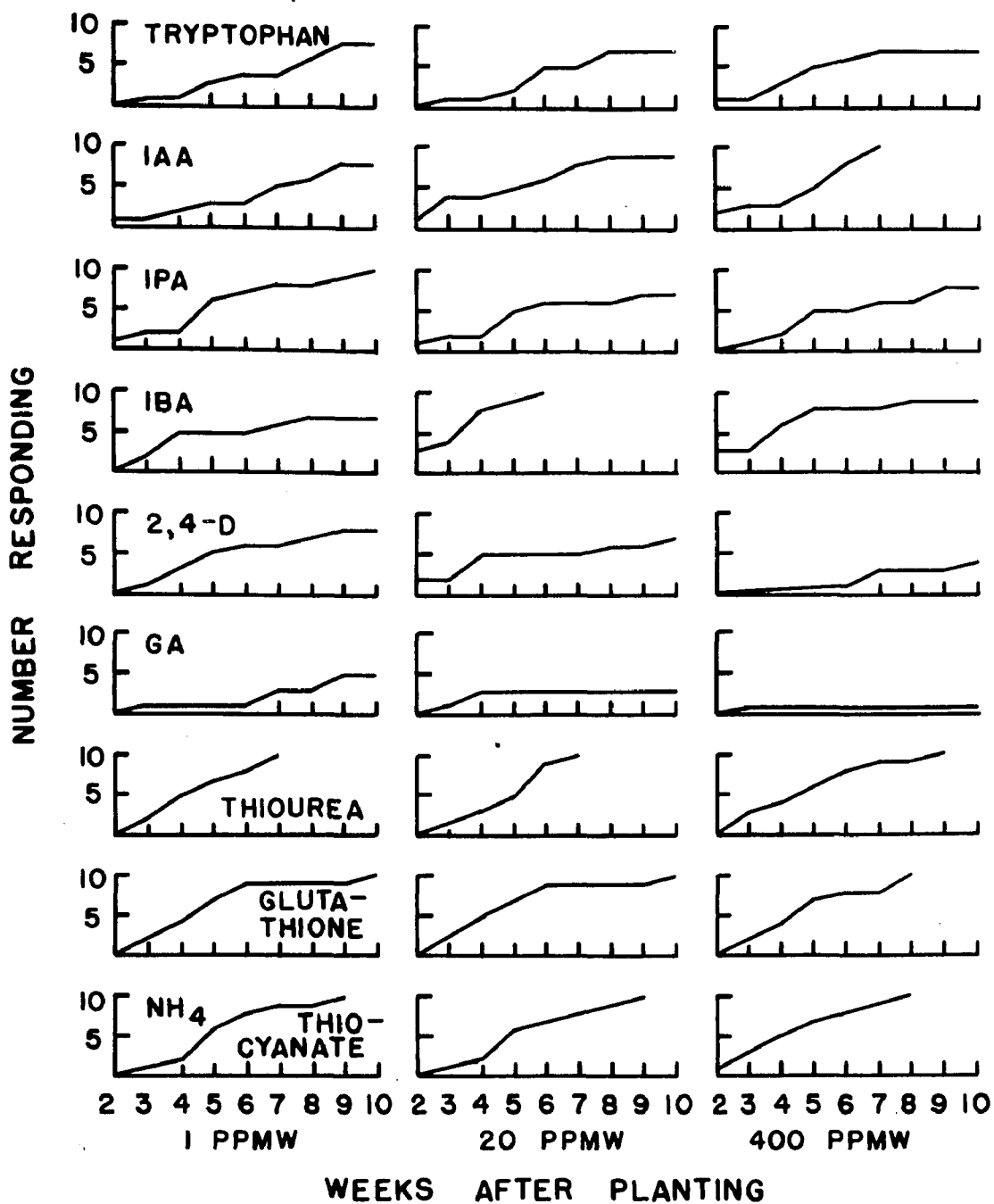


Fig. 9 (Cont'd.). Root response in the greenhouse of joints injected with 0.10 cc per joint of various chemicals at concentrations of 1, 20, and 400 ppmw.

## DISCUSSION

There are several peculiar aspects of the dormancy of jumping cholla joints. In the field, new growth on established plants begins after the start of the summer rainy season, which usually begins in early July and continues through August and part of September. Only two exceptions have been noted to the mid-summer growth of jumping cholla. Plants in northern Yuma County had new joints 1 to 2 inches long in March 1962. In May of the same year, almost all plants of a small colony of jumping cholla near Sasabe, Arizona had new joints. In all other cases, new growth has been observed only during the summer rainy season. In general, then, established plants initiate new joints during the summer rainy season.

The initiation of new shoot growth is quite different when joints are detached from the parent plant and are brought into the greenhouse for study. A study of the seasonal response of detached joints showed that the joints became dormant (delayed shoot development) during the summer rainy season and remained dormant until the following April.

Shoot dormancy of newly harvested joints started in late July and ended in February.

Thus, there are three aspects to the problem of shoot dormancy for jumping cholla: (1) established plants usually initiate new joints during the summer rainy season, (2) joints detached from the parent plant exhibited shoot dormancy from mid-summer to late winter; shoot dormancy of joints collected during that period was broken in April, and (3) joints collected from late winter to mid-summer initiate shoot development quickly in the greenhouse.

It must be granted that in defining three aspects to the problem of shoot dormancy, mature plants as well as detached joints were considered. Established plants would not necessarily be expected to exhibit the same responses as detached joints. Nevertheless, including established plants in the discussion of shoot dormancy augments the information about the species. When only the detached joints are considered, there are still two patterns of shoot dormancy. Some of the joints collected from late July to mid-February exhibited shoot dormancy which was broken in April. But joints collected from mid-February to April did not exhibit shoot dormancy. Why did not dormant joints initiate shoot growth in mid-February rather than in April? An answer to that question offers an interesting and challenging research problem.

A difference was noted between shoot response in the greenhouse and growthroom. Extended shoot dormancy in the growthroom occurred only for the October 9 collection. These joints were transferred to the greenhouse on April 16 and did not initiate shoot growth in April as was the case with other collections during the dormant period. One year and three months after collection there still was no shoot response for the eight joints exhibiting dormancy. Joints of other collection dates developed shoots within a 2 to 3-month period.

Some environmental difference caused dormancy in the greenhouse but not in the growthroom.

Length of photoperiod cannot be considered a controlling factor. Dormancy was first noted in the greenhouse for a collection of joints made on July 31. At that time the photoperiod at this latitude is 14.5

hours if morning and evening twilight, with the sun from 0 to 6° below the horizon, are included. Joints remained dormant with progressively shorter photoperiods down to slightly more than 11 hours on December 21 and then progressively longer photoperiods to about 12 hours when dormancy was broken in February. The 14-hour photoperiod maintained in the growthroom for the seasonal study was shorter than natural photoperiod at inception of dormancy and longer than natural photoperiod when dormancy was broken.

Specific work on length of photoperiod also showed that day-lengths of 10 to 14 hours did not significantly affect shoot dormancy. It must be concluded, therefore, that photoperiodism is not an operative factor in controlling the dormancy of jumping cholla.

Temperature differences between the growthroom and greenhouse are not of great magnitude. Figure 10 shows the maximum and minimum temperatures in the greenhouse during 1961. Means of consecutive 10-day periods are plotted. Also shown are the monthly maximum and minimum temperatures for Tucson during 1961 and for the growthroom from October 1961 to the end of the year. During this period joints used for testing seasonal response of roots and shoots were kept in the growthroom as well as in the greenhouse.

The temperature data are not revealing. At the time cholla joints became dormant (July 31) there was little difference between greenhouse and outside for both maximum and minimum temperatures. Also, the temperatures at that time are almost the same as those maintained in the growthroom later in the year. Since reasonably good shoot response

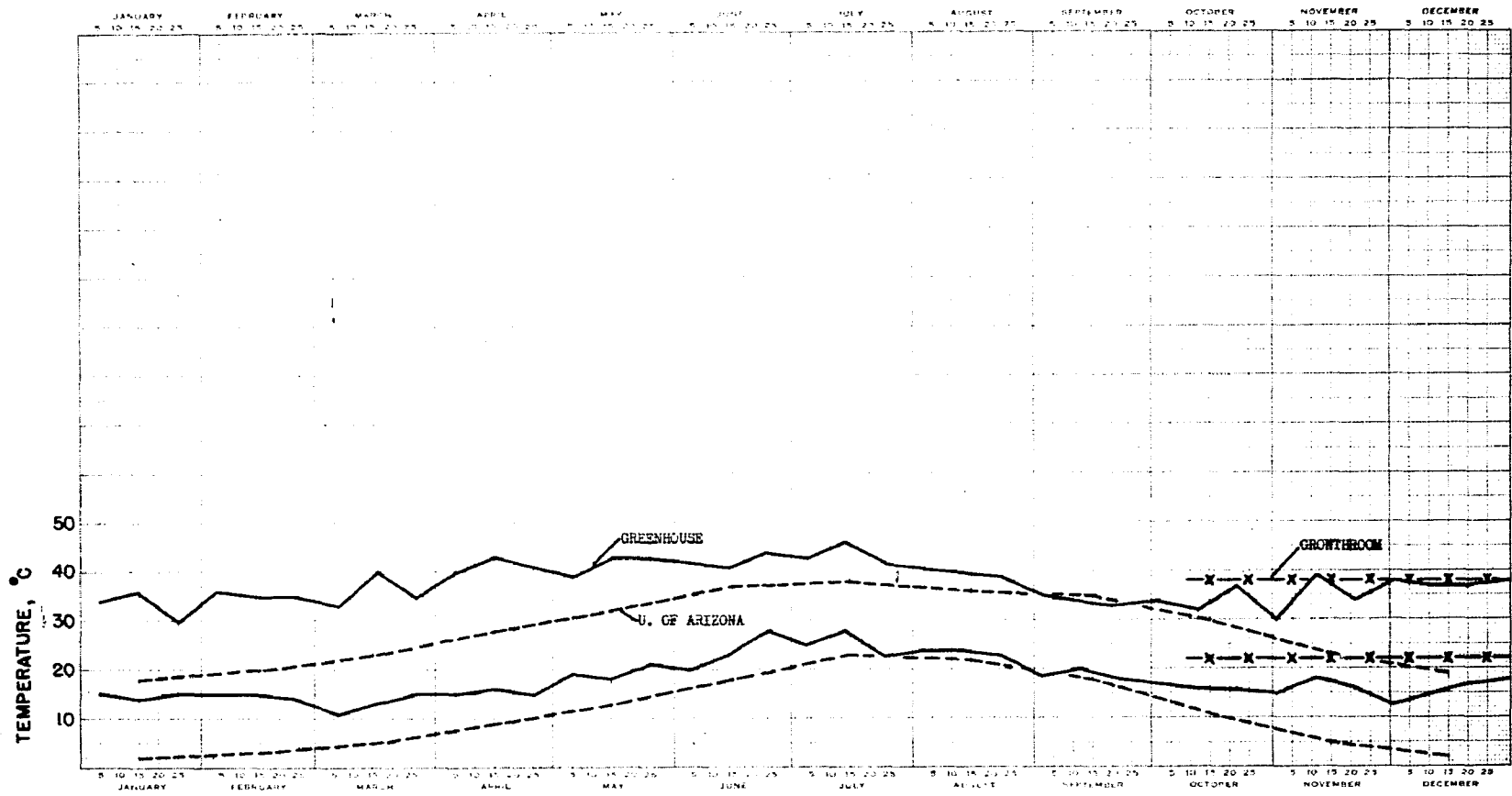


Fig. 10. Maximum and minimum temperatures for Tucson (University of Arizona), the greenhouse throughout 1961, and in the growthroom from October 9, 1961 to the end of the year.

was obtained in the growthroom, but not the greenhouse, shoot dormancy should not have occurred when it did if temperature were a controlling factor.

For the last three months of 1961, maximum temperatures were variable in the greenhouse, but were near those maintained in the growthroom. Minimum temperatures for the same period averaged 5 to 7° C below those of the growthroom. If the minimum temperature differences were to account for the differential shoot response between the greenhouse and growthroom from October to January, then shoot development should have occurred in the greenhouse during August and the first two weeks of September. Joints collected in August and September exhibited shoot dormancy in the greenhouse, however.

Temperature data do not provide a reasonable explanation for the differential response between greenhouse and growthroom.

Light intensity in the growthroom and greenhouse is about 2200 ft-c; radiant energy is about 0.1 to 0.2 g cal/cm<sup>2</sup> sec. The lack of differences between light intensity or total radiant energy in the greenhouse and growthroom precludes a discussion of those factors and their relation to shoot dormancy.

Since temperature, photoperiod and light intensity cannot be specifically implicated in joint dormancy, a variable that appears logical and may account for the different response between growthroom and greenhouse is light quality.

When the radiant energy of sunlight is compared with that of the growthroom, relative intensities differ in some portions of the spectrum. Table 9 shows the relative intensities in the spectral regions proposed

Table 9. Radiant energy of spectral bands in sunlight and growthroom.

Spectral Region	Sunlight*	Growthroom	S/GR
nm	watts/m <sup>2</sup>	watts/m <sup>2</sup>	
400-510	108	44	2.45
510-610	118	83	1.42
610-700	102	28	3.64
700-920	174	24	7.25
920-1100	96	26	3.69
1100-1400	64	34	1.88
1400-1900	49	36	1.36
1900-∞	9	36	0.25
	740	311	2.38

\*Taken from Brooks (1956): Moon's recommended sea level direct beam sunshine; solar angle = 30°, air mass = 2.

by the Dutch Committee on Plant Irradiation (Wassink, 1953) for sunlight and the growthroom. Sunlight intensity is greater for all regions except 1900  $m\mu$  to infinity.

Considering only that portion of the spectrum from 400 to 1100  $m\mu$ , the ratio of intensity in sunlight to intensity in the growthroom is relatively constant except for the regions from 510 to 610  $m\mu$  and from 700 to 920  $m\mu$ . In the first region sunlight has lower intensity and in the latter a far greater intensity. The conversion of phytochrome to the red-absorbing form is affected by the radiation in the 700 to 920  $m\mu$  region (specifically 730  $m\mu$ ).

More important than the total radiation intensity in sunlight and the growthroom are the relative intensities at 660 and 730  $m\mu$ . Such a comparison shows (Fig. 11) that in sunlight the ratio of red to far-red is 1.05 and that of the growthroom is 2.33. If the energy requirements for photoconversion are the same for both  $P_r$  and  $P_{fr}$ , the relative amounts of pigment present in a plant would be dependent on relative radiation intensity in the two regions.

The ratio of 1.05 in sunlight indicates that equimolar concentrations of the two pigment forms would be present during the light period.  $P_{fr}$  changes slowly to  $P_r$  in darkness (half-life of about 2 hours). At the end of a 10-hour dark period, only 1.56 percent of  $P_{fr}$  would remain. Equimolar concentrations would be quickly re-established after exposure to sunlight.

In the growthroom, however, the red/far-red ratio is 2.33. Using the same assumptions as above, 70 percent of the pigment would be  $P_{fr}$  at the end of a light period. A 10-hour dark period would reduce



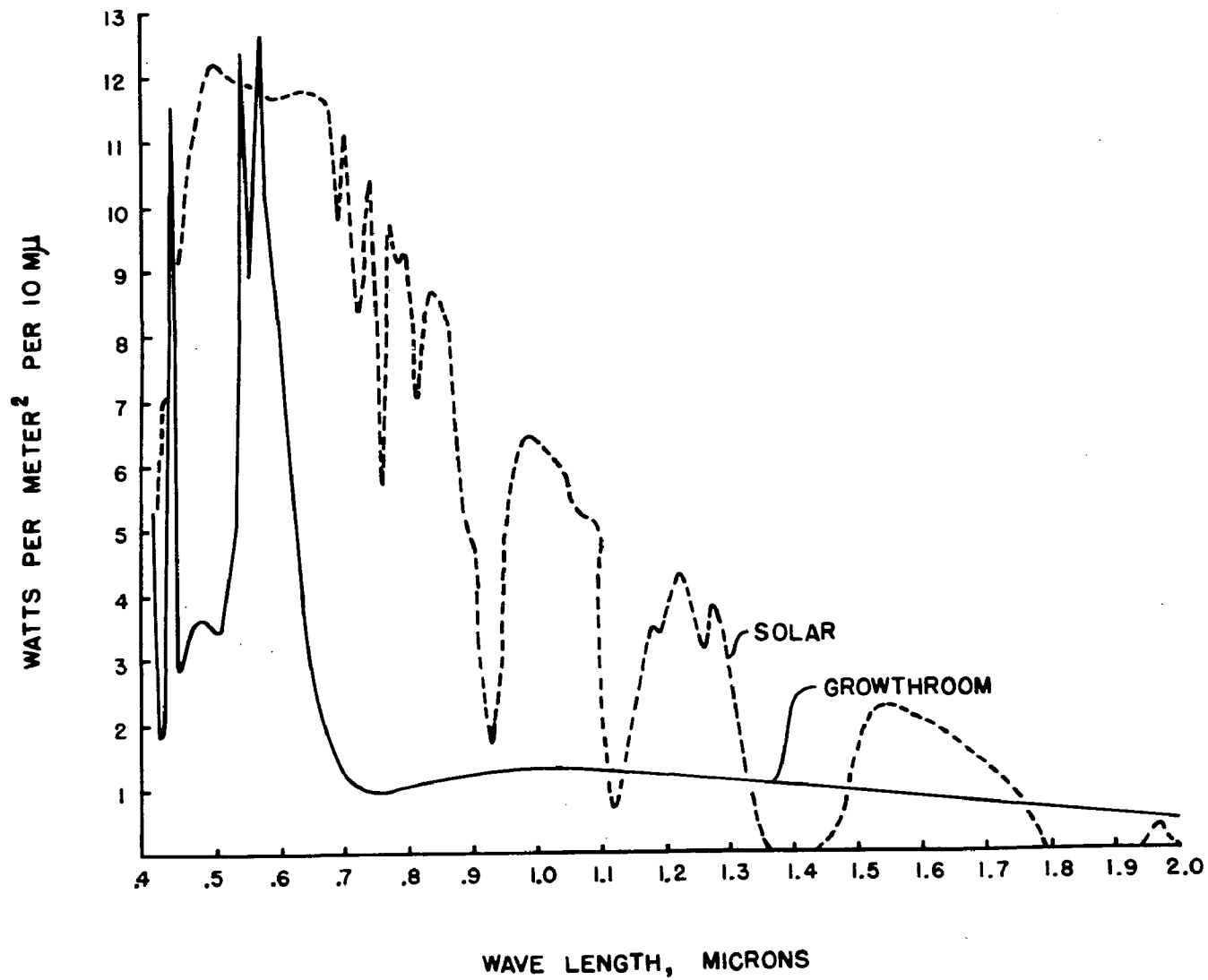


Fig. 11. Radiant energy of sunlight and lamps used in the growthroom. Solar radiation assumes a solar angle of 30° and an air mass of two.

$P_{fr}$  to 2.69 percent and 12 hours would further reduce the level to 1.35 percent, or about the same as the level reached during a 10-hour dark period for plants in sunlight. If  $P_{fr}$  is the active pigment capable of stimulating shoot development, the greater relative energy at 660 m $\mu$  in the growthroom might account for shoot development in the growthroom when it does not occur in the greenhouse.

The theory given above, which may account for differential shoot response in greenhouse and growthroom, does not explain why shoot dormancy of newly harvested joints begins abruptly in mid-summer and ends abruptly in late winter.

Temperature may offer a partial explanation for shoot dormancy. During the non-dormant season, root and shoot development occurred normally at temperatures of 45° C, but only one joint developed roots at 55° C, and no joints developed shoots. During the dormant season, however, development was repressed at a constant 40° C.

Cacti are known to be able to withstand high temperatures. McDougal and Working (1921) found that joints of Opuntia (species not given) continued to enlarge in an air temperature of 58° C when internal temperature of the joint was 56.5° C. Growth of joints stopped when the internal temperature reached 62° C, but resumed growth when the internal temperature dropped to 50° C. Young cacti and other desert plants must be able to withstand extremely high temperatures. For example, Sinclair (1922) recorded temperatures at various distances above and below the ground at the Carnegie Desert Laboratory in Tucson on a hot day in June. Temperatures at 4 and 183 cm above the soil surface and 0.4 and 2 cm below the soil surface are given in Figure 12. Maximum air temperature

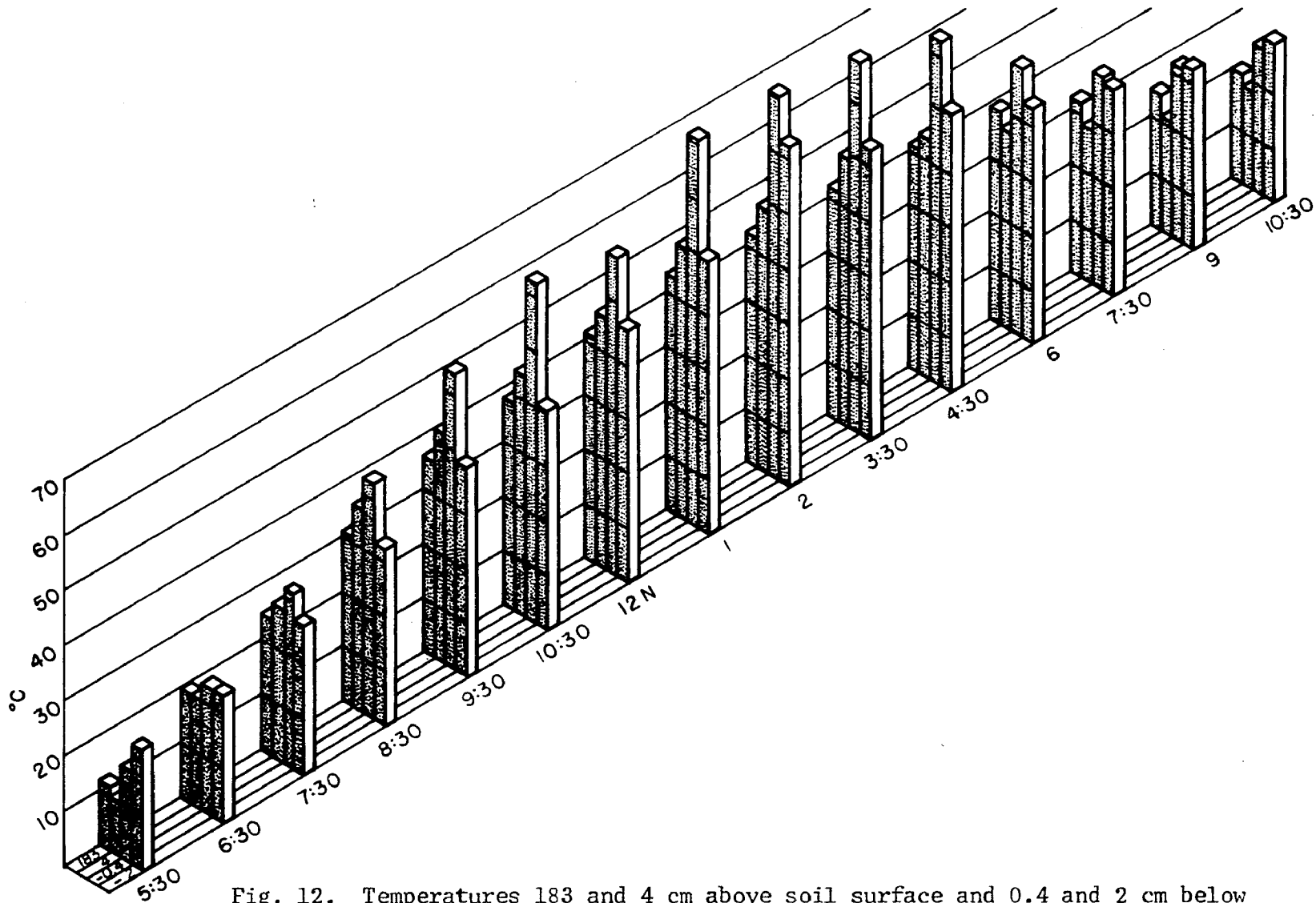


Fig. 12. Temperatures 183 and 4 cm above soil surface and 0.4 and 2 cm below soil surface on June 21, 1915 (From Sinclair, 1922).

in a standard Weather Bureau shelter (183 cm) reached  $42.5^{\circ}$  C at 1:00 PM. At the same time, temperatures were  $49.7^{\circ}$  C at 4 cm,  $71.5^{\circ}$  C at  $-0.4$  cm, and  $50.4^{\circ}$  C at  $-2$  cm. Those were the high temperatures for the day except for the  $-2$  cm thermometer which registered  $62.1^{\circ}$  C at 2:00 PM.

Such extremely high temperatures assuredly would have adverse effects on young tissue not yet insulated against temperature extremes. The difference in response between dormant and non-dormant seasons may be a mechanism to evade extreme high summer temperatures.

The highest temperatures occur from May through September. Maximum temperatures recorded from the University of Arizona weather station for that period are  $43.9^{\circ}$  C for May and  $44.4^{\circ}$  C for the other months. The driest months of the year, May and June, coincide with the highest temperatures. Precipitation data from the same weather station show an average of only 0.19 inch for May and 0.29 inch for June. Furthermore, there is an average of only one day for each month having precipitation of 0.10 inch or more.

Root and shoot response will not occur unless the joint is in contact with a moist surface. Thus, although May and June are in the non-dormant period, root and shoot response from severed joints in the field would be prevented by lack of moisture. By the time the summer rains start, accumulation of degree days may have been great enough to cause an unspecified metabolic change that induces dormancy. An essential metabolite may be thermolabile or the enzyme that catalyzes the essential metabolite may be thermolabile.

There is evidence to support the concept of high-temperature induced dormancy. Horowitz and Fling (1953) found the tyrosinase of

thermostable strains of *Neurospora* to be more thermostable than the tyrosinase of thermolabile strains. Among higher plants Bonner (1943) and Langridge and Griffing (1959) were able to partially cure temperature lesions by the addition of chemicals to the nutrient medium. The subject of biochemical adaptation was partially reviewed by Kurtz (1960).

Although temperature variation does not explain the different response in greenhouse and growthroom, it may explain dormancy during the summer rainy season.

The study on chemical injection of joints cannot be treated as a unit because some of the joints were kept in the growthroom and others in the greenhouse. Shoot growth can be disregarded. No joints developed shoots in the greenhouse; a few sprouted in the growthroom, but in no case did chemical injection induce more sprouting than occurred in the control or check. Factors that may affect the differential response between greenhouse and growthroom have already been discussed.

Rate of root response for all treatments in the growthroom did not differ greatly from the check. If a 2-week difference in rate of response between treatment and control is considered significant, root development was stimulated by alanine at 1 ppmw, asparagine at 1 and 20 ppmw, methionine at 20 ppmw, and glutamine at 1 ppmw. Using the same criteria, rooting was repressed by distilled water, valine at 20 ppmw, glutamic acid at 20 ppmw, phenylalanine at 400 ppmw, and leucine at 1 and 400 ppmw. Lack of trends with increasing or decreasing concentration cast doubt on the validity of a 2-week difference being significant, however.

In the greenhouse root response was stimulated by thiourea,

ammonium thiocyanate, kinetin, and ethylenechlorohydrin. Root response was repressed by gibberellic acid at all concentrations and by 2,4-D at 400 ppmw. Other treatments did not differ essentially from the check.

The greater repression of root response by GA as compared with 2,4-D was surprising. Although GA is known to inhibit root initiation, its effect was not expected to be so great. At the end of the study, two joints treated with GA at 20 ppmw and three at 400 ppmw had died. With 2,4-D no joints died at the two lower concentrations, but six of those treated with 400 ppmw had died.

Although a number of chemicals affected rate of root response, there was no effect on shoot response. More work is needed during both dormant and non-dormant seasons.

## RATE OF GROWTH AND POPULATION DYNAMICS

Another phase of the investigations of the ecologic relations of jumping cholla determined the approximate rate of growth. Secondary considerations were invasion potential and population dynamics. Such knowledge is important for an understanding of population fluctuations. In addition, intelligent management decisions cannot be made without a clear perception of population dynamics.

### GROWTH RATE

The study to determine growth rate was conducted on the Santa Rita Experimental Range located about 30 miles southeast of Tucson on a gently-sloping bajada dropping to the northwest from the Santa Rita Mountains. The area is Desert Grassland (Shantz and Zon, 1924) that has been invaded by woody plants, particularly mesquite (Prosopis juliflora var. velutina), cholla (Opuntia spp.) and burroweed (Haplopappus tenuisectus). The lowest elevations of the SRER are occupied by creosote bush (Larrea tridentata) with occasional palo verde (Cercidium microphyllum) and saguaro (Carnegia gigantea). More complete characterization of the Desert Grassland can be obtained from the publications of Shantz and Zon (1924), Shreve (1951) and Humphrey (1958).

Procedure -- There are many photo stations on the SRER permanently marked so that photos of the same area can be taken at any time. Not all of the photo stations were established in the same year, and retakes

were not made systematically. Since it was desirable to have the same elapsed time for all plants of jumping cholla involved in determination of growth rate, only those photo stations were selected that had been photographed in the same previous year. A sample of 126 plants was obtained from photo stations that had been photographed in 1948. Photos were again taken from these photo stations in 1960.

The 1948 photos were contact prints made with a 5 x 7 camera having a lens with a different focal length than the 4 x 5 camera currently available. A conversion factor was calculated by retaking a 1948 photograph in which a fence was present. Measurement of post height on the 1948, 5 x 7 photo and the 1960, 4 x 5 photo provided the appropriate conversion factor. Dividing the object height on the 1948 photo by 1.5 converted the height to its 4 x 5 equivalent.

A table was then prepared showing the relationship between distance from the lens in feet, actual plant height in feet and plant height on a 4 x 5 print in mm. In practice, plant height was measured at the time a photo was taken so that the distance from the lens could be determined from the table. Knowing the distance, the height of the plant on the 1948 photo could be determined and the amount of growth in the 12-year period obtained by subtraction.

Height determination from a photo was accurate to within three inches up to 85 feet and within six inches up to 150 feet. At distances greater than 150 feet the method was not reliable because of the difficulty of accurately locating the base of the plant and because very small differences on the photo represented large differences in actual plant height.



Results -- Height of the 126 plants used in the study varied from 4 to 76 inches in 1948. Plotting the mean height against growth during the 12-year period, a regression was established as shown in Figure 13. The regression coefficient of  $0.67 \pm 0.29$  represents a mean annual growth of 0.67 inches for all size classes during the 12-year period. Growth rate was greatest for small plants and there was an actual decrease in height of larger plants. The decrease in height is real. Joints and branches of senescent plants lose turgidity and the plant assumes a droopy, umbrella-like appearance. The difference between healthy and senescent plants is shown in Figure 14. As senescence progresses, there is a gradual deterioration toward the base of the plant.

Within the 95 percent confidence interval shown in Figure 13, senescence started after plants had reached a height of 48 to 70 inches. The data apply only to plants on the SRER, however. In other locations jumping cholla grows much larger.

When the data of Figure 13 were plotted to show age as a function of plant height, it was found that most jumping cholla plants on the SRER reached maximum size in about 40 years. If the curve were extrapolated beyond 40 years, senescence would be shown by a diminution of plant height. It was not possible, however, to determine the rate of senescence.

Photographic evidence from the SRER lends further support to the belief that the life span of jumping cholla is about 40 years. The series of photos shown in Figure 15 were taken from the same point over a period of about 59 years. In 1903 (approximate date) only a few

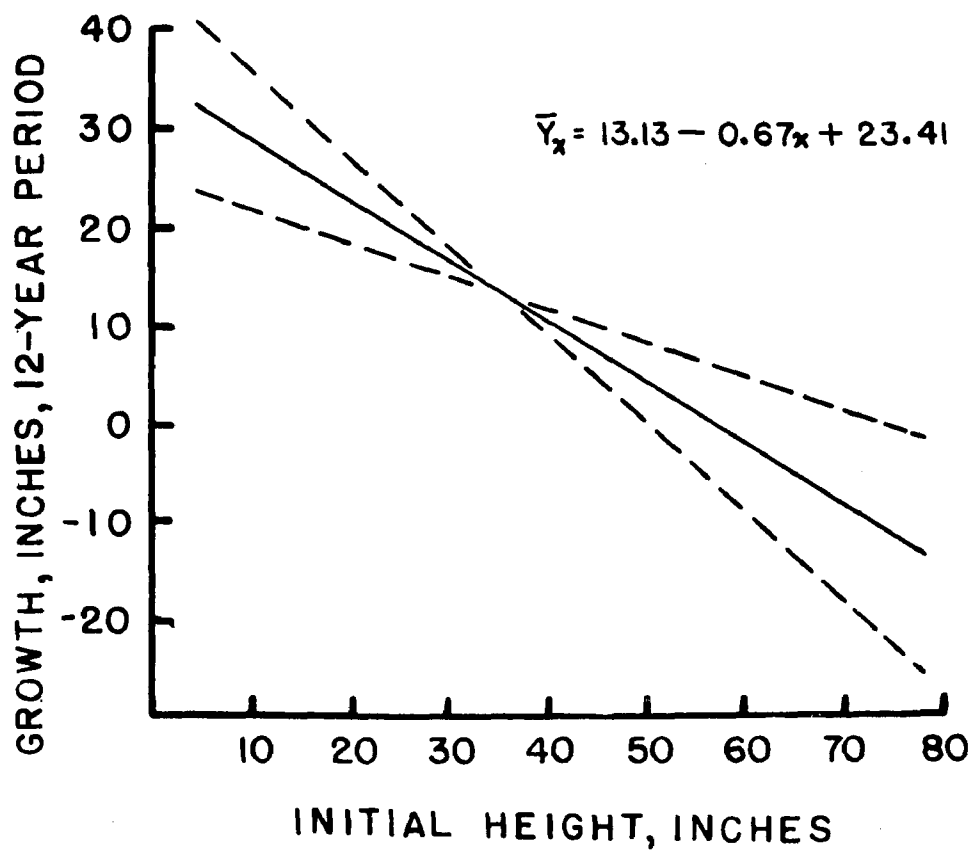
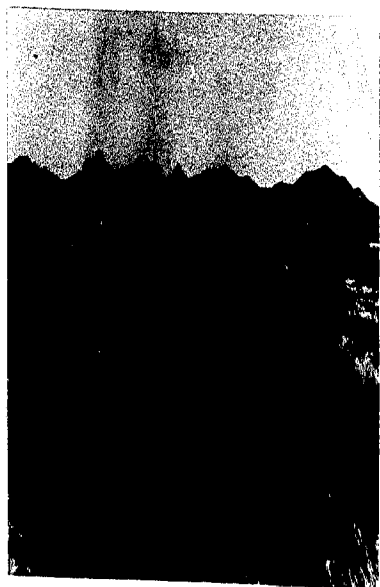


Fig. 13. Growth of jumping cholla during a 12-year period as influenced by initial height. Regression coefficient =  $0.67 \pm 0.29$ .



Fig. 14. Top: Umbrella-like appearance of a senescent plant.  
Bottom: Turgid, erect appearance of a healthy plant.



1903



1948



1960



1940



1951

Fig. 15. Invasion and retrogression of a jumping cholla population. All photos taken from the same point during a 59-year period.

mature plants of jumping cholla were present. Density increased through 1940, but by 1948 senescence and death were apparent. Only a few living plants remained in 1951 and further retrogression was evident in 1960. The life span in this case appears to be about 40 years.

#### POPULATION DYNAMICS

Cursory observations of jumping cholla populations reveal such intriguing problems as: (1) plant size variation depending on the vegetation type in which the stand is found, (2) the large number of young plants found in some stands and the complete absence of young plants in others, and (3) the die-off of jumping cholla in relatively large areas.

Procedure -- Height measurements were made in six jumping cholla populations in the Sonoran Desert and four in the Desert Grassland. Five hundred plants constituted a sample for each stand. Plant height was measured to the nearest six inches. Each stand was characterized by its associated vegetation, elevation, and precipitation at the nearest rain gauge.

Results -- Although plant size could not be correlated specifically with elevation, a difference was found when stands from the Desert Grassland sites were compared with those from the Sonoran Desert.

The Desert Grassland sites were characterized by an abundance of mesquite with an understory of burroweed and perennial grasses. Rainfall varies from 12 to 18 inches annually. Maximum plant heights on the four areas were 60, 66, 76, and 78 inches.

The Sonoran Desert sites were characterized by the presence of some mesquite associated with palo verde, saguaro, bursage (Franseria deltoidea), and annual grasses. Rainfall of 8 to 12 inches within the area where measurements were made causes a wider spacing of vegetation than in the Desert Grassland. Maximum plant heights at six areas in the Sonoran Desert were 108, 120, 132, 138, 144, and 174 inches. Clearly, jumping cholla plants are larger under more arid conditions.

An analysis of size-class distributions from the different areas shows three distinct population types. The populations may be defined as invading, mature, and senescent.

A young, invading stand is characterized by having a majority of plants in the small size classes with a decreasing number in the progressively larger size classes. A mature stand is characterized by having a large number of plants in the smallest size classes followed by a precipitous drop in numbers for the next few larger size classes and then a normal, bimodal curve for the remaining size classes. A senescent stand is characterized by a normal curve in which the highest frequencies are found in the intermediate size classes.

Curves for the three population types are shown in Figure 16. Height measurements can be used to classify stands as invading, mature or senescent. The duration of each period is not known, but the relative age can be determined by getting the closest fit to one of the three lines shown in Figure 16.

## DISCUSSION

The distribution of jumping cholla is more closely associated

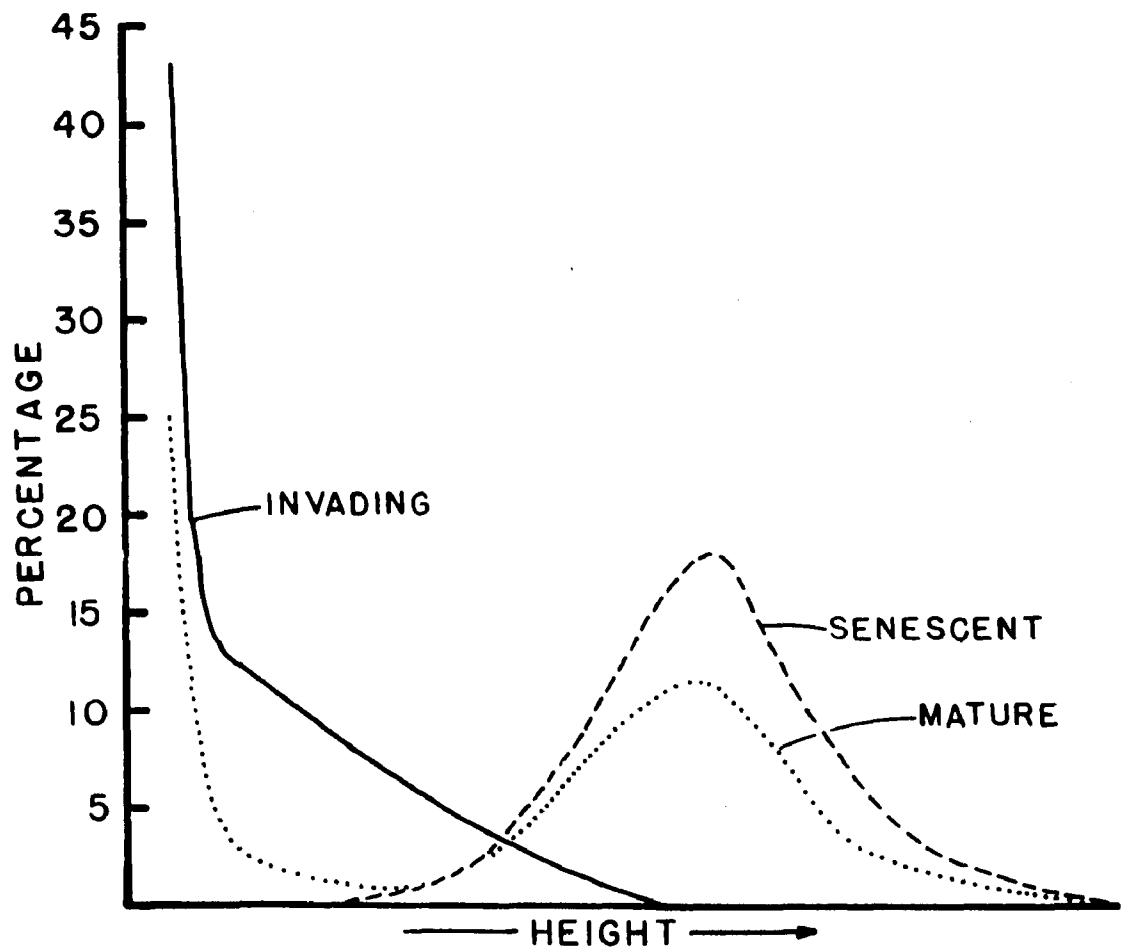


Fig. 16. Characteristic size-class frequency curves for three population types of jumping cholla.

with the Sonoran Desert and its ecotone with the Desert Grassland than with the Desert Grassland, per se. Consequently the Sonoran Desert is assumed to be the center of jumping cholla distribution. If this is true, the size of jumping cholla disagrees with the observation of Shreve (1940) that many desert plants find their optimum conditions for growth and development near the periphery of their ranges. There is no evidence to suggest that jumping cholla grows faster under more arid conditions, but plants are larger in the more arid regions of its distribution.

The distribution of size classes shown for an invading stand is expected. Jumping cholla has a high potential for vegetative reproduction so a relatively few plants in an area would provide joints for further propagation.

The size class distribution of a mature stand is also expected. Most of the plants represented in the 0.5-ft class are fallen joints that are rooted and may or may not have developed shoots. Many of these will die, so that the percentage of plants in the 1 to 3-ft classes is low. The accumulative establishment of plants over a period of years results in higher percentages for the intermediate size classes. With increasing size and age, natural mortality reduces the number of plants in the largest size classes.

The distribution of size classes in a senescent stand is surprising because the smallest size classes (less than 1.5 ft) are not represented. Joints for vegetative reproduction are still available, but they are either not viable, or die soon after establishment.

What is the reason for the natural elimination of this species



from a given locality? The explicit answer is not known, but theoretically the answer seems obvious. A pathogen has long been suspected of causing the die-off of large areas of jumping cholla and other species of cacti. Although the causative organism has not been identified, there is reason to suspect the bacillus Erwinea carnegieana Standring which causes bacterial necrosis in saguaro. Alcorn (1961) reported that jumping cholla joints inoculated with E. carnegieana progressively discolored and began to shrivel. Tissues were not observed to leak, but otherwise the symptoms were the same as for saguaro. Alcorn also isolated bacilli from jumping cholla and other cacti that appeared culturally similar to E. carnegieana. In later work Alcorn<sup>4/</sup> showed that isolates from jumping cholla used to inoculate saguaro caused typical symptoms of bacterial necrosis.

Alcorn found that infected joints usually dehisced while the symptoms were still restricted to the inoculation site. This would prevent complete infection of a mature plant and account for the slow attrition of a mature stand. The bacillus has been recovered from the soil in saguaro forests so a source of infection would be available for joints that had dropped to the ground. Infection and subsequent death of single joints would explain the absence of young plants in a senescent stand.

Vectors for E. carnegieana are not known but single joints lying on the ground could be infected as easily as mature plants. Once infected, they would be killed more easily because of the tendency for infected joints to dehisce.

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<sup>4/</sup>

Alcorn, S.M. 1962. Personal communication.

## GENERAL DISCUSSION

The study of some of the physio-ecological factors that influence jumping cholla has answered some questions and raised a host of others. That what is known increases arithmetically while what is not known increases geometrically is not a new or startling phenomenon; it is characteristic of research. There are many who would argue that research has not been properly conducted unless it uncovers more problems than it solves.

Seedlings of jumping cholla have never been found in the field. A diligent search did not uncover a single plant that could be called a seedling with absolute certainty. But since seed will germinate when properly scarified, some reproduction from seed may take place. For example, it would not be surprising to find that there is some germination after seeds have passed through the digestive tracts of birds, rodents, or other desert animals. Even though the assumption of digestive scarification is accepted, the percentage of plants established by seed germination would be extremely low.

In contrast to seed germination, vegetative reproduction by the development of roots and shoots from detached joints occurs readily and the potential for such reproduction is high. An example of successful vegetative reproduction was obtained following a chaining operation which knocked down the jumping cholla plants and scattered many joints.

An increase of more than 2000 percent in number of rooted plants was recorded one year after treatment. Many of these plants were only rooted joints that had not yet developed shoots so they could not be considered established plants. Although many will die, many will become established and 10 years from now the density of established plants will probably be as great as before chaining. The success of vegetative reproduction in this case showed unquestionably that chaining was not effective as a method for controlling the species.

Moisture undoubtedly affects joint establishment. Greenhouse studies showed that more joints developed shoots as the watering interval was increased and the same relationship was true for the dry weight of roots. Greater root and shoot development with longer intervals between watering increases the probability of plant establishment in areas of uncertain rainfall.

Field data from an area that was chained in 1958 and another that was cabled in 1961 showed more plant establishment in 1958, the year having not only the highest spring and summer rainfall, but also the most days of measurable precipitation. Despite the less favorable moisture conditions in 1961, there was still a 1750 percent increase in number of rooted plants one year after cabling. Field and greenhouse data thus showed that establishment of vegetative joints is possible not only when total rainfall for the spring and summer periods is low, but also when rainfall frequency is low.

Vegetative reproduction does not occur, however, at all seasons of the year. Joints detached from the parent plant from late July to late February exhibited shoot dormancy when placed on vermiculite in

the greenhouse. Shoot dormancy of detached joints during that period is difficult to understand because that is when new shoots are initiated on established plants in the field. The failure of detached joints to initiate shoot growth may be a mechanism to evade the extremely high temperatures at the soil-air interface during the hot summer months. Data were presented showing that air temperature at 183 cm above the ground was  $7^{\circ}$  C lower than at 4 cm above the ground surface and  $29^{\circ}$  C lower than at 2 cm below the soil surface. Thus, a joint lying on the ground would be subjected to much more severe temperatures than would joints that are still a part of an established plant.

The mean monthly temperature at the University of Arizona weather station is  $27.6^{\circ}$  C for June and  $30.1^{\circ}$  C for July. Extremely high temperatures occur at the soil-air interface in June, but detached joints are not dormant at that time. During June, however, joint establishment would be prevented by lack of moisture. In July, with the beginning of the summer rainy season, the accumulation of many high-temperature days may have effected a metabolic change in the plant that prevents shoot development on joints lying on the ground, but permits shoot development on the terminal joints of standing plants.

Compounding the problem of shoot dormancy is the fact that shoot dormancy was expressed in the greenhouse but not in the growthroom. In the discussion for the chapter on Shoot Dormancy a theory was developed to explain the difference between the response of joints in the greenhouse and growthroom on the basis of differences between solar radiation and radiation in the growthroom in the spectral region from 700 to 920  $\mu$ .

The theory was not proposed because there was adequate and reliable data to substantiate the theory, but because a single factor (light quality) offered a logical explanation for the phenomenon.

It is not unreasonable to suppose that a combination of factors was responsible. However, an explanation dealing with a combination of factors is much more subject to error than the effect of a single factor. Too little evidence was available to develop a multiple-factor theory.

The growth rate of jumping cholla in a Desert Grassland type was found to be about 0.67 inch annually for all size classes over a 12-year period. Since the life span in the same area was found to be about 40 years, an average annual growth of 0.67 inch would only account for a height of 26.8 inches. However, the larger plants used in the study of growth rate decreased in height over the 12-year period. If the plants that decreased in height were disregarded the average annual growth would be much higher.

Mean maximum plant height of jumping cholla in the Desert Grassland was about 48 inches. Assuming a 40-year life span, a mean annual growth rate of 1.2 inches would account for the plant heights that are found in the Desert Grassland.

Decreasing plant height is characteristic of senescent plants. They lose turgidity and assume a droopy, umbrella-like appearance in contrast to the turgid, erect appearance of healthy plants. Senescence is of particular interest because there are numerous sites where extensive areas of jumping cholla have died out. Where that happens, small plants die as well as large ones and the population is characterized by having the greatest number of plants in the medium size classes and

virtually no plants in the smallest size classes.

The absence of small plants in a senescent stand can be explained on the basis of disease. A bacillus, Erwinea carnegieana, is known to cause bacterial necrosis of saguaro. When jumping cholla is inoculated with E. carnegieana the symptoms, except for tissue leakage, are the same as for saguaro. Also, an organism that is culturally similar to E. carnegieana has been isolated from jumping cholla. Although the vectors for the bacillus are not known, it has been recovered from the soil and thus there would be a ready source of infection for the entire population. Joints dehisce when infected so small, several-jointed plants would be more easily killed than large plants. Consequently, a diseased population would not be expected to contain plants in the smallest size classes.

## SUMMARY

Jumping cholla (Opuntia fulgida Engelm.) is an arborescent cactus with cylindric joints found in Arizona and in the Mexican states of Sonora and Sinaloa.

Seed germination is not known to occur naturally. Seeds must be scarified by breaking away the seed coat on the radicle side of the embryo at the micropyle. Scarification in any other place did not permit radicle emergence.

Temperatures from 25 to 30° C were optimum for seed germination. No germination occurred at 20° C or at 50° C.

Germination was not affected by fruit age as had been previously reported. Tests of a large number of seed lots showed that more variation was due to seed lots than to fruit position.

One or more inhibitors are present in the fruit pulp. No germination has ever been recorded for seeds that were placed directly on fruit pulp. Inhibitors have also been reported to be present in the seed coat and embryo. This work did not verify or disprove the earlier report.

Joints of jumping cholla are severed easily from the parent plant. Since reproduction of the species takes place predominantly by vegetative means, the ease of dehiscence increases the reproductive potential.

After chaining an increase of more than 2000 percent in number of rooted plants was recorded. This emphasizes the high potential for

vegetative reproduction.

Joints grown in the greenhouse under different watering regimes showed that more joints developed shoots as the watering interval was increased and the dry weight of roots increased in a like manner.

Greenhouse-grown joints become dormant with respect to shoot development during the summer rainy season. There are three aspects to the problem of shoot dormancy: (1) established plants usually initiate new joints during the summer rainy season, (2) joints detached from the parent plant exhibited shoot dormancy from mid-summer to late winter and remained so until April, and (3) joints collected from late winter to mid-summer initiate shoot development quickly in the greenhouse.

Shoot dormancy was not expressed in the growthroom as it was in the greenhouse. A difference of light quality offered a reasonable explanation for the difference because the ratio of solar to growthroom radiant energy was much higher in the spectral region from 700 to 920 m $\mu$ . This may cause a shift in the phytochrome balance but more work is needed to define the variables precisely.

The results of injecting a large number of chemicals into jumping cholla joints for the purpose of breaking shoot dormancy were negative. Root response was affected by some chemicals, but shoot response did not differ from checks or distilled water controls.

Jumping cholla has a life cycle lasting about 40 years. In many cases, virtually all jumping cholla plants on large areas will die out. It is suspected that the die-off is caused by the same bacillus, or one closely related to, Erwinea carnegieana, that causes bacterial necrosis



of saguaro.

There are three types of jumping cholla populations. Invasion populations are characterized by having a majority of plants in the small size classes with a decreasing number in the progressively larger size classes. Mature populations are characterized by having a large number of plants in the smallest size classes followed by a precipitous drop in numbers for the next few larger size classes and then a normal, bimodal curve for the remaining size classes. Senescent populations are characterized by a normal curve in which the highest frequencies are found in the intermediate size classes.

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