ASPECTS OF THORN DEVELOPMENT ON PROSOPIS JULIFLORA

(SWARTZ) DC. VAR. VELUTINA (WOOT.) SARG.

AND CERCIDIUM AUSTRALE I. M. JOHNSTON

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES, <u>Continued</u>

LIST OF ILLUSTRATIONS

ABSTRACT

Greenhouse grown seedlings of _Prosopis juliflora_
(Swartz) DC. var. _velutina_ (Woot.) Sarg. were subjected
to various degrees of stem removal in order to deter-
mine the effects of various degrees of simulated browsing
(clipping) on thorn development. _Prosopis_ seedlings,
grown in controlled environment chambers, were also ex-
posed to varying light intensities, temperature regimes,
moisture levels and concentrations of IAA to observe the
effects of such exposure on thorn development, number
of nodes per plant and stem length. Seedlings of
Cercidium australe I. M. Johnston were included in the
light intensity experiments.

Simulated browsing did not appear to affect thorn
length of mesquite in any measurable manner, nor did the
application of IAA.

Thorn growth of both _Cercidium_ and _Prosopis_ was
found to be favored by high light intensities. Low
temperatures and high moisture levels were determined to
be important factors promoting the development of thorns
in seedlings of _Prosopis juliflora_.

INTRODUCTION

Since the time man first observed thorns on
plants, he has perhaps wondered about their origin and
speculated about their function.

Sharp-pointed projections of plants including
prickles, spines and thorns have been defined in many
ways by numerous individuals (Smith 1822; Kerner 1895;
Beecher 1898; Jackson 1900; Hodge 1938; Wilson and
Loomis 1957; Benson 1959; Dittmer 1961; Carlquist 1962;
to name a few). A spine is generally defined as a
sharp-pointed structure formed from a branch, petiole or
stipule but lacking any vascular tissue; while prickles
are developments of subepidermal tissue also containing
no vascular material. The term thorn is sometimes de-
fined as a sharp-pointed leafless branch. More commonly,
the term is used to denote any sharp process or appendage
and therefore includes both spines and prickles. The
more general term thorn will, consequently, be used here
to denote the stipular spines of _Prosopis juliflora_
(Swartz) DC. var. _velutina_ (Woot.) Sarg., velvet mesquite,
and _Cercidium australe_ I. M. Johnston, South American
paloverde.

1

There has been longstanding disagreement over the function of thorns that has persisted to the present. Dittmer (1961) states in the Encyclopedia of the Biological Sciences that, historically, thorns have been viewed as organs of survival because without them the plants would have been eliminated by herbivorous animals; or because of their reduced surface area, from that of leaves, they have less transpiring area and can therefore better withstand the buffeting of desiccating winds. He concludes by saying that neither view is acceptable. Seif El Din and Obeid (1971), on the other hand, state that in seedlings of Acacia raddiana browsing by goats produces stunted branches with stiff thorns that appear to be defensive modifications offering some protection.

Despite the controversy over the derivation and function of thorns, no one has measured variation in thorn size in relation to various environmental factors. Therefore, the main objectives of this study were: (a) to obtain data concerning the effects of simulated browsing (clipping) on thorn development, (b) to observe thorn development under various environmental conditions and (c) to evaluate some of the relationships between the degree of thorniness and environmental factors, including light intensity, moisture availability and temperature.

LITERATURE REVIEW

Differential thorn development has long been recognized by man. Linnaeus (1751) and Küchelbecker (1756) both noted that many plants appear to be less spiny when grown under cultivation than when in their native habitat. These observations of differential development and each man's own experiences with thorns gave rise to various theories as to the causes for such variation.

Functions

Protection

The concept of thorns serving as a means of protection from predation by herbivores has become one of the most widely accepted explanations (Walker 1895; McGee 1895; Hagerup 1930; Hodge 1938).

Groom (1892) wrote about the thorns of _Randia dumetorum_ Lam., a rubiaceous plant, and their role in the protection of young branches by: (1) projecting at right angles to the stem or in a slightly ascending direction and (2) developing in the same year as the stem and quickly becoming hard and lignified. Moreover, he noted

that Randia had no thorns when there were no axillary
branches and thus nothing to protect.

The long and slender spurs of Crataegus crus-galli,
cock-spur, and the means by which they protected them-
selves against browsing cattle by pricking the grazer's
noses, lips and tongues, were described by Leavitt (1905).
Disputing Leavitt's thesis, Clute (1905) wrote that at
the very time thorns would be most useful, they also
were young and tender and therefore not particularly
"obnoxious" to the browsing animals. He in turn concluded
that the reason why these plants had thorns was because
"it is their nature to."

Payne (1962) observed what he called a unique
morphological type of protective device, at least for
North American flora, on Ambrosia bryantii (Curran) Payne,
a ragweed. The plant becomes thorny because some of the
spiny fruits fail to separate from the plant; instead
they remain attached serving as armature for the entire
organism.

Decreased frequency of thorns in mature individuals
of woody thorn-bearing species, especially in lofty
branches, was noted by Hodge (1938). Leopold (1964)
discussed the juvenile characteristic of thorns and
commented that the decrease in thorniness with the

distance above ground recapitulates the ontogenetic
sequence of its changes from extreme juvenility to
maturity.

Proposed mechanisms for self-protection in plants
have not been limited to sharp-pointed projections.
Jones (1931) mentioned the use of poisonous juices by
members of the Crassulaceae. According to Fraenkel
(1959) since it is common knowledge that pigments and
flavoring substances of flowers owe their existence to
their functions as attractants for insects, it is no less
logical to conclude that substances in plants serve also
to repel insects.

Thornber (1910) related spininess to the spreading
of some plant species on the rangelands of Arizona by
grazing animals. He stated that species such as Cereus
or Larrea appeared to be immune to predation because of
the presence of spines, distasteful coatings of resins or
varnish, or bitter active principles contained within the
plant body.

One of the most detailed and extensive presenta-
tions of the protective function of spines was that of
Kerner (1895). He discussed poisons, thick cuticles,
water and in great detail "organs terminating in strong,
tapering, sharp points, which wound offenders."

Myrmecophytic (plant-ant) interactions have been noted by numerous writers (Belt 1911; Paoli 1930; Argo 1965; Hocking 1970). Janzen (1967) presented an in-depth study of myrmecophytic interactions of _Acacia cornigera_ L., bull's-horn acacia, and _Pseudomyrmex ferruginea_ F. Smith. He found that the ants were highly effective in reducing predation by animals, especially insects, by attacking any organism that came in contact with the plant. In addition, some mammals were found to avoid even the mere odor of the ants which they had come to associate with the ants' presence. Moreover, the ants were also an effective agent in reducing interspecific competition for sunlight by removing herbage from nearby plants.

Cannon (1921) and Brown (1960) both observed the lack of spines on plants in the drier portions of Australia. Brown also noted that many of the smaller shrubby acacias, grasses and shrubs of the closed forest had developed spininess. He considered this to be a development of the grazing pressure of kangaroos, smaller marsupials and rodents, while the lack of thorn development or myrmecophytic adaptations was due to the scarcity of large browsers. The "very complex" question of plant spinescence with particular reference to South African species was discussed by Schönland (1927).

Thorns were found not to be absolute barriers to predation by Hodge (1938). He noted that given a severe drought the wild asses of South America would eat Melano-cactus with its "frightful spines." The thorny acacias were ascertained to contribute the main proportion of the East African dwarf goat's browsing diet in spite of their thorns, according to Wilson (1957).

Niklitschek (1934) questioned the entire concept of the benefit of protective armament. He reasoned that thorns and poisons had less survival value than the ability of a plant to multiply and to adapt to its environment.

Discussion of spines as a means of protection has not been limited to plants. Beecher (1898) wrote extensively on the origin and significance of spines in both plants and animals, concluding that spinescence is both a means of protection and an adjustment to local conditions. More recently, Paraketsov (1958) studied the stomach contents of some 4,000 fish, both benthic and benthopelagic predators (30 species) and discovered that half of them contained members of the Cottidae, the sculpins fish family. Armed members of the Cottidae were found less frequently than unarmed forms and inversely proportional to the degree of armature.

Other Uses

Several research workers have noted other possible uses for thorns. Walker (1895) and Pijl (1951), for example, observed that certain plants employ thorns in climbing on other plants or structures, thus giving them an advantage over competitive species. A different use was discussed by Coupin (1895) who commented on the use of thorns on fruits and seeds as a means of dispersal. Aubert (1942) noted that thorny shrubs and trees along forest edges frequently have little commercial value; however, they are valuable as refuges for insectivorous birds and in protecting their nests from predators.

Morphology and Anatomy

A morphological description of the root thorns of Dioscorea prehensilis Benth. and a species of Moraea was presented by Scott (1897). He also mentioned the root spines in the genus Derris of the Leguminoseae. McArthur and Steeves (1969) described root thorns on Cryosophila guagara Allen, a Central American palm.

Both Shamel and Pomeroy (1918) and Uphof (1935) commented on the thorns of citrus which were found to be morphologically similar to branches. The morphology of the thorns of Gleditsia were described by Blaser (1956); while the anatomy and ontogeny of the thorns of some species of Lobeliaceae, found in the Hawaiian

Islands, were discussed by Carlquist (1962). Humphrey (1931) discussed thorn development in _Fouquieria splendens_ Engelm., ocotillo, and _Idria columnaris_ Kellogg, boojum tree. The growth and development of lateral shoots into thorns in _Ulex europaeus_, gorse, was described by Bieniek and Millington (1967). Thorn formation in four species of Rutaceae was compared by Roth (1969).

One family that has been the subject of a large number of papers discussing spinosity is the Cactaceae (MacDougal 1922; Grier 1926; Johansen 1931; Spillman 1905; Jones 1931; Weingart 1932; and many others).

The thorns of _Acacia seyal_ Del. were found to be filled with air which makes them white, thus enabling them to reflect light. However, this occurs only after death of the thorns because only then do the outermost cells of the cortex become filled with air (Hagerup 1930).

Environment

Thermodynamic theory was applied to desert spines by Kelso (1951) who concluded that because of the physical structure of spines, they would provide a surface, thickness, temperature and electric gradient that would enable the plant to maintain physical equilibrium with the radiational environment of the desert. Kelso (1961) also wrote that spines serve the function of either extracting

or synthesizing water from the air. However, he failed
to present any data to support either of these theories.

In 1893, Lothelier reported that in experimenting
with Berberis, barberry, and other species using con-
trolled conditions, except for one variable, he was able
to control the growth and development of thorns. He
observed that low moisture or high light intensity re-
sulted in a marked increase in the production of thorns;
while high humidity and decreased light intensity pro-
duced plants with little or no thorn development. These
same observations were made for Discaria toumatou Raoul,
a common New Zealand xerophytic shrub, by Cockayne (1905)
and separately by Robinson (1904) and Croizat (1937).

The effects of environmental stress on thorn
formation in Ulex europaeus has been recently studied by
Bieniek and Millington (1968). They found that short days
delayed thorn formation because thorn formation is corre-
lated with adult-leaf form. The appearance of adult
leaves in seedlings was delayed by exposure to short days.
Light intensity, if low enough to interfere with shoot
growth, also retarded thorn formation. Nevertheless,
thorns were produced as long as there was sufficient light
available for shoot growth. High humidity was not found
to suppress thorn formation. Decapitation allowed vege-
tative growth of secondary shoots depending on the extent

of their development as thorns. Axillary shoots at the youngest nodes developed vegetatively for several plasto-chrons, (the variable time interval between two successive repetitive events), while older induced nodes could elongate and not produce additional leaves. Accessory shoots were observed to develop in response to decapita-tion. Naphthaleneacetic acid applied to decapitated shoots suppressed the elongation response in thorn shoots and development of distal accessory buds. Application of gibberellic acid stimulated axillary shoot growth in intact shoot tips while it deferred thorn induction for several plastochrons. Young excised axillary shoots and excised shoot tips cultured in vitro differentiated as swollen thorns. Their overall conclusion was that the environmental factors tested had little or no effect on thorn formation.

MATERIALS AND METHODS

General

Prosopis juliflora and Cercidium australe seeds were obtained from Dr. Herbert M. Hull, Professor of Watershed Management, and Dr. Tien Wei Yang, Research Associate of the Department of Biological Sciences, respectively.

Germination for all trials was initiated by scarifying each seed with an emery board. The seeds were then placed in plastic trays (31 x 45 x 6 cm) between double layers of paper towels moistened with tap water. Clear plastic wrap was used to cover the trays, each of which held four rows of seeds with 25 seeds per row. The trays were placed on a desk and covered with newspaper to reduce light exposure.

Poole (1958) obtained his highest percent germination (94%) using scarified seeds, grown in the absence of light at $21^{\circ}C$; while Scifres and Brock (1969) discovered that seeds at $21^{\circ}C$ required 72 hours for emergence. Therefore, the prepared seeds in the present study were left at room temperature (approximately $21^{\circ}C$) for three days. After this period, those with emergent radicles were randomly selected using a random digits

12

table and placed in the proper containers. Greenhouse experiments were conducted using square, black, plastic pots measuring 14 x 14 x 15 cm, while growth chamber experiments employed metal flats (39 x 55 x 10 cm) to conserve space.

The planters contained 100% vermiculite as the growth medium. Glasswool was used to plug the holes in the plastic pots while paper towels served the same purpose in the metal flats. Polyethelene sheeting was used to cover the vermiculite for up to three days after transfer of the seedlings in order to reduce moisture loss.

A modified formula of the complete nutrient solution of Kurtz and Mellor (1966) was used (Appendix A) on the sixth day following scarification and thereafter at six day intervals. Stock solutions were prepared of all ingredients of the nutrient solution except for Fe-EDTA, which was weighed out into small envelopes and dissolved directly into the final solution. Nutrient solution was prepared just prior to application in 20-liter calibrated bottles using tap water. Tap water was also employed in initially wetting the vermiculite before transplanting and for all watering, usually every sixth day thereafter or as noted below. Sufficient nutrient solution or water was used to produce drainage from the bottom of the containers.

When ready for harvesting, plants were cut at
ground level and placed in envelopes, that were then
dried in an oven for 24 hours at 70°C. Thorn length
measurements were then made, using a metric ruler taped
to the stage of a dissecting scope and/or a micrometer
disc. The disc alone was employed for measurements up
to 5 mm and, when properly aligned, for measurements of
up to 10 mm, with 0.1 mm gradations. One member of each
pair of thorns was measured using the longest and
straightest member. Measurements were made from the point
at which the thorn intersected the bark to its tip, to
the nearest 0.1 mm.

Average values for thorn length, number of nodes
and stem length for each plant within a set were calcu-
lated and the t-test was used to compare differences in
mean values between treatments.

Hull (1958) showed that mesquite seedlings had
their most rapid growth rate when grown at a day tem-
perature of 30°C with a night temperature of 26°C, as
measured by fresh or dry weight, height or leaf count.
Early seedling growth was found to be favored by a con-
stant temperature of 30°C (Scifres and Brock 1969).
Peacock and McMillan (1965) found that garden populations
of Prosopis grew very poorly but that greenhouse and
growth chamber populations grew well.

Simulated Browsing

The simulated browsing experiment was conducted in a greenhouse at a maximum temperature of 30°C and a minimum of 13°C, under natural illumination from April 4, 1972 to October 21, 1972. Measurements of light intensity using a Weston Illumination Meter Model 756 showed that illumination varied from 2,000 to 10,000 foot candles depending on time of day and weather conditions. A hygro-thermograph was used to record temperature and relative humidity; the latter was found to vary from 40-100%, sometimes remaining near the 100% level for a period of 18 hours per day. The simulated browsing experiment involved eight treatments with 15 plants per treatment, randomly dispersed in the greenhouse.

Browsing was simulated by Seif El Din and Obeid (1971) in their experiments on Acacia senegal (L.) Willd. by removing the leading shoots 5-10 mm above the level of the cotyledons. Browsing on Prosopis was simulated by clipping of the main stem at various heights above ground level using a pair of pruning clippers with the cut made at right angles to the stem. Before cutting, the numbers of nodes, internodes and total stem length were counted and measured. After a growth period of 125 days set A was completely removed at ground level; sets B, C, D and E were clipped 0, 25, 50 and 75% of their total length,

respectively. Sets B thru E were completely harvested
75 days later. Concurrently, sets F, G and H were grown
for 126 days at which time 0, 10 and 20% of their main
stem was removed. These plants were again subjected to
clipping of 0, 10 and 20% of their total stem length
(present at the time of cutting) after 35 days of addi-
tional growth. Forty-two days later these individuals
were also completely harvested. In all instances the
removed portions were packaged, dried and measured as
described above.

Light Intensity

The effects of light intensity were studied
using both Prosopis juliflora and Cercidium australe.
The Prosopis experiments were conducted in an Environmental
Growth Chamber Model M2. Seedlings were grown for a
total of 51 days in the first of two experiments. A flat
containing 15 plants was elevated from the main platform
of the chamber by being suspended from clamps on a ring
stand 93 cm above the platform. Because of the conse-
quent reduced distance from the light source, this pro-
duced an increase in light intensity of some 1,500 foot
candles over the plants on the platform. Thus, those
on the platform received 2,300 foot candles while those
in the suspended flat received 3,800.

In the second experiment, which lasted 35 days, a wooden table was suspended from the ring stands (Fig. 1) and two flats with a total of 40 plants were placed on it, while an equal number of plants were placed on the main platform. Respective light intensity readings were 6,000 and 4,000 foot candles. Photoperiods for both experiments were 18 hours with temperatures maintained at $33 \pm 2^{o}C$ day and $27 \pm 2^{o}C$ night. Relative humidity was essentially constant at 50%. Daily watering was provided, except when nutrient solution was applied.

The experiment on Cercidium australe seedlings was conducted using two identical Percival Growth Chambers Model 57E. One set of 15 plants was grown in one chamber at a light intensity of 1,500 foot candles, a second was grown in the other chamber at 3,000 foot candles. Both chambers employed an 18-hour light period with day temperatures maintained at $32 \pm 2^{o}C$ and night temperatures at $28 \pm 2^{o}C$. Relative humidity varied from 35-70% during the 70-day growth period.

Indoleacetic Acid

One aspect of the study included an evaluation of the possible effects of IAA on thorn development. Aqueous solutions of 5, 7, and 9 ppm were prepared and sprayed on sets (15 plants each) of 18-day-old seedlings. All treatments, including controls sprayed with distilled
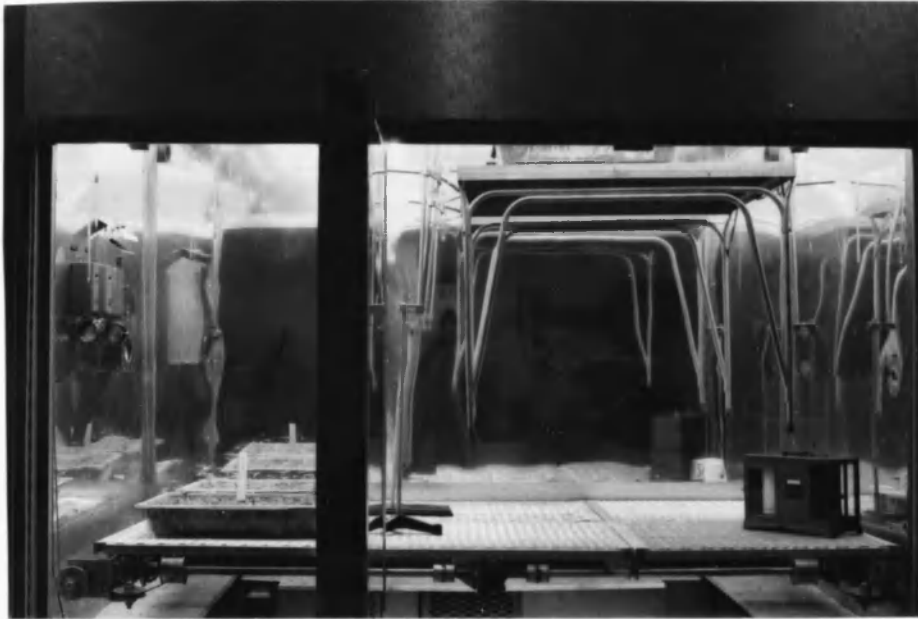
Fig. 1.   The Environmental Growth Chamber M2.

High-intensity flats can be seen on
the raised table.   The low-intensity
flats and a recording hygro-thermograph
are visible on the main platform.

water, were grown for a total of 51 days employing an 18-hour photoperiod with a light intensity of 2,300 foot candles. Day and night temperatures were maintained at $33 \pm 2^{\circ}C$ and $27 \pm 2^{\circ}C$, respectively. Relative humidity was essentially constant at 50%, with daily watering or nutrient solution provided.

Temperature and Moisture

Temperature and moisture effects were also investigated by growing duplicate sets of 20 plants each in both of the two Percival chambers. One chamber used a $35 \pm 2^{\circ}C$ day temperature with a night temperature of $21 \pm 2^{\circ}C$, while the other one utilized $24 \pm 2^{\circ}C$ and $10 \pm 2^{\circ}C$. Photoperiod was 18 hours with a light intensity of 3,000 foot candles. Relative humidity ranged from 75% to 35% in the high-temperature chamber and from 82% to 40% in the low-temperature chamber. The plants were grown for 40 days before harvesting. This experiment was repeated with a total of 40 plants (20 plants per chamber), using the same photoperiod, temperatures and light intensity. However, in this instance, daily watering or nutrient solution was provided. This produced a humidity range of 72% to 40% in the high-temperature chamber compared to 82% to 69% in the low-temperature chamber. The growth period was reduced to 23 days because the plants

in the high-temperature chamber grew so rapidly that they were about to come in contact with the top of the growth chamber.

RESULTS AND DISCUSSION

Simulated Browsing

The difficulty of determining exact field condi-
tions and of accurately measuring field-grown thorns
necessitated conducting the experiments under controlled
conditions. However, previous field observations had
suggested that thorn development on side branches of
Prosopis seemed to be inhibited near the parent stem.
Branching stimulated by clipping during the simulated
browsing experiments indicated a similar inhibition (Fig.
2). From a total of some 246 side branches from the 75
plants subjected to simulated browsing, only 9 produced
thorns on the first node of the new branch; some 120
branches produced thorns of approximately the same size
as those on the parent stem on the second node and 96
produced thorns on the third node (Fig. 3; Appendix B).

Table 1 demonstrates that as the amount of
clipping was increased the relative length of all thorns
on the regrown stems (new and old growth) compared to
those of the removed portions decreased significantly.
With 25% stem removal, there was an insigificant but
nonetheless measureable decrease in thorn length from
4.68 to 4.41 mm. This became significant with 50%
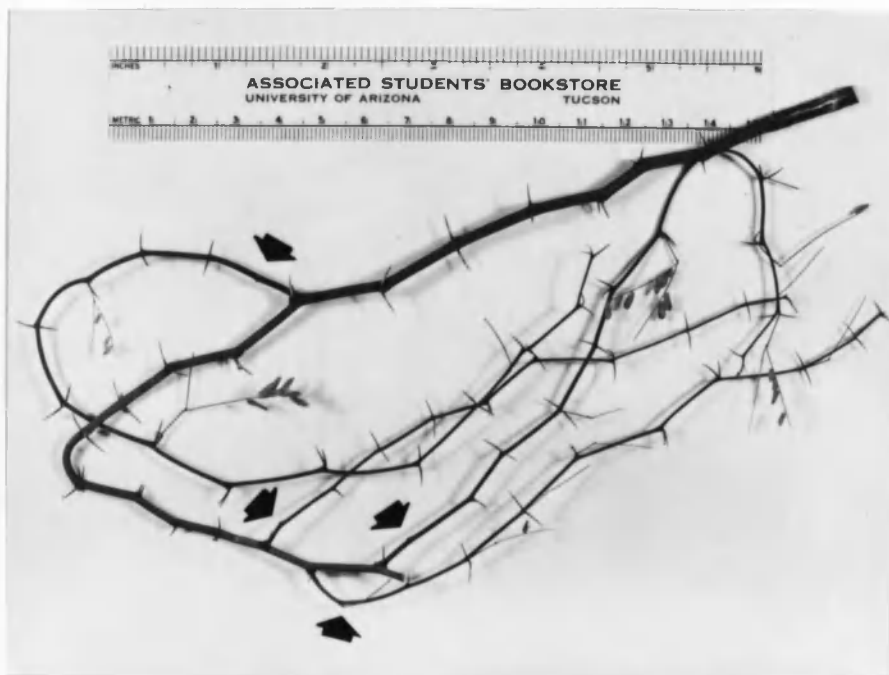
Fig. 2. A <u>Prosopis</u> <u>juliflora</u> seedling showing
differential thorn development.
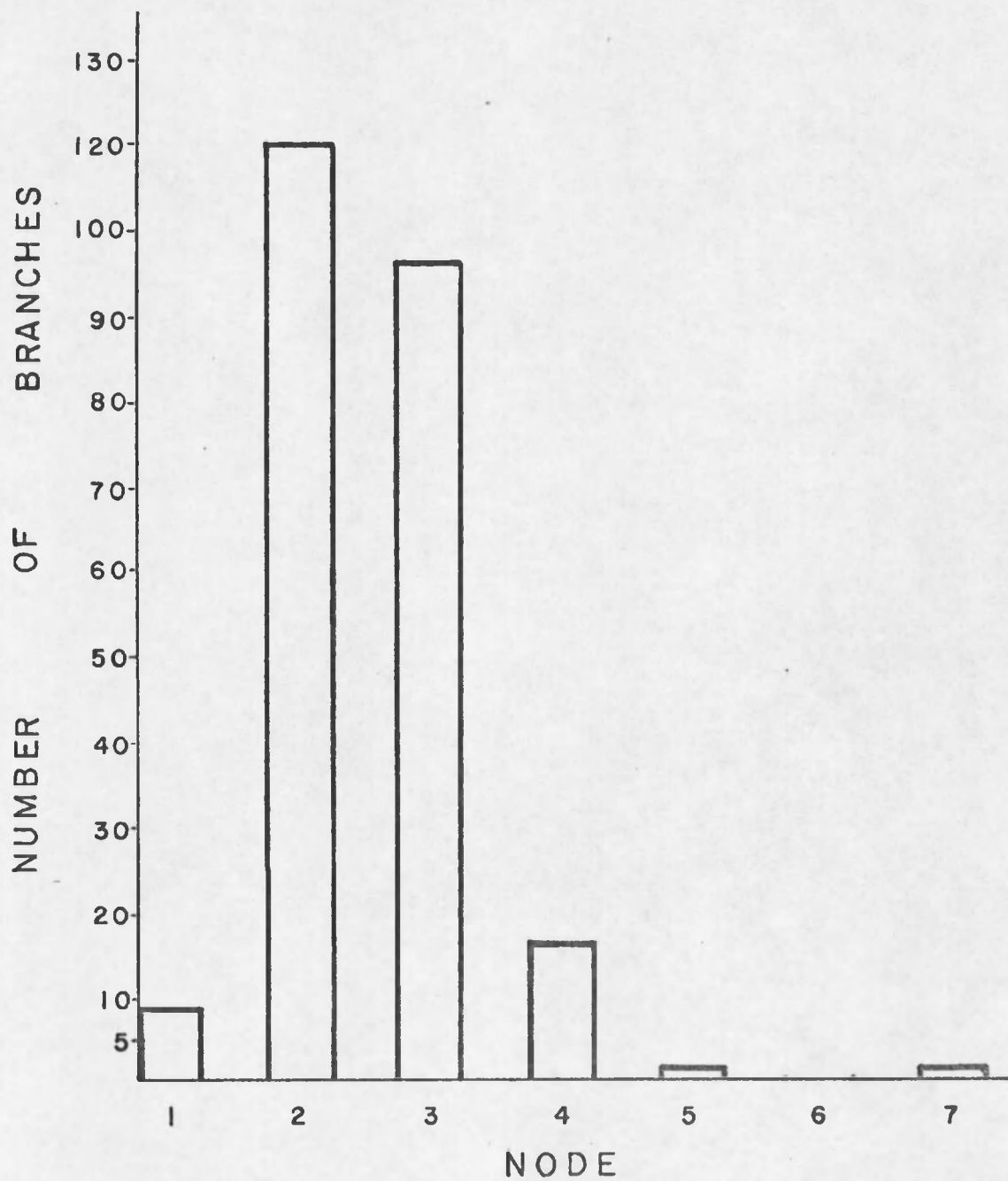
Fig. 3.   Node at which thorns first appear on newly
developed side branches.

clipping and even more so with 75% removal. From this
table it is apparent that the average length of thorns
present on the plant, even after 75 days of additional
growth, decreased with increased stem removal.

Table 1. Thorn length on portions of Prosopis juliflora
stems removed during simulated browsing, com-
pared with thorn length on the plant after 75
days of additional growth.

% removed	Thorn length (mm) on re-moved stems	Thorn length (mm) on re-grown stems 75 days later	t values
25	4.68	4.41	1.0263
50	5.19	4.10	3.1918[a]
75	4.95	3.74	4.1108[a]
100	4.69	--	0.3298
Control	--	4.81	

[a]Significance P < 0.05.

A similar decrease in length of thorns remaining
on the plant as the amount of stem removal was increased
was also noted in the sets in which the simulated browsing
treatment was repeated (Table 2). Furthermore, with in-
creased stem removal, the average length of thorns present
on the regrown stems was progressively smaller. However,

Table 2. Thorn length on portions of <u>Prosopis juliflora</u>
stems removed during repeated simulated browsing,
compared with thorn length on the plant after
additional growth time.

% removed	Thorn length (mm) on re-moved stems Days		Thorn length (mm) on re-grown stems Days	t values	
	126	161	203		
10	4.28	5.13	4.55	0.7413	1.5591
20	4.39	5.34	4.34	0.0861	1.2660

in neither case were the values statistically significant.
In addition, the maximum thorn lengths for both treatments
were obtained on the second clipping with similar lengths
to be found in both the initially removed portions and
the regrown stems.

When mean length of thorns on the plants at final
harvest were compared with those of the control set (Table
3) a similar relationship was obtained, namely, increased
stem removal resulted in a decrease in thorn length,
becoming significant at the 75% removal level. No signifi-
cant difference was found between the thorns of the plants
harvested after 125 days of growth and those cut off
after 200 days of growth. The data suggest that there is
no direct correlation between thorn length and increased
stem removal. Considerable variation exists in thorn

Table 3. Length of thorns on simulated browsed seedlings of *Prosopis juliflora*, compared with those found on unclipped controls.

% removed	Thorn length (mm)	t values
100	4.69	0.3298
25	4.41	1.2111
50	4.10	1.9388
75	3.74	3.2747[a]
Control	4.81	--
10[b]	4.88	0.1618
20[b]	4.76	0.6006
Control	4.62	--

[a] Significance P < 0.05.
[b] Clipping of seedlings was repeated.

length on different portions of the stem, longest thorns occurring near the center of the stem. This occurs because of the concentration of young immature thorns toward the younger, upper portion of the plant, as contrasted with the older stems near ground level where the older thorns are being overgrown by bark, since they no longer are growing. This variation results in a decrease in thorn length with an increase in stem removal. This is evident if one considers that many of the new thorns developed on clipped plants are on newly developed side branches, thus increasing the number of young developing thorns at the branch tips and decreasing the average length of the thorns on the plant.

The number of nodes on the plants at final harvest (Table 4) showed nothing of significance except that repeated 20% stem removal resulted in a decrease in the number of nodes, thus a reduction in the number of thorns present on the plant. This probably resulted from insufficient time for regrowth to occur. As would be expected the 75-day growth period from the initial clipping until the final harvest resulted in a significant increase in the number of nodes. The set completely harvested at the initial clipping averaged 39.0 nodes per plant whereas the control set harvested after the additional growth period had 50.5 nodes.

Table 4. Number of nodes per plant on simulated browsed
seedlings of _Prosopis juliflora_ at the time
of final harvest, compared with unclipped
controls.

% removed	Number of nodes	t values
100	39.0	3.2128[a]
25	45.2	1.1261
50	57.9	1.3398
75	54.1	0.8114
Control	50.5	--
10[b]	44.8	1.0585
20[b]	37.8	2.4302[a]
Control	49.8	--

[a]Significance P $\leqslant$ 0.05.
[b]Clipping of seedlings was repeated.

An examination of the data on the total number of nodes produced by each plant during the entire period of the experiment (Table 5), reveals a significant increase in node production with increased clipping. The number of nodes increased from 55.1 at 25% clipping to 84.0 at 75%, while the control set had a mean of 50.5 nodes per plant. With repeated clipping, however, no clear trends could be discerned.

A comparison of the total length of the plants at final harvest, including branches (Table 6), demonstrates that the only significant difference between the control groups and any of the clipping treatments was in the reduction of size of the set that was repeatedly clipped at the 20% level. The short time available for regrowth after the second clipping probably accounts for this. These findings are similar to those of Wright and Stinson (1970) in which it was noted that if mesquite plants were cut at ground line, their yield would be decreased by 75% based on oven-dried weight. The recovery of plants with their tops completely removed can perhaps be explained by the presence of large food reserves in older plants that were not available to the seedlings. Scifres and Hahn (1971) found that no mesquite seedlings survived when they were cut below the cotyledons. They

Table 5. Total number of nodes produced by a simulated
browsed seedling of <u>Prosopis juliflora</u> in its
lifetime, compared with unclipped controls.

% removed	Number of nodes	t values
100	39.0	3.2128[a]
25	55.1	0.9524
50	75.8	4.4216[a]
75	84.0	6.5817[a]
Control	50.5	--
10[b]	48.9	0.1391
20[b]	53.2	0.6449
Control	49.8	--

[a]Significance $P < 0.05$.
[b]Clipping of seedlings was repeated.

Table 6. Stem length of simulated browsed seedlings of
Prosopis juliflora at the time of final harvest,
compared with unclipped controls.

% removed	Stem length (cm)	t values
100	70.00	3.0207[a]
25	83.15	0.0948
50	83.84	0.2888
75	74.80	1.5810
Control	82.44	--
10[b]	81.96	0.2476
20[b]	59.56	2.8163[a]
Control	84.03	--

[a]Significance $P \leqslant 0.05$.
[b]Clipping of seedlings was repeated.

also noted similar results for stem length regrowth 56 days after top removal. Their data also indicated approximately equal lengths after regrowth.

Increased clipping of Prosopis resulted in a greater total stem production when removed segments were combined with the entire amount of stem created including branches (Table 7). With 25% stem removal, there was an approximate 22% increase in total stem length, while there was a 43% and 51% increase at 50% and 75% removal, respectively. In the repeat clipping treatments this relationship was not as evident but there appeared to be the same tendency.

Light Intensity

Light intensity experiments on Cercidium australe (Table 8) were inconclusive in regard to thorn length, probably because of the difficulty of working with a species in which thorn length varied greatly at any one node. Moreover, because of the fragile nature of the thorns, a great many were broken. Nevertheless, increased light intensity produced a significant decrease in stem length with non-significant increases in node number and thorn length.

Experiments using Prosopis juliflora to study the effects of light intensity (Table 9) appeared at first somewhat inconsistent. In the 51-day trial,

Table 7. Total stem length produced by a simulated
browsed seedling of <u>Prosopis juliflora</u> in its
lifetime, compared with unclipped controls.

% removed	Stem length (cm)	t values
100	70.00	3.0207[a]
25	100.10	2.2790[a]
50	117.70	6.7127[a]
75	124.72	7.8773[a]
Control	82.44	--
10[b]	95.77	1.3773
20[b]	84.35	0.0312
Control	84.03	--

[a]Significance $P < 0.05$.
[b]Clipping of seedlings was repeated.

Table 8. Effects of increased light intensity on thorn length, number of nodes per plant and stem length of <u>Cercidium australe</u> seedlings.

Light (ft-c)	Thorn length (mm)	Number of nodes	Stem length (cm)	t values		
				Thorn length	Number of nodes	Stem length
1,500	4.40	19.5	25.95	0.6119	1.7058	2.7499[a]
3,000	4.65	21.8	23.19			

[a]Significance $P < 0.05$.

significant increases were observed in thorn length, number of nodes and stem length with the 1,500 foot candle increase in light intensity. On the other hand, the 35-day experiment produced non-significant increases in thorn length, with increased light intensity. Inconsistent results were noted in the number of nodes per plant. Decreases in stem length occurred but only in one instance was the decrease significant. Careful analysis of the conditions under which the plants had been grown revealed that in the 35-day experiment the temperature on the wooden table had ranged from 3 to 5°C warmer than that on the platform or in the flat suspended from ring stands. It was also observed that throughout the experiment the plants at the lower light intensity were grown in vermiculite with a higher moisture level, thus

Table 9. Effects of increased light intensity on thorn
length, number of nodes per plant and stem
length of <u>Prosopis</u> <u>juliflora</u> seedlings.

Light (ft-c)	Thorn length (mm)	Number of nodes	Stem length (cm)	t values		
				Thorn length	Number of nodes	Stem length
Plants grown for 51 days						
2,300	2.95	23.0	33.98			
				3.5316[a]	3.3759[a]	2.8987[a]
3,800	3.74	29.2	44.97			
Plants grown for 35 days						
4,000	3.05	13.9	19.49			
				1.8915	0.8131	1.2298
6,000	3.49	14.9	17.49			
4,000	3.10	15.7	22.67			
				1.5584	0.1480	2.5410[a]
6,000	3.40	15.5	18.78			

[a]Significance $P < 0.05$.

obviating any light intensity analyses and conclusions.
However, even in the experiments in which there were no
significant differences demonstrated, both _Cercidium_
australe and _Prosopis juliflora_ produced larger thorns
on plants grown at higher light intensities. The above
finding is in agreement with those of Lothelier (1893),
Robinson (1904) and Croizat (1937). Bieniek and
Millington (1968), on the other hand, found in their study
of thorn formation in _Ulex europaeus_ that light intensity
low enough to interfere with shoot growth would prevent
the beginning of thorn formation in seedlings, but as
long as there was sufficient light intensity to permit
shoot growth, thorns would be produced. They also noted
that with decapitation of only 0.5 cm of shoot tip, terti-
ary shoots on the extended secondary axis often grew vege-
tatively for a period of time before differentiating as
thorns. They found little or no effect on thorn develop-
ment by photoperiod, light intensity, humidity, nitrogen,
decapitation, growth substances or in vitro culture.

Indoleacetic Acid

The absence of thorns on the first node of branches
newly developed after clipping and the prompt return of
thorns equal in length to those of the parent stem on the
second or third node strongly suggest hormonal regulation
of thorn development (Fig. 2; Appendix B). However,

application of IAA had no significant effect on thorn length, number of nodes or stem length of Prosopis juliflora (Table 10). This is in general agreement with the findings of Bieniek and Millington (1968). Marcelle (1971), however, was able to induce thorns on young pear trees with application of GA_3, which also promoted growth of the main stem and reduced apical dominance (Table 10).

Table 10. Effects of various concentrations of IAA on thorn length, number of nodes per plant and stem length of Prosopis juliflora seedlings, compared with untreated control plants.

IAA (ppm)	Thorn length (mm)	Number of nodes	Stem length (cm)	t values Thorn length	Number of nodes	Stem length
5	3.13	24.1	37.97	0.9915	0.6141	1.3243
7	2.77	22.7	34.85	1.0252	0.2388	0.3115
9	3.00	22.2	32.16	0.3218	0.6278	0.7357
Cont.	2.95	23.0	33.99	--	--	--

Temperature and Moisture

The two temperature regimes provided very interesting data (Table 11). There was a highly significant correlation between thorn length and decreased temperatures, longer thorns being correlated with lower temperatures. High temperatures of 35°C day and 21°C

Table 11. Effects of temperature on thorn length, number of nodes per plant and stem length of _Prosopis juliflora_ seedlings.

Temp. D/N (^{o}C)	Thorn length (mm)	Number of nodes	Stem length (cm)	t values		
				Thorn length	Number of nodes	Stem length
Plants grown for 40 days						
35/21	3.34	15.3	26.17	6.3522[a]	2.9899[a]	0.5658
24/10	4.48	13.0	27.14			
35/21	3.27	14.7	23.61	5.5525[a]	2.0491[a]	1.7415
24/10	4.33	12.6	27.07			
Plants grown for 23 days						
35/21	3.82	13.3	28.15	2.4465[a]	21.3222[a]	14.3598[a]
24/10	4.46	5.1	11.53			

[a]Significance $P < 0.05$.

night produced thorns approximately 3.3 mm in length.
Thorns grown at the lower temperatures of 24°C daytime
and 10°C nighttime, on the other hand, averaged about
4.4 mm in length. These cooler conditions also resulted
in more moisture being available to the plants; because
moisture was provided only once every three days thus
providing enough time for the vermiculite in the high
temperature chamber to almost dry out. The vermiculite
in the low temperature chamber appeared to be nearly
saturated at all times.

When this experiment was repeated using daily
watering and a shorter growth period a significant differ-
ence in thorn length was again found (Table 11). Thorns
on plants grown at the higher temperatures averaged about
3.8 mm in length, while those at the lower temperatures
averaged more than 4.4 mm.

Significant reductions were observed in the number
of nodes per plant with decreased temperatures in both
experiments. Moreover, because higher temperatures favored
early seedling growth, those grown at the higher temper-
atures were significantly larger.

In comparing the plants watered daily with those
watered only once every three days, some significant
findings are noted (Table 12). At the lower temperatures
there was a decrease in the number of nodes and the size

Table 12. Effects of watering regimes on thorn length,
number of nodes per plant and stem length of
Prosopis juliflora seedlings.

Water regime (days)	Thorn length (mm)	Number of nodes	Stem length (cm)	t values		
				Thorn length	Number of nodes	Stem length
Temperatures D/N 24/10						
1[b]	4.46	5.1	11.53	0.3103	13.5452[a]	12.1470[a]
3[c]	4.41	12.8	27.11			
Temperatures D/N 35/21						
1[b]	3.82	13.26	28.15	2.8042[a]	2.2947[a]	2.1090[a]
3[c]	3.31	14.97	24.86			

[a]Significance $P \leq 0.05$.
[b]Plants grown for 23 days with daily watering.
[c]Plants grown for 40 days and watered once every
three days.

of the plants with a shorter growth period; however, there was no difference in thorn length. At the higher temperatures, there was a significant increase in thorn length, number of nodes per plant and stem length.

Given that the watering schedule was once every three days in the 40-day experiment, the high temperature chamber was also a low moisture chamber. Therefore, it presented arid growth conditions which should have produced longer thorns than the cooler conditions of the parallel chamber, following the ideas of Henslow (1894). However, the low temperature, high moisture chamber produced thorns significantly larger. In addition, when moisture was applied daily there was still a significant difference between the thorns produced at the higher temperatures and those produced at the lower temperatures. The longest thorns were produced at the lower temperatures though the increased moisture resulted in significantly increasing the thorns grown at the higher temperature regime (Table 12).

Hull (1958) had reported that early seedling growth was favored by high temperatures. This is supported by the above data (Table 12) in regard to stem length and the number of nodes per plant; however, these conditions, as one can see from the above data, do not necessarily favor thorn development.

We are again back to the problem as to whether thorns are the product of environmental influences or an adaption to predation. There is still no possible means to definitively settle this point. However, it is now clearly evident that thorn length does indeed depend on light intensity, temperature and probably other environmental factors which are involved with hormonal regulation. Is it not, therefore, perfectly logical to view browsing as just another environmental stimulant to thorn development, indirectly if not directly?

The removal of vegetation increases the number of new branches by decreasing apical dominance and in addition the removal of vegetation decreases the amount of shading thus resulting in an increase in light intensity falling on the newly developing branches. This in turn may alter the hormonal balance of the plant producing larger thorns, which might possibly reduce browsing to some extent.

APPENDIX A

PREPARATION OF NUTRIENT SOLUTION

Table A-1. Nutrient solution.

Stock solution	Compound	Amount needed (g)	Volume water needed (ml)	Volume stock solution ml/l final solution
A	Calcium nitrate $Ca(NO_3)_2 \cdot 4H_2O$	11.7	50	5
B	Potassium nitrate KNO_3	5.0	50	5
C	Magnesium sulfate $MgSO_4 \cdot 7H_2O$	5.0	20	2
D	Potassium phosphate monobasic KH_2PO_4	1.4	10	1
E	Manganous chloride $MnCl_2 \cdot 4H_2O$	1.81		
	Boric acid H_3BO_3	2.86		
	Zinc sulfate $ZnSO_4 \cdot 7H_2O$	0.22	1000	1
	Cupric sulfate $CuSO_4 \cdot 5H_2O$	0.08		
	Molydbenum trioxide MoO_3	0.09		
F	Iron-ethylene-diamine-tetraacetic acid Fe-EDTA	1.0/ packet		0.05 g

APPENDIX B

NODE AT WHICH THORNS FIRST APPEAR

ON NEWLY DEVELOPED SIDE BRANCHES

OF SEEDLINGS EXPOSED TO SIMULATED BROWSING

Table B-1.   Node.

Amount clipped (%)	Number of branches / treatment (15 plants)	Node at which thorns first appeared						
		1	2	3	4	5	6	7
25	47	1	29	16	1			
50	73	6	36	26	5			
75	60	1	22	32	5			
10[a]	33	1	16	15	1			
20[a]	33	0	17	7	5	2	0	2
	246	9	120	96	17	2	0	2

[a]Clipping of seedlings was repeated.

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