ASPECTS OF THORN DEVELOPMENT ON PROSOPIS JULIFLORA
(SWARTZ) DC. VAR. VELUTINA (WOOT.) SARG.
AND CERCIDIIUM AUSTRALIS I. M. JOHNSTON

by

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STATEMENT BY AUTHOR

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W. VAN ASDALL
Associate Professor of Biological Sciences
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TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF ILLUSTRATIONS</td>
<td>vii</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>viii</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>LITERATURE REVIEW</td>
<td>3</td>
</tr>
<tr>
<td>Functions</td>
<td>3</td>
</tr>
<tr>
<td>Protection</td>
<td>3</td>
</tr>
<tr>
<td>Other Uses</td>
<td>8</td>
</tr>
<tr>
<td>Morphology and Anatomy</td>
<td>8</td>
</tr>
<tr>
<td>Environment</td>
<td>9</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>12</td>
</tr>
<tr>
<td>General</td>
<td>12</td>
</tr>
<tr>
<td>Simulated Browsing</td>
<td>15</td>
</tr>
<tr>
<td>Light Intensity</td>
<td>16</td>
</tr>
<tr>
<td>Indoleacetic Acid</td>
<td>17</td>
</tr>
<tr>
<td>Temperature and Moisture</td>
<td>19</td>
</tr>
<tr>
<td>RESULTS AND DISCUSSION</td>
<td>21</td>
</tr>
<tr>
<td>Simulated Browsing</td>
<td>21</td>
</tr>
<tr>
<td>Light Intensity</td>
<td>32</td>
</tr>
<tr>
<td>Indoleacetic Acid</td>
<td>36</td>
</tr>
<tr>
<td>Temperature and Moisture</td>
<td>37</td>
</tr>
<tr>
<td>APPENDIX A: PREPARATION OF NUTRIENT SOLUTION</td>
<td>43</td>
</tr>
<tr>
<td>APPENDIX B: NODE AT WHICH THORNS FIRST APPEAR</td>
<td>45</td>
</tr>
<tr>
<td>ON NEWLY DEVELOPED SIDE BRANCHES OF SEEDLINGS EXPOSED TO SIMULATED</td>
<td></td>
</tr>
<tr>
<td>BROWSING</td>
<td></td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>47</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table | Page
--- | ---
1. Thorn length on portions of *Prosopis juliflora* stems removed during simulated browsing, compared with thorn length on the plant after 75 days of additional growth. | 24
2. Thorn length on portions of *Prosopis juliflora* stems removed during repeated simulated browsing, compared with thorn length on the plant after additional growth time. | 25
3. Length of thorns on simulated browsed seedlings of *Prosopis juliflora*, compared with those found on unclipped controls. | 26
4. Number of nodes per plant on simulated browsed seedlings of *Prosopis juliflora* at the time of final harvest, compared with unclipped controls. | 28
5. Total number of nodes produced by a simulated browsed seedling of *Prosopis juliflora* in its lifetime, compared with unclipped controls. | 30
6. Stem length of simulated browsed seedlings of *Prosopis juliflora* at the time of final harvest, compared with unclipped controls. | 31
7. Total stem length produced by a simulated browsed seedling of *Prosopis juliflora* in its lifetime, compared with unclipped controls. | 33
8. Effects of increased light intensity on thorn length, number of nodes per plant and stem length of *Cercidium austral* seedlings. | 34
<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>9.</td>
<td>Effects of increased light intensity on thorn length, number of nodes per plant and stem length of <em>Prosopis juliflora</em> seedlings.</td>
<td>35</td>
</tr>
<tr>
<td>10.</td>
<td>Effects of various concentrations of IAA on thorn length, number of nodes per plant and stem length of <em>Prosopis juliflora</em> seedlings, compared with untreated control plants.</td>
<td>37</td>
</tr>
<tr>
<td>11.</td>
<td>Effects of temperature on thorn length, number of nodes per plant and stem length of <em>Prosopis juliflora</em> seedlings.</td>
<td>38</td>
</tr>
<tr>
<td>12.</td>
<td>Effects of watering regimes on thorn length, number of nodes per plant and stem length of <em>Prosopis juliflora</em> seedlings.</td>
<td>40</td>
</tr>
</tbody>
</table>
## LIST OF ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The Environmental Growth Chamber M2.</td>
<td>18</td>
</tr>
<tr>
<td>2</td>
<td>A <em>Prosopis juliflora</em> seedling showing differential thorn development</td>
<td>22</td>
</tr>
<tr>
<td>3</td>
<td>Node at which thorns first appear on newly developed side branches.</td>
<td>23</td>
</tr>
</tbody>
</table>
ABSTRACT

Greenhouse grown seedlings of *Prosopis juliflora* (Swartz) DC. var. *velutina* (Woot.) Sarg. were subjected to various degrees of stem removal in order to determine the effects of various degrees of simulated browsing (clipping) on thorn development. *Prosopis* seedlings, grown in controlled environment chambers, were also exposed 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 defined 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.
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. Self 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 themselves 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 presentations 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 *Melanocactus* 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 Fijl (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 Shame1 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 controlled 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 resulted in a marked increase in the production of thorns; while high humidity and decreased light intensity produced 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 correlated 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 vegetative growth of secondary shoots depending on the extent
of their development as thorns. Axillary shoots at the youngest nodes developed vegetatively for several plastochrons, (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 decapitation. 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°C; while Scifres and Brock (1969) discovered that seeds at 21°C required 72 hours for emergence. Therefore, the prepared seeds in the present study were left at room temperature (approximately 21°C) for three days. After this period, those with emergent radicles were randomly selected using a random digits...
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. Polyethylene 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 calculated 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 temperature 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 constant 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 additional 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 consequent reduced distance from the light source, this produced 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 $33 \pm 2^\circ C$ day and $27 \pm 2^\circ C$ 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 $32 \pm 2^\circ C$ and night temperatures at $28 \pm 2^\circ C$. 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 conditions 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 insignificant but nonetheless measureable decrease in thorn length from 4.68 to 4.41 mm. This became significant with 50%
Fig. 2. A *Prosopis juliflora* 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, compared with thorn length on the plant after 75 days of additional growth.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Thorn length (mm) on re-removed stems</th>
<th>Thorn length (mm) on regrown stems 75 days later</th>
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<td>4.41</td>
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<td>5.19</td>
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<td>3.1918^a</td>
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<td>4.95</td>
<td>3.74</td>
<td>4.1108^a</td>
</tr>
<tr>
<td>100</td>
<td>4.69</td>
<td>--</td>
<td>0.3298</td>
</tr>
<tr>
<td>Control</td>
<td>--</td>
<td>4.81</td>
<td></td>
</tr>
</tbody>
</table>

^aSignificance 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 increased stem removal, the average length of thorns present on the regrown stems was progressively smaller. However,
Table 2. Thorn length on portions of *Prosopis juliflora* stems removed during repeated simulated browsing, compared with thorn length on the plant after additional growth time.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Thorn length (mm) on removed stems</th>
<th>Thorn length (mm) on regrown stems</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Days 126</td>
<td>Days 161</td>
<td>Days 203</td>
</tr>
<tr>
<td>10</td>
<td>4.28</td>
<td>5.13</td>
<td>4.55</td>
</tr>
<tr>
<td>20</td>
<td>4.39</td>
<td>5.34</td>
<td>4.34</td>
</tr>
</tbody>
</table>

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 significant 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.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Thorn length (mm)</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>4.69</td>
<td>0.3298</td>
</tr>
<tr>
<td>25</td>
<td>4.41</td>
<td>1.2111</td>
</tr>
<tr>
<td>50</td>
<td>4.10</td>
<td>1.9388</td>
</tr>
<tr>
<td>75</td>
<td>3.74</td>
<td>3.2747(^a)</td>
</tr>
<tr>
<td>Control</td>
<td>4.81</td>
<td>--</td>
</tr>
<tr>
<td>10(^b)</td>
<td>4.88</td>
<td>0.1618</td>
</tr>
<tr>
<td>20(^b)</td>
<td>4.76</td>
<td>0.6006</td>
</tr>
<tr>
<td>Control</td>
<td>4.62</td>
<td>--</td>
</tr>
</tbody>
</table>

\(^a\) 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.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Number of nodes</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>39.0</td>
<td>3.2128a</td>
</tr>
<tr>
<td>25</td>
<td>45.2</td>
<td>1.1261</td>
</tr>
<tr>
<td>50</td>
<td>57.9</td>
<td>1.3398</td>
</tr>
<tr>
<td>75</td>
<td>54.1</td>
<td>0.8114</td>
</tr>
<tr>
<td>Control</td>
<td>50.5</td>
<td>--</td>
</tr>
<tr>
<td>10b</td>
<td>44.8</td>
<td>1.0585</td>
</tr>
<tr>
<td>20b</td>
<td>37.8</td>
<td>2.4302a</td>
</tr>
<tr>
<td>Control</td>
<td>49.8</td>
<td>--</td>
</tr>
</tbody>
</table>

*a* Significance $P < 0.05$.

*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 *Prosopis juliflora* in its lifetime, compared with unclipped controls.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Number of nodes</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>39.0</td>
<td>3.2128^a</td>
</tr>
<tr>
<td>25</td>
<td>55.1</td>
<td>0.9524</td>
</tr>
<tr>
<td>50</td>
<td>75.8</td>
<td>4.4216^a</td>
</tr>
<tr>
<td>75</td>
<td>84.0</td>
<td>6.5817^a</td>
</tr>
<tr>
<td>Control</td>
<td>50.5</td>
<td>--</td>
</tr>
<tr>
<td>10^b</td>
<td>48.9</td>
<td>0.1391</td>
</tr>
<tr>
<td>20^b</td>
<td>53.2</td>
<td>0.6449</td>
</tr>
<tr>
<td>Control</td>
<td>49.8</td>
<td>--</td>
</tr>
</tbody>
</table>

^aSignificance P < 0.05.

^bClipping 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.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Stem length (cm)</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>70.00</td>
<td>3.0207*</td>
</tr>
<tr>
<td>25</td>
<td>83.15</td>
<td>0.0948</td>
</tr>
<tr>
<td>50</td>
<td>83.84</td>
<td>0.2888</td>
</tr>
<tr>
<td>75</td>
<td>74.80</td>
<td>1.5810</td>
</tr>
<tr>
<td>Control</td>
<td>82.44</td>
<td>--</td>
</tr>
<tr>
<td>10b</td>
<td>81.96</td>
<td>0.2476</td>
</tr>
<tr>
<td>20b</td>
<td>59.56</td>
<td>2.8163*</td>
</tr>
<tr>
<td>Control</td>
<td>84.03</td>
<td>--</td>
</tr>
</tbody>
</table>

*Significance P < 0.05.

*bClipping 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 *Prosopis juliflora* in its lifetime, compared with unclipped controls.

<table>
<thead>
<tr>
<th>% removed</th>
<th>Stem length (cm)</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>70.00</td>
<td>3.0207(^a)</td>
</tr>
<tr>
<td>25</td>
<td>100.10</td>
<td>2.2790(^a)</td>
</tr>
<tr>
<td>50</td>
<td>117.70</td>
<td>6.7127(^a)</td>
</tr>
<tr>
<td>75</td>
<td>124.72</td>
<td>7.8773(^a)</td>
</tr>
<tr>
<td>Control</td>
<td>82.44</td>
<td>--</td>
</tr>
<tr>
<td>10(^b)</td>
<td>95.77</td>
<td>1.3773</td>
</tr>
<tr>
<td>20(^b)</td>
<td>84.35</td>
<td>0.0312</td>
</tr>
<tr>
<td>Control</td>
<td>84.03</td>
<td>--</td>
</tr>
</tbody>
</table>

\(^a\)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 *Cercidium australe* seedlings.

<table>
<thead>
<tr>
<th>Light (ft-c)</th>
<th>Thorn length (mm)</th>
<th>Number of nodes</th>
<th>Stem length (cm)</th>
<th>t values</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1,500</td>
<td>4.40</td>
<td>19.5</td>
<td>25.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3,000</td>
<td>4.65</td>
<td>21.8</td>
<td>23.19</td>
<td>0.6119</td>
<td>1.7058</td>
</tr>
</tbody>
</table>

<sup>a</sup>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 *Prosopis juliflora* seedlings.

<table>
<thead>
<tr>
<th>Light (ft-c)</th>
<th>Thorn length (mm)</th>
<th>Number of nodes</th>
<th>Stem length (cm)</th>
<th>Thorn</th>
<th>Number of</th>
<th>Stem length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2,300</td>
<td>2.95</td>
<td>23.0</td>
<td>33.98</td>
<td>3.5316&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.3759&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.8987&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>3,800</td>
<td>3.74</td>
<td>29.2</td>
<td>44.97</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4,000</td>
<td>3.05</td>
<td>13.9</td>
<td>19.49</td>
<td>1.8915</td>
<td>0.8131</td>
<td>1.2298</td>
</tr>
<tr>
<td>6,000</td>
<td>3.49</td>
<td>14.9</td>
<td>17.49</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4,000</td>
<td>3.10</td>
<td>15.7</td>
<td>22.67</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6,000</td>
<td>3.40</td>
<td>15.5</td>
<td>18.78</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>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 austral*e 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, tertiary shoots on the extended secondary axis often grew vegetatively for a period of time before differentiating as thorns. They found little or no effect on thorn development 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.

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

**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.

<table>
<thead>
<tr>
<th>Temp. N</th>
<th>Thorn length (°C)</th>
<th>Number of nodes</th>
<th>Stem length (mm)</th>
<th>Thorn length (cm)</th>
<th>Number of nodes</th>
<th>Stem length (cm)</th>
<th>t values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plants grown for 40 days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35/21</td>
<td>3.34</td>
<td>15.3</td>
<td>26.17</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24/10</td>
<td>4.48</td>
<td>13.0</td>
<td>27.14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35/21</td>
<td>3.27</td>
<td>14.7</td>
<td>23.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24/10</td>
<td>4.33</td>
<td>12.6</td>
<td>27.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plants grown for 23 days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35/21</td>
<td>3.82</td>
<td>13.3</td>
<td>28.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24/10</td>
<td>4.46</td>
<td>5.1</td>
<td>11.53</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 difference 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 temperatures 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.

<table>
<thead>
<tr>
<th>Water regime (days)</th>
<th>Thorn length (mm)</th>
<th>Number of nodes</th>
<th>Stem length (cm)</th>
<th>t values</th>
<th>Thorn length (mm)</th>
<th>Number of nodes</th>
<th>Stem length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1*</td>
<td>4.46</td>
<td>5.1</td>
<td>11.53</td>
<td>0.3103</td>
<td>13.5452a</td>
<td>12.1470a</td>
<td></td>
</tr>
<tr>
<td>5°</td>
<td>4.41</td>
<td>12.8</td>
<td>27.11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperatures D/N 24/10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1*</td>
<td>3.82</td>
<td>13.26</td>
<td>28.15</td>
<td>2.8042a</td>
<td>2.2947a</td>
<td>2.1090a</td>
<td></td>
</tr>
<tr>
<td>3°</td>
<td>3.31</td>
<td>14.97</td>
<td>24.86</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Temperatures D/N 35/21

**a** Significance *P* < 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.
Table A-1. Nutrient solution.

<table>
<thead>
<tr>
<th>Stock solution</th>
<th>Compound</th>
<th>Amount needed (g)</th>
<th>Volume water needed (ml)</th>
<th>Volume stock solution ml/l final solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Calcium nitrate Ca(NO₃)₂·4H₂O</td>
<td>11.7</td>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>B</td>
<td>Potassium nitrate KNO₃</td>
<td>5.0</td>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>C</td>
<td>Magnesium sulfate MgSO₄·7H₂O</td>
<td>5.0</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>D</td>
<td>Potassium phosphate monobasic KH₂PO₄</td>
<td>1.4</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>E</td>
<td>Manganous chloride MnCl₂·4H₂O</td>
<td>1.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Boric acid H₃BO₃</td>
<td>2.86</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Zinc sulfate ZnSO₄·7H₂O</td>
<td>0.22</td>
<td>1000</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Cupric sulfate CuSO₄·5H₂O</td>
<td>0.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Molybdenum trioxide MoO₃</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>Iron-ethylene-diamine-tetraacetic acid Fe-EDTA</td>
<td>1.0/0.05 g</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX B

NODE AT WHICH THORNS FIRST APPEAR
ON NEWLY DEVELOPED SIDE BRANCHES
OF SEEDLINGS EXPOSED TO SIMULATED BROWSING
Table B-1. Node.

<table>
<thead>
<tr>
<th>Amount clipped (%)</th>
<th>Number of branches / treatment (15 plants)</th>
<th>Node at which thorns first appeared</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>25</td>
<td>47</td>
<td>1</td>
</tr>
<tr>
<td>50</td>
<td>73</td>
<td>6</td>
</tr>
<tr>
<td>75</td>
<td>60</td>
<td>1</td>
</tr>
<tr>
<td>10&lt;sup&gt;a&lt;/sup&gt;</td>
<td>33</td>
<td>1</td>
</tr>
<tr>
<td>20&lt;sup&gt;a&lt;/sup&gt;</td>
<td>33</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>246</td>
</tr>
</tbody>
</table>

<sup>a</sup>Clipping of seedlings was repeated.
LITERATURE CITED


Henslow, G. 1894. The origin of plant-structures by self-adaptation to the environment, exemplified by desert or xerophilous plants. J. Linn. Soc. Bot. 30:218-263.


Jones, M. E. 1931. The spines of the cactus family. Desert Plant Life 2:140, 142-143.


