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STUDIES ON WOOD BORERS, GIRDLERS AND SEED PREDATORS OF MESQUITE

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ABSTRACT

The study was designed to determine the response of honey mesquite (*Prosopis glandulosa*) to varying levels of insect damage. Because of difficulties encountered in getting the insects to affect the plants in varying degrees, damage of the type done by the mesquite twig girdler (*Oncideres* sp.) and a node borer (family Bostrichidae) was simulated. These insects were chosen because of their particularly destructive activities. The possibility that plant water status is important to plant growth response to insect damage was included in the research design. Two plots containing 48 honey mesquite plants were established adjacent to the Jornada Validation Site. One plot received supplemental water and was fenced to guard against lagomorph pruning. The second plot received no supplemental water. Insect damage was simulated by hand on both plots, with the degree of damage varying between groups of plants. There were also control groups on both the watered and unwatered plots. Plant growth was monitored and recorded during the growing period, including leaf numbers and lengths, inflorescence numbers and lengths, and shoot numbers and lengths. Data were taken on pods until they dropped and were collected for laboratory analyses. A pressure bomb analysis showed there was a significant difference in water uptake between the two plots. However, analyses showed there were no significant differences in growth parameters between watered and unwatered mesquite and between damaged and undamaged (control) plants. This suggests that the insect activity may stimulate growth, thereby compensating for biomass loss (independent of water availability). The undamaged controls (both plots) showed no significant difference in terms of vegetative production. Reproduction did differ; the watered plants supporting about twice the biomass on the first observation. Per-node average bean biomass did not differ significantly between treatments but the per-pod biomasses were different; the unwatered pods averaged 1.21 g per pod while the watered reached 1.95 g per pod. The unwatered plants produced more total seeds per pod but the watered plants produced twice as much biomass in terms of fully developed (supposedly viable) seeds. On the basis of the seed analysis and data from other studies, it is hypothesized that *Prosopis* has developed a mechanism whereby an optimum number of seeds are produced during a growing season and the vegetative growth remains at a relatively constant rate, regardless of short-term environmental changes. Seed survival is variable according to environmental conditions. Further study is needed to determine how heavily honey mesquite depends on surface water.

INTRODUCTION

There are several insects that depend on the honey mesquite, *Prosopis glandulosa*, for a means of survival. Two of these insects, the mesquite twig girdler (*Oncideres* sp.) and a node borer of the family Bostrichidae, destroy much more than their numbers or biomasses indicate.

The twig girdler destroys the outer vascular tissues around the entire circumference of a branch and then deposits its eggs under the bark of the girdled branch where they develop, the adults emerging the following year (Polk and Ueckert 1973). Although the twig girdler attacks only branches within a specific size range, it still does significant damage to the shrubs.

The node borer causes damage by boring into and destroying a node on the branch. It destroys not only the node, but also leaves and stems above that point (Riazance and Whitford 1974).

Through their activities, both insects affect photosynthetic area and hence should affect starch reserves in new stems. This in turn should be significant in determining the growth patterns of the plant.

OBJECTIVES

The experiments were designed to determine plant response to varying levels of insect damage. The insect damage was simulated because of the difficulties encountered in getting the insects to affect plants at varying degrees.

The design provided for determination of which type of damage was most harmful to the plants and at which levels the damages were most significant. The possibility that the water status of the plants was an important determinant of the effect of insect damage and the resulting plant growth response was included in the design.

METHODS

In March 1974, 48 shrubs were selected to obtain a representative sample of the general mesquite population adjacent to the Jornada Validation Site. The plants were then divided into two plots. One plot, with 12 plants, was watered to provide each plant with approximately 165 gallons of supplemental water weekly, beginning in late March and continuing throughout the growing season. This plot was fenced to ensure that the responses measured were due only to the insect damage since initial watering studies by Cunningham (pers. comm.) showed that jackrabbits (*Lepus californicus*) selectively pruned plants with higher water content than other plants in the area. This plot supplied two types of data. First, it tested the dependency of plant response to insect damage on the water status of the plant. Second, it tested the ability of the shrubs (with the deep taproot system) to absorb surface water. The average difference in water status between the two plots and the absorption of the supplemental water was measured by pressure bomb analysis.

The second plot, with 36 shrubs, was in close proximity to the watered plot and received no supplemental water during the experiment.

Next we determined the range of twig diameter attacked by the twig girdlers. Fifty branches that had been girdled the previous year were located. The diameters of the branches immediately above the girdle were measured with a micrometer.

Insect damage on the two plots was simulated by hand. The damage mimicked the style of the insects as closely as possible. Plants were selected at random for the various treatments. Girdling activity was simulated by cutting through the phloem on various branches of selected plants. Borer activity was simulated by simply cutting off the entire terminal node.

On the watered plot the plants were divided into four groups of three plants each. In the first group 40% of the terminal nodes on the plant were destroyed with pocket knives. In the second group, 80% of the terminal nodes were destroyed in the same fashion. The third group was girdled on 50% of the branches which were within the girdling range of *Oncideres* sp. The fourth group was a control.

On the unwatered plot there were 36 plants divided into six groups of six plants each. As on the watered plot, the first two groups were treated with 40 and 80% node destruction, respectively. The next two groups were girdled at the 40 and 80% levels. In the fifth group the girdling range was doubled and 50% of the plant branches were girdled. The last group was a control.

Random nodes were marked on all plants and, throughout the growing season (from May through late October), these nodes were monitored at monthly intervals. The following data were taken according to the growth and phenology of the plant.

Leaf numbers and lengths were recorded for each month throughout the experiment. Inflorescences appeared in May and their numbers and lengths were recorded for the two months they persisted. When the June measurements were taken, very few inflorescences remained and the seed pods had begun to appear. Data were taken on the pods from June until they dropped in late July, at which time they were collected. Shoot lengths and numbers were recorded whenever they appeared and for every month from then on through October.

A pressure bomb analysis was done on the two plots simultaneously. The test was run May 27-28 during the night. Because the test measures the water potential or uptake of the plant it must be done at night when the stomata are closed.

Data for this study are stored under DSCODES A3UWK01 through WK07.

RESULTS AND DISCUSSION

The pressure bomb analysis showed conclusively that there was a significant difference in water uptake between the two plots. The measurements were taken in pounds per square inch (PSI) and the mean for each time interval was converted to pressure in atmospheres (Table 1). Pressure bomb readings were also taken before the watered plot had received its weekly watering. These initial readings were taken only minutes before sunrise (Table 2). A more striking difference between the water potential of the two plots is shown in a histogram (Fig. 1).

The difference in leaf biomass between treatments was greater than the difference in shoot biomass and consequently was subjected to further analysis. Of the 476 nodes measured only 4.5% produced new shoots; hence statistical comparisons between treatments with respect to shoot growth were not feasible. Watering and insect-damage simulation appeared to affect flowering and fruiting, and will be discussed later.

The biomass of leaves was analyzed by nested analysis of variance (Snedecor and Cochran 1968). The nested ANOVA supplies an F value between each consecutively nested level of determinations. The method takes into account the sources of variation at these different levels and estimates parameters on the basis of variance for each level of analysis, i.e., the F value *B* is the ratio of the mean square between classes and the mean square within classes.

Table 1. Results from the pressure bomb analysis of the watered and unwatered plants. Readings are given in PSI plus or minus the standard deviation

Initial Reading	Plot	1800	2000	2700	2400	200	400	600
232±61	Watered	469±35	200±39	176±24	176±22	156±22	176±33	150±22
458± 54	Unwatered	588±38	402±51	447±67	401±45	405±44	412±47	422±48
	T Statistic (Watered vs. Unwatered)							
9.518		7.817	10.703	13.175	16.095	17.317	14.101	17.691

at 95% confidence interval T statistic cutoff is 2.201

Table 2. Average per-node leaf biomass for the four watered treatments plus or minus the standard deviation. Coefficients of variance are obtained from the analysis of variance

	Control		Bored				Girdled	
Date	00 %	Coef. Vari.	40 %	Coef. Vari.	80 %	Coef. Vari.	50 %	Coef. Vari.
May	0.51±0.92	178.51	0.54±0.39	70.90	0.50±0.60	120.65	0.65±0.55	84.58
Jun	0.64±1.1	172.48	0.51±0.38	73.81	0.56±0.67	119.73	0.56±0.79	141.43
Jul	0.49±0.88	175.41	0.45±0.28	62.36	0.51±0.58	112.75	0.56±0.79	141.43
Aug	0.34±0.31	90.53	0.43±0.31	70.99	0.43±0.56	129.80	0.37±0.55	147.96
Oct	0.34±0.32	93.51	0.37±0.31	85.00	0.40±0.40	99.41	0.26±0.37	121.52

Sources of Variation	Parameters Estimated
Treatments	$\sigma^2 + n\sigma_B^2 \div cn\sigma^2$
Plants	$\sigma^2 + n\sigma_B^2$
Nodes (observations)	σ^2

This process can be repeated with each successive subsampling. The model being used is

$$x_{ijk} = \mu + A_i + B_{ij} + E_{ijk},\ i = 1 \ldots a,\ j = 1 \ldots b,\ k = 1 \ldots n$$

$$A_i = N(0, \sigma_a), B_{ij} = N(0, \sigma_b), E_{ijk} = N(0, \sigma)$$

where A refers to plants and B to leaves, the variables A_i, B_{ij} and E_{ijk} are all assumed independent.

In the completed analysis of variance (see above), the components of variance are shown. Each component of a subsample is included among those in the sample above it.

The analysis also produced the mean for each plant as well as the mean variance, standard deviation, standard error and the coefficient of variance for each individual treatment for each month. The best data were in the unwatered plot during the last three months of the growing season. This was over two consecutive sampling periods and the data were significant at the 90% confidence level. The other sampling periods in both plots did not produce any significant differences.

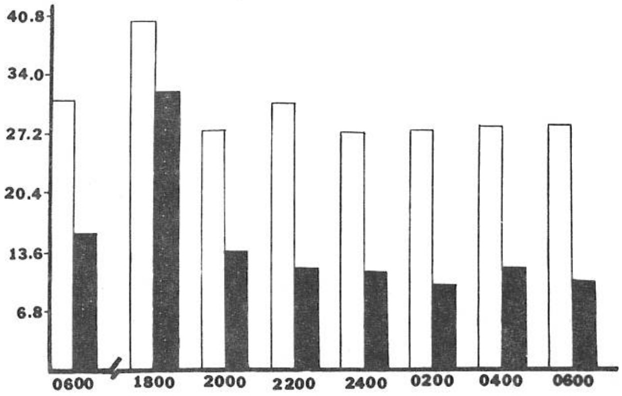

Figure 1. Results of pressure bomb analysis of the watered and unwatered plots with supplemental water applied between the initial 0600 measurement and the 1800 measurement. The vertical axis indicates pressure in bars; the horizontal axis indicates time. The open bars are unwatered plots, and the solid bars are watered plots.

The theory behind the F value states that the F ratio is a good criterion for testing the null hypothesis that populations are the same in small classes. F should be around one (1) when the hypothesis holds true and it becomes large when μ_i differ substantially.

On this basis it would seem that the simulated damage had no drastic effect on the plants and in essence the entire population studied showed no great difference in response to any of the treatments (Tables 2 and 3).

Because of the variation between plants within treatments (Figs. 2 and 3), none of the growth parameters had significant F values (Tables 4 and 5). The lack of significant differences in growth parameters between watered and unwatered mesquite and between undamaged and simulated insect-damaged plants (Figs. 4 and 5) supports the suggestion of Riazance and Whitford (1974) that the activity of girdlers and node borers stimulates stem growth, compensating for biomass lost. This response is independent of the availability of water for the shallow roots of the plant. Since even the shrubs with the highest simulated insect damage exhibited growth similar to that of controls and, in some shrubs, actually exceeded biomass production of some control shrubs, the activity of these insects has an effect similar to pruning on the growth responses of mesquite. Ueckert et al. (1971) suggested that the girdler, *Oncideres* sp., might be one means of biological control of mesquite on deteriorated rangeland. These experiments and data reported by Riazance and Whitford (1974) suggest that such efforts would be futile since the girdler has the effect of stimulating growth so there is no difference in above-ground biomass production of leaves, shoots or fruits in girdled plants as compared to ungirdled controls regardless of the water status of the plants. This might not be the case if heavy girdling damage were to occur several years in succession, which could deplete carbohydrate stores. However, testing this hypothesis would require several years of continued measurements and experiments.

COMPARISON OF WATERED AND UNWATERED CONTROLS

The watered and unwatered control plants were also compared to evaluate the effect of the supplemental water on the growth characteristics of mesquite without regard to damages done by insects.

The average leaf biomasses were compared between the two plots. Although the averages appear to be different (Table 6), the high standard deviations made these differences meaningless. A t-distribution showed that leaf production did not increase significantly due to supplemental water at any time during the experiment.

The new shoot data yielded similar results with no differences between the two plots. Of the 124 nodes measured on the nine plants (six unwatered and three watered) only four (two from each treatment) produced new shoots, and thus information gained from observing new shoots was of little value (Table 6).

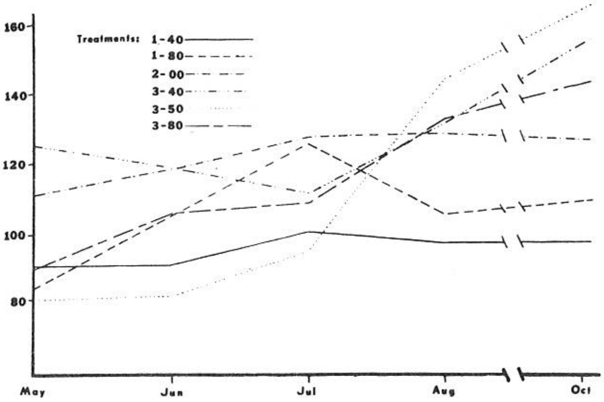

Figure 2. Coefficient of variance for the leaf biomass of the watered plot.

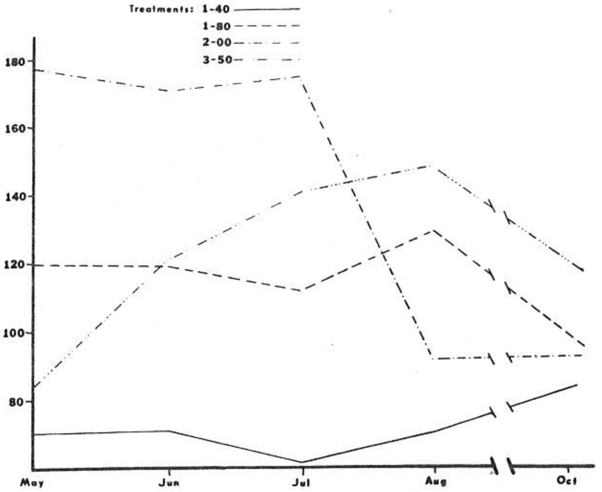

Figure 3. Coefficient of variance for the leaf biomass of the watered plot.

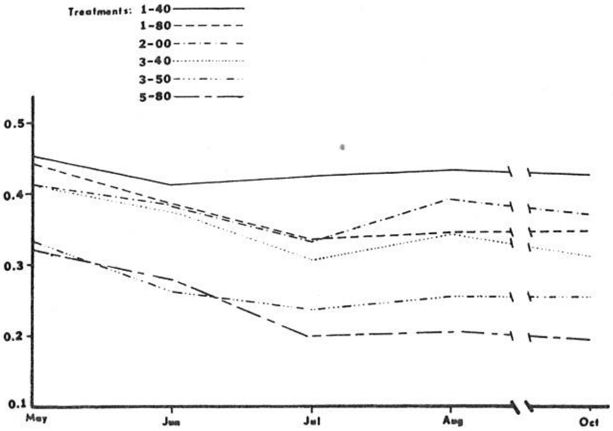

Figure 4. Average per-node leaf biomass for the six treatments of the unwatered plot. Biomass (the vertical axis) is given in grams.

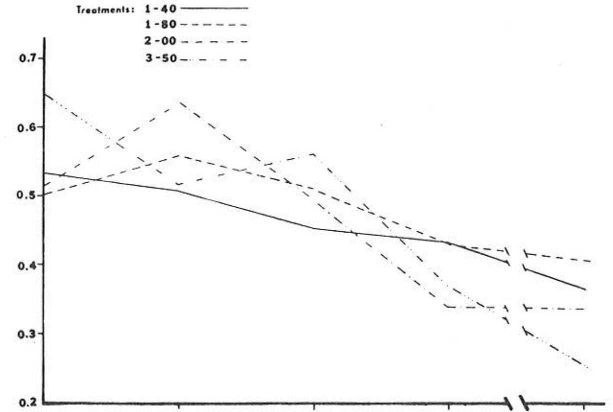

Figure 5. Average per-node leaf biomass for the four treatments of the watered plot. Biomass (the vertical axis) is given in grams.

Table 3. Average per-node leaf biomass for the six treatments of the unwatered plot plus or minus the standard deviation. Coefficients of variance are obtained from the analysis of variance

Month	00%	Coef.Vari.	40%	Coef.Vari.	80%	Coef.Vari.
May	0.41±0.46	112.06	0.45±0.42	92.63	0.34±0.31	91.47
Jun	0.38±0.46	118.94	0.41±0.38	95.53	0.27±0.28	103.86
Jul	0.33±0.42	127.00	0.42±0.43	102.17	0.24±0.29	123.38
Aug	0.39±0.51	129.23	0.43±0.42	97.14	0.25±0.26	103.76
Oct	0.37±0.47	127.17	0.43±0.42	98.04	0.26±0.28	109.16
			Bored			
Month	40%	Coef.Vari.	50%	Coef.Vari.	80%	Coef.Vari.
May	0.43±0.52	123.09	0.41±0.34	81.36	0.32±0.28	85.16
Jun	0.39±0.46	119.66	0.37±0.31	82.18	0.28±0.29	106.14
Jul	0.34±0.38	112.62	0.31±0.29	95.67	0.20±0.22	108.07
Aug	0.34±0.45	132.55	0.34±0.50	144.91	0.20±0.27	133.85
Oct	0.35±0.54	154.16	0.31±0.51	164.42	0.20±0.28	143.93

Table 4. Results from the analysis of variance of leaf biomass showing sources of variation among the six treatments of the unwatered plot, showing no significant difference among treatments

Date	Source of Variation	Degrees Freedom	Sum Squared	Mean Squared	F
May	Treatments	5	1.038	0.2076	0.31*
	Experimental Error	62	15.478	0.2496	1.74[1]
	Sampling Error	367	52.595	0.1433	
June	Treatments	5	1.344	0.2689	0.39
	Experimental Error	62	15.992	0.2579	2.14
	Sampling Error	367	44.207	0.1205	
July	Treatments	5	2.272	0.4544	1.62
	Experimental Error	62	12.733	0.2054	1.93
	Sampling Error	367	38.979	0.1062	
August	Treatments	5	2.824	0.5649	2.03
	Experimental Error	62	14.505	0.2340	1.45
	Sampling Error	367	59.061	0.1609	
October	Treatments	5	2.580	0.5160	2.61
	Experimental Error	62	11.902	0.1920	1.07
	Sampling Error	367	65.940	0.1797	

* Approximately 3.76 is significant at the 0.005 confidence interval.

[1] Approximately 1.53 is significant at the 0.005 confidence interval.

Table 5. Results from the analysis of variance of leaf biomass, showing sources of variation among the four treatments of the watered plot

Date	Source of Variation	Degrees Freedom	Sum Squared	Mean Squared	F
May	Treatments	3	0.582	0.1940	0.2969*
	Experimental Error	51	2.180	0.0427	0.07[1]
	Sampling Error	88	53.739	0.6107	
June	Treatments	3	0.335	0.1117	0.1273
	Experimental Error	51	3.354	0.0658	0.08
	Sampling Error	89	72.215	0.8114	
July	Treatments	3	0.235	0.0783	0.0972
	Experimental Error	51	3.713	0.0728	0.10
	Sampling Error	89	65.224	0.7329	
August	Treatments	3	0.198	0.0659	0.1863
	Experimental Error	51	1.086	0.0213	0.06
	Sampling Error	89	29.583	0.3324	
October	Treatments	3	0.455	0.1518	0.8166
	Experimental Error	51	1.194	0.0234	0.014
	Sampling Error	89	14.461	0.1625	

* Approximately 4.85 is significant at the 0.005 confidence interval.

[1] Approximately 1.96 is significant at the 0.005 confidence interval.

Table 6. Comparison of the vegetative production of the watered and unwatered control plants. Values are given in grams plus or minus the standard deviation

Leaf Biomass per Node (gm)

Month	Unwatered	Watered	t-stat*[1]
May	0.41±0.46	0.52±0.92	-0.597
Jun	0.37±0.45	0.64±1.10	-1.322
Jul	0.33±0.42	0.52±0.86	-1.161
Aug	0.39±0.51	0.34±0.31	0.648
Oct	0.37±0.47	0.34±0.32	0.440

*122 degrees of freedom

[1] approximately 1.65 is significant at the 0.05 level

Stem Biomass per Node (gm)

Month	Unwatered	Watered	t-stat** [1]
May	0.004±0.041	0.000±0.000	1.000
Jun	0.065±0.475	0.243±1.04	-0.920
Jul	0.075±0.514	0.214±0.919	-0.809
Aug	0.075±0.553	0.160±0.904	-0.494
Oct	0.045±0.429	0.186±0.936	-0.811

** 122 degrees of freedom

[1] approximately 1.65 is significant at the 0.05 level.

The above results indicate that watering the plants did not increase their vegetative production and if increased photosynthate was the result of supplemental water, it was not being stored in the form of shoots, as found by Meyer et al. (1971).

The reproduction of the plants did differ between the treatments. At the time of the first observation the plants of both treatments were in bloom and, at this time, the watered plants supported about twice as much biomass as the unwatered plants (Table 7). By the second observation the inflorescences were virtually gone with no difference between the treatments. No inflorescences remained on the plants by the third observation.

Table 7. Comparison of the reproductive production of the watered and unwatered control plants. Values are given in grams plus or minus the standard deviatiion

Inflorescence Biomass per Node (gm)

Month	Unwatered	Watered	t-stat*[1]
May	1.78±2.39	3.62±2.68	-3.434
Jun	0.44±1.66	0.17±0.95	1.117
Jul	0 ± 0	0 ± 0	0.0
Aug	0 ± 0	0 ± 0	0.0
Oct	0 ± 0	0 ± 0	0.0

* 122 degrees of freedom

[1] 1.96 is significant at the 95% confidence level.

Bean Pod Biomass per Node (gm)

Month	Unwatered	Watered	t-stat*[1]
May	0.0 ±0.0	0.0 ±0.0	0.0
Jun	0.02±0.23	0.0 ±0.0	1.0
Jul	0.0 ±0.0	0.02±0.10	-1.0
Aug	0.0 ±0.0	0.0 ±0.0	0.0
Oct	0.0 ±0.0	0.0 ±0.0	0.0

* 122 degrees of freedom

[1] 1.96 is significant at the 95% confidence level.

Per-node average bean biomass did not differ significantly between the watered and unwatered control plants. However, the unwatered plants released their beans about one month before the watered plants (Table 7). To investigate the effects of the water on the beans, they were collected and brought to the laboratory to be studied.

Although the per-node biomass did not differ, the per-pod biomasses were different. The actual dry weights showed that the unwatered pods averaged 1.21 g per pod while the watered pods reached 1.95 g per pod using large random samples from all the plants of the two treatments.

The number of fully developed seeds per pod was also considered since time did not permit the filing and planting of seeds to get an estimate of percent viable seeds. By counting the number of fully developed seeds and comparing them to the number of undeveloped seeds, it was determined that the number of fully developed seeds per pod did not differ between the two treatments (Table 8). However, the unwatered plants produce slightly more total seeds per pod with 11.93 compared to 10.06 for the watered plants (Table 8). Therefore, the percentage of fully developed seeds per pod was approximately 67% for the unwatered and 78% for the watered plants.

The weights of the fully developed individual seeds were compared between the plots using samples of 40 and 34 for the watered and unwatered plants, respectively. The weight of fully developed seeds was significantly different, with the seeds from the unwatered averaging nearly half the biomass of those from the watered plants (Table 8).

Table 8. Comparison of the seed production and degree of development between the watered and unwatered control plants

Fully Developed Seeds/Pod	Watered	Unwatered
Number in sample	112	136
Mean	7.85	8.01
Maximum	23	23
Minimum	0	0
Range	23	20
Standard Deviation	5.42	5.03
Upper Confidence Limit	8.85	8.85
Lower Confidence Limit	6.84	7.16
T-statistic*	0.238	

* 1.98 is significant at 97% with 120 degrees of freedom

Total Seeds/Pod	Watered	Unwatered
Number in sample	112	136
Mean	10.06	11.93
Maximum	23	25
Minimum	1	1
Range	22	24
Standard Deviation	5.13	4.85
Upper Confidence Limit	11.01	12.74
Lower Confidence Limit	9.11	11.11
T-statistic*	2.919	

* 1.98 is significant at 97% with 120 degrees of freedom

Weight of fully developed seeds (grams)	Watered	Unwatered
Number in sample	40	34
Mean	0.045	0.024
Maximum	0.0513	0.0294
Minimum	0.0326	0.0124
Range	0.0170	0.0170
Standard Deviation	0.005	0.004
Upper Confidence Limit	0.0458	0.0254
Lower Confidence Limit	0.0434	0.0233
T-statistic*	21.227	

* 2.04 is significant at 95% with 30 degrees of freedom

These data indicate that although the unwatered plants produced more total seeds per pod, they were less successful in terms of percentage of developed seeds than were the watered plants. The production of seeds consumes considerable energy from a plant and its reserves and so it is not surprising that the watered plants produced proportionally more developed seeds. Thus the energy gained through supplemental watering was used only in reproductive effort as illustrated by the drastic difference in the weight of fully developed seeds between the two treatments.

Since only the percentage of fully developed seeds per pod and the size of seeds differed and not the number of potentially viable seeds released into the environment, it is possible that *Prosopis* has evolved a mechanism by which it produces an optimum number of seeds during a growing season and grows vegetatively at a relatively constant rate without regard to short-term environmental changes. The energy expenditure in producing the optimum number of seeds, and thereby the probability that the seeds will survive, are variable according to environmental conditions. This is illustrated by the fact that the watered seeds were heavier and therefore contained more endosperm as a food source for the embryos. The energy spent and biomass added to the seeds by the plants are a function of the length of time the pods remain on the plants, which is in turn determined by the environmental conditions. This mechanism could also explain the fact that the increased inflorescence production on the part of the watered plants did not result in an increased amount of pod biomass. However, 1974 had an extremely dry spring and populations of insect pollinators for the plants could have affected fruit-set adversely.

The diverse growth forms characteristic of mesquite could also be partially explained by this mechanism. A plant in a wetter, more dependable environment would not profit from restricting vegetative production; the mechanisms would break down and larger tree-like plants could develop.

The above mechanism seems reasonable in view of the sporadic occurrence of precipitation in the environment in which the monitored plants survive. However, it is assumed by this hypothesis that mesquite depends fairly heavily on availabity of surface water and further experimentation is needed to check the validity of this assumption.

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