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The effects of twig girdlers (Cerambycidae) and node borers (Bostrichidae) on primary production in mesquite (*Prosopis glandulosa*)

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Production of leaves and shoots on branches of mesquite shrubs which had been girdled by the mesquite twig girdler (*Oncideres rhodisticta*) was compared with the production of unaffected branches on girdled and ungirdled shrubs. We made similar comparisons on mesquite which had been subjected to simulated girdling or terminal node destruction of 40–80 per cent of the branches. There was no significant difference in shoot and leaf growth in either natural or simulated damaged plants compared to controls. These studies suggest that the timing of the activity of stem-destroying insects may be important in minimizing damage to the plant.

Introduction

Most studies of the rôle of insects in ecosystems have focused on the effects of insects as herbivores and on their rôle in energy flow in ecosystems (Price, 1975). Mattson & Addy (1975) present a case for phytophagous insects serving as regulators of forest primary production. While there are numerous examples of the rôle of insect herbivores in forest ecosystems, there are few studies of the rôle of insects in desert ecosystems (Price, 1975).

Honey mesquite (*Prosopis glandulosa*) is a dominant shrub in the Chihuahuan desert in New Mexico. It occurs along the edges of water courses in creosotebush (*Larrea tridenta*) communities, and in dense stands in overgrazed areas with deep sandy soils where dunes often form around the plants (Gardner, 1951). In the rangelands of the southwestern United States mesquite is considered an undesirable species and considerable effort has been expanded to reduce its density and influence (Scifres *et al.*, 1974). Ueckert *et al.* (1971) suggested that *Oncideres* sp. mesquite-twig girdlers (Cerambycidae) might serve as a potential means of control of mesquite, and Polk & Ueckert (1973) reported on the biology of *O. rhodisticta* in West Texas. They reported that these insects killed between 10 and 40 per cent of the branches on mesquite trees in West Texas and that *c.* 90 per cent of the mesquite trees in that area were attacked. However, they did not evaluate the effect of the girdling on primary production of *Prosopis*.

Although mesquite-twig girdlers and node borers consume little biomass, their activity results in the transfer of a varying amount of live wood to the litter/decomposer portion of the ecosystem and thus may play a rôle in nutrient cycling. Branches are girdled at the end of the growing season and provide habitat and food source for a number of insects in addition to the twig-girdler larvae (Polk & Ueckert, 1973). Since the apical meristem is destroyed by the girdling, the affected stem should exhibit some difference in growth during the subsequent growing season.

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In contrast, Bostrichid node borers make holes in leaf or thorn nodes below the apical meristem, resulting in a hollow tube in which they deposit eggs. In addition to killing the apical meristem and the stem above the affected node, this eventually adds leaf and stem to the litter and, hence, to the decomposer portion of the ecosystem.

Since twig girdlers and node borers kill an unknown and variable percentage of the growing branches of mesquite on our Chihuahuan desert study area, we hypothesized that these insects would significantly reduce the production of new stems and leaves on affected plants and thus reduce their variability. The studies and experiments reported herein were designed to test this hypothesis and to add to our understanding of the rôle of these insects in a desert ecosystem.

Methods

These studies were conducted in 1974 and 1975 as part of the US/IBP Desert Biome program on the Jornada Validation Site approximately 40 km NNE of Las Cruces, New Mexico. The Jornada Validation Site is a small watershed draining the Doña Ana mountains and terminating in a small dry lake (playa). The upper alluvial slopes (bajadas) are dominated by creosotebush with mesquite abundant along larger watercourses (arroyos). Mesquite is a co-dominant shrub on the lower portion of the watershed and around the playa (ephemeral lake). The 100-year rainfall average $\pm$ one standard deviation is 211 ± 77 mm with most of the annual precipitation resulting from convectional storms in July through August.

In April 1973, 20 mesquite shrubs were selected at random along arroyos on the bajada and eight shrubs were selected at random around the fringe of the playa. Tree-like and very small shrubs were avoided.

Each mesquite was tagged with a number and its height and width were recorded. On girdled branches, each girdle was tagged with a number and the following data were recorded: diameter of branch immediately above the girdle, and the length from the girdle to the tip of the main branch. Three to five non-girdled branches were selected as controls. These were tagged with a number at a point where the branch measured from 1–2 cm in diameter, which is the diameter of stems that are normally girdled. The diameter was recorded and the length from that point to the tip of the main branch was measured.

Six of the tagged mesquites, two near the playa and four on the bajada, were later chosen at random for measurement of new growth on control branches and around girdled branches. Measurements were taken three times: in May at the start of the growing season, in July in the middle of the growing season, and in September at the end of the growing season.

In May, the following data were recorded on control and girdled branches: total lengths of new shoots, starting from either terminal or old nodes, lengths of inflorescences and numbers of leaves per old node. In July, lengths of new shoots, length of fruits, rather than inflorescences, and numbers of leaves per branch, rather than per old node, were recorded. In September, only lengths of new shoots were recorded, measured as in May, because no new leaf production was noted. Shoot lengths were corrected by subtracting the previously recorded length to obtain new shoot production for each period.

New biomass of shoots and leaves on control and girdled branches for each shrub was calculated from these data, using empirically derived equations which relate length of new shoots to (dry weight) biomass of shoots and leaves. Leaf biomass $= 0{\cdot}029L + 0{\cdot}0004L^2$, where $L =$ new shoot length. Stem biomass $= 0{\cdot}011L + 0{\cdot}0007L^2$. The relationship of leaf biomass at node (B) as a function of total leaf length (L) at the node is $B = 0{\cdot}0105L + 0{\cdot}0001L^2$. The same equations were used to calculate the biomass killed by girdlers from the length of the girdled branch.

During the month of June the tagged mesquites at the playa and bajada were examined weekly for holes bored into branch nodes by Bostrichids. When a hole was found, it was tagged with a number and the following data were recorded: diameter immediately above the hole, lengths of all old and new shoots killed by boring, from the hole to the tip of the shoot, and length of rachis of the leaves which were killed. From these data, total weight in grams of new shoots, old shoots and leaves killed by the Bostrichids was calculated for each shrub, using equations relating the length of shoots and leaves to their biomass.

In September, transects were used to estimate the frequency and extent of girdling in mesquite. A series of six random line-transects of variable length was run until 20 shrubs were encountered. For each shrub, the height, width and number and length of girdled branches were recorded. The total stem and leaf biomass killed as a result of girdling was calculated, using the appropriate regression equation. The percentage of total stem and leaf biomass killed was determined using the calculated volume of each shrub and an equation relating biomass to volume of stems and leaves (Ludwig *et al.*, 1975).

To follow the development of larvae in girdled-mesquite branches, samples of 20 branches were collected from random shrubs near the study area in February, March, May, June and July. The length of each branch from the point of girdling to its tip, its weight and the diameter immediately above the girdle were measured and recorded. Each branch was dissected and all larvae, pupae and adults found were preserved.

In 1974, we conducted studies to simulate different levels of stem damage by bostrichids and cerambycids. We selected 36 mesquite shrubs which were assigned at random to the following six treatments: 40 and 80 per cent destruction, 40, 50 and 80 per cent of branches >1·5 cm girdled and untreated controls. Insect damage was simulated by cutting a ring girdle through the phloem (girdling) or by cutting off the terminal node with a pocket knife (node boring).

Random nodes were marked on all plants and the growth data of all structures (leaves, shoots, inflorescences and seed pods) were recorded each month of the growing season as described earlier.

Results

There were no significant differences in average biomass of new shoots and leaves on girdled and control branches when comparisons were made between branches on the same shrub or when all control and girdled branches were compared (Fig. 1). There was a gradual decrease in biomass of shoots and leaves throughout the growing season.

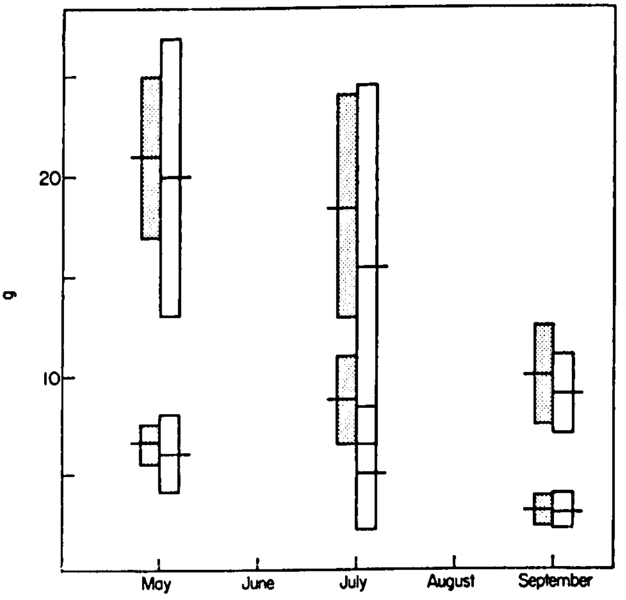

Figure 1. Leaf and new stem biomass on branches girdled by the mesquite twig girdler and on ungirdled branches. Horizontal lines represent means, and shaded and unshaded bars equal ± one standard error of the ungirdled (shaded) and girdled (unshaded) branches, respectively. Upper data are for shoots and lower are for leaves.

Of the 26 mesquite shrubs tagged to estimate Bostrichid damage, seven exhibited node destruction. Stem biomass killed by node boring ranged from 0·4 to 80·6 g, which represents between 0·01 and 0·82 per cent of the total stem biomass. Leaf death due to node boring ranged from 4·4 to 298·5 g, representing from 1·4 to 53·4 per cent of the total leaf biomass.

Twig girdlers affected 45 per cent of the mesquite bushes on the site. The number of girdled branches per shrub ranged from 1 to 17. This represents 0·08 to 0·3 per cent of the stem biomass and 0·5 to 1·8 per cent of the leaf biomass.

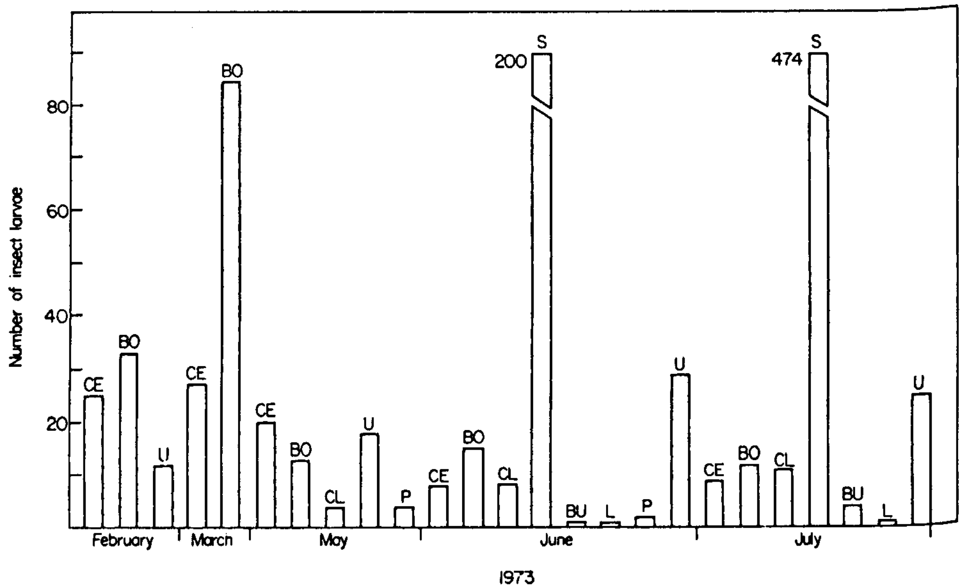

Figure 2. Numbers and taxa of insects removed from girdled mesquite branches. BO = Bostrichid, BU = Buprestid, CE = Cerambycid, CL = Clerid, L = Lepidoptera, P = Pupae, S = Scolytid and U = Unknown.

The number of girdler larvae in girdled stems descreased from 1·25 larvae stem^{-1} in February to 0·5 larvae stem^{-1} in June and July (Fig. 2). In contrast, the number of Clerids and Scolytids increased during the sampling period.

Table 1. *Average per node leaf biomass for the six treatments simulating twig girdling and node boring plus or minus the standard deviation**

Month	40%	Coeff. Var.	40%	Coeff. Var.	80%	Coeff. Var.
			Twig-girdling simulations			
May	0·41 ± 0·46	112·06	0·45 ± 0·42	92·63	0·34 ± 0·31	91·47
June	0·38 ± 0·46	118·94	0·41 ± 0·38	95·53	0·27 ± 0·28	103·86
July	0·33 ± 0·42	127·00	0·42 ± 0·43	102·17	0·24 ± 0·29	123·38
August	0·39 ± 0·51	129·23	0·43 ± 0·42	97·14	0·25 ± 0·26	103·76
October	0·37 ± 0·47	127·17	0·43 ± 0·42	98·04	0·26 ± 0·28	109·16
			Node-boring simulations			
May	0·43 ± 0·52	123·09	0·41 ± 0·34	81·36	0·32 ± 0·28	85·16
June	0·39 ± 0·46	119·66	0·37 ± 0·31	82·18	0·28 ± 0·29	106·14
July	0·34 ± 0·38	112·62	0·31 ± 0·29	95·67	0·20 ± 0·22	108·07
August	0·34 ± 0·45	132·55	0·34 ± 0·50	144·91	0·20 ± 0·27	133·85
October	0·35 ± 0·54	154·16	0·31 ± 0·51	164·42	0·20 ± 0·28	143·93

* The percentage figures refer to the percentage of branches on a shrub subject to simulated girdling or terminal node destruction. Coefficients of variation were obtained from the analysis of variance.

In the twig girdler–node borer simulations, there were no significant differences in leaf biomass between controls and any treatments (Table 1). (F ranged between 0·31 and 2·64 for the May through October measurements, which is not significant at the 0·05 level.) Shrubs with the highest level of simulated insect damage exhibited growth similar to that of controls and in some plants actually exceeded the biomass production of control shrubs.

The large coefficients of variation (Table 1) obtained in the stem damage simulations reflect the greater genetic variability and microsite variability which are not encountered when studies are made on agricultural plants or on native plants brought into the laboratory. As more investigators attempt experiments on natural populations, they should expect considerable variation particularly when dealing with complex physiological responses such as those estimated in these experiments.

Discussion

According to Meyer *et al.* (1971), mesquites store carbohydrates in young stems. These carbohydrate stores are lost to the plant when the stem is killed. Additionally, Bostrichids kill stems after the leaves have been produced, which results in variable defoliation (up to as much as 53 per cent of the total leaf biomass on our site in 1973). The hypothesis that such damage would reduce the stem and leaf production of affected plants seems logical. However, in the productivity comparisons between naturally girdled, simulated girdled and node bored plants, there was no significant change in production.

Mesquite is a deep-rooted species in which tap roots extend more than 15 m into the soil (Meyer *et al.*, 1971). It also has an extensive lateral root system (Ludwig, 1977). In the Chihuahuan desert, *P. glandulosa* is a slow-growing species. The mesquite we studied were mature (>1 m in height and diameter), having extensive root systems. Hence the energy reserves for growth after destruction of up to 80 per cent of the growth points probably came from carbohydrate stores in roots.

Although nodes above a girdle or bore hole were killed, nodes below compensated for this loss by becoming meristematic and producing new shoots and leaves. This production of necessity must come at the expense of stored energy reserves. However, it occurs rapidly (within a month), after which time the leaf biomass (hence photosynthetic area) is not significantly different from unaffected controls. Therefore, we can assume that carbohydrate production in such stems would not differ from unaffected stems from that point in time.

Polk & Ueckert (1973) reported that the number of Cerambycid (twig girdler) larvae in the branches decreased with a corresponding increase in larval predators and competitors. Our data showed that Clerids (presumably predators of Cerambycid larvae), Bostrichids and Scolytids (probably competitors) increased throughout the spring and summer as the numbers of Cerambycid larvae declined. Our observations support the contention of Polk & Ueckert (1973) that the decrease in Cerambycid larvae during the growing season is probably due to predation and competition.

The effect of twig girdlers and node borers on mesquite is similar to that of pruning. Ueckert *et al.* (1971) suggested that mesquite twig girdlers might be one means of biological control of mesquite on deteriorated rangeland. Our study suggests that such effort would be futile since these insects have the effect of stimulating growth resulting in no difference in above ground biomass production of leaves, shoots or fruits at the end of the growing season. However, this effect may not occur if large scale girdling or node destruction takes place over several years in succession. For this to occur, the girdlers and borers would have to be maintained at extremely high densities, which is highly unlikely in view of the number of probable predators and competitors we found.

This study demonstrates the importance of timing in the relationship between mesquite and the arthropods that destroy stems. Girdling of stems occurs at the end of the growing season. At that time of the year, fruits are mature and are unaffected by stem girdling. Subapical nodes below the girdled area can then grow rapidly at the beginning of the next growing season as documented in this study. Bostrichids bore into stems soon after mesquite initiates leaf growth in the spring. The timing of this activity also allows compensatory growth of undamaged portions of the stem and no measurable reduction in total stem and leaf biomass at the end of the season. If the activities of these insects were to occur in July and August, they could result in important reductions in viable fruits or in vegetative production and carbohydrate stores.

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