

The contribution of shrub pruning by jackrabbits to litter input in a Chihuahuan desert ecosystem

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Jackrabbits, *Lepus californicus*, prune stems from creosotebushes *Larrea tridentata* during the dry winter months, eating the previous season new woody stems allowing the leaves and old wood to fall to the ground. This unconsumed material was 66 kg/ha/year of stem and 35 kg/ha/year of leaves; approximately one-fifth of the quantity of shrub litter input by natural infall. Jackrabbits preferentially pruned stems of shrubs with higher tissue moisture content. Rabbits tend to prune stems from the same shrubs in successive years.

Introduction

Studies of food habits of jackrabbits, *Lepus californicus* in deserts in Nevada (Hayden, 1966) and northern Utah (Westoby, 1980) have shown that jackrabbits utilize different forage species seasonally. In southern Nevada, jackrabbits used woody perennials in late summer through winter (Hayden, 1966). Westoby (1980) and Currie & Goodwin (1966) found that jackrabbits preferred grasses and forbs in spring and summer and utilized shrubs during the autumn and winter in a northern Utah cold desert. We observed a similar pattern of shrub use by lagomorphs in the Chihuahuan desert in southern New Mexico.

Chew & Chew (1970) estimated that rabbits pruned 4 per cent of the above ground shrub production but the rabbits ate only one-half of this material. When lagomorphs use shrubs as forage, they leave considerable quantities of unconsumed plant material on the ground. That material then becomes an energy and nutrient source for the soil biota. Currie & Goodwin (1966) found that young jackrabbits ate mainly woody stems of *Artemisia tridentata* leaving younger growth on the ground. Because this wasted material is cut from living plants, the chemistry of the material, hence its decomposition, is different from naturally senescent plant material. As part of a research program on decomposition and nutrient cycling processes in Chihuahuan desert ecosystems, we measured input of non-consumed plant material by rabbit browsing and examined some of the factors that affect selection of browse by lagomorphs.

Materials and methods

Browsing activity of lagomorphs was measured on four 30 × 40 m plots on an upper bajada. Shrubs were marked by date as lagomorphs browsed individual shrubs. All uneaten stems and leaves were carefully collected, returned to the laboratory and dried at 60 °C for a minimum of 72 h. Stems and leaves were separated and weighed. Monthly samples were mixed and ground for total nitrogen analysis. Total nitrogen was measured

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by Kjeldahl titration following digestion. Lagomorph densities were estimated by flush transects. An observer walked a predetermined 2000 m transect that sampled a large portion of the upper watershed. As rabbits were flushed, the distance to the center line was estimated and the data converted to number per hectare (Pielowski, 1969).

In June 1981 we initiated a series of studies on effects of simulated rainfall on decomposition processes on a series of 3×15 m plots on the creosotebush bajada area. Three plots received 25.4 mm added water every fourth week and three plots received no water. The area wet by the simulated rainfall was larger than enclosed by fencing. In December 1981 rabbits began browsing the shrubs in the watered zone outside the plots. In order to examine water and nitrogen differences, we harvested 12 branches at random from shrubs in each plot, placed them into Zip-Lock (TM) plastic bags and returned to the laboratory. The leaves and non-edible stems were removed and the edible portion weighed and dried to estimate water content. The dried stems were ground for total nitrogen analysis.

We also estimated the percentage of shrubs in a 1 m belt around the perimeter of each plot that had been browsed and using mass-length relationships of harvested stems, estimated the quantity of leaves and stems dropped and consumed by lagomorphs. We also made numerous observations on the behaviour of rabbits feeding on *Larrea tridentata*.

Results

Jackrabbits (*Lepus californicus*) clip branches from creosotebushes at an average height of 43.6 ± 4.8 cm above the ground yielding a severed stem ranging between 30 cm and 70 cm in length and 11–50 g in mass. After cutting a branch with its incisors, a rabbit proceeds to chew off the small branchlets and new growth (light colored wood stems) allowing the leaves and lignified wood to fall to the ground. A jackrabbit may stay at a single shrub consuming the edible parts of several branches or partially consume the edible portions of a single branch and then move to another shrub. Approximately 30 per cent of the clipped branch is edible material and consumed by the rabbits, the remainder falls to the ground at the base of the shrub where the rabbit feeds.

As a general pattern, jackrabbits infrequently return to the same shrub in one season (Fig. 1). Furthermore, more than 60 per cent of the pruned shrubs had been pruned in

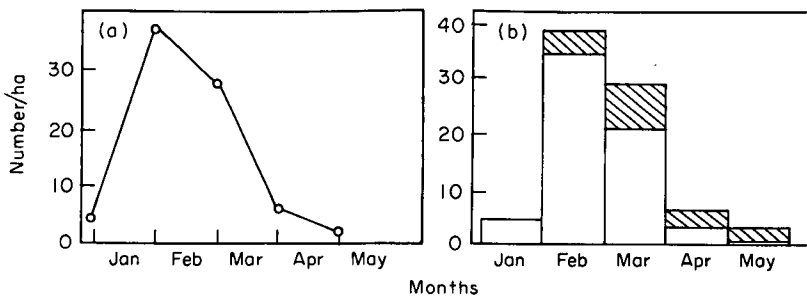


Figure 1. Seasonal variation in numbers of (a) shrubs pruned by jackrabbits (*Lepus californicus*) and (b) frequency of rabbit pruning of creosotebushes previously pruned during that year. ▨, Previously pruned; □, newly pruned.

previous years as evidenced by the old severed stems. Additional evidence that the same shrubs are pruned each year is presented in Fig. 2. In that population a cumulative total of 90 per cent of the shrubs pruned in 1979 had stems pruned in 1980. Although pruning activity was reduced in April and May, the jackrabbits previously pruned shrubs accounted for a greater percentage of the total pruned shrubs than during January,

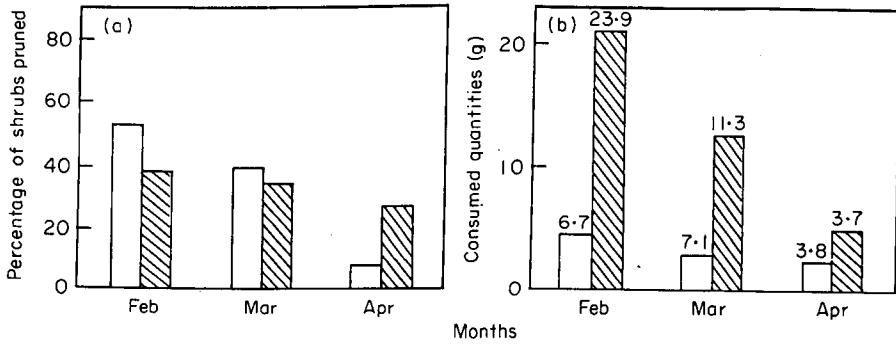


Figure 2. A comparison between (a) years of the percentage of shrubs of 200 creosotebushes pruned in 1979 and 1980 and (b) the quantities of stems and leaves unconsumed in the two years. The numbers above the bars are the standard deviations. □, 1979; ▨, 1980.

February and March. Utilization of the soft woody stems of *Larrea tridentata* peaks in February and March and decreases to near zero June through December (Fig. 1). Although the percentage of shrubs clipped by jackrabbits was relatively constant from year to year, the quantities of wasted materials varied considerably (Figs 2, 3). The average total input of unconsumed *Larrea tridentata* leaves and stems by jackrabbits was 66.1 kg/ha/year of stems and 35.0 kg/ha/year of leaves. The average jackrabbit density during the period of shrub consumption was 0.25/ha. Using the ratio of edible stem to inedible stem and leaves and the values for unconsumed stems and leaves we estimated that jackrabbits consumed approximately 50 kg/ha/year of woody material from the *Larrea tridentata* on the upper watershed.

The spatial variation in woody stem utilization shown in Fig. 3 is probably a function of soil depth and water storage. The plots where there was little jackrabbit browsing are on shallow soils where the caliche (calcium carbonate deposition) layer is within 30 cm of the surface or less. The plots where there was heavy utilization of shrubs by jackrabbits were characterized by deeper soils and better water storage.

The perimeter of our simulated rainfall plots where shrubs had an enhanced water status due to splash over were heavily browsed by rabbits. Only 2.5 per cent of the creosotebushes within 2 m of the plot fence of the unwatered plots had been browsed by jackrabbits. Around the 6.4 mm/week plots 92.5 per cent of the creosotebushes had been browsed and around the 25.4 mm/month plots 44.7 per cent of the creosotebushes had been browsed. There were between 82 and 94 shrubs in the 2 m belts around the experimental plots. The average per cent gravimetric water in edible stems on the unwatered plots was 35.67 ± 0.84 per cent, which was significantly lower ($F = 8.65$, $P < 0.015$) than stems on the 6.4 mm supplemental water plots (38.4 ± 1.9 per cent) and stems from shrubs on the 25.4 mm/month plots (38.5 ± 1.5 per cent). However there was no difference in nitrogen content of edible stems ($F = 0.62$, $P > 0.05$) unwatered 13.6 ± 0.7 mg/g, 25.4 mm rainfall/month, 13.3 ± 1.0 mg/g and 6.4 mm rainfall/week, 12.9 ± 1.3 mg/g. There was a difference in the per cent edible material when the stems from plants receiving supplemental water: (31.6 ± 3.8 per cent edible by rabbits) were compared with unwatered controls (26.7 ± 2.5 per cent edible by rabbits) ($F = 8.12$, $P < 0.01$).

Forty-six per cent of creosotebushes around the perimeter of the supplemental rainfall plots had all of the branches pruned by rabbits. Of the remaining shrubs the rabbits pruned between 93 per cent and 20 per cent of the stems ($\bar{x} = 29 \pm 24.8$ per cent).

The jackrabbits also utilized snakeweed, *Gutierrezia sarothrae*, during the months November to March which produced 0.26 kg/ha of unconsumed material. Although we did not observe jackrabbits feeding on snakeweed, the presence of leaves and old wood stems on the ground near the pruned stems provides presumptive evidence that jackrabbits were consuming only new growth stems of snakeweed.

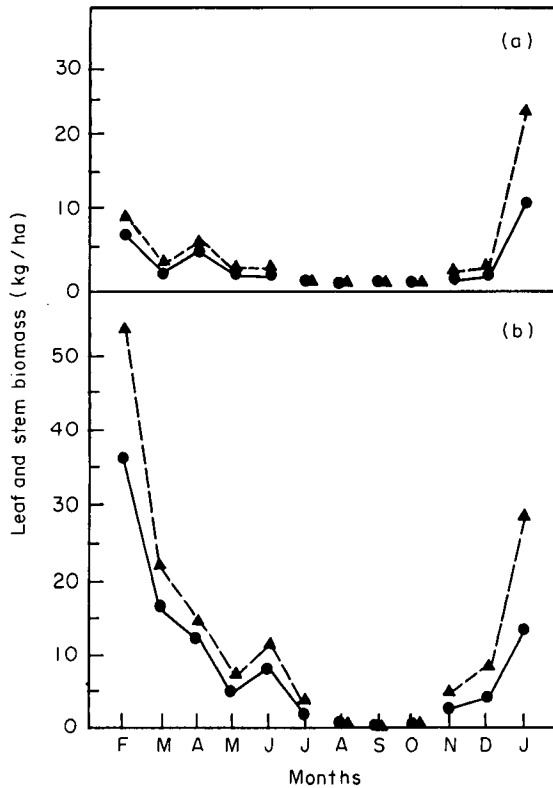


Figure 3. Comparison of jackrabbit pruning activity as measured by leaf and stem biomass wastage on plots with (a) shallow soils and (b) plots with deep soils. \blacktriangle — \blacktriangle , Stems; \bullet — \bullet , leaves.

Discussion

This study provides additional evidence to support the contention of Chew (1974) that consumers may be more important in ecosystems as regulators of processes rather than as processors of energy. Although the biomass of jackrabbits on our study area was low (0.25/ha) their impact in terms of litter input was great. The pruning activity of lagomorphs effects the growth morphology of the pruned shrubs in addition to adding the non-consumed material to the litter compartment, which provides a source of energy and nutrients to the decomposers. Jackrabbits pruning of *Larrea* added 101 kg/ha/year or approximately one-fifth of the estimated yearly total litter infall from material senescence of creosotebush parts (unpublished data). The decomposition of fresh cut creosotebush leaves differs from naturally senescent material (Fowler & Whitford, 1980) probably because the freshly cut leaves contain toxic chemicals (Rhoades, 1977).

Gutierrezia sarothrae leaves contain aromatic antiherbivore compounds that are toxic to grazing herbivores (Kingsbury, 1964) hence the feeding behavior of jackrabbits avoid the highest concentrations of these compounds by consuming the new growth woody tissue.

The results of this study document the shift to use woody shrubs in the non-growing season by jackrabbits as described in other deserts (Hayden, 1966; Westoby, 1980; Currie & Goodwin, 1966). The utilization of woody materials in the Chihuahuan desert provides not only a food source but also a source of water. The winter and early spring is typically the driest period of the year in this desert and the evergreen shrubs (*Larrea tridentata* and *Ephedra* sp.) are the only plants that contain moisture that can be obtained by jackrabbits. Further, our observations of jackrabbit feeding behavior and collections of the unconsumed materials demonstrated that the rabbits are not consuming the leaves that contain

toxins but rather are consuming the soft wood, new growth stems. The data on utilization of shrubs around the rainfall simulation plots provides an explanation for the habit of jackrabbits to prune the same shrub year after year. Creosotebushes growing in favorable microsites will have higher moisture content in their stems and a higher proportion of new growth to old growth wood. The data demonstrate that the jackrabbits can distinguish between shrubs that differ in water content to the stems. Jackrabbit pruned shrubs tend to be clustered adjacent to water courses and near depressions lending further credence to this argument. The browsed stems of snakeweed exhibited a similar spatial pattern.

The data also show that jackrabbits tend to consume the edible or desirable branches of a shrub at one feeding and not to return to that plant later in the season. When the rabbits locate creosotebushes that have a particularly favorable water status such as the shrubs next to the simulated rainfall plots, they consume every stem that is accessible to them. However few shrubs growing in natural areas had 100 per cent of the branches pruned.

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