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EFFECTS OF ARTHROPODS ON ROOT:SHOOT RATIO AND BIOMASS PRODUCTION IN UNDISTURBED AND MODIFIED MOUNTAIN SHRUB HABITATS

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ABSTRACT.—In 1987 the effects of arthropods on root:shoot ratios and biomass production were examined in southeastern Wyoming mountain shrub habitats that were undisturbed or had undergone conventional shrub management by mowing, burning, or herbicide application during the previous year. In habitats with and without shrub canopy, treatment with insecticides generally increased foliage biomass and consistently decreased root biomass, regardless of the shrub management practice. In open areas the effects of insecticide treatments on the root and shoot biomass were relatively greater in undisturbed plots than in any of the managed plots. With only one exception, the root:shoot ratio increased following application of insecticide.

The dynamic balance between root and shoot biomass, termed a functional equilibrium by Brouwer (1963), responds to biotic and abiotic environmental changes. Plants of a specific age have a characteristic root:shoot ratio in a given environment and habitat (Crist and Stout 1929, Wareing 1970). In rangeland habitats, increases in root biomass may accompany increases in aboveground plant biomass (Weaver and Zink 1946). Shariff (1988) documented increases in both root and shoot biomass in sagebrush following disturbance of the habitat by burning. Walmsley et al. (1987) showed that the altered carbohydrate distributions within grasses defoliated by grasshoppers resulted in greater shoot biomass than root biomass. Leopold (1975) suggested that root growth is limited by the amount of carbohydrates produced from shoots, while shoots are limited by the availability of minerals from the root system. This concept was refined with the "sink and source" hypothesis of Neales and Incoll (1968).

Because sagebrush is considerably less palatable than many other range plants to cattle, burning, mowing, and herbicides are commonly used to rid areas of unwanted shrubs (Powell 1970). These chemical and mechanical defoliation practices can affect root-growth dynamics. A study by Shariff (1988) found that 2,4-D application and burning as management methods significantly increased sagebrush root biomass. However, an increase in root biomass may be short-term. Sturges (1980) found that the root biomass in the top 1.2 m of soil in a sagebrush habitat treated three years previously with 2,4-D was not significantly different from undisturbed areas.

Defoliation by arthropod feeding and by chemical or mechanical means may also induce changes in root:shoot ratios in mountain shrub habitats. The purpose of this research was to determine the effects of arthropods on root:shoot ratios and biomass production in undisturbed shrub habitats and those undergoing intensive vegetation modifications.

METHODS

This study was conducted on a Wyoming big sagebrush (*Artemisia tridentata wyomingensis* Nutt.) and antelope bitterbrush (*Purshia tridentata* [Pursh] D.C.) habitat located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. The mean annual precipitation is 480 mm (mostly snow), and the mean annual temperature is 10.2 C. The daily mean temperature ranged from 21.0 to 27.0 C during the 100 days of the summer study period. The soils are brown sandy loams developed on loess, limestone, sandstone, and tuff of the North Park Formation. Limited grazing by roaming pronghorn antelope may have occurred during the study, but cattle were not present.

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In 1985 a botanical and pedological survey of the area was conducted (Powell, unpublished). Based on this work, we used sixteen 4-ha study plots that were randomly chosen from sites of similar vegetation, soil chemistry, and soil texture characteristics. Vegetation manipulations in May 1986 consisted of mowing four plots to a 20-cm stubble height, applying 2,4-D butyl ester in water at an aerial rate of 0.91 kg per hectare to four plots, and burning four plots. Four plots were left undisturbed as shrub management controls.

Two insecticides (carbaryl at 1.68 kg/ha and malathion at 1.4 kg/ha) were applied alternately every two weeks from early May through August 1987 to half of each managed and undisturbed plot. The other half of each plot was left as an untreated control. To determine effectiveness of insecticide treatments, we sampled the density of arthropods on foliage with a D-vac every 10 m along three 100-m transects in both closed (covered by shrub canopy) and open (not covered by shrub canopy) habitats in each half-plot every 10 days. The density of arthropods in litter was determined by collecting litter from 1-m^2 quadrats every 10 m along three 100-m transects in both open and closed habitats in each half-plot. Because the herbicide and burning virtually eliminated canopy cover, no samples could be obtained from closed habitats in these plots.

In August 1987 root biomass was determined by taking a 15-cm-deep and 10-cm-diameter core sample every 20 m along a 100-m transect, in 15 closed and open areas in each half-plot. On the same date, all herbaceous foliage was clipped from understory plants and overstory shrubs in 15 open and 15 closed 0.25-m^2 habitat quadrats located along three 100-m transects in each plot. Root core samples were first processed with a number 10 sieve and then with a number 18 sieve using water under pressure. Roots and foliage were dried at 75 C for three days and weighed.

Independent Students t-tests were used to determine differences in root and foliage biomass as a function of the insecticide treatments. A X^2 test of proportions was used to assess differences between root:shoot ratios as a function of insecticide treatments and shrub cover as a result of management practices.

TABLE 1. Effects of shrub management practices on sagebrush and bitterbrush canopy cover.

Management	% shrub cover[a]	
	1985 (premanagement)	1987 (postmanagement)
Undisturbed	28.1a	29.0a
Herbicide	29.6a	17.0b
Mowed	31.6a	23.0b
Burned	30.3a	6.2b

[a]Values within a management practice followed by different letters differ at the P < .05 level of significance according to the X^2 2 × 2 test of proportions.

RESULTS

All of the shrub management practices reduced ($P < .05$) the shrub cover (Table 1). Herbicide application and burning reduced shrub cover to the greatest extent; the shrub remaining after these management practices was dead and provided no distinct canopy. Because mowing left a 20-cm stubble of living shrub, a portion of the canopy remained intact. The canopy cover in undisturbed habitats did not change noticeably ($P > .05$) during the course of this study.

Insecticides reduced arthropod densities by 74–81% in the undisturbed and managed plots (Table 2). With one exception (undisturbed, closed habitats), application of insecticides to managed and undisturbed habitats significantly increased or decreased ($P < .05$) root:shoot biomass ratios, as compared to untreated controls (Table 3).

In open habitats of plots managed with the herbicide, insecticide application resulted in a 1.6-fold increase ($P < .05$) in foliage biomass and a 27% decrease ($P > .05$) in root biomass, as compared to untreated areas (Table 3). Ratio of roots to shoots decreased markedly ($P < .05$), reflecting the increase in shoot biomass after insecticide treatments.

Because mowing left a partial herbaceous canopy, the closed habitat was sampled. After application of insecticides to closed habitats, there was a 9.1-fold increase ($P < .05$) in shoot biomass and a 36% decrease in root biomass ($P > .05$), as compared to untreated areas. After insecticide applications in open areas, root biomass decreased markedly by 57% ($P < .05$) and shoot biomass decreased by only 6% ($P > .05$), compared to untreated plots. These effects were manifested by significant reductions ($P < .05$) in the root:shoot ratio, indicating a large shift toward production of shoot

TABLE 2. Effect of insecticide treatments on arthropod population densities (no./m^2) in undisturbed and managed plots.

		Undisturbed		Mowed		Herbicide		Burned	
Order	Habitat	con	trt[a]	con	trt	con	trt	con	trt
Acari	foliage	0	0	2	0	2	0	1	0
Araneae	foliage	6	1	3	0	3	1	5	2
Homoptera	foliage	218	41	31	6	33	2	21	4
Coleoptera	foliage	6	1	15	1	6	3	2	0
Diptera	foliage	13	2	3	0	2	1	3	1
Hymenoptera	foliage	64	10	73	29	80	20	13	1
Acari	litter	495	95	640	170	677	175	8	2
Araneae	litter	11	4	6	0	9	3	3	2
Homoptera	litter	14	3	11	2	10	2	3	1
Coleoptera	litter	13	0	9	0	10	2	1	1
Diptera	litter	24	5	13	1	27	9	12	5
Hymenoptera	litter	16	0	12	0	13	0	61	11
Collembola	litter	14	3	93	18	77	27	9	3
Thysanura	litter	6	1	8	0	3	0	1	0
% decrease			81%		75%		74%		77%

[a]con = control, trt = treated with insecticide.

TABLE 3. Root and foliage biomass and ratios as affected by insecticide treatments in undisturbed and intensively managed mountain shrub habitats.

Habitat	Management	Insecticide treatment	Biomass (g/.25 m^2)[a] Root	Shoot	Root:shoot ratio[b]
open	control	present	4.8 a	17.9 a	1:3 a
		absent	15.1 b	8.8 b	2:1 b
closed	control	present	7.6 a	32.8 a	1:4 a
		absent	10.0 a	47.3 b	1:5 a
open	mowed	present	2.8 a	8.1 a	1:3 a
		absent	6.5 b	8.6 a	1:1 b
closed	mowed	present	3.6 a	40.2 a	1:13 a
		absent	5.6 a	4.4 b	1:1 b
open	herbicide	present	6.5 a	13.3 a	1:2 a
		absent	8.9 a	8.5 b	1:1 b
closed	herbicide	present	NA[c]	NA	NA
		absent	NA	NA	NA
open	burned	present	1.1 a	11.5 a	1:11 a
		absent	2.3 a	8.2 a	1:4 b
closed	burned	present	NA	NA	NA
		absent	NA	NA	NA

[a]Means of foliage and root biomass within a habitat and shrub management practice followed by different letters differ at the $P < .05$ level of significance according to Students t-test.
[b]Root:shoot ratios within a habitat and shrub management practice followed by different letters differ at the $P < .05$ level of significance according to the X^2 2 × 2 test of proportions.
[c]The shrub management practice effectively eliminated the canopy, and so no closed habitats could be sampled.

biomass in both habitats after insecticide application (Table 3).

As with areas managed with herbicides, burned plots had essentially no live shrub canopy; thus, closed habitats could not be sampled. In open habitats of plots managed by burning, application of insecticide was associated with a 1.4-fold increase ($P > .05$) in foliage biomass and a 52% decrease ($P > .05$) in root biomass, compared to untreated controls. Although root and shoot biomass alone did not change significantly as a result of insecticide treatments, their combined effects resulted in a significant reduction ($P < .05$) in the root:shoot ratio, indicating an increase in the production of shoot biomass (Table 3).

Undisturbed plots that were used for assessing the role of arthropods in a natural sagebrush system clearly showed alterations in biomass production and root:shoot ratios following insecticide applications. In open areas treated with insecticides, there was a

2.0-fold increase ($P < .05$) in foliage biomass, with a 68% decrease ($P < .05$) in root biomass, compared to untreated controls. Insecticides applied to canopy-enclosed plots resulted in a 31% decrease ($P < .05$) in foliage biomass and a 24% decrease ($P < .05$) in root biomass. Root:shoot ratios reflect these changes, showing a significant shift ($P < .05$) toward shoot biomass production in open areas and a slight shift ($P > .05$) toward root biomass production in closed areas (Table 3).

Discussion

In our study all of the shrub management practices decreased root biomass relative to shoot biomass in open habitats. This result was opposite the results of Shariff's (1988) study on sagebrush habitats, which showed an increase in root biomass in managed areas. However, inasmuch as our study was conducted on the west slope and Shariff's (1988) study was performed on the east slope of the Medicine Bow Mountain range, environmental conditions were dissimilar. On the insecticide-treated plots there was generally a decrease in the absolute amount of foliage and a consistent increase in the absolute amount of root biomass. This trend was seen in the decreased root:shoot ratios following insecticide treatment in open and closed habitats, with all shrub management practices. We believe that arthropod activities (primarily feeding) influenced root and shoot biomass production in undisturbed and intensively managed mountain shrub habitats. These data do not entirely support the study of Walmsley et al. (1987), which found that while insect herbivory decreased foliage biomass, no clear differences in root:shoot ratios were evident three weeks after defoliation. Walmsley et al. (1987) conducted their study in the greenhouse using grasses fed upon exclusively by the migratory grasshopper *Melanoplus sanguinipes* (F.); therefore the study may not be comparable.

Accelerated shoot growth generally follows damage of foliage (Kleinendorst and Brouwer 1969), and this growth may partially compensate for the damage (Troughton, 1957). However, compensatory foliage growth can deplete carbohydrate reserves stored in the roots. This, in turn, may decrease root growth and root biomass (White 1973). These plant responses to herbivory are consistent with the root:shoot ratio and biomass production dynamics found in our study. A relatively higher root:shoot ratio may occur in habitats with limited resources (e.g., soil nutrients, light, and water), such as semiarid mountain shrub habitats. Conversely, an increase in shoot growth and biomass may be expected in habitats with abundant resources that permit maximum carbon gain through photosynthesis (Troughton 1977).

Grazing may also decrease root biomass by 60–70% relative to foliage biomass (Burleson and Hewitt 1982). However, this result was not observed in our study; root biomass was relatively greater in open areas (which were potentially exposed to grazing by pronghorn antelope and rodents) than in closed areas. However, the impact of grazing by vertebrates was confounded by different ecological factors in open and closed habitats; for example, grass foliage was more accessible in habitats without a shrub canopy.

The trends found in this study with regard to the role of arthropods in altering root:shoot ratio and biomass production were consistent across shrub management practices and habitats with the exception of closed areas in undisturbed plots. This exception, in which insecticides led to a significant decrease in foliage biomass, may have been a result of relatively poor penetration in insecticide in canopy-covered habitats. If the more mobile predators contacted the spatially limited insecticide more frequently than the herbivores, then there may have been a partial release of the herbivores from predation. Under these conditions a greater level of herbivory within the canopy may be expected.

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