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MEDIATION OF NUTRIENT CYCLING BY ARTHROPODS IN UNMANAGED AND INTENSIVELY MANAGED MOUNTAIN BRUSH HABITATS

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ABSTRACT.—The role of arthropods in mediating nutrient cycling on a community level was examined in a mountain shrub habitat that was managed by mowing brush to a 20-cm stubble, applying aerially 2,4-D butyl ester, or burning sixteen 4-ha study sites. Malathion and carbaryl were used to decrease arthropod populations. Higher nutrient concentrations occurred in the litter and foliage than in the soil of unmanaged habitats. Arthropods decreased nutrient concentrations in litter and foliage in unmanaged and herbicide-sprayed sites. Arthropod populations increased nutrient concentrations in mowed and burned sites. Nitrogen was consistently affected by both arthropods and brush management in all habitats.

Regulation of nutrient cycling by arthropods appears to be a function of the frequency and severity of habitat disturbance (Schowalter 1986). Arthropod responses to perturbances appear to stabilize ecosystem productivity through regulating plant, soil, nutrient, and light relations by changing plant structure and plant species biomass (Mattson and Addy 1975). In addition, the severity of a disturbance may be reduced by increasing its reliability. Plant age structure as well as plant biomass is changed as old, nonproductive plants and plant parts are eaten or reduced to litter by arthropods. This process also has an effect on nutrient release and containment in a habitat (Schowalter 1986).

Phytophagous insects require proteinaceous nitrogen for their life cycles. When the nitrogen level in plants increases, insect assimilation and growth efficiencies increase (Mattson 1980). Thus, although high nitrogen levels can be detrimental to some insects (Stark 1965), evidence suggests that insects will generally seek and respond to high nitrogen levels (Prestidge and McNeill 1965). Higher available nitrogen levels can be found in annual plants as compared to perennial plants. Being short-lived, annuals do not commit high levels of energy to defensive chemistry but allocate most of their energy to reproduction. Therefore, insect feeding can result in an increase of nutrient and energy flow in annual plants as they recover from nitrogen loss (Grimes 1979). Other inorganic elements, such as calcium, magnesium, phosphorus, potassium, and sodium, are vital to diets of many insects (Dadd 1977, 1985), and these elements are likely regulated to some extent in the environment by insects.

The role of arthropods in forest nutrient cycling has been studied by Cornaby (1977), Crossley (1977), and Webb (1977). However, few studies have been conducted on nutrient cycling in the sagebrush/bitterbrush system. Because of the lack of research in this area, we undertook this study with two objectives in mind. The first was to determine if arthropods were a mediating factor in nutrient cycling, on a community level, in a sagebrush habitat. The second objective was to determine if habitat disturbance would influence the role of arthropods in nutrient cycling.

MATERIALS AND METHODS

This study was conducted on a sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) habitat located at an elevation of 2,400 m, 12 km southeast of Saratoga, Carbon County, Wyoming. Precipitation averaged 480 mm per year, mostly in the form of snow. Temperatures ranged from 21.0 to 27.0 C during the 100 days of the summer study period though the mean annual temperature is 10.2 C. Soils are the North Park Formation of brown sandy loams developed on loess, limestone, sandstone, and tuff.

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The study site consisted of 16 blocks of at least 4 ha each. These blocks were randomly chosen from sites that had similar vegetation, soil chemistry, and soil texture characteristics. Habitat manipulation in May 1986 consisted of either mowing four 4-ha blocks to a 20-cm stubble height or applying 2,4-D butyl ester in water at an aerial rate of 0.91 kg per hectare to four 4-ha blocks. In the fall of 1986, four 4-ha blocks were burned. These treatments are used as sagebrush management practices in Wyoming. Control blocks consisted of four 4-ha, unmanaged, high-density shrub areas.

Arthropod populations were reduced using two insecticides, carbaryl (1.68 kg/ha) and malathion (1.4 kg/ha). These compounds were alternately applied every two weeks from early May through August of 1987 to half of each block in the managed and unmanaged areas. The other half of each block was left untreated as a control.

To determine effectiveness of insecticide treatments, we estimated arthropod densities using 100 sweeps of a 38-cm diameter sweep net to collect arthropods along three 100-m transects in both closed (covered by brush canopy) and open (not covered by brush canopy) microhabitats in each managed and unmanaged split-plot every 10 days.

Foliage, litter, and soil samples were collected in open and closed microhabitats in early September 1987 from fifteen 0.25-m^2 quadrats located along three 100-m transects in each split-plot. Samples were placed in paper bags, returned to the laboratory, and dried for three days at 75 C. All foliage and litter samples were ground in a Wiley Mill with a 40-mesh screen.

Total nitrogen for litter, plant, and soil material was determined by the use of a block digestion method and analysis (Jones 1971). Concentrations of magnesium, calcium, phosphorus, potassium, and sodium were determined by the Havlin and Soltanpour (1980) method of nitric digestion. All nutrient concentrations except for phosphorus, which was determined by the Olsen and Dean (1960) colorimetric method, were determined by the use of plasma spectrometry. Soil pH, electrical conductivity, and soluble cation analysis were evaluated with methods of Richards (1980). Soil organic matter was determined by combustion (Grewling and Peech 1965). Texture analysis applied the theory of particle fractionation as used by Day (1965).

TABLE 1. Vegetation parameters as determined for the baseline year (1985), treatment year (1986), and recovery year (1987).

Treatment	Year		
	1985	1986	1987
	Herbaceous biomass (g/m^2)[a]		
Unmanaged	7.0a	7.2a	5.7a
Herbicide	7.3a	16.7b	29.1c
Mowed	7.4a	24.0b	23.0b
Burned	7.2a	7.4a	4.3b
	Litter biomass (g/m^2)[a]		
Control	78.0a	79.6a	87.1a
Herbicide	75.8a	77.3a	73.1a
Mowed	79.0a	291.2b	287.6b
Burned	76.4a	77.7a	2.3b
	Sagebrush density (%)[b]		
Control	54.7a	54.8a	55.9a
Herbicide	47.9a	21.8b	18.0b
Mowed	63.7a	32.0b	38.0b
Burned	60.2a	59.7a	5.7b
	Bitterbrush density (%)[b]		
Control	54.0a	55.0a	57.0a
Herbicide	14.4a	45.7b	64.0c
Mowed	41.4a	51.4b	52.0b
Burned	47.4a	48.1a	6.3b
	Total shrub cover (%)[b]		
Control	28.1a	28.1a	29.0a
Herbicide	29.6a	17.5b	17.0b
Mowed	31.6a	24.0b	23.0b
Burned	30.3a	29.8a	6.2b

[a]Means for a parameter within a treatment between years followed by the same letter are not significantly different ($P = .05$; LSD Test [Fisher 1949]). N = 60 samples.

[b]Means for a parameter followed by the same letter are not significantly different ($P = .05$; Chi-square). N = 60 samples.

The results were analyzed as a split-plot design, and Fisher's (1949) protected least significant difference test was employed to compare specific treatment effects on nutrient content of foliage and litter. Chi-square analysis was used to assess differences in the proportions of shrub cover between management areas. In all statistical tests, differences were considered significant at $P < .05$.

RESULTS AND DISCUSSION

Disturbance of vegetation by brush management practices resulted in significant decreases in density of the major overstory plant species, sagebrush and bitterbrush (Table 1). Herbaceous biomass increased dramatically in both mowed and herbicide-sprayed blocks during and after the year of management, as

TABLE 2. Nutrient concentrations (ppm) of soil, litter, and foliage in sagebrush/bitterbrush habitats before management procedures were applied.

Nutrient[a]	Habitat	Soil	Litter	Foliage[b]
Nitrogen	Closed	21.00a	96.00c	112.00e
	Open	23.50ab	104.00d	149.00f
Potassium	Closed	.48a	2.54cd	10.75e
	Open	.54ab	1.78bc	9.68de
Magnesium	Closed	.70a	1.45d	1.01abc
	Open	.84ab	.84ab	1.90e
Sodium	Closed	.02a	.11d	.04b
	Open	.09c	.02a	.02a
Phosphorus	Closed	.69ab	.54a	1.19c
	Open	.74b	.72b	.92b
Calcium	Closed	4.98ab	8.49d	4.17a
	Open	5.23abc	5.65bc	8.10d

[a]Means for a nutrient followed by the same letter are not significantly different ($P = .05$; LSD Test [Fisher 1949]). $N = 60$ samples.
[b]Closed foliage indicates shrubs and open foliage indicates grass.

often occurs with the decline of the shrub layer (Barbour et al. 1980). Litter biomass significantly increased during and after the year of mowing. Both herbaceous and litter biomass decreased significantly after being burned.

In undisturbed sites the vegetation component contained higher concentrations of nitrogen, potassium, and magnesium than the litter, which had higher concentrations than the soil (Table 2). Phosphorus levels were higher in shrub vegetation than in any other component. This was probably due to long-term accumulation of this element in the woody portion of shrubs, as is known to occur in forest habitats (Horn 1974). Calcium was highest in the litter of closed microhabitats and in grasses. Sodium concentrations were highest in litter located under shrubs. Sodium is readily leached from open litter (Forth and Turk 1972). Thus, sodium concentration under shrubs may have been higher due to more protection from precipitation and leaching.

Insecticide applications reduced arthropod densities by 82% in unmanaged areas, 76% in mowed areas, 74% in herbicide-applied areas, and 78% in burned areas (Table 3). All orders were clearly diminished by the insecticides, although Acari generally fared better than the insect orders.

The nutrient levels in unmanaged habitats with intact arthropod communities compared well with previous measurements in sagebrush (Gough and Erdman 1980). Arthropods in open microhabitats of unmanaged blocks significantly increased nitrogen, magnesium, and calcium in both litter and foliage (Table 4). Phosphorus was significantly decreased in foliage of open microhabitats by arthropods. Foliage potassium significantly increased in insecticide-treated, open areas. Arthropods significantly increased nitrogen in both litter and foliage of closed microhabitats and significantly increased potassium in litter. Arthropods significantly decreased magnesium and sodium in both litter and foliage in closed microhabitats and significantly decreased phosphorus in foliage of closed microhabitats.

Decreases in the level of a nutrient following insecticide applications indicate that arthropods have some direct or indirect effect on the release of these nutrients. In particular, arthropods are clearly acting to increase plant nitrogen, since this element decreased significantly in foliage and litter of open and closed microhabitats after insecticide treatments. There is some evidence that insect feeding may stimulate plant growth (Walmsley et al. 1987), and this effect may account for the impact of arthropods on plant nitrogen levels. Since arthropods function in unmanaged sagebrush habitats to increase the levels of nitrogen in plant material, the indirect impacts of widespread applications of broad-spectrum insecticides on western prairies for control of grasshoppers should be considered (Hewitt and Onsager 1983).

Insects may also be functioning to directly mobilize nutrients; aphids are a good example of how insects may mediate nutrient cycling. As a group, aphids are generally inefficient at energy conversion of plant sap; only 5% of the potential dietary energy is utilized, and the remainder is excreted as honeydew (Hagen et al. 1951). This product is nutritionally important to a number of animals and fungi (Wilson 1971). As such, honeydew production functions as an important and rapid return of energy and nutrients to the local habitat. Soluble nutrients in the phloem are absorbed by aphids and provide food to other organisms through honeydew or indirectly through predation. Therefore, aphids and other arthropods may act as nutrient-storage organisms or sinks for plant nutrients in a small scale (Way and Cammell 1970). Joy (1967) reported that local amino acid synthesis can be induced from nutrients contained in the aphid sink.

The reduction of arthropod population density by insecticides in herbicide-treated sites

TABLE 3. Effects of insecticide treatments on arthropod population densities (no./m^2) in unmanaged, mowed, and herbicide-managed blocks averaged over the study.

Order	Habitat	Unmanaged		Mowed		Herbicide	
		Treated	Control	Treated	Control	Treated	Control
Acari	foliage	0	0	2	0	2	0
Araneae	foliage	6	1	2	0	3	1
Homoptera	foliage	218	41	35	10	39	7
Coleoptera	foliage	6	1	15	1	6	3
Diptera	foliage	16	2	3	0	2	1
Hymenoptera	foliage	62	10	72	29	85	24
Acari	litter	495	95	640	170	677	175
Araneae	litter	9	2	6	0	7	1
Homoptera	litter	11	0	11	2	12	4
Coleoptera	litter	13	0	9	0	10	2
Diptera	litter	24	5	13	1	25	7
Hymenoptera	litter	16	0	12	0	13	0
Collembola	litter	14	3	93	18	63	16
Thysanura	litter	6	1	8	0	3	0
% decrease			82%		76%		74%

TABLE 4. Arthropod effects on nutrients (ppm) in unmanaged sagebrush/bitterbrush habitats treated with insecticides.

Nutrient[a]	Habitat	Foliage		Litter	
		Treated	Untreated	Treated	Untreated
Nitrogen	Closed	100.00cde	112.00f	69.00a	96.00cd
	Open	87.00cb	149.00e	82.00b	104.00ed
Magnesium	Closed	1.29cd	1.01abcd	1.94g	1.45def
	Open	0.92cab	1.90g	0.75a	0.84ab
Calcium	Closed	4.17a	4.17a	8.87cd	8.49d
	Open	4.78ab	8.10d	4.78ab	5.65c
Sodium	Closed	<.01a	0.04abc	0.14e	0.11d
	Open	0.04abc	0.02ab	<.01a	0.02ab
Potassium	Closed	11.51g	10.75g	1.58ab	2.45cd
	Open	8.51f	5.59e	1.00ab	0.54a
Phosphorus	Closed	1.61g	1.19ef	0.56abc	0.54abc
	Open	1.15e	0.92d	0.57abc	0.72abc

[a]Means for a nutrient followed by the same letter are not significantly different (P .05, LSD Test [Fisher 1949]). N 60 samples.

resulted in a significant decrease of all litter nutrients except sodium (Table 5). However, only phosphorus was significantly decreased in foliage. Again, the decrease of nutrients when arthropod populations were reduced in herbicide-treated areas could be the result of arthropods being storage components in the community as in undisturbed sites. The application of herbicide effectively eliminated the closed microhabitat.

In herbicide-treated mountain brush habitats, arthropods functioned to generally increase litter nutrient levels. Whether insects directly (via death and decomposition) or indirectly (via secretions and excretions) elevate litter nutrient levels is yet to be determined. The general lack of change in foliage nutrient levels suggests that the loss of nutrients in litter following insecticide treatments did not result in the effective mobilization of the nutrients for uptake by grasses. Many of the annual grasses may not have been in a phenological stage suitable to exploit the available resources as they became available in mid- to late summer.

Application of insecticides to mowed sites caused significant increases of litter nitrogen, potassium, and phosphorus in open microhabitats (Table 6). The increase in phosphorus could be an artifact from application of the organophosphorous insecticide. Canopy-covered litter in insecticide-treated plots had significant increases in nitrogen, magnesium, and calcium. There were significant decreases of foliage magnesium and phosphorus in

TABLE 5. Arthropod effects on nutrients (ppm) in herbicide-treated sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Open	142.00b	142.00b	55.00a	146.00b
Magnesium	Open	0.91ab	0.86ab	0.91ab	1.03c
Calcium	Open	6.62b	6.30b	4.05a	6.42b
Sodium	Open	<.01a	0.04a	0.32b	<.01a
Potassium	Open	7.12c	7.12c	0.47a	1.12b
Phosphorus	Open	0.98b	1.24c	0.24a	0.94b

[a]Means for a nutrient followed by the same letter are not significantly different (P .05, LSD Test [Fisher 1949]). N 60 samples.

TABLE 6. Arthropod effects on nutrients (ppm) in mowed sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Closed	122.00c	120.00c	117.00c	99.00b
	Open	114.00c	139.00d	119.00c	85.00a
Magnesium	Closed	1.13cd	1.48e	1.48e	0.68a
	Open	1.17cd	0.96bcd	0.93bc	0.88ab
Calcium	Closed	4.71a	6.78abcd	9.05g	6.78ef
	Open	5.94abcde	5.12abc	5.07ab	5.63abcd
Sodium	Closed	<.01a	0.03a	<.01a	0.30b
	Open	<.01a	0.03a	<.01a	0.04a
Potassium	Closed	11.13g	10.79g	2.05abcd	0.85ab
	Open	0.74a	6.24ef	5.34e	0.93abc
Phosphorus	Closed	0.98f	1.40g	0.53abc	0.33ab
	Open	0.58cd	0.66de	0.70e	0.32a

[a]Means for a nutrient followed by the same letter are not significantly different (P = .05, LSD Test [Fisher 1949]). N = 60 samples.

TABLE 7. Arthropod effects on nutrients (ppm) in burned sagebrush/bitterbrush habitats treated with insecticides.

		Foliage		Litter	
Nutrient[a]	Habitat	Treated	Untreated	Treated	Untreated
Nitrogen	Open	NA	NA	215.00a	204.00a
Magnesium	Open	NA	NA	3.60a	2.85b
Calcium	Open	NA	NA	8.65a	7.69a
Sodium	Open	NA	NA	0.04a	<.01a
Potassium	Open	NA	NA	43.57a	29.52b
Phosphorus	Open	NA	NA	2.30a	1.83b

[a]Means for a nutrient followed by the same letter are not significantly different (P = .05; LSD Test [Fisher 1949]). N = 60 samples. NA = not applicable.

canopy-covered microhabitats. Foliage in insecticide-treated, open microhabitats had significant decreases in nitrogen, potassium, and phosphorus (Table 6).

In mowed mountain brush habitats, arthropods functioned to restrict the flow of nutrients from foliage to litter or, conversely, to accelerate the flow of nutrients from litter to foliage. Earlier work on sagebrush habitats showed that insects are critical components in the process of litter decomposition (Christiansen and Lockwood, unpublished data). Thus, we suggest that the application of insecticides decreased the breakdown of litter by arthropods and thereby reduced the nutrients available to plants. The fact that arthropods apparently had the opposite effect on mobilization of nutrients in mowed and herbicide-treated habitats may have been a result of the functional differences in these treatments; the overstory plants were rapidly recovering following mowing but were effectively eliminated by herbicide applications.

Burning a habitat dramatically altered the plant architecture, leaving no closed microhabitats. In burned sites treated with insecticides, magnesium, potassium, and phosphorus were all significantly increased in litter (Table 7). As with mowing, significant nutrient increases in litter indicate that insects are important in mobilizing nutrients. Burned habitats had properties of herbicide-treated habitats (elimination of the canopy) and mowed habitats (ongoing recovery of the overstory plants, although insufficient for sampling). Plants under various stresses respond differently (Hale and Orcutt 1987), and it is not unexpected that the interacting impacts of arthropods and management practices resulted in different alterations in nutrient cycling.

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Literature Cited

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980. Terrestrial plant ecology. The Benjamin/Cummings Publ. Co., Inc., Menlo Park, California. 604 pp.

Cornaby, B. W. 1977. Saprophagous organisms and problems in applied resource partitioning. Pages 96–100 *in* W. J. Mattson, ed., The role of arthropods in forest ecosystems. Springer-Verlag, New York. 104 pp.

Crossley, D. A., Jr. 1977. The role of terrestrial saprophagous arthropods in forest soils: current status of concepts. Pages 49–56 *in* W. J. Mattson, ed., The role of arthropods in forest ecosystems. Springer-Verlag, New York. 104 pp.

Dadd, R. H. 1977. Qualitative requirements and utilization of nutrients: insects. Pages 305–346 *in* M. RechCigil, ed., Handbook series in nutrition and food. CRC Press, Cleveland, Ohio. 561 pp.

______. 1985. Nutrition: organisms. Pages 313–390 *in* G. A. Kerkut and L. I. Gilbert, eds., Comprehensive insect physiology, biochemistry and pharmacology. Vol. 4. Regulation: digestion, nutrition, excretion. Pergamon Press, New York. 639 pp.

Day, P. R. 1965. Particle fractionation and particle size analysis. Pages 425–442 *in* C. A. Black, ed., Methods of soil analysis. Part I. Agronomy 9. Amer. Soc. of Agron., Madison, Wisconsin. 1,188 pp.

Forth, H. D., and L. M. Turk. 1972. Fundamentals of soil science. John Wiley and Sons, New York. 454 pp.

Fisher, R. A. 1949. The design of experiments. Oliver and Boyd, Edinburgh. 456 pp.

Gough, L. P., and J. A. Erdman. 1980. Seasonal differences in the element content of Wyoming big sagebrush. J. Range Manage. 33: 374-378.

Grewling, T., and M. Peech. 1960. Chemical soil tests. Cornell Univ. Agric. Expt. Sta. Bull. No. 960. 362 pp.

Grimes, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York. 222 pp.

Hagen, K. S., R. H. Dadd, and J. Reese. 1984. The food of insects. Pages 79–112 *in* C. B. Huffaker and R. L. Rabb, eds., Ecological entomology. Wiley and Sons, New York. 844 pp.

Hale, G. M., and D. M. Orcutt. 1987. The physiology of plants under stress. John Wiley and Sons, New York. 206 pp.

Havlin, J. L., and P. L. Soltanpour. 1980. A nitric acid plant tissue digest method for use with inductively coupled plasma spectrometry. Comm. Soil Science and Plant Analysis 11: 969–980.

Hewitt, G. B., and J. A. Onsager. 1983. Control of grasshoppers on rangeland in the United States—a perspective. J. Range Manage. 36: 202–207.

Horn, H. S. 1974. The ecology of secondary succession. Ann. Rev. Ecol. System. 5: 25–37.

Jones, J. B. 1971. Laboratory procedures for the analysis of soils, feed, water, and plant tissues. Soil Testing and Plant Analysis Laboratory, Athens, Georgia. 534 pp.

Joy, K. W. 1967. Carbon and nitrogen sources for protein synthesis and growth of sugar-beet leaves. J. Exp. Bot. 18: 140–150.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119–161.

Mattson, W. J., Jr., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. Science 190: 515–522.

Olsen, S. R., and L. A. Dean. 1965. Phosphorus. Pages 403–430 *in* C. A. Black, D. D. Evans, L. E. Ensminger, J. L. White, F. E. Clark, and R. C. Dinauer, Methods of soil analysis. Amer. Soc. Agr. Inc., Madison, Wisconsin. 1,159 pp.

Prestidge, R. A., and S. McNeill. 1983. The importance of nitrogen in the ecology of grassland Auchenorrhyncha (Homoptera). Symp. Brit. Ecol. Soc. 7: 117–124.

Richards, L. A. 1980. Diagnosis and improvement of saline and alkali soils. Agric. Handbook No. 60. USDA, Washington, D.C. 158 pp.

Schowalter, T. D. 1986. Adaptations of insects to disturbance. Pages 235–251 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York. 472 pp.

Stark, R. W. 1965. Recent trends in forest entomology. Ann. Rev. Entomol. 10: 303–324.

Walmsley, M. R., J. L. Capinera, J. K. Detling, and M. I. Dyer. 1987. Growth of blue grama and western wheatgrass following grasshopper defoliation and mechanical clipping. J. Kansas Entomol. Soc. 60: 51–57.

Way, M. J., and M. Cammell. 1970. Aggregation behaviour in relation to food utilization by aphids. Pages 229–247 *in* A. Watson, ed., Animal populations in relation to their food resources. Blackwell, Oxford. 477 pp.

Webb, D. P. 1977. Regulation of deciduous forest litter decomposition by soil arthropod feces. Pages 57–69 *in* W. J. Mattson, ed., The role of arthropods in forest ecosystems. Springer-Verlag, New York. 104 pp.

Wilson, E. O. 1971. The insect societies. The Belknap Press, Cambridge, Massachusetts. 548 pp.