

By

H. F. Mayland and R. B. Murray^{1/}INTRODUCTION

All life forms absorb minerals, which are generally used in cellular metabolism. These minerals may be secreted during normal metabolism or mineralized after cellular death. The cycle can then be repeated.

Our studies of mineral cycling within the sagebrush (*Artemisia*) ecosystem attempt to explain why the productivity of one site is different from that of another. We may also want to know if enough minerals are available to support a shrub-to-grass conversion project or if the site provides adequate nutrition to herbivores. The mineral content of *Artemisia*, for example, has been used as a means of detecting precious metals in the subsoil. This procedure, known as biogeochemical prospecting, is commonly used in north-central Asia. The mineral enrichment studies comparing *Artemisia* in areas downwind and upwind from factories provide a base line for monitoring mineral fallout (Conner et al. 1976, Gough and Severson 1976, Severson and Gough 1976). Mineral cycling information also helps us to interpret the effects of fire, grazing, or erosion on the mineral status of a given site.

Literature

The English language literature on mineral cycling in the woody *Artemisia* includes G. E. Fogg's translation of the text by Rodin and Bazilevich (1965), two dissertations from Washington State University, and a series of International Biome Program-Desert Biome studies, some of which are in press. Other pertinent studies published in English will be mentioned below.

Much of the Russian work, except for Fogg's translation, is available only through the American Chemical Society's Chemical Abstracts, and even that is of limited value, because the data are presented on the basis of ash rather than dry matter. These data would be more useful if they were also given on the basis of

herbage dry matter. Lavrenko and Borisova (1976) have edited a 3-volume Russian language series entitled 'Biocomplex Investigations in Kazakhstan'. Sections of this work by Miroschnichenko on ash composition of *Artemisia pauciflora* and *Atriplex* associations and by Gagarin and Miroschnichenko on mineral composition of vegetation growing on the steppes, semidesert and deserts of central Kazakhstan should be of interest. An English translation is not available yet.

The objectives of this paper are to briefly describe the cycling process and to give some data on the dry matter biomass, litter fall and decomposition, mineral concentration and mass, and mineral turnover for *Artemisia tridentata*. These data are supplemented by data on *Artemisia sieberi*.

Artemisia pauciflora is woody and 10 to 25 cm in height. It provides feed for sheep, horses, goats and camels. *Artemisia sieberi* is also woody and 20 to 35 cm tall (Polyakov 1961).

Readers interested in the methodology of measuring production and developing nutrient budgets in an ecosystem should refer to Chapman (1976). Those interested in a broader discussion of mineral cycling in rangeland ecosystems of the world should read the papers by Charley (1977) or West (In Press).

Process

The fate of minerals on a given site includes the cycling from soil to plant to litter and again to soil where the process is repeated. The time needed for the minerals to cycle through this closed system is call turnover time. It can be most accurately determined using mineral isotopes, a costly and time-consuming process. Turnover time may, however, be estimated as the mineral content in the biomass divided by that in the annual litter. This estimate assumes a steady state growth and decomposition, and it is often calculated for above-ground plant parts only.

Minerals can be lost from this system as volatile gases like N₂, NO, NH₃, and SO₂ or in volatile organic compounds. Fire results in gaseous losses of some N

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and S and perhaps other minerals that escape in the smoke and particulate matter. Some mineral mass leaves the system through wind or water erosion. Minerals in forage may contribute to the growth of herbivores, or they may be carried off site before they are excreted.

Minerals can be added to this system by dust, rain, animal excrement, fallout from factories, or even fertilizer. Biological fixation of N_2 or foliar absorption of NH_3 , SO_2 , F and some of the heavy metals can occur.

Readily mobile elements like K can be translocated from leaves back to the rest of the plant before senescence. Water soluble elements can be leached from the plant, thus entering the soil mineral pool.

Biomass

Data in Table 1 illustrate nearly an order of magnitude range in the above-ground biomass for *Artemisia tridentata* at five sites in southern Idaho and a sixth in south-central Washington. Sites 1 to 4 represent a dry to wet gradient. Soil moisture at site 5 is less than at site 1, whereas moisture at site 6 is intermediate to that at sites 1 and 2. Perennial plant parts and dead parts increase in mass as the age of the shrub stand increases. *Artemisia* roots at sites 5 and 6 make up 20 to 50% of the total biomass, respectively. Roots made up 27 to 57% of the *Artemisia sieberi* communities shown in Table 2. The community information in Table 2 represents shrubs plus grasses, whereas the information in Table 1 is for the *Artemisia tridentata* component only.

Litter Fall

The leaves of *Artemisia tridentata* consist of large (>30 mm) leaves produced in early spring and small (<30 mm) leaves produced in late summer. The large leaves begin senescing and falling in late spring (Figure 1). The small leaflets do not drop at any particular time. The inflorescence parts do not drop until late winter; the drop is enhanced by cold temperatures, snow and wind.

The annual parts of *Artemisia tridentata* constitute 150 to 1100 kg/ha (Table 1). Stem loss is generally a small part of litter fall and apparently

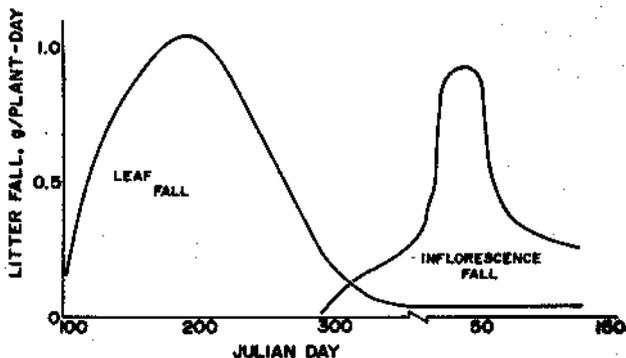


Figure 1. *Artemisia tridentata* leaf and inflorescence fall. Accumulative leaf fall was 135g/plant and accumulative inflorescence fall was 53g/plant. (Adapted from Mack 1971).

is not related to seasonal changes. We, therefore, assumed that the production of annual parts is nearly equivalent to litter fall. Mack (1971) collected 34 kg/ha of leaves and 28 kg/ha of inflorescences of *Artemisia tridentata* annually in litter traps. In another year he estimated 108 kg/ha-year leaf fall and 10 kg/ha-year inflorescence fall (Mack 1977). These amounts and proportions vary considerably from plant to plant and year to year. Root sluffing and decay also occur but are difficult to estimate.

Litter fall in the plant community may be much larger than these values shown for just the *Artemisia* component. Litter fall values of 500 to 2400 kg/ha are given in Table 2. Root residues contribute 26 to 46% of the litter fall.

Decomposition

The decomposition rate is generally measured as the loss of dry matter from material enclosed in fine mesh (<1-mm openings) bags. In reality this measures the rate of mastication or fragmentation to smaller particle sizes allowing escape from the bag. Murray (1975) found that 32 to 49% of the leaf litter remained at the Idaho study sites after 1 year (Table 3). Mack (1977) noted that 50% of the leaf litter remained after 1 year on the Washington study area and Comanor and Staffeldt (1978) reported that 47 to 57% of the leaf litter remained after 1 year near Reno. Mack (1971) found that less than 50% of the inflorescence litter remained at 1 year.

Comanor (1976) reported that 50% of the leaf and

twig mass remained at 19 months when *Artemisia tridentata* samples were buried at either 5 or 10 cm. About 63% of the small stem mass and 70% of both small and large root mass litter remained at 19 months. Over 90% of the stem mass placed on the soil surface remained after 19 months which substantiates the long residence time observed in the field. Conditions leading to litter burial obviously increase the decomposition rate.

Comanor (1976) also reported 6-hour respiration (CO_2 evolution) rates of litter exposed to various environmental conditions. The respiration process accounted for a large portion of the decomposition loss. The losses were generally greater for wet (-0.1 bar) than dry (-70 bar) samples, decreased with a decrease in temperature (range of 5 to 35 C), were greater for stems than roots, and greater for old leaves than for young leaves. The laboratory respiration measurements supported the decomposition data obtained from the buried litter studies.

Mineral Concentration and Mass

The ash elements (e.g. Si, K, Ca, Mg, P) of the Syrian desert *Artemisia* communities (Table 2) ranged from 79 to 461 kg/ha-year, of which 42 to 53% was returned by above- and below-ground litter fall. About 20 to 42% of this came from the roots, and less than 11% came from the standing green parts.

The distribution of N and the ash elements in the *Artemisia sieberi/Poa sinaica* community is given in Table 4. In this community N, Si and Ca make up 73% of the mineral element mass. Mineral concentration data showed that N, Si, Ca and K make up about 82% of the mineral mass of the shrub, and, if Mg is included, 85%.

Mineral concentration data are also given for several *Artemisia* species grown in the western United States (Table 5). The data reflect differences in mineral concentration caused by soil fertility and differences in physiological maturity of the plant parts sampled.

Mineral mass in various *Artemisia tridentata* plant parts is given in Table 6. The N mass is given in Table 1. The leaves contain 2 to 4% of the mineral elements and 15% of the N measured in the above ground parts. The roots contained 15, 37, 21 and 44% of the K, Mg, P and Ca respectively in the shrub. The K, Mg, P and Ca in the biomass are only 0.7, 0.1, 2.0 and 0.03% respectively of that available

from soil (Table 6). The biomass (including litter) N represents 6% of the total N in the soil, which occurs predominately in organic forms.

When we compare mass and distribution of the elements in *Artemisia tridentata*, we note that a relatively larger portion of the total ecosystem N is found in the biomass and second that a relatively larger portion of the total N is cycled in litter (leaf and root) fall. Thus N may be the first most limiting element in the system. Phosphorus may be the second most limiting macroelement that restricts plant growth.

Mineral Turnover

Rodin and Bazilevich (1965) reported 40 to 50% of the mineral mass in the community biomass was returned annually in the litter fall (Table 2). About 6 to 26 kg N/ha were also in the litter fall. These values are lower than those anticipated for *Artemisia tridentata* (Table 1), if we assume that more than 8% of the root mass sluffs off annually. Mack (1971 and 1977) also gives data (Table 6) on the mass of *Artemisia tridentata* plant parts and the amounts of K, Mg, P and Ca contributed by leaf and inflorescence fall. The leaf litter and sluffed roots are undoubtedly the major source of minerals returned to the soil as organic matter decomposes. The amount of mineral remaining after incubating *Artemisia tridentata* leaves on the ground for 1 year is given in Table 3. Mineral losses were generally described best by the equations $Y=AX^B$ or $Y=1/(A+BX)$. The averaged correlation coefficient for the four sites and 10 elements was $r^2=0.82$.

The mobile K is easily leached from the leaf samples. However, more than 50% of the N, Mn and Cu remained in the sample at 1 year. The leaf N is not readily lost from the sample because the microorganisms recycle the N during C respiration. This process reduces the C/N values from about 36 (Mayland, Unpublished) in leaves and 65 in roots to values approaching 6 in the soil.

We estimate that the C loss resulting from the decomposition of leaf and root litter ranges from 150 to 950 g C/m²-year. This assumes that 50% of the root matter sluffs annually.

Mineral turnover for four *Artemisia tridentata* sites in southern Idaho is given in Table 3. These values are calculated as the mineral mass in the above ground biomass divided by the mineral mass in

the leaves plus inflorescences. Phosphorus, S, Ca, Mg and K cycle in the shrub system more rapidly than do N, Na, Zn, Mn and Cu. Mineral turnover for the entire community is about twice as rapid as for the shrub component alone. This accelerated turnover of the community mineral mass occurs because grasses and forbs contribute a large portion of their biomass to the annual litter fall.

Discussion

The minerals contained in the shrub and community biomass turn over in 9 to 43 years and 5 to 16 years, respectively. During this period the additional minerals required by the plants must be obtained from mineralized soil organic matter or from exchangeable sources in the soil. The large soil reservoir of minerals (Table 6) provides more than adequate amounts of these minerals, except for N and occasionally P and Zn.

Plant-induced soil chemical patterns are significant in desert shrub communities (Charley and West 1975). These horizontal and vertical patterns develop as the shrub roots absorb minerals from the soil and concentrate them, via the litter fall, in the upper part of the soil profile under the shrub canopy. This process is particularly important for organic N and C. Vertical gradients are also noted for available P and C/N where higher values occurred near the soil surface. Charley and West (1977) reported larger amounts of mineralized N under shrub canopies than in the interspace areas. However, the amount of N mineralized versus the amount present was not different for the two areas. Charley and West (1975) found that the process of converting *Artemisia* communities to grass obliterated the horizontal N and C patterns. Incorporating shrub litter into the soil increases the decomposition rate and release of minerals.

Burning shrub communities quickly releases mineral elements for subsequent vegetative growth. The increased productivity that frequently occurs after fire is evidence that even N must be more available than before the fire. Some N, perhaps as much as 50% (Murray 1975) in the above-ground biomass might be lost by high temperature volatilization. This would normally be a very small part of the total N in the system.

West and Skujins (1977) have developed a N balance for *Atriplex confertifolia*-dominated system and have made some reference to *Artemisia*. The amount of N lost by denitrification and volatilization or gained by dust fallout, blue-green algal fixation (Rychert and Skujins 1974), and symbiotic fixation in *Artemisia ludoviciana* (Clawson 1973) have no large effect on the size of the N pool. Klubek (In Press) summarized N_2 -fixation and denitrification in arid soil cryptogamic-crust microenvironment. In general these processes do not significantly change the size of the main N pool.

Sulfur is subject to many of the same processes as N. Other mineral elements, although not generally subject to volatilization, may cycle from organic to inorganic forms in soil. These forms may be freely available, sparsely available or unavailable to plants.

Soil moisture has the major effect on plant growth. Only when moisture is abundant, especially for several years in succession, will shrubs respond to supplemental N and perhaps other mineral elements (James and Jurinak 1978).

- Chapman, S. B. 1976. Production ecology and nutrient budgets. p 157-228. In S. B. Chapman (ed.). *Methods in Plant Ecology*. Blackwell Sci. Publ. Oxford.
- Charley, J. L. 1977. Mineral cycling in rangeland ecosystems. p 215-256. In R. E. Sosebee (ed.). *Rangeland plant physiology*. Society for Range Management. Denver, Colorado.
- Charley, James, and Neil E. West. 1975. Plant-induced soil chemical patterns in some shrub dominated semi-desert ecosystems of Utah. *J. Ecol.*, 63, 945-964.
- Charley, J. L. and N. E. West. 1977. Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biol. Biochem.* 9:357-365.
- Clawson, M. A. 1973. Nitrogen fixation by *Artemisia ludoviciana* (gray sagewort), characterization of the endophyte and factors influencing nodulation. Brigham Young Univ. M. S. Thesis. Provo, Utah.
- Comanor, P. L. 1976. Decomposition and mineralization in an *Artemisia tridentata* community in northern Nevada. US/IBP Desert Biome Res. Memo. 76-30. Utah State Univ., Logan. 8pp.
- Comanor, P. L. and E. E. Staffeldt. 1978. Decomposition of plant litter in two western Northern American deserts. In N. E. West and J. J. Skujins (ed.) *Nitrogen in desert ecosystems*. Dowden, Hutchinson & Ross. Stroudsburg, PA. (In Press).
- Connor, J. J., J. R. Keith and B. M. Anderson. 1976. Trace-metal variation in soils and sagebrush in the Powder River basin, Wyoming and Montana. *J. Res. U. S. Geol. Surv.* 4:49-59.
- Gough, L. P. and R. C. Severson. 1976. Impact of point source emissions from phosphate processing on the element content of plants and soils, Soda Springs, Idaho. *Trace Substances in Environmental Health* 10:225-233.
- Harner, R. F. and K. T. Harper. 1973. Mineral composition of grassland species of the eastern Great Basin in relation to stand productivity. *Canadian J. Botany*. 51:2037-2046.
- James, D. W. and J. J. Jurinak. Nitrogen fertilization of dominant plants in the northeastern Great Basin. p 219-231. In N. E. West and J. J. Skujins (ed.). *Nitrogen in desert ecosystems*. Dowden, Hutchinson & Ross. Stroudsburg, PA. (In Press).
- Klubek, B. P. Nitrogen fixation and denitrification in arid soil cryptogamic crust micro-environment. p 543-552. In W. E. Krumbein (ed.) *Environmental Biogeochemistry and Geomicrobiology*. Ann Arbor Science. Ann Arbor, Michigan. (In Press).
- Lavrenko, E. M. and I. V. Borisova. 1976. Biocomplex investigation in Kazakhstan. Vol. 1. Main plant communities of the Kazakhstan steppes and desert. Vol. 2. Main plant and animal communities of the Kazakhstan steppes and desert. Vol. 3. Main Plant communities of central Kazakhstan desert steppe. (Russian). Nauka, Leningrad.
- Mack, R. N. 1971. Mineral cycling in *Artemisia tridentata*. Ph.D. dissertation, Washington State University, Pullman, 96pp.
- Mack, R. N. 1977. Mineral return via the litter of *Artemisia tridentata*. *Amer. Midland Naturalist* 97:189-197.
- Marchand, D. E. 1973. Edaphic control of plant distribution in the White Mountains, eastern California. *Ecology* 54:233-250.
- Murray, Robert Burns. 1975. Effect of *Artemisia tridentata* removal on mineral cycling. Ph.D. dissertation, Washington State University, Pullman, 203pp.
- Polyakov, P. P. 1961. *Artemisia*. In: V. L. Komarov (ed.). *Flora USSR* 26:425-631.
- Rodin, L. E. and N. I. Bazilevich. 1965. Production and mineral cycling in terrestrial vegetation (Russian). English translation by G. E. Fogg and published by Oliver and Boyd, London. 1967. 288 p.
- Rodin, L. E., N. I. Bazilevich and Y. M. Miroshnikchenko. 1972. Productivity and biogeochemistry of *Artemisia* in the Mediterranean area. p. 193-198. In USSR Academy of Sciences. *Eco-physiological foundation of ecosystems productivity in arid zone*. Proceedings International Biological

Rychert, R. C. and J. Skujins. 1974. Nitrogen fixation by blue-green algae lichen crusts in the Great Basin Desert. *Soil Sci. Soc. Amer. Proc.* 38:768-771.

Severson, R. C. and L. P. Gough. 1976. Concentration and distribution of elements in plants and soils near phosphate processing factories, Pocatello, Idaho. *J. Environmental Quality*. 5:476-482.

Wallace, A., E. M. Romney and V. Q. Hale. 1973. Sodium relations in desert plants: 1. Cation contents of some plant species from the Mojave and Great Basin Deserts. *Soil Sci.* 115:284-287.

West, N. E. Nutrient cycling in desert ecosystems. In I. Noy-Meir (ed.). Short term dynamics of arid ecosystems. Cambridge University Press. In Press.

West, N. E. and J. Skujins. 1977. The nitrogen cycle in North American cold-winter semi-desert ecosystems. *Oecologia Plantarum* 12:45-53.

Table 1. Biomass statistics for *Artemisia tridentata* at Saylor Creek (site 1 near Glenns Ferry, Idaho), Piemeisel (site 2 near Twin Falls, Idaho), Mayfield (site 3 between Boise and Mountain Home, Idaho, Sand Creek (site 4 near St. Anthony, Idaho), Hanford (site 5 in Columbia Basin of south central Washington), and Big Southern Butte (site 6 near Arco, Idaho). Nitrogen data are included for site 6. Data for site 1 through 4 are from Murray, 1975. Data for site 5 are from Mack, 1971 and for site 6 are from West, Mayland, and Welch, unpublished.

Component	Biomass						N
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 6
	kg DM/ha						kg N/ha
<i>Artemisia tridentata</i>							
Annual parts	200	1100	300	400	150	1000	13
Perennial parts	2600	9500	3500	4600	7700	10,400	46
Dead parts	1500	3900	400	200	3400	5100	29
Roots	Not determined				3000	16,800	150
Litter	Not shown					150	9
Mixed soil & litter	Not determined					500	27
Other forbs, grasses							
& shrubs	800	100	200	500 [†]		600	5
Litter	Not determined					200	1
Cryptogams & fungi	Not determined					500	12
Soil N in upper 60 cm	4000	6400	3400	7800			4500

[†]Plus nearly 5000 kg/ha *Parshia tridentata* above ground biomass.

Table 2. Biomass statistics in an (1) *Artemisia sieberi/Poa sinaica*, (2) *Artemisia sieberi/Poa sinaica/Carex pachystilis/Aspicilia esculenta*, and (3) *Artemisia sieberi/Poa sinaica/Aspicilia esculenta* communities of the Syrian desert. (Adapted from Table 44 of Bodin and Bazilevich, 1965).

Component	Community		
	1	2	3
Biomass, kg/ha	6100	940	1600
Green parts, %	3	14	12
Perennial parts, %	40	59	44
Roots, %	57	27	44
Litter fall, kg/ha	2400	500	700
Green parts, %	8	26	28
Perennial parts, %	46	48	35
Root residues, %	46	26	37
Mineral elements			
in biomass, kg/ha	461	79	106
In green parts, %	3	10	11
In perennial parts, %	55	70	59
In roots, %	42	20	30
Returned with litter fall, %	42	53	46
N returned with litter fall, kg/ha	26	6	8
In green parts, %	12	37	40
In perennial parts, %	42	41	32
In root residues, %	46	22	28

Table 3. Leaf decomposition and mineral turnover time in *Artemisia tridentata* and mineral turnover time for the entire community at Saylor Creek (Site 1), Piemeisel (Site 2), Mayfield (Site 3), and Sand Creek (Site 4). Data are from Murray 1975.

Site	Weight	N	P	S	Ca	Mg	K	Na	Zn	Mn	Cu
Leaf decomposition, percent remaining at 1 year, %											
1	45	74	43	38	58	38	11	34	-	56	68
2	49	79	50	34	47	32	9	35	-	83	123
3	46	81	39	35	22	24	3	29	-	69	84
4	32	79	41	31	16	21	2	23	-	46	85
Mineral turnover in <i>Artemisia tridentata</i> , years											
1	-	25	19	11	11	13	14	20	42	19	46
2	-	14	14	19	16	12	11	30	42	29	35
3	-	12	7	5	3	2	3	24	49	15	33
4	-	16	9	6	6	8	6	21	40	8	24
Mineral turnover for entire community, years											
1	-	3	2	2	4	4	3	5	6	5	8
2	-	11	10	16	13	11	9	28	27	26	31
3	-	5	3	4	3	2	2	15	17	10	18
4	-	5	3	3	4	3	2	7	8	4	7

Table 4. Mineral element concentration in *Artemisia sieberi* shrub parts and mineral content in annual litter fall from the *Artemisia sieberi/Poa sinaica* community in the Syrian desert (from Table 45 and Figure 52 respectively of Rodin and Bazilevich, 1965).

Component	Mineral Concentration			Mineral Content		
	Leaves	Perennial above ground parts	Roots	Green parts	Perennial above ground parts	Roots
		%			kg/ha	
N	2.5	1.9	0.8	2	12	12
Si	.35	.37	.15	2	40	12
Ca	1.2	1.7	1.5	1	41	20
K	2.8	.7	.5	3	1	3
Mg	.43	.26	.12	1	1	2
P	.22	.09	.05	<1	7	3
Al	.12	.13	.05	<1	8	4
Fe	.12	.12	.06	<1	7	2
Mn	-	-	-	1	2	2
S	.37	.16	.21	1	1	1
Na	.23	.04	.13	2	<1	1
Cl	.44	.11	.05	1	<1	1
					Dry Matter Production	
					kg/ha	
Biomass				200	1100	1100

Table 5. Mineral concentration data for *Artemisia* species of the Great Basin and eastern California regions and the Syrian *Artemisia sieberi*.

Species, Plant Part	Mineral Concentration					
	Si	Ca	K	Mg	P	N
	%					
<i>arbuscula</i> ^{1,2/}	0.06	0.57	0.8	0.15	0.08	-
<i>arbuscula</i> ^{1,3/} } <i>nova</i>	-	0.54	1.5	-	0.12	0.67
<i>tridentata</i> ^{4/}						
leaves	-	0.67	1.8	0.25	-	-
stems	-	0.62	1.1	-	-	-
<i>tridentata</i> ^{5/}						
leaves	-	1.02	1.0	0.40	0.19	1.2
<i>sieberi</i> ^{6/}						
leaves	0.35	1.22	2.8	0.43	0.22	2.5
branches	0.37	1.69	0.7	0.26	0.09	1.9
roots	0.15	1.53	0.5	0.12	0.05	0.8

^{1/} Presumed to be standing shrub biomass.

^{2/} Marchand 1973.

^{3/} Harner and Harper 1973.

^{4/} Wallace et al. 1973

^{5/} Charley 1977.

^{6/} Rodin et al. 1972.

Table 6. Biomass and mineral mass of *Artemisia tridentata* plant parts and available soil mineral mass in the 0 to 100 cm depth. From Mack 1971 and 1977.

Component Part	Mineral Mass				
	Biomass	K	Mg	P	Ca
	----- kg/ha -----				
Leaves ^{1/}	150	1.3	0.3	0.1	1.1
Inflorescence ^{1/}	10	0.06	0.02	0.02	0.05
Stems	7700	20.0	4.6	3.9	22.0
Deadwood	3400	8.8	2.0	1.7	10.0
Roots	3000	5.3	4.1	1.5	26.0
Soil Minerals	-	3600	4500	130	22000

^{1/} These data are equivalent to annual litter fall.