

STANDING CROPS AND DYNAMICS OF PHYTOMASS AND MINERALS IN TWO SALT DESERT SHRUB COMMUNITIES

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ABSTRACT.—Of two salt desert shrub communities studied in Curlew Valley, Utah, the *Atriplex confertifolia*-dominated community had 15% greater total midsummer phytomass than the *Ceratoides lanata* community. The larger *Atriplex* shrubs contained much more woody tissue for support of photosynthetic tissues than did *Ceratoides*. *Atriplex* aboveground phytomass and litter were about twice those of *Ceratoides*. *Ceratoides* litter was generally fine and easily decomposable, but *Atriplex* litter contained about equal proportions of coarse, resistant woody tissues and fine, easily decomposable material. *Atriplex* root phytomass was 1.3 times that of *Ceratoides* at the 2–30 cm depth, but at depths below 30 cm, *Ceratoides* exhibited up to three times greater root phytomass and had 23% more root mass overall.

Net aboveground community primary production was estimated to be about one-third greater in the *Atriplex* than *Ceratoides* community. Turnover times for readily decomposable aboveground litter were quite similar, but, because *Atriplex* produced coarser litter, its overall rate was somewhat slower than that of *Ceratoides*.

Analyses of selected minerals in plant parts, litter, and soil revealed that about 90% of the mineral capital is in the soil, mostly within organic matter. Nearly equivalent pools of mineral elements were found in the two communities, except for greater Na in the *Atriplex* community.

Primarily because of relatively low productivities, insignificant nutrient losses by leaching, and slow losses due to biological export, primary production (Caldwell 1975) and nutrient cycling processes (West 1981) of arid grazing lands have received little basic study. Disturbance of desert vegetation is followed by slow recovery. If soil erosion is great, nearly permanent damage to site potential can occur during periods of diminished vegetation. Knowledge of ecosystem structure will aid interpretations of and decisions for managing these areas.

In the interests of providing data for comparison purposes, we report the following study of standing crops and dynamics of phytomass and selected mineral elements in communities dominated by nearly pure stands of *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale) and *Ceratoides lanata* (Pursh.) J. T. Howell (winterfat), two major, perennial species of the salt desert shrub type (West 1983) in the intermontane basins of the interior western United States. Estimates of net aboveground primary productivity and turnover rates of litter are made for both communities.

Ceratoides is more palatable to livestock and has been widely replaced by the less palatable *Atriplex confertifolia* or annual weeds (West 1982). We wished to compare production and nutrient-cycling processes on sites dominated by perennial species to anticipate whether further losses of *Ceratoides* dominance had unfavorable implications from primary production and nutrient-cycling viewpoints.

METHODS

Plant, litter, and soil samples were collected in Curlew Valley of northwestern Utah (41°52'N, 113°5'W). The sites selected were on nearly level, lacustrine soils covered by pluvial Lake Bonneville prior to about 7000 years ago (Eardley et al. 1957). The soil profiles of both sites were classified as belonging to the fine silty mesic family of Xerollic Calciorthids, Thiokol Series (A. R. Southard, pers. comm.) and were 0.8 km apart on the 1350 m contour. Previous investigators of soil chemical (Gates et al. 1956) and physical characteristics (Mitchell et al. 1965) had concluded that the soils under *Atriplex* and

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Ceratoides in this area did not differ in a statistically significant sense.

The vegetation was composed of nearly monospecific stands of the two dominant plants, *Atriplex confertifolia* and *Ceratoides lanata* (see Mitchell et al. 1965). Total higher plant cover (line intercept method) averaged 22% in the *Atriplex* and 20% in the *Ceratoides* community. *Ceratoides* plants are small half-shrubs quite evenly dispersed, whereas *Atriplex* plants are true shrubs from 5 to 20 times larger and less uniformly distributed (West and Baasher 1968). The area had been used by livestock since at least the 1870s. Because open water is at least 6 km distant, most of the livestock use was in winter by sheep. This comparatively light use has apparently allowed the more palatable species to persist in pure stands. Plots used in this study were fenced in 1967 with sheep-, cattle-, and rabbit-proof netting.

Each community was subdivided into four major components: shoots, roots, litter, and soil. A single annual sampling of each compartment was made in late July or early August of 1968, 1969, and 1970. This sampling followed the period of maximum growth of the shrubs and water-stress-induced drop of ephemeral leaves (West and Gasto 1978). Aboveground phytomass (living + standing dead plants and litter) estimates were made by harvesting plants from randomly selected 1- and 4-m² plots in *Ceratoides*- and *Atriplex*-dominated vegetation, respectively. Quadrat dimensions and numbers were predetermined to yield phytomass estimates within 15% of the true mean ($P \leq 0.1$). Plants were clipped at ground level and separated from adhering soil and litter.

Aboveground net primary community production was estimated by a technique using the ratio between the oven dry masses of old and new growth (Whittaker 1961) of 40 individual plants of each species. Plant numbers were predetermined to estimate this ratio within 10% of the true mean ($P \leq 0.1$).

Litter was collected from the total area of each plot after removal of aboveground plant parts. In *Atriplex* plots, the litter could be divided into two classes, a coarse fraction that was resistant to decay and composed of woody material such as dead stem bases, and a fine, easily decomposable fraction of leaves

and finer stem material. Surface soil particles were removed by shaking the litter on a 1.6-mm sieve, followed by washing and flotation. The *Ceratoides* litter was virtually all of fine composition, so that fractionation was not necessary. Distinctly standing dead material was included in the litter fraction. Woody, aboveground portions of shrubs with distinctly live tissue were included in the shoot fraction. Root phytomass and soil bulk density values were determined from randomly placed 8.4-cm-diameter core samples taken with a bucket auger from the aboveground biomass sampling plots, at depth increments of 2-30, 30-60, and 60-90 cm. This sampling depth included 98% of the root mass (Gasto 1969).

Roots were partially separated from soil using a 1.6-mm sieve, followed by washing and flotation.

Old shoot growth, new shoot growth, root mass, and litter were dried with forced air at 60 C for 48 hr and ground to pass a 40-mesh sieve. Samples were analyzed for total N by semimicro Kjeldahl techniques. To determine P, K, Na, Ca, and Mg content, a 1.0 g sample was digested for 2 hr with 16 ml HNO₃ + 2.4 ml HClO₃ + 1.6 ml H₂SO₄, after which it was cooled, filtered, and diluted to an appropriate volume. Phosphorus was determined colorimetrically as phospho-vanado-molybdate and other elements were measured by atomic absorption spectrophotometry. Only soil organic carbon is included here since total carbon budgets of these ecosystems had been previously considered by Caldwell et al. (1977).

The soil organic carbon was determined by wet combustion in an excess of potassium dichromate solution. Excess dichromate was reduced by addition of ferrous ammonium sulfate solution, which in turn was titrated with standardized potassium permanganate solution. The difference between the amount of standardized potassium permanganate used in titrating blanks and soil samples served as the basis for calculation of organic carbon. Since soil samples contained appreciable quantities of carbonate and chloride salts, concentrated sulfuric acid containing 25 g of silver sulfate per pound was used to drive off inorganic carbonates and prevent interference of chlorides by precipitating with the silver ion (Jackson 1958).

The soil separated from each of the root mass samples was air dried prior to chemical analysis. Total N was determined by the Kjeldahl procedure. Soil P was extracted by .5 N NaHCO₃ and determined by the phosphovanado-molybdate method, and other minerals were determined by atomic absorption on a HNO₃-HCO₃ (3:1) digestion.

Total soluble salt content of soil was determined by measuring resistance of the saturated soil paste and converting the temperature-adjusted values according to method 5 (U.S. Salinity Laboratory 1954).

RESULTS AND DISCUSSION

Phytomass

Total midsummer phytomass, as well as the amounts in most compartments, significantly differed between communities (Table 1). Total plant and litter weights in the *Atriplex* community were about 15% greater than those found in the *Ceratoides* community. *Atriplex* showed about 60% greater total shoot phytomass than *Ceratoides*. The *Atriplex* litter phytomass fractions were over twice as

great as that of the *Ceratoides*-dominated community. It is particularly significant that the current year's aboveground growth of *Atriplex* was about 20% greater than that of *Ceratoides*. Not all this new growth in *Atriplex* is photosynthetic. Caldwell et al. (1977) reported about 19% of the new shoot growth fractions of this plant to be non-photosynthetic. Much less (about 10%) was nonphotosynthetic in *Ceratoides*. A principal difference between the aboveground phytomasses of *Atriplex* and *Ceratoides* communities appeared to be in the woody nature of the former. New growth in *Atriplex* occurs on old, woody stems, but much of the new growth of *Ceratoides* originates from a woody base, there being no hard wood in the form found in Curlew Valley. The woody, spiny nature of *Atriplex* makes it comparatively more resistant to browsing than is *Ceratoides* (Gasto 1969).

Only in total belowground phytomass did the *Ceratoides* system exceed *Atriplex*. *Atriplex* had somewhat more root mass in the upper 30 cm of the soil profile, but only 42% as much as *Ceratoides* was found below 30 cm.

The distribution of root biomass was closely related to soil-textural conditions and total soluble salt distribution in the two soil profiles (Fig. 1). The *Atriplex*-dominated site had higher clay content in the upper part of its soil profile. This soil has a slower infiltration rate and under equal rainfall wets to shallower depths than the *Ceratoides* soil (Gasto 1969).

The greater woodiness and concentration of roots of *Atriplex* closer to the soil surface contrasts with less woodiness and continuance of high densities of *Ceratoides* roots to greater depths. The two species thus had tissue concentrations in somewhat different microenvironments both above- and belowground. Both species had very high root:shoot ratios, also typical of dominants in cold-winter temperate deserts elsewhere (Rodin and Basilevich 1967). Brewster (1968) and Wagner (1980) have speculated that the high proportion of roots is related to most of the soil moisture coming from winter snowmelt. Cold to cool season precipitation is the only input that normally infiltrates to great enough depths to escape evaporation in such environments (Caldwell et al. 1977). Arrested

TABLE 1. Midsummer phytomass (oven-dry g m⁻²) in *Atriplex confertifolia* and *Ceratoides lanata*-dominated communities, by compartments, Curlew Valley, Utah. Average of 1968, 1969, and 1970 midsummer samples ± 90% confidence intervals.

| Compartment | Depth cm | Community type | |
|-------------------------------------|-------------|-----------------|-------------------|
| | | <i>Atriplex</i> | <i>Ceratoides</i> |
| SHOOTS | | | |
| New growth | | 84 ± 11 | 70 ± 13 |
| Old growth | | 333 ± 25 | 172 ± 22 |
| Total shoot phytomass | | 417 ± 36 | 241 ± 35 |
| ROOTS ¹ | | | |
| | 0-30 | 945 ± 62 | 721 ± 69 |
| | 30-60 | 292 ± 35 | 668 ± 42 |
| | 60-90 | 76 ± 9 | 218 ± 30 |
| Total root phytomass | 0-90 | 1,313 ± 76 | 1,607 ± 90 |
| LITTER | | | |
| Coarse | | 446 ± 20 | — |
| Fine | | 403 ± 26 | 400 ± 26 |
| Total litter weight | | 849 ± 36 | 400 ± 26 |
| TOTAL PLANT AND LITTER WEIGHT | | | |
| | | 2,579 ± 141 | 2,249 ± 119 |

¹Estimate includes root litter

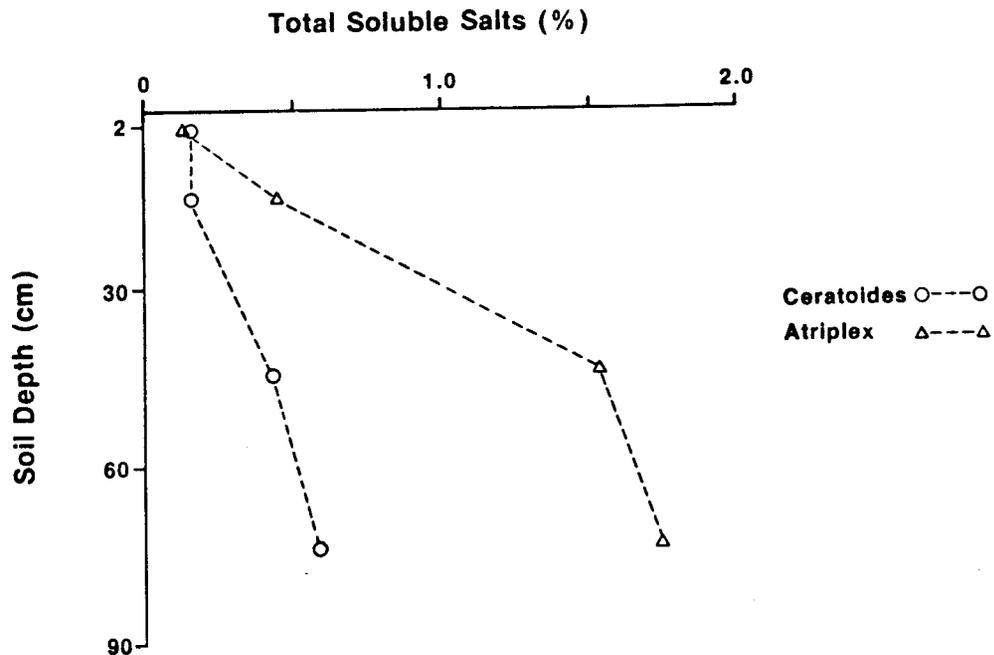


Fig. 1. The vertical distribution of total soluble salts (%) in soils under the *Atriplex* and *Ceratoides*-dominated communities, July 1968.

growth and a dieback of some aboveground tissues are usually related to the water stresses experienced during the summer (Love and West 1972).

Net Aboveground Primary Production

Estimates of average aboveground net primary production in the *Atriplex* community were significantly higher than for the *Ceratoides* community (Table 2). Only during 1968 did aboveground production of *Ceratoides* exceed the aboveground production of *Atriplex*. The differences were not statistically significant, however. Although a single end-of-growing-season harvest nearly always

underestimates net aboveground primary production and the data in Table 2 should be more properly labeled "new green growth," single-harvest data prevail in the literature dealing with this type of vegetation.

Similar between-communities differences in average net aboveground primary production were found in other phytomass and production studies of chenopod shrublands in Curlew Valley (Caldwell et al. 1977). In their studies, addition of litter that had fallen prior to clipping accounted for only 2% to 9% of their annual shoot production estimates. Fetcher and Trilica (1980), using six years of data gathered from the same area, reported that annual aboveground production of *Atriplex* and *Ceratoides* (also estimated from a single midsummer clipping of new growth) was well correlated with growing season (March-June) precipitation ($P \leq 0.10$ and $P \leq .009$, respectively).

The comparison of these phytomass and aboveground production data with salt desert shrub communities elsewhere (Rodin and Basilevich 1967, Holmgren and Brewster 1972, Branson et al. 1976, Osmond et al.

TABLE 2. Estimates of net annual aboveground primary production ($\text{gm m}^{-2} \text{yr}^{-1} \pm 90\%$ confidence intervals) in *Atriplex-confertifolia*- and *Ceratoides-lanata*-dominated communities.

| Year | Community type | |
|------|-----------------|-------------------|
| | <i>Atriplex</i> | <i>Ceratoides</i> |
| 1968 | 78 ± 9 | 83 ± 5 |
| 1969 | 61 ± 6 | 50 ± 4 |
| 1970 | 113 ± 12 | 76 ± 5 |
| Mean | 84 ± 7 | 70 ± 4 |

1980) is difficult because of differing environments, definitions, and methodologies. Herbivory and amounts of prior leaf fall are, like herein, often ignored, as are increments to stem wood on the irregularly shaped stems of these shrubs. The weight of developing fruit is included here. A greater problem, however, is determination of live and dead tissues. Desert shrubs such as *Atriplex* have a large fraction of standing dead wood. It is difficult on some *Atriplex* plants to decide what part of the plant is alive.

The reason for the small differences in means and confidence intervals for new shoot growth in Table 1 and 2 is that the former are plot based, and the latter are determined from a random selection of individual plants.

Our estimates of the weights of aboveground litter (Table 3) probably exceed the long-term averages due to drought-induced increases in mortality of plant parts following a period of above-normal precipitation prior to and early in our study period (West and Gasto 1978).

For a detailed discussion of below ground plant community dynamics at this study site see Caldwell and Fernandez (1975) and Caldwell et al. (1977). Belowground production was roughly 3.5 times that of aboveground.

Litter Turnover

Estimates of litter turnover are crucial to our considerations of mineral cycling since litter represents the largest and most readily available source of organically incorporated nutrients. Turnover of soil surface litter and the standing dead portion was estimated by dividing estimates of mean net aboveground

primary production by mean aboveground litter fractions (Table 4). This was done on the assumption that, if the communities were successional stable, or nearly so, the long-term values for new growth should equal litter fall. The true turnover coefficients are probably higher than the values in Table 4 due to likely underestimations in net primary production discussed previously.

The decomposition of *Atriplex* and *Ceratoides* fine shoot litter was quite comparable, but when the coarse litter of *Atriplex* was added, a much slower recycling of minerals was suggested. The overall differences in litter turnover were closely related to growth habit (Table 4). *Atriplex* plants were larger and had a high proportion of hard, woody tissue. *Ceratoides* stems were generally less than 0.5 cm in diameter and more easily decomposed. *Atriplex* coarse litter was derived from woody stem tissue that accumulates over the life of an individual plant. More rapid decomposition of litter in the *Atriplex* community was suggested when only fine litter was considered (Table 4). Greater N content of *Atriplex* new growth compared to *Ceratoides* may be causally associated with this difference.

Root litter production could not be reliably estimated because of the difficulty in separating live and dead roots. Descriptions of the problems involved and initial attempts to deal with these important processes can be found in Caldwell and Camp (1974) and Caldwell and Fernandez (1975). Hodgkinson et al. (1978) suggests that less than 10% of the root phytomass in *Atriplex confertifolia* communities may be alive, leading to the possible conclusion that most of the belowground phytomass is litter.

TABLE 3. Estimates of aboveground litter standing crops (oven-dry gm m⁻²) in *Atriplex*- and *Ceratoides*-dominated communities, Curlew Valley, Utah. Midsummer values for the years 1968-1970.

| Component | Year | Type | Community type | |
|--------------|---------|--------|-----------------|-------------------|
| | | | <i>Atriplex</i> | <i>Ceratoides</i> |
| Shoot litter | 1968 | Coarse | 446 | — |
| | | Fine | 426 | 381 |
| | 1969 | Coarse | 479 | — |
| | | Fine | 380 | 355 |
| | 1970 | Coarse | 413 | — |
| | | Fine | 397 | 465 |
| Average | 1968-70 | Coarse | 446 | — |
| | | Fine | 403 | 400 |

TABLE 4. Turnover coefficients (fraction decomposed each year) and turnover time for soil surface litter (years) in *Atriplex*- and *Ceratoides*-dominated communities based on 1968-70 phytomass estimates and aboveground new growth fractions, assuming steady state conditions.

| | Community type | |
|----------------------|-------------------------|-------------------|
| | <i>Atriplex</i> | <i>Ceratoides</i> |
| Turnover coefficient | 0.09 (.21) ^a | 0.17 |
| Turnover time (yr) | 10.1 (4.8) ^a | 5.71 |

^a Turnover time for easily decomposable fine litter fraction only in parentheses

Mineral Concentrations within the Compartments

Tables 5 and 6 list means and standard deviations in concentrations of selected mineral elements in various plant parts, litter, and soil in the two community types. Discussion of some major (statistically significant = within one standard deviation, to include the mean 68% of the time) descriptive differences will be followed by other reorganizations of the data, attempting to rank the elements in order of their probable roles in limiting community functions.

Concentrations of K, Na, Ca, and Mg in the new shoot growth fraction of *Atriplex* were significantly higher ($P \leq .001, .001, .15,$ and $.3,$ respectively) than in *Ceratoides*. The concentrations of elements in old shoot growth were comparable between the two species except that Na was significantly higher in *Atriplex*. The two species had similar ratios of elemental concentrations in new to old shoot growth, except for N, P, Na, Ca, and Mg. This similarity, coupled with the observation that N, K, Na and Mg concentrations were significantly higher in the new growth fraction in both species, hints at their possible limiting function (Charley 1977). In Curlew Valley, K, Na, and Mg are very abundant and soluble in soil solutions and may be taken up in quantities far in excess of metabolic need (luxury consumption).

Elemental concentrations in litter were comparable between communities except that Na was higher in the fine fraction of *Atriplex* and K was higher in *Ceratoides* litter. Statistically significantly higher Na concentrations appeared in upper-level *Atriplex* roots, and Ca was higher throughout all root depths of *Ceratoides*. Concentrations of elements in the soils showed pronounced, similar decreases of C, N, and K with increasing depth in both community types. *Atriplex* soils had significantly greater P and Na at all depths.

Interpretations of nutrient concentrations at one point in time and space are limited in value because of translocation and the known seasonal dynamics of the elements (Breckle 1976). Nevertheless, some relationships with anatomical and physiological knowledge can be discussed.

Direct comparison of these data with those of prior studies (Wiebe and Walter 1972, Moore et al. 1972, Breckle 1974, 1976) at the same site is difficult since the earlier studies dealt with soluble forms (including some anions) in expressed sap from fresh growth of leaves and stems rather than the ash form concentrations presented here. The same general species differences, however, were found in the new growth fractions.

Atriplex is known to accumulate salts in vesicular epidermal cell leaf hairs that eventually rupture and deposit salts on the leaf

TABLE 5. Means and standard deviations of elemental concentrations (mg g^{-1}) in various components of a *Ceratoides-lanata*-dominated ecosystem, Curlew Valley, Utah. Average of 1968, 1969, and 1970 samples.

| | C | N | P | K | Na | Ca | Mg |
|---------------|----------|----------|--------|----------|---------|----------|----------|
| SHOOTS | | | | | | | |
| New growth | | 11.9±2.4 | 1.1±.1 | 13.5±1.0 | .9±.1 | 19.5±2.5 | 3.95±.47 |
| Old growth | | 10.9±1.2 | 1.1±.1 | 6.6±.8 | .8±.1 | 22.2±2.2 | 3.53±.61 |
| LITTER | | | | | | | |
| | | 13.7±1.4 | 1.2±.2 | 4.0±0.4 | .5±1.7 | 15.7±1.7 | 2.97±.43 |
| ROOTS | | | | | | | |
| 0-30 | | 16.3±1.5 | 1.4±.1 | 5.1±.9 | 2.0±1.2 | 47.5±5.5 | 5.14±.94 |
| 30-60 | | 16.1±1.8 | 1.5±.1 | 5.1±.7 | 3.4±1.5 | 52.9±3.9 | 6.68±.47 |
| 60-90 | | 18.1±2.6 | 1.6±.1 | 5.1±.6 | 3.5±1.3 | 53.1±3.3 | 6.91±.51 |
| SOIL | | | | | | | |
| 0-2 | 14.8±1.6 | 1.2±.3 | .8±.1 | 2.5±.5 | .3±.2 | 5.8±.9 | .33±.02 |
| 2-30 | 7.9±1.7 | .7±.1 | .6±.1 | 2.0±.4 | .5±.3 | 5.4±1.3 | .31±.05 |
| 30-60 | 6.5±1.0 | .6±.1 | .6±.1 | 1.9±.3 | 1.8±.5 | 4.9±1.0 | .37±.07 |
| 60-90 | 5.3±1.0 | .4±.1 | .6±.1 | 1.6±.4 | 3.3±.8 | 4.8±1.4 | .45±.11 |

surface (Osmond et al. 1980). *Atriplex confertifolia* sampled elsewhere had high concentrations of Na and other alkaline elements (Wallace and Romney 1972, Wallace et al. 1973a, 1973b, 1974, 1975). *Ceratoides* is thought to exclude Na and some other cations at the root-soil interface (Breckle 1976). It accumulates Ca, however, particularly in the roots. Classification of *Atriplex* as a euhalophyte and *Ceratoides* as a calciohalophyte (Walter 1979) is supported by these data.

It is interesting that the two species differed in Ca distribution patterns between new and old aboveground growth and root phytomass. Ca metabolism has been linked with the salinity tolerance of certain crop species (Epstein and La Haye 1969). The Ca:Na ratios differ in the two species studied here and, at least in Curlew Valley, *Atriplex* takes root in a saltier soil than does *Ceratoides* (Fig. 1). Seasonal variation in Ca:Na ratios of plant tissue of the species are known (Breckle 1976); nevertheless, Ca:Na interactions are worthy of further investigation. Breckle (1974, 1976) ascribed a possible functional role to the high Na content of *Atriplex confertifolia*, hypothesizing that it allows this species to take up soil moisture and carry on photosynthesis for a longer period through

the summer than can *Ceratoides*. The lower anionic concentrations he found may have been related to the bonding of cations by high amounts of organic acids (chiefly oxalic) in these chenopods (Wiebe and Walter 1972). How much this mechanism differs between the two species is unknown.

Mineral Content of the Ecosystems

Comparisons of mineral contents at the ecosystem level require multiplication of compartmental elemental concentrations by phytomass and soil bulk density to derive standing crops of minerals (mineralomasses, Duvigneaud and DeSmet 1975). Although this approach overlooks the seasonal variation in both mineral concentrations and phytomass, it allows a graphical comparison (Fig. 2) of the pools of the various minerals to be expected during midsummer. For most elements, the beginning of the growth period in spring is the time of highest mineral concentrations (Caldwell et al. 1971, West 1972, Breckle 1976) in new growth fractions. There is not as much seasonal variation in either the old growth aboveground phytomass or the mineral content of surface litter, belowground phytomass, and soil compartments (Caldwell et al. 1971, West 1972,

TABLE 6. Means and standard deviations of elemental concentrations (mg g^{-1}) in various components of an *Atriplex-confertifolia*-dominated ecosystem, Curlew Valley, Utah. Average of 1968, 1969, and 1970 samples. P = probability level at which a given value for *Atriplex* is different from that of *Ceratoides*.

| | C | N | P | K | Na | Ca | Mg |
|---------------|----------|----------|--------|------------|----------|-----------|------------|
| SHOOTS | | | | | | | |
| New growth | | 13.9±2.6 | 1.0±.2 | 21.5±1.1** | 8.1±.2** | 31.3±5.0† | 5.92±1.44† |
| Old growth | | 9.8±.8 | 1.0±.1 | 9.5±3.1 | 5.7±.7** | 18.2±5.4 | 3.56±1.00 |
| LITTER | | | | | | | |
| Fine | | 12.6±1.3 | 1.5±.2 | 3.0±.3 | 1.8±.2 | 15.7±.7 | 2.57±.21 |
| Coarse | | 10.0±1.0 | .9±.1 | 3.2±.5 | 1.9±.4 | 14.5±3.2 | 2.07±.67 |
| ROOTS | | | | | | | |
| 0-30 | | 16.7±1.3 | 1.5±.2 | 6.3±1.3 | 4.4±1.0† | 32.8±7.7† | 5.96±2.20 |
| 30-60 | | 17.2±2.0 | 1.6±.2 | 6.7±1.2 | 5.1±1.3 | 35.6±8.2† | 6.14±2.20 |
| 60-90 | | 18.8±2.3 | 1.8±.1 | 7.0±1.1 | 5.7±1.3 | 38.2±9.0† | 6.35±2.22 |
| SOILS | | | | | | | |
| 0-2 | 17.6±1.2 | 1.6±.6 | 1.1±.1 | 2.6±.5 | .9±.2† | 5.7±1.5 | .33±.05 |
| 2-30 | 8.4±1.0 | .8±.1 | .9±.2 | 2.7±.6 | 2.7±.9† | 5.3±1.1 | .27±.06 |
| 30-60 | 7.5±.7 | .6±.1 | .8±.1 | 1.8±.4 | 5.8±1.4* | 5.3±.7 | .39±.09 |
| 60-90 | 6.7±.7 | .5±.0 | .7±.1 | 1.2±.4 | 7.2±1.2* | 5.4±.9 | .60±.05 |

†P ≤ .3

‡P ≤ .15

*P ≤ .05

**P ≤ .001 Probability level at which the given value for *Atriplex* ecosystems differs from the parallel value for the *Ceratoides* ecosystem (Table 5)

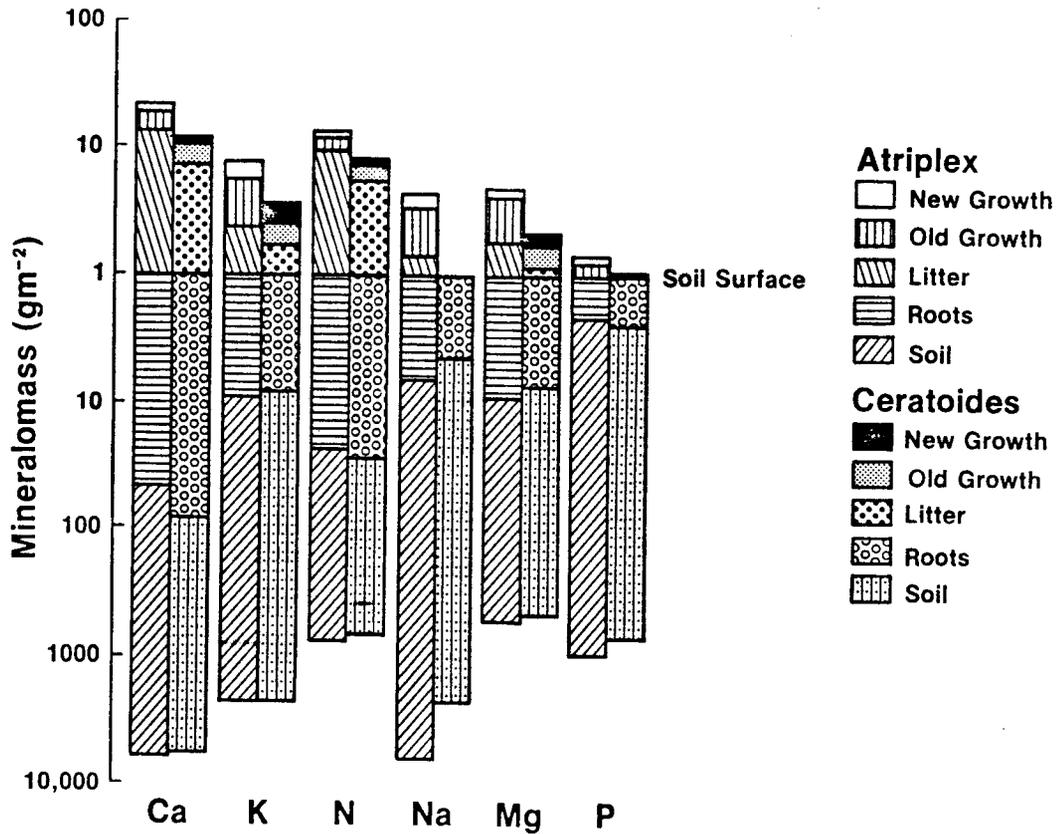


Fig. 2. Graphical comparison of mineral mass of various mineral elements in *Atriplex*- and *Ceratoides*-dominated ecosystems. Average of element concentration times average phytomass values for 1968, 1969, and 1970. Soil profile considered to a depth of 90 cm July 1968 only.

Breckle 1976). Nitrogen is an exception to the above generalization, which has been extensively discussed elsewhere (West and Skujins 1977, 1978).

Nearly equivalent pools of mineral elements were found in the two ecosystems. Carbon has been discussed elsewhere (Caldwell et al. 1977). Ca was the greatest contributor to the mineral mass of both ecosystems. The *Atriplex*-dominated ecosystem had slightly higher accumulations of Ca, but *Ceratoides* had more in new aboveground growth and plant tissue in general. There is less K accumulated aboveground, particularly in the new growth portion of the *Ceratoides* system. More nitrogen was accumulated in the *Atriplex* system. The soils of the *Atriplex* system also had more Na and distinctly more was incorporated into phytomass, making the differences the greatest of any of the elements studied. The *Atriplex* ecosystem had

the most plant-incorporated Mg and P, with the highest proportions in aboveground compartments. This is directly related to the small differential concentrations in aboveground and belowground fractions and the somewhat higher aboveground production of *Atriplex*.

Concentrations or pools tell us nothing definitive about nutrient availability. In fact, we know that much of the soil organic matter reserve is "bound" and may be entirely of microbial origin (Kang and Felbeck 1965). Nutrient turnover time for the aboveground portion of the system could be approximated by dividing litter by new growth phytomass (Table 4). To estimate nutrient turnover in the entire community, belowground production has to be estimated and heroic assumptions about community stability made. Although such calculations would have suggested which elements might be in critical

supply, we did not calculate them because of problems discussed above.

Another way of inferring which elements could be limiting is to look at the presence or absence of biological magnifications during the decomposition of fine litter compared to new growth (Charley 1977). Such an analysis can be used as a basis for separating the major minerals analyzed into two groups. N and P show increased concentrations in partially decomposed litter compared to new growth, whereas K and Na concentrations are less in litter compared to new growth. N and P remain in short supply in soil until they become excess metabolites in the absence of suitable high carbon substrates. K and Na are easily leached and are generally not needed in large quantities for decomposition processes. They also appear in excessive quantities as soluble soil salts.

Table 7 shows amounts of nitrogen and phosphorus taken up in annual shoot production in *Atriplex* and *Ceratoides* communities. These amounts are very small in comparison to total inventories. They are significant, however, when compared to amounts in easily decomposable high carbon substrates such as fine litter. When N in new growth was compared to N in litter, average turnover times of 4.6 and 6.8 years were computed for *Atriplex* and *Ceratoides*, respectively. These values compare closely to those computed on a phytomass basis (Table 4). Close monitoring of inorganic soil nitrogen supported this concept, showing gradual buildup of NH_4^+ and NO_3^- in the surface soil (Bjerregaard 1971). This is later carried into the rooting zone by significant rainfall (Osmond et al. 1980).

Carbon:nitrogen ratios can be used to determine the extent of decomposition of carbon-based substrates as mineralization occurs (West and Skujins 1977, 1978). *Ceratoides*

and *Atriplex* fine litter exhibit C:N ratios of 38.4 and 41.4, respectively. The *Atriplex* coarse litter C:N ratio is 46.5. C:N ratios in soil varied from 10.5 at the surface to 13.3 at 60–90 cm for *Atriplex*, and from 10.7 to 15.7 for *Ceratoides*. "Terminal" or steady state soil C:N ratios appear to be related to increasing soluble salt concentrations (Fig. 1), and maximum ratios occur at 60–90 cm depths.

Although these data and inferences are intrinsically interesting and valuable for related considerations such as animal nutrition, much remains to be done to discover what soil-held nutrients are limiting to plant growth in deserts once the primary constraint of available soil moisture is exceeded (West 1983). Further inferences as to which elements may act as secondary limiting factors can only be definitively stated after direct experimentation.

Since the *Atriplex*-dominated community is more productive than the *Ceratoides*-dominated community and has somewhat greater plant litter and microphytic crusts that stabilize the soil and fix more nitrogen (Bjerregaard 1971), we should not be concerned that the probable replacement of *Ceratoides* by *Atriplex confertifolia* on the sites studied (Dzurec 1981) will necessarily result in greater erosion. Although primary productivity is higher with *Atriplex*, its spines protect it from heavy livestock utilization. This appears to be a feedback mechanism protecting the land as well as the plants from individual damage.

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TABLE 7. Estimates of nitrogen and phosphorus uptake in aboveground production of *Atriplex*- and *Ceratoides*-dominated communities. Averages of 1968–70 production estimates were used.

| Nutrient | Community type | | | |
|------------|-------------------------|-------------------|-------------------------|-------------------|
| | <i>Atriplex</i> | | <i>Ceratoides</i> | |
| | mg g ⁻¹ D.W. | g m ⁻² | mg g ⁻¹ D.W. | g m ⁻² |
| Nitrogen | 14 | 1.2 | 12 | 0.8 |
| Phosphorus | 1.0 | 0.9 | 1.1 | 0.1 |

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