Comparative Nutrient Relations in Adjacent Stands of Chaparral and Coastal Sage Scrub[1]

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Abstract: Productivity and nutrient cycling parameters were measured in mature stands of chaparral and coastal sage scrub in the Santa Monica Mountains, California, USA. Net annual production and the magnitude of annual nutrient transfers were much greater in the evergreen chaparral. The chaparral had considerable stores of nutrients in wood biomass, low leaching rates, and a conservative and efficient use of most mineral elements. The drought-deciduous community was characterized by a high annual turnover of nutrients, high leaching rates, and considerable variation in foliar nutrient concentration during the year.

Several attributes of mediterranean-type ecosystems make them attractive systems in which to study plant nutrition, including low soil fertility, the predominance of sclerophylly, and the recycling of minerals by fire. Nutrient studies in these plant communities have traditionally focused on one or more of these attributes (e.g., Beadle 1966, Christensen and Muller 1975, Hellmers et al. 1955a, Specht and Groves 1966). However, our understanding of the complete nutrient cycle in mediterranean-type ecosystems is very limited, especially in comparison to forested ecosystems (Gray and Schlesinger 1981a). There is a conspicuous need for detailed studies of nutrient pools, transfers, and regulating processes in mature scrub communities.

In response to this situation, a nutrient study was conducted in the chaparral of southern California (Gray 1981). The goal of this research was twofold: (1) to quantify nutrient pools and annual transfers in the chaparral for several years; and (2) to compare and contrast the pattern of nutrient cycling and nutrient resource-use in two communities dominated by shrubs with different leaf types. The communities were evergreen chaparral and drought-deciduous coastal sage scrub, which are closely associated with one another in the coastal mountains of southern California.

SITE DESCRIPTION AND METHODS

The research site was located in the Santa Monica Mountains, 100 km north of Los Angeles, Calif., USA. Adjacent stands of chaparral and coastal sage were found at 150 meters elevation, 3 km inland. The two communities established after a fire 22 years ago on the same aspect, slope, soil, and rock formation (Gray 1981).

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It is generally recognized that coastal sage scrub and chaparral are distributed along a moisture gradient in the southern California mountains (Harrison et al. 1971, Mooney and Dunn 1970). The drought-deciduous growth form appears to be an adaptation to very dry, seasonal conditions, and is normally found at low elevations. At mid-elevations a mosaic may be formed as coastal sage species are replaced by evergreen chaparral, the well-known mediterranean-type sclerophyllous vegetation of California.

The chaparral community chosen for this study was a pure stand of *Ceanothus megacarpus*. This species establishes only by seed after a fire and forms dense, rapidly-growing stands with a closed canopy of 3-4 meters height (Schlesinger and Gill 1980). In contrast, the coastal sage stand was co-dominated by two shrubs, *Artemisia californica* and *Salvia leucophylla*. Other occasional species include *Yucca whipplei* and *Eriogonum parvifolium*, and scattered herbs and grasses (Gray and Schlesinger 1981b). The two "sage" shrubs establish by seeds and resprouting after a fire, and form a relatively low, open community that is essentially leafless during the dry summer months.

The standing biomass in each community was determined by harvesting large samples of each shrub species and forming dimension analysis regressions (Whittaker and Woodwell 1968). Net annual aboveground production was measured for the dominant species for two years. A random sample of each species was harvested monthly and the dry weight of all plant parts was determined. Net production was calculated as the sum of positive biomass increments during the year on an areal basis, using the "mean-tree" approach (Ovington and Pearsall 1957, Gray and Schlesinger 1981b). Litterfall was collected monthly for two years in randomly-placed trays beneath the canopy of both stands.

The nutrient pool in the standing vegetation was determined by standard analysis of all harvested tissues in the lab. Nitrogen was measured as total Kjeldahl-N with an ion-specific electrode (NH_4); phosphorus by an ammonium metavandate colorimetric technique; and the major cations by atomic absorption spectrophotometry (Gray 1981). Nutrient analysis of the monthly harvested tissues provided a measurement of annual nutrient accumulation.

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Nutrient return was measured as the nutrient content of the monthly litterfall, and the elemental content of throughfall and stemflow collections following the techniques of Eaton et al. (1973), using randomly-placed collectors.

STANDING BIOMASS AND NUTRIENT POOLS

The peak aboveground live biomass of the *Ceanothus* chaparral was greater than the coastal sage by a factor of six (Table 1). The biomass of these two stands represent the highest and lowest values of 14 mediterranean-type ecosystems from around the world as summarized in Gray and Schlesinger (1981a). Dead wood accounted for 15 and 21 percent of the aboveground biomass in the chaparral and coastal sage, respectively. The coastal sage had a greater proportion of its peak standing biomass in foliage than in the chaparral (Table 1). However, during the summer months of August and September, only 15-30 percent of the deciduous foliage biomass remains (Gray and Schlesinger 1981b).

In the coastal sage scrub, 39-42 percent of the total nutrient pool in the vegetation was present in the foliage. In contrast, this value was only 12-23 percent for all elements in the chaparral. The smaller allocation of nutrients to the foliage compartment in the chaparral is due in part to the large amount of wood accumulation, and to the low concentration of mineral elements in the evergreen foliage.

Unlike forest ecosystems, where 60-70 percent of the aboveground nutrient pool is stored in the litter layers (Lang and Forman 1978), a comparatively smaller nutrient pool was found in the litter of the chaparral and coastal sage (Table 1). Non-limiting elements such as calcium and magnesium accumulated in the litter layer, while potassium which is easily leached from litter by rainfall was only present in small quantities. The relative impoverishment of nitrogen and phosphorus in the litter layers may be a result of a greater retranslocation of these elements before abscission. Schlesinger and Hasey (1981) have shown that in chaparral ecosystems, rates of decomposition are relatively rapid, preventing the accumulation of large nutrient pools in the litter.

ANNUAL PRIMARY PRODUCTION AND NUTRIENT ACCUMULATION

In the mediterranean climate of southern California, both evergreen and drought-deciduous shrubs begin their aboveground growth soon after the winter rains (Mooney et al. 1977). This period of measurable growth varies for each species and from year to year. For the drought-deciduous shrubs, there is a 5-8 month period of leaf production, followed by a short period of flowering, and 2-4 months of drought dormancy (Gray 1981, Gray and Schlesinger 1981b). The evergreen shrub, *Ceanothus*, produces flowers and leaves in the spring, while woody increment may extend throughout the summer. The possession of evergreen foliage in *Ceanothus*

Table 1-- Peak aboveground standing biomass and nutrient pools in the chaparral and coastal sage.

	Dry Matter	Nutrient Pool				
		N	P	K	Ca	Mg
				g/m^2		
CHAPARRAL						
Live aboveground biomass	6482	40.8	2.8	16.0	33.5	4.2
Percent foliage	8	20	13	12	13	23
Community aboveground total[1]	9651	68.6	3.9	23.4	65.2	11.5
Percent litter layer	21	30	15	19	39	58
COASTAL SAGE SCRUB						
Live aboveground biomass[2]	925	5.5	0.7	5.6	4.1	1.0
Percent foliage[2]	12	39	39	40	42	39
Community aboveground total[1]	2034	12.5	1.5	9.2	15.0	5.1
Percent litter layer	30	37	26	20	60	60
MEDITERRANEAN-TYPE ECOSYSTEMS[3]						
Mean, aboveground biomass	3729	21.1	1.6	13.4	25.5	3.8

[1]Includes dead wood, litter layer mass, and biomass of subordinate species.
[2]Values for the dominant shrubs *Salvia* and *Artemisia* only.
[3]From Gray and Schlesinger (1981a).

Table 2-- Annual production, litterfall, nutrient accumulation, and nutrient return in the chaparral coastal sage. Values are a mean of two years.

	Dry Matter	N	P	K	Ca	Mg
				g/m²/yr		
ANNUAL ACCUMULATION[1]						
Chaparral	1056	13.11	0.74	4.61	7.39	1.38
Coastal Sage[3]	291	3.19	0.42	3.58	2.39	0.51
ANNUAL RETURN[2]						
Chaparral	801	7.30	0.32	4.06	9.54	1.77
Coastal Sage[3]	199	2.01	0.18	3.14	3.87	0.99

[1]Accumulation = peak nutrient content of annual production.

[2]Return = nutrient content of litterfall, throughfall, and stemflow.

[3]Values for the dominant shrubs, *Salvia* and *Artemisia* only.

allows for the potential of year-round photosynthesis (Gray 1981, Mooney and Dunn 1970).

The annual aboveground production was greater in the *Ceanothus* chaparral than in the coastal sage as shown in Table 2. In the chaparral, 52 percent of the production (1056 $g/m^2/yr$) was foliage, compared to 38 percent of the production (291 $g/m^2/yr$) in the coastal sage. Both communities allocated 50 percent of total production to twig growth and radial wood increment. This relatively high rate of wood accumulation in both communities is reduced partially by the death of attached stems, estimated at 74 and 20 $g/m^2/yr$ in the chaparral and coastal sage, respectively (Gray 1981).

Not surprisingly, nutrient accumulation in the annual production was greater in the chaparral (Table 2). Nutrient accumulation in *Adenostoma fasciculatum* (chamise), another evergreen chaparral dominant, appears to be much less than found in *Ceanothus*. Annual accumulation of nitrogen and phosphorus in a chamise community was only equivalent to that found in the coastal sage scrub (Mooney and Rundel 1979).

In both the chaparral and coastal sage, 60-70 percent of the annual primary production was returned in litterfall (Table 2). The majority of the annual nutrient return was contained in this litterfall; potassium is a notable exception because it is so easily leached from plant leaves (Tukey 1970). The time and magnitude of leaching by winter rains vary from year to year, but generally coincide with the appearance of new, nutrient-rich leaves on all the shrubs.

NUTRIENT RELATIONS

Foliar Concentrations

The concentration of mineral elements, particularly nitrogen and potassium, is usually lower in coniferous and evergreen foliage (van den Driessche 1974). For all the major elements, *Ceanothus* had a lower concentration than either *Artemisia* or *Salvia* as shown in Table 3. *Ceanothus megacarpus* had much higher values for nitrogen and phosphorus than reported in the needle-like leaves of *Adenostoma fasciculatum* (chamise), the most wide-

Table 3-- Mean elemental concentrations (pct. dry weight) in leaves of the dominant shrubs. Mean derived from 24 monthly collections, 8 samples per month; coefficient of variation in parentheses.

Species	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Artemisia californica	1.88 (29)	0.225 (29)	1.42 (33)	0.94 (25)	0.267 (19)
Salvia leucophylla	1.85 (31)	0.200 (30)	1.54 (44)	1.41 (16)	0.298 (19)
Ceanothus megacarpus	1.69 (12)	0.081 (20)	0.45 (22)	0.87 (12)	0.160 (12)

spread chaparral shrub in California (Mooney and Rundel 1979). Ceanothus also had moderately high concentrations compared to six other chaparral shrubs in San Diego County where nitrogen and phosphorus concentrations ranged from 0.91-1.61 and 0.06-0.13 percent, respectively (Mooney et al. 1977).

The nitrogen:phosphorus ratios in the drought-deciduous shrubs were between 8 and 9, while in Ceanothus, it was 20. The optimal ratio for productivity in many agricultural plants is between 15-20 (van den Driessch 1974). The high ratio in Ceanothus implies that nitrogen is probably not limiting at this site.

Symbiotic nitrogen fixation occurs in the genus Ceanothus (Delwiche et al. 1965), although no nodules were observed on the roots of the shrubs at the research site. Kummerow et al. (1978) suggest that nodulation of the roots of C. greggii in the chaparral is rare because of xeric soil conditions; they estimate that symbiotic nitrogen fixation contributes less than 0.01 $g/m^2/yr$ in the chaparral.

Thus, in comparison to the drought-deciduous species, and many other evergreen chaparral shrubs, Ceanothus appears to have a relatively high nitrogen requirement. It also appears that in the chaparral, Ceanothus may not depend upon nitrogen fixation to meet this requirement, although this suggestion deserves careful attention in the future.

The monthly variation of nitrogen and phosphorus concentration in the leaves of the three species is presented in Figure 1. This fluctuation is due primarily to the production of new, nutrient-rich leaves and the subsequent reduction in their concentration as they age. In the evergreen shrub, Ceanothus, the annual variation was lower; the coefficient of variation for all elements over two years was only 12-20 percent (Table 3). In Salvia and Artemisia, the concentration of elements in the leaves varied greatly throughout the year, depending primarily upon the season in which the leaves were produced. Coefficients of variation for the drought-deciduous shrubs ranged from 16-44 percent (Table 3).

Turnover Rates

Turnover rates of dry matter and nutrients are primarily a function of the magnitude of the standing biomass and the nutrient pools. In the high biomass chaparral, the percent of the total biomass returned to the environment each year was only 12 percent, compared to 22 percent in the coastal sage as shown in Table 4. In both communities, the order of nutrient turnover from fastest to slowest was Mg, Ca, K, N, and P. The essential elements nitrogen and phosphorus were both closely coupled to dry matter turnover. The nutrient turnover rates in the chaparral were twice that found in the coastal sage. The turnover rates of non-limiting elements, calcium and magnesium were very rapid in the coastal sage community.

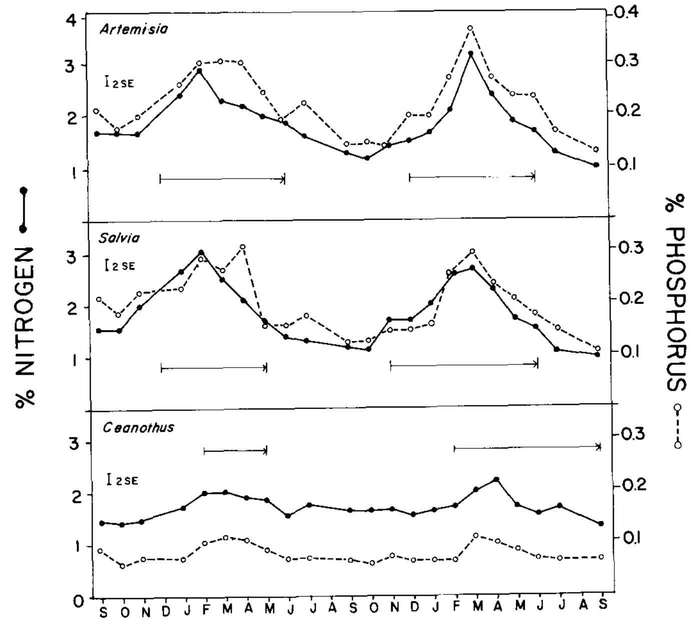

Figure 1--Monthly nitrogen and phosphorus concentrations (pct. dry weight) in the foliage of the dominant shrubs of the coastal sage and chaparral. The largest two standard errors for any month are shown. The spring period of leaf production is indicated by the lines with arrows.

Leachability

Plant foliage is subject to nutrient losses by leaching, although the magnitude differs depending upon the leaf morphology and the element in question (Tukey 1970). The leachability of each community, expressed as the total nutrient loss in throughfall and stemflow as a percent of the nutrient pool in the canopy (i.e., leaves and flowers) during the winter months is presented in Table 4. The coastal sage showed a high leaching rate for all elements: the leachability ratio was 2-3 times greater than in the chaparral. The overall rate of leaching in the coastal sage community was surprisingly high in light of the fact that the canopy was open and sparse. In contrast, the canopy of the chaparral was closed and over 50 percent of the incident precipitation was intercepted (Gray 1981).

Redistribution of Mineral Elements

Mobile mineral elements are translocated from leaves into living stems before abscission (Williams 1955). The extent of this recovery process varies, depending upon the plant species and the plant nutrient status (Chapin 1980). Clearly, in nutrient-limiting situations, greater redistribution would be of a selective advantage. Using the mass balance relationships defined by Turner et al. (1976), the amount of the annual nutrient accumulation provided by redistribution can be calculated for the species in the chaparral and coastal sage scrub. As presented in Table 4, only the

Table 4-- Elemental characteristics of the chaparral and coastal sage scrub. All values represent a mean of two years.

	Dry Matter	N	P	K	Ca	Mg
TURNOVER RATE[1]						
Chaparral	12	17	11	25	28	42
Coastal Sage	22	36	26	56	94	99
LEACHABILITY[2]						
Chaparral	-	3	0	41	17	29
Coastal Sage	-	8	0	76	54	59
REDISTRIBUTION[3]						
Chaparral	-	44	56	12	0	0
Coastal Sage	-	36	57	12	0	0
EFFICIENCY RATIO[4]						
Chaparral	-	86	1944	156	66	358
Coastal Sage	-	72	805	46	37	146

[1]Total annual nutrient return/nutrient pool in the standing biomass.
[2]Annual leaching losses/ leaf and flower nutrient pool during winter months.
[3]Percent of annual nutrient accumulation provided by retranslocated minerals.
[4]Annual dry matter production of leaves and flowers/annual nutrient return.

common limiting elements, nitrogen and phosphorus, were conserved to any significant degree. There was no redistribution of calcium and magnesium, the former being associated with cell wall deposition and not freely transported within the plant (Clarkson and Hanson 1980). Magnesium has a multiplicity of roles in plant metabolism and is relatively mobile. Any redistribution of magnesium may have been masked by the high leaching rate of this element, particularly in the coastal sage.

Although Ceanothus had a high nitrogen requirement and did not appear to be nitrogen-limited, the shrub showed a high dependency on internal sources of nitrogen and a great capacity for the storage of this nutrient. The redistribution values for Ceanothus can be compared to chamise, where redistribution of nitrogen and phosphorus has been estimated at only 24 and 46 percent, respectively (Mooney and Rundel 1979). Values reported for other wild plants in the literature range from 0-83 percent and no consistent relationship between growth form and redistribution ability is evident yet.

Efficiency Ratio

Nutrient-use efficiency can be defined in a variety of ways, depending upon which nutrient process of the plant being investigated (i.e., acquisition, transport, or utilization). On a community level, a production efficiency ratio can be defined as the annual production of dry matter per amount of mineral element returned to the environment each year. This is a composite index across the species in the community that incorporates production with nutrient uptake, accumulation, and loss (Gray 1981). To the extent that greater production leads to greater reproduction and/or longevity, this index may be a measure of the potential competitive abilities under nutrient-limited conditions.

For all the major elements, the evergreen shrub, Ceanothus, had a greater production efficiency (Table 4). This is particularly true for phosphorus, potassium, and magnesium. Ceanothus had a very low requirement for these three elements, and was less susceptible to leaching of the latter two nutrients than Salvia or Artemisia.

DISCUSSION AND CONCLUSIONS

Chaparral ecosystems are relatively short-lived because of recurring fires. Ecologists have traditionally thought that in the absence of fire, many chaparral communities become "senescent" (Hanes 1977). In these communities, it has been suggested that as more of the soil mineral resources are tied up in the vegetation and litter layer, production will become nutrient-limited (Rundel and Parsons 1980).

However, the present work indicates that in mature stands of Ceanothus chaparral and coastal sage, there is considerable net production and nutrient accumulation. The high foliar concentrations in the two drought-deciduous shrubs and in Ceanothus are equal to or greater than the levels in most chaparral shrubs (Mooney et al. 1977) and suggest no nutrient limitation. This conclusion is similar to that of Schlesinger and Gill (1980), who found no decline in foliar nitrogen concentrations in stands of C. megacarpus from 6-22 years near Santa Barbara, California.

With regard to the coastal sage scrub, there was considerable turnover of dry matter and nutrients each year; 26-36 percent of the standing nitrogen and phosphorus pools were returned annually to the soil. The stand was relatively productive and did not appear to be impoverished of mineral elements. This high rate of nutrient turnover and productivity implies that there may be a close coupling of nutrient release (i.e., decomposition and mineralization) and nutrient uptake by the plants. Drought-deciduous shrubs like Artemisia and Salvia are well adapted to form this type of nutrient cycle by virtue of their shallow roots (Hellmers et al. 1955b), rapid response to winter rains (Gray and Schlesinger 1981b, Harvey and Mooney 1964), and fast, inherent growth rates (Gray 1981).

The Ceanothus chaparral was more productive than the coastal sage community, and the magnitude of the nutrient transfers was considerably larger. Also, in contrast to the rapid turnover of nutrients in the coastal sage, the nutrient cycle in the chaparral was characterized by several important differences.

First, there were considerable stores of nutrient in the biomass of the chaparral. Therefore, only a small turnover of minerals occurred annually. Second, the evergreen shrub had low leaching rates, a high redistribution ability, and an efficient use of nutrients in the production of dry matter. These attributes of the evergreen shrub made it very conservative in its use of nutrients, particularly nitrogen and phosphorus. Third, because of the great extent to which Ceanothus used internal sources of nitrogen and phosphorus, it may have been less dependent upon soil nutrient availability during any given year compared to the coastal sage.

In the early development of a Ceanothus community the high nutrient-use efficiency may favor the rapid accumulation of biomass and nutrients typical of this species (Schlesinger and Gill 1980). This same conservative and efficient use of mineral elements in a mature stand may also permit the formation of a comparatively balanced and self-regulated nutrient cycle, which in turn may lead to the high rate of biomass accumulation found in these mature stands. The extent to which this nutrient cycle is characteristic of other evergreen chaparral communities is unknown and deserves future attention before management questions involving chaparral nutrient relations can be fully answered.

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