

Productivity and Nutrient Cycling in the Early Postburn Chaparral Species *Lotus scoparius*¹

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Nutrient circulation through the biomass of Southern California chaparral is most heavily influenced by frequent fires. The fire cycle of 20- to 40-year interval (Byrne et al., 1977) significantly disrupts the chaparral nutrient circulation (Gray & Schlesinger, 1981). Considerable quantities of nutrients, particularly carbon and nitrogen, are lost through volatilization and smoke during these frequent fires (DeBano and Conrad, 1978). The remaining nutrients are deposited on the soil surface as ash. These post-burn nutrients are in available forms subject to export from the community by leaching or by erosion (Christensen and Muller, 1975; DeBano and Conrad, 1978).

The nitrogen cycle is critical to the development of chaparral stands because chaparral soils tend to be poor in available nitrogen, and productivity of mature stands may be nitrogen-limited (Hellmers et al., 1955). Chaparral stands receive only limited inputs of nitrogen from atmospheric sources (1.0 kg of ha⁻¹ yr⁻¹, Schlesinger and Hasey, 1980) and nitrogen fixation (0.1 kg ha⁻¹ yr⁻¹, Kummerow et al., 1978). During a fire over 100 Kg ha⁻¹ of nitrogen can be lost by volatilization and an additional 15 Kg ha⁻¹ of nitrogen can be lost by erosion in the first year following a fire in a chaparral community with a biomass of 3000 g/m² (DeBano and Conrad, 1978). The nitrogen remaining on the site after volatilization is only a small portion of the nitrogen in a mature chaparral stand. Even though the total soil pool of nitrogen is large in chaparral regions, the concentrations of available soil nutrients below the surface ash are characteristically low. Since inputs of nitrogen into

Abstract: The frequent fires in southern California have a pronounced influence on many aspects of chaparral shrub communities, particularly nutrient relationships. Nutrient accumulation, and productivity were studied for the post fire species *Lotus scoparius*. This stand of *Lotus scoparius* was approaching maximum biomass yet there was significant net production and a large transfer of nutrients to the detrital compartment. These productivity and nutrient relationships suggest that early post-burn dominance by fast-growing deciduous perennials may be important for nutrient conservation following fire.

chaparral stands after a fire are small, the limitation of nitrogen export following a fire can be critical for later community development.

Deerweed was chosen for this investigation because of its ubiquitous distribution in southern California burn sites and because this species often dominates young post-burn chaparral regions. This investigation examined productivity and nutrient accumulation by deerweed in a four-year old post-burn site. The seasonality of productivity, phenology, and nutrient accumulation was evaluated, and a yearly nutrient budget was compiled for *Lotus scoparius*. These investigations were conducted to evaluate deerweed as a nutrient conserving agent in chaparral following fire. The nitrogen cycle in particular was investigated because of its critical influence on later community development.

SITE DESCRIPTION

A four-year-old post-burn site was chosen for this investigation in the Santa Ynez Mountains 10 km north of the Pacific Ocean near Santa Barbara, California. This was a southeast-facing slope of 15° at 800 m elevation. The soil texture was a sandy loam (65% sand, 25% silt and 10% clay) of sandstone parent material. Kjeldahl nitrogen content of the upper 10 cm was 1.6%, nitrate and ammonium ion concentrations were less than 1 µg.g⁻¹ dry weight, and organic matter was 8% by loss-on-ignition. Before the most recent fire in 1974 the site was dominated by *Adenostoma fasciculatum* (chamise). During this 1979 investigation, *Lotus scoparius* accounted for 40% cover and 22 other shrub species accounted for 45% cover. Annuals were of very low importance.

METHODS AND MATERIALS

Climatic measurements were made at 910 m elevation on a south slope 3 km east of the research site. Temperature and relative humidity were recorded with a hygrothermograph (Weather-measure Model H311) and rainfall was measured with a standard 8-inch rain gauge. Photoperiod

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was calculated as the number of hours with an irradiance greater than $100 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$.

A 0.5-ha plot was chosen in the center of the burn site and divided into 5 x 5 m quadrats. Three of these quadrats were randomly chosen to be used as permanent quadrats for phenology measurements. Within these permanent quadrats two to four canopy branches on each *Lotus scoparius* plant were labeled for phenological measurements. This resulted in 125 monitored canopy branches. Measurements of plant growth characteristics were made every two weeks from January 1979 to August 1979. Relative plant water relations were measured by determining predawn xylem pressure potential of *Lotus scoparius* at 2-week intervals on 25 canopy branches collected in the immediate proximity of the permanent quadrats.

Standing biomass and productivity were measured with a sequential harvest technique. Fifteen randomly chosen 1 x 1 m quadrats were harvested on five occasions from August 1978 to November 1979. All the *Lotus scoparius* plants were collected at ground level in each quadrat and the harvested quadrats were labeled to prevent resampling. Each harvest was separated into live wood, leaves, dead wood, and reproductive tissue, dried at 70°C in a forced air oven for 48 h, and weighed to obtain dry weight/area. Productivity was calculated from the increments in standing live biomass.

On each phenology sampling date, plant material was collected for tissue nutrient analysis. Five canopy branches were collected from 10 plants in each permanent quadrat. These were oven-dried at 70°C for 48 h and ground in a Wiley Mill. Phosphorus was determined by the molybdovanadate reaction and the cationic concentrations were determined by atomic absorption spectrophotometry (Likens and Bormann, 1970).

In addition, concentrations of nitrogenous compounds were analyzed in both dried and fresh samples. Immediately after milling, the dried samples were assayed for NO_3^- , NH_4^+ , and total (Kjeldahl) nitrogen. Nitrate was determined by the "known addition" technique (Orion, 1977) using a nitrate-specific ion electrode (Orion Model 93-07). Total free and exchangeable ammonium ion was measured with an Orion ammonia electrode (Model 95-10). Kjeldahl nitrogen (total nitrogen less NO_3^-) was extracted with a micro-Kjeldahl technique (McKenzie and Wallace, 1954). The concentration of nitrogen in the digest was measured with the Orion ammonia-specific electrode.

RESULTS

Climatic conditions during 1979 were characteristic for this region of southern California. Temperature gradually increased from a mean minimum of 4°C in January to a mean maximum

of 29°C in July (Figure 1). Along with the increase in temperature, vapor pressure deficit also increased to a maximum in July of 2.90 KPa. Rainfall began in December and continued through March resulting in a total of 37 cm. No precipitation occurred after March. The pre-dawn xylem pressure potential (a relative indication of water availability) increased to its least negative value in March indicating high moisture availability. After the precipitation stopped and the vapor pressure deficit began to increase, plant pre-dawn xylem pressure potential slowly decreased to the lowest value in August. These climatic data indicate low physiological stress from January to May and high physiological stress from June through August.

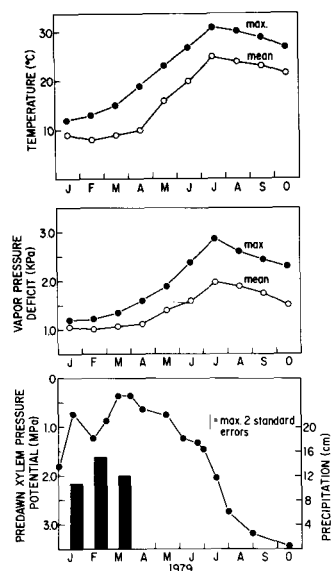


Figure 1. Climatic conditions for an elevation of 910 m in the Santa Ynez Mountains of southern California. Pre-dawn xylem pressure potentials are for a 4-year-old stand of *Lotus scoparius* subject to the represented climatic conditions.

One of the primary environmental cues for growth in deerweed is water stress (Nilsen and Muller, 1980a) as is shown by the phenology results (Figure 2). The number of leaves per branch is a general indication of the plants ability to capture carbon for biomass production in the absence of limiting environmental factors. The leaf number per branch increased to maximal values from May through June during the warmest period of the year (Figure 2).

Indexes of relative plant activity can be found through measurements of the rates of certain plant growth characteristics. The rate of leaf production indicates maximal plant activity in late February and May. The high leaf production rate in February is due to bud burst of many small leaves. Therefore maximum leaf production occurred during May. Similarly maximal shoot elongation

occurred during May and early June as well as maximal flower production. These relative indicators of plant activity point to May through June as the period of greatest plant growth. Leaf abscission occurred very synchronously during late June and early July when the dawn xylem pressure potential reached -2.0 mPa. Previous experiments with deerweed phenology indicated that -2.0 mPa is a critical predawn xylem pressure potential for leaf abscission (Nilsen and Muller, 1980b). All the phenology indices indicate a precipitous decrease in plant activity functions incident with hot and dry climatic conditions.

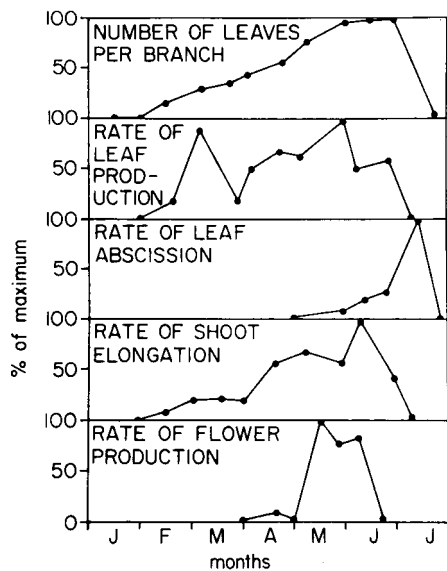


Figure 2. Phenological characteristics for a population of *Lotus scoparius* in the Santa Ynez mountains of Southern California, 1979.

The seasonal progression of biomass components (Figure 3) indicate a slow increase in biomass during the beginning of the growing season (January-March) followed by a sudden jump in deerweed biomass in May through June. The rapid increase in total biomass during May was due to the rapid increase in leaf biomass. Woody biomass increased at a constant rate from January through May. Following the dry season from July through October total biomass decreased to a value similar to the initial November biomass. The reduction in total biomass during the dry season is due to leaf fall and die back of the woody compartment. These data indicate that this 4-year old stand of deerweed is close to a steady state biomass condition where net production is similar to litter fall.

Primary production of deerweed at this research site was characterized by similar magnitudes of stem-wood and leaf production (Table 1). Production of reproductive tissues

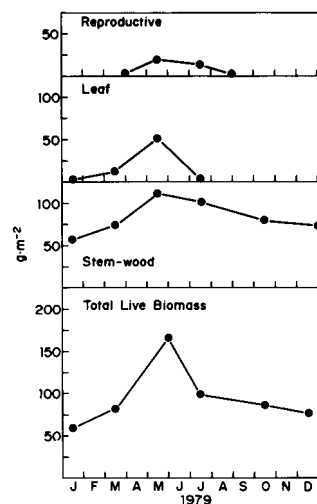


Figure 3. Seasonal changes in biomass components for a stand of *Lotus scoparius* in the Santa Ynez mountains of southern California, 1979.

was only one third that of stems and leaves. Detrital production (biomass of each component entering the litter layer) was a large portion of net production. All the leaf and reproductive biomass entered the litter layer in July and 28.5 OIL of stem wood died and entered the standing dead wood or the litter layer between July and October. This resulted in a small true increment of biomass equal to only 16.5% of net production (% retention in Table 1). The high productivity in relation to biomass results in a low biomass accumulation ratio. Indicating that the total biomass of this four-year-old (close to steady state) stand of deerweed can be turned over into the litter layer every 1.57 years.

Table 1. Net production characteristics of a 4-year-old post-burn *Lotus scoparius* population

Characteristic	Stem	Leaf	Fruit	Total
Max. Biomass (g/m ²)	105.6	42.1	16.7	164.4
Net Primary Production (g/m ² /yr)	45.7	42.1	16.7	104.5
Detrital Production (g/m ² /yr)	28.5	42.1	16.7	87.3
True increment (g/m ² /yr)	17.2	0.0	0.0	17.2
% Retention (g/m ² /yr)	37.6	0.0	0.0	16.5
Biomass accumulation ratio (years)	2.31	-	-	1.57

$$\text{Biomass accumulation Ratio} = \frac{\text{maximum biomass}}{\text{net primary production}}$$

$$\% \text{ Retention} = \frac{\text{True increment}}{\text{net primary production}} \times 100$$

Yearly seasonal nutrient concentrations are shown in Figure 4 on a leaf area basis. The specific leaf weight increased dramatically from May through June when the vapor pressure deficit was highest and the plants were enduring greater water stress. The increase in specific leaf weight had significant influences on all nutrient concentrations. In particular Ca, Mg, and K increased greatly during this specific leaf weight increase. Nitrogen and phosphorus were the only measured nutrients which decreased in concentration during January through April. This decrease in N and P indicates that these nutrients were being diluted in the biomass, therefore, accumulation of N and P from root and soil resources may be limited later in the growing season.

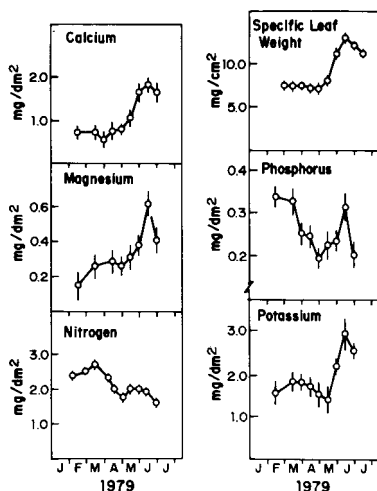


Figure 4. Seasonal concentrations of major nutrients in leaves of *Lotus scoparius* during 1979.

Stem nutrient concentrations show only small gradual seasonal nutrient changes. For this reason average nutrient concentration for stems and reproductive tissues are represented along with average leaf, deadwood, and abscised leaf nutrient concentrations (Table 2). Only winter concentrations of N in stems were significantly higher than summer concentrations. Also, nutrient content of deadwood was insignificantly different from summer stem nutrient concentrations. Abscised leaf concentrations of N, P, and K are significantly lower than the average leaf content on the plant, while calcium concentration is higher in abscised leaves. This indicates that significant reabsorption of N, P, and K may occur from pools of these nutrients allocated to leaves before leaf abscission.

Nitrogen components were investigated separately because nitrogen may be an important limiting factor in chaparral vegetation (Figure 5). Total protein decreased throughout the growing season in accordance with total nitrogen.

Table 2. Average nutrient concentrations in above-ground biomass components for *Lotus scoparius*

Component	Ca	K % oven-dry weight	Mg	N	P
Leaves	1.12 (0.17)	2.16 (0.15)	0.34 (0.05)	2.1 (0.54)	0.30 (0.06)
Abscised Leaves	1.53 (0.28)	1.30 (0.07)	0.46 (0.14)	1.0 (0.05)	0.07 (0.1)
Stem (summer)	0.38 (0.02)	0.75 (0.05)	0.12 (0.01)	0.85 (0.11)	0.09 (0.01)
stem (winter)	0.48 (0.04)	0.88 (0.10)	0.14 (0.01)	1.42 (0.24)	0.09 (0.01)
Dead wood	0.40 (0.02)	0.0 (0.05)	0.10 (0.01)	0.88 (0.10)	0.09 (0.01)
Flowers and Fruits	0.63 (0.20)	1.74 (0.20)	0.26 (0.06)	0.76 (0.25)	0.24 (0.06)

() = 2 standard errors.

Ammonium ion content remained unchanged until the leaf specific weight increased. The seasonal cycle of nitrate ion concentration contrasted with that of the other components. During the end of the growing season nitrate increased in concentration more than the increase in specific leaf weight. Nitrate concentration in abscised leaves was higher than leaves in July even though

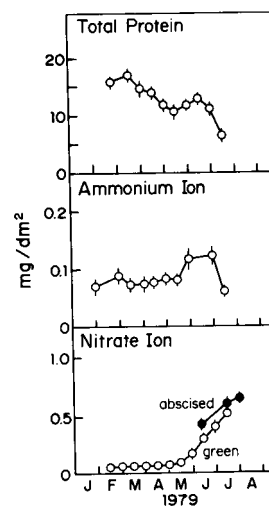


Figure 5. Seasonal concentrations of nitrogenous compounds in leaves of *Lotus scoparius* during 1979.

the specific leaf weight of abscised leaves was lower than that of the leaves on the plant in July.

The ability of *Lotus scoparius* to accumulate nutrients in above-ground biomass and litter is an important part of this investigation. Table 3 represents the combination of net primary productivity and tissue nutrient concentration; yielding nutrient accumulation characteristics for this stand of *Lotus scoparius*. Accumulation of nutrients by this stand are lower than accumulation rates of local chaparral and coastal sage communities (Gray and Schlesinger, 1981a; Schlesinger and Gill, 1980) but they are higher than a stand of chamise chaparral (Mooney and Rundel 1979) which had a far greater biomass. The true increment of nutrients for *Lotus scoparius* at this site was low in all cases and the detrital production of nutrients was a large part of the total accumulation. Only P, N, and K had a percent retention in standing biomass close to 50% of the yearly accumulation. The less mobile Ca and Mg had very low retention in the standing live biomass.

Nitrogen and phosphorus are thought to be critical limiting factors for chaparral development (Hellmers et al., 1955) and large amounts of these nutrients are lost from chaparral following fire (DeBano and Conrad 1978). Therefore, a nitrogen and phosphorus budget has been composed for this stand of deerweed (Figure 6). Flux rates (transfers between compartments) for N and P were large in comparison to the pool size of each compartment. For example the N accumulation ratio in above-ground parts (biomass N-pool/N accumulation) was 1.78 years indicating that the above ground N-pool is replaced rapidly. Also, 0.65gm⁻² of nitrogen was introduced as litter into the chaparral system and 41% of the accumulated nitrogen was transferred into the roots at the end of the growing season. This nitrogen and phosphorous budget then indicates

Table 3. Net production, maximum pool size, true increment, and total detrital production for dry weight and nutrients in a 4-year-old stand of *Lotus scoparius*.

Nutrients and units	Net primary production and nutrient accumulation				True increment	Detrital	% Retention
	stem	leaf	fruit	total			
Dry Weight (g/m ² /y)	45.7	42.1	16.7	104.5	17.2	87.3	16.5
Ca (g/m ² /y)	0.18	0.49	0.11	0.78	0.07	0.69	12
R	0.35	0.94	0.29	1.58	0.13	0.86	46
Mg	0.07	0.15	0.04	0.26	0.03	0.21	19
N	0.41	0.84	0.13	1.38	0.16	0.75	53
P	0.02	0.13	0.04	0.19	0.08	0.09	53

N and P Budget for *Lotus scoparius* (4 year old stand) (g·m⁻²)

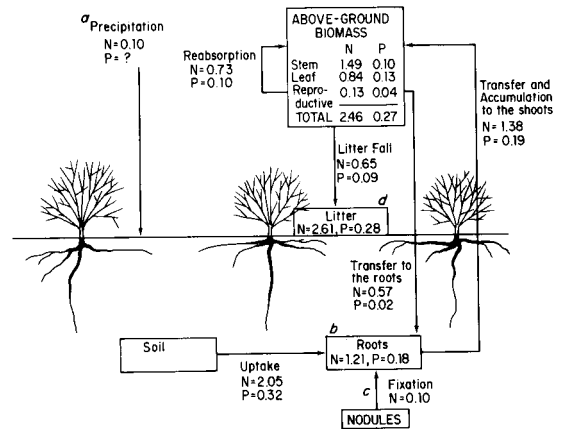


Figure 6. Nitrogen and Phosphorus budget for a stand of *Lotus scoparius* in the Santa Ynez Mountains of southern California, 1979. a = data from Schlesinger & Hasey 1980; b = Root biomass calculated from a lab derived Root to Shoot Ratio; c = data from Kummerow et al. 1978; d = assuming a litter residence time of 4 yr.

a nutrient cycle with short residence time in biomass components but considerable nutrient uptake from the environment.

DISCUSSION

The phenology, productivity, and nutrient accumulation data presented in this investigation clearly indicate that maximal plant activity occurs during the latter part of the growing season. Although the initial plant activity of deerweed occurs in February most productivity and nutrient accumulation occurs in May through June. Nitrogen and phosphorus are the only nutrients which indicate an initial accumulation in February through March and a dilution in the biomass during the maximum productivity period. High productivity during the late growing season is closely associated with increasing temperatures. Although deerweed has favorable water relations characteristics early in the growing season only limited productivity occurred during the period of low temperatures. Temperature has previously been found as a factor speeding physiological functions in deerweed (Nilsen 1980a).

There have been only few investigations of productivity and nutrient accumulation in southern California chaparral (Mooney and Rundel 1979, Schlesinger and Gill 1980, Gray & Schlesinger 1981). In these studies, chamise productivity ranged from 362 to 67 g · m⁻² · yr⁻¹, *Ceanothus* productivity was 850 g · m⁻² · yr⁻¹ with considerable year to year variation, aril coastal sage productivity was 255 g · m⁻² · yr⁻¹. These productivity values are greater than that of *Lotus scoparius* (105 g · m⁻² · yr⁻¹) but

Lotus scoparius is a small shrub (biomass = 164 g m^{-2}) in comparison to chaparral shrubs ($2,127 \text{ g m}^{-2}$ Mooney and Rundel to $7,506 \text{ g m}^{-2}$ Cray and Schlesinger 1981b) and coastal sage scrub ($1,417 \text{ g m}^{-2}$ Cray & Schlesinger 1981). Lotus scoparius also has a shorter growing season (3-4 months) in comparison to chamise chaparral (6-8 months, Mooney and Rundel 1979) and coastal sage scrub (4-6 months, Gray & Schlesinger 1981). Taken together, the productivity, biomass and growing season data from this investigation indicate that this early post-burn shrub rapidly replaces its biomass with newly accumulated tissues. The low biomass accumulation ratio (BAR) for this stand of deerweed (1.57) in comparison to other chaparral communities (BAR = 3 to 10, Cray & Schlesinger 1981h) further supports the rapid replacement of biomass.

Nutrient circulation in a community with rapid biomass turnover, such as this 4-year old burn site, should also have high nutrient flux rates from the environment to the detrital layer. These high flux rates in comparison to nutrient pool sizes were found in Lotus scoparius (Figure 5). Therefore, even though deerweed has a small biomass in relation to other chaparral shrubs the rapid nutrient cycling fluxes in stands of Lotus scoparius can accumulate considerable quantities of nutrients from the environment in standing biomass and litter. This capacity to accumulate nutrients following fire may be particularly important for nitrogen and phosphorous. The ability of Lotus scoparius to grow in high density after fire, the high nutrient uptake and flux rates, and the potential N-fixation ability of deerweed all point to the importance of nutrient accumulation by Lotus scoparius in latter chaparral community development. Lotus scoparius is particularly suited for rapid nutrient accumulation because of its deciduous phenology and high productivity in relation to biomass. Post-burn annuals are of lesser importance to nutrient accumulation following fire because they only have short term residence following fire due to germination requirements. Young evergreen species are also of lesser importance because their density is lower and growth rates are slower than that of the deciduous perennials in early post burn environments. Even though the quantitative importance of Lotus scoparius as a nitrogen source (by fixation) has yet to be evaluated, the role of Lotus in the conservation of mobile nutrients may be very important to later community development in southern California chaparral.

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