BIOGEOCHEMICAL CYCLING IN ANNUAL GRASSLAND ECOSYSTEMS[1]

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INTRODUCTION

Factors controlling biogeochemical cycling in annual grasslands are generally the same as in perennial plant-dominated ecosystems. An important difference, however, is that most annual herbaceous vegetation (except seeds) dies at the end of each growing season. Thus, herbaceous vegetation in the annual grasslands does not internally recycle and store nutrients from one season to the next. As a result, amounts of nutrients entering and leaving vegetation are large compared to other systems (Cole et al., 1968; Rosswall, 1976; Bormann et al., 1977; Clark, 1977; Likens et al., 1977; West and Skujins, 1977; Woodmansee et al., 1978). Most nutrients in the current year's vegetation are derived from direct mineralization of plant and soil microorganism residues.

The discussion in this paper is limited to factors controlling cycling of nitrogen (N), phosphorus (P), and sulfur (S). Sufficient quantitative data are not available on potassium (K), calcium (Ca), molybdenum (Mo), and

TABLE I

Ranges of annual outputs, inputs, and distribution of N, P, and S in annual grassland system. We assume C to N to P to S ratios of 60:9:1:0.5.

Inputs, outputs, and distribution	N (kg·ha⁻¹)	P (kg·ha⁻¹)	S (kg·ha⁻¹)
Belowground			
Inert	—	6,000–12,000	100
Organic	2,000–5,000	1,500–3,500	750–1,750
Mineral available	1–10	1–20	1–10
Roots	20–80	2–8	2–15
Microbes	10–40		
Aboveground			
Plant tops	35–80	2–35	2–4
Herbivores	2–12	1–10	0.1–0.6[a]
Dung and urine	10–50	0.7–25	0.5–12.0
Carnivores		0.15–15	
← Leaching and runoff	13–63	0–0.5	1–20
→ Rain	3.0–10.0	0.04–0.5	1–20
→ Fertilizer		← as desired →	
→ Feed supplements	0–100	0–12	0–6
← Animal products	2–20	0.2–4	0.1–2
→ N fixation	5–50	—	—

[a] 0.2 to 0.9 sheep·ha⁻¹.
← Losses.
→ Gains.

other micronutrients for complete discussion of their cycling. We will discuss the sources of N, P, and S available to plants and the mechanisms for their loss from the soil-plant system, by tracing and attempting to quantify the pathways of these elements through some representative annual grassland ecosystems.

NITROGEN

Nitrogen is an element that frequently limits growth of herbaceous vegetation in annual grasslands, even in dry years (Martin, 1958; McKell et al., 1960; Duncan and Reppert, 1961). Production of vegetation often responds directly to additions of N from natural processes (fixation of N_2) or from fertilization. In many locations symbiotic N fixation was enhanced by addition of P and S (Martin, 1958).

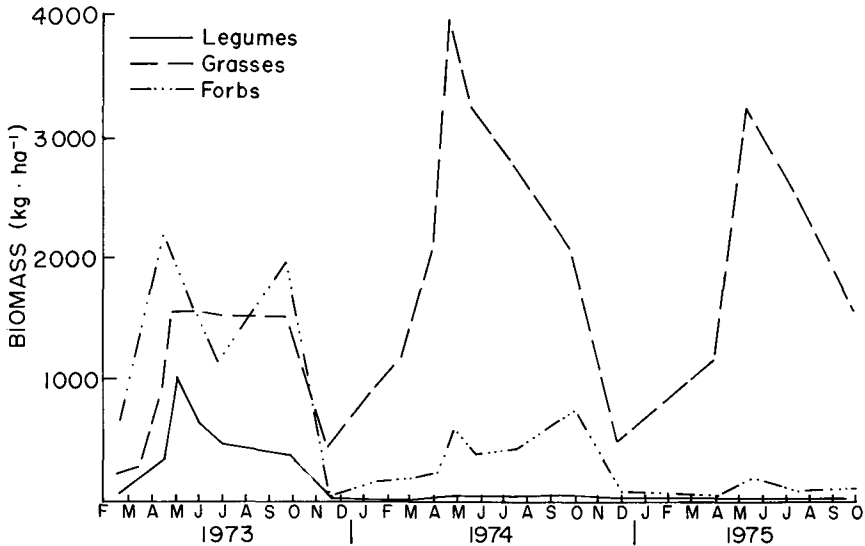Nitrogen is a very dynamic element, having several gaseous phases

Fig. 1. Nitrogen budget for a representative ungrazed pasture for the 1973–1974 growing season at San Joaquin Experimental Range. (a) Relative values for A, B, C, and D are unknown, but combined they apparently add to 39 kg $N \cdot ha^{-1} \cdot yr^{-1}$. (b) For this figure we assumed that E was zero because the flow could not be estimated, but some amount of A probably would be reabsorbed by the plant canopy and that amount would be subtracted from uptake by tops. (c) Steady-state assumption applied to yield a value of 6 kg $N \cdot ha^{-1} \cdot yr^{-1}$. (d) After Junge (1958) and Woodmansee (1978). (e) These flows were not estimated by Woodmansee and Duncan (1978) and would depend on management practices. (f) The value for litterfall is the amount that fell before the next growing season (1974–1975). F represents an unknown amount that fell and was mineralized during the growing season. (g) The value for root death is the amount that died after peak standing crop. F represents an unknown amount that died and was mineralized during the growing season. (h) The bulk of this flow was drained from plant material produced the previous year.

and a very mobile anion, NO_3^-, in solution. The N cycle is "open," meaning that inputs and losses may be relatively large (Odum, 1969). Values of N inputs, outputs, and distribution that can be expected in a broad range of annual grassland ecosystems are shown in Table I. Actual values for any one system in any single year depend on amount and timing of precipitation, abundance of legumes in both current and preceding years, degree of utilization, and fertilization, to name only a few important controlling factors.

Important components and transfers of N in a representative annual grassland ecosystem adjacent to the San Joaquin Valley in a nonextreme year are shown in Fig. 1; pertinent biomass data used to develop Fig. 1 are in Table II and Fig. 2 (from Duncan and Woodmansee, in preparation). The budget represents movement of N during a complete growing season, from seed germination through vegetation death by desiccation.

Organization of components of the nitrogen submodel of the annual

Fig. 2. Biomass dynamics of legumes, grasses, and forbs other than legumes in an ungrazed pasture at the San Joaquin Experimental Range. The principal winter and spring vegetation germinated in mid-November 1972, mid-October 1973, and early November 1974. Death of vegetation occurred from early to mid-May each year.

grassland simulation model is shown in Fig. 3 (Pendleton et al., submitted). Components of the conceptual models are arranged differently because of different research objectives and assumptions (Figs. 1 and 3). However, some interesting inferences about dynamics of ecosystems were gained from the simulation model and will be discussed.

Sources of Nitrogen

Nitrogen that can be utilized by organisms, especially vegetation, can originate in several ways: from direct addition of mineral N as NH_4^+ and NO_3^- by wet deposition in rain or by dry deposition in dust and aerosols; from symbiotic and nonsymbiotic fixation; from mineralization of soil organic matter of dead but discernible plant, microbial, and animal matter; from direct uptake of ammonia (NH_3) by foliage and soils and subsequent conversion to NH_4^+; and from fertilizer. Generally, the relative contribution of each of these sources is not precisely known but undoubtedly varies with time and place. Available evidence indicates non-symbiotic fixation to be on the order of 1 kg $N \cdot ha^{-1} \cdot year^{-1}$ (Delwiche and Wijler, 1956).

Atmospheric deposition.—According to Hutchinson (1944), the sources of combined N in atmospheric precipitation are soil, the ocean, fixation of N in the atmosphere, industrial and agricultural activities, and urban

TABLE II

Distribution of biomass (kg·ha⁻¹) near "peak standing crop" in 1973, 1974, and 1975 and for two subsequent dates in 1973 and 1974 following death of the principal vegetation in an ungrazed annual grassland ecosystem (after Duncan and Woodmansee, in preparation).

Vegetation	1973			1974			1975
	1 May[a]	21 May[b]	27 Jun[c,d]	25 April[a]	21 May[b]	10 July[c]	12 May[a]
Aboveground parts							
Grasses[e]	1,540	1,550	1,450	3,950	3,040	2,800	3,240
Forbs[f]	2,000	1,590	1,380[g]	590	370	400	170
Legumes[h]	1,030	650	470	30	20	10	20
Subtotal	4,570	3,790	3,300	4,570	3,430	3,210	3,430
Roots (live and dead)	7,570	6,210	7,590	6,260	5,650	7,020	4,450
Litter (including seeds and some shattered root crowns)	1,740	3,340	2,980	1,570	4,520	3,860	—[i]
Total	13,880	13,340	13,870	12,400	13,600	14,090	—[i]

  [a] All living.
  [b] Living and dead.
  [c] All vegetation dead except summer annuals.
  [d] 0.2 cm rainfall, 26 June.
  [e] *Bromus mollis, Bromus rigidis, Festuca* spp., miscellaneous grasses.
  [f] *Erodium* spp., miscellaneous forbs.
  [g] Includes about 250 kg·ha⁻¹ summer annuals above ground and we assume a similar amount below ground.
  [h] *Lotus purshianus, Trifolium* spp., miscellaneous legumes.
  [i] No data for 1975.

areas. The relative importance of these sources is unknown and varies with location. In fact, very large differences in NH_4^+ and NO_3^- concentrations in precipitation have occurred at different locations in California (Junge, 1958).

Nitrate measured in rainfall at the Hopland Site in northern California for 2 years totaled 1.25 kg·ha⁻¹ for the 1973–1974 season and 0.78 kg·ha⁻¹ for 1972–1973, an average of 1.0 kg·ha⁻¹·yr⁻¹ (Jones et al., 1977). Nitrogen returned as ammonia in rainfall generally exceeds that returned as nitrate by a factor of two (Allison, 1965). Thus, total input of N in rainfall at Hopland would be about 3 kg N·ha⁻¹·yr⁻¹. Based on midcontinent data, $NH_4^+{:}NO_3^-$ ratios were estimated to be 1; this would result in an input of 2 kg N·ha⁻¹·yr⁻¹ at Hopland, where pollution effects are minimal
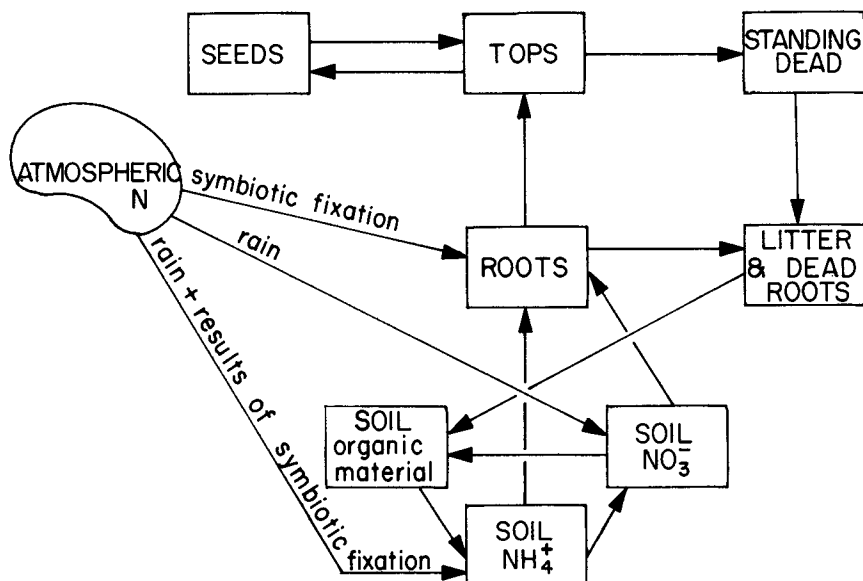
Fig. 3. Box and arrow diagram of the N submodel of the annual grassland ecosystem model ELMAGE (from Pendleton et al., 1978).

(Woodmansee, 1978). Adding 25% to the adjusted data[2] of Junge (1958) to account for dry deposition (Robinson and Robbins, 1968), we estimated that inputs to the Hopland Site were about 2 to 3 kg $N \cdot ha^{-1} \cdot yr^{-1}$ and to the San Joaquin Experimental Range (SJER), about 5 to 10 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 1). The higher values at San Joaquin result largely from pollution from agricultural and urban sources (Junge, 1958). These amounts would account for 1% to 3% of the N taken up and leached from a good range land soil in 1 year at Hopland (Jones et al., 1974) and for about 5% to 10% at San Joaquin. These percentages are quite low compared to the potential contribution of N from the atmosphere to systems dominated by perennial vegetation (Rosswall, 1976; Likens et al., 1977; Woodmansee et al., 1978).

Direct absorption of NH_3 from the atmosphere by foliage has been studied extensively by many workers (Hutchinson et al., 1972; Porter et

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[2] Concentrations of N ions were averaged for 3-month periods: January–March; April–June; July–September; and October–December (Junge, 1968). Fertilization of cropland and biological activity generally start in March in the Central Valley of California; therefore, we used March precipitation data with April–June NH_4^+ concentration data to calculate the upper limit of the values presented.

al., 1972; Denmead et al., 1976). The work of the last two groups, with plants of agronomic importance, indicates that plants may be a natural sink for atmospheric NH_3; furthermore, amounts of N received by this pathway may constitute a significant portion of the crop's total N intake. In highly productive Australian grasslands with large inputs of N from *Trifolium subterraneum* L., significant amounts of NH_3 were lost from the soils; but most of this gas was absorbed by the foliage as it diffused through the plant canopy (Denmead et al., 1976), suggesting that plant foliage is capable of absorbing significant quantities of N from the atmosphere. This pathway is probably significant, though wholly unquantified, in grasslands of North America.

Studies conducted in cultivated fields in New Jersey (Malo and Purvis, 1964; Hanawalt, 1969) showed that soils are capable of absorbing NH_3 from the atmosphere and that absorption depends on N content of the atmosphere, soil type, temperature, and velocity of air movement across the soil surface. Organic matter at or near the surface could fix NH_3 from the atmosphere (Mortland, 1958), but whether this process is of consequence in annual grasslands is unkown.

Symbiotic N fixation.—The abundance of N-fixing plants, mostly of the legume family (Leguminosae), in the annual grassland varies widely from place to place and from year to year. Botanical composition was determined for 11 grazed pastures in California, extending from Los Angeles County in the south to Tehama County in the north, where fertilizer trials had been made (Jones et al., 1961). The percentage of legumes varied from <1 to 16. The pastures having the higher percentages of legumes had been sown to a mixture of *Trifolium hirtum* All. and *T. subterraneum* L. Nine unsown, unfertilized pastures varied from 0 to 13%, with an average of 4%, legumes. In natural ungrazed range at peak standing crop at the San Joaquin Experimental Range, legumes were 23% in 1973 and <1% in both 1974 and 1975 (Table III; Duncan and Woodmansee, in preparation). Several other studies have indicated that if P and S levels are adequate, increases in the clover component are striking; total amounts of up to 70% have been measured (Jones, 1964).

If grasses and legumes must compete for nutrients, grasses are favored because their fibrous root systems absorb nutrients more efficiently. Thus, if N levels are adequate for luxuriant grass growth, legumes may be suppressed by shading (Stern and Donald, 1962). From the San Joaquin data (Woodmansee and Duncan, submitted), we infer that the good legume year, 1973 (with coincident N-fixation), may have resulted in natural "fertilization" of grasses, and consequently poor legume growth, in 1974 and 1975 (Fig. 2). As N levels become inadequate for vigorous grass growth, legumes, being able to fix N from the atmosphere, may have the advantage, especially if levels of P, S, Mo, and perhaps other nutrients

TABLE III

Contribution of legumes to biomass and N in the aboveground portions of annual grassland ecosystems in 1957 at Hopland (Jones, 1964) and 1973 at San Joaquin (Woodmansee and Duncan, submitted).

Month	Total biomass (kg·ha⁻¹)		Total N (kg·ha⁻¹)		Legume biomass (%)		Legume N (%)	
	Hopland	San Joaquin	Hopland	San Joaquin	Hopland	San Joaquin	Hopland	San Joaquin
March	910	1,800	24	38	31	10	43	20
April	2,330	3,390	57	51	31	9	53	20
May	3,530	4,570	66	65	51	23	73	40

are adequate to supply legume needs. We can see a striking similarity between these annual grassland ecosystems and the lake ecosystems described by Schindler (1977). He reasoned that in systems able to fix carbon and nitrogen, the element limiting productivity may be P or some micronutrient.

The amount of N fixed by legumes also varies from year to year and from site to site (Jones, 1963; Woodmansee and Duncan, submitted). Table III shows typical late-season growth of legumes and the resulting increased rate of N-fixation. Even though the contribution by legumes was considerably larger at Hopland than at San Joaquin in the years compared, in both cases this group of plants made substantial contributions to N budgets of both systems. Much of the N thus fixed becomes available to other plants and microorganisms the following year.

If we assume that the N in legumes was fixed by them[3] and that root N occurs in the same proportion as top N, we can conclude that legumes fixed 53.9 kg·ha⁻¹ in the 1972–1973 growing season at San Joaquin Experimental Range (Table IV; Woodmansee and Duncan, submitted). By contrast, 2.5 and 0.9 kg N·ha⁻¹ were fixed in the 1973–1974 and 1974–1975 seasons, respectively. In another study, Jones (1967) found that uptake was 230 kg N·ha⁻¹ on plots with substantial *T. subterraneum* fertilized with P and S in a wet year, but only 85 kg N·ha⁻¹ in a dry year. Grass contribution in this study was not separated. Williams et al. (1977) estimated that vigorous stands of field-grown annual legumes fixed 99 kg N·ha⁻¹ annually.

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[3] Certainly, legumes will draw from soil solution reserves to fulfill their N requirements. However, we assume that growing legumes also contribute N to the soil system by root sloughing and exudation during growth. Thus, lacking precise information, we assume that uptake from the soil solution is balanced by losses by sloughing and exudation, resulting in a net exchange of zero.

TABLE IV

Distribution of N (kg·ha⁻¹) near "peak standing crop" in 1973, 1974, and 1975 and for two subsequent dates in 1973 and 1974 following death of the principal vegetation in an ungrazed annual grassland ecosystem. Soil organic N was about 3,185 kg N·ha⁻¹ and was assumed unchanged during the 3 years of the study. Ammonium and nitrate were sampled during April 1974 and, combined, totaled 1.2 kg·ha⁻¹. We assume all available N in the system is tied up in discernable plant material. (After Woodmansee and Duncan, submitted.)

	1973			1974			1975
Vegetation	1 May[a]	21 May[b]	27 June[c,d]	25 April[a]	21 May[b]	10 July[c]	12 May[a]
Aboveground parts							
Grasses[e]	17.9	7.6	4.3	36.0	12.3	11.2	34.1
Forbs[f]	20.8	10.4	8.2[g]	6.1	2.3[h]	2.4[h]	1.5
Legumes[i]	26.3	7.6	3.7	1.1	0.3	0.2	0.4
Subtotal	65.0	25.6	16.2	43.2	14.9	13.8	36.0
Roots (live and dead)[j]	68.1	56.8	68.3[g]	56.3	50.8[h]	63.3	39.5
Litter (including seeds and some shat-tered root crowns)	19.2	63.2	46.4	14.0	43.3	42.8	—[k]
Total	152.3	145.6	130.9[g]	113.5	109.0	119.9	

[a] All living.
[b] Living and dead.
[c] All vegetation dead except summer annuals.
[d] 0.2 cm rainfall, 26 June.
[e] *Bromus mollis, Bromus rigidis, Festuca* spp., miscellaneous grasses.
[f] *Erodium* spp., miscellaneous forbs.
[g] Includes 7.2 kg·ha⁻¹ in living summer annuals, of which we assume 7.0 are new growth, since peak standing crop and some of its source of N may be from deeper soil strata than that sampled. We further assume that a smaller amount, maybe 2.0 kg·ha⁻¹, is in new root growth. Also, after the "peak standing crop" sampling, there was some additional legume growth. Thus, when the 172.3 value is adjusted to account for summer-annual and late-season legume growth, the amount of N tied up in the system before death and after death is identical, indicating little if any is lost from senescent plant material.
[h] Includes a small amount of summer annual growth. This growth is sufficient to account for increase, presuming our estimates are precise.
[i] *Lotus purshianus, Trifolium* spp., miscellaneous legumes.
[j] Roots are assumed to contain 0.9% N (after Clark, 1977; Woodmansee et al., 1978, 1978b).
[k] No data for 1975.

In a lysimeter study by Jones et al. (1974), a *T. subterraneum* grass mix yielded 180 kg N·ha⁻¹. Grass growing alone yielded 50 kg N·ha⁻¹, giving an apparent 130 kg N·ha⁻¹ fixed by the clovers, not counting the roots. The apparent N fixed by a *T. hirtum* grass mixture was 60 kg

$N \cdot ha^{-1}$. The apparent fixed N leached in their study was 7 and 5 kg $N \cdot ha^{-1}$ from the *T. subterraneum* grass and *T. hirtum* grass mixes, respectively. These values are 4-year averages, indicating that legumes make an important contribution and that, in terms of uptake relative to the amount of N leached, this N is very efficiently used.

Clearly, legumes can be an extremely important source of N in the ecosystem. They not only contribute substantially to the yield in some years but also fix N. To fix N_2 effectively, however, rhizobia are needed in adequate numbers. When new legumes, such as *T. subterraneum,* are introduced, large *Rhizobium* populations must be introduced with the legume seed. Resident rhizobia often infect these introduced plants but are ineffective as N-fixers on them. Introduced clovers will not survive without effective N-fixing root nodules; but with high populations of effective rhizobia they are much more productive than native species.

As indicated in the foregoing discussion, legumes growing in annual grasslands can add significant amounts of N to the soil-plant systems by fixation of N_2.

Fertilization.—From 1% to 2% of the annual rangeland of California was fertilized with N each year (Wagner and Jones, 1968). The amount of N applied depends on economic relationships, climatic conditions, government policy, and desires of individual ranchers. Grazing studies were carried out over a wide area of annual grasslands of California, over a 5-year period (Martin and Berry, 1970). This work indicated that for each kilogram of N fertilizer applied in the fall, meat production increased 1.5 kg during the winter and spring. Furthermore, N fertilizers were most effective where rainfall was 400 to 650 mm. Nitrogen should be applied in the fall in the form of ammonium to reduce leaching. Nitrogen broadcast before the first fall rains resulted in more winter forage than when applied later (Jones, 1960). Pasture fertilized with 70 $kg \cdot ha^{-1}$ is usually ready for grazing about 6 weeks earlier than unfertilized pasture. Where needed, phosphorus and S should be applied with N to maximize benefits from N. The later N is applied in the growing season following first fall rains, the less effective it is in stimulating winter forage production.

Use of N induces important changes in the botanical and chemical composition of the pasture. Increase in production results mainly from increased growth of grasses and broad-leaved plants, such as *Erodium* spp. When fertilized with N, these species generally grow rapidly during the first part of the growing season, crowding out the less competitive legumes. All annual grassland species grow most in spring, but under N-deficient conditions legumes grow relatively more than other species in spring, when both moisture and temperature are favorable.

Protein level in plants is generally increased by N fertilization during winter and early spring. This is not particularly beneficial for grazing

animals, since protein levels are adequate without applications of N during this period. As the season advances, protein levels drop more rapidly where N has been applied. Thus, at the end of the growing season, protein levels where N was applied the previous fall are usually equal to or less than protein levels in unfertilized grass. Crowding out of legumes by grasses also lowers protein content of the forage. An exception to this rule is that when rainfall is insufficient, moisture limits plant growth early in spring. Under these conditions, fertilized plants mature with higher levels of protein than unfertilized plants (McKell et al., 1960). Also, application of N in spring has increased the protein level in mature forage but has not substantially increased dry matter production.

Nitrogen, being more subject to leaching in areas with annual rainfall >650 mm, is made even less desirable in those areas because highly productive stands of clover are relatively easier to establish with high rainfall.

Supplemental feeding.—When and where practiced, supplemental feeding of livestock is probably an important N input to grassland ecosystems. Using Katznelson's (1977) P data and assuming a N:P ratio of 9:1, we have determined that supplemental feeding could contribute up to 100 kg $N \cdot ha^{-1}$. A more complete discussion of our assumptions is given in the phosphorus section.

Losses of N from the Ecosystem

Nitrogen can be lost from ecosystems by runoff either in solution or in sediments, by leaching of NO_3^- through the soil profile and below the rooting zone, by volatilization of NH_3 or of N_2O and N_2 following denitrification, and by removal of plant and animal products. Ammonium ions can also be fixed in the crystal lattices of clay minerals, but we have no data for this process and assume it to be inconsequential. Actual and relative values of these losses are extremely difficult to measure; but, as with sources of N added to the system, they probably vary greatly with time and place.

Loss of N in runoff.—Losses of N in runoff from lysimeters were practically nil (Jones et al., 1977). Losses from fields have not been measured directly but seem to be minor, since erosion is negligible except under very unusual circumstances, such as when soil has been disturbed by cultivation or trees have been removed. In general we estimate that the losses of N by runoff or soil erosion are negligible on the annual grasslands of California.

Loss of N by leaching.—Nitrate levels tend to increase in the absence of living roots during summer, even though soils are dry. Evolution of CO_2 from soils continues throughout the summer, though at reduced rates

(Coleman and Pigg, in preparation). This evolution indicates microbial activity and the possibility of nitrification. With the first fall rains, ammonification of organic matter increases rapidly and nitrification may occur; thus, NO_3^--N may be lost from the soil-plant system by leaching.

Germination of annual plants is quite rapid after the first fall rains. After germination, plants have a great propensity to absorb mineral N, and there is some evidence that nitrification may be inhibited by actively growing plants (Clark and Paul, 1970). Consequently, NO_3^--N decreases to base levels in groundwater and outflow streams after a first flush of leachate has passed, usually by January or February (unpublished data from Hopland).

We have some evidence that N lost by leaching can be substantial, depending on amount and distribution of rainfall. Leaching occurred at SJER some years but not others, while at Hopland it would be unusual not to have some leaching every year (Williams et al., 1964). In one lysimeter study, about 70 kg $N \cdot ha^{-1} \cdot yr^{-1}$ was leached over a 4-year period (Jones et al., 1974). This value is probably high because lysimeters tend to intensify the leaching process; however, these facts do indicate that leaching losses, which occur mostly in November and December, can be substantial.

Gaseous losses.—A 3-year study indicated that when ^{15}N was applied to a pure grass stand, virtually no volatilization or denitrification occurred during the winter months on a well-drained soil (Jones et al., 1977). However, when 500 kg $N \cdot ha^{-1}$ was applied to a pure stand of *T. subterraneum,* loss by volatilization of NH_3 or by denitrification was substantial, providing some evidence that there is a potential for N loss. Because no losses occurred where 100 kg $N \cdot ha^{-1}$ was applied to grass, they may not be a serious problem where soils are well drained.

During some wet seasons substantial areas of the annual grasslands can be saturated with water for several weeks, creating anaerobic conditions conducive to denitrification. Even on hilly land there is evidence of anaerobic conditions, as indicated by extensive mottling in soils; however, estimating the amount of N lost by denitrification under a wide range of conditions is impossible at this time.

Apparently, gaseous losses of N compounds from grazed pasture can constitute a large part of the N turnover in a grazing system (Denmead et al., 1974). They state that N input to leguminous pastures by symbiotic N fixation varies with plant species and growing conditions, but annual amounts of from 100 and 200 kg $N \cdot ha^{-1}$ have often been reported. In addition, rain adds small quantities of N, which Denmead et al. (1974) estimated at about 5 kg $N \cdot ha^{-1} \cdot yr^{-1}$. Of these, about 50 kg $\cdot ha^{-1}$ remain in the soil and the equivalent of about 20 kg $\cdot ha^{-1}$ remain in the animals. Thus, annual loss of N from the system is often about 100 kg $\cdot ha^{-1}$, an

average of 0.27 kg $N \cdot ha^{-1} \cdot day^{-1}$. This value matches almost exactly measurements made of NH_3 and other N compounds above a grazed pasture at Canberra, Australia.

Losses to animal and plant products.—Dean et al. (1975) and Woodmansee (1978) estimated that 17% of the N ingested by steers was retained in the tissues of the growing animals. Thus, loss of N from pastures by export of the animals represents a loss from the ecosystem, but that loss is totally controlled by factors that influence stocking rates (i.e., forage production, grazing pressure, and season of grazing).

The amount of N contained in pasture herbage will vary widely, depending on the site selected, time of year, amount of rainfall, botanical composition, and soil fertility. Many annual grassland soils produce about 2,500 kg dry matter $\cdot ha^{-1}$. If this herbage were about 2% N, it would contain about 50 kg $N \cdot ha^{-1} \cdot yr^{-1}$. Hence, in the example cited, there was about 66 kg $N \cdot ha^{-1}$ at Hopland (Jones, 1963). Table IV shows the amount of N in the herbage at the San Joaquin site for 3 years. In Oregon, Dawson (1974) found that a S-deficient pasture yielded about 79 kg $N \cdot ha^{-1}$, but when the pasture was fertilized with P, S, and Mo, the value rose to 213 kg $N \cdot ha^{-1}$. Dawson (1974) also found no yield response from applied N when ryegrass was grown in pots containing soil from pastures stocked at 10 ewes $\cdot ha^{-1}$ for 12 years. Furthermore, the yield and N content of ryegrass grown on this soil were significantly higher than those of ryegrass grown on the same soil without grazing, indicating the extent of the impact of the grazing animal on available N in the soil. Dawson (1969) estimated that dung and urine excreta would likely return 167 kg$\cdot$ $ha^{-1} \cdot yr^{-1}$.

A fattening animal may excrete >90% of N ingested; a dairy cow, about 75% (Walker et al., 1954). In a 1-year Australian study Merino sheep (assumed to be in nutrient balance) on annual pasture ate 454 kg of dry matter (Barrow and Lambourne, 1962). This feed had an average composition of 3.2% N. Of the 15 kg of N consumed, 3.8 kg was excreted in the feces and about 0.45 kg was used in the production of wool. Thus, about 10.7 kg, or 70% of the ingested N, was excreted in the urine. In a trial using Romney wethers, 70% of the total excreted N was in the urine and 30% in the feces (Sears and Newbold, 1942). Availability of the N in the feces was unquestionably low (return of dung alone gave no increase in yield of grasses), and the amount mineralized and utilized by plants during 1 year is very small. Barrow (1961b) found that the amount of N mineralized from feces was closely related to N content of the feces. Because feces were more resistant to decomposition than was plant material, a smaller proportion of N was mineralized from the feces than from plant material. According to Doak (1952), on the other hand, about 90% of urine-N is urea and amino-N, all of which may be assumed to be

immediately available to plants. However, workers in Australia found that from 50% to 80% of urea-N could be volatilized as NH_3 under dry, warm conditions (Watson and Lapins, 1969; Barlow, 1974). Such conditions may occur often in California during spring, summer, and fall.

Nutrients are transferred from the pasture to bedding grounds. Studies with sheep in Australia indicated that 22% of the feces were deposited on 3% of the area and 34% were deposited of 10% of the area (Hilder, 1964). We have no data on the distribution of urine, but we presume its distribution is similar to that of feces.

For example, if a pasture where N uptake by plants was 66 kg· $ha^{-1} \cdot yr^{-1}$ were stocked at a rate to return 75% of this N, 50 kg N·ha^{-1} would be returned to the pasture by the animals. On the 90% of the pasture receiving 66% of the excreta, only 33 kg N·ha^{-1} would be returned. Of this, about one-third, or 11 kg, would be in the feces and relatively unavailable during the year, leaving 22 kg N·ha^{-1} in the urine. Of this, from 11 to 18 kg·ha^{-1} would be volatilized, leaving 4 to 11 kg for plant growth. Using slightly different assumptions, Woodmansee (1978) calculated that losses of N from the San Joaquin Site, if grazed during the growing season, were 11 kg·ha^{-1}.

Losses from herbage.—In *T. subterraneum*, N loss from standing herbage began with seed set (Lapins and Watson, 1970). In the annual grass *Bromus mollis* the loss began at flowering and continued until senescence. Nitrogen lost from herbage may be translocated to fruit and seeds, leached by rain and dew, and volatilized as NH_3 to the atmosphere. The litter values in Table IV indicate that much of the N in the aboveground biomass was in seeds, which fell when plants became senescent. The litter also probably included some roots that shattered immediately below the soil surface and were collected as litter rather than with the root cores (Woodmansee and Duncan, submitted). When ground-up plant material was added to soil on which grass was growing, from 19% to 74% of the N in that material could not be accounted for in the soil or in the uptake by grass and was presumed to be lost by volatilization and by leaching (Watson and Lapins, 1972).

The distribution of N in an ungrazed pasture at the San Joaquin Site at peak standing crop and soon after most plants had died is given in Table IV. About 20 kg N·ha^{-1} were lost from the entire system within 2 months after peak standing crop in 1973, but no significant amount was lost in 1974; in fact, a slight increase was noted. Woodmansee and Duncan (submitted) inferred from the information of Lapins and Watson (1970) that losses noted in 1973 were caused partly by volatilization of NH_3 from legumes, while in 1974 losses were not observed because of the dominance of grasses and the lack of legumes. Nitrogen in plant material at peak standing crop was 25% less in 1973 than in 1974. Plant-

available N losses were probably caused by a combination of leaching, volatilization of NH_3, and possibly an accretion of soil organic matter.

Transfers of N within Ecosystems

Mineralization of slowly cycling soil organic matter (humus).—Analysis of four soils from 22 sites near Hopland in 1976 showed that N concentrations in the A horizon ranged from 0.10% to 0.55% and in the B horizon from 0.04% to 0.19%. Ranges in bulk densities of the two horizons were 1.25–1.75 and 1.45–1.75, respectively; and total N in the two horizons varied from 230 to 4,250 kg·ha^{-1}. There was as much variation within soil types as between soil types. The Awahnee soils of the San Joaquin Experimental Range were about 0.09% N in the surface–10 cm, 0.03% N in the next 38 cm (A12 horizon), and 0.01% N in the B horizon (15 cm). Average bulk density was 1.3 in, and 1.4 below, the A11 sub-horizon (Woodmansee and Duncan, submitted). Thus, there were 3,185 kg N·ha^{-1} at the San Joagquin Site (Fig. 1). If we assume an average turnover time of 500 years, we can calculate a steady-state input of N for any 1 year. The 500-year turnover time is a crude estimate based on the fact that although much of the soil humus has an estimated turnover time of several thousand years (Allison, 1973), other fractions have much faster turnover times (Clark, 1977). Thus, the range of input values at the Hopland Site is about 0.5 to 8.5 kg N·ha^{-1}, while the value at San Joaquin is 6.4 kg N·ha^{-1}. However, if we assume that the system is approximately in steady state, then an equal amount of humus must be synthesized each year and the net contribution would be zero. Actually, we view this N pool as a large, slowly cycling buffer that in some years may contribute a net amount of N to the active system and in other years may immobilize more N than it contributes (Woodmansee, 1978).

Mineralization of actively cycling nitrogen in organic matter.—Actively cycling organic N is defined as discernible plant and animal fragments whose N turnover times are a few years or less. Annual turnover rates for litter and dead roots were estimated to be 77% and 79%, respectively (Duncan and Woodmansee, in preparation; Woodmansee et al., submitted). Thus, using data from Table IV and assuming that all N in the aboveground parts became litter, Woodmansee and Duncan (submitted) calculated that the size of the litter compartment decreased by 5 kg·ha^{-1} between 1973 and 1974 and that 70 and 56 kg N·ha^{-1} for litter and roots, respectively, were mineralized in 1974. From the 1974 crop, 43 and 44 kg N·ha^{-1} for litter and roots, respectively, were made available for the 1974–1975 growing season (Fig. 1, Table IV). Thus, empirically, the greatest proportion of mineral N made available in native annual grasslands apparently came from the previous year's plant material.
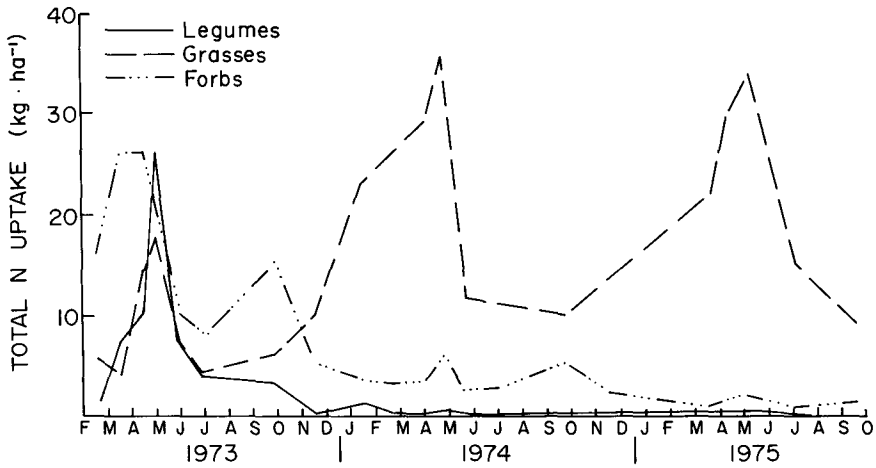
Fig. 4. Nitrogen dynamics of legumes, grasses, and forbs other than legumes in an ungrazed pasture at the San Joaquin Experimental Range. The principal winter and spring vegetation germinated in mid-November 1972, mid-October 1973, and early November 1974. Death of vegetation occurred from early to mid-May each year.

Data from CO_2-evolution studies in the San Joaquin soils (Coleman and Pigg, in preparation) support the following sequence of mineralization processes in annual grasslands. Following the first rains in fall, microbial populations proliferate, utilizing the rich carbon sources of tops and roots. Immobilization of N probably occurs immediately after initiation of microbial growth, but as fall and winter progress, microbial N requirements are satisfied and mineralization of N commences. Microbial activity remains surprisingly high throughout the winter, suggesting that mineralization processes are also occurring. At that time N becomes available for utilization by plants but also becomes vulnerable to loss by leaching, runoff, and volatilization. In late winter and early spring, as temperatures increase, microbial activity increases, then continues at high rates until summer drought again reduces microbial activity to low levels (but not to zero).

Uptake of N by plants.—Curves illustrating the annual dynamics of N in aboveground material at SJER imply a period of rapid N uptake after germination associated with rapid decomposition of dead organisms and mineralization of N from residues of the previous season (Fig. 4). This burst of activity occurs when both temperature and soil water are adequate to support growth of organisms. After this initial burst the rate of uptake declined because of lower winter temperatures. Uptake during this period of slow growth came from N mineralized during the first

growth phase and from that released by mineralization during the winter. We postulate that if temperatures are not too low, substrate is relatively easy to decompose and mineralize by microorganisms and plant biomass is large enough to continue to accumulate N. Thus, curves resembling those for 1973–1974 result (Fig. 4), showing that the rate of uptake was appreciable during winter periods. By contrast, when these conditions are not met, curves representing uptake may resemble those in 1974–1975 (Fig. 4). In these instances, growth started early; material easily decomposed and mineralized may have been utilized before the onset of winter; and winter temperatures were lower, resulting in depressed uptake rates during winter. Similar patterns of uptake occurred with simulation modeling studies (Pendleton et al., submitted).

After the period of depressed uptake rates of winter, both the data and model showed a period of rapid N uptake associated with rapid growth of vegetation and high decomposition and mineralization rates as temperatures rose in spring (Fig. 4; Pendleton et al., submitted). After the vegetation matured, seeds fell to the ground and the N content of the standing vegetation rapidly decreased. The increase of N in the summer of 1973, and to a lesser extent in 1974, resulted from growth of summer annual plants, which may obtain water and N from below the rooting zone of the spring vegetation (Duncan and Woodmansee, in preparation). Much of the vegetation remained standing following death until the fall rains (Fig. 4).

We cannot construct similar curves for roots, because we do not know their N concentrations at the various stages of growth. Thus, our estimates of uptake by roots are quite empirical (Fig. 1).

Total uptake by plants at SJER during the 1973–1974 growing season was estimated to be about 87 kg $N \cdot ha^{-1}$ (Woodmansee and Duncan, submitted). Results from the simulation model indicated somewhat higher uptake by plants. The simulation model probably describes the real dynamics better than the empirical data because the model accounted for death, litterfall, and rapid mineralization of plant-material N during the growing season. We have no data from which to estimate these processes, especially during the rapid growth phase of vegetational development. The data and model descriptions disagree because, during this phase of growth and N uptake, decomposition processes are also optimal; thus, young, succulent vegetation that dies because of suppression by more vigorous plants can quite conceivably be decomposed, mineralized, and have their nitrogen recycled very rapidly (i.e., between standard field sampling periods).

Litterfall.—Nitrogen stored in aboveground parts returns to the soil surface as litter and seeds. We have used data combining dead plant parts and seeds because the two components were not separated during sam-

pling (Woodmansee and Duncan, submitted; Fig. 1 and Table IV). How-
ever, seeds may represent a large proportion of the total N that falls in
organic material.

To illustrate this situation, we assumed that all standing plant matter
at peak standing crop in 1973 was the amount that fell to the soil surface
as litter for the 1973–1974 growing season (Fig. 1; Woodmansee and Dun-
can, submitted). Using the simulation model, we estimated somewhat
higher amounts of litterfall (50%) because the model accounted for plant
death and litterfall during the growing season (Pendleton et al., submit-
ted). We believe that the data of Woodmansee and Duncan are a minimum
estimate of litterfall, while the model response may be high but not un-
reasonable (Pendleton et al., submitted; Woodmansee and Duncan, sub-
mitted).

Root death.—Data from Woodmansee and Duncan (submitted) sug-
gested the amount of N contained in live roots at peak standing crop (Fig.
1). As with litterfall, they assumed that the amount of N transferred to
dead roots was the amount contained in the roots at peak standing crop
of the previous year. We assume that that estimate is minimal because
it does not account for intraseasonal death.

We did not use simulation model results here because the model for-
mulation was highly empirical, because of our ignorance of root dynam-
ics.

Annual variation.—The study of Woodmansee and Duncan (submitted)
illustrated the realities of annual variation in N dynamics (Fig. 4 and
Table IV). Following the large amount of N fixation the first year, the
system apparently declined, as discussed. Uptake of N by plants also
declined appreciably following the high fixation rate the first season. Ap-
parent losses of N from the system are not well understood, although
some combination of losses by leaching, volatilization, or immobilization
into recalcitrant soil organic matter may have been responsible. We be-
lieve this kind of variation is the rule rather than the exception.

Utilization of herbivores.—The study of Woodmansee and Duncan
(submitted), summarized in Figs. 1 and 4 and Tables II and IV, is used
here to represent typical N dynamics in an annual grassland ecosystem
ungrazed by domestic herbivores. Certainly, grazed pastures would vary
somewhat from the pasture represented, depending largely on intensity
of grazing, season of grazing, or class of animal (Fig. 1). However, the
fundamental differences would be changes in botanical composition due
to grazing and in transfer rates between some of the aboveground com-
ponents, perhaps increased losses of N by volatilization of NH_3 from
urine and feces, and some horizontal movement of minerals by ungulates.
Fertilization would alter the supply of N to plants, microbial populations,
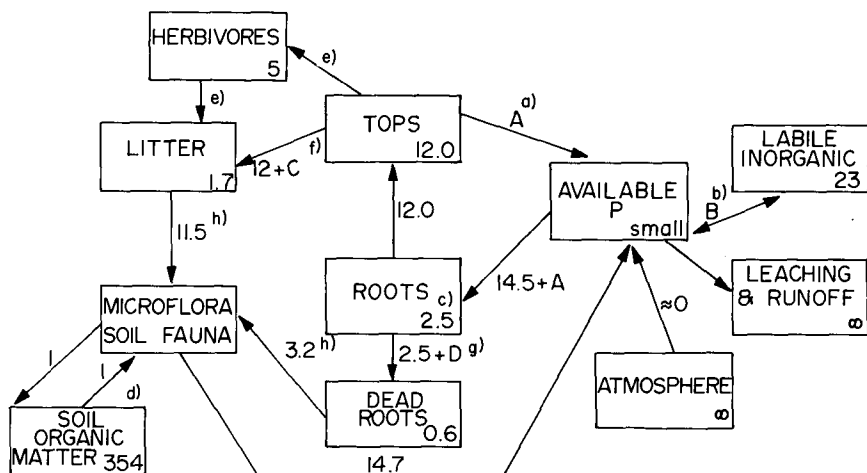and animals.

Fig. 5. Phosphorus budget for a representative ungrazed pasture for the 1973–1974 growing season at San Joaquin Experimental Range. (a) We cannot estimate these values but assume that P leached out of the canopy is reabsorbed and recycled to younger, growing tissues in the canopy. (b) Relative contribution of the labile inorganic pool to growing plant parts is unknown empirically. (c) Roots are assumed to contain 0.5% P (C. V. Cole, personal communication). (d) Steady-state assumption. (e) Depends largely on management practices. (f) Value for litterfall was the amount that fell before the next growing season (1974–1975). C represents an unknown amount that fell and was mineralized during the growing season. (g) Value for root death is the amount that died after peak standing crop. D represents an unknown amount that died and was mineralized during the growing season. (h) The bulk of this flow was derived from plant material produced the previous year.

PHOSPHORUS

Phosphorus, an element in short supply in some annual grassland ecosystems (e.g., Hopland) but not in others (e.g., SJER), is an essential element, is relatively nonmobile in forms available to organisms, and has no gaseous phases. As a result, it tends to exist in relatively constant amounts in any given ecosystem over periods of years. It cycle is relatively closed (Odum, 1969); however, amounts allocated to the various components of the system may vary from year to year.

Amounts of P in components of annual grassland ecosystems vary greatly (Table I). Distribution at peak standing crop and estimates of annual flows of P for one growing season at one site (SJER) are shown in Fig. 5. We assume that production at the SJER is not limited by P (Woodmansee and Duncan, submitted). Distribution of P for peak standing crop in 1973, 1974, and 1975 and two subsequent sampling dates in 1973 and one date in 1974 are given in Table V. As with N, we will discuss the source and magnitude of inputs and losses of P and the intrasystem pathways and magnitude of transfers within the SJER ecosystem.

TABLE V

Distribution of P (kg·ha⁻¹)near "peak standing crop" in 1973, 1974, and 1975 and
for two and one subsequent dates, respectively, in 1974 and 1975 following death
of the principal vegetation in an ungrazed annual grassland ecosystem for 1973,
1974, and 1975 (after Woodmansee and Duncan, submitted).

	1973			1974		1975
Vegetation	1 May[a]	21 May[b]	27 June[c,d]	24 April[a]	21 May[b]	12 May[a]
Aboveground parts						
Grasses[e]	3.6	2.5	1.7	10.0	4.9	8.0
Forbs[f]	2.5	2.4	1.4[g]	1.9	1.0	0.5
Legumes[h]	4.0	0.8	0.6	0.1	0.1	0.1
Subtotal	10.1	5.7	3.7	12.0	6.0	8.6
Roots (live and dead)[i]	3.8	3.5	3.8[g]	3.1	2.8	2.2
Litter (including seeds and some shattered root crowns)	2.4	6.9	6.8	1.7	6.5	—[j]
Total	16.3	16.1	14.3[g]	16.8	15.3	—[j]

[a] All living.
[b] Living and dead.
[c] All vegetation dead except summer annuals.
[d] 0.2 cm rainfall, 26 June.
[e] *Bromus mollis, Bromus rigidis, Festuca* spp., miscellaneous grasses.
[f] *Erodium* spp., miscellaneous forbs.
[g] Includes about 2 kg·ha⁻¹ in living summer-annual growth that was not present at last
sampling (24 April). Source of the P may be below 30 cm in the soil. Also included is P in
plants that grew following April sampling and died before late May.
[h] *Lotus purshianus, Trifolium* spp., miscellaneous legumes.
[i] Roots are assumed to contain 0.05% P (C. V. Cole, personal communication).
[j] No data for 1975.

Assumptions used to develop the P budget were the same as those for
the N budget, except for the following.

(1) Normal inputs and outputs of P are very small.
(2) A relatively large pool of labile inorganic P exists and is in rapid
    equilibrium with solution or available P.

The key point to be emphasized about the P budget is that adequate P
was available in dead plant material from the preceding year (1973) to
support new plant growth during the 1973–1974 growing season (Fig. 5).
We assumed that living plant material contained more P in the 1972–1973
season than in the 1971–1972 season. The 1971–1972 growing season
yielded relatively low amounts of plant material because of drought (D.
A. Duncan, personal communication). We presume that the source of the

additional P was the labile inorganic P pool, which is an important buffering component of the system (Cole et al., 1977).

Sources of Phosphorus

Natural sources of P available to organisms are from atmospheric deposition, both wet and dry. Some P is made available by weathering of soil minerals, but this source is probably trivial. The largest portion of available P is that cycled from the mineralization of soil organic matter and discernible plant, microbial, and animal material. Anthropogenic sources of P are fertilizer and supplemental feeds for domestic animals.

Atmospheric deposition.—The contribution of dust to the annual grasslands of California is probably insignificant in most instances. Rain can contribute from 0.04 to 0.5 kg $P \cdot ha^{-1}$, according to Katznelson (1977). We have made no direct measurements for dust or rain as the source of P.

Inputs from primary minerals.—Inputs of P to grassland ecosystems from weathering of primary minerals are considered to be very small (Cole et al., 1977; Katznelson, 1977); we assume that they are trivial over short periods of time (several years).

Fertilization.—The amount of P added by fertilization is determined by the rancher. Current recommendations range from 10 to 50 kg $P \cdot ha^{-1}$ on very P-deficient virgin land, with about 10 kg $P \cdot ha^{-1}$ applied as a maintenance dose biennially. Fertilization can drastically change the uptake of P. In one 4-year study, 4.4 kg $P \cdot ha^{-1}$ were taken up where no P was applied, but applications of mineral P increased the uptake to about 20 kg $\cdot ha^{-1}$ in some instances (Jones and Ruckman, 1973).

Supplemental feeding.—Supplemental feeding can result in substantial additions of P to pastures. Katznelson (1977) gives several examples of feeding procedures customary in Israel. One kilogram of concentrate contains 8 g P; 1 kg of cottonseed cake contains 11 g P, of which 5 to 6 g appear rather quickly in the feces. A cow whose diet is supplemented with 0.5 kg cottonseed cake per day for 150 days in the summer receives 850 g P. If the cow uses 2.5 ha of pasture, she receives 350 g $P \cdot ha^{-1}$. In comparison, the dry P utilized by that cow from that pasture may be 1,500 kg organic matter, including 1.2 to 1.5 kg P. A ewe licking 3 to 4 g of minerals per day ingests 60 g P per year in addition to that obtained from the pasture. Of course, distribution of the dung-P will be poor, as discussed in the nitrogen section (Hilder, 1964). Over decades, the impact on the availability of P is probably significant in heavily grazed areas, where most of the transfer is from the pasture to the bedding grounds.

Losses of P from the Ecosystem

Losses of P by leaching and erosion are believed to be negligible on annual grasslands, but the evidence for this is partly indirect. We have

measurements of residual fertilizer effects for up to 16 years; the apparent recovery of applied P over a long period of time is very high (M. B. Jones, unpublished data).

Losses of P to animal and plant products are probably less than 1 kg·ha^{-1}·yr^{-1}, based on calculations of Till and Blair (1974) and extrapolated to stocking rates of 1 sheep·ha^{-1}. At higher stocking rates cycling by the grazing animal would be a much bigger factor and would affect fertilized and improved pastures. Katznelson (1977) puts losses to animal products at from 1 to 10 kg P·ha^{-1}·yr^{-1}, depending on pasture production and stocking rate.

Transfers of P within Ecosystems

Mineralization of slowly cycling organic matter (humus).—As with N, we presume that the magnitude of mineralization of humus is small, on the order of 1 kg P·ha^{-1}·yr^{-1}, and that over a number of years it is in equilibrium.

Mineralization and leaching from actively cycling P in organic matter.—Most of the P used by plants and microorganisms in two perennial grassland ecosystems was obtained from readily decomposable plant and microbial material (Cole et al., 1977). Our data suggest that for the years 1974 and 1975, enough P was in the plant material of a given year's crop to support the following year's demand (Table V). We assume that P is mineralized at least as fast as N, as discussed; thus, at least 77% of the P in litter and 79% of that in dead roots became available for growth of the next year's crop.

Leaching from standing plant parts.—Of the total P in ground-up plant material, from 60% to 83% was water soluble and most was inorganic (Broomfield and Jones, 1972). Continuous leaching equivalent to 24.4 cm of rain was required to leach more than 90% of the P from certain samples of all ground-up plant material, but leaching rates equivalent to 1.25 cm over 96 h quite effectively removed up to 60%. Whether P is leached from living plants in annual grasslands is not known but could be a significant pathway of recycling.

Labile inorganic P in the soil.—The inorganic labile pool of P was estimated to be about 20 to 25 kg·ha^{-1} in April, near peak standing crop, in 1973 (Woodmansee and Duncan, submitted). Slightly more P was in this pool than in the plant material alone. The inorganic labile pool was considered to be in equilibrium with the soil solution; consequently, plants and microorganisms had available P from this source as well as from mineralization of, and leaching from, plant parts. We presume that all significant amounts of P entering living organisms must pass through the soil solution.

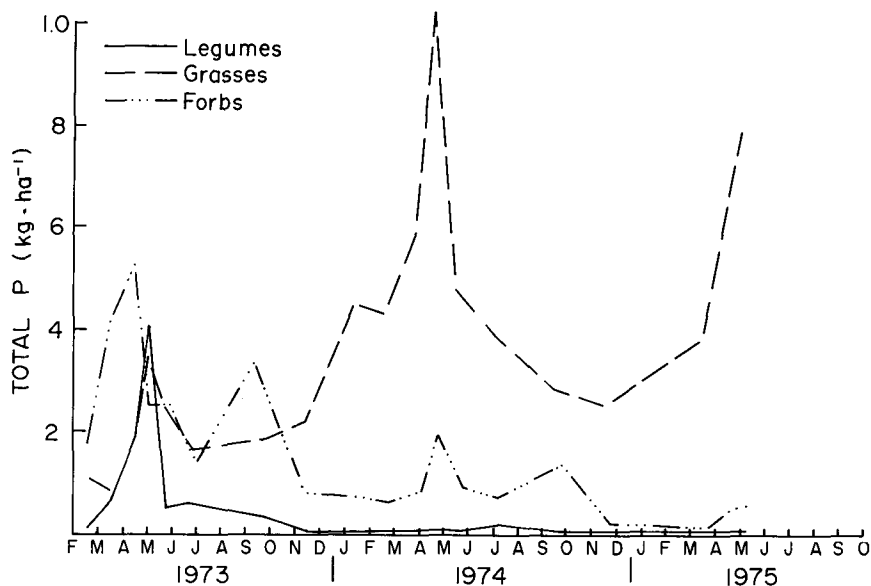Although data suggest that grasslands at SJER are not deficient in P

Fig. 6. Phosphorus dynamics of legumes, grasses, and forbs other than legumes in an ungrazed pasture at San Joaquin Experimental Range. The principal winter and spring vegetation germinated in mid-November 1972, mid-October 1973, and early November 1974. Death of vegetation occurred from early to mid-May each year.

(Woodmansee and Duncan, submitted), many grasslands in other parts of the state do appear to be deficient. For example, on one P-deficient soil average upake by aerial plant parts over a 4-year period was about 4.4 kg·ha^{-1} (Jones and Ruckman, 1973). Average annual uptake of P on 19 sites near Hopland was 4.3, with a range of from 1.0 to 10.5 kg·ha^{-1}. Comparing these values with those at SJER, we conclude that the grasslands in the Hopland area of California are much lower in available P than those at SJER (Table V).

Uptake of P by plants.—Trends in annual dynamics of P in aboveground material at SJER were, in general, similar to those for N, as discussed (Fig. 6). Integrated results of the ecosystem behavior indicate that at least 14.5 kg P·ha^{-1} were taken up by vegetation (Fig. 5). This is a minimal estimate of apparent uptake, as was that for N, because of intraseason death, leaching from foliage, and decomposition.

Litterfall and root death.—Litterfall and root death showed P trends similar to those for N, as discussed (Fig. 5 and Table V).

Annual variation.—Data from SJER (Table V) show the distribution of P in various parts of an annual grassland ecosystem at the dates in 1973, 1974, and 1975 when living biomass is near peak standing crop (Woodmansee and Duncan, submitted): Aboveground parts of plants contained
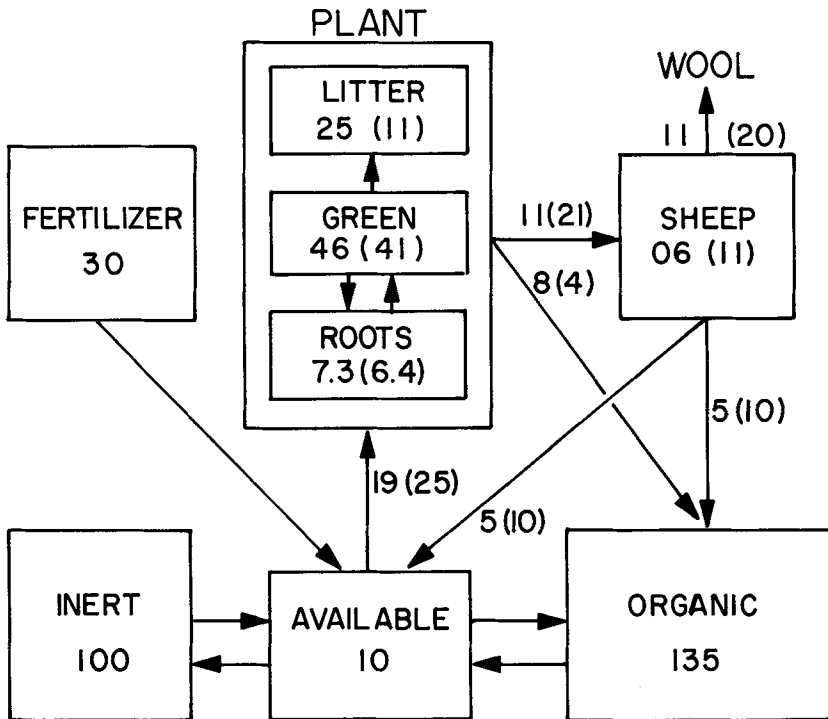
Fig. 7. Sulfur cycling in pasture grazed at two stocking rates (10 and 20 sheep·ha⁻¹). Boxes represent pools (kg S·ha⁻¹); arrows indicate flows (kg S·ha⁻¹·yr⁻¹). Unbracketed numbers show flow rates at 10 sheep·ha⁻¹; numbers in parentheses show flow rates at 20 sheep·ha⁻¹ (from Till and Blair, 1974).

10.1, 12.0, and 8.6 kg·ha⁻¹; roots (live and dead) were estimated to contain 3.8, 3.1, and 2.2 kg·ha⁻¹ for the 3 years, respectively; and litter contained 3.1 and 2.0 kg·ha⁻¹ in 1973 and 1974, respectively. In 1973 and 1974, aboveground production was the same, but species composition was different (Table II). Phosphorus contained in the entire plant system was about the same both years.

SULFUR

Sulfur, an element that frequently limits production of plants in annual grassland ecosystems (Wagnon et al., 1958; McKell and Williams, 1960; Jones, 1964), may act directly in plant metabolism to increase production of biomass by ameliorating deficiencies. It may also stimulate bacteria in the legume-*Rhizobia* relationship, thereby increasing legume production and N-fixing efficiency and thus N available for plant growth.

We will discuss S only briefly because sulfur was not studied as part of the US/IBP Grassland Biome and information is limited. Sulfur cycling in *T. subterraneum* pastures in New South Wales, Australia, was summarized by Till and Blair (1974), who gave the size of sulfur pools and rates of cycling at two stocking rates (Fig. 7). Expected ranges of outputs, inputs, and distribution of S within annual grassland ecosystems are shown in Table I.

Sources of Sulphur

Atmospheric inputs of S.—The soil at SJER absorbed about 0.1 kg $S \cdot ha^{-1} \cdot yr^{-1}$, as estimated by McKell and Williams (1960) using lead candles. Similar lead candles placed at Hopland indicated that atmospheric S was extremely low (M. B. Jones, unpublished data).

McKell and Williams (1960) reported that 23.5 kg $S \cdot ha^{-1}$ was added by rainfall in 1957–1958 at the San Joaquin Range. This appears to have been an extreme year, however, for Williams et al. (1964) reported values of 3.6, 4.6, and 1.6, for 1958–1959, 1959–1960, and 1960–1961, respectively. These values were similar to those found at Hopland, where over a 17-year period, 1958 to 1975, the mean was 3.0 $kg \cdot ha^{-1} \cdot yr^{-1}$. Most of this S probably comes from the sea, since the prevailing winds are from west to east, but sulfur from land sources is included in these values. For most California rangeland, the S input by rain is the major outside source.

Fertilization.—Research during the 1950's indicated that S deficiencies are widespread in California (Martin, 1958), and later work has confirmed this. Applications of S have frequently resulted in large increases in production, especially where annual clovers are a significant component of the plant cover, but in many instances, P is also required to increase plant production (Conrad et al., 1948; Bentley et al., 1958; Martin, 1958; Jones, 1964; Martin and Walker, 1966; Dawson, 1969).

An increase in clover growth in the year S was applied to S-deficient pastures, followed by an increase in grass in subsequent years, has been recorded (Bentley et al., 1958; Conrad et al., 1948). However, the decrease in clover and increase in grass need not follow in subsequent years, if adequate S for legume growth is maintained (Jones, 1964). Clover apparently requires higher levels of available S than the annual grasses. As legumes build N levels in the soil, the grasses compete more intensely with the legumes. Adequate grazing pressure, especially early in the growing season, is needed to maintain a stand of *T. subterraneum* and high-quality forage later in the season as herbage matures.

Sulfur fertilization of annual grassland reduced the proportion of weedy plant; increased protein, phosphorus, and calcium levels in the forage; and increased steer gains during the dry season (Green et al., 1958). Protein, soluble carbohydrates, and digestibility increased with increasing

levels of S in a greenhouse study (Jones et al., 1970). Lambs made better weight gains when fed on alfalfa with adequate S than when fed alfalfa deficient in S (Rendig and Weir, 1957).

Supplemental feeding.—If we assume a P:S ratio of 2:1, supplemental feeding would contribute up to 6 kg S·ha⁻¹ in some instances.

Losses of S from Ecosystems

Runoff.—Evidence is scant for S losses from annual grasslands in California by either direct runoff of surface flowing water or erosion; rather, most losses, if any, are by leaching.

Loss of S by leaching.—There is much evidence, both direct and indirect, that S is lost by leaching through the soil. The rate of leaching depends on amount and distribution of rain, temperature, soil type, chemical form of S in the soil, and vegetation growing on the soil.

Most leaching in California occurs where rainfall is greater than 630 mm. Leaching can occur in drier areas if heavy rains come in a short period, especially early in the season before plants are well established. Higher temperatures increase the activity of soil organisms that break down organic S to SO_4-S, which is leachable. Lysimeter work on the SJER and Hopland sites has indicated leaching losses can be great (McKell and Williams, 1960; Williams et al., 1964; Jones et al., 1968).

Organic S and elemental S are not leached but must be oxidized to SO_4-S. Particle size determines surface area, which is directly related to the rate of oxidation of elemental S; thus, large particles of elemental S remain in the soil much longer than fine particles of S (Jones and Ruckman, 1969).

Work in places as widely separated as Oregon, New Zealand, and Australia has shown that some soils have a much greater ability to hold SO_4-S against leaching than others (Chao et al., 1962, 1963; Barrow et al., 1969; Saunders and Cooper, 1975). We have observed evidence of this in California (Jones, unpublished data).

Gaseous loss of S.—In saturated and anaerobic soils, S is reduced to sulfide forms. Hydrogen sulfide is lost from estuaries and bays, but the magnitude of this loss is not known (Cadle, 1975). However, lysimeter work at Hopland has indicated that very little S is lost as H_2S from waterlogged rangeland soils (Jones et al., 1971); rather, S is reduced to insoluble sulfides, such as FeS. When soils were drained and became aerobic, S was available for leaching and plant uptake, indicating that little, if any, gaseous loss had occurred in temporarily waterlogged soils during winter.

Losses to animal and plant products.—The amount of S utilized by animals and removed in animal products depends on stocking rate and season of use. Much of the S ingested by animals is returned to the

pasture in urine and dung. Cycling rates are difficult to measure at low stocking rates, say 1 sheep·ha^{-1}, but as rates go to 3 or 4 sheep·ha^{-1} or higher, cycling becomes increasingly important. The distribution over the pasture is influenced by the same factors described for N.

Transfers of S within Ecosystems

Mineralization of organic material.—During soil formation, sulfides are the primary minerals converted to SO$_4$-S, which is changed in turn to many organic compounds by microorganisms, plants, and animals; thus, many forms of S can be found in soils (Freney and Swaby, 1975).

In surface horizons of well-drained noncalcareous soils in humid regions, most S accumulates in organic forms; whereas in arid zones and calcareous soils, large quantities of inorganic sulfate accumulate. Appreciable quantities of sulfides are found in waterlogged soils. Because soils of annual grasslands are humid and leached in winter and dry in summer, most S is in organic form, and sulfides occur for only short periods under waterlogged conditions (Jones et al., 1971).

Organic S is converted to inorganic sulfate mainly by soil microorganisms (Alexander, 1961); thus, any variable affecting the growth of microorganisms will affect mineralization of S. These factors include temperature, moisture, pH, and availability of food supply (organic matter and its quality).

In soils planted to *T. subterraneum,* SO$_4$-S accumulated during the summer immediately after senescence of the pasture (Williams, 1968). Concentrations remained high from summer to fall, then decreased to low values from winter to spring. The higher values in summer probably resulted from mineralization of organic S under favorable moisture and temperature conditions and lack of plant uptake. The low levels in winter were probably caused by leaching, plant uptake, and the lower rates of mineralization resulting from low soil temperatures. These experiments were carried out in New South Wales, Australia, where summer rainfall occurs. Also, sulfates are released from soil organic matter by desiccation (Freney, 1958; Barrow, 1961a; Williams, 1967; Tabatabai and Bremner, 1972). In a Mediterranean climate, Barrow (1966) ascribed the higher summer levels of sulfate to this phenomenon. In general, fluctuations of mineral S parallel those of nitrate.

Uptake of S by plants.—Uptake of S by grassland species has been found to be about the same order of magnitude as that deposited by rainfall, that is, 3 to 4 kg S·ha^{-1}·yr^{-1} (Jones, 1964; Jones and Ruckman, 1969). For maximum production, S uptake generally must be increased to about 10 to 12 kg S·ha^{-1}·yr^{-1} by fertilization. If uptake is less than this, S can limit forage growth (Martin and Walker, 1966).

SUMMARY

We have discussed the cycling of N, P, and S. These elements are essential nutrients for the maintenance of annual grassland ecosystems because they are important elements in the synthesis of organic matter. Many other elements are also essential, but were not included in the discussion, because little information about the characteristics of their cycling is available.

Nitrogen occurs principally in organic forms in ecosystems, but most of it is bound in very slowly cycling forms. Most N used by organisms is mineralized from plant residues of the previous growing season. The N cycle is open, meaning that significant amounts of the element may be added to the ecosystem from natural external sources: as NH_4^+ and NO_3^- from the atmosphere and as N_2 from fixation by plants. However, significant amounts of N may be lost from the system by leaching, volatilization of NH_3, and denitrification. Nitrogen plays a very important role in ecosystem functioning and can be manipulated by fertilization or legume management.

Phosphorus occurs in both organic and inorganic forms. As with N, organic forms occur in both slowly cycling and fast-cycling forms. The fast-cycling forms are very important sources of P for organisms, especially in ecosystems where it is in short supply. In addition to the organic forms of P, a labile inorganic pool can be very important. In some ecosystems this pool is sufficiently large to supply adequate amounts of P for plant growth, while in other systems it is small and P can limit vegetation production. In some systems P can stimulate legume development, thereby improving the N status of the community. The P cycle is relatively closed, compared to the N cycle, and natural additions and losses are very small. Where P is in limited supply, fertilization can be beneficial.

As with N, sulfur occurs principally in organic forms and its cycling properties are generally similar to those of N. The "openness" of the S cycle is probably intermediate between N and P. Plant production responds to additions of S in many ecosystems. The response may be caused by amelioration of S deficiencies in many types of plants of the ecosystem, or the S may stimulate legume production, resulting in increased N production.

SUMMARIO

Hemos discutido el proceso cíclico del nitrógeno, fósforo, y azufre. Estos elementos son nutrimentos esenciales para el mantenimiento de los

ecosistemas de pastos anuales porque son elementos importantes en el síntesis de la materia orgánica. Muchos otros elementos son esenciales, pero no fueron incluidos en la discusión porque no es disponible mucha información en cuanto a sus características cíclicas.

El nitrógeno ocurre principalmente en las formas orgánicas en los ecosistemas, pero la mayoría se asocia en las formas cíclicas muy lentas. Casi todo el nitrógeno utilizado por organismos se mineraliza de los residuos vegetales del crecimiento del año anterior. El ciclo de nitrógeno es abierto, lo que quiere decir hay cantidades significantes del elemento que se pueden ser añadidas al ecosistema de fuentes externos naturales: como NH_4^+ y NO_3^- de la atmósfera, y como N_2 de la fijación planta. Sin embargo, hay cantidades significantes de nitrógeno que se pueden ser perdidas del sistema por la lixiviación, la volitalización de NH_3, y la desnitrificación. El nitrógeno desempeña un papel importante en el funcionar del ecosistema y se lo puede manipular por la aplicación de fertilizantes y el manejo de las leguminosas.

El fósforo ocurre en las ambas formas orgánicas e inorgánicas. Así como nitrógeno, las formas orgánicas se encuentran en las dos formas cíclicas lentes y rápidas. Las formas del ciclo rápido son fuentes importantes de fósforo para organismos, especialmente en los ecosistemas donde escasea. Además de las formas orgánicas de fósforo, una reserva labil inorgánica puede ser muy importante. En unos ecosistemas este surtido de reserva es bastante grande para suplir cantidades adequadas de fósforo para el crecimiento vegetal, mientras que en otros sistemas esta reserva es pequeña y el fósforo puede limitar la producción vegetal. En algunos sistemas el fósforo puede estimular el desarrollo de las leguminosas, así mejorando el estado de nitrógeno en la communidad. El ciclo de fósforo es relativamente cerrado, comparado al ciclo de nitrógeno, y las aportaciones y perdidas naturales son muy insignificadas. Donde el fósforo no se abunda, la aplicación de fertilizantes puede ser beneficial.

Así como el nitrógeno, el azufre se encuentra principalmente en formas orgánicas y sus características cíclicas son generalmente semejantes a las del nitrógeno. Lo "abierto" del proceso cíclico de azufre es probablemente intermedio entre el nitrógeno y el fósforo. La producción vegetal responde a la adiciones del azufre en muchos ecosistemas. Este efecto puede resultar del mejoramiento de deficiencias de azufre en muchos tipos de plantas del ecosistema, o el azufre puede estimular la producción de las leguminosas, resultando en la aumentada producción del nitrógeno.

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