

Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California

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Abstract

The monthly deposition of total nitrogen, phosphorus, potassium, calcium and magnesium via canopy throughfall, and various components of the litterfall was measured for 31 months under mature *Quercus douglasii* and in the bulk precipitation in the surrounding open grassland. Seasonal patterns of nutrient concentration in leaf litter, throughfall, and precipitation were also measured. Total annual subcanopy deposition exceeded open precipitation deposition by approximately 45–60× for nitrogen, 5–15× for phosphorus, 30–35× for potassium, 25–35× for calcium, and 5–10× for magnesium. Total annual subcanopy deposition was low in comparison to other oak woodland sites reported in the literature. Throughfall and leaf litter were the primary sources of nutrients and thus determined the seasonal peaks of nutrient deposition. The first autumn rains and leaf fall were associated with one peak in nutrient deposition, and throughfall during early spring leaf emergence was associated with a second peak in potassium, magnesium and phosphorus. Non-leaf plant litter (excluding acorns) provided approximately 15–35% of most nutrients, with twigs and bark depositing over 12% of the annual calcium flux in 1987–1988, and flower litter depositing over 8% of the annual nitrogen flux in 1986–1987. Acorns had high concentrations of phosphorus and nitrogen and during the mast season of 1987–1988 they contained a large proportion of the total subcanopy annual flux of these elements. With acorns excluded, total annual nutrient deposition was similar between years, but timing of nutrient deposition differed. Late summer leaf fall associated with drought, variation in precipitation, and variation in deposition of non-leaf parts were associated with seasonal differences in nutrient deposition between years.

Introduction

Quercus douglasii H. and A. (blue oak) is the dominant tree on an estimated 3 million ha in California woodlands and savannas, and has a substantial effect on subcanopy plants, microbiota, and soils. Total and available soil nutrients are higher under *Q. douglasii* canopies than in surrounding open grassland (Callaway et

al., in press; Holland, 1973; Holland and Morton, 1980; Kay 1987), and appears to be the result of nutrient uptake by the deeper rooted trees and the subsequent deposition of nutrients at the soil surface via litterfall and throughfall. High soil fertility associated with *Q. douglasii* has been reported to improve understory productivity under some trees (Callaway et al., in press; Holland, 1973; 1980), and appeared to

improve grassland productivity in some areas when trees were removed (Jansen, 1987; Kay, 1987; Murphy and Crampton, 1956).

In addition to increasing the total annual nutrient inputs, *Q. douglasii* canopies alter the seasonal patterns of nutrient deposition. Nutrient availability in mediterranean-climate ecosystems is largely dependent on favorable combinations of warm temperatures, high soil moisture and available organic material, which occur in the spring and fall. This is also the time of maximum nitrogen uptake (Jackson et al., 1988) for the annual plants that dominate the grassland. Oak canopy-mediated changes in nutrient inputs during these months may have a significant effect on subcanopy productivity and species composition.

Although the contribution of *Q. douglasii* to nutrient cycles in California grasslands is significant, no quantitative analyses of nutrient fluxes in litterfall or throughfall have been conducted. In this paper we describe the seasonal patterns of deposition of total nitrogen, phosphorus, potassium, calcium, and magnesium in various components of the litter fall, and in the throughfall beneath *Q. douglasii* trees and compare subcanopy nutrient deposition to that in the precipitation in the open grassland.

Methods

Study area and species

We conducted this study at the University of California Hastings Natural History Reservation in the Santa Lucia Mountains of central California. The climate is mediterranean, with 90% of the average annual precipitation of 54 cm occurring between November and April. Mean minimum temperatures range from 1.4°C in January to 9.7°C in August, and mean maximum temperatures range from 8.5°C in January to 20.1°C in July.

The study site was a *Q. douglasii* woodland with a density of approximately 690 stems ha⁻¹. *Q. douglasii* are difficult to age, primarily due to rotten centers in older trees. However, we estimated that our sample trees ranged from 80 to 250 years, based on trunk core samples. The

range of sizes of our sample trees was representative of trees at the study site. The site had not been grazed for over 60 years. Soils at the study site are coarse, loamy, mixed mesic Entic Haploxerolls, with surface soil textures ranging from sandy loam to sandy clay loam. Surface soils under *Q. douglasii* canopies average 6.3 in pH (unpub. data), 6.7 mg g⁻¹ total N, 0.3 mg g⁻¹ total P, 2.1 mg g⁻¹ total K, 4.5 mg g⁻¹ total Ca, and 2.0 mg g⁻¹ total Mg. (Callaway et al., in press). In the open grassland, surface soils average 6.0 in pH, (unpub. data), 2.9 mg g⁻¹ total N, 0.15 mg g⁻¹ total P, 1.9 mg g⁻¹ total K, 3.0 mg g⁻¹ total Ca and 1.9 mg g⁻¹ total Mg (Callaway et al., in press). Soils at the site are underlain by a Cretaceous quartz diorite parent material.

Q. douglasii, an oak in the *Leucobalanus* subgenus, is a California endemic, but it is widespread within the state and is the dominant tree on much of the eastern side of the coastal ranges and the western foothills of the Sierra Nevada (Griffin and Critchfield, 1976). Its size is variable and acorn-bearing individuals may range from 5 m to 20 m in height and 20 cm to over 100 cm in diameter at breast height. Although it occurs in a climate characterized by winter rain and summer drought, *Q. douglasii* is winter-deciduous. Leaves usually emerge by mid-March and drop between October and January. Although winter-deciduous oaks do exist in southern Europe, no other region with a mediterranean climate has such large areas that are dominated by winter-deciduous perennials.

Data collection

Litterfall was collected monthly between June 1986 and December 1988, which spanned three autumn leaf-shedding events. Six trees, scattered throughout the woodland were chosen nonrandomly to encompass the wide range of variation in size (Callaway, 1990). The litterfall from each tree was collected using plastic buckets 25 cm in diameter and 30 cm deep attached to steel tripods 1.5 m tall at five fixed stations that had been randomly located under the canopy. Litter was dried at 60°C immediately after collection and divided into leaf, twig and bark, lichen, acorn, flower, and miscellaneous categories. The

miscellaneous category consisted mostly of unidentifiable fragments, bud scales, and insect frass. Because virtually all acorns that fall to the ground are removed by predators under natural conditions (pers. obs., see Borchert et al., 1989) and are unlikely to contribute directly to soil nutrient pools available to understory plants, they were not included in the monthly totals of nutrient deposition.

Nutrient concentrations were measured in all leaf litter bulked by month. In several winter months when leaf fall was very low, leaves could not be collected from all of the sample trees, and these concentrations are based on small amounts of leaves. Initial analyses of lichen litter revealed that concentrations of nutrients were not different between months or seasons, so total lichen litter was combined by year and analyzed in eight subsamples. Each of the other litter fractions were combined by the fall, winter, spring and summer seasons and analyzed for nutrient concentration in eight subsamples for each category in each season. Total nitrogen, phosphorus, potassium, calcium, and magnesium concentrations were determined after samples were ionized in a Technicon BD/20/40 Block Digester. Nitrogen was sampled using a modified indophenol method (Setaro and Jones, 1989), phosphorus using a modified molybdenum blue assay (Setaro and Jones, 1989), and total cations using a Perkin-Elmer atomic absorption spectrophotometer. After concentrations were determined, they were used with the litterfall weights to estimate monthly nutrient fluxes.

Throughfall and incident precipitation were collected monthly during the wet seasons of 1986–1987 and 1987–1988. Collectors consisted of 10-cm diameter funnels attached by Tygon tubing to 1-L Nalgene bottles. Collectors were fastened to steel stakes 50 cm tall and the tygon was looped to slow evaporative loss. Litter was blocked from entering the funnels with aluminum mesh and glass wool. Four collectors were placed under each of the trees that were sampled for litter fall and four were placed in the open. One mL of formaldehyde was added each month to prevent bacterial and algal growth and the bottles were scrubbed with a brush to collect any build-up of organic material. Collected water was frozen for up to six months before nutrient

analyses. Twenty-five mL of each sample was digested separately, and post-digest analyses followed those for litter. Both litterfall and throughfall were collected near the middle of each month, although the day of collection was not always the same. Time between collections ranged from 28 to 33 days.

Results

Over 80% of the annual canopy deposition (excluding acorns) for each element was in the throughfall and leaf fall (Table 1). Thus, the seasonal variation in these sources generally determined the seasonal trends in total deposition. Throughfall provided high percentages of total phosphorus, potassium, and magnesium. Thus, total deposition of these nutrients (Figs. 1, 2, and 3) in winter and spring was much higher than for nitrogen and calcium (Figs. 4 and 5) which were deposited primarily in leaf fall between August and January.

Nutrient deposition via non-leaf plant parts contributed significantly to the total annual nutrient flux (Table 1), and was the primary source of some nutrients in several months. Flowers were the primary source of nitrogen and calcium in May 1987, a period when throughfall and leaf deposition were low. Twig and bark litter contained over 12% of the total (excluding acorns) calcium flux in 1987–1988, and was the primary non-leaf source of this element. The 1987–1988 season was a mast year for oaks in the region. Thus, annual nutrient flux via acorn litter ranged from 20% of total magnesium to 55% of total phosphorus. The total amounts of nutrients deposited by lichen litter did not exceed 5% annually, and peaks of deposition were associated with exceptionally large pieces falling into single collectors and not with any seasonal or phenological pattern.

Excluding acorns, annual nutrient fluxes were similar (Table 1). Monthly patterns of nutrient deposition, however, varied widely between years (Figs. 1–5). The autumn rains began in October in 1987 but not until November in 1986, and the former were more highly concentrated in potassium and magnesium (Fig. 6). Early rains, with high nutrient concentrations, and more

Table 1. Mean annual biomass and nutrient deposition (\pm one S.D., $n=6$ trees) under *Quercus douglasii* via litterfall and throughfall and in open grassland via bulk precipitation. Data are total nutrients after Kjeldahl digests (kg ha^{-1})

	Litter weight	N	P	K	Ca	Mg
Subcanopy deposition						
<i>June 1986–May 1987</i>						
Leaves	2514 \pm 611	31.3 \pm 0.2	0.8 \pm 0.2	10.4 \pm 2.5	22.5 \pm 5.7	3.3 \pm 0.7
Twigs and bark	314 \pm 123	2.6 \pm 1.0	0.1 \pm 0.1	1.3 \pm 0.5	2.7 \pm 1.1	0.3 \pm 0.1
Lichen	166 \pm 168	2.2 \pm 2.3	—	0.5 \pm 0.6	0.4 \pm 0.4	0.1 \pm 0.1
Miscellaneous	316 \pm 214	5.3 \pm 3.6	0.2 \pm 0.1	1.8 \pm 1.3	2.7 \pm 1.8	0.6 \pm 0.4
Acorns	39 \pm 42	0.3 \pm 0.4	—	0.2 \pm 0.2	0.3 \pm 0.3	0.4 \pm 0.4
Flowers	146 \pm 139	3.5 \pm 3.4	0.1 \pm 0.1	0.9 \pm 0.9	0.6 \pm 0.6	0.2 \pm 0.2
Throughfall	—	1.6 \pm 0.4	0.7 \pm 0.2	9.9 \pm 3.3	5.0 \pm 2.9	2.6 \pm 0.8
Total	—	43.3	1.9	25.0	34.2	7.5
Open PPT deposition	—	0.9 \pm 0.1	0.3 \pm 0.1	0.7 \pm 0.2	1.6 \pm 0.1	1.8 \pm 0.2
<i>June 1987–May 1988</i>						
Leaves	2227 \pm 537	25.6 \pm 5.9	0.8 \pm 0.1	7.7 \pm 1.6	18.4 \pm 5.1	3.7 \pm 0.8
Twigs and bark	676 \pm 395	5.6 \pm 3.3	0.1 \pm 0.1	2.7 \pm 1.6	5.7 \pm 3.4	0.7 \pm 0.4
Lichen	202 \pm 108	2.7 \pm 1.4	—	0.7 \pm 0.3	0.5 \pm 0.3	0.2 \pm 0.1
Miscellaneous	259 \pm 91	4.3 \pm 1.5	0.1 \pm 0.1	1.5 \pm 0.6	2.2 \pm 0.8	0.5 \pm 0.2
Acorns	1930 \pm 2654	17.2 \pm 23.6	1.8 \pm 2.5	8.5 \pm 11.7	14.5 \pm 20.0	2.0 \pm 2.7
Flowers	68 \pm 53	1.7 \pm 1.3	—	0.4 \pm 0.3	0.3 \pm 0.2	0.1 \pm 0.1
Throughfall	—	1.0 \pm 0.2	0.5 \pm 0.1	8.7 \pm 3.3	5.1 \pm 3.1	2.7 \pm 0.9
Total	—	58.1	3.3	30.2	46.7	9.9
Open PPT deposition	—	0.8 \pm 0.2	0.2 \pm 0.1	1.1 \pm 0.3	1.3 \pm 0.1	0.9 \pm 0.1
<i>June 1988–December 1988^a</i>						
Leaves	1756 \pm 622	21.6 \pm 8.0	0.5 \pm 0.2	4.7 \pm 1.5	14.2 \pm 5.1	2.1 \pm 0.7

^a Annual leaf fall was complete by this date, other litter components were not annual totals.

abundant rain in the autumn and winter resulted in much higher fall nutrient deposition via throughfall during these months in 1987–1988 than in 1986–1987. Conversely, spring rainfall was higher in 1986 than in 1987, and spring throughfall nutrient deposition was also higher (Figs. 1–5). In general, high throughfall concentrations were associated with the presence of leaves and low monthly rainfall totals.

Variation in the seasonal patterns of nutrient deposition between years was also associated with early leaf abscission in the summers and autumns of 1987 and 1988 (Figs. 1–5), which were the second and third years of a drought in central California. The combination of earlier leaf fall and higher nutrient concentrations of leaf litter in the summer and early autumn than in later months (Fig. 7) resulted in higher nutrient fluxes via leaves in the autumns of 1987 and 1988 than in 1986. Total leaf fall decreased in each of the consecutive years of the study, and

was probably due to the cumulative effects of the drought.

Seasonal nutrient concentrations in leaf litter varied differently for each nutrient (Fig. 7). Nitrogen concentrations dropped by 50% between August and September of 1986, but in the following two drought years concentrations began decreasing earlier in the summer and decreased at a lower rate. Calcium, which is not retranslocated from leaf tissues, was at higher concentrations in the winter than in the other seasons. Phosphorus concentrations in the leaf litter decreased slowly during the fall and winter and increased sharply with leaf emergence. Potassium and magnesium concentrations began to decrease later in the fall than nitrogen concentrations, which may explain the exceptionally high concentrations of these elements in the October 1987 throughfall (Fig. 6) in comparison to the November throughfall collected during the first rains of 1986.

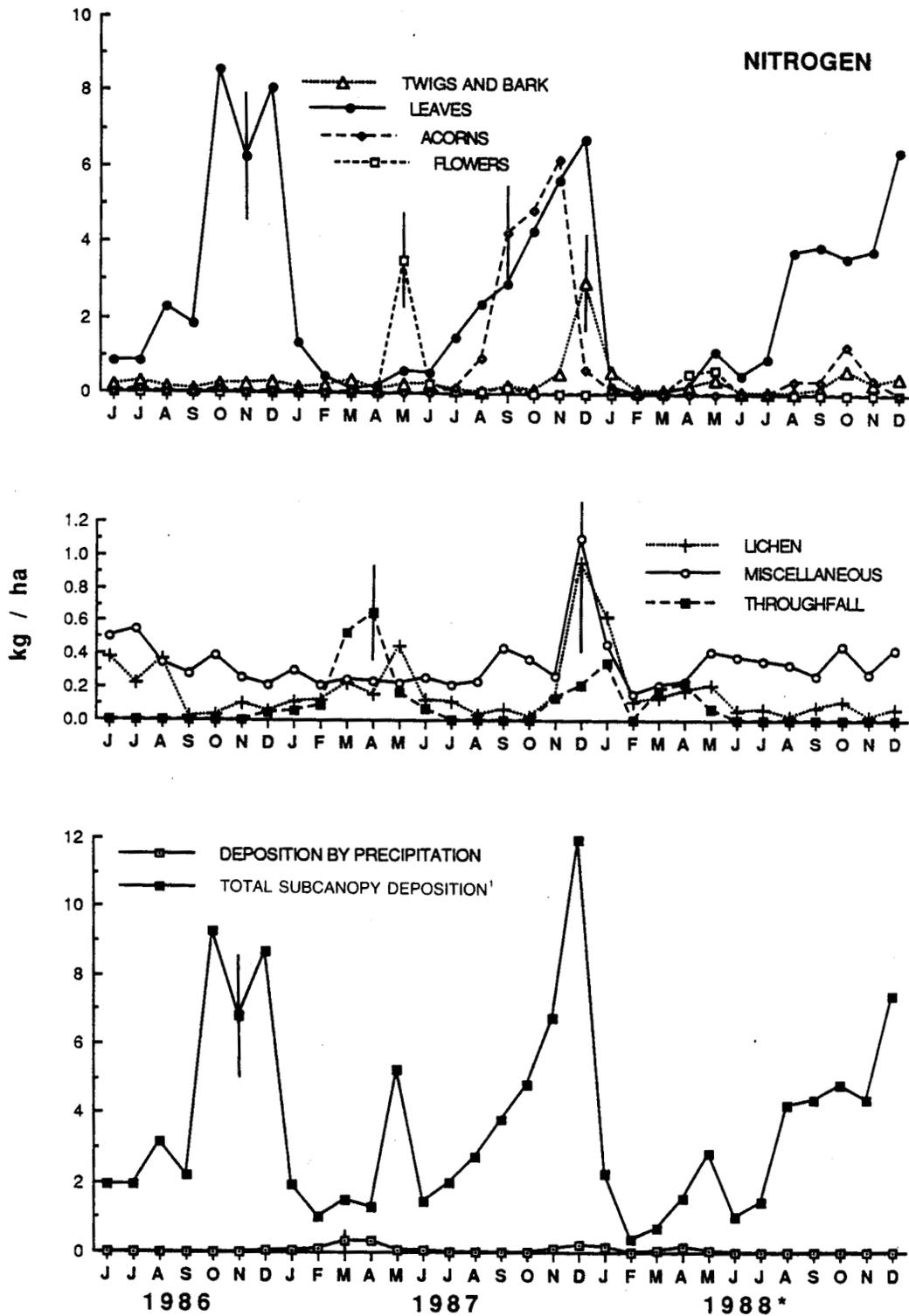


Fig. 1. Total nitrogen deposition under *Quercus douglasii* canopies and in the open grassland. 1 = not including acorns, see Methods for explanation. * = throughfall and precipitation were not measured in 1988. Error bars show two standard errors on each side of means with the largest standard error for each litter fraction, n = 6.

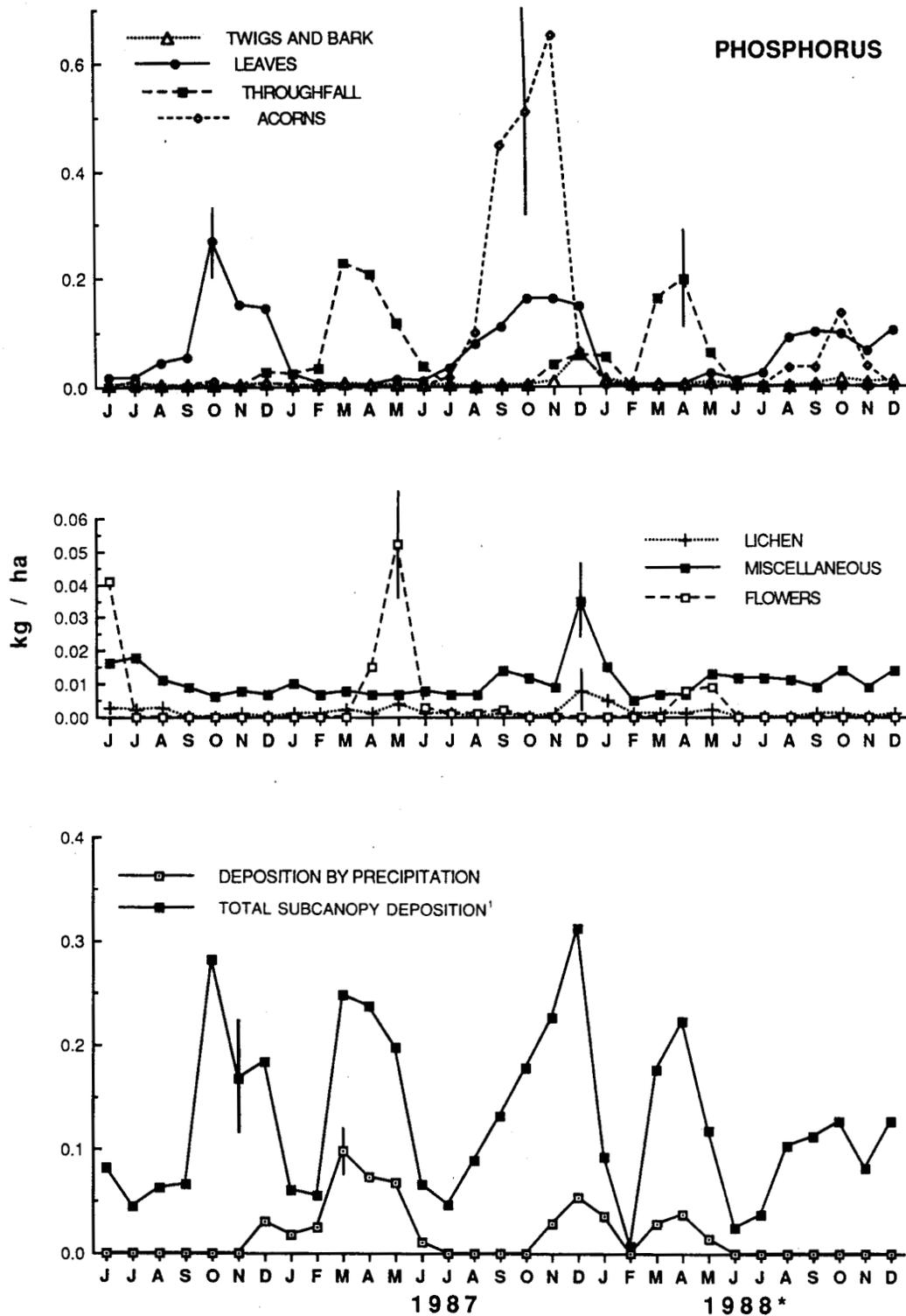


Fig. 2. Total phosphorus deposition under *Quercus douglasii* canopies and in the open grassland. 1 = not including acorns, see Methods for explanation. * = throughfall and precipitation were not measured in 1988. Error bars show two standard errors on each side of means with the largest standard error for each litter fraction, n = 6.

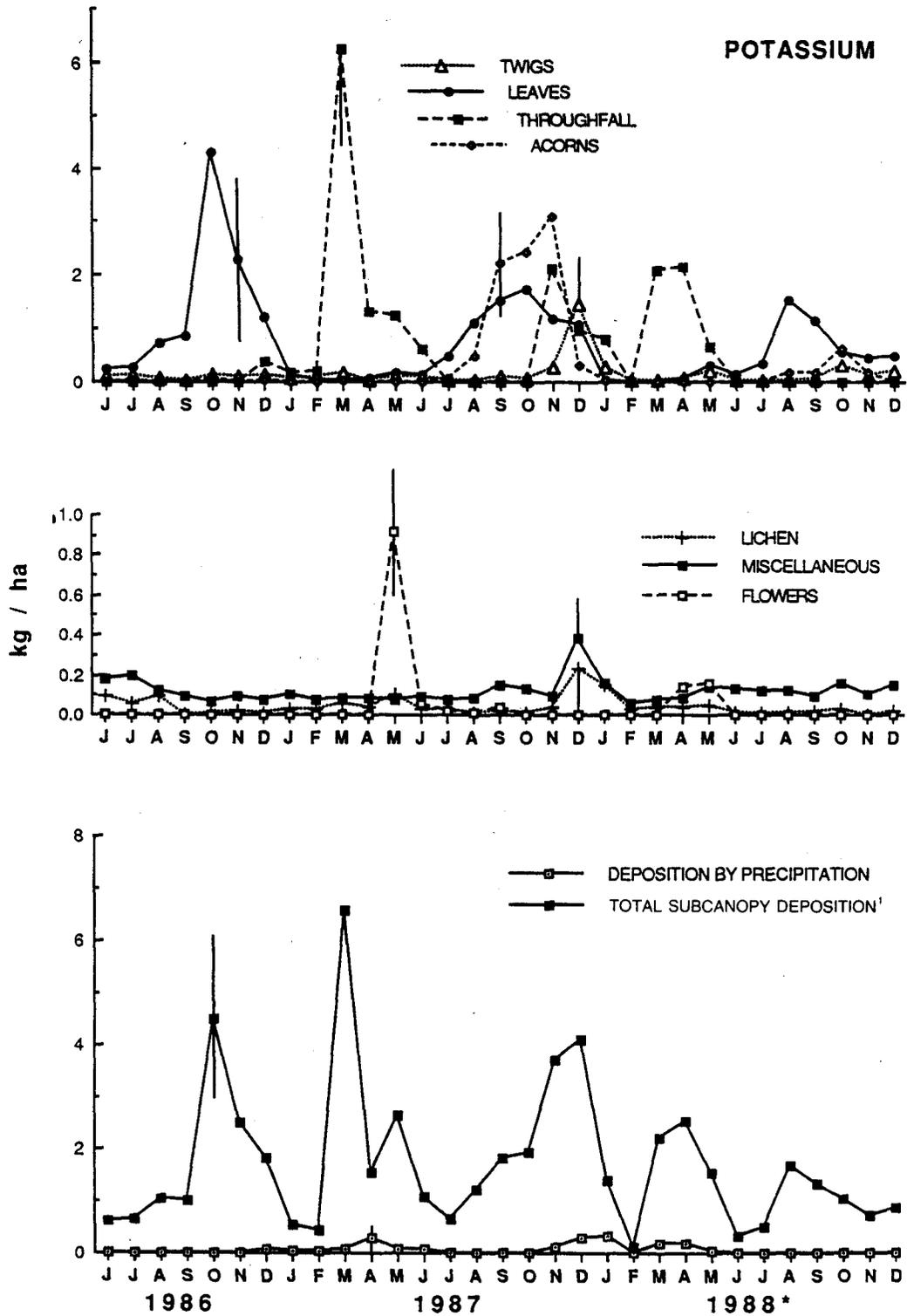


Fig. 3. Total potassium deposition under *Quercus douglasii* canopies and in the open grassland. 1 = not including acorns, see Methods for explanation. * = throughfall and precipitation were not measured in 1988. Error bars show two standard errors on each side of means with the largest standard error for each litter fraction, n = 6.

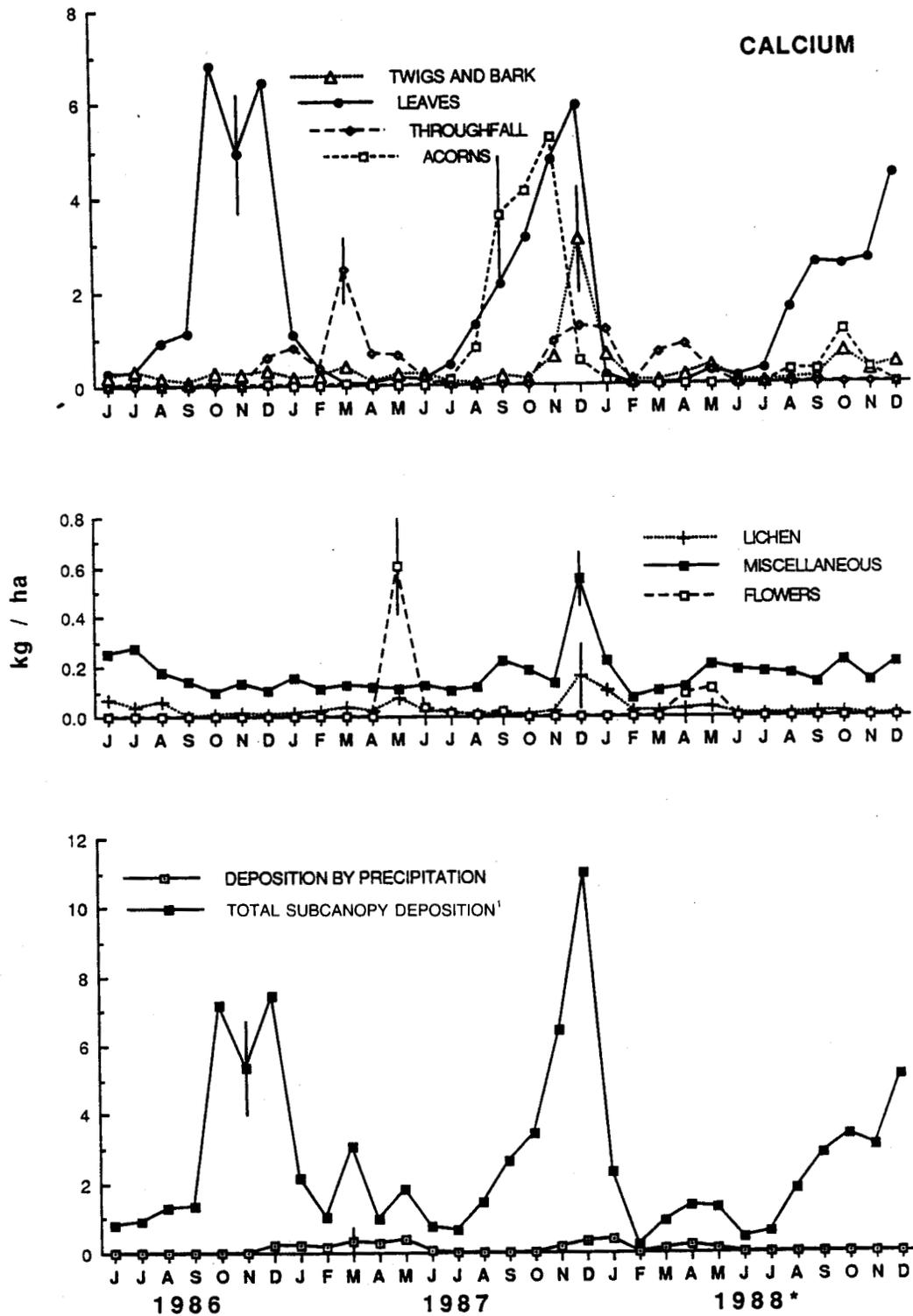


Fig. 4. Total calcium deposition under *Quercus douglasii* canopies and the open grassland. 1 = not including acorns, see Methods for explanation. * = throughfall and precipitation were not measured in 1988. Error bars show two standard errors on each side of means with the largest standard error for each litter fraction, n = 6.

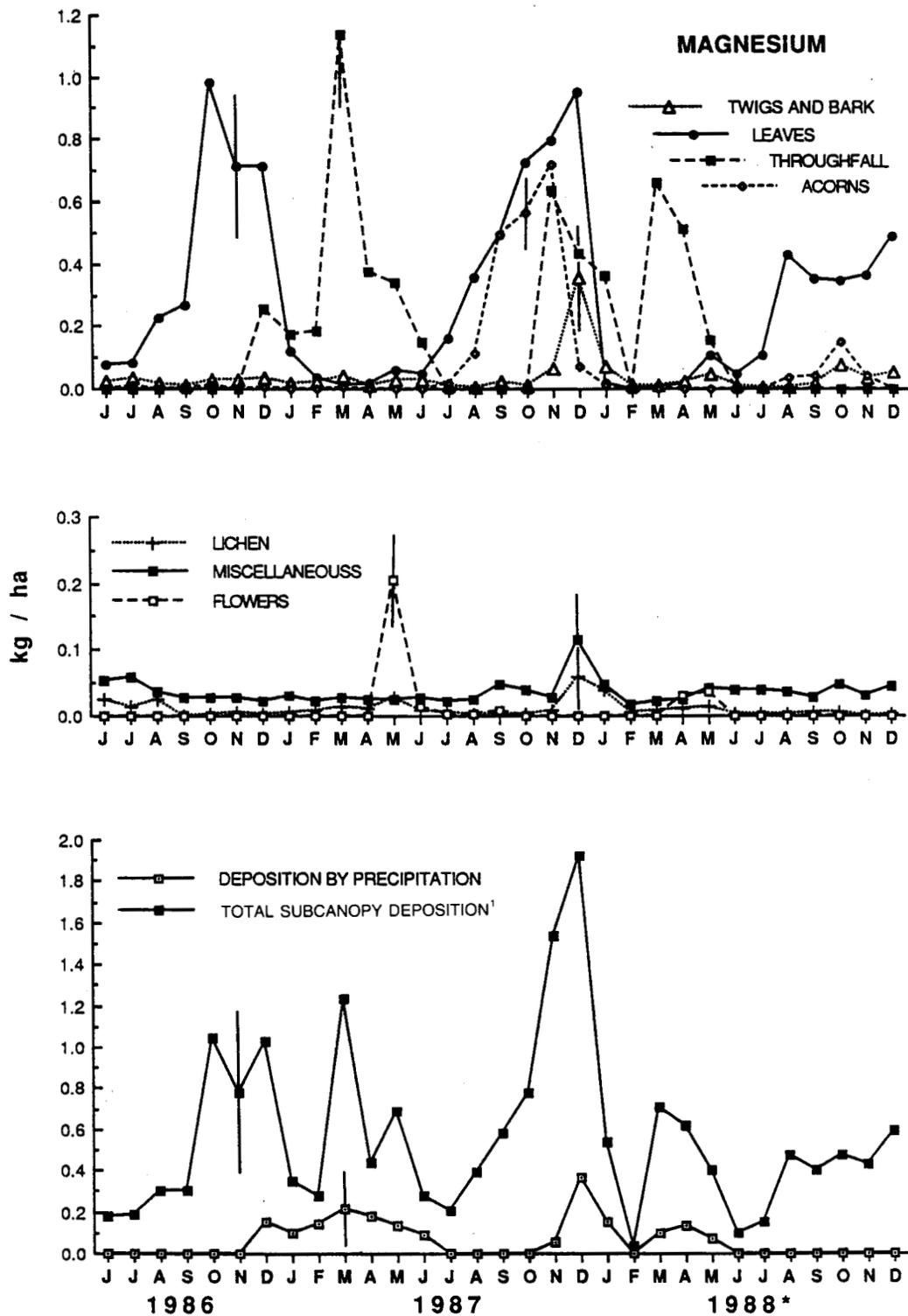


Fig. 5. Total magnesium deposition under *Quercus douglasii* canopies and in the open grassland. 1 = not including acorns, see Methods for explanation. * = throughfall and precipitation were not measured in 1988. Error bars show two standard errors on each side of means with the largest standard error for each litter fraction, n = 6.

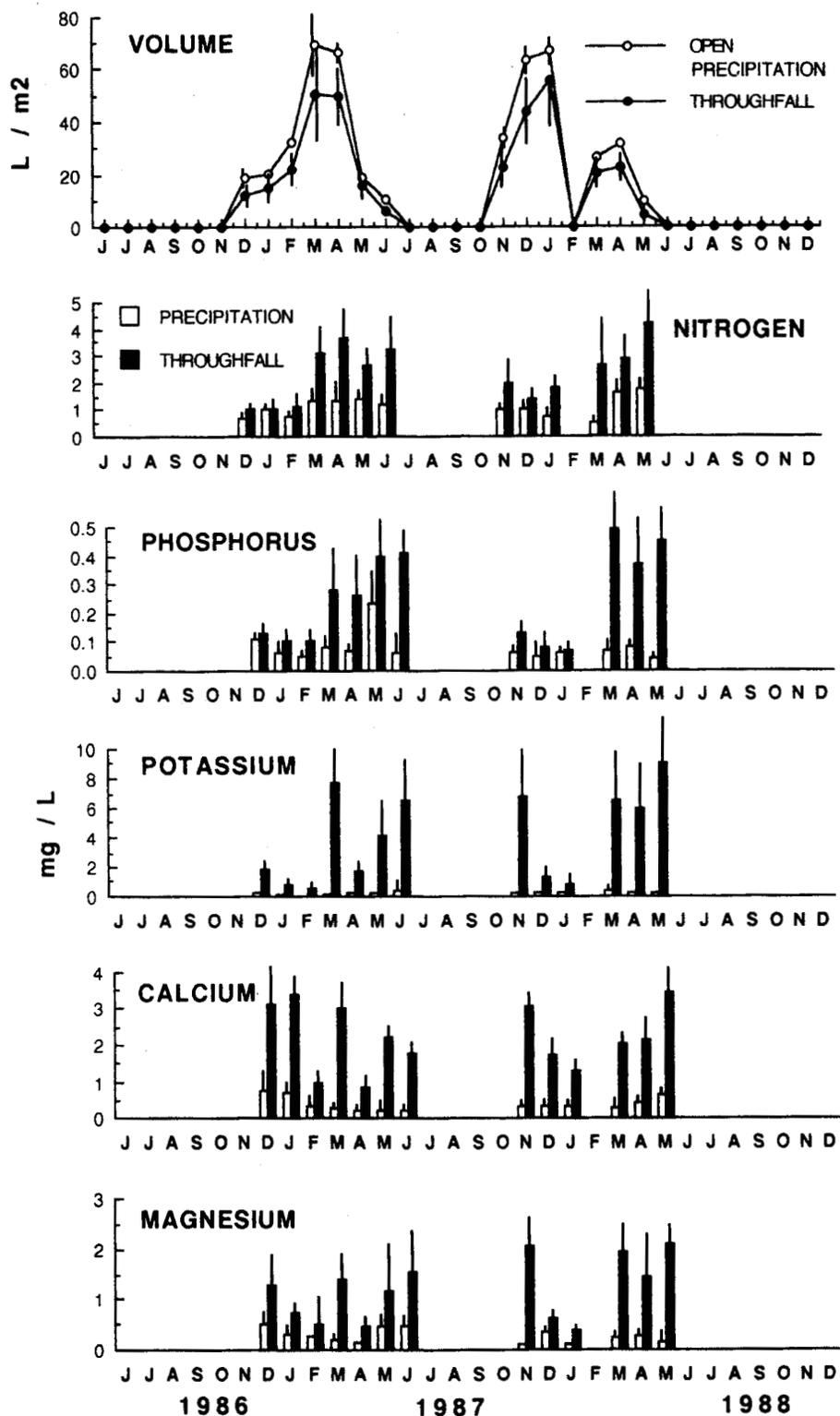


Fig. 6. Volume of throughfall and precipitation, and concentration of nutrients in throughfall and precipitation under *Quercus douglasii* canopies and in the open grassland. Error bars show two standard errors, n = 6.

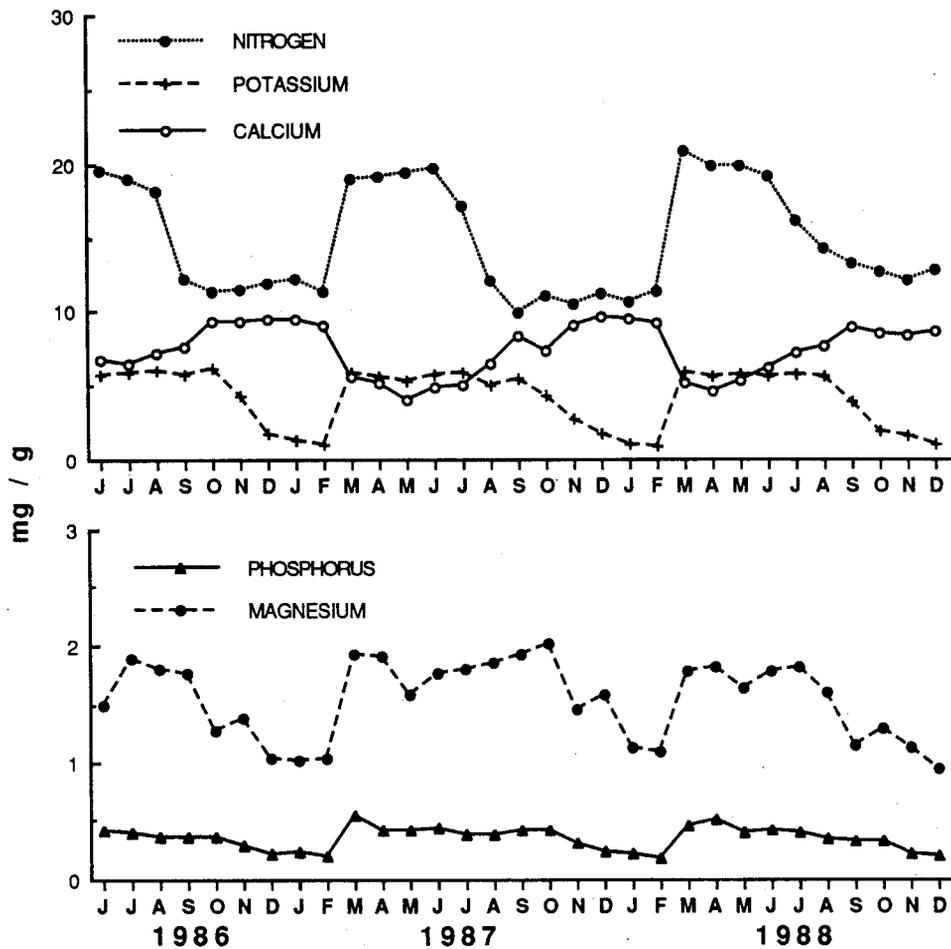


Fig. 7. Concentrations of nutrients in leaf litterfall under *Quercus douglasii* canopies.

Discussion

Total nutrient deposition was lower than has been reported for woodlands dominated by winter-deciduous oaks in northern England (Carlisle et al., 1966a; 1966b), several sites in Belgium (Duvigneaud and Denaeyer-De Smet, 1971), the eastern Soviet Union (Duvigneaud and Denaeyer-De Smet, 1971), and the eastern (Monk and Day, 1985), central (Johnson and Risser, 1974; Rochow, 1974) and northern United States (Killingbeck and Wali, 1978; Reiners, 1972). Total nutrient deposition was also lower than in evergreen oak woodlands in the Himalaya (Mehra et al., 1985), and in southern France (Rapp, 1969). In general, low throughfall deposition in the woodland we studied was the

primary reason for the lower total deposition. Although throughfall nutrient concentrations were relatively high in this *Q. douglasii* woodland, other winter-deciduous oak woodlands generally receive more total rainfall. Additionally, precipitation during our collection period was below average, thus in other years total deposition should be higher. In temperate climates, rainfall is common during the summer months when leaves are present, and summer peaks of throughfall nutrient deposition have been reported from other winter-deciduous oak woodlands (Reiners, 1972). In California oak woodlands, a large percentage of total annual precipitation falls when the trees are leafless. Thus, leaves are rarely leached during summer.

The relative quantities of nutrients in litter in

most winter-deciduous oak woodlands is $\text{Ca} > \text{N} > \text{K} > \text{Mg} > \text{P}$ (Duvigneaud and Denaeyer-De Smet, 1971; Johnson and Risser, 1974; Killingbeck and Wali, 1978; Monk and Day, 1985; Ostman and Weaver, 1982; Reiners, 1974; Rochow, 1974). The relative quantities of nutrients in the oak woodland studied here, however, were $\text{N} > \text{Ca} > \text{K} > \text{Mg} > \text{P}$. The high quantities of nitrogen in the litter and throughfall relative to calcium (which is not retranslocated) suggests that nitrogen use in *Q. douglasii* woodlands may be inefficient in comparison to deciduous oak woodlands in temperate climates. Leaf abscission in *Q. douglasii* appears to occur over longer periods of time than for oaks in habitats with severe winters, which may affect the efficiency of nitrogen retranslocation. Although the relative amounts of nutrients may vary for many reasons, the relatively low amount of calcium in the litter was probably not due to low availability because calcium was abundant in the soil at our site under trees and in the open grassland (see Methods).

Throughfall contributed only 3.7% and 1.7% of the canopy nitrogen deposition in 1986–87 and 1987–1988, respectively. Low throughfall nitrogen fluxes are common in winter-deciduous oak woodlands (Killingbeck and Wali, 1978; Monk and Day, 1985; Reiners, 1972) and net canopy uptake of nitrogen was reported by Carlisle et al. (1966b) and Ostman and Weaver (1982). Carlisle et al. (1966b) suggested that leaf and bark adsorption, microflora assimilation, leaf absorption, and uptake by epiphytic mosses and lichens may have contributed to the net loss. The latter possibility is supported by the findings of Lang et al. (1976) who found that several species of lichens removed ammonium and nitrate from experimental solutions, but leaked potassium, magnesium and calcium into the solutions. Epiphytic lichens were common on all of our sample trees.

Non-leaf parts provided approximately 15–35% of the total nutrient budgets, which is comparable to reports from other oak woodlands (Carlisle et al., 1966a; Gosz et al., 1972; Killingbeck and Wali, 1978; Monk and Day, 1985). The summer deposition of flowers and the non-seasonal deposition of twig and bark, lichen and miscellaneous litter provided important sources

of nutrients during mid-summer and mid-winter when leaf and throughfall deposition was low. The importance of non-leaf parts to annual and seasonal fluxes of nutrients was also reported by Carlisle et al. (1966a) who found that large quantities of nitrogen, phosphorus and potassium fell in flowers, twigs, bark, bud scales and insect frass several months prior to leaf fall in a winter-deciduous *Q. petraea* woodland in England.

Nutrient deposition via *Q. douglasii* canopies has significant effects on understory soil nutrients and herbaceous productivity and appears to affect species composition. Callaway et al. (in press) examined light, temperature, soil moisture, soil nutrients, and fine tree root distributions under *Q. douglasii* canopies in order to determine how variations in these factors were associated with widely varying differences in sub-canopy herbaceous production. They found that soil under all trees sampled was higher in nutrients than under treeless grassland, and had the potential to facilitate the growth of herbaceous understory plants. Facilitative effects in the field, however, were determined by tree root morphology, with high understory productivity being associated with low biomass of fine oak roots, and low understory productivity being associated with high biomass of fine oak root. Under oaks with low understory productivity, root exclosures significantly improved herbaceous growth.

Variation in the temporal pattern of nutrient availability also may affect the productivity and species composition of *Q. douglasii* understories. High deposition in fall and spring corresponds with periods of maximal nitrogen uptake in California grasslands (Jackson et al., 1988) and may have substantial positive effects on overall productivity. Because most nitrogen deposition under *Q. douglasii* canopies was in leaf litter, nitrogen availability is dependent on mineralization rates, which may not co-occur with maximum deposition rates. However, Callaway et al. (in press) found that in autumn, available ammonium and nitrate were significantly higher under *Q. douglasii* trees ($\text{NH}_4 = 12\text{--}17 \mu\text{g g}^{-1}$, $\text{NO}_3 = 21\text{--}23 \mu\text{g g}^{-1}$) than in the open grassland ($\text{NH}_4 = 7 \mu\text{g g}^{-1}$, $\text{NO}_3 = 8 \mu\text{g g}^{-1}$). Growth phenologies of many California annual species do not overlap completely (Chiarellio, 1989).

Thus, early annual species may have an advantage in seasons with high deposition in the fall, whereas late annuals may benefit from high spring deposition. Canopy-mediated soil fertility may also contribute to the displacement of *Avena fatua* L. and other open grassland dominants by *Bromus diandrus* Roth. and other understory dominants as has been suggested for *Q. agrifolia* by Parker and Muller (1982).

We found that nutrient deposition in *Q. douglasii* woodlands was much higher under tree canopies than in the open grassland. However, most of the nutrient deposition was in organic form and not immediately available for plant uptake. Additionally, only deposition via precipitation was measured for deposition in the open grassland, which underestimates total deposition, and the contribution of the herbaceous plants to the overall nutrient cycle (e.g. Carlisle et al., 1967) was not measured. Analysis of decomposition rates and non-plant sinks and losses (e.g. Jackson et al., 1988) is required to fully understand the effects of the fluxes described here.

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