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Herbivory and the cycling of nitrogen and phosphorus in isolated California oak trees

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Summary. Nitrogen and phosphorus flow in litterfall and throughfall were studied in two California *Quercus* species (the evergreen *Q. agrifolia* and deciduous *Q. lobata*) before, during, and after an outbreak of the California oak moth, *Phryganidia californica.* All of the foliage of both oak species was removed by the herbivore during the course of this outbreak. During the outbreak, total N and P flow to the ground more than doubled from *Q. agrifolia* and increased to a lesser extent from *Q. lobata* over the previous year. The composition of the litter during the outbreak year shifted so that in *Q. agrifolia*, almost 70% of the total N and P flow to the ground moved through frass and insect remains, while in *Q. lobata*, approximately 60% of the N and 40% of the P moved through frass and insect remains. Short-term leaching experiments showed that nitrogen was far more rapidly lost from *Phryganidia* frass than from leaf litter of either species. These results and the relative frequency of *Phryganidia* outbreaks suggest that this herbivore has significant effects on the nutrient cycling beneath these trees.

Key words: Herbivory – Nutrient cycling – *Quercus* – Evergreen – Deciduous

The oaks of the central coastal California Foothill Woodland community are regularly attacked by a native lepidopteran, the California oak moth, *Phryganidia californica* Packard (Lepidoptera; Dioptidae). In the study area, *Phryganidia* is bivoltine with summer and winter generations. The larvae do not diapause but feed continuously. The evergreen *Quercus agrifolia* Nee is utilized by *Phryganidia* in the winter while the summer generation feeds primarily on *Quercus lobata* Nee (Puttick 1986).

The population density of *Phryganidia* typically fluctuates widely, reaching peak densities every five years on average (Harville 1955). These peak densities are followed by a population collapse after which few of the insects may be found. Typically, during the peak year of a population outbreak, all of the *Q. agrifolia* trees in an area will be completely defoliated by the winter brood while the deciduous oaks will be defoliated by the following summer brood.

During the course of this study, population densities of *Phryganidia* at the study area increased dramatically such that most trees of both oak species were totally defoliated in 1981. The loss of foliage by these trees was far higher than the 10% loss to herbivores commonly observed in forested ecosystems (Bray 1964; Gosz et al. 1972; Schowalter et al. 1981; Ohmart et al. 1983). High foliage losses have been recorded during periodic outbreaks of other herbivores (Carlisle 1966a; Swank et al. 1981; Morrow 1977, but see Ohmart et al. 1983), but there are probably few forested systems in the world which experience such regular and intense herbivory.

A consequence of the massive loss of foliage experienced by these oaks is that the processes of nutrient retranslocation is largely bypassed so that nitrogen, phosphorus and other mineral elements cycle mainly through an external pathway of frass and insect remains. The effect of this change is considered in the context of speculation concerning the influence of insects in regulating system productivity or nutrient cycling.

Methods

This study was conducted at Stanford University's Jasper Ridge Biological Preserve, 12 km west of Palo Alto, California. Foliage and litterfall were collected from two *Q. lobata* and two *Q. agrifolia* trees from January of 1980 until January of 1983. Throughfall was collected from beneath the same trees during 1980 and 1981. All trees occurred as isolated individuals.

Leaves and litter were collected monthly or twice monthly during spring leafout and at times of maximum *Phryganidia* activity. Leaves were collected in a stratified random manner by walking around the trees and reaching into the canopies to remove samples. Approximately 20 leaves were collected per *Q. lobata* tree and an equal number of each age class (current year and previous year leaves) were collected per *Q. agrifolia* tree. Litter was recovered from four one-meter tall plastic barrels (0.19 m^2) located beneath each tree. Plastic colanders were placed inside the barrels to hold the litter above the bottom of the container which was pierced for drainage. The leaf area index (LAI) for each species was calculated from the annual weight of the leaf litter (collected before the *Phryganidia* outbreak) divided by the weight per unit area of that litter. In *Q. agrifolia*, the figure derived in this manner was multiplied by two since mean leaf retention in this species is two years (Hollinger 1984). Litter and leaves were dried

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Table 1. Litterfall (g m^{-2} yr^{-1}) (means for 2 trees of each species)

	Quercus agrifolia				*Quercus lobata*			
	Year			Total	Year			Total
	1980	1981	1982	1980–1982	1980	1981	1982	1980–1982
Brown lvs	518	383	100	1,001	302	181	203	685
Green lvs	25	56	87	167	10	15	10	35
Twigs	125	121	238	484	217	221	174	612
Fruit	154	15	36	204	14	9	16	39
Flowers	17	32	7	56	25	8	0	33
Misc.	2	4	6	12	6	12	11	28
Subtotal	841	610	473	1,924	573	446	414	1,432
Frass	155	863	87	1,106	46	214	61	321
Insects	1	87	1	89	2	35	2	40
Total	997	1,560	561	3,119	621	695	477	1,793

(Individual values may not sum to totals because of rounding.)
All trees had highest total litterfall during outbreak year of 1981 (exact probability = 0.012)
In each year both *Q. agrifolia* trees produced more litter than either *Q. lobata* tree (exact probability assuming independence of each years result = 0.005)

overnight in a forced draft oven at 80° C immediately after collection. Litter samples were separated into green leaves, brown leaves, twigs, frass, fruits, flowers, insect remains and other material. All samples were then weighed and ground in a Wiley mill to 20 mesh size. Material from each tree was analyzed separately.

Throughfall was collected immediately after each storm from two collectors located beneath each tree. Collectors consisted of 15 cm polypropylene funnels fitted tightly into 4 l plastic containers. The funnels were located 1 m above the ground. Glass wool was fitted into each funnel to exclude leaves and other debris. Subsamples were bulked for each tree and stored at −20° C until analysis. Leaching loss was calculated as the difference in nutrient (N or P) concentration between throughfall and precipitation multiplied by the amount (volume) of throughfall.

Total nitrogen and phosphorus were determined in Kjeldahl digests of the leaf, litter, and throughfall samples. A Technicon Block Digestor was used for the Kjeldahl digestions and an AutoAnalyzer II for the colorimetric nitrogen and phosphorus determinations.

Exact probabilities of occurrences were calculated by considering the possible permutations or combinations of the sample data.

Leaching experiment

Rapid loss of nitrogen and phosphorus from five replicate frass and leaf litter samples from each species of *Quercus* was measured by placing 1.0 gm of dried, freshly collected material in 20.0 ml of deionized water. Leaves were cut in half with one half being placed in the deionized water while the other half was retained for N and P analysis of the dry material. This permitted a determination of the relative amount of N and P leached from each sample as well as total N and P leached. Aliquots were withdrawn after 1 h, 6 h and 24 h and analyzed for total N and P by the methods described previously.

Results

Litterfall

Litterfall from *Q. agrifolia* over the 1980–1982 period averaged approximately 1,040 g m^{-2} yr^{-1}, compared to approximately 598 g m^{-2} yr^{-1} recovered from *Q. lobata* (Table 1). In each year each *Q. agrifolia* tree produced more litter than either *Q. lobata* tree. Assuming independence between years, the probability of such an occurrence is <0.01. Approximately 50 and 38 percent of the three year fall from *Q. agrifolia* and *Q. lobata* respectively occurred during the oakmoth outbreak year of 1981. In the year following the *Phryganidia* outbreak, approximately 18 and 27 percent of the three year litter fall from *Q. agrifolia* and *Q. lobata* occurred (Fig. 1).

The largest proportion of material falling from the *Q. agrifolia* trees during the three year period consisted of frass (35.5%) with lesser amounts of brown leaves (32.1%), twigs (15.5%), fruit (6.6%), green leaves (5.4%) and other material (Table 1 and Fig. 1). During the outbreak year of 1981, *Phryganidia* frass accounted for 55.3% of total *Q. agrifolia* litterfall compared to 15.6% in both the preoutbreak and postoutbreak years. Brown leaves accounted for 52% of the litterfall in the year before the outbreak, but made up only 24.5% of the litter during the outbreak and 17.7% of the material following defoliation by *Phryganidia.* Twigs increased as a percentage of litter mass from 12.5% of the total before oakmoth outbreak to 42.4% following the outbreak. The absolute amount of twigfall in 1982 was approximately double that of 1980. Approximately 15.5% of the preoutbreak litterfall in *Q. agrifolia* consisted of fruit (acorns and caps). This declined to less than 1% during the oakmoth outbreak and increased to 6.3% of total litterfall in 1982. Because of the relatively light litterfall during 1982, however, total fruit litterfall in that year was actually only 23% of fruit litterfall in the predefoliation year of 1980.

In contrast to the results for *Q. agrifolia*, in *Q. lobata*

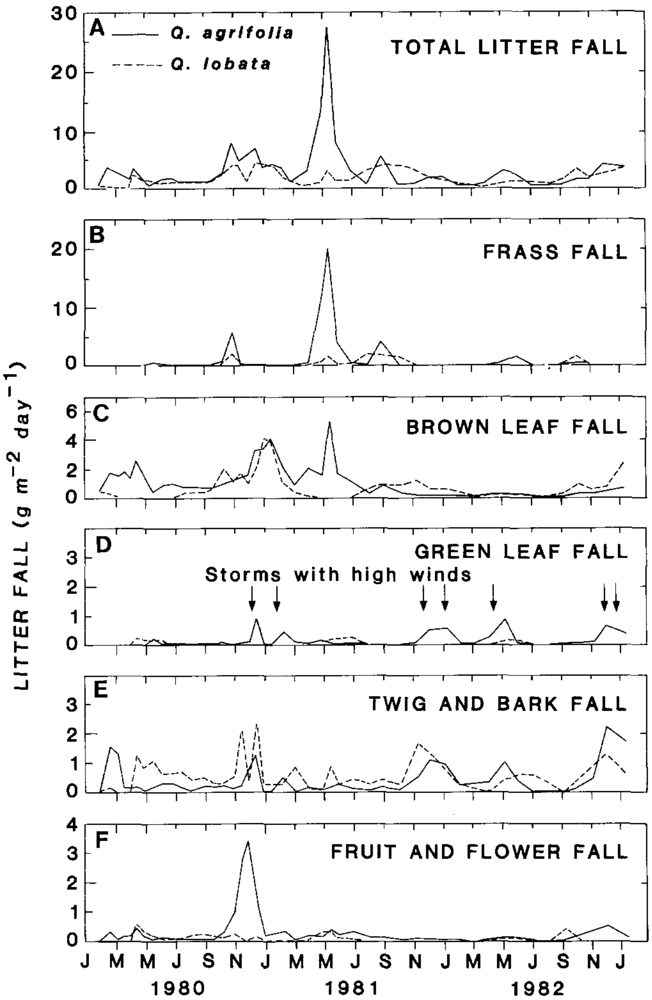

Fig. 1A–F. Litterfall from *Q. agrifolia* and *Q. lobata*

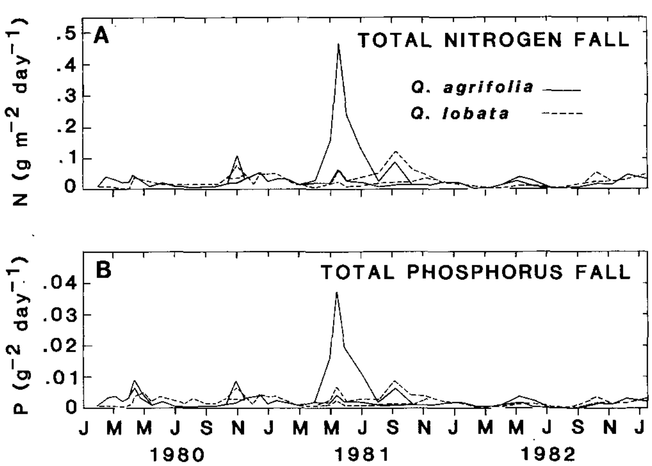

Fig. 2A, B. Total dry nitrogen and phosphorus fall from *Q. agrifolia* and *Q. lobata*

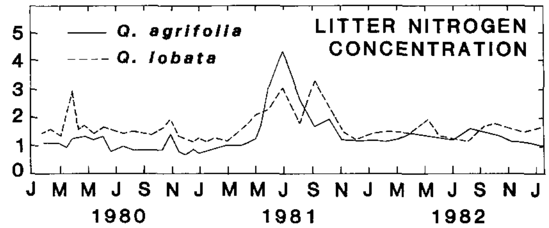

Fig. 3. Mean nitrogen concentration of material caught in litter traps

brown leaves made up the largest fraction of litterfall during the 1980–1982 period; 34.1% of the material consisted of twigs while most of the remaining material consisted of frass (17.9%) (Table 1). Brown leaves comprised 48.6% and 42.5% of the litter from the *Q. lobata* trees during the preoutbreak and postoutbreak years respectively, but only 26.1% during the *Phryganidia* outbreak when a greater amount of the foliage was converted to frass. Approximately 7.3 and 12.8 percent of the litterfall in the years before and after the outbreak consisted of frass. This amount rose to 30.8% of the total during the *Phryganidia* outbreak. Twigs comprised about one-third of the litterfall throughout the 3 year study period. This is in contrast to the results from *Q. agrifolia* where twigs made up about an eighth of the preoutbreak litter and increased substantially following defoliation. There were few fruits produced by the *Q. lobata* trees during this study.

The seasonal pattern of litterfall (Fig. 1) clearly shows the two annual generations of *Phryganidia* (Fig. 1B) as well as the marked decrease in brown leaf litterfall from the *Q. agrifolia* trees following defoliation (Fig. 1C). Fruit and flower litterfall decreased during and after oakmoth outbreak (Fig. 1F) in both species of *Quercus*. Also apparent is a correlation between storms with high winds and green leaf and twig fall (Fig. 1D and E).

Nitrogen and phosphorus in litterfall

Total nitrogen fall from both oak species during this study was controlled by the herbivore *Phryganidia* (Fig. 2A). N loss from each of the study trees was highest in year 1981 ($P = 0.012$). Both the total amount of litterfall (Fig. 1) and the nitrogen concentration of the litterfall increased during the outbreak. The latter increased dramatically (Fig. 3) because of the higher nitrogen concentration of frass relative to brown leaves, twigs and fruits, and because of the very high nitrogen concentrations (9–10%) of dead *Phryganidia* larvae and adults. The importance of the insects as vectors for nitrogen and phosphorus flow is shown in Tables 2 and 3. Insects comprised in mass only about 2.8% of the three year litterfall from the *Q. agrifolia* trees (Table 1), but carried with them 21.1% of the total nitrogen fall and 20.8 percent of the total phosphorus fall (Table 2). Insects made up 2.2% of the three year litterfall from the *Q. lobata* trees but contained 13.4% and 11.8% of the nitrogen and phosphorus fall respectively.

In *Q. agrifolia*, 34.6% of the three year nitrogen fall was contained in the frass while 21.3% of the nitrogen fall was found in frass from *Q. lobata*. Brown leaves contained a lower percentage of nitrogen (21.0%) than frass in *Q. agrifolia* but a greater percentage (35.6%) than frass in *Q. lobata*. Fruits were relatively impoverished in nitrogen while flowers were relatively enriched in this nutrient (Table 2). The mean nitrogen concentration of *Q. lobata* litter was higher than *Q. agrifolia* litter before the defoliation of both species.

The pattern of total phosphorus in the litterfall was similar to that of nitrogen (Fig. 2B) with all trees losing

Table 2. Nitrogen and phosphorus flow (g m^{-2} yr^{-1}) (means for 2 trees of each species)

	Quercus agrifolia						*Quercus lobata*					
	1980		1981		1982		1980		1981		1982	
	N	P	N	P	N	P	N	P	N	P	N	P
Brown lvs	4.31	0.37	3.71	0.23	1.07	0.08	4.29	0.33	3.03	0.20	3.70	0.23
Green lvs	0.34	0.03	0.82	0.06	1.40	0.11	0.28	0.04	0.28	0.03	0.24	0.02
Twigs	1.11	0.08	1.11	0.09	2.07	0.10	2.48	0.31	2.27	0.24	1.85	0.15
Fruit	1.01	0.12	0.09	0.01	0.40	0.04	0.15	0.02	0.12	0.01	0.19	0.02
Flowers	0.52	0.10	0.70	0.06	0.17	0.02	0.57	0.06	0.17	0.02	0.01	0.00
Misc.	0.06	0.01	0.09	0.01	0.18	0.02	0.11	0.01	0.22	0.02	0.22	0.02
Frass	2.24	0.22	11.37	0.96	1.37	0.11	0.95	0.09	4.42	0.31	1.22	0.08
Insects	0.12	0.01	8.96	0.72	0.05	0.00	0.19	0.01	3.76	0.27	0.20	0.01
Total dry	9.71	0.92	26.85	2.13	6.72	0.48	9.02	0.88	14.27	1.10	7.63	0.53
Leached from canopy	3.68	0.30	2.25	0.22	[a]	–	1.10	0.33	1.36	0.24	–	–
Total	13.39	1.22	29.10	2.35	10.40	0.78	10.12	1.21	15.63	1.34	8.74	0.86

(Individual values may not sum to totals because of rounding.)
[a] Not measured in 1982; total values for 1982 assume leaching losses equal to those recorded in 1980

Table 3. Nitrogen and phosphorus rapidly leached from litter and frass (mg N and P g^{-1}) (mean and standard deviation)

Sample	% N	% P	Loss after 24 h	
			% Total N	% Total P
Q. lobata				
Litter	1.70 (0.38)[a]	0.105 (0.016)[a]	9.4 (4.5)[a]	45.7 (11.4)
Frass	1.65 (0.22)[b]	0.079 (0.011)[b]	42.3 (1.8)[a b]	51.9 (13.9)
Q. agrifolia				
Litter	0.76 (0.21)[a b]	0.038 (0.028)[a b c]	5.9 (2.1)[b]	44.7 (6.3)[a]
Frass	1.18 (0.13)	0.090 (0.037)[c]	27.5 (2.8)[a b]	63.3 (12.2)[a]

Means in each column with same letter significantly different ($P < 0.05$, Tukey's test)

the largest amount of phosphorus during the outbreak year ($P = 0.012$). About 50% of the three year total *P* in *Q. agrifolia* litterfall returned to the ground as frass or insect remains during the outbreak year, and about 31% in *Q. lobata* returned in this way. Twig litter and brown leaf litter from *Q. lobata* contained similar amounts of phosphorus (27.8% of the three year total compared to 30.2%) while in *Q. agrifolia*, twig litter contained less than one-half the phosphorus of brown leaf litter (7.7% of the three year total compared to 19.2%).

Nitrogen and phosphorus in throughfall

Total nitrogen in precipitation amounted to approximately 0.46 g m^{-2} yr^{-1} in 1980 and less than the detection limit of approximately 0.27 g m^{-2} yr^{-1} in 1981 (Table 5). Total phosphorus in precipitation was less than the detection limit of approximately 0.07 g m^{-2} yr^{-1} for both years.

Total nitrogen leached via throughfall from the canopies averaged 2.97 g m^{-2} yr^{-1} from *Q. agrifolia* and 1.23 g m^{-2} yr^{-1} from *Q. lobata*. Total phosphorus leached into throughfall was similar for both species, averaging 0.26 g m^{-2} yr^{-1} from *Q. agrifolia* and 0.29 from *Q. lobata* (Table 2). These values represent approximately 23 and 12% of the preoutbreak total annual amount of nitrogen and 22 and 25% of the preoutbreak total annual amount of phosphorus returned to the soil per unit area from *Q. agrifolia* and *Q. lobata* respectively.

Litter and frass leaching

Significantly more nitrogen was rapidly leached from frass samples than from leaf litter samples in both *Q. lobata* and *Q. agrifolia* (Fig. 4). During all time periods, N loss from *Q. lobata* frass >N loss from *Q. agrifolia* frass >N loss from *Q. lobata* leaf litter >N loss from *Q. agrifolia* leaf litter. After 24 h 42% of the nitrogen in *Q. lobata* frass was lost compared to only 9% of the nitrogen in *Q. lobata* leaf litter (Table 3). Similarly, after 24 h 28% of the nitrogen in *Q. agrifolia* frass was lost while only approximately 6% of the nitrogen in *Q. agrifolia* leaf litter was lost.

Phosphorus loss was measured after 24 h of sample leaching. Significantly more P was leached from *Q. agrifolia*

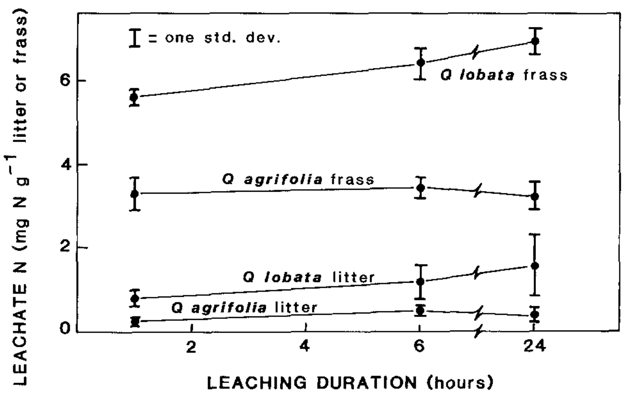

Fig. 4. Nitrogen leached from *Quercus* foliage litter and *Phryganidia* frass as a function of immersion time

frass than leaf litter (Table 3). However, P loss from *Q. lobata* frass and litter were not significantly different. Relatively more phosphorus than nitrogen was leached from all samples after 24 h.

Discussion

Comparison to other systems

Leaf nitrogen and phosphorus concentrations in both species studied here are relatively high compared to other values reported for *Quercus* (Table 4). The leaf specific weights in the California oaks are also considerably higher than in the other species reported, and may represent an adaptation common to plants occurring in a mediterranean-type environment (Mooney et al. 1977). The leaf area index of the evergreen *Q. agrifolia* is considerably higher than that of the deciduous species reported here, but in the range of other evergreens reported by Larcher (1980). The LAI of *Q. lobata* is somewhat lower than that of the other *Quercus* species. Because of the high leaf specific weight and high nitrogen concentration, however, there is actually a greater content of nitrogen per unit ground area in *Q. lobata* than in the deciduous trees of the *Q. coccinea* and *Q. alba* forest (Woodwell et al. 1975) or the *Q. stellata* and *Q. marilandrica* forest (Johnson and Risser 1974).

Litter and nutrient flow to the soil beneath *Q. lobata* and *Q. agrifolia* is high (Table 5). This probably reflects both the climate in which these species occur and their growth form as isolated trees. The mediterranean-type climate of California is characterized by a long growing season and high irradiances, both conducive to high productivity. In addition, the isolated growth of the trees in this study allows them to exploit the resources of large soil and aerial volumes without competition from other trees. The high production of litter by the *Quercus* species suggest that their primary productivity would be high. The average deposition of frass beneath the trees under study here is also high, indicating that high rates of production are not inconsistent with relatively high rates of herbivory.

Herbivory

Phryganidia severely impacted the litterfall and nutrient dynamics of *Q. lobata* and *Q. agrifolia* during this study. If we assume that this outbreak of *Phryganidia* was typical, and take the average outbreak frequency as 5 years (Harville 1955), then even if there is no loss to herbivory during the remaining years, on average about 25 percent of *Q. agrifolia* litter is composed of *Phryganidia* frass and insect remains. A somewhat smaller amount, 12 percent of the litter mass, is returned as frass and insect remains beneath *Q. lobata*. Each gram of *Phryganidia* frass litter collected represents approximately 1.10 grams of *Q. agrifolia* foliage and 1.39 grams of *Q. lobata* foliage (Puttick, personal comm.), the difference reflecting the higher quality of *Q. lobata* as a larval food source. Thus, assuming a 5 year cycle of defoliation consisting of three years as reported in this study and two years with no defoliation but production identical to the values before the outbreak, *Phryganidia*, on average, consumes about 35% of the annual foliage production in *Q. agrifolia* and 25% in *Q. lobata*. During peak years, *Phryganidia* removes most or all of the foliage of both species. Note that this represents 2 years worth of production for the evergreen. *Q. agrifolia* individuals that grew adjacent to deciduous oaks suffered losses in addition to these during the outbreak year. After the initial defoliation in June, the *Q. agrifolia* trees produced new leaves. In August, late instar *Phryganidia* larvae were observed leaving their defoliated deciduous hosts, and climbing the trunks of adjacent *Q. agrifolia* individuals which were then defoliated for the second time in three months. Assuming that this double defoliation has a negative effect on the *Q. agrifolia* individ-

Table 4. Comparison of *Quercus* leaf characteristics

Deciduous Trees	Location	% N	% P	sp wt. ($g\ m^{-2}$)	LAI
Q. lobata[a]	California	2.35	0.140	159	2.6
Q. coccinea[b]	New York	0.79	0.049	121	3.4
Q. alba[b]	New York	0.79	0.063		
Q. stellata[c]	Oklahoma	1.54	0.144	119	4
Q. marilandrica[c]	Oklahoma	1.38	0.124		
Q. kelloggii[d]	California	2.23	0.120		
Evergreen Trees (old and new leaves)					
Q. agrifolia[a]	California	1.38	0.095	221	6.5
Q. ilex[e]	France	1.33	0.140		
Q. wislizenii[d]	California	1.49	0.086		
Q. chrysolepis[d]	California	1.20	0.080		
Q. agrifolia[f]	California	1.15	0.08	130	3.6

[a] Current study (1980 midsummer values)
[b] Woodwell et al. 1975
[c] Johnson and Risser 1974
[d] Wheeler 1975
[e] Rapp 1969b
[f] (Shrub form) Mooney et al. 1977

Table 5. Comparison of annual litter and nutrient flow in several tree species ($g\ m^{-2}\ yr^{-1}$)

Deciduous Trees	Foliage biomass	Total litter biomass	Frass litter biomass	Nutrient flux					
				Thrufall		Litter		Total	
				N	P	N	P	N	P
Q. lobata[a]	411	621	45.6	1.2	0.29	9.0	0.88	10.2	1.17
Q. stellata[b] *Q. marilandrica*[b]	476	514		1.0	0.09	4.1	0.36	5.1	0.45
Q. petraea[c]	382	386	16.8	−0.1	0.09	4.1	0.22	4.0	0.31
Hubbard Brook[d]	315	559	18.0	1.0	0.07	5.3	0.36	6.3	0.43
Evergreen Trees									
Q. agrifolia[a]	1,422	997	155.2	3.0	0.26	9.7	0.92	12.7	1.18
Q. ilex[e]	700	542		0.5	0.26	6.0	0.62	6.5	0.86

[a] Present study (pre-outbreak year only)
[b] Johnson and Risser 1974
[c] Carlisle et al. 1966a, b
[d] Whittaker et al. 1974, 1979; Gosz et al. 1972
[e] Rapp 1969a, b; Lossaint 1973

uals, this phenomenon would contribute to a locally disjunct distribution of the evergreen and deciduous oaks.

The average foliage losses for these California *Quercus* are considerably higher than the 3 to 11% of annual foliage production lost to herbivores in other forest systems (Bray 1964; Whittaker and Woodwell 1969; Gosz et al. 1972; Larsson and Tenow 1980; Ohmart et al. 1983), and compare well with peak losses during outbreaks of phytophagous insects in other systems. Carlisle et al. (1966a) reported a peak loss of 24% of the annual foliage production in a *Quercus petraea* forest during an outbreak of *Tortrix viridana* (Lepidoptera) while Waide et al. (unpublished, cited in Swank et al. 1981) noted that 33% of the foliage in a mixed hardwoods forest was consumed by the fall cankerworm, *Alsophila pometaria* (Lepidoptera: Geometridae) during an outbreak of this herbivore. Only in a few forest systems do losses equal those experienced by *Q. agrifolia* here. For example, Miller (1966) reported total loss of current year foliage for two years running by *Abies balsamea* to the blackheaded budworm, *Acleris variana* (Lepidoptera: Tortricidae). Budworm outbreaks appear to be much less frequent than those of the California oakmoth, however, occurring at intervals of 10–15 years (Miller 1966) or even less often (Blais 1965).

The frequency and extent of defoliation in these *Quercus* species means that on average, 37% of the nitrogen and phosphorus returning to the soil beneath *Q. agrifolia* trees flows through insect frass or dead insects. In *Q. lobata*, the figures are respectively 24% of the nitrogen flow and 18% of the phosphorus flow to the ground. Leaching of N and P from the canopy did not apparently increase during the *Phryganidia* outbreak, probably because of the seasonal nature of precipitation at the study site. In a more mesic site, however, partial defoliation increased leaching loss of cesium-134 (a potassium analogue) from red pine (Kimmins 1972).

It appears that since *Phryganidia* strongly affects both the quantity and quality (leachability) of litterfall in these oaks, *Phryganidia* also probably exerts strong control on the subsequent processes of decomposition, mineralization, immobilization and uptake beneath these trees. It should be clear, however, that as a consequence of the evergreen growth form, the effect of *Phryganidia* on *Q. agrifolia* during outbreak years is far more severe in terms of the total quantity of biomass and nutrients lost than the effect of this herbivore on *Q. lobata*. These data support the hypothesis of Mooney and Hayes (1973) who, in finding that the bulk of the carbohydrate reserves of *Q. agrifolia* were contained in the leaves, speculated that this species might be more vulnerable to defoliation than a deciduous species which stored carbohydrates throughout the plant.

Many researchers have hypothesized recently that herbivores may increase plant fitness (Owen and Wiegert 1976; Owen 1980) or regulate system productivity and nutrient cycling (Chew 1974; Mattson and Addy 1975; Kitchell et al. 1979). Most of these hypotheses explicitly relate a beneficial or regulatory effect of herbivory to the increased flow of nutrients through herbivore frass which then presumably stimulates primary productivity. In this system, however, the seasonal nature of precipitation and large quantities of easily leached frass and insect remains suggest that with the first rains of the season large pulses of N and P would be released from the litter. It appears likely that here, herbivory leads to increased losses of nitrogen and possibly phosphorus. These potential system loses need to be quantified. Such herbivore induced losses of ecosystem N have been seen in other systems (Swank et al. 1981).

There is also no evidence to suggest that productivity is enhanced by defoliation in this system. Instead, productivity is apparently high despite *Phryganidia*. Both oak species, however, produced less foliage and litter following defoliation. Reproduction was also reduced or eliminated during and following defoliation.

Conclusions

During normal years, *Q. agrifolia* and *Q. lobata* produce relatively large quantities of litter which carry large amounts of nitrogen and phosphorus to the soil surface while a lesser fraction is leached directly from the canopy by rain throughfall. The total fluxes of N and P during these years are more similar between these two species than they are to fluxes in other oaks in other parts of the world, even though one of the species is deciduous while the other is evergreen. This suggests that the climate, substrate and perhaps isolated growth of the trees under study was more important than their lifeform *per se* in regulating nutrient fluxes.

During an oakmoth outbreak (approximately 1 out of 5 years), essentially all individuals of both species were defoliated. The nitrogen and phosphorus contained in the easily leached frass and dead insects represented 41 to 130 percent of the average input of these nutrients into the litter. The effect of this enormous pulse of N and P on decomposition and other soil processes remains unexplored, although it is likely that decomposition rates will be accelerated. The frequency of oakmoth outbreak suggests that N and P cycling in these Californian oaks are strongly influenced if not "controlled" by this herbivore. However, there is no evidence that productivity or reproduction in these oaks is enhanced by *Phryganidia* herbivory.

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