# The Influence of Epiphytic Lichens on the Nutrient Cycling of a Blue Oak Woodland[1]

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***Abstract:*** *We evaluated the importance of epiphytic lichens in the nutrient cycling of a blue oak (*Quercus douglasii*) woodland in California. Each oak tree contained an average of 3.8 kg lichen biomass, totaling 590 kg per ha. For comparison, oak leaf biomass was 958 kg per ha. We compared tree growth, volume and composition of throughfall (rainfall falling though the tree canopy), litterfall, and soil nutrients under 20 trees from which we removed the lichens to 20 control trees. The removal of lichens had no effect on the growth of the oak trees, but it did influence nutrient cycling fluxes significantly. We calculated an enhanced atmospheric deposition for nitrogen of 2.85 kg/ha/yr and for phosphorus of 0.15 kg/ha/yr. This is caused by the presence of epiphytic lichens in the canopy where they act as an intercepting surface, enhancing dry deposition into the tree canopy. Thus, epiphytes can significantly influence nutrient fluxes in blue oak woodlands. This also supports the hypothesis that the tree canopy influences atmospheric deposition and that this, in turn, contributes to the observed "canopy effect" on the understory productivity in oak savannas.*

A large part of the California landscape is made up of oak woodlands, and in the past 20 years considerable research has focused on understanding the functioning of these ecosystems. Most of these studies have focused on the dominant growth forms in these ecosystems, and consequently, there is abundant evidence that oak trees and the annual grass understory both influence energy, water, and nutrient balances (Callaway and others 1991, Gordon and Rice 1992, Holland 1973, Huenneke and Mooney 1989, Jackson and others 1990, McNaughton 1968, Mooney and others 1986). However, one understudied group is the epiphytic community, which can make up a substantial part of the aboveground biomass in oak woodlands (Boucher and Nash 1990, Callaway and Nadkarni 1991). Epiphytes are known to affect ecosystem processes in various forest ecosystems (Knops and others 1996, Lang and others 1980, Nadkarni 1986, Pike 1978). In this study, we examine whether epiphytes are a significant part of California oak woodlands.

Lichens are the dominant taxonomic group of epiphytes present in Californian oak woodlands, and *Ramalina menziesii* (lace lichen) is the most conspicuous lichen in the coastal foothill oak woodlands (Larson and others 1985, Rundel 1974) and is considered the unofficial State lichen of California (Hale and Cole 1988). *Ramalina menziesii* occurs along the coast from Baja California to southern Alaska. It is very sensitive to air pollution (Boonpragob and Nash 1991, Sigal and Nash 1983) and is especially abundant in areas with frequent fog (Larson and others 1985). This is partly because lichens do not tap into the vascular system of their host trees, but they depend entirely on rainfall, dew, fog, and atmospheric water vapor (Matthes-Sears and Nash 1986).

## Study Area and Methods

This research was conducted at the Hastings Natural History Reservation, which is a field station of the University of California at Berkeley. Hastings is located in the Santa Lucia Mountains in the central coast of California (Carmel Valley, Monterey County) approximately 20 km east of the Pacific Ocean and 42 km

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southeast of Carmel. Hastings has a typical Mediterranean climate with winter rains and summer droughts. Annual rainfall averaged 524 mm over the past 55 years, with a mean monthly minimum temperature ranging from 1.4 °C in January to 9.7 °C in August and the mean maximum ranging from 15.6 °C in January to 30.4 °C in July. Coastal fog occasionally reaches the study site in the spring and early summer; however, the effect of the fog on the vegetation and specifically on the epiphytic lichens is minimal (Matthes-Sears and others 1986).

Our study site was a south-facing blue oak (*Quercus douglasii)* woodland (elevation 550 m), with a tree density of 157 trees per ha and a canopy cover of 58 percent. A 0.65-ha area was fenced with a deer-proof fence in December 1989. A factorial experiment was established with combinations of two factors: canopy with and without lichens, and soil with and without lichens as a component of the litterfall. This experimental design allowed us to examine independently the effect of epiphytic lichens in the canopy and the effects of lichen decomposition on the ground. We selected 40 trees within our study site and randomly divided them into four groups of 10 trees, with individual trees as the basic sampling units. The lichen removal trees were stripped of canopy and branch lichens in December 1989. The soil treatments were established by either removing or not removing the lichen litterfall on a monthly basis, the lichen litter from the treatment with canopy lichens (but no lichen litter) was moved to the treatment of no-canopy lichens but with lichen litter starting in February 1990.

Throughout 3 years we measured the effect of the treatments on litterfall, throughfall (rainfall falling through a tree canopy), soil nitrogen and phosphorus, and tree growth. In addition, atmospheric deposition was measured outside the canopy, and we measured oak leaf and lichen litter decomposition in a separate experiment. A complete description of all experimental methods is given by Knops (1994). In short, litterfall was measured, in 200 black plastic plant pots (top diameter 50 cm and 40 cm high) on a monthly basis in five collectors under each tree, beginning March 20, 1990. Throughfall was collected in a bottle with a funnel on the top, starting February 20, 1990. Soil nutrients were measured both as total nitrogen and phosphorus and available nitrogen and phosphorus. The latter were measured by using ion exchange resin bags, buried in the field from October 1992 through April 1993. Tree growth was measured by comparing the annual amount of leaffall and acorn litterfall under each tree and by measuring the tree ring width. Tree ring width was measured on two 5-cm-long cores taken on opposite sides of the tree, using an increment borer, processed and measured following standard dendroecological methods (Phipps 1985). Atmospheric deposition was measured in two Aerochem Metrics automated wetfall/dryfall collectors and in 10 throughfall collectors placed outside the canopy. Litter decomposition was measured in litterbags, for a 4-year period, starting in January 1990. We constructed 160 litterbags containing either oak leaves, or a mixture of equal amounts of oak leaves and lichen litter. Twenty litterbags of each type were collected each year. Chemical analyses of rainfall, throughfall, litter, and soil samples were performed with standard autoanalyzer techniques following a persulfate digestion for measurements of total nitrogen and phosphorus in liquid samples. Throughfall and rainfall were also analyzed for chloride, sulfate, nitrate, ammonium, calcium, magnesium, sodium, and potassium (cations on an atomic absorption spectrometer and anions on an ion chromatograph).

## Results and Discussion

We removed all epiphytic lichens from 21 blue oak trees and these trees contained on average 3,794 ± 658 g dry lichen biomass per tree (average ± 1 S.E.). One tree was a hybrid (between *Quercus douglasii* and *Quercus lobata*) and was used only to calculate the lichen biomass. There were 101 trees in our 0.65-ha experimental area,

so the standing crop of epiphytic lichens was 590 kg per ha. *Ramalina menziesii* was the dominant lichen species, contributing 78 percent of the biomass, followed by *Usnea* spp. (20 percent). All other lichen species contributed less than 2 percent.

Rainfall was 463 mm from July 1, 1990 through June 30, 1991, and 545 mm in the following year, giving an average of 504 mm (*table 1*). The average throughfall

***Table 1—Total annual deposition of the throughfall, nitrogen (N) and phosphorus (P)*** [1]

| Element | Year | Treatments | | | *F*-values | |
|---|---|---|---|---|---|---|
| | | Bulk deposition | Canopy without lichens | Canopy with lichens | Canopy versus bulk deposition | Canopy with versus Canopy without lichens |
| | | *mm* | | | | |
| Throughfall | 90-91 | 463 ± 3 | 422 ± 8 | 387 ± 10 | 17.59 *** | 7.09 * |
| Throughfall | 91-92 | 545 ± 4 | 515 ± 11 | 468 ± 14 | 7.76 ** | 6.89 * |
| | | $g/m^2$ | | | | |
| Total N | 90-91 | 95 ± 12 | 261 ± 14 | 299 ± 18 | 47.67 *** | 2.66 |
| Total N | 91-92 | 141 ± 7 | 283 ± 16 | 329 ± 17 | 44.40 *** | 3.88 |
| | | $g/m^2$ | | | | |
| Total P | 90-91 | 13 ± 4 | 166 ± 13 | 145 ± 14 | 55.55 *** | 1.28 |
| Total P | 91-92 | 43 ± 8 | 218 ± 17 | 195 ± 17 | 43.84 *** | 0.86 |

[1]The means ± 1 S.E. are given for the canopy without lichens ($n$=20), canopy with lichens ($n$=20), and the bulk deposition (90–91 $n$ = 16, 91–92 $n$ = 10). Data were collected monthly and tabulated by year from May 16, 1990 through May 16, 1991, and from May 16, 1991 through July 16, 1992. The two canopy treatments and the canopy-versus-bulk deposition were compared with an ANOVA, and the F-values associated with the treatments are given (*$P$<0.05; **$P$<0.01; ***$P$<0.001). The two canopy treatments were combined to compare canopy versus open deposition (resulting in a sample size of 40 for the canopy).

amount was 428 mm under the trees with epiphytic lichens and 469 mm under the trees from which we removed the epiphytic lichens. Thus, a tree canopy without lichens intercepts 7 percent of the rainfall; a tree canopy with lichens, 15 percent; and the lichens in the tree, 8 percent. Our canopy cover was 58 percent, which implies that the presence of epiphytic lichens lowers the total rainfall reaching the soil by 5 percent. We should keep in mind here that most of the rainfall occurs in the winter months and that this reduction in rainfall is not likely to influence the growth of the trees or the grass, because the oak trees are leafless and inactive and the grass productivity during the winter months is limited by the low temperatures. We found no differences in xylem water potential of the trees in the different treatments in late summer, the time when blue oak trees have the highest water stress (Griffin 1973, Knops 1994, Knops and Koenig 1994). However, the total runoff and groundwater recharge is likely to be lowered, resulting in a lowered water yield, but also lower rates of soil erosion.

Because blue oak woodlands frequently occur on low-fertility soils and understory productivity is often limited by nitrogen and/or phosphorus (Menke 1989), we focused most of the research on these two elements.

In the short term, phosphorus cycling is controlled by biological processes, and the phosphorus availability is primarily dependent on the rates of litter decomposition and mineralization of soil organic matter (Cross and Schlesinger 1995). Globally, the largest pool of phosphorus is in rocks and ocean sediments, and the long-term main source of phosphorus for terrestrial plants is rock weathering (Schlesinger 1991). We did not study rock weathering, because it is not likely that epiphytes have any measurable effect on this.

Global nitrogen pools are strongly dominated by the atmosphere, because air contains 78 percent nitrogen ($N_2$). However, this form of nitrogen is inert and not available for plants. Transformations from atmospheric $N_2$ to plant-available nitrogen are through biological fixation by micro-organisms (Schlesinger 1991), but these rates are generally low in California oak woodlands (Ellis and others 1983). Consequently, intrasystem recycling is the dominant source of plant-available nitrogen (Woodmansee and Duncan 1980). However, nitrogen is much more mobile than phosphorus, and ecosystems in general are much less closed, so that inputs and outputs of nitrogen compounds are important on time scales of decades in natural ecosystems. Atmospheric deposition is the main input pathway of nitrogen into ecosystems, and air pollution episodes show that we can influence the productivity of an ecosystem with the amount of nitrogen in atmospheric deposition (Vitousek 1994).

Atmospheric deposition (bulk deposition) of nitrogen was 1.18 kg/ha/yr and that of phosphorus was 0.28 kg/ha/yr (*table 1*). These values, especially for nitrogen, are very low, and there is no indication of air pollution at this site. The throughfall amounts of both nitrogen and phosphorus are much higher because a substantial amount of both elements can be leached from the oak leaves. In addition, there is also an accumulation of dry deposition (dust) into the tree canopy, which can be washed off by rainfall. Dry deposition is difficult to quantify because it is indistinguishable from the leached nitrogen and phosphorus, but dry deposition is potentially important as a nutrient input (Johnson and Lindberg 1991). Dry deposition rates are strongly influenced by the intercepting surface. Although we cannot determine the exact dry deposition of both elements in our study, we can get an indication of its importance by subtracting the amount of throughfall in a tree canopy without lichens from the amount of throughfall in a tree canopy with lichens. Because lichens have no vascular connection to the soil, the depletion or enrichment of nutrient elements in throughfall must be caused by dry deposition onto the lichen thallus surface. We calculated this for nitrogen and phosphorus and found that the throughfall was enriched by 42 mg $N/m^2/yr$ (i.e. 299+329-261-283) and depleted by 22 mg $P/m^2/yr$ (i.e. 145+195-166-218) (*table 1*).

Lichens also take up nutrients for their growth and incorporate these into their thallus. If we assume that the canopy lichen biomass is in a steady state (i.e., their loss of biomass in the litterfall is balanced by their growth), we can use the amount of lichen litterfall as an index of their growth. The lichen litterfall contained 445 mg $N/m^2/yr$ (i.e. (0.39+0.52)/2) and 48 mg $P/m^2/yr$ (i.e. (0.045+0.051)/2) (*table 2*). If these amounts are added to the throughfall amount, this suggests that 497 mg $N/m^2/yr$ and 26 mg $P/m^2/yr$ are deposited by dry deposition into the tree canopy as a result of the presence of epiphytic lichens as an intercepting surface in the canopy. For our study site, which has a tree cover of 58 percent, this is equivalent to 2.85 kg nitrogen (N) and 0.15 kg of phosphorus (P) per hectare per year. Thus, epiphytic lichens substantially enhance atmospheric deposition of nitrogen into these ecosystems. We do not know how much additional dry deposition occurred on oak leaves and branches; however, this would likely add substantially to these dry deposition estimates. If the deposition on leaves is proportional to their surface area and we assume that their surface area per amount of mass is half that of the lichens, then atmospheric deposition of nitrogen is approximately 5 kg/ha/yr. This is substantially higher than our bulk deposition estimates and implies that atmospheric deposition is an important component of the available nitrogen in this ecosystem; by comparison, we estimate the nitrogen mineralization in the soil at approximately 50 kg/ha/yr (Knops 1994).

Despite the large quantity of lichen biomass present, we found no major effects of our experimental removal of lichens on the growth of oak trees. Trees in the different treatments produced the same amount of leaves and/or

acorns *(table 2)* and tree ring growth did not differ between the treatments *(table 3)*. There are several likely explanations for the lack of a significant effect of our experimental treatments on tree growth and nutrient dynamics. First, plants occupying infertile environments are often not very responsive to nutrient additions (Chapin and others 1986, Koide and others 1988). Second, it is possible that a different factor, such as water availability, limited tree growth. Water correlates strongly with the annual ring width increment in *Quercus douglasii* at Hastings (Knops and Koenig, unpublished data[5]) and throughout its range (Kertis and others 1993). Third, the intrasystem nutrient pools are large, compared to the change in nutrient fluxes induced by our experiment, so the enhanced deposition might be too small to be detected in soil fluxes and pools in 3 years. Surface soils under *Quercus douglasii* at Hastings average 6.7 mg N/g soil and 0.3 mg P/g soil (*table 4*, Knops 1994), with a bulk density of 1.0 g/cm$^3$ (Callaway and others 1991). For the upper 30

***Table 2—Total annual litterfall biomass*** [1]

| | Category | Treatments | | | | *F*-values | | |
|---|---|---|---|---|---|---|---|---|
| | | Canopy without lichens, litter without lichens | Canopy without lichens, litter with lichens | Canopy with lichens, litter without | Canopy with lichens, litter | Canopy | Litter | Canopy by litter |
| | | *g/m²* | | | | | | |
| Biomass | Total biomass | 246 ± 20 | 302 ± 17 | 377 ± 36 | 377 ± 35 | 13.27** | 0.95 | 1.00 |
| | Oak leaves | 139 ± 13 | 175 ± 9 | 179 ± 14 | 168 ± 13 | 1.71 | 1.06 | 3.51 |
| | Acorns | 18 ± 7 | 18 ± 5 | 22 ± 4 | 20 ± 4 | 0.23 | 0.01 | 0.07 |
| | Miscellaneous | 79 ± 8 | 96 ± 9 | 143 ± 24 | 138 ± 24 | 8.76** | 0.11 | 0.37 |
| | Lichens | 9 ± 1 | 11 ± 1 | 33 ± 5 | 50 ± 12 | 23.96*** | 2.31 | 1.26 |
| | | *g/m²* | | | | | | |
| Nitrogen | Total biomass | 2.05 ± 0.17 | 2.51 ± 0.16 | 3.01 ± 0.25 | 2.96 ± 0.21 | 12.64** | 1.11 | 1.60 |
| | Oak leaves | 0.97 ± 0.08 | 1.22 ± 0.07 | 1.21 ± 0.10 | 1.18 ± 0.10 | 1.30 | 1.57 | 2.56 |
| | Acorns | 0.12 ± 0.04 | 0.13 ± 0.04 | 0.16 ± 0.03 | 0.14 ± 0.03 | 0.41 | 0.00 | 0.22 |
| | Miscellaneous | 0.84 ± 0.08 | 1.01 ± 0.09 | 1.25 ± 0.14 | 1.13 ± 0.09 | 6.37* | 0.05 | 1.93 |
| | Lichens | 0.11 ± 0.02 | 0.14 ± 0.02 | 0.39 ± 0.06 | 0.52 ± 0.10 | 30.74*** | 1.68 | 0.59 |
| | | *g/m²* | | | | | | |
| Phosphorus | Total biomass | 0.462 ± 0.040 | 0.583 ± 0.039 | 0.633 ± 0.049 | 0.594 ± 0.048 | 4.23* | 0.85 | 3.26 |
| | Oak leaves | 0.326 ± 0.034 | 0.414 ± 0.026 | 0.427 ± 0.033 | 0.403 ± 0.035 | 1.98 | 0.97 | 3.03 |
| | Acorns | 0.015 ± 0.006 | 0.018 ± 0.005 | 0.020 ± 0.004 | 0.019 ± 0.004 | 0.50 | 0.02 | 0.15 |
| | Miscellaneous | 0.108 ± 0.010 | 0.134 ± 0.016 | 0.140 ± 0.013 | 0.121 ± 0.011 | 0.53 | 0.08 | 3.16 |
| | Lichens | 0.013 ± 0.002 | 0.017 ± 0.002 | 0.045 ± 0.007 | 0.051 ± 0.010 | 28.28*** | 0.63 | 0.01 |

[1] All data are 3-year means ± 1 s.e., $n = 10$ trees in all cases. $F$ values are from a two-way ANOVA with 36, 1, 1, 1 degrees of freedom (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

cm, this translates to 2,100 g/m$^2$ of nitrogen and 90 g/m$^2$ of phosphorus. We found an enhanced atmospheric deposition because of the epiphytic lichens of 497 mg N/m$^2$/yr and 26 mg P/m$^2$/yr. Thus, annual enhancement of either nutrient is minor compared to the total soil nutrient pools and the annual mineralization in these pools, which is approximately 1-3 percent annually (Jackson and others 1988, Knops 1994). The past contribution of lichens to the soil pool of nitrogen, a development process likely occurring over centuries, is unknown, and its estimate is beyond the scope of our data.

[5]Unpublished data on file at the Hastings Natural History Reservation, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924

*Table 3—Annual relative tree ring width* [1]

| Year | Treatments | | | | *F*-values | | |
|---|---|---|---|---|---|---|---|
| | Canopy without lichens, litter without lichens | Canopy without lichens, litter with lichens | Canopy with lichens, litter without lichens | Canopy with lichens, litter with lichens | Canopy | Litter | Canopy by litter |
| | N | | | | | | |
| | 10 | 9 | 7 | 8 | | | |
| 1990 | 0.71 ± 0.04 | 0.71 ± 0.04 | 0.89 ± 0.16 | 0.63 ± 0.10 | 0.33 | 2.17 | 2.14 |
| 1991 | 1.49 ± 0.18 | 1.41 ± 0.12 | 1.34 ± 0.08 | 1.23 ± 0.14 | 1.28 | 0.44 | 0.01 |
| 1992 | 1.48 ± 0.20 | 1.39 ± 0.10 | 1.27 ± 0.07 | 1.40 ± 0.27 | 0.29 | 0.01 | 0.33 |
| 1993 | 1.91 ± 0.14 | 1.95 ± 0.21 | 1.73 ± 0.19 | 1.97 ± 0.31 | 0.14 | 0.41 | 0.21 |
| Total | 5.59 ± 0.48 | 5.47 ± 0.37 | 5.24 ± 0.31 | 5.23 ± 0.74 | 0.33 | 0.02 | 0.01 |

[1] All data are expressed as annual growth divided by the average growth from 1984 through 1989 and are means ± 1 s.e. *F*-values are from a two-way ANOVA with 30, 1, 1, 1 degrees of freedom (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

*Table 4—Soil total nitrogen (N) and phosphorus (P) and absorption of ions on ion exchange resin bags* [1]

| Soil Element | Treatments | | | | *F*-values | | |
|---|---|---|---|---|---|---|---|
| | Canopy without lichens, litter without lichens | Canopy without lichens, litter with lichens | Canopy with lichens, litter without lichens | Canopy with lichens, litter with lichens | Canopy | Litter | Canopy by litter |
| | *mg/g* dry soil | | | | | | |
| Total N | 1039 ± 73 | 1292 ± 68 | 1185 ± 48 | 1120 ± 34 | 0.05 | 2.64 | 7.59** |
| Total P | 462 ± 29 | 473 ± 54 | 414 ± 22 | 437 ± 34 | 1.29 | 0.21 | 0.02 |
| ----- Resin -- | *mg/L* effluent | | | | | | |
| Ammonium | 4.23 ± 0.43 | 3.58 ± 0.40 | 4.20 ± 0.58 | 3.74 ± 0.31 | 0.02 | 1.55 | 0.05 |
| Nitrate | 18.5 ± 3.0 | 21.6 ± 7.0 | 19.7 ± 3.7 | 22.6 ± 4.8 | 0.05 | 0.39 | 0.00 |
| Nitrogen | 22.7 ± 3.4 | 25.2 ± 7.3 | 23.9 ± 4.2 | 26.4 ± 5.1 | 0.05 | 0.23 | 0.00 |
| Phosphate | 44.0 ± 3.8 | 35.1 ± 3.9 | 46.2 ± 4.5 | 37.8 ± 2.9 | 0.43 | 5.14 * | 0.00 |

[1] All data are means ± 1 s.e., $n$=10 in all cases. Samples were collected on April 17, 1992. *F*-values are from a two-way ANOVA with 36, 1, 1, 1 degrees of freedom (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

## Summary and Conclusions

Nutrient availability is higher under the blue oak canopy relative to the surrounding grasslands and it increases understory productivity and species composition (Callaway and others 1991, Frost and McDougald 1989, Holland 1980, McClaran and Bartolome 1989). This canopy effect has also been observed under different oak species in California (Parker and Muller 1982) and in other savannas throughout the world (Belsky 1992, 1994 ; Belsky and others 1989; Kellman 1979; Ko and Reich 1993; Vetaas 1992). The higher local fertility under oaks has been attributed to the presence of a reservoir of organic matter under the tree canopy resulting in higher rates of mineralization and consequently higher availability of nutrients (Jackson and others 1990). However, this does not explain the long-term origin of this organic matter and, thus, the ultimate cause of this canopy effect. The accumulation of the organic matter can be caused by at least three processes. First, trees are thought to concentrate nutrients by taking up from deeper soil layers or intercanopy areas, thereby inducing greater spatial heterogeneity by influencing nutrient cycling within the ecosystem (Vetaas 1992). Second, large herbivores, like cattle and deer, often aggregate for extended periods under tree canopies, concentrating their dung under the canopy

area. Third, the canopy may enhance atmospheric deposition (Kellman 1979, Kellman and Carty 1986) and thereby produce a spatial heterogeneity of nutrient input. Our study provides further evidence that tree canopies enhance atmospheric deposition and that epiphytes can influence these nutrient fluxes.

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## References

Belsky, A. Joy 1992. **Effects of trees on nutritional quality of understory gramineous forage in tropical savannas**. Tropical Grasslands 26: 12-20.

Belsky, A. Joy 1994. **Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition**. Ecology 75: 922-932.

Belsky, A.J.; Amundson, R.G.; Duxbury, J.M.; Riha, S.J.; Ali, A.R.; Mwonga, S.M. 1989. **The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya**. Journal of Applied Ecology 26: 1005-1024.

Boonpragob, Kansi; Nash, Thomas H., III. 1991. **Physiological responses of the lichen *Ramalina menziesii* Tayl. to the Los Angeles urban environment**. Environmental and Experimental Botany 31: 229-238.

Boucher, V.L.; Nash, T.H., III. 1990. **The role of the fructicose lichen *Ramalina menziesii* in the annual turnover of biomass and macronutrients in a blue oak woodland**. Botanical Gazette 151: 114-118.

Callaway, Ragan M.; Nadkarni, Nalini M. 1991. **Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California**. Plant and Soil 137: 209-222.

Callaway, Ragan M.; Nadkarni, Nalini M.; Mahall, Bruce E. 1991. **Facilitation and interfering of *Quercus douglasii* on understory productivity in central California**. Ecology 72: 1484-1499.

Chapin, F. Stuart, III; Vitousek, Peter M.; Van Cleve, Keith. 1986. **The nature of nutrient limitation in plant communities**. American Naturalist 127: 48-58.

Cross, Anne Fernald; Schlesinger, William H. 1995. **A literature review and evaluation of the Hedley fractionation: applications to the biogeochemical cycle of soil phosphorus in natural ecosystems**. Geoderma 64: 197-214.

Ellis, Barbara A.; Verfaillie, Joseph R.; Kummerow, Jochen. 1983. **Nutrient gain from wet and dry atmospheric deposition and rainfall acidity in southern Californian chaparral**. Oecologia 60: 118-121.

Frost, William E.; McDougald, Neil K. 1989. **Tree canopy effects on herbaceous production of annual rangeland during drought**. Journal of Range Management 42: 281-283.

Gordon, D.R.; Rice, K.J. 1992. **Partitioning of space and water between two California annual grassland species**. American Journal of Botany 79: 967-976.

Griffin, James R. 1973. **Xylem sap tension in three woodland oaks in Central California**. Ecology 54: 152-159.

Hale, Mason E, Jr.; Cole, Mariette. 1988. **Lichens of California**. Berkeley: University of California Press; 254 p.

Holland, V.L. 1973. **A study of vegetation and soils under blue oak compared to adjacent open grassland**. Berkeley: University of California. Ph.D. dissertation; 369 p.

Holland, V.L. 1980. **Effect of blue oak on rangeland forage production in Central California**. In: Plumb, Timothy R., technical coordinator. Proceedings of the symposium on ecology, management and utilization of Californian oaks; 1979 June 26-28; Claremont, CA. Gen. Tech. Rep. PSW-44. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 314-318.

Huenneke L.F.; Mooney, H.A. 1989. **Grassland structure and function: California annual grasslands**. Dordrecht: Kluwer Academic Press; 220 p.

Jackson, L.E.; Strauss, R.B.; Firestone, M.K.; Bartolome, J. 1988. **Plant and soil nitrogen dynamics in Californian annual grassland**. Plant and Soil 110: 9-17.

Jackson, L.E.; Strauss, R.B.; Firestone, M.K.; Bartolome, J. 1990. **Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna**. Agriculture, Ecosystems and Environment 32: 89-105.

Johnson, D.W.; Lindberg, S.E. 1991. **Atmospheric deposition and nutrient cycling in forest ecosystems**. New York: Springer Verlag; 707 p.

Kellman, Martin. 1979. **Soil enrichment by neotropical savanna trees**. Journal of Ecology 67: 565-577.

Kellman, M.; Carty, A. 1986. **Magnitude of nutrient influxes from atmospheric sources to a central American *Pinus caribaea* woodland**. Journal of Applied Ecology 23: 211-226.

Kertis, Jane A.; Gross, Rob; Peterson, David L.; Arbaugh, Michael J.; Standiford, Richard B.; McCreary, Douglas D. 1993. **Growth trends of blue oak (*Quercus douglasii*) in California**. Canadian Journal of Forest Research 23: 1720-1724.

Knops, Johannes M.H. 1994. **The influence of epiphytic lichens on the nutrient cycling of an oak woodland**. Tempe: Arizona State University; 146 p. Ph.D. dissertation.

Knops, Johannes M.H.; Koenig, Walter D. 1994. **Water use strategies of five sympatric *Quercus* species in central coastal California**. Madroño 41: 290-301.

Knops, Johannes M.H.; Nash, Thomas H., III; Schlesinger, William H. 1996. **The influence of epiphytic lichens on the nutrient cycling of an oak woodland**. Ecological Monographs 66: 159-180.

Ko, Leonora J.; Reich, Peter B. 1993. **Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin**. American Midland Naturalist 130: 31-42.

Koide, R.T.; Huenneke, L.F.; Hamburg, S.P.; Mooney, H.A. 1988. **Effects of applications of fungicide, phosphorus and nitrogen on the structure and productivity of an annual serpentine plant community**. Functional Ecology 2: 335-344.

Lang, Gerald E.; Reiners, William A.; Pike, Lawrence H. 1980. **Structure and biomass dynamics of epiphytic lichen communities of balsam fir forests in New Hampshire**. Ecology 61: 541-550.

Larson, D.W.; Matthes-Sears, U.; Nash, T.H., III. 1985. **The ecology of *Ramalina menziesii*. I. Geographical variation in form**. Canadian Journal of Botany 63: 2062-2068.

Matthes-Sears, U.; Nash, T.H., III. 1986. **The ecology of *Ramalina menziesii*. V. Estimation of gross carbon gain and thallus hydration source from diurnal measurements and climatic data**. Canadian Journal of Botany 64: 1698-1702.

Matthes-Sears, U.; Nash, T.H., III; Larson, D.W. 1986. **The ecology of *Ramalina menziesii*. III. *In situ* diurnal field measurements at two sites on a coast-inland gradient**. Canadian Journal of Botany 64: 988-996.

McClaran, Michael P.; Bartolome, James W. 1989. **Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient**. Madroño 36: 141-153.

McNaughton, S.J. 1968. **Structure and function in California annual grassland**. Ecology 49: 962-972.

Menke, J.W. 1989. **Management controls on productivity**. In: Huenneke, L.F.; Mooney, H., eds. **Grassland structure and function**. Dordrecht: Kluwer Academic Publishers; 173- 200.

Mooney, H.A.; Hobbs, R.J.; Gorham, J.; Williams, K. 1986. **Biomass accumulation and resource utilization in co-occurring grassland annuals**. Oecologia 70: 555-558.

Nadkarni, Nalini M. 1986. **The nutritional effects of epiphytes on host trees with special reference to alteration of precipitation chemistry**. Selbyana 9: 44-51.

Parker, V.T.; Muller, C.H. 1982. **Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland**. American Midland Naturalist 107: 69-81.

Phipps, Richard L. 1985. **Collecting, preparing, crossdating, and measuring tree increment cores.** Reston, VA: U.S. Geological Survey, Water-Resources Investigations Report 85-4148.

Pike, Lawrence H. 1978. **The importance of epiphytic lichens in mineral cycling**. Bryologist 81: 247-257.

Rundel, Philip W. 1974. **Water relations and morphological variation in *Ramalina menziesii***. Bryologist 77: 23-32.

Schlesinger, William H. 1991. **Biogeochemistry. An analysis of global change**. San Diego: Academic Press; 443 p.

Sigal, Lorene L.; Nash, Thomas H., III. 1983. **Lichen communities on conifers in southern California mountains: an ecological survey relative to oxidant air pollution**. Ecology 64: 1343-1354.

Vetaas, Ole R. 1992. **Micro-site effects of trees and shrubs in dry savannas**. Journal of Vegetation Science 3: 337-344.

Vitousek, Peter M. 1994. **Beyond global warming: ecology and global change**. Ecology 75: 1861-1876.

Woodmansee, R.G.; Duncan, D.A. 1980. **Nitrogen and phosphorus dynamics and budgets in annual grasslands**. Ecology 61: 893-904.