# Microhabitat and Environmental Relationships of Bryophytes in Blue Oak (*Quercus douglasii* H. & A.) Woodlands and Forests of Central Coastal California[1]

Mark Borchert Daniel Norris[2]

**Abstract:** Microhabitat preferences and species-environment patterns were quantified for bryophytes in blue oak woodlands and forests of central coastal California. Presence data for mosses collected from 149 400 $m^2$ plots were analyzed using canonical correspondence analysis (CCA), a multivariate direct gradient analysis technique. Separate ordinations were performed for terricolous, saxicolous and epixylic mosses using 14 environmental variables. Fifty-six species of bryophytes were collected from the study area. Only the terricolous moss CCA was shown to be significantly related to environmental variables. Thirty-nine soil bryophyte species were arranged along 4 environmental gradients: potential annual solar insolation, moderate soil trampling, tree density and overstory crown cover. The significance of each environmental factor is discussed in relationship to the ecology of the species.

Bryophytes and lichens are an important component of the flora in blue oak woodland and forests. Despite a high abundance and diversity in this type, bryophytes have received very little study. An extensive list of lichens is available for blue oak in the San Joaquin Experimental Range (Herbert and Meyer 1984) but there are no comparable lists of bryophytes in blue oak. In the extensive range literature for blue oak and related annual grasslands, Heady (1956) briefly describes fluctuations in the cover of soil mosses that paralleled changes in vascular plant cover, but he did not identify bryophyte species.

We collected presence data for bryophytes in conjunction with a study to classify blue oak vegetation in southern San Luis Obispo and northern Santa Barbara counties, California. The objectives of this paper are: (1) to give a descriptive account of bryophytes and their microhabitat preferences in blue oak woodlands and forests on the Central Coast and (2) to identify bryophyte species-environment relationships.

## STUDY AREA

The study area includes 6 7.5'topographic quadrangles and is a patchwork of blue oak woodland and forest in southern San Luis Obispo and northern Santa Barbara Counties at the juncture of three mountain ranges: the La Panza Range, Garcia Mountain, and the Sierra Madre Mountains. The center of the study area (35° 10'N, 122° 10'W) is located approximately 52 km ESE of San Luis Obispo. The climate is mediterranean. Average annual precipitation at Pozo (9.5 km west of San Luis Obispo, CA) is 526 mm. In 1986 precipitation was 713 mm, higher than the average, and 269 mm in 1987, well below the average.

Eight allotments within the study area have been grazed almost continuously by cattle since 1900. Allotment grazing regimes have been highly variable historically. Currently three allotments are grazed year around and the others are grazed from one to five months. None of the plots had burned within a period of 5 years before the study.

## METHODS

Plot data were collected from the study area over a period of two years from late March to late May. In 1986 and 1987, 69 plots were sampled in the area from Pozo to the Cuyama River west of Branch Mountain. In 1987, 80 plots were sampled in the area from the Cuyama River to Miranda Pine Mountain.

Plots of 400 $m^2$ were subjectively located in stands where blue oak overstory crown cover was at least 20 percent and understory herbaceous cover exceeded 60 percent. A stand was sampled only if oaks were relatively evenly distributed over the plot on the same slope and aspect.

Slope angle, aspect, elevation, landform, slope position, and within-plot vertical and horizontal micro-relief were recorded for each plot. Slope and aspect were used to obtain an estimate of potential annual solar insolation using the tables of Frank and Lee (1966).

Bryophytes were collected from soil, rocks, downed logs and tree boles within each plot. Bole mosses were collected to 3 m. Percentage foliar cover of all vascular plant species was estimated visually and recorded into a modified Braun-Blanquet

[1]Presented at the Symposium on Oak Woodlands and Hardwood Rangeland Management, October 31-November 2, 1990, Davis, California.

[2]Forest Ecologist, Los Padres National Forest, Goleta, Calif.; Professor, Department of Biological Sciences, Humboldt State University, Arcata, Calif.

cover scale: 0-1 percent, 2-5 percent, 6-25 percent, 26-50 percent, 51-75 percent, and 76-100 percent. Midpoints of each of these cover classes were used to calculate total understory cover used in the data analysis. The cover of overstory trees was measured with a spherical densiometer (Lemmon 1956) by averaging five values taken in the plot: one at plot center and the others 7.5 m parallel and perpendicular to the slope contour from plot center. Trees larger than 5 cm dbh were counted, and their diameters measured at 1.4 m.

A soil pit was excavated in each plot to a depth of 100 cm or bedrock, whichever was encountered first. Soil characteristics taken for the A horizon and subsoil included: color, texture, pH, percentage coarse fragment and horizon thickness. Soil structural characteristics were used to create classes of soil trampling: light, moderate, heavy and severe. Lightly trampled soils had well developed A horizons with granular structure. At the other end of the gradient severely trampled soils had platy structure or no structure (massive) in the A horizons, and, in some cases, were heavily eroded. Seven soil textural classes were used in the analysis: loam, sandy loam, gravelly loam, gravelly sandy loam, fine sandy loam, sandy clay loam, and clay loam.

## DATA ANALYSIS

We analyzed bryophyte presence data using canonical correspondence analysis (CCA)(Ter Baak 1986). CCA is designed to detect unimodal relationships between species and external variables by performing a correspondence analysis ordination but with the added feature of canonical ordination. Ordination axes extracted by this method are required to be a linear combination of environmental variables. Axes appear in order of the variance explained.

Continuous variables used in the CCA analysis included elevation, aspect, slope, solar insolation, basal area, tree density, overstory crown cover, total understory cover and soil pH. If necessary, continuous variables first were normalized and then standardized to a mean of 0 and standard deviation of 1. Categorical variables used in the analysis included slope position, within-plot horizontal and vertical microrelief, trampling class and soil texture.

Because bryophytes usually have very specific microhabitat preferences, we separately performed ordinations of the terricolous, saxicolous and epixylic species. Too few plots had logs for analysis. Total understory cover, soil texture, and trampling class were used only for the analysis of terricolous mosses.

Species with less than 20 percent of the most frequent species were down-weighted by reducing abundance values in proportion to their frequencies of occurrence. A Monte Carlo test (Ter Baak 1986) was used to determine if the first canonical axis of each ordination was significantly related to environmental variables.

## RESULTS

### *Terricolous Mosses*

Fifty-six bryophyte species were collected from the 149 plots. Thirty-four were primarily found on soil and, of these, 21 were uncommon or rare (<4 occurrences)(table 1).

Thirty-nine species in 101 plots entered the CCA analysis of terricolous mosses. Species on the first canonical axis were significantly related (p=0.01) to the environmental variables. Moderate trampling is positively correlated and solar insolation negatively correlated with the first canonical axis (table 2). Density and overstory cover are positively correlated with the second and third axes, respectively (table 2). Density and overstory cover were moderately correlated (r=0.52) but moderate trampling and solar insolation were uncorrelated (r=-0.07).

The relationship of ground bryophytes to environmental variables is presented in the CCA ordination (biplot) diagram (fig. 1). Arrow length in the CCA ordination diagram is propor-

**Table 1—*Terricolous moss specks. Species are listed by the number of occurrences in all microhabitats (N) and percent frequency by microhabitat.***

| | | Microhabitat | | | |
|---|---|---|---|---|---|
| Species | N | Logs | Boles | Rocks | Soil |
| *Brachythecium velutinum* (Hedw.) B.S.G. | 8 | — | — | 13 | 87 |
| *Brachythecium albicans* (Hedw.) B.S.G. | 15 | — | 20 | — | 80 |
| *Bryum lisae* DeNot. | 4 | — | — | — | 100 |
| *Bryum* spp. | 7 | — | 14 | 14 | 72 |
| *Ceratodon purpureus* (Hedw.) Brid. | 6 | — | — | — | 100 |
| *Fissidens bryoides* Hedw. | 30 | — | 3 | — | 97 |
| *Fossombronia pusilla* (L.) Dum. | 20 | — | — | 15 | 85 |
| *Funaria hygrometrica* Hedw. | 6 | — | — | — | 100 |
| *Homalothecium arenarium* (Lesq.) Lawt. | 30 | 3 | 20 | 3 | 74 |
| *Phascum cuspidatum* Hedw. | 6 | — | — | — | 100 |
| *Targionia hypophylla L.* | 6 | — | — | 23 | 67 |
| *Timmiella anomala (B.S.G.)* Limpr. | 27 | — | — | 7 | 93 |
| *Weissia controversa* Hedw. | 6 | — | — | — | 100 |

Species with N <4 that were collected exclusively from soil: *Acaulon muticum* (Hedw.) C. Muell., *Anatolia menziesii* (Turn.) Par., *Anthoceros fusiformis* Aust., *Asterella bolanderi* (Aust.) Underw., *Claopodium bolanderi* Best, *Didymodon vinealis* (Brid.) Zander, *Ephemerum serratum* (Hedw.) Hampe, *Fissidens sublimbatus* Gront, *Funaria muehlenbergii* Hedw. f. ex Lam. and DC., *Phaeoceros bulbiculosus* (Brut.) Prosk., *Pleuridium subulatum* (Hedw.) Rabenh., *Pottia bryoides* (Dicks.) Mitt., *Pottia davalliana* (Sm.) Jens., *Pottia lanceolata* (Hedw.) C. Muell., *Pottia starckeana* (Hedw.) C. Muell. *Pterygoneuron subsessile* (Brid.) Jur., *Riccia nigrella* DC., *Scleropodium touretii* (Brid.) L. Koch, *Tortula bolanderi* (Lesq.) Howe, *Tortula inermis* (Brid.) Mont and *Tortula princeps* DeNot.

**Table 2**—***Canonical coefficients and intraset correlations of the CCA for terricolous bryophytes. Only correlation coefficients equal to or greater than 0.40 on one of the first 3 axes are shown. The first 3 axes accounted for 82 percent of the variance in the weighted average of the species with respect to environmental variables.***

| Axis variable | Canonical coefficients | | | Correlation coefficients | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 1 | 2 | 3 |
| Solar insolation | -.59 | .26 | -.06 | -.62 | .08 | .08 |
| Moderate trampling | .33 | -.03 | .13 | .40 | -.08 | .13 |
| Density | .20 | .38 | .29 | .30 | .46 | .00 |
| Overstory tree cover | .04 | -.14 | -.55 | .28 | .16 | -.48 |

tional to the strength of the correlation between environmental variables and ordination axes. Arrow direction indicates whether a variable is positively or negatively related to the axis. A species point projected perpendicularly onto each environmental axis corresponds approximately to the ranking of the weighted average of the species with respect to that environmental variable. The weighted averages are approximated in the diagram as deviations from the grand mean of each variable. The origin of the plot represents the grand mean.

As an example, we show frequency histograms of *Homalothecium arenarium* for solar insolation, moderate trampling and tree density (figs. 2a-c) to illustrate the position of this species in the biplot diagram. *Homalothecium arenarium* shows a preference for low-solar insolation (mesic) sites (fig. 2a) that are moderately trampled (fig. 2b). It is also more frequent in stands with high tree densities but this preference is less pronounced (fig 2c). The position of this species in the biplot diagram clearly reflects its distribution on these gradients.

The overall pattern of species in figure 1 shows that they are equally distributed on the solar insolation gradient but that more species are associated with higher than average tree densities especially in high-solar insolation (xeric) sites (fig. 1; upper left quadrant). Species that inhabit low-solar insolation stands are most prevalent on moderately trampled soils independent of tree density.

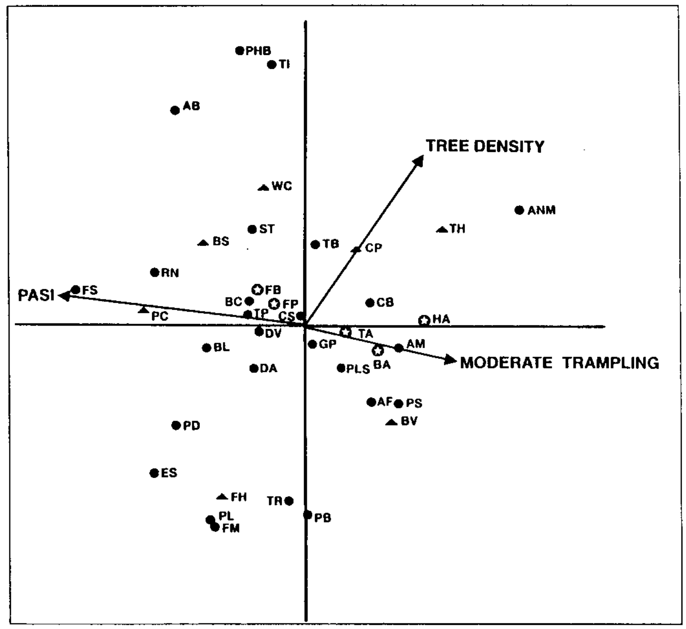


**Figure 1**—CCA ordination diagram with species and environmental variables (arrows) for the 101 plots. First axis is horizontal, second axis is vertical. Species with N> 15 are starred; those with 5< N < 15 are indicated with triangles and species with N< 5 are indicated with dots. Species are as follows: *Asterella bolanderi* (AB), *Anthoceros fusiformis* (AF), *Acaulon muticum* (AM), *Anatolia menziesii* (ANM), *Brachythecium albicans* (BA), *Bryum capillare* (BC), *Bryum lisae* (BL), *Bryum* spp. (BS), *Brachythecium velutinum* (BV), *Claopodium bolanderi* (CB), *Ceratodon purpureus* (CP), *Crossidium squamiferum* (CS), *Didymodon australasiae* (DA), *Didymodon vinealis* (DV), *Ephemerum serratum* (ES), *Fissidens bryoides* (FB), *Funaria hygrometrica* (FH), *Funaria muehlenbergii* (FM), *Fossombronia pusilla* (FP), *Fissidens sublimbatus* (FS), *Grimmia pulvinata* (GP), *Homalothecium arenarium* (HA), *Pottia bryoides* (PB), *Phascum cuspidatum* (PC), *Pottia davalliana* (P D), *Phaeoceros bulbiculosus* (P H B), *Pottia lanceolata* (PL), *Pleuridium stramineum* (PLS), *Pterygoneron subsessile* (PS), *Riccia nigrella* (RN), *Scleropodium touretii* (ST ), *Timmiella anornala* (TA), *Tortula bolanderi* (TB), *Targonia hypophylla* (TH), *Tortula inermis* (TI), *Tortula princeps* (TP), *Tortula ruralis* (TR), and *Weissia controversa* (WC). *Pottia starckeana* is not shown but is positioned in the upper left quadrant

## Epixylic Mosses

Twenty species in 143 plots entered the CCA for this group. The 1st canonical axis was significantly related (p=0.05) to environmental variables but none of the correlation coefficients equaled or exceeded 0.40. Species of the genus *Orthotrichum* clearly dominate this group and *Tortula laevipila* and *Orthotrichum lyellii* are nearly ubiquitous (table 3). Both species consistently grow at the bases of trees and in low solar insolation environments. Where there is ample fog, *O. lyellii* extends into the canopy on larger branches.

## Saxicolous Mosses

Twenty-eight species in 30 plots entered the CCA analysis of rock mosses (table 4). The 1st canonical axis was not related to the environmental variables (p=0.21). In general, rocks are infrequent in the study area and where present, their cover seldom exceeds 4 $in^2$ (1 percent). Not unexpectedly, the genus *Grimmia is* best represented in this microhabitat.

## Mosses Distributed Among Several Microhabitats

Species without a clear microhabitat preference are listed in Table 5. *Antirichia californica* is one of a large number of western North American species that can be found as readily on trees as on rocks. The microhabitat amplitude of the other species is largely due to their preference for rocks or trees that have a thin layer of sediment deposition.

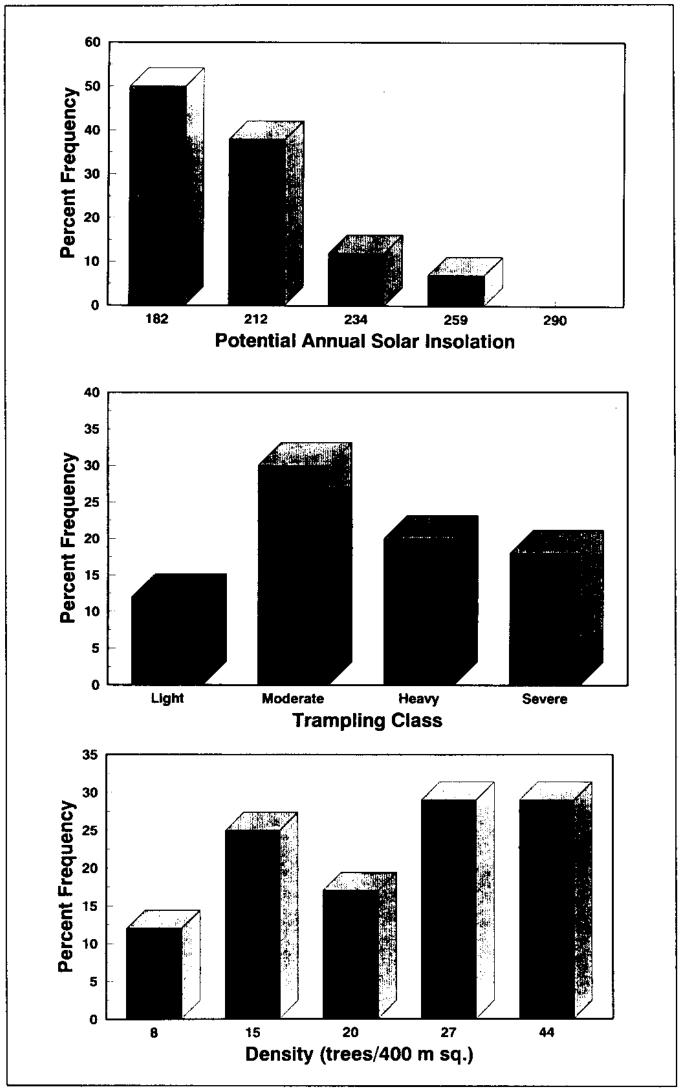


**Figure 2—**Frequency histograms for Homalothecium arenarium for (a) solar insolation, kcal/cm$^2$/yr (b) trampling class, and (c) tree density. Frequencies are for 5 classes of solar insolation and four classes of tree density. The values on the x axes of (a) and (c) are the means for each class.

**Table 3—*Epixylic bryophyte species. Species are listed by occurrence in all microhabitats (N) and percent frequency by microhabitat.***

| | | Microhabitat | | | |
|---|---|---|---|---|---|
| Species | N | Logs | Boles | Rocks | Soil |
| *Homalothecium nuttallii* (Wils.) Jaeg. | 12 | — | 100 | — | — |
| *Orthotrichum lyellii* Hook. and Tayl. | 128 | 2 | 98 | — | — |
| *Orthotrichum pumilum* Sw. | 6 | — | 100 | — | — |
| *Orthotrichum tenellum* Bruch ex Brid. | 8 | — | 100 | — | — |
| *Tortula laevipila* (Brid.) Schwaegr. | 130 | 6 | 92 | 2 | — |

Species with N <4 that were collected exclusively from tree boles: *Amblystegium varium* (Hedw.) Limpr., *Fabronia pusilla* Raddi, *Orthotrichum diaphanum* Schrad. ex Brid., and *Scleropodium cespitans (C.* Muell.) L. Koch. *Dicranoweisia cirrata* (Hedw.) Lindb. in Milde was collected only from logs.

**Table 4—*Saxicolous brypohyte species. Species are listed by occurrence in all microhabitats (N) and percent frequency by microhabitat.***

| | | Microhabitat | | | |
|---|---|---|---|---|---|
| Species | N | Logs | Boles | Rocks | Soil |
| *Grimmia laevigata* (Brid.) Brid. | 5 | — | — | 100 | — |
| *Grimmia pulvinata* (Hedw.) Sm. | 11 | — | — | 91 | 9 |

Species with N <4 that were collected exclusively from rocks: *Bryum pseudotriquetrum* (Hedw.) Gaertn., *Grimmia alpestris* (Web. and Mohr) Schleich ex Nees, *Grimmia ovalis* (Hedw.) Lindb., Meyer and Scherb., *Homalothecium pinnatifidum (Sull.* and Lesq.) Lawt.

**Table 5—*Bryophyte species without strong microhabitat preferences. Species are listed by occurrence in all microhabitats (N) and percent frequency by microhabitat.***

| | | Microhabitat | | | |
|---|---|---|---|---|---|
| Species | N | Logs | Boles | Rocks | Soil |
| *Antitrichia californica Sull.* in Lesq. | 15 | 27 | 60 | 13 | — |
| *Crossidium squamiferum* (Jur.) Giac. | 4 | — | — | 50 | 50 |
| *Didymodon australasiae* (Hook. and Grev.) Zander | 11 | — | 18 | 36 | 45 |
| *Didymodon vinealis* (Brid.) Zander | 55 | — | 38 | 16 | 46 |
| *Tortula ruralis* (Hedw.) Gaertn., Meyer and Scherb. | 38 | 3 | 53 | 32 | 13 |

Species with N <4 on trees and rocks: *Bryum capillare* Hedw., *Didymodon rigidulus* Hedw., and *Grimmia trichophylla* Grev. occurred on soil, trees and rocks.

## DISCUSSION

Terricolous mosses are the dominant (70 percent) species group in blue oak on the Central Coast and show definite species patterns in relation to macroenvironmental gradients. Other ordination studies of terricolous moss assemblages have centered almost entirely on plant communities well to the north of blue oak: artic (LaFarge-England 1989), subartic forest-tundra (Robinson and others 1989), and boreal forest (Lechowicz and Adams 1974; Johnson 1981; Brumelis and Carleton 1989). Species patterns in these studies were correlated with soil chemistry (Johnson 1981; LaFarge-England 1989; Robinson and others 1989), soil texture (Robinson and ethers 1989), slope (LaFarge-England 1989), light and temperature regimes (Lechowicz and Adams 1974; Johnson 1981; Brumelis and Carleton 1989) and disturbance (Johnson 1981; Brumelis and Carleton 1989).

Terricolous mosses in blue oak woodlands are organized along at least four environmental gradients, the strongest of which is solar insolation. Solar insolation is a complex gradient and may be a surrogate for soil moisture. Although soil moisture was not measured, field observations on the rate of drying of annual plants indicated that low-solar insolation sites remained moist much longer than high-solar insolation sites. Species distributions of vascular plant vegetation also are correlated with solar insolation (r=-0.69) (Borchert and others 1990). Nevertheless, slope angle, a significant environmental variable (r=0.44) for vascular plants (Borchert and others 1990), is not important to soil mosses.

Tree density and overstory cover may reflect gradients in light and/or soil nutrients. Overstory cover in blue oaks is predominately composed of branch, twig and bole cover with a relatively smaller percentage furnished by foliage. Moreover, because woody cover is present year around, it constitutes a more constant source of shade than deciduous foliage. In addition to light, bryophytes may be responding to a density-related gradient in soil nutrients or soil structure. Blue oak litter increases soil nutrients, organic material, friability, water holding capacity and creates a more equitable soil temperature regime (Holland 1973; Callaway 1990). Thus, regardless of solar insolation, dense stands may provide a better microclimate and soil environment for terricolous mosses than low-density stands. Vascular plant species were also significantly related (r=0.40) to overstory cover.

The emergence of moderate trampling as a significant variable suggests that disturbance plays a role in the distribution of ground mosses in low-solar insolation sites. The impact of livestock trampling on soils is complex. Hoof action can cause vegetation injury and loss, compaction of the soil surface and reduced infiltration (Abdel-Magid and others 1987). Observations indicate that trampling produces extremely variable microtopography. Hooves create small cutfaces that, if left undisturbed, are colonized by bryophytes, as are the small mounds of soil pushed up at bases of the cutfaces. Where trampling is very heavy, however, mosses are completely eliminated but it is not clear why mosses are not also associated with lightly grazed sites.

Semiarid blue oak woodlands are comparatively rich in bryophyte species. For example, a similar number of plots in coast redwood (*Sequoia sempervirens*) forests in southern Monterey County, California produced only 16 bryophyte species (in prep.). Future studies of bryophytes in blue oak should concentrate on terricolous species with a particular emphasis on low-solar insolation environments where this group has the highest cover. Successional studies on species in mesic sites would be of particular interest because mosses may be more sensitive indicators of livestock grazing effects than vascular plants.

## ACKNOWLEDGMENTS

We thank Patti Krosse for describing the soils and Juanita Freel and Maile Neel for the graphics.

## REFERENCES

Abdel-Magid, A.H.; Trlica, M.J.; Hart, R.H. 1987. Soil and vegetation responses to simulated trampling. Jour. of Range Management 40(4):303-306.

Borchert, M.; Davis, F.W.; Allen-Diaz, B. 1990. Environmental relationships of herbs in blue oak (*Quercus douglasii*) woodlands of central coastal California. Madrono. In press.

Brumelis, G.; Carleton, T.J. 1989. The vegetation of post-logged black spruce lowlands in central Canada. II. Understorey vegetation. Journal of Applied Ecology 26:321-339.

Callaway, R.M. 1990. Effects of *Quercus douglasii* on grassland productivity and nutrient cycling in Cental California. Santa Barbara, CA: University of California. p. 150. Dissertation.

Frank, E.C.; Lee, R. 1966. Potential solar beam irradiation on slopes: tables for 30° to 50° latitude. USDA For. Ser., Rocky Mtn. For. Range Exp. Sta. Res. Pap. RM-18.

Heady, H.F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37: 798-812.

Herbert, J.R.; Meyer, R. W. 1984. Lichens of the San Joaquin Experimental Range, California. The Bryologist 87:234-252.

Holland, V.L. 1973. A study of soil and vegetation under *Quercus douglasii* H. & A. compared to open grassland. Berkeley, CA: University of California. p. 358. Dissertation.

Johnson, E.A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology 62(l):200-215.

LaFarge-England, C. 1989. The contemporary moss assemblages of a high arctic upland, northern Ellesmere Island, N.W.T., Canada. Canadian Journal of Botany 67:491-504.

Lechowicz, M.J.; Adams, M.S. Ecology of Cladonia lichens. 1974. I. Preliminary assessment of the ecology of terricolous lichen-moss communities in Ontario and Wisconsin. Can. J. Bot. 52:55-64.

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory crown density. Forest Science 2:314-320.

Robinson, A.L.; Vitt, D.H.; Timoney, K.P. 1989. Patterns of bryophyte and lichen distribution in relation to latitudinal and edaphic gradients in the Canadian subarctic forest-tundra. Nova Hedwigia 49(1-2):25-48.

Ter Baak. CJ.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.