

## Spatial Variation in Herbivory by Forest Canopy Arthropods Along an Elevation Gradient

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**ABSTRACT** Spatial variation has recently been recognized as an important component in ecological processes. Elevation differences are an obvious example of spatial variation, but little is known about the influence of elevation on canopy insect herbivory. We examined elevation effects on canopy insect herbivory in an eastern deciduous forest. Percentage leaf area removed and canopy arthropod guild structure were measured at 3 sites along an elevation gradient in the southern Appalachians. *Acer rubrum* L. was sampled at all sites; *Quercus rubra* L. at the lowest and highest sites. Upper and lower canopies of *A. rubrum* were sampled at the highest site. Canopy walkways were used in most sampling. Our 1st hypothesis was that percentage leaf area removed would decrease as elevation increased because of decreases in temperature. Percentage leaf area removed decreased significantly for both tree species as elevation increased. We also hypothesized that percentage leaf area removed would be greater in the lower canopy, because shade leaves are reportedly more palatable to herbivores. Percentage leaf area removed was significantly greater in the lower canopy compared with the upper canopy of *A. rubrum*. Our 3rd hypothesis was that arthropod guild structure would vary along the elevation gradient because of environmental differences reflecting elevation differences. Arthropod guild structure was significantly different for *A. rubrum* at all sites but similar for *Q. rubra*. Spatial variation, in terms of elevation differences, was shown to have a significant effect on forest insect herbivory and arthropod guild structure.

**KEY WORDS** herbivory, forest insects, elevation gradient, leaf area removed, canopy walkways, spatial variation

CANOPY ARTHROPODS PLAY a major role in forest ecosystem function. For example, they are important components in the regulation of nutrient cycling (Kimmins 1972, Chew 1974, Mattson and Addy 1975, Wickman 1980, Wickman and Starr 1990). Swank et al. (1981) measured increased stream export of nitrate nitrogen during a defoliation event by the fall cankerworm, *Alsophila pometaria* (Harris). Other measured effects were as follows: (1) decrease of wood production but increase in leaf production; (2) large inputs of frass to the forest floor; (3) large increases of litterfall; (4) increased nitrogen inputs via canopy throughfall during the period of defoliation; and (5) significant increases in pools of available nutrients (especially mineral N) in upper soil horizons. Risley and Crossley (1988) and Risley (1986) have found that greenfall (green leaves which fall as a direct result of herbivore feeding) occurs throughout the growing season, and thus should be included in measures of herbivory. Nitrogen measured in greenfall was greater than that of senescent leaves; therefore, greenfall should be a high-quality substrate for decomposers. Greenfall appears to be one manner in which insect herbivores accelerate nutrient cycling (Risley and Crossley 1992).

Canopy arthropods also can cause major changes in forest stand composition. This effect was documented by MacLean (1990) for spruce budworm, *Choristoneura fumiferana* (Clemens), in spruce-fir forests and by Gansner and Herrick (1987) for gypsy moth, *Lymantria dispar* (L.), defoliation in oak forests.

Furthermore, canopy arthropods may affect primary productivity (Heichel and Turner 1983), although some investigators (Romme et al. 1986, Schowalter et al. 1991) have found evidence for compensation from low to moderate foliage losses. In feeding on tree leaves, canopy arthropods may have direct effects on primary productivity and indirect effects on nutrient cycling. Thus, quantifying percentage leaf area removed by arthropod feeding can be a significant measure of canopy arthropod activity. Because "leaves are the platforms of interaction between forest and atmosphere" (Parker 1989), removal of some or all of a leaf by insects is an important component of forest canopy processes. In a summary study, Coley and Aide (1991) reported annual rates of herbivory in temperate forests of  $\approx 7.5\%$ . Many of these reported values may be underestimates because most studies did not include leaves that were completely consumed (Wallace and O'Hop 1985, Coley and Aide 1991), those which

left the trees as greenfall (Risley 1986), or leaves in the upper canopy (Basset 1991, Lowman 1992).

Insect herbivore populations are influenced by a host of factors. As pointed out by Hunter and Price (1992a), insect populations are affected by top-down forces (such as predators) and bottom-up forces (such as plant chemistry), but the relative importance of these forces will vary with environmental heterogeneity or spatial variation.

Spatial variation now is recognized as a vital component in ecological processes (Kareiva 1994). Variations in plant secondary compounds have been correlated with elevation differences (Louda and Rodman 1983), and patterns of foliage consumption may be correlated with spatial variation in environmental conditions (Louda et al. 1987).

One obvious component of spatial variation in the southern Appalachians is elevation, but little is known about its influence on canopy arthropod feeding activity. Elevation could affect percentage leaf area removed, because variations in plant secondary compounds have been correlated with elevation differences (Louda and Rodman 1983), but there is little information available about the specific influence of elevation on percentage leaf area removed. Of the few studies that dealt with insect herbivores, 2 reports on galling species found decreased numbers of species with increases in elevation (Lawton et al. 1987, Fernandes and Lara 1993). Lowman (1992) measured 12.3% annual leaf area loss in *Doryphora sassafras* Endlicher in a cool temperate site with increases to 17.6% in the canopy of the same tree species at a lower elevation in a warm temperate site in New South Wales.

The research reported here continues studies on canopy insects on low- and mid-elevation watersheds at Coweeta Hydrologic Laboratory, U.S. Forest Service, Otto, NC (Swank and Crossley 1988, Blanton 1989). However, this project includes measurements at a higher elevation and higher in the canopy than previous studies.

The primary objective of this study was to measure differences (if any) in canopy chewing herbivory, measured as percentage leaf area removed, along an elevation gradient. Our hypothesis was that percentage leaf area removed would decrease as elevation increased, since cooler temperatures at higher elevations (Hoover and Crossley 1995) would decrease insect feeding activity and trees at higher elevations have a growing season almost a month shorter than those at lower ones (B.C.R., unpublished data). Measurements of arthropod densities also were made to examine possible relationships to percentage leaf area removed.

A 2nd objective was to learn if there were any differences in percentage leaf area removed between upper and lower canopies of the same trees, as reported by Basset (1991) and Lowman (1985, 1992) for Australian forests, or differences in insect abundance between the canopy layers, as found by Majer et al. (1990) in Australian eucalypt forests. We hypothesized that percentage leaf area removed

would be greater in the lower canopy because shade leaves are often reported to be more palatable to insects (Lowman 1985, Maiorana 1981) and microclimate conditions might be more favorable for insects (i.e., less exposure to heat and desiccation). Developmental changes in host resistance also could affect herbivore distribution (Kearsley and Whitham 1989). The last objective was to examine differences in insect feeding guilds (Crossley et al. 1976, Moran and Southwood 1982) along the elevation gradient. Because feeding guilds represent the exploitation of the same class of environmental resources in a similar way (Root 1967), differences in guild structure along the gradient could reflect environmental differences related to elevation.

### Materials and Methods

This study was conducted at the Coweeta Hydrologic Laboratory, NC, operated by the U.S. Forest Service (Swank and Crossley 1988). Three plots of similar aspect but differing elevations were selected from the 3 gradient plots established for an ongoing Long Term Ecological Research (LTER) gradient project (Hoover and Crossley 1995).

The low site is a north-facing slope with an elevation of 795 m. The cove terrain forest includes chestnut oak, *Quercus prinus* L.; red oak, *Quercus rubra* L.; red maple, *Acer rubrum* L.; tulip poplar, *Liriodendron tulipifera* L.; sweet birch, *Betula lenta* L.; and hickory, *Carya* sp.

The midelevation mixed-oak forest site faces northeast, at 1,001 m. Important tree species include red maple; chestnut oak; red oak; sweet birch; striped maple, *Acer pensylvanicum* L.; and eastern hemlock, *Tsuga canadensis* (L.) Carr.

The highest study site also faces northeast, at an elevation of 1,347 m. Common tree species in this northern hardwood stand include red oak; red maple; striped maple; and yellow birch, *Betula lutea* Michaux, with an understory of rhododendron, *Rhododendron maximum* L.; flame azalea, *Rhododendron calendulaceum* (Michaux) Torrey; and sweet pepper bush, *Clethra acuminata* Michaux.

Access to the canopy has been a major obstacle for canopy research. Although recently developed techniques have largely overcome these difficulties (Lowman et al. 1993), methods such as the canopy raft (Halle and Pascal 1992) or construction cranes (Parker et al. 1992) are expensive. Technical climbing (Lowman 1984) may present physical challenges to many investigators. Canopy walkways (Lowman and Bourcius 1993) are relatively inexpensive and are easier to use than technical climbing techniques. For these reasons, we used canopy walkways for access to the canopy. Walkways at the 3 sites consisted of canopy bridges 20 m long suspended between platforms built into the crowns of carefully selected trees,  $\approx 20$ –40 m tall (Reynolds and Crossley 1995).

Crown height from which the samples were taken ranged from 7 m on the high site to 14 m on the low

site. Samples were taken using a 15-ft pole pruner and plastic bags (Crossley et al. 1988). A nylon drawstring bag on a hoop was placed over the selected branch and the drawstring pulled when the branch was cut by the pruners; a plastic bag liner inside the drawstring bag contained the sample. Arthropods inside the plastic bag were anesthetized with a chloroformed cotton ball placed in the bag. Clipping of individual branches rather than spraying with a knockdown insecticide was done to obtain data on arthropod weights or numbers of individuals on a foliage weight basis (Majer and Recher 1988). Blanton (1989) found clipping to be more reliable than fogging and gave a better estimate of total resident arthropod biomass. Clipping also allowed separation between upper and lower canopy samples.

Trees sampled from the canopy bridges were *A. rubrum* on mid- and high-elevation sites, and *Q. rubra* on low and high sites. These 2 species were chosen because they are among the dominant trees on all sites (Hoover and Crossley 1995). On the high-elevation site, 2 *Q. rubra* and 1 *A. rubrum* were sampled from the walkways. Some outer branches of *A. rubrum* growing along the road by the high site also were sampled. On the middle site, 3 *A. rubrum* trees were sampled from the walkways and on the low site, 1 large *Q. rubra* could be reached. In August, a 2nd *Q. rubra*, which had recently fallen, was sampled for leaf area removed only. *A. rubrum* branches sampled on the low site were taken from trees growing along a road or a power line, where microclimate conditions such as solar radiation would be similar to that of upper canopies. Branches from *A. rubrum* on the high site also were taken from the understory, to compare leaf area removed, arthropod feeding guilds, and arthropod density (Root 1973, Crossley et al. 1988) between the upper (>20 m) and lower (<8 m) canopy.

Sampling was done monthly from June through September 1994. Every month, 7–10 branches were collected from each site, representing 3 *A. rubrum* from the middle site, 2 *Q. rubra* and usually 2 *A. rubrum* from the high site, and 1 *Q. rubra* and 3 *A. rubrum* from the low site. The high site was usually sampled in midmorning and the middle site in the early afternoon. The low site was usually sampled the following morning. Care was taken that no tree had more than a small percentage of its branches removed.

In the laboratory, leaves were removed from the branches and arthropods were picked off and kept frozen until they were identified. Every branch was carefully examined for abscission scars, although none were found in this study. Arthropods were dried at 50°C for 24 h and weighed to 0.001 mg on an analytical balance. All leaves were photocopied, dried at 50°C and weighed; the photocopies were digitized for leaf area removed using a video camera interfaced with a microcomputer (Hargrove and Crossley 1988). No attempt was made to separate young from old leaves.

To study the functional structure of canopy arthropod communities, arthropods were sorted into feeding guilds (Root 1973) based on compartments for forest canopy arthropods suggested by Crossley et al. (1976), Moran and Southwood (1982), and Stork (1987). The guilds recognized were phytophages (divided into chewers and suckers), floral feeders, ants (regarded as omnivores), tourists (insects that do not feed in the canopy, such as aquatic emergents), predators (divided into insect predators and other predators, such as spiders) and parasitoids. Arthropod density was calculated as the ratio of the number of arthropods per 100 g dry foliage (Root 1973).

Statistical analysis on percentage leaf area removed data was done on log-transformed data. Analysis of variance (ANOVA) was used to evaluate relations between percentage leaf area removed and other variables; the Tukey studentized range (HSD) test was used to compare means (SAS Institute 1988). Differences among guild structures were calculated using the chi-square test (Bishop 1966).

## Results

In total, 119 branches were collected in 1 summer (1994), with 2,788 *Q. rubra* leaves and 7,735 *A. rubrum* leaves measured for percentage leaf area removed. The 588 arthropods counted on these leaves weighed 579 mg; the foliage they were on weighed 3,414 g.

**Percentage Leaf Area Removed.** Seasonal averages for percentage leaf area removed ranged from 4.5% for *Q. rubra* on the high site to 9.6% for *A. rubrum* on the low site (Fig. 1). These values are similar to those listed by Coley and Aide (1991) for temperate forests and to those previously measured at Coweeta (Blanton 1989). Monthly averages for percentage leaf area removed were as low as 1.69% for *A. rubrum* on the high site (Fig. 1A) and as high as 19.06% for *Q. rubra* on the low site (Fig. 1B).

Elevation had a detectable effect on percentage leaf area removed for both *Q. rubra* ( $F = 31.2$ ,  $P = 0.001$ ,  $n = 2,788$ ) and *A. rubrum* ( $F = 435.9$ ,  $P < 0.001$ ,  $n = 6,650$ ), with percentage leaf area removed decreasing as elevation increased (Fig. 1). The difference in mean percentage leaf area removed at each site on the elevation gradient for the sampling season was significant ( $F = 42.3$ ,  $P = 0.001$ ,  $n = 2,788$  for *Q. rubra*;  $F = 575.3$ ,  $P < 0.001$ ,  $n = 6,650$  for *A. rubrum*; Tukey,  $\alpha = 0.05$  for both) and the mean seasonal percentage leaf area removed decreased with increasing elevation (Table 1).

Our hypothesis was that percentage leaf area removed would decrease as elevation increased from decreasing temperatures and shorter growing seasons at higher elevations. However, when average monthly temperature at each site was added to the statistical model, it showed no relation with *A. rubrum* percentage leaf area removed. For *Q. rubra* percentage leaf area removed, the relationship was significant ( $F = 17.0$ ;  $P < 0.001$ ;  $n = 2,788$ ), although

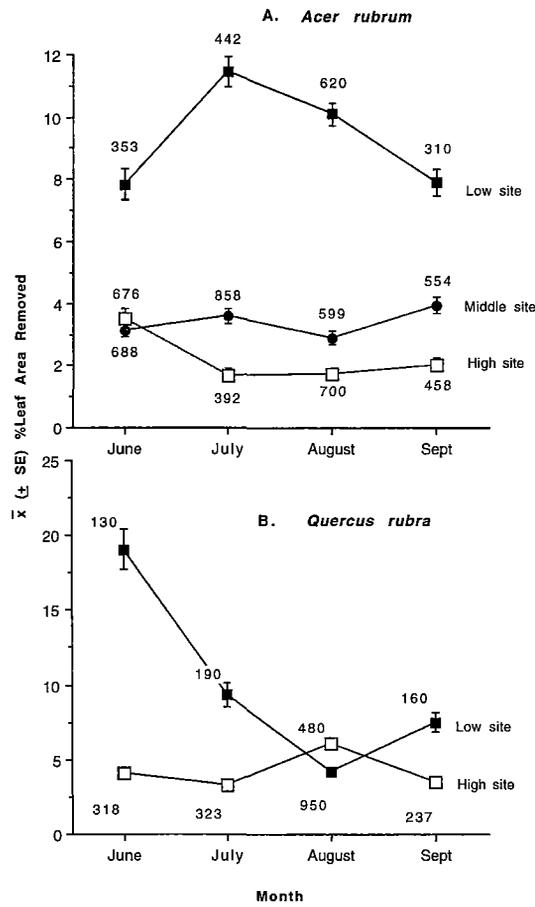


Fig. 1. Monthly percentage leaf area removed for *A. rubrum* at 3 elevations (A) and for *Q. rubra* at 2 elevations (B). Values are mean percentage leaf area removed  $\pm$  SE for all samples per date and site. Numbers of leaves measured for each data point are shown.

the percentage of variation accounted for was still low (1%).

Factors other than elevation that contributed to differences in percentage leaf area removed were date of sampling ( $F = 40.9, P < 0.001, n = 9,438$ ) and variation among samples ( $F = 37.07, P = 0.001, n = 9,438$ ) for *Q. rubra* and *A. rubrum*.

**Canopy Arthropod Densities.** The densities of canopy arthropods showed a strong elevation pat-

Table 1. Seasonal average percentage of leaf area removed from *A. rubrum* and *Q. rubra* on sites of different elevations at Coweeta Hydrologic Laboratory, North Carolina, 1994

Site	Elevation, m	Mean $\pm$ SE % leaf area removed	
		<i>A. rubrum</i>	<i>Q. rubra</i>
Low	795	9.6 $\pm$ 0.23	6.58 $\pm$ 0.26
Middle	1,001	3.39 $\pm$ 0.11	NA
High <sup>a</sup>	1,347	2.33 $\pm$ 0.12	4.48 $\pm$ 0.16

<sup>a</sup>Data for high site are upper canopy only. NA, not applicable.

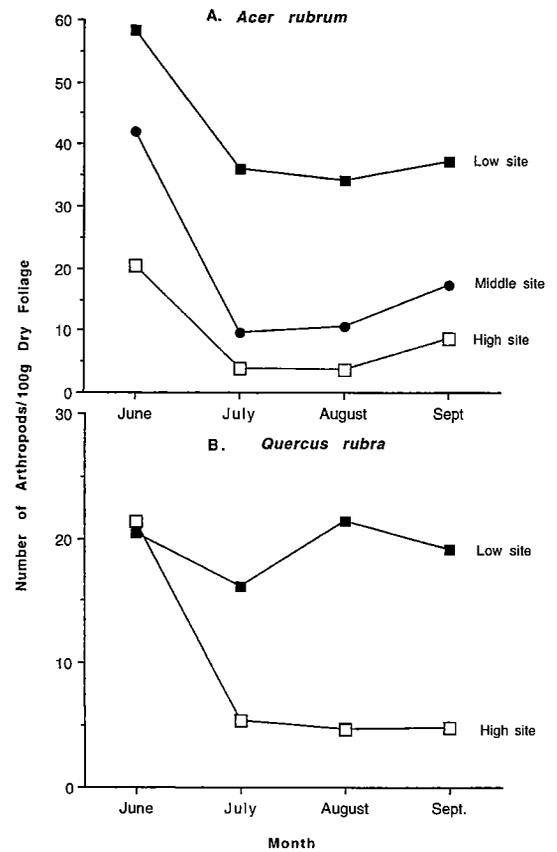


Fig. 2. Monthly arthropod density on *A. rubrum* at 3 elevations (A) and on *Q. rubra* at 2 elevations (B).

tern (Fig. 2). For *A. rubrum* (Fig. 2A), the low site had the highest density for all 4 mo. The middle site had consistently lower densities than the low site, and the high site had values 1/2-1/3 those of the middle site. Average values for the entire collection season were 39.9, 18.1, and 9.3 arthropods per 100 g dry foliage for the low, middle, and high sites, respectively.

For *Q. rubra* (Fig. 2B), the situation was similar, except in June. Although canopy arthropod density was nearly equal for the low and high sites in June, for the following 3 mo the low site densities were 3-5 times greater than the high site. The average values for the season were 19.3 arthropods per 100g dry foliage for the low site and only 9.5 for the high site.

Seasonal differences for canopy arthropod density usually showed peak densities in the spring (except *Q. rubra* on the low site), and a smaller peak in September for *A. rubrum* on all sites (Fig. 2). For every site, greater percentage leaf area removed was significantly related to greater density of canopy arthropods ( $F = 14.59, P < 0.001, n = 7,735$  for *A. rubrum*, including upper and lower canopy on the high site;  $F = 104.67, P < 0.0001, n = 2,788$  for *Q. rubra*).

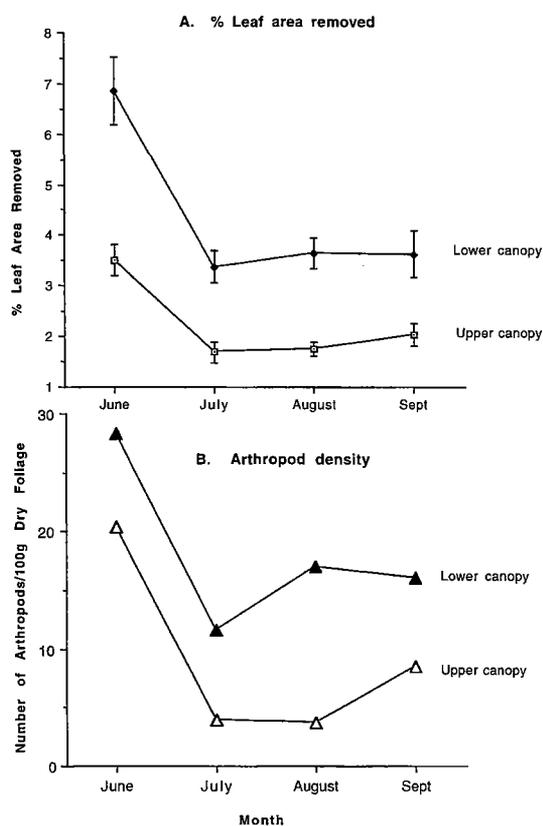


Fig. 3. Monthly percentage leaf area removed (A) and arthropod density (B) in upper and lower canopy of *A. rubrum* on the high site.

**Upper and Lower Canopy.** The percentage leaf area removed was affected by height in the canopy ( $F = 223.3$ ,  $P < 0.001$ ,  $n = 3,311$ ); seasonal average percentage leaf area removed in the lower canopy of *A. rubrum* on the high site was 4.31% but almost half that (2.33%), in the upper canopy (Fig. 3A). Herbivory was greater in the lower canopy for every sampling date (Fig. 3A). The difference between these percentage leaf area removed values was significant ( $F = 17.2$ ;  $P < 0.001$ ,  $n = 3,311$ ; Tukey,  $\alpha = 0.05$ ). Variation among individual samples also was related to percentage leaf area removed ( $F = 16.46$ ,  $P = 0.001$ ,  $n = 3,311$ ).

Greater arthropod densities were again associated with higher percentage leaf area removed. In all 4 mo, density in the lower canopy, where percentage leaf area removed was greater, was as much as 4 times greater than the upper canopy (Fig. 3B). The seasonal average was 9.3 arthropods per 100 g leaves for the upper canopy and 17.6 for the lower.

**Functional Group Analysis.** Chi-square analysis of the distribution of arthropod density indicated that proportions of the 3 dominant functional groups (chewers, suckers, and spiders) were similar on both sites for *Q. rubra* (Fig. 4A;  $\chi^2 = 1.445$ ,  $df = 2$ ,  $P = 0.5$ ). Suckers outnumbered chewers; non-

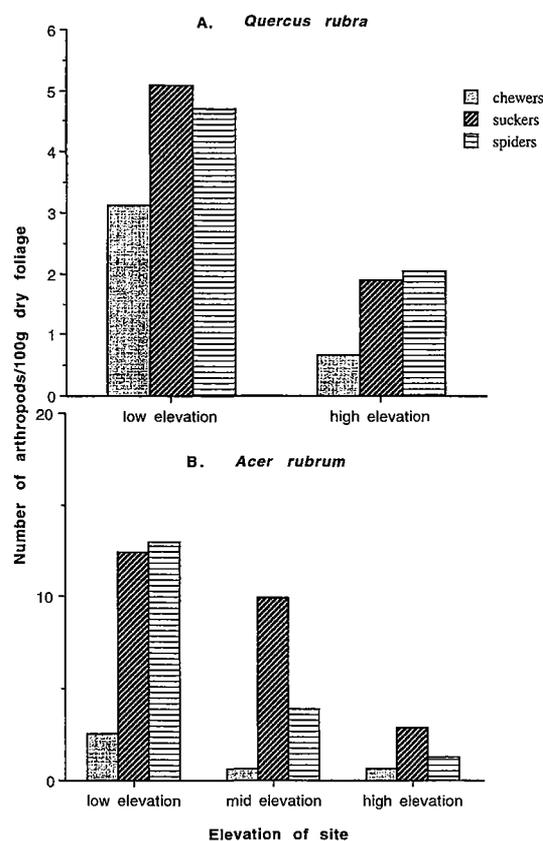


Fig. 4. Arthropod density for guild structure of 3 most important groups on *Q. rubra* (A) and on *A. rubrum* (B).

sect predators (i.e., spiders) were similar in number to suckers. For *A. rubrum* on all sites, chi-square analysis showed significant differences ( $\chi^2 = 14.86$ ,  $df = 4$ ,  $P = 0.005$ ) for arthropod density proportions (Fig. 4B).

## Discussion

Canopy arthropod density and leaf area removed decreased as elevation increased. Canopy arthropod populations could have been affected by top-down forces, such as predators. The species of insectivorous birds change along this gradient. For example, at the low site, black-throated green warblers, *Dendroica virens* Gmelin, are a common breeding species, whereas at the middle and high sites, black-throated blue warblers, *Dendroica caerulescens* Gmelin, are common (B.C.R., unpublished data). Different predators at the 3 sites could have different effects on the canopy arthropod population. Bottom-up forces, such as plant chemistry, also could affect arthropod populations. Louda and Rodman (1983) have shown that plant secondary compounds can vary with differences in elevation.

Although average monthly temperature showed no relation with leaf area removed in *A. rubrum* and

accounted for little of the variation in *Q. rubra* leaf area removed, it is possible that daily temperatures or differences in degree-days for insect development could have been important abiotic factors. We think that meteorological effects on leaf area removed are probably more complex than simple monthly means suggest. Differences in soil chemistry along this gradient (J. Knoepp, U.S. Forest Service, Otto, NC, personal observation) also could have affected leaf chemistry. Phenological effects may be the most obvious source of variation in leaf area removed because trees at Coweeta have a longer growing season at lower elevations.

Although one would expect that percentage leaf area removed would accumulate over the growing season, only *A. rubrum* on the middle site showed an increase (Fig. 1A). *A. rubrum* percentage leaf area removed peaked in July on the low site, and in June on the same site for red oak (Fig. 1B). Subsequent decreases in percentage leaf area removed could be caused by new leaves flushing, total consumption of leaves by herbivores, clipping of fed-upon leaves by herbivores (Heinrich 1979, Heinrich and Collins 1983), or abscission of damaged foliage by the tree (Risley 1986). Measurements of greenfall or monitoring of individual leaf fates would give some explanation of why these decreases in percentage leaf area removed occur.

This dynamic pattern of percentage leaf area removed, rather than steady accrual, has been reported by Crossley et al. (1988) for *Quercus prinus* L. at Coweeta in 1981 and by Risley (1986) in 1983. Hargrove (1988) found decreases in percentage leaf area removed for *Q. prinus* in 1984 and for *A. rubrum* in 1985 at Coweeta.

Significant differences were found between percentage leaf area removed in lower and upper canopy samples from *A. rubrum* on the high site, the only site where there was a lower canopy of *A. rubrum* branches (Fig. 3A). Greater percentage leaf area removed was measured in lower branch samples. These differences may in part be caused by within tree variation in leaf chemistry (Hunter and Price 1992b), such as differences in palatability between sun and shade leaves (Lowman 1985, Maiorana 1981), but also they may reflect differences in microclimate (Bassett 1991). These data may indicate that many measurements of percentage leaf area removed, using samples taken from lower in a tree, may be biased toward higher values.

Guild structure varied significantly along the gradient for *A. rubrum* (Fig. 4B). On the low site, suckers and spiders (including Opiliones) predominated with similar densities, whereas on the middle and high sites, suckers were more than twice as abundant as spiders. The densities of other groups, such as floral feeders and parasitoids, also varied among the sites. These differences also could reflect differences in top-down or bottom-up effects along the gradient. Proportions of major functional groups found in this study are similar to those reported in

earlier, lower elevation studies at Coweeta (Blanton 1989).

In conclusion, our results indicated that spatial variation, either on the scale of 500-m differences in elevation, or within the canopies of individual trees, was an important factor influencing herbivory by forest canopy arthropods. Spatial variation affected both the percentage leaf area removed by various insect herbivores and the guild structure of the arthropod community.

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