

# Diel Patterns of Canopy Arthropods Associated with Three Tree Species

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**ABSTRACT** Canopy arthropods on dogwood, *Cornus florida* L.; red maple, *Acer rubrum* L.; and yellow poplar, *Liriodendron tulipifera* L., were bag-sampled during the day and night on six dates from July through September 1986 in the southern Appalachians of North Carolina. Diurnal and nocturnal comparisons were made for arthropod community composition and similarity. Overall numbers of canopy arthropod taxa were similar both between and within tree species, as was relative taxon abundance as assessed by community diversity measures. However, there were substantial differences in faunal composition and weighted arthropod numbers between daytime and nighttime canopies. Diel differences in canopy faunal composition is related to differential periods of activity among some canopy arthropods. These data suggest that canopy foliage may support greater densities and kinds of arthropods than those previously reported based on daytime sampling only. Experimental designs that include diel sampling would provide a more complete assessment of the structure and composition of canopy communities by taking into account the dynamic component of these communities.

**KEY WORDS** Insecta, arthropod communities, diel activity, canopy arthropods

AT PRESENT, our understanding of the nature of canopy arthropod communities is based upon, and limited to, information obtained in the sampling and analysis techniques used to measure the arthropod populations comprising these communities. To date, most investigations into the structure and makeup of canopy arthropod communities have employed diurnal sampling regimes (e.g., Crossley et al. 1976, Schowalter et al. 1981, Southwood et al. 1982a, Stork 1987a) despite nocturnal activity on the part of numerous arthropod species representing many orders.

Although some of these nocturnal arthropods lie quiescent in the canopy during the day and thus would be counted in a diurnal sampling regime, there is evidence that many arthropods migrate to the canopy at night from diurnal resting places on the ground, in understory vegetation, or on the bole of the host tree (e.g., Adams 1941, Heinrich 1979, Larsen & Whalon 1987). Hence, little is known about the nocturnal aspects of canopy arthropod communities or, more important, the extent to which neglecting night-active arthropods may result in misrepresentation of arthropod species and abundance distributions within these communities. This may, in turn, lead to underestimation of the amount or rate of herbivory and of the quantity of community biomass supported by trees. In addition, neglect of the nocturnal dimension of canopy communities results in an incomplete understanding of the dynamic, temporal aspect of these communities.

In an attempt to evaluate the potential significance of neglecting the temporal dimension of can-

opy arthropod communities, our study compares both the diurnal and nocturnal composition of the canopy arthropod communities of three common tree species to assess possible diel patterns in species composition and diversity. This was accomplished by analyzing the diel distribution of taxa and of individuals comprising these taxa, and faunal similarities between and within tree species.

## Methods and Materials

Foliage and associated arthropods were sampled from a reforested watershed at the USDA-Forest Service Coweeta Hydrologic Laboratory, 25 km south of Franklin, N.C. (35° N 83° 25' W). Foliage was sampled from canopies of dogwood, *Cornus florida* L.; red maple, *Acer rubrum* L.; and yellow poplar, *Liriodendron tulipifera* L. Samples were taken from tree foliage on watershed 7, a 59-ha north-facing watershed clear-cut by cable logging in 1975-1976 (Swank & Crossley 1987) and since permitted to regenerate undisturbed. All sampling was performed at medium elevations ( $\approx 850$  m) using a modified, long-handled insect net with a drawstring closure and a 1-m-deep plastic bag insert (see Blanton 1990). All samples were taken from a height of 3-5 m from the ground; small branches and associated arthropods were captured by enclosing a branch, pulling the drawstring, and pruning the branch free. Chloroform-soaked cotton balls were added to the bagged samples to immobilize trapped arthropods.

Ten samples were taken from each tree species between 0900 and 1200 hours (EST) and again

between 2100 and 2400 hours on six dates during the summer of 1986: 2 July, 16 July, 30 July, 19 August, 11 September, and 26 September. Each of the 10 samples were taken from different individual trees of the same species; these same individuals were sampled on all six dates.

Samples were stored at 5°C for 1–3 d until they were processed in the laboratory. In processing, leaves were removed from branches, and all leaves and branches were inspected for arthropods. Leaves from each sample were dried at 50°C for 24 h and weighed. Arthropods were collected, stored in vials, and frozen for later identification. Insects were identified to family or superfamily and noninsects were identified to order.

Community composition was analyzed by comparisons of day–night arthropod taxa and abundance distributions. Day–night taxa distributions for individual and pooled sampling dates were compared using corrected  $\chi^2$  goodness-of-fit tests. Raabe's percentage of faunal similarity was used to determine degrees of faunal overlap between and within tree species (Southwood 1966): between-tree comparisons used the total faunal compositions of paired tree species, and within-tree comparisons paired the diurnal faunas with the nocturnal faunas for each tree species.

Further day–night comparisons were made with two measures of diversity: the Shannon-Weiner diversity index and the evenness index (Zar 1984). The Shannon-Weiner index ( $H'$ ) measures diversity in terms of numbers of taxonomic classes present and relative abundance of those classes. The evenness index ( $J'$ ) is expressed as the ratio of  $H$  to  $H_{max}$ , the maximum possible diversity for the observed number of taxonomic classes.

A nonparametric two-factor analysis of variance (ANOVA) by ranks, the Kruskal-Wallis test (Zar 1984), was employed to analyze day–night distributions of weighted arthropod numbers between and within tree species. The two factors tested are tree species and day–night. Arthropod numbers were weighted by sample foliage weight to standardize for sample size and were averaged over the 10 samples for each sampling date; these are expressed as mean arthropod numbers per 100 g (dry weight) of foliage.

## Results

The day–night distributions of taxa for each tree species are presented in Table 1. There were no differences in numbers of arthropod families between daytime and nighttime canopies for either individual sampling dates or pooled sampling dates ( $\chi^2$  goodness of fit tests,  $P > 0.05$  for all tests). The Shannon-Weiner diversity index (Table 2) further indicates the comparable overall faunal diversity of day and night canopies. However, day and night taxonomic distributions show that an average of 19.5% of all observed families were found only during the day and an average of 36.3% were found

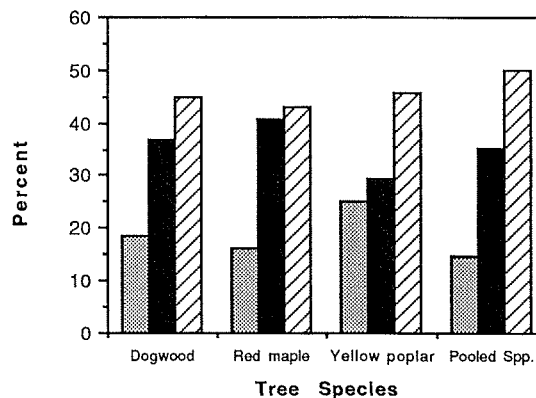


Fig. 1. Percentage temporal distribution of arthropod families for dogwood, red maple, yellow poplar, and pooled species;  $n = 49, 48,$  and  $44$  taxa for the three tree species, respectively. Note the large percentages of groups found only day or night. □, day; ■, night; ▨, day and night.

only at night (Fig. 1). Raabe's percentage of similarity, based upon numbers and relative abundance of arthropod taxa, indicates that the canopy arthropod communities of the study tree species possess a relatively high degree of faunal overlap (Table 3). Percentage similarities between the daytime and nighttime canopies of each individual tree species also indicate a high degree of faunal overlap (Table 3). Of central importance here is not the percentage of diel faunal overlap per se, but rather the percentage of nonoverlap. These nonoverlapping groups (by definition present only in the daytime or nighttime canopies, but not both) constitute a differential in diel faunal groups.

Thus, although the absolute numbers of families remained much the same day and night, several families were found only during the day or only at night (see Fig. 1 and Table 1 for details). Because many of the families observed both day and night may contain species that are day- and night-specific, estimates of diurnal–nocturnal specificity based upon the relative proportion of groups found only in the day or only at night are probably conservative. It is concluded that there exists a partial diel shift in the faunal composition of the canopy arthropod communities of these tree species, and that this shift occurs while preserving the overall structure of the community.

The mean weighted numbers of arthropods found in the daytime and nighttime canopies of the study tree species are presented in Table 4. The Kruskal-Wallis ANOVA by ranks (Table 5) suggests that there are significant differences in arthropod numbers between tree species and between day and night canopies ( $P < 0.0001$  for each factor and the factor interaction). Moreover, the evenness indices (Table 1) display changes in day–night taxon evenness for two of the three tree species considered, indicating a shift in the relative numbers of indi-

Table 1. Taxa found in 120 daytime and 120 nighttime canopy samples of dogwood, red maple, and yellow poplar

Taxon	Dogwood		Red maple		Yellow poplar	
	Day	Night	Day	Night	Day	Night
Coleoptera						
Anobiidae	0	3	0	0	0	0
Bruchidae	1	0	0	1	0	0
Buprestidae	0	0	1	0	0	0
Chrysomelidae	0	0	3	0	0	0
Cleridae	0	0	1	1	1	1
Coccinellidae	0	3	1	2	0	2
Curculionidae	2	1	3	0	1	0
Dermestidae	0	1	0	0	0	0
Elateridae	0	1	0	0	2	3
Lagriidae	0	0	0	1	0	0
Lathridiidae	0	0	0	0	0	1
Melandryidae	0	0	0	2	0	0
Mordellidae	0	0	0	0	0	1
Oedemeridae	0	0	0	0	1	0
Phalacridae	1	0	0	0	0	0
Ptilodactylidae	0	1	0	0	0	1
Staphylinidae	0	0	0	0	1	0
Tenebrionidae	1	1	0	0	0	0
Collembola						
Entomobryidae	0	1	0	0	0	0
Diptera						
Anthomyiidae	0	1	0	0	0	0
Asilidae	0	0	0	0	1	0
Cecidomyiidae	4	4	1	1	37	28
Ceratopogonidae	0	0	0	1	0	0
Chironomidae	0	0	3	1	0	0
Dolichopodidae	0	2	0	0	0	0
Drosophilidae	0	1	0	3	0	0
Empididae	0	1	1	0	0	2
Leptogastridae	0	1	0	0	0	0
Milichiidae	0	0	0	1	0	0
Mycetophilidae	2	2	2	1	0	0
Phoridae	1	1	0	0	0	0
Platysotmatidae	0	0	0	0	1	0
Psychodidae	0	2	1	0	1	0
Sciaridae	5	1	1	4	2	1
Stratiomyiidae	0	0	0	0	1	0
Syrphidae	0	0	0	1	0	0
Tachinidae	0	0	0	1	0	0
Tephritidae	0	0	0	1	0	0
Tipulidae	3	3	0	1	0	0
Ephemeroptera						
Heptageniidae	0	0	0	1	0	0
Hemiptera						
Lygaeidae	0	0	0	1	0	0
Miridae	4	5	6	4	4	9
Pentatomidae	2	3	0	2	2	3
Phymatidae	1	0	0	0	0	0
Reduviidae	3	6	6	4	3	3
Homoptera						
Aleyrodidae	1	0	0	0	0	1
Aphididae	0	2	1	2	102	104
Cercopidae	6	8	0	0	4	5
Cicadellidae	16	57	19	32	12	31
Derbidae	0	0	0	0	1	0
Flatidae	5	5	3	6	2	3
Membracidae	0	0	3	0	0	1
Psyllidae	1	1	1	1	0	1

Table 1. Continued

Taxon	Dogwood		Red maple		Yellow poplar	
	Day	Night	Day	Night	Day	Night
Hymenoptera						
Bombidae	0	1	0	0	0	0
Braconidae	0	1	2	2	1	1
Chalcididae	4	9	3	7	11	4
Cynipidae	0	0	0	1	0	1
Formicidae	2	2	5	18	3	2
Ichneumonidae	1	1	0	1	1	0
Proctotrupoidae	1	1	0	3	0	0
Vespidae	0	0	0	0	1	0
Lepidoptera						
Adults	1	9	0	7	2	3
Larvae	6	7	8	5	10	17
Neuroptera						
Chrysopidae	1	0	0	1	2	1
Coniopterygidae	1	0	0	3	0	0
Orthoptera						
Acrididae	0	0	0	0	0	3
Gryllidae	11	3	5	2	2	3
Tettigoniidae	1	0	1	1	1	4
Psocoptera						
Polypsocidae	0	0	2	0	0	0
Psocidae	0	0	0	0	0	1
Thysanoptera						
Merothripidae	1	0	0	0	0	0
Phlaeothripidae	0	1	2	0	0	0
Thysanura						
Lepismatidae	2	0	1	2	0	0
Acarina	0	2	0	0	0	1
Araneida	34	33	18	31	33	43
Diplopoda	0	2	0	0	0	0

Day samples were taken between 0900 and 1200 hours and night samples between 2100 and 2400 hours on each of six dates in the summer of 1986: 2, 16, 30 July; 19 August; 11, 26 September.

viduals in some taxa. The third species, yellow poplar, displayed only a slight difference.

### Discussion

Faunal similarity measures are usually composed of two components: taxonomic composition and relative numbers of taxon representatives. Consideration of these components individually can provide further insights in addition to those gained by considering the similarity index calculated with the two together.

With regard to taxonomic composition, our data suggest that some of the taxa comprising overall community trophic structure display diel shifts; that

is, community composition may change while overall structure remains the same. In this study, community composition is assessed primarily with the use of family-level taxonomic data. While use of such data poses problems (e.g., differential sampling probabilities which are contingent upon relative species richness between families, and the inclusion of quiescent or inactive arthropods present on foliage during periods of inactivity), they are nonetheless adequate for analyses of diel compositional differences. This is because any differences observed at the family level must reflect dif-

Table 2. Shannon-Weiner diversity index ( $H'$ ) and evenness index ( $J'$ ) for day and night canopies of dogwood, red maple, and yellow poplar (Zar 1984)

Index	Dogwood		Red maple		Yellow poplar	
	Day	Night	Day	Night	Day	Night
$H'$	2.76	2.75	2.89	2.92	2.14	2.30
$J'$	0.804	0.746	0.858	0.792	0.630	0.659

Table 3. Raabe's percentage of similarity between paired "habitats," based upon numbers of arthropod taxa and proportionate makeup of those taxa

Comparisons	Paired "habitats"	% Similarity
Tree spp.	Dogwood-Red maple	71.02
	Dogwood-Yellow poplar	46.46
	Yellow poplar-Red maple	42.76
Diel	Dogwood day-night	62.38
	Red maple day-night	60.07
	Yellow poplar day-night	80.66

**Table 4.** Mean numbers of arthropods per 100 g (dry weight) foliage

Sample date (1986)	Dogwood		Red maple		Yellow poplar	
	Day	Night	Day	Night	Day	Night
2 July	13.28	40.26	6.76	26.85	27.80	37.59
16 July	16.32	33.67	8.04	18.03	23.70	27.02
30 July	20.80	52.15	13.76	26.50	15.75	23.83
19 August	16.73	33.03	20.56	26.49	24.90	24.57
11 Sept.	19.15	24.24	15.69	31.43	19.0	18.40
26 Sept.	13.18	50.28	14.05	24.10	11.39	20.04

$n = 10$  samples day and night per tree species per sample date.

ferences at the species level as well, although the actual extent of these species differences is not known.

We suggest that diel species shifts are the consequence of differential time periods of activity on the part of some or all of the species comprising a community. Lewis & Taylor (1964) record such periodicity of activity for some 400 flying taxa representing 46 "habitats." Thus, the extent to which a given species contributes to a diel shift hinges upon its period or periods of activity in the daily 24-h cycle.

Many species display a periodicity of activity that is neither diurnal nor nocturnal. These species are active at certain times both day and night, although the onset of daytime or nightfall may trigger the initial bout of activity in the daily cycle. The eastern tent caterpillar, *Malacosoma americanum* (F.), exemplifies this type of activity pattern (Fitzgerald 1980); species such as this would not contribute to a faunal shift. Other species are temporally specific with respect to their activity periods. Some such species remain in the canopy when quiescent (e.g., *Callosamia* spp.) and also would not contribute to a faunal shift. Those that actively migrate to the canopy at night and leave in the daytime or vice versa, however, collectively constitute a faunal shift. The cicadellid *Paraphlepsius irroratus* (S.) displays the former movement pattern (Larsen & Whalon 1987), and Heinrich (1979) suggests that many caterpillar species may employ diel canopy migration-emigration as a predator avoidance strategy. The latter pattern was found by Lewis & Taylor (1964), who found more canopy-dwelling taxa by day than by night in their suction traps and suggested that diurnal periodicity of activity is related to light intensity.

Even in the absence of faunal shifts of the kind described here, daytime and nighttime canopies can be quite different owing to changes in the second component of faunal similarity measures: relative abundance of taxa. The Kruskal-Wallis test, which makes comparisons based solely on this measure, indicates highly significant differences in numbers of individuals between tree species and, most important to this discussion, between day and night canopies (Table 5).

**Table 5.** Summary table for Kruskal-Wallis analysis of variance of ranks performed on ranked mean numbers of arthropods per 100 g foliage from day-night canopies of dogwood, red maple, and yellow poplar

Source	SS	df	H statistic
Cells	6,562.5	5	
Trees (factor A)	4,288.75	2	0.5366*
Day-night (factor B)	5,962.28	1	0.7461*
A × B	-3,688.52	2	-0.4616*

\*,  $P < 0.0001$  (Kruskal-Wallis ANOVA by ranks [Zar 1984]). Total mean square = 7,991.5.

These differences are further evidenced by the similarity measures. Raabe's percentage of similarity (Table 3) indicates that the day-night canopies of dogwood and red maple are  $\approx 60\%$  similar, whereas those of yellow poplar display greater similarity (80%). The evenness index (Table 2) reflects this pattern as well; day-night arthropod communities of dogwood and red maple have a greater disparity in evenness than those of yellow poplar. The changes in these similarity measures stem from differences in relative abundance of taxa representatives.

Both the faunal shift phenomenon and species abundance-distribution data hold certain implications for the assessment of the structure and composition of canopy arthropod communities. In particular, our data suggest that canopy foliage may support greater densities and kinds of canopy arthropods than are typically estimated from daytime samples. Investigations into the nature of canopy arthropod communities usually involve measures of arthropod taxa and biomass distributions within a guild model, as first described by Root (1967, 1973). The community structure perceived is therefore contingent upon the method and protocol of sampling. Most investigations have employed either knockdown sampling, bag sampling, or light-trapping.

Knockdown sampling entails fogging the canopy with an insecticide or some other knockdown agent and collecting arthropods which fall onto sheets of known area for a set period of time following fogging (usually 1 or 2 h). Among other investigations, this sampling method has been used to compare guild biomass and composition between tree species (Moran & Southwood 1982, Stork 1987b), assess the number and biomass proportions of guilds (Brown & Southwood 1983, Stork 1987a), measure the overall faunal abundance and biomass of arthropod communities (Southwood et al. 1982a), and analyze the seasonal and spatial distribution of certain taxa (Barnard et al. 1986). The bag sampling technique we used has been employed to assess arthropod community structure (Crossley et al. 1976, Schowalter et al. 1981, Schowalter 1989) and nutrient distribution within communities (Schowalter et al. 1981, Schowalter & Crossley 1983). Light trapping is also commonly employed in the assessment of diversity and niche breadth of var-

ious taxa (e.g., Sutton & Hudson 1980, Broadhead 1983, Rees 1983).

The problem with the sampling regimes employed in these studies is that they are temporally constrained; in all cases, the faunal lists and biomass measures are based upon arthropods collected in either diurnal or nocturnal sampling regimes. Although such sampling constraints are often unavoidable owing to considerations of finance, logistics, or safety, it remains that neglecting inactive arthropods bears upon the perceived community structure and makeup because a certain proportion of the arthropods comprising this structure and makeup are found at one or the other time of day.

The extent of the effects of neglecting inactive arthropods on guild and biomass measurements is unknown. Southwood et al. (1982b) report parallels in measures of species richness between six knock-down-sampled British tree species and faunal lists drawn from the literature for those tree species. The fact that the samples in this study were diurnal suggests that the effects of neglecting nocturnal arthropods are negligible, although there exists the possibility that faunal lists taken from the literature are also largely based upon diurnal collections. Stork (1987b), however, reports that misplacement of even a few species in guild assignments can cause important differences in the proportions of those guilds. Stork (1987b) further states that these differences can greatly affect the results of sample comparisons and guild analyses. These findings of Stork suggest that the absence of just a few crepuscular or nocturnal species from samples may be significant because the misplacement of a species in a guild is conversely the absence of that species from its proper guild.

These potential problems often are easily mitigated. Where possible, diel replication should be adopted in studies that address canopy arthropod community composition and secondary production. In this way, representation of the full complement of arthropod species and their relative abundance in the community may be more closely approached, and the corresponding measures of community biomass and species distribution will be more accurate. Such a sampling regime recognizes that communities are not wholly static or unidimensional but possess dynamic components which vary in space and time.

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