*Selbyana* 19(2): 141–146

# CANOPY AND GROUND LEVEL INSECT DISTRIBUTION IN A TEMPERATE FOREST

EVAN PREISSER[1], DAVID C. SMITH

Biology Department, Williams College, Williamstown, Massachusetts 01267

AND MARGARET D. LOWMAN

Marie Selby Botanical Gardens, 811 South Palm Street, Sarasota, Florida 34236

ABSTRACT. We tested for the effect of height on the number of flying insects at one site in a mixed hardwood temperate forest in Williamstown, Massachusetts, by trapping insects at two heights, 0 and 20 meters above the ground, using two types of traps, light traps and malaise traps, from May through September 1992. Overall, insects were approximately eight times more abundant in traps at ground level than in the canopy. Of 101 insect families collected, 86 families (85%) were more abundant in the ground level traps than in the canopy traps. For most groups, these abundance differences with height were consistent in both types of trap. Our results contrast with previous work, done in tropical forests, which has consistently shown more insects in the canopy than in the understory. Our results suggest that the canopy, which supports a major component of insect diversity in the tropics, might not directly support the bulk of insect diversity in temperate forests.

## INTRODUCTION

The high species diversity of tropical forest arthropods is sustained in part by the large number of insects in the canopy (Erwin 1982, 1983): tropical rainforest insects are more abundant in the canopy than near the forest floor (Erwin 1982, Smythe 1982, Erwin 1983, Sutton *et al.* 1983, Stork and Brendell 1990, Stork 1991). Recent studies suggest that the diversity of arthropods in the canopies of temperate forests is substantially less than in the tropics (Schowalter 1989, Simandl 1993, Schowalter 1995). However, the height distributions of insect abundance, comparable to those reported in tropical forests (Smythe 1982, Sutton *et al.* 1983, Stork and Brendell 1990, Stork 1991), have not been measured in temperate forests. The aim of this study was to compare the number of insects in the canopy of a temperate forest with that at ground level. We sampled adult insects at two levels, through most of a growing season, at a canopy walkway site in a temperate deciduous forest in northwestern Massachusetts.

## MATERIALS AND METHODS

Our study site was in the Hopkins Memorial Forest, a northern hardwood forest near Williams College, Williamstown, Massachusetts, USA. The Hopkins Memorial Forest is a mosaic of stands at different successional stages. The site chosen for canopy sampling was in a stand of mature red oak (*Quercus rubra),* with an understory of red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and hornbeam (*Ostrya virginiana*). The top of the canopy of these trees was 45 m, while densest canopy foliage was found at 30 m. We used a walkway (at 20 m above the ground), to gain access to the canopy.

We used four traps: a zero meter (ground level) light and malaise trap, and a twenty meter (canopy level) light and malaise trap. The 0 meter (m) light trap was placed 3 m from the base of the tree supporting the main canopy platform. The 20 m light trap was placed at the level of the main canopy platform. The 20 m trap was positioned directly above the 0 m trap. Thick understory growth prevented either light trap from being directly visible at any time from the other.

The 0 m malaise trap was erected in a small clearing 10 m from the 0 m light trap to ensure that the light trap would not be directly visible from the malaise trap. The 20 m malaise trap was placed in the middle of the canopy walkway, suspended between the two trees that supported the walkway. Because of walkway limitations it was impossible to ensure that no interference occurred between the 20 m light and malaise traps; however, the malaise trap was placed in the area of lowest possible interference on the side of the tree opposite that of the light trap.

Light traps were run two nights per week beginning 4 June and ending 30 September 1992. The light traps ("Pennsylvania" type described by Southwood 1966, in Smythe 1982) have four perpendicular plastic vanes (each 0.06 $m^2$) with

[1] Current address: 215 S 4th Ave., 1st floor, Highland Park, New Jersey 08904.

an ultraviolet lamp (30 cm Sylvania #350 blacklight) in the middle. Insects attracted to the light hit the vanes and fell into a bucket suspended underneath. Light traps were turned on from approximately 1700 to 0630 each night (about 13.5 hours). Seventeen trapping dates were missed because of rainy weather, so that samples were obtained on sixteen nights spaced throughout the trapping period.

Malaise traps were run every other week beginning 11 June and ending 29 September 1992. The malaise traps were of the standard "tent" type (Matthews & Matthews 1971); they consist of a hanging net (2.5 $m^2$), with netting above and to either side. A piece of insecticide (Vapona brand) in the collecting bottle was used to kill the insects.

After collection, insects were placed in 70% ETOH or placed in bags and frozen. Each sample consisted of all insects captured over a 7 day period; the date for each sample is the middle date of each sample. Seven malaise samples and sixteen light trap catches were obtained, representing week long and daily collections respectively.

All collected specimens longer than 5 mm were counted, and more than 95% of these were identified to family. We excluded insects less than 5 mm because they were often badly damaged by larger insects; they included fewer than 10% of all insects counted, and they were a small fraction of the insect biomass that we captured.

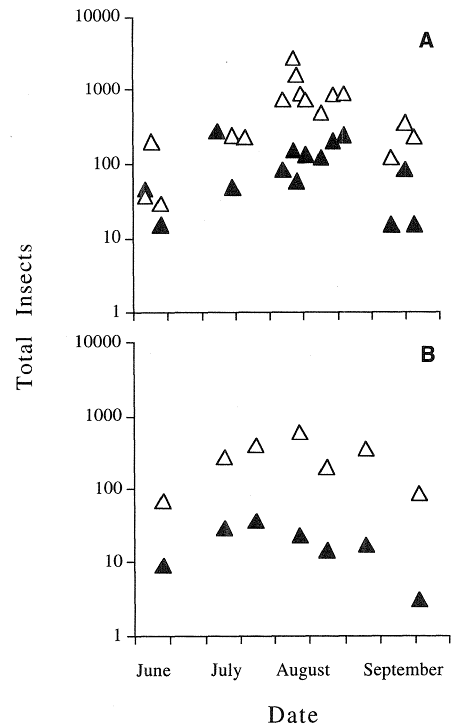


FIGURE 1. Insects captured in light traps (A) and malaise traps (B). Solid triangles are insects caught at 20 meters, and open triangles are insects caught at 0 meters. Ground level traps caught over seven times as many insects as canopy traps. The seasonal pattern of captures was similar at both levels and in both trap types.

## RESULTS

During the trapping period, we caught 13,333 insects in 101 families representing 11 orders. Trap height dramatically affected the overall capture rates (FIGURE 1; note the logarithmic scale). Traps at 0 m caught 11,744 insects, whereas those at 20 m caught 1,589 insects (a ratio of 7.39 to 1). This difference between high and low traps was consistent for both light and malaise traps, although light traps caught more insects than malaise traps, and malaise traps were more affected by height than were light traps. As expected, most insects were caught in the warmer months of July and August.

We found similar patterns when the orders and families were analyzed separately. Of 101 insect families identified, 86 (85%) were more abundant in the ground level traps than in the canopy; all but two of the 20 most abundant families were caught more frequently at ground level than in the canopy (TABLE 1). Of these families, only the Miridae (Hemiptera) were caught more often in the canopy traps than at ground level. Three of the six common orders, Diptera, Hymenoptera, and Lepidoptera, were more abundant near the forest floor than in the canopy, although there was no clear difference related to height in total counts of Coleoptera, Hemiptera or Trichoptera (FIGURE 2).

We obtained extensive light trap capture data on a number of insect taxa: the scarab genus *Phyllophaga,* the two Lepidopteran families Noctuidae and Geometridae, the two Dipteran families Mycetophilidae and Tipulidae, and the Trichopteran family Lepidostomatidae. All six taxa were much more abundant in the ground level traps than at 20 m, consistently so in all but the Lepidostomatidae (FIGURE 3).

## DISCUSSION

Although temperate canopy arthropods are now being studied extensively (Schowalter 1989, 1995, Simandl 1993, Winchester 1997), our data appear to be the first to compare canopy and understory arthopod abundance in a temperate forest. The relative abundance of insects

TABLE 1. Number of insects caught in the canopy and at ground level in the 20 most abundantly trapped families.

| Order<br>Family | 0 m<br>Total | 20 m<br>Total | Trap<br>total | Percent<br>at 0 m |
|---|---|---|---|---|
| Coleoptera | | | | |
| Cantharidae | 73 | 38 | 111 | 65.8 |
| Elateridae | 111 | 20 | 131 | 84.7 |
| Lycidae | 59 | 8 | 59 | 86.4 |
| Scarabaeidae | 141 | 12 | 153 | 92.2 |
| Diptera | | | | |
| Culicidae | 41 | 41 | 82 | 50 |
| Empididae | 26 | 2 | 28 | 92.9 |
| Muscidae | 133 | 13 | 146 | 91.1 |
| Mycetophilidae | 2,135 | 124 | 2,259 | 94.5 |
| Rhagionidae | 155 | 5 | 160 | 96.9 |
| Sarcophagidae | 27 | 8 | 35 | 77.1 |
| Tipulidae | 467 | 88 | 555 | 84.1 |
| Hemiptera | | | | |
| Miridae | 18 | 79 | 97 | 18.6 |
| Hymenoptera | | | | |
| Braconidae | 42 | 5 | 47 | 89.4 |
| Ichneumonidae | 120 | 8 | 128 | 93.8 |
| Lepidoptera | | | | |
| Arctiidae | 448 | 8 | 456 | 98.2 |
| Geometridae | 602 | 50 | 652 | 92.3 |
| Lasiocampidae | 33 | 3 | 36 | 91.7 |
| Noctuidae | 5,685 | 478 | 6,163 | 92.2 |
| Trichoptera | | | | |
| Lepidostomatidae | 562 | 247 | 809 | 69.5 |
| Phygranaeidae | 65 | 7 | 72 | 90.3 |

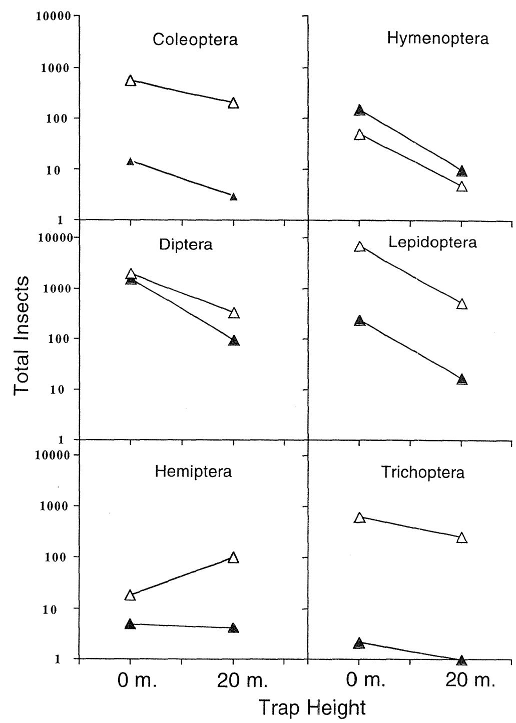


FIGURE 2. The effect of height and trap type on the number of insects caught in the six most common orders. Open triangles are light traps, and solid triangles are malaise traps.

near the forest floor in our study contrasts with the well established pattern of flying adult insects in tropical forests. Studies in several forest habitats using sampling schemes similar to ours indicate that in tropical forests, canopies hold more insects than the understory. In Panama, light traps caught as many or more insects at 20 or 26 meters than at ground level; this difference held for Coleoptera, Ephemeroptera, Hemiptera, Hymenoptera and Lepidoptera (Smythe 1982). In lowland rain forest sites in Brunei, Panama, and Papua New Guinea, canopy light traps caught more insects of most groups, including Coleoptera, Diptera, Hemiptera, Homoptera, and Hymenoptera, at 30 and 20 m than at ground level (Sutton *et al.* 1983). Kitching *et al.* (1993) also found more insects in the canopy than in the understory in an Australian tropical rain forest, in contrast to a subtropical rain forest site, where they found slightly more insects in the understory than in the canopy.

Compared to tropical species, many of the temperate forest insects that we trapped have life histories that may tie them closely to resources near the ground. Four of the six taxa that we sampled most extensively have major feeding life stages near the ground. Lepidostomatidae (Trichoptera) have exclusively aquatic larvae, flying as adults for only brief periods (Ito 1981, 1984). Tipulidae (Diptera) live as larvae in streams or in wet wood or soil (Fuller & Hynes 1987, Pritchard & Hall 1971, Hofsvang & Hagvar 1976). Mycetophilidae (Diptera) are also ground based, feeding on fungi or building web systems used for travel and to capture prey (Peck & Russell 1976, Arnett 1985). Adult Mycetophilidae engage in mating flights near ground level rather than in the canopy (Peck & Russell 1976). Even *Phyllophaga* beetles (Scarabeidae: Coleoptera), some of which swarm as adults in the canopy, feed as larvae in soil, with most flights closer than 5 m to the ground (Guppy 1982, Stone 1986, Kard & Hain 1990). In contrast, many abundant tropical insect species appear to be tied throughout their life cycle to the canopy (Erwin 1982). Wilson and Holldobler (1990) noted that tropical forests hold some specialist ant species (Formicidae: Hymenoptera) that live exclusively in the canopy, and this

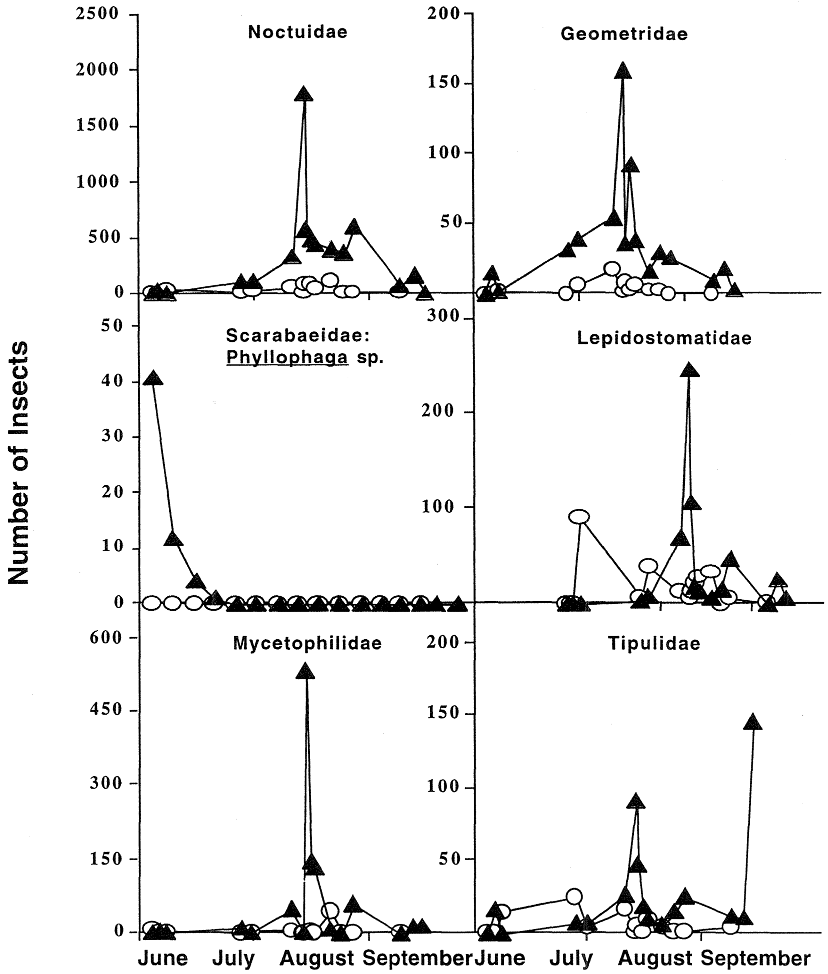


FIGURE 3. Seasonal capture patterns in light traps for the five most common families, and for the genus *Phyllophaga* (Coleoptera: Scarabaeidae). More insects are found near ground level throughout the season in all groups except for the Lepidostomatidae. Solid triangles are ground traps, and open ovals are canopy traps.

pattern may well hold true for tropical forest insects in general.

The most likely explanation of the predominance of ground-based insects in temperate forests may relate to the structure of the temperate forest itself. Temperate forests are much more seasonally variable in climate than are tropical rainforests, with corresponding changes in the vegetation. Temperate forest canopies undergo a drastic change in winter, losing all of their leaves and many of their hiding places. Unlike the rain forest, the temperate forest does not have vegetation throughout the year sufficient to support a permanent population of canopy feeders. Moreover, since the temperate forest has a relatively restricted growing season, many trees which make up the canopy leaf out synchronously, creating only a brief period when phytophagous insects have abundant new vegetation available. During much of the growing season, the temperate forest trees have older, tougher leaves with higher levels of lignins and tannins (Lowman 1985). In addition, temperate forests may provide substantial food resources near the ground. Understory herbs may have vegetation that is eaten more readily than is canopy vegetation. Much of the canopy vegetation is not eaten by herbivores at all, but enters the detritus food chain in the soil, where it is heavily exploited by insects.

This explanation may not hold, however, for the two common Lepidoptera families, Geometridae and Noctuidae. The larvae of these moths are leaf and stem feeders, and they are known to feed in both temperate and tropical forest canopies (Yela and Herrera 1993). Their combined presence can defoliate entire trees (Arnett 1985). We would therefore expect these two families to have substantial flight activity at least during the egg laying and mating periods which occur in late summer and early autumn in the temperate deciduous forest. Most of the moths that we captured were presumably participating in these flights, yet they were primarily captured near the ground. Perhaps the most plausible explanation is that the adults of both families drop near ground level to travel from one site to another, because the forest is more open at that level and dense foliage does not impede movement.

Our results may have general implications for patterns of insect biodiversity. Working in tropical forests, Erwin (1982, 1983) fogged tropical trees and found large numbers of specialist species in the canopy. His findings were the basis for dramatically increased estimates of global arthropod biodiversity. In our temperate forest study, we found that the proportion of canopy insects was low, when compared to tropical studies using similar techniques; furthermore, many of the common taxa have life history stages that depend on resources near or on the ground. This difference suggests that the presence of canopy specialists in tropical forests, and their relative scarcity in similar canopy-level temperate habitats, may account substantially for the increase in diversity as one moves towards the tropics.

In this study, we were able to gain access to only one site in the canopy; this prevented us from obtaining replicated samples at several locations in the local forest. But the patterns that we found are so pronounced, in the number of insects, in the consistent difference between high and low catch rates in so many families, and over an extended sample over an entire season, using two types of traps, that it seems unlikely that additional nearby samples would appreciably change our results. Our findings do indicate, though, that added samples from other temperate forest sites, analogous to those already available from several widely scattered tropical localities, are highly desirable.

## Acknowledgments

David Young and Rob Van Gent both deserve thanks for summer trapping. E.P. thanks his parents Julie and Thomas Preisser. E.P. was supported by Williams College research funds, and M.L. received an environmental grant from the Miller Foundation to construct the canopy walkway system. Thanks also to Canopy Construction Associates for their design and construction of the Williams College walkway.

## Literature Cited

ARNETT R.H. JR. 1985. American insects. Van Nostrand, Reinhold & Co. New York, New York. 850 pp.

ERWIN T.L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. The Coleopterists Bull. 36(1): 74–75.

——— 1983. Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. *Tropical rain forest: ecology and management.* Special Publication No. 2 of the British Ecological Society. Blackwell Scientific Publications. Boston, Massachusetts. 59-75.

FULLER R.L. AND H.B. HYNES. 1987. The life cycle, food habits, and production of *Antocha saxicola* o.s. (Diptera: Tipulidae). Aquat. Insects. 9: 129–136.

GUPPY J.C. 1982. Effects of temperature and light intensity on nocturnal activity patterns of the Northern June Beetle *Phyllophaga fusca* and the Common June Beetle *Phyllophaga anxia* (Coleoptera: Scarabaeidae). Canad. Entomol. 114: 1151–1158.

HOFSVANG T. AND S. HAGVAR. 1976. Density and composition of crane fly larvae (Diptera: Tipulidae) from an alpine wet meadow at Stigstuv Hardangervidda, South Norway. Norwegian J. Entomol. 23: 41–43.

ITO T. 1981. Morphological and ecological studies on the caddis-fly genus *Dinarthrodes* in Hokkaido, Japan (Trichoptera: Lepidostomatidae). Kontyu 48: 311–320.

——— 1984. Three new species of *Dinarthrum* (Trichoptera: Lepidostomatidae). Kontyu 52: 1–20.

KARD B.M.R. AND F.P. HAIN. 1990. Flight patterns and white grub population densities of three beetle species (Coleoptera: Scarabaeidae) in the mountains of northwestern North Carolina USA. J. Entomol. Sci. 25: 34–43.

KITCHING R.L., J.M. BERGELSON, M.D. LOWMAN, S. MCINTYRE, AND G. CARRUTHERS. 1993. The biodiversity of arthropods from Australian rain forest canopies: general introduction, methods, sites, and ordinal results. Australian J. Ecol. 18: 181–191.

LOWMAN M. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. Australian J. Ecol. 10: 7–24.

MATTHEWS R.W. AND J.R. MATTHEWS. 1971. The malaise trap: its utility and potential for sampling insect populations. The Michigan Entomol. 4: 117–122.

PECK S.B. AND D.R. RUSSELL. 1976. Life history of the fungus gnat *Macrocera nobilis* in American caves (Diptera: Mycetophilidae). Canad. Entomol. 108: 1235–1241.

PRITCHARD G. AND H. HALL. 1971. An introduction to the biology of crane flies in a series of abandoned beaver ponds with an account of the life cycle of *Tipula sacra* (Diptera: Tipulidae). Canadian J. Zool. 49: 467–482.

SCHOWALTER T.D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. Canad. J. Forest Res. 19: 318–322.

——— 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. For. Ecol. and Manag. 19: 115–125.

SIMANDL J. 1993. Canopy arthropods on Scots pine: influence of season and stand age on community structure and the position of sawflies (Diprionidae) in the community. For. Ecol. and Manag. 62: 85–98.

SMYTHE N. 1982. The seasonal abundance of night-flying insects in a neo-tropical forest. Pp. 309–318 *in* The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institute Press. Washington, DC.

STONE J.D. 1986. Time and height of adults of adults of white grubs (Coleoptera: Scarabaeidae) in the southwestern United States. Environ. Entomol. 15(1): 194–197.

STORK N.E. AND M.J.D. BRENDELL. 1990. Variation in the insect fauna of Sulawesi trees with season, altitude, and forest type. Pp. 173–190 *in* Insects and the rain forests of south east Asia (Wallacea). The Royal Entomological Society of London. London, England.

STORK N.E. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. J. Tropical Ecol. 7: 161–180.

SUTTON S.L., C.P.J. ASH AND A. GRUNDY. 1983. The vertical distribution of flying insects in lowland rainforests of Panama, Papua New Guinea, and Brunei. Zool. J. Linnean Soc. 78: 287–297.

YELA J.L. AND C.M. HERRERA. 1993. Seasonality and life cycles of woody plant feeding noctuid moths (Lepidoptera: Noctuidae) in Mediterranean habitats. Ecological Entomol. 18: 259—269.

WILSON E.O. AND R. HÖLLDOBLER. 1990. The ants. Belknap Press. Cambridge Massachusetts. 732 pp.

WINCHESTER, N.N. 1997. Canopy arthropods of coastal Sitka spruce trees on Vancouver Island, British Columbia, Canada. Pp. 151–168 *in* Canopy arthropods. Chapman and Hall. London, England.