

A review of methods for sampling arthropods in tree canopies

*Y. Basset, N.D. Springate, H.P. Aberlenc
and G. Delvare*

ABSTRACT

A review of most of the 'non-fogging' methods which have been used to sample arthropods in tree canopies, particularly in tropical forests, is presented, emphasizing the strengths and limitations of each method, as well as the rationale for its use. In particular, methods used with the canopy raft are examined. The review is supplemented with a comparison of the selectivity of four methods used in Papua New Guinea for collecting adult leaf-feeding beetles: pyrethrum knockdown, composite flight-interception traps, branch clipping and hand-collecting/beating. The total number of species collected was highest with composite flight-interception traps, whereas the number of species collected and known to feed on the tree species sampled was highest with hand-collecting/beating. The results emphasize the need for spatial and seasonal replicates in faunal surveys and the abundance of transient species in these replicates. None of the sampling methods examined can be considered as a panacea for investigating a wide range of topics. It is imperative that several, complementary methods should be used for general arthropod surveys. A key is provided to assist ecologists in selecting sampling methods appropriate for their research.

INTRODUCTION

Early studies on canopy arthropods were more concerned with taxonomic inventories than with investigation of specific ecological topics. With improvements in gaining access to the canopy and the development and refinement of several sampling methods, the study of canopy

arthropods has matured and now embraces a wide range of ecological issues, as this book testifies. In this chapter, the term 'canopy' is used in its broader sense, meaning the crown of trees, whereas its stricter sense, 'canopy ecotone', refers to the interface between the uppermost layer of leaves and the atmosphere (Hallé and Blanc, 1990).

The growing scientific interest in canopy arthropods emphasizes the need for appropriate sampling methods. Obviously, it is important to standardize techniques whenever studies attempt to answer similar questions at different locations. However, it would be misleading to assume that one or a few sampling methods would be appropriate to overcome the numerous challenges that the ecologist faces when studying canopy arthropods. Each method has its inherent advantages and biases and some may be more appropriate than others to investigate specific topics (Southwood, 1978). For example, pyrethrum knockdown is a productive method which has been used widely both in temperate and tropical forests (Stork and Hammond, 1997, Chapter 1, this volume). However, this method would be unsuitable to study arthropod diel activity in tree canopies, since the same tree cannot be re-sampled within a few hours (since full recolonization cannot be expected during that period of time).

Instead, this review examines these concerns and acknowledges the strengths and the limitations of each method, as well as the rationale for its use. It is intended primarily for the ecologist, is focused on sampling tropical arthropods, and provides representative examples rather than an exhaustive list of references. It is based on field experience and is supplemented with a comparison of four methods used for sampling leaf-feeding beetles at one tropical location. Students interested in sampling canopy arthropods may wish to consult, in addition to textbooks on statistics and multivariate analyses, papers covering important topics which are not discussed here. These include protocols for quantitative studies of assemblages, sample dimensions and complementarity, and the extrapolation of species richness (Hutcheson, 1990; Coddington *et al.*, 1991; Eberhardt and Thomas, 1991; Hammond and Harding, 1991; Colwell and Coddington, 1994; Hammond, 1994; Longino, 1994).

Before commencing the review of sampling methods, it should be mentioned that there are a number of methods for gaining access to the canopy or for establishment of sampling equipment in the canopy, such as the spikes-and-belt method, single-rope technique, towers, cranes, walkways, dirigible and canopy raft (reviewed in Mitchell, 1982; Lowman *et al.*, 1993a; Moffett, 1993). Since it is possible to use a wide range of sampling methods with the recent innovation of the canopy raft, a separate section is devoted to the latter.

A REVIEW OF METHODS

Insecticide knockdown

Stork and Hammond (1997, Chapter 1, this volume) review the use of insecticide for sampling canopy arthropods. The main advantage of this method includes relatively quick implementation (making it suitable for short-term studies), high productivity (high numbers of arthropods collected) and 'clean' samples, which may be processed easily. The method appears ideal for general surveys of forest tracts and large-scale taxonomic work (Erwin and Scott, 1980; Erwin, 1983; Stork, 1987a,b). However, sampling may be highly dependent on weather conditions and, usually, needs to be performed when air conditions are calm, e.g. at daybreak. Where an emphasis is on the determination of arthropod densities (expressed by the number of arthropods collected per surface area of tray) (Greenwood, 1990; Stork and Brendell, 1990, 1991; Stork, 1991; Russell-Smith and Stork, 1994), the sample size represented by each fogging tray is known imprecisely, since the amount of foliage above it is difficult to quantify. Usually, arthropods are collected dead (but see Paarmann and Stork, 1987; Adis *et al.*, 1997, Chapter 4, this volume; Paarmann and Kerck, 1997, Chapter 3, this volume) and their origin from a specific habitat within the tree sampled may be difficult to trace with confidence. Another restriction, as emphasized previously, is that it is not possible to re-sample the same tree before allowing for recolonization. The cost of equipment and chemicals and the time required to both clear the area beneath the target tree and emplace the collecting trays must be taken into consideration.

Foliage samples

Most methods targeting foliage arthropods, including those in flowers and seeds, are grouped here. Limitations of these methods include: (i) the disturbance of foliage causing active insects to fly or jump off, although this is less of a problem when using cranes; (ii) depending on which method is used to gain access to the canopy (e.g. single-rope technique), it is often impossible to sample in the periphery of the crown, unless access is gained from adjacent trees (but see discussion on the canopy raft); and (iii) it is difficult to sample from moist foliage. Most of these methods are inexpensive, with the possible exception of 'gassing', but often time consuming.

Hand-collecting

The most direct technique is the inspection of foliage and subsequent collection of arthropods in tubes or with entomological nets or aspirators/pooters (Morris, 1955; Moran *et al.*, 1994; Basset, 1997, Chapter 12, this

volume). The origin of specimens is known and they may be collected alive. However, the method is not productive and its results are considerably dependent on the experience of the investigator. Direct examination of leaves has provided estimates of densities of minute arthropods, such as mites (Walter *et al.*, 1994).

Extraction

Minute arthropods associated with leaves, flowers and seeds may be extracted using Berlese-Tullgren apparatus or similar devices (Harris, 1971; Basset, 1985). The method is destructive, but sample size can be determined easily so that both numbers of individuals and species may be compared among samples. Small arthropods may be extracted from leaves by exposing them to the vapour of certain chemicals or washed from leaves using various solutions (Southwood, 1978).

Branch clipping

A few branches are cut and enclosed in a large plastic bag, whose content is later examined in the laboratory (Ohmart *et al.*, 1983; Majer and Recher, 1988; Costa and Crossley, 1991; Basset *et al.*, 1992a) (Figure 2.1). Blanton (1990) described a convenient collapsible-bag sampler and compared samples taken with this technique with those obtained with pyrethrum knockdown. Arthropods can be anaesthetized by dropping a small ball of cotton-wool, saturated with ethyl acetate, inside the bag. Sample size (leaf area) can be determined, usually with precalculated regressions of dry weight against leaf area. It is an inexpensive method to estimate the actual density of foliage arthropods, despite being destructive, biased towards sedentary taxa and relatively non-productive. Further, individual bags often sample such a small portion of habitat that they must be pooled to be sufficiently representative (Blanton, 1990).

'Gassing'

This is a small-scale variation of the fogging method, also known as the 'selecteur' or 'restricted canopy fogging' (Lepointe, 1956; Dempster, 1961; Basset, 1985, 1990). A few branches are enclosed in a container or a plastic bag, which is then gassed with carbon dioxide, for example, and the anaesthetized arthropods retrieved. Leaves may be cut or counted to estimate sample size and to provide estimates of arthropod densities. This method has been used for studying arthropod stratification within tree crowns (Basset, 1992). However, the method is inadequate for sampling arthropods from the trunk and large limbs and the foliage is disturbed when the container or bag is positioned.

Beating

A beating tray is held under a few branches, which are then struck with a stick. Usually, fallen arthropods are collected with aspirators (Lepointe, 1956; Harris *et al.*, 1972; Turner, 1974; New, 1979; Mouna *et al.*, 1985). However, quantitative samples may be derived by collecting most arthropods into a large plastic funnel, fitted with a collecting jar filled with fluid (Wilson, 1962; Basset, 1985; unpublished data). Insects and falling debris may be pushed gently into the collecting jar with a brush. Sample size may vary considerably, depending on the type of foliage. This method is particularly effective for dislodging free-living caterpillars, but less so for active or small arthropods.

Sweeping

This is a popular method for sampling arthropods in the field layer, in which the vegetation is swept with a net. Since sweeping requires perambulation, this method has been used rarely in tree crowns (Dowdy, 1950; Lepointe, 1956; Lowman *et al.*, 1993a,b). Like beating, sample size (measured here as one or a few sweeps) can vary considerably, depending on the nature of the foliage and, therefore, samples are difficult to compare. Sweeping is less effective in dense vegetation and depends on the experience of the investigator (Lamotte *et al.*, 1969). Active arthropods tend to be better sampled than sedentary ones (Noyes, 1989) and small specimens tend to be overlooked (Hespenheide, 1979). To remedy the latter problem and to process large numbers of arthropods, LeSage (1991) proposed a sweeping technique in which the entire contents of the net are placed in a killing jar. A study comparing the relative efficiency of pyrethrum knockdown, beating and sweeping for sampling arboreal arthropods is in progress (M.D. Lowman, personal communication).

Non-attractive traps

The methods reviewed in this section do not provide a measurement of density, but relative measurement of activity. Flying insects are targeted, but adult Lepidoptera are difficult to identify after being immersed in or entrapped by the collecting agent (although killing-jars may be used). Non-attractive traps may provide less biased general surveys than attractive traps. The former are often inexpensive, but the investment in time for cleaning the samples must be considered. Several authors have used various criteria to compare the effectiveness of non-attractive and attractive traps (see p. 33; Juillet, 1963; Southwood, 1978; Hosking, 1979; Osmelak, 1987; Noyes, 1989; Hammond, 1990; Muirhead-Thomson, 1991).

Malaise traps

These refer to a class of tent-like traps of different designs. They have been used extensively in the field layer, but less so within tree-crowns (Crossley *et al.*, 1973; Basset, 1985; Hammond, 1990) (Figure 2.1). In the field layer they are supported by ropes and pegs, but require suspension within a rigid frame for use in the canopy. They target insects whose tendency is to fly upwards when encountering a vertical surface, and are particularly effective for collecting Diptera and Hymenoptera. Dufour (1980) described a trap combining features of Malaise and light trap, suitable for sampling arthropods both during day- and night-time.

Flight-interception traps

These consist of vertical panels and collecting trays, the latter filled with water or other collecting fluid, which have been used in tree canopies (Merrill and Skelly, 1968; Crossley *et al.*, 1973; Hosking and Knight, 1975). They are more effective for collecting arthropods, such as Coleoptera, which fall when encountering vertical surfaces. Masner and Goulet (1981) described a model on which contact insecticide is applied, thus increasing the effectiveness of collection of minute and slow-flying taxa. Wilkening *et al.* (1981) illustrated an inexpensive omnidirectional flight trap suitable for sampling in tree-crowns.

Composite flight-interception traps

These traps combine features of both Malaise and flight-interception traps, thus resulting in less bias toward specific taxa (Basset, 1988; Basset *et al.*, 1992b) (Figure 2.1). One recent model (Springate and Basset, 1996) was particularly well-adapted for selective sampling of tree-crown faunas. The main body of the trap consists of a rectangular cross-panel of black netting with a roof of white netting, connected to a collecting jar via a clear plastic tube. A clear plastic funnel is attached below the main body of the trap and connected to a large collecting jar. In the lower collecting jar, a solution of water saturated with salt is used as collecting fluid, which remains effective even during heavy rainfall. The width (80 cm) and height (250 cm) of the trap allow convenient emplacement and re-positioning after survey within tree-crowns. Similarly, Robert (1992) described a model combining features of Malaise, window, water and pitfall traps ('piège entomologique composite') and illustrated its use within the tree layer in Madagascar. A recent study showed that a trapping period of 24 hours with this model was sufficient to characterize entomological samples obtained at different sites, but further trapping was required to estimate total species richness at these sites (J.C. Robert, personal communication).

Sticky traps

Sticky traps (wood, plastic or stout cardboard coated with glue) have been used in tropical tree-crowns relatively rarely (Sutton and Hudson, 1980; House, 1989). Recently, these traps were used on a large scale in Papua New Guinea, for collecting arboreal weevils (O. Missa, personal communication), using a small roof in order to protect the glue from rain and falling debris. This method is inexpensive, hence enabling a large number of replicates to be taken, and is highly suitable for the study of arthropod spatial distribution and stratification. However, the glue is difficult to apply and removal and identification of trapped specimens, particularly fragile insects, are difficult. The traditional removal of insects using non-polar (and usually carcinogenic) solvents is being superseded by the use of citrus oil (Miller *et al.*, 1993). Sticky traps may be modified with different coloured surfaces and chemical baits to become attractive (Knodel and Agnello, 1990; Muirhead-Thomson, 1991).

Photo-electors

Usually, arboreal photo-electors consist of black funnels surmounted by clear collecting containers, affixed to tree trunks. These traps target arthropods foraging on tree trunks (Funke, 1971; Adis, 1981; Nicolai, 1986; New *et al.*, 1991) and may be modified to study upward or downward migration of arthropods (Moeed and Meads, 1983; Adis and Schubart, 1984).

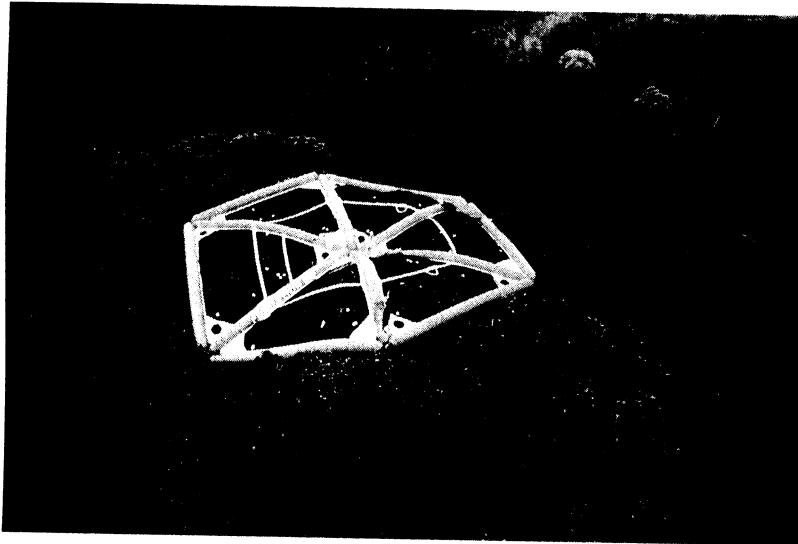
Attractive traps

As in the previous section, the emphasis is on recording arthropod activity. Since the attractiveness of the trap may vary from one taxon to another, the strength of a certain trap model for particular taxa may become a weakness when used in general surveys. The distance from which insects are attracted is often difficult to evaluate, so that selective sampling of the fauna associated with particular tree species may be less effective than that with non-attractive traps, since non-resident arthropods may well be included in any sample.

Light traps

Nocturnal insects which may be attracted to light, such as many species of moths, are often trapped with this technique in tree canopies (Sutton, 1979; Wolda, 1979; Sutton and Hudson, 1980; Smythe, 1982; Rees, 1983). Several models of light traps are available, combining different designs

(a)



(b)

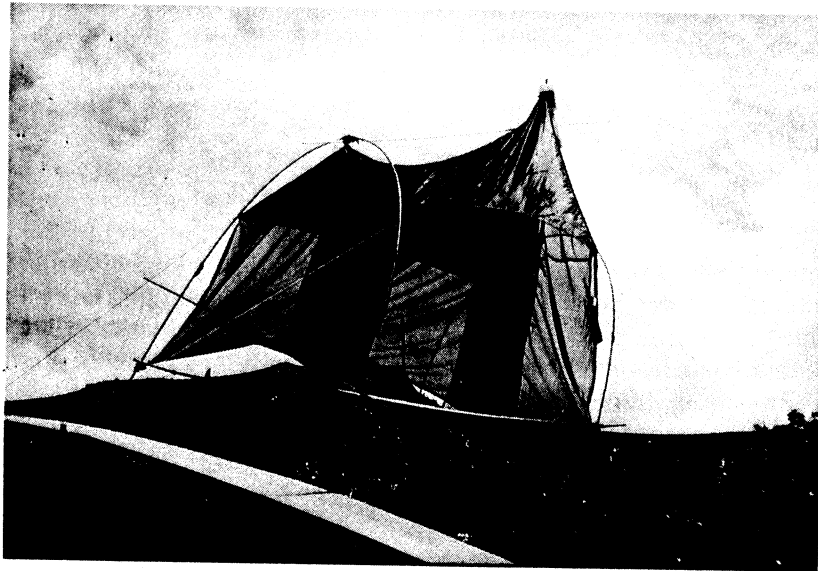


Figure 2.1 Some entomological methods used with the canopy raft. (a) The canopy raft emplaced (Cameroon, Campo, October 1991; photograph P. Gard). (b) A Malaise trap on the canopy raft (French Guiana, Petit-Saut, October, 1989; photograph G. Delvare). (c) A composite flight-interception trap lowered to ground-level (Cameroon, Campo, October 1991; photograph

(c)



(d)



R. Gaillarde, Gamma). (d) The first author examining the content of a branch-clipping sample in the laboratory with six Berlese funnels, of Orousset's (in press) design, in the background (Cameroon, Campo, October 1991; photograph H. Setsumasa).

and light sources, the latter including acetylene lamps, tungsten filament electric lights, mercury-quartz lamps, 'black' lamps, etc. (reviewed by Southwood, 1978). Gerber *et al.* (1992) described a portable, solar-powered charging system for blacklight traps. Robert (1983) devised a model of directional light trap used at different heights to study arthropod stratification in Madagascan forests. Light trapping often provides high numbers of specimens. However, for comparison between traps, correction factors must be computed for the effects of temperature, moonlight, cloud cover and background illumination (Bowden, 1982). The cost of equipment and its operation is often high, particularly if a high number of replicates are required, although this may be remedied by a recent and inexpensive version of the Robinson-pattern mercury-vapour lamp moth-trap, costing about \$US 30.00 (G. Robinson, personal communication).

Baited traps

This category includes traps which are designed specifically to catch a narrow spectrum of taxa. Various trap models and baits have been employed, the former ranging from small plastic bottles to large buckets (Togashi, 1990; Allemand and Aberlenc, 1991) and the latter from food-matter to pheromones or their mimics (Hammond, 1990; Togashi, 1990; Muirhead-Thomson, 1991). Austin and Riley (1995) describe two models of a portable bait trap for butterflies, discuss their use (usually hung between 5–10 m) with fruit- and 'stink'-baits in the Neotropical region and provide a useful set of references about trap design. They noted that 'stink'-baits proved effective in trapping Orthoptera, Hemiptera, Diptera and Hymenoptera, in addition to Lepidoptera. Sourakov and Emmel (1995) discuss briefly the use of three types of bait trap, at several heights (up to 20 m) and with various lures, in Kenya. Allemand and Aberlenc (1991) described an inexpensive trap made from a plastic water bottle, which proved efficient and less selective. A liquid bait based on red wine was often used, but other successful baits included beer, fermented fruit, fish, shrimps, cheese, meat and excrement. It is possible to collect live insects with this method, depending on the bait used. Usually, specimens require cleaning and rinsing before storage or mounting.

Water pan traps

Usually, these consist of shallow card, plastic or aluminium food containers, painted yellow and filled with water and detergent (although other colours may be used with success; see Kirk, 1984). These traps have been used extensively in the field layer but less so in tree-crowns

(Krizelj, 1971; Couturier, 1973; Basset, 1985). They are particularly attractive for Diptera, Hymenoptera and Thysanoptera and high numbers of replicates are reasonably inexpensive. However, their ultimate effectiveness is likely to depend upon trap specification and siting. A disadvantage of these traps is their sensitivity to rainfall, wind and desiccation, which may easily ruin catches, thus requiring frequent servicing.

Other methods

D-Vac sampler

Some authors have used suction apparatus fixed on towers or suspended within trees to vacuum arthropods from the surrounding foliage (Lepointe, 1956; Rees, 1983). A more promising approach is the use of portable D-Vac samplers with long, flexible pipes (Dietrick, 1961). These devices have been used frequently to vacuum arthropods from the field layer but, to date, do not appear to have been used on a large scale in tree canopies. The apparatus may be carried conveniently and models relying on both electrical and combustion engines are available, the latter being more powerful and of higher autonomy. It is possible to modify inexpensive commercial leaf-blowers (Wilson *et al.*, 1993). Arthropods could also be sampled from other habitats than foliage (e.g. trunk, branches). However, disadvantages include cost, weight, exhaust gases, clogging with debris, possible damage to specimens and the definition of sample size.

Extraction of epiphytes

Inhabitants of epiphytes and of 'suspended soils' in the canopy have been sampled using Berlese-Tullgren apparatus or Winkler/Moczarski eclectors (Delamare-Deboutville, 1951; Nadkarni and Longino, 1990; Paoletti *et al.*, 1991). Depending on the robustness of the taxa, large volumes of samples can be sifted and processed with Winkler/Moczarski eclectors, which are independent from power source and light and permit the extraction of live arthropods (Besuchet *et al.*, 1987). A convenient, light and collapsible Berlese-Tullgren apparatus has been devised by Orousset (in press).

Rearing of branch and other samples

Arthropods from specific arboreal habitats may be obtained by rearing galls, leaf mines, stem-borers and samples of flowers, fruits, seeds, dead branches, etc. collected in the canopy. Living or dead branches may be cut, left for a few weeks or months and then placed in rearing cages

(Owen, 1989, 1992), plastic bags (C.R. Vardy, personal communication) or Tullgren extraction apparatus (Paviour-Smith and Elbourn, 1993). In French Guiana, this technique is being used on a large scale for assessing the host-specificity of longicorn beetles, by felling many trees which are later cut up and placed in rearing cages (G. Tavakilian, personal communication). Emergence traps for bark-dwelling arthropods (Glen, 1976) are an alternative method, but their effectiveness and results depend on the state of decay of the habitat sampled (Basset, 1985).

SAMPLING METHODS USED WITH THE CANOPY RAFT

The 'canopy raft' ('radeau des cimes') represents a recent development for investigating selectively the canopy ecotone of tropical forests. This is a large-scale operation in which an air-inflated dirigible is used to transport and emplace a hexagonal platform of 580 m² on the canopy (Cleyet-Marrel, 1990; Ebersolt, 1990) (Figure 2.1). Investigators use single-rope techniques to gain access to the platform (the raft), which consists of air-inflated beams and Aramide netting. Descriptions of the operation, as well as examples of scientific projects performed with the canopy raft, are reported in Hallé and Blanc (1990) and in Hallé and Pascal (1992).

A wide range of methods for sampling arthropods has been used from the canopy raft. During the first scientific expedition in French Guiana, Delvare and Aberlenc (1990) used hand-collecting, sweeping, Malaise traps, light traps, baited traps and rearing. In addition, they used a large net towed by the dirigible at night and illuminated by 500-W lights, thus creating a mobile light trap above the canopy. They concluded that Malaise and light traps were effective for entomological survey of the canopy, but some moths flying upward to the light trap were unlikely to be canopy residents. Nancé (1990) used beating and sweeping to collect spiders in the canopy.

During the second expedition in Cameroon, Basset *et al.* (1992a,b) used branch clipping, Malaise traps and composite flight-interception traps. They concluded that branch clipping was appropriate to estimate densities of sedentary arthropods and that composite flight-interception traps provided a wider spectrum of taxa than Malaise traps for general surveys. Lowman *et al.* (1992, 1993a) used sweeping for general surveys, while McKey (1992) and Dejean (1992) used hand-collecting and direct observation to study ants and Yumoto (1992) netted insect pollinators.

Both expeditions provided the opportunity to test methods for obtaining botanical and entomological samples from a variety of locations in the canopy. A small triangular platform of 16 m² ('sledge' or 'luge') was suspended 10 m below the dirigible, as the latter glides over the canopy at low speed (Ebersolt, 1990; Lowman *et al.*, 1993a). The

sledge is suitable for three investigators, who may command its precise placement. Two teams of investigators took entomological samples using different methods: Basset *et al.* (1992a,b) used branch clipping, whereas Lowman *et al.* (1992, 1993a) used sweeping. Both teams concluded that the sledge is effective, since it allowed rapid access to many otherwise inaccessible locations. The use of D-Vac samplers, both on the raft and with the sledge, appears to be particularly promising for future expeditions.

A COMPARISON OF FOUR METHODS IN PAPUA NEW GUINEAN TREES

Materials and methods

From the above discussion it can be seen that while certain methods may be appropriate for sampling a particular target group of arthropods, or a specific habitat within the canopy, no single method exists as a sampling panacea for general surveys. For the future it may be useful to select several, complementary methods for use in a 'sampling package' (Stork, 1994). These need not be expensive and may provide much useful and comparable data from a variety of habitats (Gadagkar *et al.*, 1990). To illustrate such a review and the use of a sampling package, data are presented comparing four methods used in a survey of leaf-feeding beetles (i.e. Chrysomelidae, Curculionidae, Lagriidae, etc.). Beetles associated with 10 tree species were sampled during one year of field work on the slopes of Mount Kaindi, near Wau, Papua New Guinea (details in Basset, 1997, Chapter 12, this volume). Here, the question whether certain sampling methods provided a better general survey of beetle species and of specialists than others is investigated.

Beetles were collected using four methods:

1. Hand-collecting/beating: these two methods were considered jointly, since the foliage was struck immediately after its visual inspection. These samples represented, for each tree species, about 50 hours of hand-collecting activity and 300 beating samples, distributed among different trees.
2. Branch clipping represented, for each tree species, 55 samples of about 33 m² of leaf surface, obtained from different trees.
3. One composite flight-interception trap was established in the crown of one individual of each tree species. The trap collected insects continuously during an entire year and was surveyed approximately every 11 days.
4. One individual of each tree species was sampled using pyrethrum knockdown (5% Pyranone® and kerosene), using 12–20 trays (1 m²

Table 2.1 Number of individuals and morphospecies of adult leaf-feeding beetles and mean body length (and standard error) of morphospecies collected with each sampling method and within each feeding category. HC/B, hand-collecting/beating; BC, branch clipping; FIT, composite flight-interception traps; FOG, pyrethrum knockdown

Category	HC/B		BC		FIT		FOG		All methods	
	No. of individuals	No. of morpho-species	No. of individuals	No. of morpho-species	No. of individuals	No. of morpho-species	No. of individuals	No. of morpho-species	No. of individuals	No. of morpho-species
Specialists	413	40	94	20	319	29	177	20	1003	40
Generalists	370	32	98	11	457	13	272	14	1197	33
Uncertains	32	13	1	1	137	4	13	4	183	13
Incidentals	230	93	100	21	302	44	693	23	1325	99
Additional	1	1	19	13	647	146	263	66	930	197
Proven feeders	815	85	193	32	913	46	462	38	2383	86
Leaf-feeding beetles	1046	179	312	66	1862	236	1418	127	4638	382
Mean body length (mm) (standard error)	6.32 (0.399)		5.10 (0.883)		5.64 (0.278)		4.62 (0.268)		5.56 (0.195)	

surface area), depending on tree size (total 159 trays used for all tree species).

The first three of these methods were used during both day and night, whereas pyrethrum knockdown was performed at daybreak only.

Live beetles were stored in plastic vials, at room temperature and in conditions of near-saturated relative humidity. They were provided with fresh foliage and tested for feeding. These tests (details in Basset, 1997, Chapter 12, this volume) allowed the assignment of beetles into the following categories: (i) 'specialists', i.e. feeding only on one tree species; (ii) 'generalists', feeding on two or more tree species; (iii) 'uncertains', feeding, but not enough information to assign either to specialists or generalists; (iv) 'incidentals', not feeding; and (v) 'additional', collected dead, by various methods and, therefore, not tested. Categories (i), (ii) and (iii) were referred to as 'proven feeders', i.e. species known to feed on the foliage of tree species sampled.

Since sampling effort, as well as the number of habitats (trees) sampled, varied for each method, it is difficult to compare the effectiveness of the different methods for surveying foliage beetles. In particular, no attempt was made to use rarefaction techniques to estimate the number of species for a common sample size since the results of these computations would be heavily dependent upon the arbitrary definition of a 'sample' for each method (e.g. 1 hour or 1 day of hand-collecting, one week or one month of trap-collecting, one or several fogging trays, etc.). Further, the accuracy and precision of the jack-knife estimate is highly dependent upon the number of replicates (samples) available (Coddington *et al.*, 1991). As an alternative, for each sampling method, the rate of species accumulation within the cumulative number of individuals collected was considered. Thus, to some extent, a comparison could be made between the rates of discovery of 'new' species within the entire material sampled and this within the different feeding categories defined.

Results and discussion

A total of 4638 leaf-beetles, representing 382 morphospecies in the families Chrysomelidae, Curculionidae and Lagriidae, were collected with the four sampling methods. The total numbers of individuals and species collected with each method and within each feeding category of beetles are indicated in Table 2.1. While the total number of morphospecies collected was greatest with the traps, the number of species of specialists and proven feeders was particularly high using hand-collecting/beating. These totals were lower for the trap, fogging and branch clipping samples. This was not unexpected since hand-collecting/beating

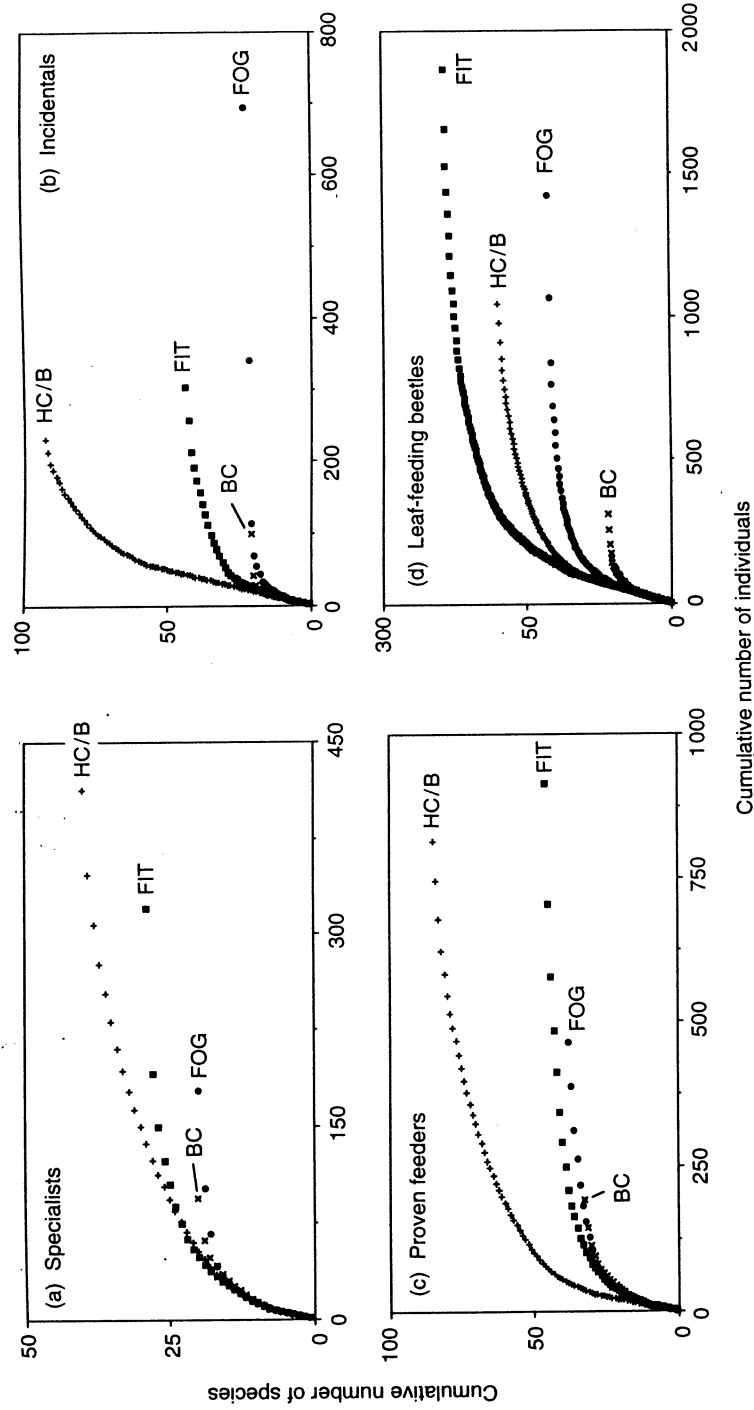


Figure 2.2 Cumulative number of individuals plotted against cumulative number of species for (a) specialists, (b) incidentals, (c) proven feeders and (d) all leaf-feeding beetles detailed by sampling method. HC/B, hand-collecting/beating (+); BC, branch clipping (x); FIT, composite flight-interception traps (■); FOG, pyrethrum knockdown (●).

was performed on several trees of the same species, at different periods of the year (as was branch clipping), while the traps sampled arthropod populations obtained from one tree, but at different periods of the year, and fogging focused on one individual at one period of time.

Despite high proportions of incidental species being collected with hand-collecting/beating and trapping, the number of species collected with each sampling method was distributed uniformly when the proven feeder and incidental categories were compared (G-test, $G = 5.38$, $P = 0.146$). However, a similar comparison of the distribution of the number of individuals collected was non-uniform, with a high proportion of incidentals collected by fogging ($G = 439.4$, $P < 0.001$).

Figure 2.2 shows the cumulative plots of the number of individuals and species for each sampling method and for selected feeding categories. If a common sample size among the different sampling methods of, for example, 300 individuals, is considered, the above observations remain valid. It is probable that trapped material will be more speciose than that derived from other methods, when all leaf-feeding beetles are considered. However, it is probable that when proven feeders or specialists are considered, material obtained by hand-collecting/beating will be more speciose. However, this effect is only likely to be noteworthy for material containing more than 300 individuals.

Several interesting observations may be inferred from these plots:

1. Spatial as well as seasonal replicates ensure that samples are representative of the total species richness present. Here, the apparent poor performance of pyrethrum knockdown is explained by the lack of such replicates. For proven feeders, spatial replicates appear more important than seasonal replicates, as few differences existed between trap and fogging curves (Figure 2.2c). For the purpose of this study, hand-collecting/beating was the superior method, since many more trees were visited during the time needed to sample different trees with pyrethrum knockdown or with composite flight-interception traps. However, it is evident that the applicability of the hand-collecting/beating method is highly dependent on the ease of gaining access to the canopy.
2. Sampling other habitats will result in collecting more incidentals and, therefore, more transient species. It is probable that 'incidentals' included both transients and species genuinely associated with tree species studied, but which were feeding on parts other than the foliage. The relation between transient species and the diversity of tropical vegetation is discussed elsewhere (Basset, 1997, Chapter 12, this volume). Since the arthropod fauna associated with vegetation surrounding the trees sampled will change throughout the year, seasonal replicates may yield more transient species. Similarly,

diurnal/nocturnal replicates may also influence species richness (Blanton, 1990)

3. Branch clipping was the least effective of all methods, but was unique in providing a precise estimate of the amount of habitat sampled. This technique should be used to compare relative densities of arthropods, rather than estimating species richness.

Some 120 beetle species were collected exclusively with the traps, 68 by hand-collecting/beating, 53 by fogging and only 10 by branch clipping. To some extent, this reflects the effectiveness of the different methods with the present sampling protocol. Not unexpectedly, a cluster analysis with the 382 species of leaf-feeding beetles (data not presented) showed that hand-collecting/beating and branch clipping were the closest of the four methods, with trapping and fogging more distant. This reflects that the first two methods target foliage arthropods, whereas the others sample indiscriminately the fauna foraging on the foliage, trunk and branches (some weevil species in the 'incidental' and 'additional' categories may be wood-borers).

Further analysis indicated that the average body size of morphospecies collected varied significantly between sampling methods (Kruskal-Wallis $W = 17.113$, $P < 0.01$). In particular, the average body size of morphospecies collected with hand-collecting/beating was higher than that collected with pyrethrum knockdown (Table 2.1). Either this reflects the poor performance of hand-collecting/beating at collecting small species, or the poor performance of pyrethrum knockdown at collecting large species, or possibly both.

CONCLUSION: CHOOSING AN APPROPRIATE COLLECTING METHOD

Both the literature review and the comparison of sampling methods for surveying leaf-feeding beetles in Papua New Guinea support the contention that none of the methods examined can be considered as the panacea for investigating a wide range of ecological topics. Rather, and in particular for general surveys, the implementation of a range of methods, used in conjunction and providing spatial, seasonal and diurnal replicates, will provide larger and more diverse samples. For example, a combination of hand-collecting/beating, composite flight-interception traps and pyrethrum knockdown may be one such strategy. Depending on the research goals of the investigator, other techniques, used singly or in conjunction, may be more suitable.

The few studies of the stratification of arthropods in tropical forests and of the entomofauna of the canopy ecotone suggest that the faunal composition of the canopy is very different from that found in lower

Table 2.2 Key to assist the ecologist in the choice of a method for sampling arthropods in tree canopies (numbers in parentheses refer to pages in the text)

1. No emphasis on sampling particular habitats within trees.....	2
- Emphasis on sampling particular habitats within trees.....	9
2. Emphasis on estimating relative activities of arthropods, regular sampling of the same individual tree; flying arthropods targeted.....	3
- Emphasis on estimating actual densities of arthropods and not based upon regular sampling from the same individual tree; both flying and flightless arthropods targeted.....	insecticide knockdown (29)
3. Emphasis on nocturnal arthropods.....	light traps (33)
- No emphasis on nocturnal arthropods.....	4
4. Non- or relatively non-specific sampling of arthropod faunas.....	5
- Specific taxon or taxa targeted.....	8
5. Emphasis on studying spatial distribution, particularly with a high number of replicates.....	sticky traps (33)
- Emphasis on studying seasonal distribution.....	6
6. Traps not particularly biased towards either light or heavy arthropods.....	composite flight-interception traps (32)
- Trapping method with known tendency to selectivity.....	7
7. Traps biased towards Diptera and light arthropods.....	Malaise traps (32)
- Traps biased towards Coleoptera and heavy arthropods.....	flight-interception traps (32)
8. Visual attractants.....	water traps (36)
- Olfactory attractants.....	baited traps (36)
9. Emphasis on foliage arthropods.....	10
- No emphasis on foliage arthropods.....	16
10. No emphasis on comparing samples of known size.....	11
- Emphasis on comparing samples of known (or relatively known) size...	12
11. Electrical/solar power source or fuel available for sampling over long duration.....	D-Vac sampler (37)
- No power source or fuel available.....	hand-collecting (29)
12. Emphasis on estimation of actual densities of arthropods.....	13
- Emphasis on estimation of relative densities of arthropods.....	15
13. Minute arthropods targeted.....	extraction of leaves (30)
- Minute arthropods not targeted.....	14
14. Volume sampled relatively small (destructive method).....	branch clipping (30)
- Volume sampled higher (method not necessarily destructive).	gassing (30)
15. Perambulation possible; active arthropods targeted.....	sweeping (31)
- Perambulation restricted; sedentary arthropods targeted.....	beating (31)
16. Emphasis on concealed fauna.....	rearing (37)
- Emphasis on 'exposed' fauna.....	17
17. Emphasis on epiphytic fauna.....	extraction of epiphytes (37)
- Emphasis on trunk-foraging fauna.....	photo-electors (33)

strata (Sutton and Hudson, 1980; Delvare and Aberlenc, 1990; Basset *et al.*, 1992a,b; J.C. Robert, personal communication). This difference emphasizes the need for selective sampling of the canopy ecotone, which, to date, can be achieved with the canopy raft and sledge alone, and, in a more restricted way, by cranes. Furthermore, the variety of sampling methods used on the canopy raft emphasizes that different methods are needed to pursue specific research goals.

Based on field experience and a literature review, a key (Table 2.2) is provided to assist (rather than direct) the ecologist in the selection of suitable methods for sampling arthropods in tree canopies. It should be noted that certain methods could be placed in different sections or may appear twice, particularly where they have multiple functions. Additional factors the ecologist should consider are the efficiency of methods in relation to both cost and investment of time, and the suitability and sensitivity of a particular method to climatic conditions in tropical forests.

Acknowledgements

The assistance in French Guiana and Cameroon of Francis Hallé, Gilles Ebersolt, Dany Cleyet-Marrel and the staff of Opération Canopée is gratefully acknowledged. In Papua New Guinea, the first author acknowledges the assistance of Nathan Daniel and Martin Kasbal and the support of Harry Sakulas and the staff of the Wau Ecology Institute. G.A. Samuelson checked the assignment of beetles to morphospecies. Many colleagues commented on earlier drafts of the manuscript and provided us with unpublished information, particularly Nigel Stork, Peter Hammond, Daniel Burckhardt, Willy Matthey, Scott Miller, Jeremy Holloway, Gaden Robinson, Barry Bolton, Paul Williams, Steve Brooks, Tom Huddleston and Andrew Polaszek. Studies with the canopy raft were funded by the Elf Foundation, Opération Canopée and other sponsors indicated in Hallé and Blanc (1990). Studies in Papua New Guinea were funded in part by a grant from the Swiss National Science Foundation to the first author and were made possible by Bishop Museum technical staff. The manuscript was prepared while the first author was in receipt of a Christensen Research Institute Fellowship and National Science Foundation grant DEB-94-07927 (with Scott Miller and Allen Allison). This is contribution no. 150 of the Christensen Research Institute.

REFERENCES

Adis, J. (1981) Comparative ecological studies of the terrestrial arthropod fauna in Central Amazonian inundation forests. *Amazoniana*, 7, 87–173.

- Adis, J. and Schubart, H.O.R. (1985) Ecological research on arthropods in Central Amazonian forest ecosystems with recommendation for study procedures, in *Trends in Ecological Research for the 1980s* (eds J. Cooley and F.B. Golley), Plenum Press, New York, pp. 111–44.
- Adis, J., Paarmann, W., Fonseca, C.R.V. da and Rafael, J.A. (1997) Knockdown efficiency of natural pyrethrum and survival rate of arthropods obtained by canopy fogging in Central Amazonia, in *Canopy Arthropods* (eds N.E. Stork, J. Adis and R.K. Didham), Chapman & Hall, London, pp. 67–79 (this volume).
- Allemand, R. and Aberlenc, H.-P. (1991) Une méthode efficace d'échantillonnage de l'entomofaune des frondaisons: le piège attractif aérien. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 64, 293–305.
- Austin, G.T. and Riley, T.J. (1995) Portable bait traps for the study of butterflies. *Tropical Lepidoptera*, 6, 5–9.
- Basset, Y. (1985) Comparaison de quelques méthodes de piégeage de la faune dendrobie. *Bulletin Romand d'Entomologie*, 3, 1–14.
- Basset, Y. (1988) A composite interception trap for sampling arthropods in tree canopies. *Journal of the Australian Entomological Society*, 27, 213–19.
- Basset, Y. (1990) The arboreal fauna of the rainforest tree *Argyrodendron actinophyllum* as sampled with restricted canopy fogging: composition of the fauna. *The Entomologist*, 109, 173–83.
- Basset, Y. (1992) Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree. *Ecological Entomology*, 17, 8–16.
- Basset, Y. (1997) Species abundance and body size relationships in insect herbivores associated with New Guinea forest trees, with particular reference to insect host specificity, in *Canopy Arthropods* (eds N.E. Stork, J. Adis and R.K. Didham), Chapman & Hall, London, pp. 237–64 (this volume).
- Basset, Y., Aberlenc, H.-P. and Delvare, G. (1992a) Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology*, 17, 310–18.
- Basset, Y., Aberlenc, H.-P. and Delvare, G. (1992b) Abundance, diversité et stratification verticale de l'entomofaune d'une forêt tropicale humide africaine, in *Biologie d'une Canopée de Forêt Equatoriale – II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun* (eds F. Hallé and O. Pascal), Fondation Elf, Paris, pp. 45–52.
- Besuchet, C., Burckhardt, D. and Löbl, I. (1987) The 'Winkler/Moczarski' extractor as an efficient extractor for fungus and litter Coleoptera. *The Coleopterists' Bulletin*, 41, 392–4.
- Blanton, C.M. (1990) Canopy arthropod sampling: a comparison of collapsible bag and fogging methods. *Journal of Agricultural Entomology*, 7, 41–50.
- Bowden, J. (1982) An analysis of the factors affecting catches of insects in light traps. *Bulletin of Entomological Research*, 72, 535–56.
- Cleyet-Marrel, D. (1990) Bilan technique partie dirigeable, in *Biologie d'une Canopée de Forêt Equatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française* (eds F. Hallé and P. Blanc), Montpellier II et CNRS-Paris VI, Montpellier/Paris, pp. 11–14.
- Coddington, J.A., Griswold, C.E., Dávila, D.S., Peñaranda, E. and Larcher, S.F. (1991) Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems, in *The Unity of Evolutionary Biology* (ed. E.C. Dudley), Proceedings of the Fourth International Congress of Systematics and Evolutionary Biology. Dioscorides Press, Portland, pp. 44–60.
- Colwell, R.K. and Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B*, 345, 101–18.

- Costa, J.T. III. and Crossley, D.A.J. (1991) Diel patterns of canopy arthropods associated with three tree species. *Environmental Entomology*, **20**, 1542–8.
- Couturier, G. (1973) Etude éthologique et biocénotique du peuplement d'insectes dans un verger naturel. *Travaux et Documents O.R.S.T.O.M.*, **22**, 1–96.
- Crossley, D.A.J., Coulson, R.N. and Gist, C.S. (1973) Trophic level effects on species diversity in arthropod communities of forest canopies. *Environmental Entomology*, **2**, 1097–100.
- Dejean, A. (1992) Les relations plantes-fourmis, in *Biologie d'une Canopée de Forêt Equatoriale – II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun* (eds F. Hallé and O. Pascal), Fondation Elf, Paris, pp. 74–75.
- Delamare-Deboutville, C. (1951) *Microfaune du Sol dans les Pays Tempérés et Tropicaux*, Hermann, Paris.
- Delvare, G. and Aberlenc, H.P. (1990) Des entomologistes sur la canopée, in *Biologie d'une Canopée de Forêt Equatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française* (eds F. Hallé and P. Blanc), Montpellier II et CNRS-Paris VI, Montpellier/Paris, pp. 211–21.
- Dempster, J.P. (1961) A sampler for estimating populations of active insects upon vegetation. *Journal of Animal Ecology*, **30**, 425–7.
- Dietrick, E.J. (1961) An improved back pack motor fan for suction sampling of insect populations. *Journal of Economic Entomology*, **54**, 394–5.
- Dowdy, W.W. (1950) A community study of an Oak–Hickory association with special reference to invertebrates. *American Midland Naturalist*, **43**, 667–95.
- Dufour, C. (1980) Un nouveau piège lumineux pour la capture des Tipulidae et autres Diptères Nématocères: une tente 'Malaise' lumineuse. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **53**, 313–20.
- Eberhardt, L.L. and Thomas, J.M. (1991) Designing environmental field studies. *Ecological Monographs*, **61**, 53–73.
- Ebersolt, G. (1990) Bilan technique partie radeau, in *Biologie d'une Canopée de Forêt Equatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française* (eds F. Hallé and P. Blanc), Montpellier II et CNRS-Paris VI, Montpellier/Paris, pp. 15–26.
- Erwin, T.L. (1983) Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging, in *Tropical Rain Forest: Ecology and Management* (eds S.L. Sutton, T.C. Whitmore and A.C. Chadwick), British Ecological Society Special Publication 2, Blackwell Scientific Publications, Oxford, pp. 59–75.
- Erwin, T.L. and Scott, J.C. (1980) Seasonal size and patterns, trophic structure, and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *The Coleopterists' Bulletin*, **34**, 305–22.
- Funke, W. (1971) Food and energy turnover of leaf-eating insects and their influence on primary production. *Ecological Studies*, **2**, 81–93.
- Gadagkar, R., Chandrashekara, K. and Nair, P. (1990) Insect species diversity in the tropics: sampling methods and a case study. *Journal of the Bombay Natural History Society*, **87**, 337–53.
- Gerber, G.H., Walkof, J. and Juskiw, D. (1992) Portable, solar-powered charging system for blacklight traps. *The Canadian Entomologist*, **124**, 553–4.
- Glen, D.M. (1976) An emergence trap for bark-dwelling insects, its efficiency and effects of temperature. *Ecological Entomology*, **1**, 91–4.
- Greenwood, S.R. (1990) Patterns of herbivory on the edge of the tropical forest in North Sulawesi, in *Insects and the Rain Forests of South East Asia (Wallacea)* (eds W.J. Knight and J.D. Holloway), The Royal Entomological Society of London, London, pp. 309–12.

- Hallé, F. and Blanc, P. (eds) (1990) *Biologie d'une Canopée de Forêt Equatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française*. Montpellier II et CNRS-Paris VI, Montpellier/Paris.
- Hallé, F. and Pascal, O. (eds) (1992) *Biologie d'une Canopée de Forêt Equatoriale – II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun*. Fondation Elf, Paris.
- Hammond, P.M. (1990) Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region, in *Insects and the Rain Forests of South East Asia (Wallacea)* (eds W.J. Knight and J.D. Holloway), The Royal Entomological Society of London, London, pp. 197–254.
- Hammond, P.M. (1994) Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London, Series B*, **345**, 119–36.
- Hammond, P.M. and Harding, P.T. (1991) Saproxyllic invertebrate assemblages in British woodlands: their conservation significance and its evaluation, in *Pollard and Veteran Tree Management* (ed. H.J. Read), Richmond Publishing, Slough, pp. 30–7.
- Harris, J.W.E., Collis, D.G. and Magar, K.M. (1972) Evaluation of the tree-beating method for sampling defoliating insects. *The Canadian Entomologist*, **104**, 723–9.
- Harris, M. (1971) Sampling pear foliage for nymphs of the pear *Psylla*, using the Berlese-Tullgren funnel. *Journal of Economic Entomology*, **64**, 1317–18.
- Hespenheide, H.A. (1979) Are there fewer parasitoids in the tropics? *American Naturalist*, **113**, 766–9.
- Hosking, G.P. (1979) Trap comparison in the capture of flying Coleoptera. *New Zealand Entomologist*, **7**, 87–92.
- Hosking, G.P. and Knight, F.B. (1975) Flight habits of some Scolytidae in the spruce-fir type of northern Maine. *Annals of the Entomological Society of America*, **68**, 917–21.
- House, S.M. (1989) Pollen movement to flowering canopies of pistillate individuals of three rain forest tree species in tropical Australia. *Australian Journal of Ecology*, **14**, 77–94.
- Hutcheson, J. (1990) Characterization of terrestrial insect communities using quantified malaise-trapped Coleoptera. *Ecological Entomology*, **15**, 143–51.
- Juillet, J.A. (1963) A comparison of four types of traps used for capturing flying insects. *Canadian Journal of Zoology*, **41**, 219–23.
- Kirk, W.D. (1984) Ecologically selective coloured traps. *Ecological Entomology*, **9**, 35–41.
- Knodel, J.J. and Agnello, A.M. (1990) Field comparison of nonsticky and sticky pheromone traps for monitoring fruit pests in western New York. *Journal of Economic Entomology*, **83**, 197–204.
- Krizelj, S. (1971) L'entomofaune circulante dans une chênaie à charmes de haute Belgique, in *Productivité des Ecosystèmes Forestiers* (ed. UNESCO), UNESCO, Paris, pp. 397–402.
- Lamotte, M., Gillon, D., Gillon, Y. and Ricou, G. (1969) L'échantillonnage quantitatif des peuplements d'invertébrés en milieux herbacés, in *Problèmes d'Ecologie: l'échantillonnage des Peuplements Animaux des Milieux Terrestres* (eds M. Lamotte and F. Bourlière), Masson, Paris, pp. 7–54.
- Lepointe, J. (1956) Méthodes de capture dans l'écologie des arbres. *Vie et Milieu*, **7**, 233–41.
- LeSage, L. (1991) An improved technique for collecting large samples of arthropods. *Entomological News*, **102**, 97–104.

- Longino, J.T. (1994) How to measure arthropod diversity in a tropical rainforest. *Biology International*, **28**, 3–13.
- Lowman, M.D., Moffett, M.W. and Rinker, B. (1992) Insect sampling in forest canopies: a new method, in *Biologie d'une Canopée de Forêt Equatoriale - II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun* (eds F. Hallé and O. Pascal), Fondation Elf, Paris, pp. 41–44.
- Lowman, M., Moffett, M. and Rinker, H.B. (1993a) A new technique for taxonomic and ecological sampling in rain forest canopies. *Selbyana*, **14**, 75–9.
- Lowman, M., Taylor, P. and Block, N. (1993b) Vertical stratification of small mammals and insects in the canopy of a temperate deciduous forest: a reversal of tropical forest distribution? *Selbyana*, **14**, 25.
- Majer, J.D. and Recher, H.F. (1988) Invertebrate communities on western Australian eucalyptus, a comparison of branch clipping and chemical knock-down procedures. *Australian Journal of Ecology*, **13**, 269–78.
- Masner, L. and Goulet, H. (1981) A new model of flight-interception trap for some hymenopterous insects. *Entomological News*, **92**, 199–202.
- McKey, D. (1992) Interactions between ants and plants: comparison of canopy, understory and clearing environments, in *Biologie d'une Canopée de Forêt Equatoriale - II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun* (eds F. Hallé and O. Pascal), Fondation Elf, Paris, pp. 66–73.
- Merrill, W. and Skelly, J.M. (1968) A window trap for collection of insects above the forest canopy. *Journal of Economic Entomology*, **61**, 1461–2.
- Miller, R.S., Passoa, S., Waltz, R.D. and Mastro, V. (1993) Insect removal from sticky traps using a citrus oil solvent. *Entomological News*, **104**, 209–13.
- Mitchell, A.W. (1982) *Reaching the Rain Forest Roof*, Leeds Philosophical and Literary Society, Leeds.
- Moeed, A. and Meads, M.J. (1983) Invertebrate fauna of four tree species in Orongorongo Valley, New Zealand, as revealed by trunk traps. *New Zealand Journal of Ecology*, **6**, 39–53.
- Moffett, M.W. (1993) *The High Frontier. Exploring the Tropical Rainforest Canopy*. Harvard University Press, Cambridge, MA.
- Moran, V.C., Hoffmann, J.H., Impson, F.A.C. and Jenkins, J.F.G. (1994) Herbivorous insect species in the tree canopy of a relict South African forest. *Ecological Entomology*, **19**, 147–54.
- Morris, R.F. (1955) The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. *Canadian Journal of Zoology*, **33**, 225–94.
- Mouina, M., Bigot, L. and Fabre, J.P. (1985) Comparaison des communautés frondicoles des Coléoptères du Cèdre (*Cedrus atlantica* Massetti) en France (Provence) et au Maroc (Moyen-Atlas). *Vie et Milieu*, **35**, 99–106.
- Muirhead-Thomson, R.C. (1991) *Trap Responses of Flying Insects*, Academic Press, London.
- Nadkarni, N.M. and Longino, J.T. (1990) Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica*, **22**, 286–9.
- Nancé, E. (1990) Recherches arachnologiques sur la canopée. *Biologie d'une canopée de forêt équatoriale*, in *Biologie d'une Canopée de Forêt Equatoriale. Rapport de Mission. Radeau des Cimes Octobre-Novembre 1989, Guyane Française* (eds F. Hallé and P. Blanc), Montpellier II et CNRS-Paris VI, Montpellier/Paris, pp. 205–7.
- New, T.R. (1979) Phenology and relative abundance of Coleoptera on some Australian Acacias. *Australian Journal of Zoology*, **27**, 9–16.
- New, T.R., Adis, J.U., de Morais, J.W. and Gomes Rodrigues, J.M. (1991) Notes on phenology and abundance of Psocoptera from primary and secondary dryland forest in Central Amazonia, Brazil. *Studies on Neotropical Fauna and Environment*, **26**, 243–7.
- Nicolai, V. (1986) The bark of trees: thermal properties, microclimate and fauna. *Oecologia*, **69**, 148–60.
- Noyes, J.S. (1989) A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, **23**, 285–98.
- Ohmart, C.P., Stewart, L.G. and Thomas, J.R. (1983) Phytophagous insect communities in the canopies of three *Eucalyptus* forest types in south-eastern Australia. *Australian Journal of Ecology*, **8**, 395–403.
- Orousset, J. (1997) Les techniques de récolte des coléoptères hypogés (4e partie). *Supplément au Bulletin de liaison de l'ACOREP*, Paris (in press).
- Osmelak, J.A. (1987) A comparison of five different traps for monitoring leafhopper activity (Homoptera). *General and Applied Entomology*, **19**, 49–56.
- Owen, J.A. (1989) An emergence trap for insects breeding in dead wood. *British Journal of Entomology and Natural History*, **2**, 65–7.
- Owen, J.A. (1992) Experience with an emergence trap for insects breeding in dead wood. *British Journal of Entomology and Natural History*, **5**, 17–20.
- Paarmann, W. and Kerck, K. (1997) Advances in using the canopy fogging technique to collect living arthropods from tree crowns, in *Canopy Arthropods* (eds N.E. Stork, J. Adis and R.K. Didham), Chapman & Hall, London, pp. 53–66 (this volume).
- Paarmann, W. and Stork, N.E. (1987) Canopy fogging, a method of collecting living insects for investigations of life history strategies. *Journal of Natural History*, **21**, 563–6.
- Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H. and Benzing, D.H. (1991) Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *Journal of Tropical Ecology*, **7**, 373–83.
- Paviour-Smith, K. and Elbourn, C.A. (1993) A quantitative study of the fauna of small dead and dying wood in living trees in Wytham Woods, near Oxford. *English Nature Science*, **7**, 33–57.
- Rees, C.J.C. (1983) Microclimate and the flying Hemiptera fauna of a primary lowland rain forest in Sulawesi, in *Tropical Rain Forest: Ecology and Management* (eds S.L. Sutton, T.C. Whitmore and A.C. Chadwick), British Ecological Society Special Publication 2, Blackwell Scientific Publications, Oxford, pp. 121–38.
- Robert, J.C. (1983) Le piégeage lumineux directionnel. Ses utilisations. *Cahiers de Liaisons O.P.I.E.*, **17**, 21–6.
- Robert, J.C. (1992) Le piège entomologique composite (P.E.C): une technique d'échantillonnage à large spectre de l'entomofaune terrestre circulante. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **65**, 395–411.
- Russell-Smith, A. and Stork, N.E. (1994) Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. *Journal of Tropical Ecology*, **10**, 545–58.
- Smythe, N. (1982) The seasonal abundance of night-flying insects in a Neotropical forest, in *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (eds E.G. Leigh Jr, A.S. Rand and D.M. Windsor), Smithsonian Institution Press, Washington, pp. 309–18.
- Sourakov, A. and Emmel, T.C. (1995) Bait trapping for butterflies in Kenya. *Tropical Lepidoptera*, **6**, 1–2.
- Southwood, T.R.E. (1978) *Ecological Methods, with Particular Reference to the Study of Insect Populations*, 2nd edn, Chapman & Hall, London.

- Springate, N.D. and Basset, Y. (1996) Diel activity of arboreal arthropods associated with Papua New Guinean trees. *Journal of Natural History*, **30**, 101–12.
- Stork, N.E. (1987a) Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology*, **12**, 69–80.
- Stork, N.E. (1987b) Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology*, **12**, 219–26.
- Stork, N.E. (1991) The composition of the arthropod fauna of Bornean lowland rainforest trees. *Journal of Tropical Ecology*, **7**, 161–80.
- Stork, N.E. (1994) Inventories of biodiversity: more than a question of numbers, in *Systematics and Conservation Evaluation* (eds P.L. Forey, C.J. Humphries and R.I. Vane-Wright), Systematics Association Special Volume No. 50, Clarendon Press, Oxford, pp. 81–100.
- Stork, N.E. and Brendell, M.J.D. (1990) Variation in the insect fauna of Sulawesi trees with season, altitude and forest type, in *Insects and the Rain Forests of South East Asia (Wallacea)* (eds W.J. Knight and J.D. Holloway), The Royal Entomological Society of London, London, pp. 173–190.
- Stork, N.E. and Brendell, M.J.D. (1991) Arthropod abundance in lowland forest of Seram, in *Natural History of Seram* (eds I.D. Edwards, A.A. Macdonald and J. Proctor), Intercept, Andover, pp. 115–30.
- Stork, N.E. and Hammond, P.M. (1997) Sampling arthropods from tree-crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park, UK, in *Canopy Arthropods* (eds N.E. Stork, J. Adis and R.K. Didham), Chapman & Hall, London, pp. 3–26 (this volume).
- Sutton, S.L. (1979) A portable light trap for studying insects of the upper canopy. *The Brunel Museum Journal*, **4**, 156–60.
- Sutton, S.L. and Hudson, P.J. (1980) The vertical distribution of small flying insects in the lowland rain forest Zaire. *Zoological Journal of the Linnean Society*, **68**, 111–23.
- Togashi, I. (1990) Symphyta (Hymenoptera) lured to benzyl acetate and alphapyrene in traps. *Transactions of the Shikoku Entomological Society*, **19**, 117–25.
- Turner, B.D. (1974) The population dynamics of tropical arboreal Psocoptera (Insecta) on two species of conifers in the Blue Mountains, Jamaica. *Journal of Animal Ecology*, **43**, 323–37.
- Walter, D.E., O'Dowd, D. and Barnes, V. (1994) The forgotten arthropods: foliar mites in the forest canopy. *Memoirs of the Queensland Museum*, **36**, 221–6.
- Wilkening, A.J., Foltz, J.L., Atkinson, T.H. and Connor, M.D. (1981) An omnidirectional flight trap for ascending and descending insects. *The Canadian Entomologist*, **113**, 453–5.
- Wilson, L.F. (1962) A portable device for mass-collecting or sampling foliage-inhabiting arthropods. *Journal of Economic Entomology*, **55**, 807–8.
- Wilson, S.W., Smith, J.L. and Purcell, A.H. (1993) An inexpensive vacuum collector for insect sampling. *Entomological News*, **104**, 203–8.
- Wolda, H. (1979) Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecological Entomology*, **4**, 181–90.
- Yumoto, T. (1992) Pollination ecology in a tropical rain forest canopy in Cameroon, in *Biologie d'une Canopée de Forêt Equatoriale – II. Rapport de Mission: Radeau des Cimes Octobre-Novembre 1991, Réserve de Campo, Cameroun* (eds F. Hallé and O. Pascal), Fondation Elf, Paris, pp. 110–114.