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# Methodological advances and limitations in canopy entomology

Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching


## ABSTRACT

Many of the earlier studies of canopy arthropods relied upon indirect sampling methods, such as light trapping or pyrethrum knockdown (canopy fogging). Usually, observers were limited to ground level, with few opportunities to study canopy organisms directly. Life histories and population dynamics could only be inferred from such data. In addition to improvements in fogging techniques, recent methodological developments (such as construction cranes, canopy towers, canopy rafts, aerial sledges, aerial walkways or single rope techniques) have broadened our ability to access the canopy and allow the observation and collection of canopy arthropods *in situ*. Collecting methods are accordingly much more diverse and reflect the increasing complexity of the questions that are pursued by canopy biologists. In this chapter, we review past and recent methods of canopy access that have allowed entomologists to sample arthropods in tropical forest canopies. In doing so, we stress the advantages and limitations of each method, from an entomological viewpoint. We further review key problems in tropical canopy entomology and discuss possible remedies.


## INTRODUCTION

Logistical problems in tropical canopy entomology are dictated by the physical environment and canopy access, as well as by the formidable biodiversity present in the canopy. How to sample efficiently the canopy habitat, how to document adequately the life history of its inhabitants, how to perform manipulative experiments there and how to archive the ensuing data and collections efficiently are recurrent problems. It is not an exaggeration to state that the resolution of these interrelated problems would take us a large step closer to understanding the diversity and distribution of life on Earth.

Surveys of arthropods in the canopy of tropical rainforests are a recent field of investigation. The oldest attempt to collect quantitative information on the invertebrates in the canopy of tropical rainforests appears to be the pioneering efforts led by O. W. Richards, who hoisted light traps up in the canopy in 1929 during the Oxford University expedition in Guyana (Hingston, 1930, 1932; Sutton, 2001). With the exception of the erection of towers and occasional insect collection from these in the 1950s (Haddow *et al.*, 1961; Haddow & Ssenkubuge, 1965), the mass collection of arthropods from the canopy did not progress notably until the development of ground-based fogging and light-trapping techniques in the 1970s (fogging: Roberts, 1973; Erwin & Scott, 1980; Gagné & Howarth, 1981; light trapping: Sutton, 1979; Sutton & Hudson, 1980; Holloway, 1984a). From then, methods adopted by entomologists to access, collect and experiment in the canopy greatly diversified. Canopy access and canopy entomology in the tropics are reviewed historically in Mitchell (1982), Erwin (1989, 1995), Moffett (1993), Moffett and Lowman (1995), Lowman and Wittman (1996) and Sutton (2001), among others.

This contribution examines recent advances and the most significant remaining limitations in canopy entomology. Improved canopy access, which in recent years has represented the most significant development in canopy entomology and science (Barker & Pinard, 2001), is discussed at more length.

## ADVANCES IN CANOPY ENTOMOLOGY

### Canopy access

Recent progress in canopy access has allowed entomologists to sample arthropods *in situ*, in better conditions and for longer periods of time than previously, and to increase notably the number of spatial replicates. A brief review of the main methods of canopy access favoured by entomologists follows. These methods are further compared in terms of spatial and temporal replicates, time investment in the field and productivity of arthropod material (Table 2.1) and some are illustrated in Fig. 2.1.

*Ground-based techniques and their evolution*

Ground-based techniques that provide indirect access to the canopy have always been popular with entomologists. For example, out of 17 tropical studies reported in Stork *et al.* (1997a), 12 were based on the ground and did not include direct access to the canopy and sampling or observation *in situ* of its arthropod inhabitants. An increasing number of studies are concerned with sampling arthropods *in situ*, as the present volume attests (about half of contributions relied on some form of canopy access, the other half were ground based).

The favourite technique, insecticide knockdown (known as canopy fogging or canopy misting), includes hoisting in the canopy a radio-controlled fogging or misting machine that dispenses insecticide in different directions. The dying arthropods fall on collecting trays located just above ground level. Alternatively, one may fog or spray from the ground. Other popular ground-based methods include hoisting light traps (or other types of trap) in the canopy using pulley systems, which allows convenient surveys of the traps. For protocols, advantages and limitations of these and other techniques used in canopy entomology, see Erwin (1983b), Stork and Hammond (1997), Basset *et al.* (1997b), Adis *et al.* (1998b) and Kitching *et al.* (2000).

The first attempts to use insecticide knockdown in the tropics often targeted plantations or relatively open and low vegetation (e.g. Gibbs *et al.*, 1968; Roberts, 1973; Gagné & Howarth, 1981; Room, 1975). Other studies performed in primary and tall rainforests followed and sparked a vigorous interest in both canopy arthropods and the techniques of insecticide knockdown itself (e.g. Erwin & Scott, 1980; Adis *et al.*, 1984, 1997; Stork, 1987b; Paarman & Kerck, 1997). The main advantages of this technique are the quick implementation of a systematic and productive protocol (Table 2.1) that produces reasonably clean samples and that it is ideal for general surveys of forest tracts and large-scale taxonomic work, as well as comparative studies. Apart from some technical limitations (e.g. dependence upon weather conditions, sampling often limited to daybreak, etc.), the main disadvantages include the fact that the specimens collected are dead or moribund, the difficulty in tracing the precise origin of the specimens to a specific habitat within the tree fogged, the often low number of spatial replicates available, and the likely escape of larger and more robust individuals. In addition, selective sampling of the upper canopy in tall forests is difficult, as the method yields a mixture of specimens originating from different forest strata.

In recent years insecticide knockdown has been improved significantly by several techniques.

- The observer controls directly the action of the fogging machine by climbing the tree with the single-rope technique (see below); this improves the efficiency of fogging, particularly within tall trees (e.g. Erwin, 1989; Basset, 1995; Floren & Linsenmair, 1997b).
- The collecting trays are set up immediately below the foliage or tree parts fogged (e.g. Ellwood & Foster, 2000; Ch. 34). This prevents the drift of small specimens away from trays located at ground level.
- Particular tree species are selectively fogged by stretching a cotton roof, preventing collection of arthropods from neighbouring trees (Floren & Linsenmair, 1997b).
- Reducing the insecticide concentrations enables live insects to be collected for rearing and observation (e.g. Adis *et al.*, 1997; Paarmann & Kerck, 1997).

Fogging methods and results are discussed further in Chs. 13–16, 18, 19, 29 and 34.

The interest in traps, especially light traps, for sampling the canopy fauna originated from several studies, particularly those of Wolda (1979) and Smythe (1982) on Barro Colorado Island, Panama, of Sutton (1979) in Brunei, and of Sutton and Hudson (1980) in Zaire. These traps are highly productive for nocturnal insects, particularly moths and beetles (Table 2.1). The size and composition of catches in such light traps, however, is highly dependent on environmental factors such as temperature, relative humidity, other ambient light sources and air movement. Correction factors can be computed but are likely to be region or even site specific (e.g. Bowden, 1982). The range of attraction to traps depends on taxa and is often difficult to estimate. The usual response to these various problems has been to

Table 2.1. *Comparison of canopy access methods with regard to spatial and temporal replicates, duration of field work and arthropod material produced. Representative references have been selected to cover different forest types. Note that sites may have been defined differently among studies, and that the productivity of studies depend on many parameters, including collecting method, target group and forest type*

| Method/reference | Tree species | Tree individuals | Sites | Duration | Individuals collected | Collecting method | Target group |
|---|---|---|---|---|---|---|---|
| **Ground-based techniques** | | | | | | | |
| Erwin, 1983b | ? | 10 | 4 | 2 months | 24 350 | Pyrethrum knockdown | Arthropods |
| Stork, 1987b | 5 | 10 | 1 | 12 days | 23 874 | Pyrethrum knockdown | Arthropods |
| Kitching *et al.*, 1993 | 10 × 10 m plots | Various | 16 | 3 years | 32 951 | Pyrethrum knockdown | Arthropods |
| Allison *et al.*, 1997 | 6 | 51 | >3 | >2 weeks | 45 464 | Pyrethrum knockdown | Arthropods |
| Floren & Linsenmair, 1997b | 3 | 10 | >2 | ? | 155 000 | Pyrethrum knockdown | Arthropods |
| Wagner, 1998 | 4 | 64 | 3 | ? | 3952 | Pyrethrum knockdown | Chrysomelidae |
| Missa, 2000 | 17 | 38 | 1 | 13 months | 7899 | Pyrethrum knockdown | Curculionidae |
| Wolda, 1982 | 1 | 1 | 1 | 4 years | 87 547 | Light trap | Homoptera |
| Sutton *et al.*, 1983a | 4 | 4 | 4 | 38 days | 98 569 | Light trap | Arthropods |
| **Single rope technique** | | | | | | | |
| Basset, 1996 | 10 | >100 | 2 | 1 year | 52 858 | Hand-collecting/beating | Insect herbivores |
| **Platforms, towers and walkways** | | | | | | | |
| Corbet, 1961b | >2? | >4? | 1 | 3 months | 1951 | Light trap | Culicidae |
| Kato *et al.*, 1995 | 1? | 1? | 1 | 1 year | 1 023 008 | Light trap | Arthropods |
| *Canopy crane* | | | | | | | |
| Blüthgen *et al.*, 2000b | 27 | 66 | 1 | 3 months | ? | Hand-collecting/baiting | Ants and homopterans |
| Ødegaard, 2000a | 24 | 37 | 1 | 2 years | 35 479 | Hand-collecting/beating | Phytophagous beetles |
| Y. Basset & H. Barrios, unpublished data | >80 | >100 | 1 | 1 year | >2000 | Hand-collecting/beating | Curculionoidea |
| **Canopy raft** | | | | | | | |
| Basset *et al.*, 1992 | 15 | >15 | 4 | 4 days | 2271 | Beating | Insect herbivores |
| Dejean *et al.*, 1999, 2000e | *c.* 30 | 34 | 3 | Several days | >10 000 | Hand collecting | Ants |
| Basset *et al.*, 2001 | >10 | >10 | 3 | 15 days | 9026 | Beating/different traps | Insect herbivores |
| **Canopy sledge** | | | | | | | |
| Dejean *et al.*, 1992b, 1999 | 62 | 167 | Many | *c.* 6 hours | >50 000 | Hand collecting | Ants |
| Dejean *et al.*, 1998, 1999 | *c.* 60 | 71 | Many | *c.* 3 hours | >20 000 | Hand collecting | Ants |
| Dejean *et al.*, 2000b | 106 | 220 | Many | Several days | >60 000 | Hand collecting | Ants |
| Basset *et al.*, 2001a | 56 | 78 | Many | *c.* 16 hours | 626 | Beating | Insect herbivores |
| **Treetop bubble** | | | | | | | |
| Basset *et al.*, 2001a | >30[a] | >30[a] | 2 | 4 days | 4003 | Sticky traps | Insect herbivores |

[a]Depends on the length of the transect

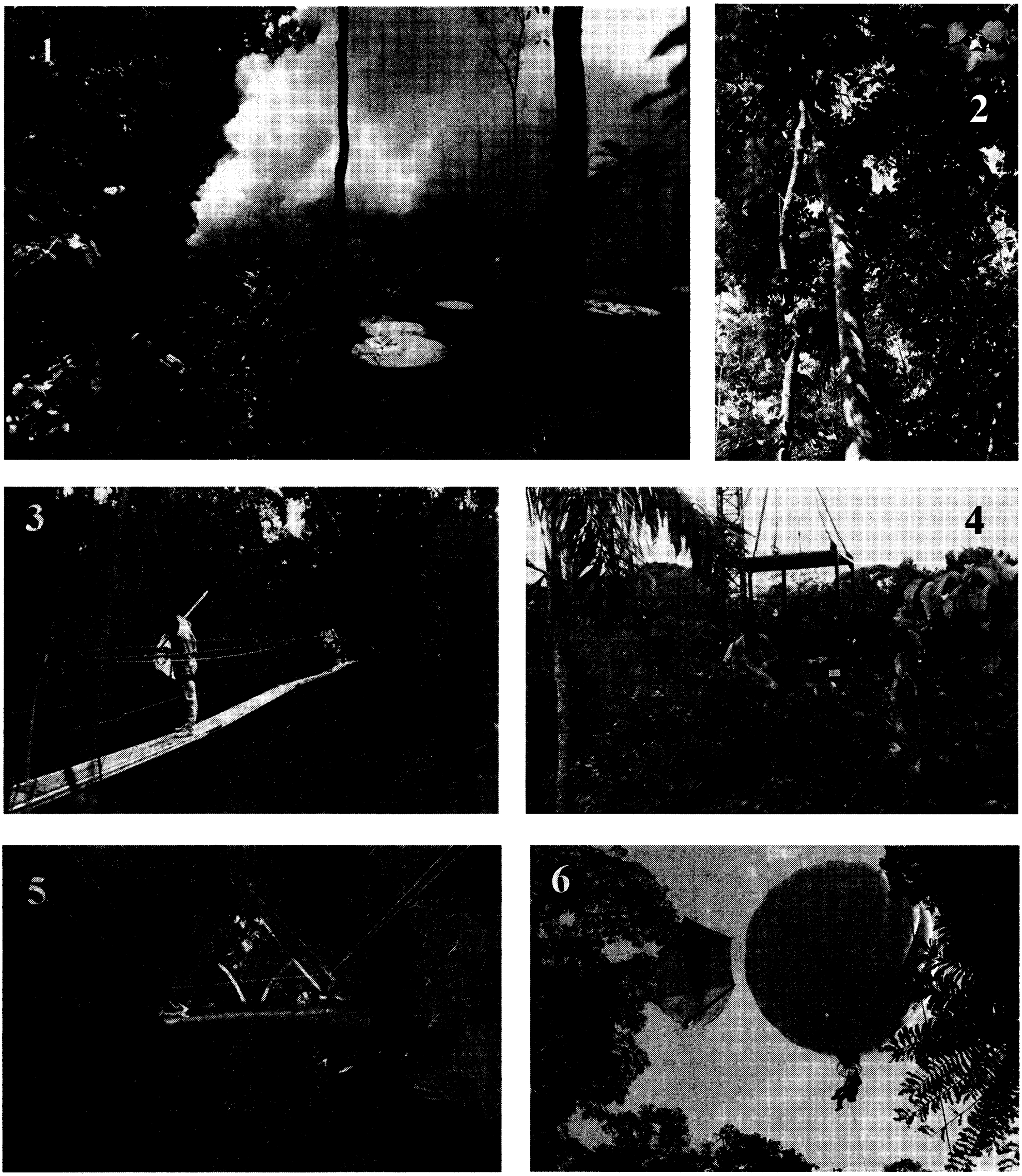


**Fig. 2.1.** Methods of canopy access and entomological techniques. 1. Mist-blowing in Australia (photo H. Setsumasa). 2. Beating the foliage with single-rope techniques in Papua New Guinea (photo Y. Basset). 3. Netting insects on a walkway in Sarawak (photo H. Setsumasa). 4. Observation of foliage with the canopy crane near Colon, Panama (photo M. Guerra). 5. Harvesting foliage samples with the canopy sledge, Cameroon (photo H. Setsumasa). 6. Surveying interception-flight traps with the treetop bubble, Gabon (photo H. Setsumasa).

use more traps more often. Recent studies have used light traps on towers erected in rainforests (e.g. Kato *et al.*, 1995; Willott, 1999; Chs. 7 and 12) or suspended from ropes in the high canopy (Kitching *et al.*, 2000).

### *Single-rope technique*

Perry (1978) appears to have been the first scientist to modify the single-rope technique used in caving to climb tall rainforest trees. The observer climbs with harnesses and jumars on a static rope anchored at ground level. For later developments and safety hints, see Perry and Williams (1981), Whitacre (1981), Landsberg and Gillieson (1982), Dial and Tobin (1994), Laman (1995), Barker (1997) and Barker and Sutton (1997). The equipment is inexpensive and allows a protocol to be developed based on spatial replication (Table 2.1). However, in addition to safety and liability concerns, the mobility of the climber is often restricted (but see description of the more unrestrained arborist method in Dial & Tobin (1994)) and the upper canopy or the crown periphery are often out of reach, unless climbing from emergent trees. In addition, the availability of suitable branches able to bear the weight of climber and equipment necessarily place constraints on precisely which locations can be accessed.

Entomologists have used this technique to sample the fauna of epiphytes (e.g. Nadkarni & Longino, 1990; Rodgers & Kitching, 1998; Ch. 10), to study herbivory (e.g. Lowman, 1985; Sterck *et al.*, 1992; Barone, 2000), to set up and survey various traps (e.g. Basset, 1991a; Ch. 6) or to collect live arthropods *in situ* (e.g. Basset, 1996; Longino & Colwell, 1997). The technique is also increasingly used to test or improve the efficiency of insecticide knockdown (e.g. Ellwood & Foster, 2000; Ch. 18). Regular improvements in speleological equipment (such as the improved ascender developed by the PETZL™ company, which may save up to 30% in energy during the climb) promise that entomologists will still be using this method in the future, particularly to reach the lower parts of the canopy and as a complement to the more intensive kinds of access provided by other methods discussed below.

### *Platforms and towers*

Medical entomologists often set up platforms and towers in rainforests to study insect vectors, as did Bates (1944) in Columbia, Galindo *et al.* (1956) in Panama, and Haddow *et al.* (1961) and Haddow and Ssenkubuge (1965) in East Africa. Paulian (1947) used a sophisticated system of platforms and lifts to collect various taxa in the canopy of a lowland rainforest in Ivory Coast. Le Moult (1955) collected butterflies from platforms in French Guiana, and Cachan (1964) studied the seasonality and vertical stratification of Scolytinae from a tower located in the Ivory Coast. McClure (1966) collected various insect taxa from his platform in Malaysia. These structures tend to be relatively inexpensive and may also be replaced by cheaper scaffoldings (e.g. Jackson, 1996). However, their fixed access cannot be chosen randomly: appropriate clearings, adjacent trees or other constraints associated with tower construction impose limitations. In addition, foliage, flowers or fruits may be difficult to reach by the observer. Using a different approach, some workers have established small individual platforms in trees (Nadkarni, 1988). A new generation of larger tree platforms shaped like icosahedrons, which can be conveniently set up within tree crowns and moved elsewhere, seem promising for many sampling purposes including the light trapping of insects (Ebersolt, 2000; Hallé *et al.*, 2000). In the present volume, several authors relied on towers for canopy access (Chs. 7 and 34). A different technique, the canopy boom, is mentioned here in the interests of completeness but did not generate wide enthusiasm among entomologists following the initial pollination studies performed with it in Malaysia (e.g. Ashton *et al.*, 1995).

### *Walkways*

Canopy walkways to conduct scientific research were first built in Malaysia to study ecto- and endoparasites of mammals (Muul & Lim, 1970; Muul, 1999). Other walkways were constructed in Panama, Papua New Guinea and Sulawesi (Sugden, 1985) and, among other work, were used to study herbivory (Wint, 1983). More recently, walkways have been in use in Australia, Belize and Peru to study herbivory and to survey arboreal mites (Walter & O'Dowd, 1995; Lowman, 1997; Walter *et al.*, 1998). These structures may well be affordable by research institutions and are safe (e.g. Lowman & Bouricius, 1993). They expand canopy access for sampling from points to transects, in contrast with platforms, towers and single-rope access (Muul & Lim, 1970). Access to the upper canopy, however, is difficult. A recent trend has been to combine platforms and walkways, such as at Blue Creek, Belize (Lowman & Bouricius, 1995), or towers and walkways as in the

Canopy Observation System in Lambir Hills, Sarawak (Inoue *et al.*, 1995; Yumoto *et al.*, 1996). Numerous entomological contributions resulted from the latter effort, with a special emphasis on insect pollination and seasonality (e.g. Kato *et al.*, 1995; Momose *et al.*, 1996; Sakai *et al.*, 1999a). In Ch. 12, Itioka *et al.* used walkways to gather entomological data.

*Canopy cranes*

Several construction tower cranes have been erected in tropical rainforests, such as in Panama (two cranes), Venezuela, Australia and Sarawak (Parker *et al.*, 1992; Wright, 1995; Wright & Colley, 1996; Stork *et al.*, 1997c). A crane operator controls the position of the crane gondola, from which observers can perform a variety of tasks. Many entomological studies have been performed or initiated with tropical canopy cranes, using different sampling methods (e.g. Roubik, 1993; Ødegaard, 2000a; Ødegaard *et al.*, 2000; Blüthgen *et al.*, 2000b; Basset, 2001a). The main advantages are the safety and excellent access within much of the canopy (less so in the lower part), and the possibility of obtaining many temporal replicates (Table 2.1). This is particularly useful for behavioural and life-history studies. Problems related to pseudoreplication at the meso-scale are acute within the relatively small and fixed crane perimeter (seldom exceeding 1 ha in area), and the costs of purchasing, erecting and maintaining a crane are expensive, particularly in remote locations. Crane use may be restricted during stormy or windy weather. One exciting development of canopy cranes is the Canopy Operation Permanent Access System (COPAS), currently being developed in French Guiana (Lohr, 2000). This system is similar to that using canopy cranes but the gondola is supported by a helium balloon and moves across a triangular line supported by three masts. Masts could be moved or added after the triangular area has been well studied, thus providing improved spatial replication. Several contributions in this volume present data that have been obtained using canopy cranes: Chs. 20, 21, 23, 25, 28 and 32.

*Canopy raft and sledge*

The canopy raft ('*Radeau des Cimes*') is a 580 $m^2$ platform of hexagonal shape, consisting of air-inflated beams and Aramide$^{TM}$ (polyvinyl chloride) netting. An air-inflated dirigible of 7500 $m^3$ raises the raft and sets it upon the canopy. The raft is positioned on particular sites upon the canopy and moved every 2 weeks by the dirigible. Access to the raft is provided by single-rope techniques (Hallé & Blanc 1990; Ebersolt, 1990). The sledge ('*Luge des Cimes*') is a triangular platform of about 16 $m^2$ that is suspended below the dirigible and 'glides' over the canopy at low speed (Ebersolt, 1990; Lowman *et al.*, 1993a). Several entomological teams have worked with either the canopy raft or sledge, using a variety of collecting methods (e.g. Basset *et al.*, 1992, 1997b, 2001a; Dejean *et al.*, 1992b, 1998, 1999, 2000b,e; Sterck *et al.*, 1992; Lowman, 1997). The mobility of the raft, and particularly of the sledge, is ideal to obtain spatial replicates (Table 2.1). The infrastructure needed is expensive, however, and long-term temporal replicates are difficult to obtain. Access to the foliage is mainly restricted to the periphery of the raft. Flights with the sledge are restricted to the early mornings and times of good weather. In this volume, Chs. 10, 27 and 30 present data obtained with either the canopy raft or sledge.

*Treetop bubble*

The Treetop bubble ('*Bulle des Cimes*') is an individual 180 $m^3$ helium balloon of 6 m in diameter that runs along a fixed line set up in the upper canopy (Hallé *et al.*, 2000; Cleyet-Marrel, 2000). The system is independent from the canopy raft and sledge although the dirigible used to move the canopy raft is used to install the transect line. The observer is seated in a harness suspended below the balloon. He or she moves along the line with jumars. Different transects of several hundred metres have been set up, but longer transects of several kilometres are planned. So far, the bubble has been used to set up and survey different traps in the upper canopy (Basset *et al.*, 2001a), but other entomological applications are certainly possible. The equipment needed is relatively inexpensive and spatial replicates along line transects can be easily obtained (Table 2.1). Long-term temporal replicates along these transects could also be achieved. Possible limitations may be the relative instability of the observer because of the buoyancy of the balloon, and the difficulty in accessing the lower canopy. One promising development may be to elaborate protocols that would allow setting up the line with professional tree-climbers, instead of relying on the dirigible. This would make the method affordable to many research institutions. In Ch. 27, Basset *et al.* report data obtained with the treetop bubble.

**Sampling and performing experiments in the canopy**

With enhanced canopy access, entomologists can now focus their attention on the one hand in expanding their spatial and temporal replicates and, on the other, carrying out detailed process studies at selected 'super-access' locations. Basset *et al.* (2001a), for example, reported on one of the first attempts to factor out the effects of site, stratum and time in the distribution of arthropods in a tropical rainforest, using different methods of canopy access and sampling. They found that the effects of stratum were most important, representing between 40 and 70% of the explained variance in arthropod distribution, depending on the collecting method used. Site effects represented between 20 and 40% of the variance, whereas time effects (diel activity) explained a much lower percentage of variance (6–9%). These data stress the importance of replication among canopy sites and the appreciably different arthropod fauna that forages in the understorey compared with the upper canopy, where microclimatic conditions appear to be very different.

Enhanced access to the canopy also means that entomologists can now perform extensive and selective sampling with sufficient replicates in key canopy habitats, as opposed to more systematic sampling of individual trees. Targeting key habitats such as the upper canopy layer, blooming trees, lianas, epiphytes or dead suspended wood may be one strategy to refine relevant hypotheses on habitat and resource use in the canopy. This line of research is evident in recent studies (e.g. Nadkarni & Longino, 1990; Berkov & Tavakilian, 1999; Compton *et al.*, 2000; Ellwood & Foster, 2000; Ødegaard, 2000a; Basset *et al.*, 2001a), and in many contributions to this volume.

Manipulative experiments *in situ* are also needed to improve our understanding of arthropod distribution in the canopy. To date, few such examples exist, but they are bound to increase in the future. For example, Dial and Roughgarden (1995) removed *Anolis* lizards from tree crowns in Puerto Rico and monitored the resulting changes in the food-web, particularly within arthropod groups. V. Novotny (unpublished data) has likewise performed multiple-choice feeding experiments *in situ* in the canopy in Panama, using canopy cranes. Mark-recapture experiments would also help greatly to study arthropod dispersal in the canopy. However, these experiments are likely to be challenging for some time (T. Roslin, personal communication), given the relatively low arthropod densities in the canopy (Basset, 2001b), their high spatial aggregation (Novotny & Leps, 1997; Novotny & Basset, 2000) and the difficulties in accessing multiple sites in the canopy.

The collection and rearing of live specimens from the canopy also represents another recent trend in the study of canopy arthropods that is promising (e.g. Paarmann & Paarmann, 1997; Novotny *et al.*, 1999b; Ch. 25). Rearing juvenile specimens provides adult specimens tractable for taxonomic studies, and the behaviour of live specimens can be studied either *in situ* or in the laboratory. Specimens collected alive can also be used subsequently in a variety of experiments, investigating, for example, resource use.

**Archiving of data and collections**

Recently, several projects have documented the rich tropical insect fauna by training local people ('parataxonomists') in the basics of insect collecting, mounting and sorting morphospecies; digital photography; and the use of simple, yet powerful computer databases (e.g. Janzen *et al.*, 1993; Longino & Colwell, 1997; Novotny *et al.*, 1997; Basset *et al.*, 2000). To date, none of these efforts has targeted specifically the canopy habitat, but it is only a question of time before entomologists train efficient parataxonomists on a large enough scale to cope with the enormous arthropod diversity in the canopy. These strategies can yield high-quality insect material and data, which are also available for subsequent taxonomic studies, within a relatively short time.

The identification of specimens collected in the canopy and their permanent storage are other problems that entomologists must face (see below). We expect some improvements in the routine identification of specimens that belong to known, and named, species. Extended computer hardware and software now allows the routine inclusion of digital pictures of specimens and characters in sophisticated databases, and this information can be circulated readily among colleagues over the internet and worldwide web. Large public databases, such as Ecoport (www.ecoport.org) and taxonomic tools are beginning to be available widely on the internet. As access to the internet, worldwide web and the nodes of expert taxonomists and their taxonomic tools from tropical countries improves, identification of specimens belonging to described species should be facilitated, and the ecological information linked to these species should expand. For a discussion on networking, entomological databases and the worldwide web, see Miller (1994).

## CAVEATS AND LIMITATIONS IN CANOPY ENTOMOLOGY

The caveats and limitations in canopy entomology can be grouped in four categories: sampling limitations, taxonomic limitations, interpretation of ecological data, and conservation threats.

### Sampling limitations

One recurrent problem in canopy entomology is low sample size, not so much in terms of number of specimens collected but rather in terms of number of replicates available for statistical analysis. This often results from difficult, expensive, partial or constrained canopy access. It often leads to pseudoreplication within the sampling universe and to disturbance and possible interference with the object being studied (Barker & Pinard, 2001). To what extent this problem may be serious may be dependent upon both taxa and scale. Data about larger, more active, stronger flying, better dispersing arthropod taxa are more likely to suffer from pseudoreplication than those related to more sedentary and physically smaller taxa, as sampling units are more likely to be independent in the latter. For similar taxa, the scale at which their distribution is analysed (e.g. microsites on a leaf, leaves, branches, crown segments, trees or forest plots) is also crucial.

For example, the study of insect host specificity in tropical rainforests appears to be constrained by at least three critical issues: sample size, number of singleton and rare species, and aggregation patterns of arthropods. Since the vegetation is highly diverse in rainforests, the sample size needed to estimate the true range of a species of herbivorous insect must be high, although no guidelines exist at the moment. Sufficient spatial and temporal replicates need to be combined with natural history data. Insufficient sampling and the mass effect described by Shmida and Wilson (1985) partly explain why so many species are represented by singletons in canopy samples (e.g. Morse *et al.*, 1988; Allison *et al.*, 1997). In tropical rainforests, the distribution of many insect herbivores is aggregated on the foliage, even for generalist species (Basset, 2000). This is reflected in their apparent high host specificity and rarity at low sample size (Novotny & Basset, 2000). This issue is also discussed in Ch. 29.

The positioning of access systems in the canopy is almost always nonrandom and opportunistic, particularly for fixed structures. An associated potential limitation is that samples obtained may not be representative of the fauna of the wider but less-accessible canopy (Barker, 1997).

Once sampling methods have been selected appropriately to investigate particular hypotheses, protocols should, as far as possible, be standardized (e.g. Adis *et al.*, 1998b, Kitching *et al.*, 2001, for insecticide knockdown). This will ensure subsequent comparison of valuable data across studies (Erwin, 1995; Stork *et al.*, 1997b). In practice, this comparability has seldom been sought.

### Taxonomic limitations

Sampling techniques have greatly influenced present knowledge of canopy invertebrates. Invertebrates other than arthropods, although often abundant in epiphytic habitats, phytotelmata and perched litter, are little studied. The abundance of several arthropod groups, such as Acari, Collembola and Isoptera, is almost certainly seriously underestimated. The meagre taxonomic information available is usually focussed on a few relatively better known groups, such as Coleoptera and Lepidoptera (Basset, 2001b).

In addition to this conspicuous lack of information at the higher taxonomic level, many challenges are inherent in dealing with more detailed analyses of tropical arthropods. Taxonomic sufficiency, or using the level of identification appropriate to the study question, is important (Pik *et al.*, 1999; Slotow & Hamer, 2000): some studies may be accomplished with resolution at the level of order, genus or functional group, whereas other studies require species or morphospecies. Identification to species involves three steps: (i) sorting specimens into similar groups based on external characters; (ii) refining these groups based on detailed examination of accepted taxonomic characters (often including genitalic dissection) or external knowledge of patterns of polymorphism, sexual dimorphism, etc.; and (iii) associating these groups of specimens with formal names, based on literature, reference collections and comparisons with type specimens. Many early ecological studies on tropical arthropods only went to the first step, resulting in many errors. The present standard of practice is the second step, which we refer to as a morphospecies (although some authors use the same term for the first step). This can effectively be done with parataxonomists, if sufficient training, identification aids and quality control are provided (Cranston & Hillman, 1992; Basset *et al.*, 2000). The third level often requires collaboration with professional taxonomists, as well as access to type specimens scattered in European museums. Because of the cost in money and time of accomplishing the third step, many studies have assigned numbers and voucher specimens to their morphospecies, thus providing an 'interim taxonomy' (Erwin, 1991b) that allows the species to be referenced and its identity to be verified in the future.

Of all the species collected in canopy arthropod studies, few are identified as described species (e.g. Erwin, 1995; Ch. 21). Further, in most studies only very narrow taxonomic groups are actually taken fully through the third step above by exhaustive comparisons with type specimens (e.g. Roberts, 1993; Curletti, 2000). Our own work in Papua New Guinea has found, however, that a surprisingly high portion of morphospecies can be linked to names if sufficient effort is made (S. E. Miller, unpublished data). With the continuing crisis in systematics (e.g. Miller, 1991, 2000), description of new species collected in the canopy is going to be an increasingly difficult task (e.g. Kitching, 1993). Although coded morphospecies resolve many of the taxonomic problems in local studies, examination of ecological information associated with these unnamed species across multiple localities or studies is difficult. One solution will be to deposit and link information on the morphospecies (e.g. digital pictures, genitalia drawings, ecological data, etc.) into large public databases, such as Ecoport (www.ecoport.org), but this not an ideal solution without the features of a full taxonomic framework. In addition, the permanent storage of the material collected is also problematic (Stork & Gaston, 1990). Means of streamlining taxonomic practices have been suggested (e.g. Erwin & Johnson, 2000), but until images of old type specimens are routinely available in searchable databases, associating names with tropical arthropods will remain challenging.

Several major taxonomic initiatives have been proposed (such as the Global Taxonomy Initiative (GTI), BioNet International, Systematics Agenda 2000, All Taxa Biodiversity Inventories (ATBI), Global Biodiversity Information Facility (GBIF), All Species Inventory), which, *inter alia*, would build the capacity for taxonomic understanding of canopy arthropods (Cracraft, 2000). These approaches vary in their feasibility but, at this point, they remain largely unfunded. There has been widespread recognition of the crisis in staffing and available expertise in arthropod taxonomy since the 1980s (Wilson, 1985; Hawksworth & Ritchie, 1993; Miller & Rogo, 2002) but, in general, there has been little response from government agencies and other funding bodies. More progress is being made in databasing of existing formal collections, in cataloguing already named species and in documenting available expertise. Nevertheless, the parataxonomic approaches already described will likely remain the methodology of choice for canopy ecologists for some time to come.

For studies dealing with the biology of particular species, it is especially important that voucher specimens of both insects and host plants be placed in appropriate repositories for future reference (Huber, 1998; Ruedas *et al.*, 2000).

### Interpretation of ecological data

To date, most of the information on canopy arthropods results from surveys of the canopy habitat, isolated from other forest habitats (but see Stork & Brendell, 1993; Kitching *et al.*, 2001; Chs. 9 and 26). Whether the canopy should be studied on its own or jointly with other forest habitats, such as soil and litter, is debatable. Many insect herbivores, such as some chrysomelids and curculionids, feed on roots as larvae and later migrate into the canopy to feed as adults on leaves. Although it is relatively easy to report differences in the occurrence of particular species of beetles in the adult stage either in the soil or in the canopy, our understanding of the relationships between the canopy and soil should also proceed by assessing how many insect species depend on the soil/litter habitat during their juvenile stages and on the canopy during their adult phase. Understanding the distribution of adult insects in the canopy may require solid data on their distribution as larvae in the soil (Basset & Samuelson, 1996). Further, comparison between the litter and canopy faunas may emphasize specific adaptations of arboreal invertebrates that may be important from a conservation viewpoint. Nevertheless, multimethod, multihabitat studies are essential if statements are to be made about the overall arthropod diversity of the forest: the assumption, tacit since Erwin & Scott's (1980) article, that the species richness of the forest is totally canopy dominated is certainly not true.

Rightly, Stork *et al.* (1997b) advised that entomological studies in the canopy should be integrated with other groups of organisms and studies of ecosystem processes. A sound understanding of biotic relationships in the canopy may require baseline knowledge of the entire rainforest ecosystem, an additional challenge in itself.

### Conservation threats

The habitats that are the objects of study of canopy entomologists are disappearing fast (e.g. Bowles *et al.*, 1998), and with them an unknown but presumably vast number of arthropod species (e.g. Lawton & May, 1995). Canopy entomologists can play an active role in forest conservation by focussing their technical research on topics directly relevant to nature conservation issues (see the concluding chapter of this volume). In particular, they should attract the attention of the media, public and policy-makers by disseminating popular accounts of the tropical canopy and its arthropod inhabitants, aimed at both developing and developed countries (e.g. Basset & Springate, 1993; Floren & Linsenmair, 2000b; Novotny, 2000; Ødegaard, 2000b).

## CONCLUSION

The limitations of each method of canopy access are obvious, as are those of each collecting method. There is no doubt that the choice of access technology and sampling methods must be tailored to the particular scientific questions being posed. For example, with regard to invertebrate samples obtained *in situ*, seasonal aggregation may be better studied with construction cranes, whereas spatial aggregation may be better studied with mobile devices such as the canopy raft or the canopy sledge (Table 2.1). This multifaceted approach calls for increasing collaborative effort (e.g. Nadkarni & Parker, 1994; Stork & Best, 1994; Erwin, 1995), involving not only researchers but also parataxonomists, and the use of multiple and complimentary techniques to create, for example, a 'canopy station' (e.g. A. W. Mitchell (cited in Lowman *et al.*, 1995); Hallé *et al.*, 2000; Mitchell, 2001). In particular, the more 'mobile' methods (single-rope technique, raft, sledge, treetop bubble) could be used to assess the representativeness of samples and observations obtained with 'fixed' methods (towers, walkways, cranes). One can also imagine merging different methods of canopy access and sampling, such as, for example, performing insecticide knockdown with the canopy sledge.

Not only do canopy entomologists need to expand greatly their sampling universe in the canopy, they also need to study the distribution of canopy arthropods at a much finer scale than done previously, by accurately tracking arthropod resources in space and time. Ideally, manipulative experiments should be performed at these meso- and microscales. One way to succeed in tackling these various problems would be to develop local inventories near or at canopy stations, as suggested by several authors (e.g. Janzen, 1993a; Stork, 1994; Godfray *et al.*, 1999). Significant progress in understanding arthropod distribution in the canopy requires us to solve these different challenges.