5. The International Canopy Crane Network: Key findings in canopy science

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Introduction

In this chapter, we summarize the key scientific findings contributed by the International Canopy Crane Network (ICCN) since 1990. Also, we place the results of these investigations in the larger context of the study of process, structure, and function in forests. The reader interested in particular research topics in canopy science may wish to consult the following recent compilations: Lowman and Nadkarni (1995) and Linsenmair *et al.* (2001), on canopy forest process and canopy science; Mitchell *et al.* (2002) on canopy access and methods of study of forest canopies; Mulkey *et al.* (1996b) on tropical forest ecophysiology; Gash *et al.* (1996) on climate change and deforestation; and Stork *et al.* (1997b) and Basset *et al.* (2003a) on canopy biodiversity. Overviews of the importance of canopy science and the canopy crane network to global issues are provided by Ozanne *et al.* (2003) and Stork *et al.* (1997a).

The ICCN is composed of 11 crane facilities, of which one is no longer operational, located in eight countries. The oldest crane facility is that of Parque Natural Metropolitano, which started its activities in 1990. The most recent crane facilities of the Network are those of Leipzig and Münich, constructed in 2001. A new facility, the Canopy Operation Permanent Access System, will soon be in operation in French Guiana. Since only six crane facilities have been active for more than 5 years, much research within the network is on-going and has yet to be published. Not unexpectedly, the oldest crane facilities have been the most productive in terms of numbers of research articles published (e.g., Panama, Surumoni, Wind River, Tomakomai). Most crane facilities are located in lowlands (mean altitude of research facilities = 207m, highest location = Basel, 550m). Only two are located in predominantly coniferous forests (Solling and Wind River) and none is located in Africa. The height of the cranes ranges from 25m (Tomakomai) to 85m (Lambir Hills). The average area covered by a crane is only 1.06ha (smallest area = Solling, 0.2ha; largest = Wind River, 2.3ha) and the total area of forest covered by the network amounts to 11.7ha.

Given this rather modest infrastructure, the network collectively has been extremely successful in producing high quality science that sheds light on the maintenance of complex forest processes. Below we summarize key findings, grouped under the broad headings of canopy structure, plant phenology, local maintenance of biodiversity, biotic interactions, canopy microclimate and plant growth, and plant physiological responses to a changing environment.

Canopy structure

Remote sensing is defined as the measurement or acquisition of information of a particular property of an object or phenomenon, by a recording device that is not in physical or intimate contact with the object or phenomenon under study. It involves measuring force fields, electromagnetic radiation, or acoustic energy employing cameras, lasers, radio frequency receivers and radar systems. It is widely regarded as a powerful set of tools to (a) describe canopy structure and composition (Fig. 103); (b) understand physical phenomena such as canopy light interception and deciduousness; and (c) scale up some of the processes and mechanisms occurring in the canopy (Shaw *et al.*, Chapter 4.2.6; Nakashizuka *et al.*, 4.3.3; Bohlman, 4.3.5). In particular, a portable LIDAR ('light detection and ranging' or laser altimetry) device has been used at nine crane sites to produce detailed foliage-height profiles and highresolution and three-dimensional views of canopy elements (G.G. Parker, pers. comm.). LIDAR metrics are strongly correlated with forest structural characteristics, such as basal area, mean stem diameter and above-ground biomass (Drake *et al.*, 2003). Thus, crane sites are increasingly used as sites for validation of data quality for newly developed remote sensing technologies ('ground-truthing'; Shaw *et al.*, 4.2.6; Stork & Cermak, 4.3.1; Bohlman, 4.3.5).

Measurements of canopy structure with a portable LIDAR device confirmed that old-growth forests, in comparison with those younger, have a more uneven canopy surface (i.e., the canopy surface increases as the forest matures) and have a more complex distribution of canopy elements over height (Lefsky *et al.*, 2002; Parker *et al.*, 2002). For example, the canopy/ground ratio was 1.2 for a secondary stand in French Guiana, whilst it was nearly twice as high (2.1) for a primary stand nearby (Birnbaum, 2001). There are several implications of these important findings. (a) Models of ecosystem fluxes treat the canopy as a simple surface and they should be improved to account for the complex vertical structure of the canopy in old-growth forests (Ryan, 2002). (b) For stands situated at similar latitudes, of similar composition and area occupied, the evapotranspiration and carbon sequestration rates may be potentially higher in old-growth forests than in younger forests, thus emphasizing the value of the former. (c) The distribution of organisms over height (stratification) is likely to be more complex (and probably more sensitive to natural and anthropogenic changes) in old-growth than those younger. (d) Oldeman (1992) developed the 'folded forest theory' which envisaged the canopy surface as a folded green carpet, including a hierarchical nesting of folds from the landscape level to the level of the leaf structure. The large canopy surface in old-growth forests and the fractal dimension of vegetation may imply that more habitats may be available in the upper canopy of these forests for small organisms, such as arthropods (Morse *et al.*, 1985). In addition, large temporal changes in canopy surface and volume that may occur even for a stand of a given class age (Parker, 1995) may influence the functional parameters of the stand and the distribution of organisms within.

Bohlman (4.3.5) stated that in seasonal tropical forests, deciduousness affects mostly the upper canopy and, therefore, the canopy should be represented by at least two layers in carbon models that are based on remote-sensing data. A portable LIDAR device can accurately estimate the rate of absorption of photosynthetically active radiation (PAR) and define the location and depth of the zone where the maximum rate of PAR absorption occurs (Parker, 1997; Parker *et al.*, 2001). Since light absorption is correlated with other physiological plant activities, models derived from accurate identification of maximum PAR absorption zones should improve emission models for gaseous molecules, including isoprene, that affect climatic changes (Lerdau, 4.3.5).

Plant phenology: changing canopy structure and resources

Plant phenology (the seasonal dynamics of leaves and reproductive parts) is paramount to understand both the ecosystem functioning of forests and the subtle biotic interactions within (Fig. 104). Since leaf, flower, fruit and seed production are typically higher in the upper canopy than in the understorey (e.g., the understorey represents only 20% of the total leaf area index at the Wind River crane site, Thomas & Winner, 2000), the need for accurate phenological data in the canopy cannot be overstated. Further, since plant phenology and ecophysiology are related, phenological data are crucial to improve regional models of plant evapotranspiration and productivity (Wright & Colley, 1994). Understanding the local and regional importance of mass and general flowering (i.e., the production of flowers and seeds at irregular, multi-years intervals) may also be fundamental for the conservation and sustainable use of forests (Ishida & Hiura, 2002; Nakashizuka *et al.*, 4.3.3). Last, phenological data may help to comprehend and predict the distribution of primary consumers and their suite of predators and parasites.

Fig. 103. Geoffrey Parker and Alan Smith measuring canopy structure at Parque Natural Metropolitano, Panama (photo Marcos Guerra).

Fig. 104. Mirna Samaniego and Osvaldo Calderón performing plant phenology censuses at San Lorenzo, Panama (photo Marcos Guerra).

Vertical profiles of leaf area densities may vary strikingly between tree species, even in temperate forests (Häberle *et al.*, 4.2.2). These profiles are complicated by complex patterns of leafing and flowering within and among tree species (Morawetz & Horchler, 4.2.3, 4.3.4; Wright & Samaniego, 4.3.5), which may also include the production of epicormic foliage (lateral sprouting from dormant buds; Shaw *et al.*, 4.2.6). Dynamic changes in canopy leaf numbers have implications for several levels of forest organization. Leaves produced in different seasons may also differ in morphology and physiology in a manner suitable for the wet, cloudy conditions of the rainy season or the dry, sunny conditions of the dry season (Kitajima *et al.*, 1997a). In addition to dynamic patterns in trees, the phenology of epiphytes (Freiberg, 4.3.1; Zotz, 4.3.5) and lianas (Avalos & Mulkey, 1999; Wright & Samaniego, 4.3.5) also influence the productivity of the forest and the distribution of primary consumers.

Seasonal leaf dynamics affect annual carbon gain and water vapour loss at the level of forest stands. Accurate models of the contribution of tropical forest to global carbon balances need to include accurate estimates of leaf area seasonality (Wright & Colley, 1994). Resource seasonality (vegetative and reproductive parts of plants) is also likely to affect the distribution and behaviour of primary consumers (Wright *et al.*, 1999), which, in turn, contribute to the integrity of the forest via pollination (Roubik, 2000), seed dispersal and return of nutrients to the ground by way of herbivory. Thus, plant phenology represents one of the important components of any research concentrated on the forest canopy.

Local maintenance of biodiversity

All crane sites are concerned to some extent with surveying, mapping and studying the distribution of the rich biodiversity in the forest canopy, including taxa as diverse as trees, lianas, epiphytes, fungi, lichens, mosses, arthropods, birds and mammals (Fig. 105). All studies confirm the high organismic and genetic diversity in temperate and tropical forests, especially in the canopy (e.g., Stork *et al.*, 1997b). Studies with canopy cranes often provided the first insights into the magnitude of local species richness for a range of taxa (e.g., fungi, Morawetz & Horchler, 4.2.3, 4.3.4; epiphytes, Zotz, 4.3.5; beetles, Ødegaard, 4.3.5), although global estimates derived from a small crane perimeter (e.g., herbivorous beetles: Ødegaard, 2000b) are more difficult to substantiate (Ødegaard, 4.3.5; Novotny *et al.*, 2002). Studies examining the relationships between biodiversity and productivity (or other variables accounting for the functioning of ecosystems) have been restricted to impoverished or artificial systems (Chapin *et al.*, 1997). Crane access enables experimental tests of diversity-function relationships for organisms for which relevant spatial scale can be replicated within the crane's perimeter (Hiura, 4.2.5). As pointed by Zotz (4.3.5), whereas many permanent tree plots have been established word-wide, similar plots for canopy organisms (such as epiphytes) have yet to be established. Such plots could be developed conveniently at 'canopy stations' centered on a crane site (Chapter 3).

The distribution of canopy organisms may be affected by horizontal (e.g., different host plants), vertical (e.g., stratification) and temporal factors (e.g., plant phenological changes). The use of canopy cranes can provide useful insights into the relative importance of these different factors for a range of unrelated taxa. Within the crane perimeter, the distribution of small organisms can be studied from the levels of the leaf to the individual tree. Many studies within the crane network are concerned with the vertical distribution of organisms. Indeed, canopy cranes provide unique opportunities to investigate at a fine scale the vertical distribution of abiotic factors and resources and the ensuing stratification of many organisms. The latter contributes to the coexistence of high numbers of species in forests, particularly in tropical rainforests (Basset *et al.*, 2003b).

The distribution of canopy plants such as mistletoes (Shaw *et al.*, 4.2.6), lianas (Morawetz & Horchler, 4.3.4) and epiphytes (Winkler & Listabarth, 4.3.4) depends greatly on light conditions and, as such, often shows a clear vertical distribution. However, the irregular canopy surface at the Surumoni site prevented a strong stratification of epiphytes. This emphasizes the importance of quantifying canopy structure for a sound understanding of patterns of distribution in canopy organisms (e.g., Engwald *et al.*, 2000). Lianas represent important primary producers that support a rich fauna of primary consumers, such as phytophagous beetles (Ødegaard, 2000a) and sap-sucking homopterans (Blüthgen *et al.*, 2000; Blüthgen & Fiedler, 2002). Some of these interactions appear to be rather host-specific, such as many of the weevil species that scrape the tendrils of lianas (Ødegaard, 2000a), others, such as membracid species that suck the sap of lianas, are much less so (Y. Basset & H. Barrios, unpubl. data).

The distribution of mosses, macro-fungi, leaf-surface fungi, slime moulds and lichens have been well investigated at a number of crane sites (Morawetz & Horchler, 4.2.3; Shaw *et al.*, 4.2.6; Winkler & Listabarth, 4.3.4.; Morawetz & Horchler, 4.3.4; Gilbert *et al.*, 4.3.5). There is wide concordance in the results of these investigations in indicating that (a) the habitat preferences of these organisms can be rather narrow, even at the leaf level; (b) leaf-surface fungi share common attributes suited to growth in the harsh conditions of the forest canopy; (c) the increase in air temperature and decrease in relative humidity from the understorey to the upper canopy induces a strong stratification of mosses, fungi and lichens, which can, however, be mitigated by illumination; and (d) the species richness of lichens usually increases from the understorey to the canopy, whereas that of fungi and mosses usually shows a reverse pattern. Further, at the Wind River site, a unique lichen community occurs in the upper canopy (McCune *et al.*, 2000).

Fig. 105. Lukas Cizek and David Hauck collecting insects visiting flowers with large butterfly nets in the canopy of San Lorenzo, Panama (photo Marcos Guerra).

A wide range of arthropod taxa (insects, spiders and mites) have been studied at multiple crane sites. Arthropod occurrence often depends on the presence of particular habitats or host-plants (Häberle *et al.*, 4.2.2; Schowalter & Ganio, 1998; Ødegaard, 4.3.5; Basset & Barrios, 4.3.5), but is also strongly affected by seasonal events, such as rainfall, leafing or flowering (Stork & Cermak, 4.3.1; Nakashizuka *et al.*, 4.3.3; Winkler & Listabarth, 4.3.4; Basset & Barrios, 4.3.5). In temperate forests, the structural features of the canopy appear to be important for certain arthropods that hibernate there during winter (Häberle *et al.*, 4.2.2). Contrary to popular wisdom, the host-specificity (degree of overlap between different hosts) of herbivorous insects in tropical rainforests appears to be lower than previously thought. This concerns a range of leaf-feeding (Ødegaard, 2000b; Novotny *et al.*, 2002; Y. Basset & H. Barrios, unpubl. data) and flower-feeding insects (Kirmse *et al.*, 2003). As a result, the highest estimates of global biodiversity, based on an assumption of a high host-specificity of tropical insects (Erwin, 1983), are difficult to support (Basset *et al.*, 1996; Ødegaard, 2000b; Novotny *et al.*, 2002).

Many arthropod groups show clear patterns of stratification in forest canopies, particularly in tropical rainforests (Basset *et al.*, 2003b), which are sometimes mitigated by the preferential and seasonal use of certain food resources (Roubik, 1993). Depending on their ecology, certain groups show a preferential distribution near ground level (many scavengers) or in the upper canopy (many herbivores; Basset *et al.*, 2003b). Even within the relatively short Tomakomai forest, the vertical distribution of flying insects, such as drosophilid flies, closely follows the stratified structure of the vegetation (Tanabe, 2002) and it is probable that seasonal changes in the leaf quality of canopy trees cause the migration of caterpillars (Wada *et al.*, 2000). As a consequence of differing abiotic and biotic conditions in the understorey and upper canopy of tropical rainforests, conspecific seedlings and mature trees support different suites of insect herbivores (Basset, 2001b; Barrios, 2003). In particular, various studies in Panama suggest that the higher availability of food resources, such as young foliage, in the canopy than in the understorey, perhaps combined with other factors such as resource quality and enemy-free space, may generate complex gradients of abundance and species richness of insect herbivores in wet closed tropical forests (Basset & Barrios, 4.3.5).

Small organisms, such as arthropods, often exploit the environment in a more discriminating way than larger organisms do. Therefore, vertical stratification of the former is more likely than for the latter. However, stratification patterns are also apparent for larger animals, such as certain birds and mammals. Various studies at the Wind River crane site implied that the structure and resources of the upper canopy of old-growth forests are more important for birds than previously thought (Shaw *et al.*, 4.2.6). At the Surumoni crane site, about 42% of bird species prefer to forage in the upper canopy (Winkler & Preleuthner, 2001). These preferences in vertical distribution may, in part, relate to the effectiveness of certain behaviours, such as vocal communication and sexual displays (Winkler & Listabarth, 4.3.4).

The various studies summarized in this section suggest two important implications for the conservation of forests and their biodiversity. First, old-growth forests, with their high tree diversity and structural diversity, represent unrivaled repositories of organismic and genetic diversity. Typically, species observed near ground level represent only a fraction of the total biodiversity supported by these forests. Simplifying these ecosystems by management and removal of tree species will result in a severe loss of species. The magnitude of these losses is difficult to estimate, since baseline information is missing for many diverse but poorly-studied groups. Second, the bulk of biodiversity includes many small organisms, poorly known, but with specific habitat and food-resource requirements. In particular, survival of many of these organisms may be linked to the presence of specific abiotic and biotic conditions along the vertical forest profile. Alterations of the canopy structure (e.g., by selective logging) may change these conditions and lead to important losses of species. For example, a diverse and distinct community of insect herbivores is restricted to the few uppermost metres of the upper canopy of a tall closed African rainforest (Basset *et al.*, 2001). Similar communities may exist at other locations and would be the first affected by slight openings in the forest canopy.

Biotic interactions

The functioning of all ecosystems depends on biotic interactions among species. The cranes of the network allow convenient observations and experimentation *in situ* in the canopy for a wide range of crucial biotic interactions. Although the potential for such studies across the network is large, the number of biotic interactions investigated at crane sites represents only a small fraction of the total. Protocols dedicated to the study of biotic interactions in the canopy depend on spatial and temporal replication, to evaluate the consistency of the interactions. Whereas good temporal replication can be achieved at individual crane sites, the crane network is essential to ensure spatial replication.

Estimates of herbivory at the scale of the forest ecosystem are crucial to studies of the return of nutrients to the ground and their re-cycling in forest systems. However, such studies are difficult since herbivory is likely to vary greatly at smaller scales, such as between leaves, individual trees or forest strata (Lowman, 1995). A research group lead by Margaret Lowman (Selby Botanical Gardens, Sarasota) has developed a protocol to measure herbivory within a relatively small volume of forest and to scale up to the forest stand level. The protocol has been validated and improved using several crane sites (e.g., Leipzig, Wind River, San Lorenzo, etc.).

Herbivory may be influenced by many factors. One study in Panama demonstrated that vertebrate predators, such as birds, regulate herbivory in the canopy. These effects were more pronounced at the dry, less diverse, crane site than at that wetter and more diverse. This implies that local bird decline or extinction could affect significantly local leaf damage and forest health (Van Bael, 4.3.5).

Sound understanding of biotic interactions requires that interactions be studied within the whole forest system, i.e. both in the understorey and upper canopy. This is perhaps best exemplified by studies of pollination. For example, the fruit production of understorey herbs within the Hokkaido crane site is affected by the flowering intensity of canopy trees via the activities of pollinators (Hiura, 4.2.5). Various studies at the Lambir Hills and Panama cranes suggest that relationships between plants and pollinators are rather specialised in the understorey, and less specialised in the upper canopy. In Panama, thrips and bees were the principal potential pollinators in the canopy and their abundance shifted greatly from year to year for many plant species. Many plants possessed loose pollination niches and the introduced African honeybees played a prominent role as flower visitors (Sakai & Roubik, 4.3.5).

Whereas studies of post-dispersal seed attack in tropical rainforests are relatively common, pre-dispersal seed attack (i.e., attack of seeds in the canopy, before they are dispersed) has rarely been studied. A study at the crane site in the dry forest in Panama indicated that four species of insects and one of fungi collectively kill 99.6% of the flower buds initiated by a common canopy tree (Wright & Samaniego, 4.3.5). This impressive figure would warrant similar studies for other tree species and within different forest types. One may speculate that at higher latitudes, the demise of the reproductive parts of canopy trees depends more on the action of abiotic factors than that of biotic factors.

Many birds, bats and arboreal mammals represent important agents for the dispersal of seeds and fruits from the canopy (terrestrial mammals often perform this task with fallen fruits in the understorey). Frugivory has been well studied at the Surumoni crane site, where fruit standing crop is actually higher in the mid-canopy than in the upper canopy. Various studies indicated that frugivorous birds were difficult to classify as specialists or generalists with regard to fruit consumption, as fruit choice was dependent on the abundance of alternative fruits, fruit accessibility, and secondary metabolite content (Schaefer *et al.*, 2002, 2003; Winkler & Listabarth, 4.3.4).

Insect-plant relationships often involve ants, which represent a conspicuous and abundant, sometimes dominant, element of many tropical forest canopies (e.g., Tobin, 1991). Therefore, it is hardly surprising that ant-plant relationships have been the subject of a number of detailed studies at different tropical crane sites. Several studies examined the resources on which arboreal ants depend, which often involve extrafloral nectaries (i.e., glands secreting sugars often located on leaves) and honeydew which is produced by colonial homopterans (scale insects, membracids, etc.) attended by ants (Blüthgen *et al.*, 2000; Blüthgen & Fiedler, 2002). This confirms that the predatory role of arboreal ants may often be exaggerated (Tobin, 1991; Davidson, 1997).

Nevertheless, ants may act as predators of other arthropods in the canopy and thus protect plants from herbivores. Conversely, they may rob nectar from flowers without contributing to pollination. One study at the Surumoni crane site evaluated the role of ants as flower visitors, contrasting savannah and forest canopy habitats. It concluded that flowers in the canopy have probably adapted to tolerate ants rather than to repel them, since ants might benefit plants and their flowers by providing protection against herbivores (Jaffé *et al.*, 2003).

Relationships between ants and plants can be rather specialized and subtle. This can involve ants nesting in plant stems, such as *Cecropia* or *Macaranga* (Itino & Itioka, 4.3.3), or the so-called 'ant gardens', which develop from an arboreal ant nest around the roots of one or more epiphytes. Plants benefit from the relationship via nitrogen fixing cyanobacteria that are dispersed by the ants together with the seeds, whereas ants benefit through increased nest stability and nutrition on extrafloral nectaries or seeds. Ant gardens have been well studied at the Surumoni crane site. They are most abundant in the sunniest sectors of the crane plot and their microclimate is affected by El Niño events (Cedeño *et al.*, 1999). Since epiphytes are often limited by the low availability of suitable substrates and nutrients in tropical rainforests, their distribution and growth may be promoted by ant gardens, which include high concentrations of nutrients (Blüthgen *et al.*, 2001).

In conclusion, biotic interactions in the canopy have been studied at the crane sites mainly with respect to herbivory, pollination, frugivory and ant-plant interactions. Other important processes, such as decomposition, are yet to be addressed adequately. Although the majority of decomposition is likely to occur at ground level, there are often important stocks of suspended dead wood in the canopy, particularly in old-growth forests (e.g., Martius & Bandeira, 1998) and epiphytes accumulate relatively large quantities of soil in the canopy (e.g., Nadkarni & Longino, 1990). Further, species difference in physiological and chemical traits of leaves (e.g., leaf longevity, photosynthetic rates and nitrogen levels) may affect decomposition rates (Santiago, 2003). Other notable biotic interactions that have been less well studied include pre-dispersal seed attack, predation and parasitism, the latter likely to represent one of the most important regulatory forces of herbivory.

The canopy microclimate and plant growth

Plant ecophysiology may be studied at the level of the cell, individual leaf, individual branch, individual tree, or the forest community. The challenge is to scale up or down between these different levels of organization, to obtain mechanistic understanding of the functioning and the responses (see next section) of the plant and, ultimately, of the forest (Mulkey *et al.*, 1996b). Since trees are large, integrated organisms rather than mere collections of leaves, the appropriate scale for characterizing physiological behaviours that contribute to their survival, growth and reproductive success is often the entire individual. Further, studies are often performed with the help of environmental growth chambers, where conditions are distant from those experienced *in situ* by canopy leaves of mature trees (Norby *et al.*, 2001). Hence, canopy cranes represent exciting opportunities for studying *in situ* large trees as whole, integrated organisms, and validate measurements obtained with growth chambers (Fig. 106).

At the leaf tissue level, leaves of canopy trees often absorb much more light than is used in photosynthesis. Excess energy must be safely dissipated without damaging the photosynthetic apparatus through various photoprotective mechanisms including photoinhibition, i.e., a reversible reduction in photosynthetic ability (Krause *et al.*, 1995; Thiele *et al.*, 1997; Barth *et al.*, 2001). A study at a crane site found that young leaves are particularly well protected through the presence of xanthophyll pigments (Königer *et al.*, 1995).

Fig. 106. Manuel Lerdau and Heather Throop measuring photosynthesis, transpiration, and isoprene emission at Parque Natural Metropolitano, Panama (photo Marcos Guerra).

At the leaf level, physiological activity varies within the three-dimensional structure of the canopy. Some leaves receive high levels of illumination whilst others are always shaded. Photosynthetic capacity of leaves, measured as the light saturated CO_2 assimilation rates (A_{max}), was found to be a good predictor of the daily net photosynthetic production by individual leaves (Zotz *et al.*, 1995). The photosynthetic capacity of young mature leaves differ among species in relation to their life history traits (e.g., higher for pioneers) and leaf longevity (e.g., higher for short-lived leaves; Mulkey *et al.*, 1995; Zotz & Winter, 1996). Further, leaves produced right before the dry season that experience higher light availability exhibit higher A*max* compared to the leaves produced during the early wet season that experience heavier cloud cover through most of their lives (Kitajima, 4.3.5). Leaves adjust to variation in light availability within and among branches through adjustment of photosynthetic capacity and leaf orientation (J.M. Posada, pers. comm.). Leaf age-related declines in A_{max} reflect development of self-shading above individual leaves, but also reflect species differences in leaf longevity in a manner predicted by a cost-benefit theory of leaf longevity (Kitajima *et al.*, 1997b, 2002). Different rates of leaf metabolism, either along vertical transects or among leaf cohorts, are likely to influence the spatial and temporal distribution of primary consumers within trees. Studies at this scale have rarely been attempted, particularly in tropical closed rainforests where spatial variation in light is often extreme, but could be conveniently performed with canopy cranes.

Leaves in the treetops often suffer severe water stress (Nakashizuka *et al.*, 4.3.3). Thus, seasonal patterns of leaf-level photosynthesis consist of interactions between the suite of ambient environmental conditions and the species-specific sensitivity to the combination of those factors (Murakami & Hiura, 4.2.5), as well as the hydraulic characteristics of the whole plant. High radiation load and rapid loss of water on a sunny day often result in closure of stomata (microscopic pores in the leaf underside), thereby decreasing the uptake of carbon dioxide (Zotz & Winter, 1996). The carbon isotope composition of leaves is generally accepted as an indicator of photosynthetic water use efficiency, but a study at Parque Metropolitano indicated that leaf age significantly modifies this relationship (Terwilliger *et al.*, 2001), warranting further investigation of isotopic signatures in canopy trees. Control of stomatal closure in tropical leaves by rising air temperatures also warrants further investigation with respect to global warming (Clark *et al.*, 2003), as well as the effect of whole-plant hydraulic characteristics to stomatal closure (Meinzer, 2003).

Within a species, photosynthesis (and productivity) of canopy leaves was found to decline with tree age and size due to the increase of hydraulic limitation for broad-leaved temperate trees at the Tomakomai crane (Murakami & Hiura, 4.2.5), as well as for coniferous trees at the Wind River crane (Lewis *et al.*, 2000). Douglas-fir roots absorb water from wetter, deeper portions of the soil depth profile, and then loose water to drier, more superficial portions of the soil profile (Brooks *et al.*, 2002). Large trees also rely on rechargeable stem water storage for a larger fraction of their daily water use than small trees (McDowell *et al.*, 2002). Both of these findings have important implications for adaptation of Douglas-fir to summer drought, for ecosystem-level hydrology, and therefore timber production of watersheds occupied by stands of different ages (Shaw *et al.*, 4.2.6).

No similar evidence on hydraulic limitation due to size and age is found in tropical trees, for which stem-water storage capacity as well as deep roots may contribute to maintenance of water supply to tall trees (Meinzer, 2003). Regulation of water use among taxonomically, phylogenetically and architecturally diverse tree species converge substantially (Meinzer, 2003). On a leaf area basis, the resistance to water flow through the tree was found to be the major determinant of differences in stomatal regulation of transpiration among species. Utilization of water stored in stems and other organs was found to lower the effective resistance of the hydraulic pathway by transiently uncoupling canopy transpiration from water absorption by roots. Reliance on stored water to temporarily replace transpirational losses thus appears to be an important homeostatic mechanism for maintaining photosynthetic gas exchange as hydraulic path length and potential resistance increases with tree size and canopy height (Meinzer *et al.*, 4.3.5).

At the level of the forest community, investigations have focused on competitive interactions between species (Häberle *et al.*, 4.2.2), manipulation of nutrient and water input and their impact on forest growth and productivity (Bredemeier *et al.*, 4.2.4), and on attempts to estimate carbon flux through the whole forest as a function of nitrogen flow through the plants (Murakami & Hiura, 4.2.5). Moreover, it is also essential to examine age-related changes in plant physiology and to perform these studies on mature forest stands (Ryan, 2002). Climate seasonality greatly influences ecophysiological processes in plants. The harshness of the winter at higher latitudes, which often imposes deciduousness, is one of many examples. The contrasting seasonality of water and light availability in tropical rainforests (the rainy season is typically cloudy whilst light is abundant during the dry season) represents another example (Mulkey *et al.*, 1996a; Fig. 107). Thus, any change in climatic variables, such as rising global air temperatures, is likely to affect plant machinery from the level of the cell to the level of the stand. Therefore, *in situ*, non-destructive studies replicated seasonally in the canopy where most gas exchange occurs, appear crucial to understand the proximate effects of global climate change on plants.

Plant physiological responses to a changing environment

Plants are exposed to fluctuations in precipitation, light, temperature, relative humidity, and atmospheric gases. Seasonal variation in temperature, available water and nutrients further influence plant physiological processes such as gas exchange between plants and the atmosphere. In order to evaluate global models of carbon and ozone fluxes, detailed information on temporal or quantitative differences in production and consumption of these gases is needed. Studies on photosynthesis and transpiration of forest trees are important for understanding the role of forests in regional and global hydrological and carbon budgets. Collecting data during both dry and wet seasons provides further parameters for these budgets. Most studies have been performed with saplings, shrubs and low trees. Only recently has it been possible to measure these parameters directly on mature canopy trees under natural conditions.

A sound understanding of global hydrological and carbon budgets starts with assessing the local energy budget of the canopy, as was performed at the Surumoni crane. During daytime solar radiation on the canopy is converted into fluxes of sensible and latent heat. During the night, heat is lost through radiation, and sensible as well as latent heat, via condensation, contribute to the energy budget of the canopy. Some heat also flows from the ground layer. Accordingly, temperature fluctuates by almost 10°C in the upper canopy and only slightly near the ground (Anhuf & Rollenbeck, 2001; Szarzynski & Anhuf, 2001). About 45% of the annual precipitation is transpired. Remarkably, the lower portion of transpiration loss measured and extrapolated in this study sheds new light on extant climatic models (Winkler & Listabarth, 4.3.4).

Fig. 107. Steve Paton surveying meteorological equipment at the top of the San Lorenzo crane, Panama (photo Marcos Guerra).

The next step is to evaluate local budgets of carbon, as is being attempted at the Wind River, Australian and Lambir Hills crane sites. The old-growth Wind River site is considered to be in the long-term a slight sink of carbon dioxide (Shaw *et al.*, 4.2.6). At the Australian crane site, Cyclone Rona altered the micro- and meso-climate of the area dramatically by removing almost all foliage and bringing the canopy boundary layer almost to ground level. A team of researchers are studying how carbon, heat and water fluxes change over time as the canopy recovers from the cyclone. They are also trying to identify the main species responsible for shifting the carbon balance (Stork & Cermak, 4.3.1). At the Lambir Hills site, the emphasis is on refining carbon dynamics by paying attention to the mosaic of different regeneration stages. The decomposition of fallen trees causes emission of carbon into the atmosphere, while growing young trees absorb carbon. Such heterogeneity detected by analyzing the three-dimensional structure of the forest and its dynamics will be combined with analyses of carbon flux measurements. In addition, researchers at Lambir Hills also consider the influence of global meteorological events such as El Niño-Southern Oscillation (ENSO), which affects tropical forest climates and, hence, their carbon dynamics (Nakashizuka *et al.*, 4.3.3).

Eventually, the response of mature trees to elevated levels of CO_2 must be studied *in situ*. Körner and Würth (1996) experimented with small, light-weight cups mounted on the lower side of rigid leaves at the top of tall trees in Panama. These cups were supplied with CO_2-enriched air derived from a low-technology air mixing device utilizing CO_2 generated by decomposition and respiration of soil organisms at the forest floor. Total non-structural carbohydrates (TNC) reached a new steady state concentration after less than 4 days of exposure to twice ambient CO_2 concentration. Against expectation, all four tree species investigated accumulated significant amounts of TNC (+ 41 to + 61%) under elevated CO_2. TNC accumulation reflects a tissue response specific to elevated CO_2, presumably unrelated to sink limitations. Thus, leaves of tropical forests will most likely contain more non-structural carbohydrates in a CO_2-rich world (Würth *et al.*, 1998).

Somewhat contrasting results were found at the same site with small open-top chambers that enclosed branchlets of a canopy tree in Panama (Fig. 108). Elevated concentrations of CO_2 increased photosynthetic rates and decreased stomatal openness, but did not influence the growth of leaf area per chamber, the production of flower buds and fruits, nor the concentration of non-structural carbohydrates within leaves. However, elevated levels of CO_2 did increase the concentration of non-structural carbohydrates in woody stem tissue and the ratio of leaf area to total biomass of branchlets, suggesting complex changes of growth and allocation patterns of mature trees in a CO_2-rich world (Lovelock *et al.*, 1999).

While both CO_2 and light are resources for photosynthesis, plants respond differently to changes in their availability. Heavy tropical cloud cover can reduce irradiance and limit photosynthesis even for exposed canopy leaves (Mulkey *et al.*, 1996a). The implications for global carbon uptake are significant if carbon uptake by tropical trees is limited by year-to-year variation in cloud cover and irradiance. Graham *et al.* (2003) installed high-intensity lamps above the Parque Natural Metropolitano forest canopy and supplemented light whenever cloud cover reduced photosynthetic photon flux density. During a representative cloudy day, photosynthesis increased with augmented light from the lamps for randomly chosen leaves and increased daily net carbon gain by an average of 18.4%. Unlike the response to elevated to CO_2, higher photosynthetic productivity in response to greater light availability translated to increased vegetative and reproductive growth without accumulation of total non-structural carbohydrates. Year-to-year climate variability may thus influence net CO_2 uptake and growth through variation in solar irradiance caused by clouds and atmospheric particulates (Graham *et al.*, 2003).

Large scale experiments, such as the web-FACE (Free Air CO_2 Enrichment) facility developed at the Basel crane, further facilitate the evaluation of the response of mature trees to elevated levels of CO_2 *in situ*. In this experiment, considerable intraspecific and interspecific variation in the response to elevated levels of CO_2 occurred. For example, in broad-leaved trees leaf stomatal conductance was reduced by circa 15% on average. None of the conifers showed a significant difference. Consistent with these results, sap flux data for the same year suggest a reduction of transpiration by almost 10%. Conversely, tree growth showed no clear trend up to the present. The feeding behaviour of a generalist herbivore, *Lymantria dispar*, yielded quite contrasting responses to altered food quality. The latter result highlights once more the importance of a multi-species approach to study biotic reactions to global change (Körner & Zotz, 4.2.1).

Fig. 108. Catherine Lovelock and Aurelio Virgo monitoring CO_2 levels in small open-top chambers at Parque Natural Metropolitano, Panama (photo Marcos Guerra).

Other significant studies of gas exchange with canopy cranes concern ozone, isoprene and reactive nitrogen. At the Kranzberg forest, research has concentrated on the regulation of carbon allocation with ozone exposure and determination of eco-physiological threshold levels in ozone sensitivity of mature forest trees. The results suggest that beech leaves developed visible symptoms and accelerated autumnal senescence due to the elevated ozone regime whereas spruce appeared to be less susceptible (Nunn *et al.*, 2002). An important finding is that responses from containerised young plants cannot be extrapolated to the performance of adult trees under ozone stress (Häberle *et al.*, 4.2.2).

Isoprene is a volatile hydrocarbon emitted by many plants. It quickly breaks down in the atmosphere to form hydroxyl ions that affect atmospheric chemistry. Keller & Lerdau (1999) showed that calculations describing emission controls of isoprene for temperate plants are inappropriate for tropical trees. Whereas temperate plants show isoprene emissions that saturate at approximately one half of full sun intensity, that from tropical trees does not show light saturation. In addition, isoprene emission from tropical trees saturates at a higher temperature than does emission from temperate trees. These results mean that previous models of isoprene emissions from tropical forests may have underestimated emissions by 20%-50%. In other words, tropical forests play a much larger role in global atmospheric chemistry than previously supposed, especially in controlling the dynamics of ozone and methane in the lower atmosphere (Lerdau, 4.3.5).

Current atmospheric models concentrate on soil emission rates of reactive nitrogen (NO_x) as biogenic input to tropospheric chemistry. However, plants absorb nitrous oxide (NO_2) through their leaves, and this uptake has been ignored in current atmospheric models. Sparks *et al.* (2001) demonstrated interspecific differences in the leaf level uptake rates of nitrous oxide and found that these rates were sensitive to stomatal conductance, the amount of photosynthetic enzymes in the leaf, and the concentration of NO_2 in the atmosphere. Interestingly, leaves appear to have the ability to both take up and emit reactive nitrogen depending on the concentration of NO_2 in the surrounding atmosphere. A calculation scaled to the entire canopy suggests that soil NO_2 emission rates to the atmosphere are modified by ~ ±19% by the overlying canopy depending on the ambient NO_2 concentrations. As humans release more reactive nitrogen in the atmosphere through pollution and biomass burning, understanding nitrogen cycling in forests will help us predict the sustainability of natural, urban and agricultural ecosystems worldwide (Sparks, 4.3.5).

Long term changes in canopy processes are far from being well understood (Ryan, 2002). Permanent canopy access with canopy cranes can greatly improve long-term measurements. For example, the continuous records of vertical microclimate being obtained at the Wind River crane represent the only such data available for old-growth coniferous forests (Shaw *et al.*, 4.2.6). Körner and Zotz (4.2.1) emphasize that knowledge of short-term reactions to elevated CO_2 may have little bearing on long-term responses and that it is essential that experiments such as those developed in Basel operate for several years. Further, the responses of primary consumers to altered leaves, wood, seeds or fruits may be complex and subtle, and may vary among different herbivore guilds (Whittaker, 1999). These responses are also likely to depend on subtle biotic interactions, such as predation and parasitism, which need to be studied *in situ*. There are also mounting concerns that the effects of rising air temperature and levels of tropospheric ozone may be more damaging to plants and animals than rising levels of CO_2 per se (e.g., Dury *et al.*, 1998; Percy *et al.*, 2002).

Overall, the results achieved collectively by the crane network constitute an impressive contribution to canopy science in general, in all major fields reviewed above. Many crane sites have just initiated their research programmes and their research productivity is to increase dramatically. In the next and concluding chapter of this book, we explore promising avenues for collaboration among crane sites in the larger context of forest canopy research.

6. Conclusion: The future of the International Canopy Crane Network

6

Conclusion: The future of the International Canopy Crane Network

Yves Basset, S. Joseph Wright & Nigel E. Stork

In this concluding chapter, we discuss promising topics of research that could be developed as collaborative projects among several sites within the International Canopy Crane Network (ICCN). More generally, we review factors that could improve the efficiency and productivity of the network. As reviewed in the preceding chapter, canopy cranes have been instrumental for many studies performed at the levels of the leaf, tree or forest stand. Comparisons among crane sites may help to develop theories of general relevance and to reduce pseudoreplication at the tree or stand level. The important data that individual crane sites can provide to the scientific community concern issues such as how biodiversity is maintained locally, which biotic interactions appear primordial to maintain the integrity of the forest ecosystem and its functioning, how plant metabolism realistically operates at the top of the canopy, and how plants and primary consumers will respond to elevated air temperature and increased levels of CO_2 and pollutants in the atmosphere. All of these represent key parameters needed to improve knowledge of environmental threats identified in international conventions (see Chapter 2). A comparative and collaborative approach within the network could greatly enhance the flow of information relevant to these parameters.

The Global Canopy Programme (GCP, Chapter 2) has already identified several research topics related to forest canopies that could be easily implemented at different sites. These include measurement and comparison of the canopy structure; insect stratification (Häberle *et al.*, 4.2.2; Stork & Cermak, 4.3.1; Basset & Barrios, 4.3.5); comparison of herbivory at the stand level; and the effects of bird predation on herbivory (Van Bael, 4.3.5, see also Shaw, 2002). We will discuss below these and other projects related to the four main themes of research developed within the network (see preceding chapter): canopy structure, maintenance of biodiversity, plant ecophysiology and the response of plants to a changing climate. However, we feel compelled to emphasize that this research must consider the 'canopy' as part of the whole forest ecosystem and not as an isolated habitat.

Relationships between the forest canopy and the forest ecosystem

Canopy science emphasizes the importance of the canopy, not that the canopy is distinct from the rest of the forest ecosystem. Canopy processes must be linked to other forest components for a sound understanding of the functioning of the forest ecosystem. For example, studies to quantify herbivory and frass (faeces) fall in conjunction with decomposition on the forest floor are likely to enable a better mapping of nutrient cycling than if these components are studied in isolation (Lowman, 2001). In particular, defoliation may influence positively decomposition on the forest floor by increasing carbon, nitrogen, and phosphorus available to the decomposer community. This may occur via the fall of insect frass, greenfall (leaf fragments dropped by defoliators), prematurely-abscised leaves, and rainfall which collects dissolved insect frass and modified leachate from damaged foliage (Rinker *et al.*, 2001). Indeed, Schowalter and Sabin (1991) reported increases in litter arthropod diversity and abundance following defoliation of saplings.

Moffett (2002) rightly remarks that it is unlikely that a forest will harbour a significant canopy flora and fauna in isolation of the ground and soil biota. In fact, levels of biodiversity above and below ground are often correlated (Hooper *et al.*, 2000). Perhaps the necessity to study the canopy in conjunction with other forest habitats is best illustrated in entomological studies. Many insect herbivores, such as some leaf beetles and weevils, feed on roots as larvae and later migrate into the canopy to feed as adults on leaves (Fig. 109). In inundation forests in Brazil, some soil and leaf litter insects migrate to the canopy when the forests are flooded (Adis, 1997). 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). Surprisingly little analysis of the use of different strata (soil, leaf litter, tree trunks, canopy) by different insects and their life stages has been carried out in European temperate forests. Further, comparison between the litter and canopy faunas may emphasize specific adaptations of arboreal invertebrates which may be important from a conservation viewpoint. Nevertheless, multi-method, multi-habitat studies are essential if statements are to be made about the overall arthropod diversity of forests: the assumption, tacit since Erwin & Scott's (1980) article, that the species richness of the forest is totally canopy-dominated is certainly not true. Thus, sound understanding of biotic relationships in the canopy may require baseline knowledge of the entire rainforest ecosystem, an additional challenge in itself (Basset *et al.*, 2003c).

Canopy structure

At present, measurement of canopy structure, such as those obtained with remote sensing (Lefsky *et al.*, 2002), are mostly used for descriptive purposes. In fact, these measurements should be at the core of multidisciplinary studies, since mapping canopy structure is equivalent to mapping forest productivity. A description of canopy structure can also be used to study the finer distribution of organisms, or variation in plant ecophysiological processes. One may imagine studying the relationships between leaf area density or woody structures and the vertical flight distribution of insects, for example. In this case the priority of the entomological protocol would be on spatial replication, with the use of numerous, small collection devices placed throughout the vertical profile of the forest. Such a replicated study at different crane sites would be able to compare patterns of insect stratification among different forest types and canopy structures. Forest structure measurements could also be crucial in ecophysiological studies concerned with the scaling up of processes from the leaf to the forest stand levels. Possibly, studies of canopy structure could evaluate the intriguing 'inversion surface' (*surface d'inversion*) of Oldeman (1974) in tropical rainforests. It is surprising that the biological significance of this concept has never been assessed. Briefly, this is the zone where water becomes the limiting factor for tree growth and where photosynthesis is performed with a minimum of transpiration. It roughly corresponds to the first branching of dominant trees (Oldeman, 1974). In French Guiana, Sterck and Bongers (2001) recently showed that regressions of plant traits against tree height were linear with study trees below 25 m in height, and become non-linear with taller trees. Light availability was not considered to be an important selection force acting on architectural changes with tree height. Forest structure measurements might help to describe such branching patterns, and, further, these data might conveniently be related to ecophysiological measurements with the help of canopy cranes.

Biodiversity and biotic interactions

With regard to the international conventions discussed in Chapter 2, one may remark that estimates of rates of carbon sequestration, or of gaseous pollutants in the atmosphere, have notably improved since the 1990's, whereas estimates of rates of species loss remain vague and controversial. In part, this may have resulted from funding being channeled towards studies of global change rather than towards biodiversity studies. The magnitude of the effort necessary for adequate surveys of biodiversity and implementation of conservation policies may also be overwhelming to many organizations, institutions and individuals (see Chapter 2; Fig. 110).

In a sense, it is puzzling to observe that scientists have managed to focus public attention on complex problems of gas exchange and nutrient cycling (involving many primary reactions not visible with the bare eye), such as the 'ozone hole', whereas they have largely failed to focus public attention on the fundamental and unanswered question of how many species inhabit Earth, what proportion of these have been named and described, and how widely they are distributed. One of the reasons accounting for this state of affairs may be that global cycles of gases and nutrients can now be well explained. In contrast, the local maintenance of biodiversity is far from being reasonably captured. For example, knowledge of local food-webs, especially in the tropics, is still rudimentary (e.g., Godfray *et al.*, 1999). In short, the inability of the scientific community to document species diversity, and hence its changes including decline, is hugely detrimental to the credibility of the conservation movement (e.g., Mann, 1991).

Fig. 109. This undescribed weevil species of *Exophthalmus* is relatively common in the canopy of the San Lorenzo forest, where it feeds on the foliage of several tree species. However, its larvae are unknown and most probably feed on roots in the soil (photo Marcos Guerra).

Fig. 110. Countless invertebrates in the canopy of tropical rainforests are unknown to science yet. The biology of many others is hardly known. For example, the bug *Macrotingis zeteki* (Tingidae) was described in 1950 from a single male collected in Barro Colorado Island in Panama, possibly one of the most thoroughly studied location in the tropics. This species was never found again until collections in 1998 in the canopy of the San Lorenzo forest, on mature trees of *Pourouma bicolor*, revealed this species to be extremely common there. Both larvae and adults feed on mature trees and were never collected on conspecific saplings in the understorey (photo Marcos Guerra).

Promoting local studies of food-webs may represent one way to improve knowledge about the maintenance of biodiversity (the study of regional and historical factors represents another). There have been repeated pleas to initiate large-scale inventories of invertebrates, particularly in the tropics (e.g., Janzen, 1993; Stork, 1994; Godfray *et al.*, 1999; Basset, 2001a). Smaller inventories, but with convenient access to all levels in the forest, such as within the perimeters of canopy cranes, may be easier to implement. Such inventories could be coupled with detailed studies of ecophysiology and energy budgets, and efficiently compared among different biogeographical regions (crane sites). There is nothing really new with this methodology (e.g., Morawetz, 1998), but in practice, it has yet to be implemented. The network could facilitate this approach, by testing different protocols at different crane sites (in their area of excellence for example) and then implement them sequentially at each site concerned.

Many studies within the network are concerned with the vertical distribution of organisms. Many reported that the occurrence of organisms along vertical transects is linked to specific abiotic and biotic conditions. One interesting question is to know whether rising air temperatures (with concomitant changes in plant metabolism) may alter this equilibrium and result in further species extinction. For example, rising temperature may cause spatial shifts of arthropod species, particularly sedentary ones, that may threaten their survival (e.g., specialised species of the upper canopy may move down, to cooler levels where their resources may be less abundant). These effects are likely to be of greatest magnitude in tall, closed tropical rainforests, where biodiversity is also greatest.

Lawler *et al.* (2001) considered several ways in which studies of biodiversity could best address conservation-related problems. The two following items appear to be of particular relevance to the study of forest canopies: (a) research that builds tools for predicting which sort of ecosystem failures are likely with the loss of particular species or functional group of species; and (b) the role of exotic species. Research into item (a) could be promoted by studying the effects of canopy opening by logging. These effects have not been well investigated to date. For example, specialised insect herbivores of the upper canopy are unlikely to fare well in the understorey since forest gaps typically include different plant species (pioneers) than are present in the mature canopy (shade-tolerant species). Taxa less tied to resources occurring specifically in the upper canopy, such as dung beetles, do not appear to suffer much from canopy loss and survive well in the understorey of disturbed forests (Davis & Sutton, 1998). Some crane sites could be used as controls of undisturbed canopy, in comparison to natural and anthropogenic forest gaps. With regard to (b) an important question would be to evaluate the ecological consequences of a canopy constituted mostly of exotic species, such as in certain plantations. Ideally this would include establishing a crane in a plantation not far away from a control crane-site, but perhaps manipulative experiments with smaller plants, such as epiphytes, may also be possible.

Studies of biotic interactions in the forest canopy should also move towards assessing the influence of biodiversity (species richness) on forest productivity and functioning. This might be best investigated by coupling studies of herbivory, predation, parasitism and plant productivity, and comparing patterns among crane sites.

Plant ecophysiology and the changing climate

Beside the effects of rising pollutants in the atmosphere, one worrying aspect of global climate change is the increase in air temperature per se. Rising air temperatures are likely to involve cascading effects starting from the level of the leaf (e.g., Clark *et al.*, 2003), continuing at the level of primary consumers (e.g., Percy *et al.*, 2002), and culminating at the level of ecosystems (see Chapter 2). The hypothesis that the control of stomatal closure will be greatly affected in tropical trees by rising air temperatures warrants further investigations, since this affects the likelihood that tropical forests act as either sources or sinks of carbon (Clark *et al.*, 2003). Therefore, studies related to this topic and performed in different forest types (temperate, tropical) and at different ambient temperatures would be instructive.

More generally, the above remark emphasizes the crucial effect of changes in limiting resources for plants. Another example is the negative effects of increased nitrogen deposition. Anthropogenic burning of fossil fuels and addition of fertilizers have more than doubled the nitrogen flux through natural ecosystems. The problem is particularly acute in densely populated and heavily industrialized areas, and is largely limited to higher latitudes where nitrogen limits most natural systems (Galloway & Cowling, 2002). With nitrogen limitation removed, species must operate under novel constraints such as inadequate phosphorus and water supplies. How are the performance of organisms and the operation of larger ecological processes affected by rapid changes in their chemical environment for which they have no evolutionary background and to which they are not adapted (Vitousek *et al.*, 1997b)? The ICCN could tackle stepwise these complex problems by sharing investigations on particular limiting resources for plants among different crane sites.

Körner & Zotz (4.2.1) have stressed the importance to adopt a multi-species approach to study biotic reactions to global change. Natural forest canopies accessible from canopy cranes represent an ideal arena for such studies, in contrast to artificial systems such as, for example, the Ecotron, an integrated series of environmental chambers in which physical conditions are controlled (Lawton *et al.*, 1993). These artificial systems can include only few species and appear very simplified in comparison with natural systems. The challenge, for the ICCN, is to develop several crane sites fully dedicated to the study of global change (such as Basel, 4.2.1 and Kranzberg, 4.2.2), and to implement similar protocols at these sites.

Bridging the gap between research and policy

One of the challenges for the ICCN and canopy researchers in general is to make their research more available and relevant to policy makers who are attempting to change the way that we manage human impacts on the environment. Bridging the gap between research and policy is a problem shared by all scientists and policy makers and yet some have been more effective than others. In his address at the second International Canopy Conference in Florida, Chief Scientist of the International Union for Conservation of Nature and Natural Resources (IUCN), Jeff McNeely identified the differences between policy makers and researchers and suggested ways in which canopy research could become more relevant to policy (McNeely, 1998, see also Stork, 2001). For example, he suggested that if disturbance of forests was a critical issue for policy makers then surely we should be placing cranes in heavily disturbed or secondary forests. Fortunately, we now have a crane in a heavily disturbed forest in Queensland, Australia, which was hit by a category three cyclone within three months of the crane being installed. Research from this crane is showing how rapidly forests recover from such events. McNeely listed some of the critical issues where canopy science could and should have an impact, such as sustainable use, climate change, extinction rates, ecosystem integrity, interactions among species and disturbance. The next important phase for canopy science though has begun and that is the start of a dialogue between research and policy makers. A first result of this is the inclusion of a section on the need for forest canopy science in the recommendations of the latest Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA) report to the Convention on Biological Diversity (SBSTTA Recommendations VII/6 on Forest Biological Diversity, to COP6; see http://www.biodiv.org/doc/meetings/cop/cop-06/other/cop-06-pr-end-en.pdf). The Cairns Declaration on Forest Canopy Research (http://www.biodiv.org/doc/ref/for-cairns-canopy-en.pdf) which resulted from a subsidiary meeting of the third international canopy conference in Cairns, 2002, is also an attempt to bridge the gap.

Improving the International Canopy Crane Network

The efficiency of the present network could be greatly improved by taking a series of different steps, which may start by improving the crane sites themselves.

1) Improve canopy access at each crane site. This is needed to appreciate the representativeness of the data obtained and to reduce pseudoreplication. Two crane sites include scaffoldings, towers or walkways (Kranzberg, 4.2.2; Lambir Hills, 4.3.3) and one other is movable on rails (Leipzig, 4.2.3; as was Surumoni, now defunct). Canopy access can be expanded at crane sites by creating a web of platforms accessed by the single rope technique, walkways and other techniques, as discussed in Chapter 3.

2) Improve the quality of long-term research at each crane site. To this end, combining local expertise is important, such as, for example, the need to combine micrometeorology and plant ecophysiology at flux sites to assess the effects of global change on ecosystem functioning (Buchmann, 2002). Development of long-term research goals is crucial as it may increase the value of crane sites which may ultimately be viewed as Long-Term Ecological Research (LTER) sites (see Nakashizuka & Stork, 2002).

Fig. 111. Jerry Franklin talking to a group during an 'educational lift' at the Wind River crane facility (photo Mark Creighton).

3) Augment educational activities at each crane site. These activities should include university classes and students, teachers, policy makers, personnel of natural resource agencies, legislators, media and lay persons. Although all crane sites undertake limited educational activities, only one site includes them as a routine activity (Wind River, 4.2.6, Fig. 111). Canopy tourism ventures are rapidly growing such as those in Queensland, Australia, and these offer the opportunity to promote the relevance of the ICCN and canopy research in general to a wider audience.

4) Adopt joint sampling protocols and perform a few key projects at each and every crane site. The use of a standard methodology would ensure that data points are truly comparable among sites.

5) Improve relationships with other scientific networks. The ICCN currently enjoys good relationships with other networks, such as GCP, ICAN and FLUXNET (see Chapter 2), but these links should be nurtured and expanded to other networks related to forest research. This can be accomplished via common research projects and the organization of international meetings.

6) Increase the number of crane sites and improve the representativeness of the network. Other crane sites should be implemented in different forest types (boreal forests, plantations, dry tropical forests, etc.), to improve both the overall representativeness of the network and its intrinsic value. The establishment of new crane sites evidently depends on many factors, but research needs should be carefully considered. There are currently no crane sites in Africa or in montane forests. With regard to biodiversity studies, currently only three crane sites are located in the 25 'biodiversity hotspots' (regions that harbour a great diversity of endemic species and, at the same time, have been significantly impacted and altered by human activities) recognized by Myers *et al.* (2000). Two are in Mesoamerica (two crane sites in Panama) and one in Wallacea (Lambir Hills).

7) Augment the exchange of researchers, including students, among crane sites. Forests represent complex ecosystems in which it is difficult to control all putative factors in manipulative experiments. Often, the interpretation of results is hampered by lack of expertise in all of these putative factors. Locally, it is often difficult to pool all the necessary expertise to obtain a better interpretation of experiments performed. Sharing expertise across the network would greatly help in this regard. Further, more ambitious studies could be implemented stepwise with an increased mobility of scientists among crane sites.

Conclusions

Each canopy crane site has produced or promises to produce substantial research that sheds new light on complex ecological processes occurring in forests and forest canopies. The International Canopy Crane Network promises to be a vehicle to tackle more ambitious studies, and to test the general relevance of new hypotheses. The network could be improved and expanded as outlined above. Improving the network and implementing new collaborative studies is going to be difficult without substantial help from donors and sponsors. However, one approach to initiate rapidly small-scale research projects would be collaborative ventures where several projects are agreed upon and performed at different crane sites by pooling resources. We hope that this booklet will help to focus discussion on these research opportunities. We look forward to a renewed interest in the study of one of the most complex systems on Earth, the forest canopies and their inhabitants.

Fig. 112. A panorama of the canopy at the Australian Canopy Crane Research Facility (photo Liz Poon).

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This publication describes the development and the achievements of a worldwide network of construction cranes, dedicated to the scientific study of one of the most important habitats on Earth: forest canopies. The International Canopy Crane Network includes 11 crane facilities, including temperate sites in Asia, Europe and North America, and both seasonal and evergreen tropical sites in Australasia and Central America. Key scientific findings at each crane facility are summarised and discussed under the broad headings of canopy structure, plant phenology, local maintenance of biodiversity, biotic interactions, the canopy microclimate and plant growth, and plant physiological responses to a changing environment.