Ecology for tropical forest management

DOUGLAS SHEIL and MIRIAM VAN HEIST

Center for International Forestry Research, P.O. Box 6596, JKPWB, Jakarta 10065, Indonesia
Email: d.sheil@cgiar.org

SUMMARY

There is a considerable body of ecological information relevant to the management of tropical forests, but in practice, little of this is used. We demonstrate how ecology helps us understand forests and forest change and argue an urgent need for a wider appreciation and utilisation of current knowledge. We illustrate how forest managers must take a holistic, long-term landscape-level view, and how change in itself is inevitable. We start by considering familiar concerns relating to silviculture and canopy disturbance. From this basis, we move into the neglected biology of tree pollination and seed dispersal and the risks associated with animal loss. We identify the increasing threats from fire, exotic species, and habitat fragmentation. Finally, we consider the difficult balance between timber production and conservation related values. We then suggest how our ecological overview, with its mixture of common sense and more subtle insights, might be translated into beneficial actions and conclude that considerable progress is attainable, but requires collaboration between ecologists and forest managers. Initiatives that seek to reform forest practices in the tropics require a sound ecological basis to better address the many challenges facing modern forestry in these regions – such a basis is, in large part, already available for wider use. We provide some illustrations as to how management may be improved. Fundamental to these is the recognition that ecological knowledge is crucial to forestry but currently too often ignored, and that considerable and rapid progress is possible if ecologists, foresters, and others can find ways to work together and address this directly.

Keywords: biodiversity, conservation, education, landscape ecology, rainforest, reduced impact logging, tropical silviculture.

INTRODUCTION

Ecology provides the foundation for forest management. However, the relationship between management and ecology can sometimes appear obscure. Lowe (1995) for example recently claimed that ecology 'has contributed little of practical use to tropical silviculture'. We disagree (e.g. see Sheil and Hawthorne 1995), but the relationship between forestry and ecology can certainly be improved. The prominence of 'ecological issues' and ecologists in the mounting opposition to forest harvesting in many parts of the world has lead to a view that ecology is somehow 'anti-production', and has been symptomatic of deterioration in the relationship between biological scientists and forest managers. At the same time, there is an ever growing pressure on foresters to review their practice and adapt to changing demands. We strongly believe that ecology is fundamental to progress, and that a cooperation between ecologists and foresters is needed. Here we are particularly addressing those concerned with the practical aspects and implications of tropical forest management.

Tropical ecologists, seeking research funding, frequently emphasize how little is known about tropical forests. This can be misinterpreted – 'lack of knowledge' does not excuse the prevalence of poor practices, and enough is known to make improvements. There is a considerable body of potentially useful information. A problem remains that many of those involved in the management of tropical forests have limited access to such ecological knowledge and insights, or indeed lack the means to translate such information into real actions. Recognizing this concern is a first step in developing remedial activities, and it is the purpose of this article to show that this goal is important and realistic.

It would be ideal if we could simply present ecological facts and the recommendations they inspire. However, applications will always depend on many factors and while we do not examine policy, economics, regulations, enforcement or management-capacity here, we recognize the demanding context in which most managers operate. What we provide are insights that demonstrate how ecology helps us understand forests and their behaviour. Stakeholders must decide what changes are acceptable or preferred. We emphasize the broad range of factors requiring forest managers to take a holistic, long-term landscape-level view. An in-depth account of everything is impossible in this short note and some crucial aspects (e.g. soil ecology and genetics) cannot be considered. Nor are we able to discuss important related themes such as further research, indigenous knowledge and the role of local communities. Our intention then is to emphasize the very practical need for ecology by outlining a range of topics, and discussing some principles and recommendations.

THE ECOLOGY OF SILVICULTURE

Harvesting as disturbance

Disturbance as an ecological term is generally used for any rapid release or reallocation of community resources such as light, water or soil nutrients (e.g. Clark 1990, Glenn-Lewin and van der Maarel 1992, Roberts and Gilliam 1995). Much ecological work has examined the effects of *disturbance* in plant communities. Intensity, scale and frequency of disturbances are thought to be key aspects and can be readily interpreted in harvesting terms.

A useful distinction can be made between *intrinsic* and *extrinsic* disturbances. *Intrinsic* disturbances are inherent to all forest formations, i.e. tree falls, whereas logging is an *extrinsic* disturbance. It is sometimes suggested that if processes of harvesting would create disturbance patterns similar in size and intensity to such *intrinsic* processes, this would cause least change (e.g. Skorupa and Kasenene 1984). However, 'replicating natural processes' would require that only dead or vulnerable trees were impacted, whereas harvesting is always an addition to intrinsic processes. Change after harvesting is therefore inevitable and 'naturalness', and any of the values uniquely associated with it (e.g. wilderness value), cannot be sustained. The responsibility of managers is rather to minimise deleterious changes while maintaining future stand productivity and management options.

In forestry, the *intensity* of harvesting generally determines the reduction in basal area (Johns 1988, Skorupa 1988, Favrichon 1998), which is closely correlated to changes in canopy cover and thus understorey light. As foresters know, and ecologists have examined, increased illumination affects tree growth and regeneration, but responses can be greatly influenced by species, and context (Silva *et al.* 1996, Whitmore and Brown 1996). *Guilds* provide convenient classes of species responses to such changes in illumination. Hawthorne's (1996) system is particularly useful as it is explicitly related to silvicultural characteristics (Table 1). It is at this level, in combination with knowledge of regeneration requirements (see below), that foresters have modified forest composition and productivity through the control of canopy opening.

Foresters typically distinguish between *monocyclic* and *polycyclic* harvesting systems where ecologists might emphasize the types of regeneration involved (e.g. Swaine 1996). In a monocyclic system, all the standing timber in a compartment is cut at one time. Future harvests depend on regeneration from seeds in the soil prior to cutting [the seed-bank, dominated by pioneer species] - or from seeds arriving from outside [the 'seed-rain'], often depending on animals for dispersal, or remnant mother trees. Such seed rain is also important in the recovery of open and damaged areas such as log–collection areas (Hladik and Miquel 1990).

On the other hand, in a highly selective or polycyclic system only a limited proportion of stems, usually the largest, are cut. The same compartment will be revisited after the younger trees [the 'advanced regeneration' or 'seedling bank'] that survived the harvesting process have grown sufficiently (Hartshorn 1978, Clark 1994, Whitmore and Brown 1996, Brown and Jennings 1998). This advanced regeneration is especially important for many timber species with seeds that are only briefly viable and germinate rapidly under natural circumstances (Ng 1983, Vazquez-Yanes and Orozco-Segovia 1993). An additional form of regeneration is presented by species that coppice. Such regeneration is probably much more common than generally recognized, particularly amongst small stems, and is particularly important in the ecology of areas of the world that suffer intermittent storm damage (e.g. Bellingham *et al.* 1994). Although it has not attracted much attention in tropical silviculture (aside from teak, *Tectona grandis*) some timber species do coppice well (e.g. *Milicia*).

Canopy gaps have dominated ecological ideas on rainforest dynamics for much of the last decade and more (e.g. Brokaw 1987, Denslow 1987, Brandani *et al.* 1988). It now appears that in most circumstances the composition and richness of natural forests is little influenced by the nature of natural gaps which are generally small and quickly filled by advanced regeneration (e.g. Brown and Jennings 1998, Hubbell *et al.* 1999). However, in harvested forest, gaps are generally larger and in higher densities than in unlogged forest, and advanced regeneration is often destroyed. In such cases pioneer vegetation, germinating from seed, can dominate initial regrowth (Swaine and Hall 1983, Denslow *et al.* 1990, Silva *et al.* 1996, Pelissier *et al.* 1998). According to an extensive review by Hawthorne et al. (*in*

TABLE 1 *Some guild definitions, based on Hawthorne (1995)*

		Seedlings found	
		Almost exclusively in non deep-shade areas	In shaded (gap free forest)
Adults found	Almost exclusively in non deep-shade areas	*Pioneers* Seedlings develop most profusely in open areas and canopy gaps. Seedlings may be found in shade but seldom survive long in such locations. Includes many low light-timber species	*(Cryptic Pioneers)*
	In shaded (gap free forest)	*Non Pioneer Light Demanders (NPLDS)* Seedlings may be found under closed canopy, but illumination is needed for further development. Includes many high value (medium density) timber species	*Shade bearers* All sizes >5cm dbh can be found under closed canopy, and will persist in these conditions. Generally very high-density timbers.

press) a few broad generalizations are available: NPLDs (see Table 1) generally benefit from some canopy opening, while shade-bearers generally decline in all canopy-opening processes and regeneration far from undisturbed forest suffers. Loading bays and logging roads favour pioneers over NPLDs, but skid trails and felled tree gaps support a higher concentration of NPLDs. Areas close to intact forest usually recover more quickly from any clearance. The maintenance of scattered 'reserves' within a managed forest is justified as a practical precaution.

Excessive canopy opening can lead to regeneration problems especially in exposed conditions where soils dry out rapidly and nutrient loss through run-off is common. Herbaceous vegetation associated with severe opening can interfere with regeneration and impedes recovery (Epp 1987, Hawthorne 1993, 1994), e.g. *Pennisetum* (Kasenene and Murphy 1991) and *Imperata* grass in Uganda, and *Chromolaena* in Ghana (Hawthorne 1993, 1994, 1996). Areas of low regrowth attract ground herbivores which may also damage regrowth and maintain open areas (Laws *et al.* 1975, Struhsaker *et al.* 1996).

Tree reproduction and survival

Thus far, we have considered familiar silvicultural issues; we now extend our considerations to tree reproduction, a comparatively neglected topic. Trees do not generally have the ability to flower and set seed until they have reached some minimum size, and greatest fecundity is normally found in the largest stems (Appanah and Mohd-Rasol 1990, Chapman and Chapman 1997, Thomas 1996). Plumptre (1995) found that the seedling densities of four canopy species, including *Khaya anthotheca*, were strongly dependent on the abundance of potential parent trees (diameter > 50cm). Thus, removal of larger stems can impair subsequent regeneration due to loss of fruit and seed sources. The use of a 'minimum felling size' as sole silvicultural control is inadequate to protect seed production.

Even when potential parent trees are present, reproduction processes may require further protection. The role of many animal species in pollination and seed dispersal is underlined by research. Though a complex body of ecological knowledge exists on these roles, it is often species specific and thus not readily generalized (Gautier-Hion *et al.* 1985). Knowledge of timber tree reproduction remains surprisingly limited, e.g. the primary pollinators of the 'African mahogany' species (e.g. *Khaya, Entandrophragma, Lovoa* spp.) remains uncertain, while bats are required for the effective seed dispersal of the probably wind pollinated and dioecious *Milicia* (Osmaston 1965). Recent research has also indicated that seed dispersal distances are characteristically much lower than previously thought even for animal dispersed species (e.g. Hubbell *et al.* 1999), a realization that suggests the need for denser or at least more even distribution of retained mother trees. Guiding principles should be available soon when such assessment is coupled with advances in seed and fruit classification (e.g. Gautier-Hion 1985, Howe and Westley 1988).

Ultimately dispersal and pollination syndromes and potential fecundity must help determine choice of mother tree retention and associated site management (Baur and Hadley 1990, Schupp 1990). As an example, dioecious trees should probably be at twice the density of equivalent hermaphrodite species (Lawton 1955, Kigomo *et al.* 1994, note that important timber species such as *Milicia,* and possibly *Entandrophragma* are dioecious), but there are few data to define adequate pollination densities for any tropical tree species (e.g. Stacy *et al.* 1996, Ghazoul *et al.* 1998).

Protecting mother trees and unharvested 'reserves' within the forest landscape offer some insurance, but the maintenance of key animal populations is also necessary to ensure long- term viability and this may require additional attention (e.g. Howe and Westley 1988, Parren 1991, Bakuneeta *et al.* 1995, Hawthorne and Parren 2000). Gordon *et al.* (1990) have shown that crucial Central-American forest pollinators can themselves be dependent on non-forest areas outside of gazetted reserves, implying that such areas and functions need to be included in long-term management

Remnant trees are influential as more than seed sources. Most trees survive and grow better near sources of mycorrhizae, such sources often being other trees (Alexander *et al.* 1992, Hogberg and Alexander 1995, Moyersoen *et al.* 1998). Some fruit trees provide a strong catalytic function by drawing in fruit dispersing vertebrates and enriching the local seed-rain (Guevara 1986, Hietz-Seifert *et al.* 1996). Protecting or planting these species can accelerate forest recovery in degraded sites.

FOREST FOOD, HABITAT AND WILDLIFE

Animals play a major role in maintaining forest vegetation through pollination and seed dispersal. Wildlife *can* be compatible with managed forest (Johns 1997) and is often a major value in itself, providing vital food for local communities, and/or ensuring a high conservation status for the forest.

Manipulation of forest composition has implications for hungry wildlife. While the chemistry of forest vegetation is complex (e.g. Gartlan *et al.* 1980, Waterman 1983, Waterman *et al.* 1988), it is generally true that heavy timbered species are generally better defended against browsers and support fewer animals than faster growing, lighter species (e.g. Janzen 1979, Gartlan *et al.* 1980, Loehle 1988). Fruit availability shows a roughly similar pattern: pioneer species generally have wind-dispersed or small-fruited (bird-dispersed) seeds (Loiselle *et al.* 1996), NPLDs (Table 1) include many species with larger fleshy fruits (e.g. Sapotaceae, Moraceae), while many shade-tolerant species have gravity-dispersed seeds. There is thus often a low abundance of edible fruit and vegetation in dense old-growth forest. These patterns, and the occurrence of herbaceous growth in clearings, explain why young or disturbed areas frequently support higher densities of wildlife than old-growth forests. However, it must be emphasised that 'specialist' species

associated with old growth forests may have a higher conservation status and are more vulnerable to eradication. Some trees, most notably figs (*Ficus* spp.), are especially important for wildlife as they provide fruit throughout the year, and fulfil vital nutritional needs, such as the calcium needed by vertebrates living on otherwise mineral-poor diets (see O'Brien *et al.* 1998).

Large, old and hollow trees have considerable significance for many forest taxa that utilize or are dependent on them, e.g. hornbills (Datta 1998, Whitney and Smith 1998, Whitney *et al.* 1998), woodpeckers (McNally and Schneider 1996), hyraxes and other hollow tree nesters (Zahner 1993). This includes important pollinators like bees (Kerr *et al.* 1994, McNally and Schneider 1996) and seed dispersers (Whitney and Smith 1998, Whitney *et al.* 1998). The loss of such large stems can thus have long-term influences (Gordon *et al.* 1990) and, although not well documented, is potentially involved in otherwise inexplicable decline or failure in forest regeneration in various parts of the world (H.C. Dawkins and J. Palmer *pers. comm.*).

Lianas have been shown to exacerbate the effects of logging, and cutting prior to felling is often advised (e.g. Liew 1973, Appanah and Putz 1984, Putz 1984). However, these can also provide habitat and food for a number of specialized fauna. Protected liana and climber species already occur in some silvicultural prescriptions, e.g. in recognition of a key fruit source (F.E. Putz *pers. comm.*).

Hunting frequently poses a *greater* threat to larger forest fauna than does timber harvesting. However, hunting pressure itself is often related to forestry roads and the provisioning of logging camps (Robinson *et al.* 1999). Many large mammals have been exterminated from areas well within their historical ranges even when suitable habitats remain. The widespread loss of larger forest wildlife throughout the tropics has been called the 'empty forest' syndrome, and some already view such forests as 'ecologically dead' (Redford 1992). The longer-term impacts of animal loss remain hard to specify since we lack basic information, but they are likely to be substantial involving changes in forest composition and structure (De la Cruz and Dirzo 1987, Campbell 1991, Sheil 1998). Forest managers need to consider their responsibility to control excessive hunting and ensure the protection of important habitat features, such as sites that provide vital mineral nutrients directly through soil or salt springs (e.g. Klaus *et al.* 1998).

RISKS AND THREATS

Loss of animals is not the only looming problem in tropical forests; *fire*, *exotic species*, and *forest fragmentation* are all increasingly familiar concerns. Until recently fire had not been a concern in many tropical forest countries, but this is changing. For deciduous and semi-deciduous forest fire is now seen as the greatest risk associated with selective harvesting in some regions (Hawthorne 1994). Risk factors are dry debris and improved access (Buechner and Dawkins 1961, Phillips 1987). Even under moist conditions fire risk is substantially higher in logged forest than in primary forest, especially after periods of drought, and in areas of fragmented cover (Malingreau *et al.* 1985, Bertault 1990). Managers should look at ways to maintain evergreen undergrowth where possible, especially at forest edges.

Another global problem is invasion by non-native plants and animals (*exotics*). While the ability of exotic plants to colonize intact continental rainforest is debated, the problem on islands is often considerable (Whitmore 1991, Cronk and Fuller 1994). The presence of such plants can severely reduce options for maintaining productive natural vegetation after harvesting (Sheil 1994, Rejmanek *et al.* 1996). Invasion can progress very slowly; an interesting example of which is the spread of the exotic tree *Broussonetia papyrifera* (L.) Vent. (Moraceae), a growing problem in both Uganda (Sheil 1994) and Ghana (Hawthorne 1995). This species is unusual in having the tendency to sucker vegetatively from roots or fallen stems. These young sucker shoots dominate the understorey around adult trees and pre-empt other regeneration – while physical control is difficult (the species also coppices well), the existence of a linked root network suggests that poisoning may be an efficient control option. If not recognized in time, such 'slow problems' may nonetheless become ultimately catastrophic and control options unaffordable.

Recent ecological research has begun to clarify how invasive species might be identified from general principles. Rejmanek (1999) provides a scheme for screening out high-risk woody exotics and notes that early maturity associated with high seed outputs and long-distance dispersal is particularly dangerous. The threat is not restricted to plants, but involves a wide range of organisms. Introduced fungi are already seen as a potential threat to native forests in some locations (e.g. *Phytophera* in Australia, Brown 1976) and measures are needed to ensure minimal transfer of soil and other potentially infected material between sites. General recommendations are to eliminate local exotics before they spread over large areas, to be aware of which species have caused problems elsewhere, not to transfer known pest species between sites, and to monitor recovering areas.

The *fragmentation* of forest cover has profound ecological significance. This is a controversial topic with much recent research (e.g. Turner 1996, Laurance and Bierregaard 1997), but there are some generally accepted relationships. Small isolated areas of forest cannot maintain as many species in the longer-term as the same area would if part of some larger tract. Small populations, such as arise in fragmented or heavily harvested landscapes, run much greater risks of reduced reproduction, genetic deterioration and extinction (Nason and Hamrick 1997). The effects will be least if the distances between forest patches are low, and recent research has highlighted the importance of maintaining 'forest-like' or patchy 'forest stepping stone' habitats in the intervening landscape (Laurance and Bierregaard 1997, Gascon *et al.* 2000). Some wildlife is especially vulnerable to habitat fragmentation, and will not cross open areas, even avoiding forest margins. For example, Newmark (1991)

indicates that forest corridors need to be at least 200m wide to allow the free movement of sensitive East African forest birds. Some more general patterns are also emerging based on species characteristics. It appears that nocturnal flying animals (including pollinators and seed dispersers) tend to be less effected by fragmentation than are species which are active in the day, i.e. moths are less sensitive than butterflies, bats than birds (Daily and Ehrlich 1996). Forest fragments are also especially vulnerable to fire (Buechner and Dawkins 1961), invasion by weedy species, and other processes of habitat erosion (Gascon *et al.* 2000). There is a real need to maintain forest connectivity, minimize road width, and avoid unnecessary edge creation. Regulations requiring maintenance of forest cover along stream and river margins (theoretically this should provide a widely linked corridor network) is clearly useful.

BALANCING CHOICES

Timber production versus conservation

There is a conflict between common silvicultural objectives (leading to 'high disturbance') and generally stated conservation goals ('low disturbance'). This choice is well illustrated in Uganda where the majority of preferred timber species grow best in open or disturbed environments (e.g. *Maesopsis eminii* Engl.), and many do not regenerate adequately without significant canopy opening (Meliaceae). A long-standing aim of forestry in Uganda has been to deplete and eradicate the originally widespread but low-yielding old-growth formations in favour of the earlier successional timber forests (Dawkins 1958, Dawkins and Philip 1998). The elimination of native species is no longer considered compatible with modern environmental standards, and as already noted, many non-timber species previously controlled by poisoning (e.g. *Ficus*) are now known to serve important ecological roles.

Similarly, the maintenance of animal populations is not without cost. For example elimination of browsing animals can lead to a substantial improvement in regeneration densities of some timber species – this was the primary reason that the Uganda Forest Department invested heavily in the control of elephants (Laws *et al.* 1975). The acceptability of such measures is a separate matter.

The benefits of encouraging a broader range of harvestable species are equivocal: yields and management options are theoretically increased, but there is also potential for greater forest degradation when regulations cannot be enforced. R.A. Plumptre (1996) provides a useful review showing how higher timber volumes can be extracted from tropical forests if more species are accepted (this being an issue of marketing and treatment). He shows how this would greatly improve the economics of harvesting, but emphasizes that this should not go beyond the ecological limits.

Despite many debates, there is little doubt that many conservation values can theoretically be maintained in managed forest (e.g. Johns 1997) even though such forest is not going to be the 'pristine' entity that some conservationists seek (e.g. Struhsaker 1997). Many areas that have been harvested for timber maintain high conservation significance (e.g. the Bwindi National Park, Uganda, still contains a high proportion of the world's mountain gorillas). While quantitative information is scarce, all harvesting appears to reduce large-scale tropical forest diversity (Struhsaker 1997, Bawa and Seidler 1998). There are vulnerable species that are likely to require protected areas or special management. Hawthorne and Abu-Juam (1995) have made intensive reviews and studies, but are still willing to contend that timber harvesting has not caused any plant extinction in Ghana. However, care is needed, because the presence of species does not mean that long-term ecological viability is assured. For example, trees may live for many centuries despite not being able to regenerate - hence the 'living dead' may be recorded simply 'present' in surveys (c.f. Turner *et al.* 1996, Hawthorne and Parren 2000). The 'empty forest' syndrome already discussed poses an unknown threat, and the effects of forest fragmentation, fires, exotic species, and climate change (see e.g. Markham 1998) pose many additional concerns that urge against complacency.

A common misunderstanding caused by ecologists and conservationists, arises in equating concern about 'biodiversity' with the ecologists classical measures of species richness, and hence into some form of management criteria. However, species are not equal and species counting does not reflect value. Conservation needs to ensure the long-term protection of vulnerable and threatened taxa – not to maximize the number of species recorded in some discrete area. Disturbance in old-growth forest will often promote increased species richness - the added species are generally robust common species, while old-growth forest is rare. Thus, while an increase in the number of tree species after harvesting or disturbance is not unusual (Plumptre 1996, Sheil 1998, Cannon et al. 1998), the conservation relevance is unclear. A more detailed study in Malaysia has indicated that unharvested forest had a much higher 'conservation value' defined by weighting tree species according to their rarity and vulnerability – globally rarer species appear to become disproportionately rarer in areas that have been harvested (Chua *et al.* 1998). The generality of these patterns remains unclear but species counting is definitely a poor way to assess management objectives (Sheil *et al.* 1999).

Ecologists frequently compare managed forests with 'undisturbed', 'pristine' or 'natural' vegetation but caution is required when any notions of a 'stable unchanging natural state' are invoked. Ecologists now recognize that all forests are changing and will continue to change, with or without interventions, fire and exotic species (e.g. Sheil 1996, Phillips and Sheil 1997, Whitmore and Burslem 1998). One of the clearest explanations for this instability lies in the volatile nature of the world's climate which has always been changing and is now doing so even more rapidly as a result of human activities. Even areas set aside for conservation may ultimately require active management if values are to be maintained in the longer term.

DRAWING IT ALL TOGETHER: A BASIS FOR BETTER MANAGEMENT

Presenting available ecological information like the examples presented above into a more accessible and practical form remains a challenge. Ecologists need to derive and develop guidelines and recommendations that are useful and appropriate to local circumstances. Consider three example questions that might arise naturally from our previous account: How do managers know 1) how to define an 'adequate' retention of mother trees, 2) which exotic species to control, and 3) which management practices are needed to sustain vital pollinators? If we are willing to aim at management *improvement* rather than *perfection,* incremental gains are readily available. Regarding the first question: a minimum density for mother trees would be derived as a series of recommendations based on current knowledge of the species (or similar species). Information to be summarized would include minimum-size of reproductive stems, normal density and spacing (as well as pollination biology, type of fruit and seed and requirements of known dispersal agents). This would then be translated back into practical guidelines for forest harvesting operations (e.g. 'over 40% of class A species in the over 80 cm dbh class will be maintained, and over 25% of class B in the over 50 cm dbh class, total canopy opening should not surpass 30% in any given 10 ha block, etc.').

For exotic species there could be a list of species known to cause trouble or with attributes that make problems likely (possibly based on an international agreement and updated as needed). Associated guidelines would be required for managers to carefully assess any introductions, identify problems rapidly and ensure effective control whenever needed.

To maintain 'key pollinators', management plans should include specific reference of what is known about the life history of the important trees and their dependencies (i.e. against a pre-defined checklist). Planning should then take this knowledge into account by ensuring key aspects are protected (e.g. 'pollinators require neighbouring grasslands within 500 m of the forest area to be maintained, these will be gazetted as etc.') – or indicate collaboration with national forest bodies in targeted research to clarify further what is needed. Lists, and derived guidelines, could similarly be used to specify the resources and species to which managers need pay special attention in order to fulfil local and regional conservation and co-operative management objectives.

The development of programmes such as 'codes of practice', 'criteria and indicators' and certification schemes may provide a potential context in which the more demanding ecological issues can be brought to the mainstream. In this way, the likely costs of improved management may not disadvantage the conscientious managers. It is not realistic that either foresters or ecologists working alone could do all this – it requires partnership and informed consultation.

The problem of information access remains. Most information is found in academic books and journals, and is not easily accessible to the general forestry community. This may be improved by Internet libraries and abstracting services (e.g. the CABI tree CD service) and increasing education and training activities by international environmental organizations and cooperative programs. However, in many tropical countries, ecologists are too often seen as opponents rather than providers of positive advice, and working on a better mutual understanding is an important step.

We have discussed how improvements are attainable, but we do not wish to give the impression that the best management can be attained through prescriptions, regulations and bureaucratic procedures alone. The best management practices will only be achieved if trained, experienced and motivated forest managers are available on site to address ecological concerns on a day-to-day basis. Our suggestions require the acceptance of a greater emphasis on ecological information and ecologists in the planning, implementation, and control of forest management and a genuine willingness to improve current practices. Certainly more research will uncover new insights and factors that may be relevant, but this should not stop the development of a range of guidelines, and local management codes can be useful now.

CONCLUSION

Ecology provides a vital component of the understanding needed to reconcile the long-term viability of tropical forests with human needs. Though tropical forests remain incompletely understood, this cannot excuse the current prevalence of poor management practices – enough is known to manage tropical forests much better than is generally the case. Forest managers and ecologists must work together to face the considerable challenges to tropical forests in the new millennium.

While we have presented a number of ecological principles and ideas through the text, these serve as illustrations only, and are neither definitive nor comprehensive. We conclude with some more general propositions (Table 2).

TABLE 2 *Ecology for tropical forest management: some general propositions*

- Ecology is vital to good forest management, not opposed to it. Any definition of 'good practice' or 'sustainability' that neglects a comprehensive treatment of ecological principles will be incomplete.
- There is already a vast amount of ecological information that can be used to guide management, but managers require various types of support to be able to make better use of this.
- Wider availability of information (Internet etc.) may help, but more importantly, ecologists and foresters must seek a constructive alliance in which the best ecology is made available as a basis for management.
- Ecologists must not merely criticize management practices but should seek ways by which they can be improved. Nor should ecologists expect to tell forest managers what they can and cannot do – there is a need for dialogue to find the most acceptable compromises.
- An alliance between ecologists, foresters, and others is needed to combat the many threats facing forests.
- We support the many initiatives looking at codes of conduct, criteria and indicators, certification, forestry education etc. but suggest that there is a need to provide adequate ecological support (information, training, materials, incentives, access to expertise) to those responsible for forest management.

ACKNOWLEDGEMENTS

We thank Andrew Plumptre, Derek Pomeroy, Henry Osmaston, Michael Spilsbury, Dennis Dykstra, Francis (Jack) Putz, Carol Colfer, Jeff Sayer, Arnold Grayson, Alan Pottinger and referees for their comments, encouragement and criticisms, and Melinda Wan, Rosita Go, and the CIFOR library staff for their help.

REFERENCES

ALEXANDER, I., AHMAD, N. and SEE, L.S. 1992 The role of mycorrhiza in the regeneration of some Malaysian forest trees. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **335**: 379-388.

APPANAH, S. and MOHD.-RASOL, A.M. 1990 Smaller trees can fruit in logged dipterocarp forests. *Journal of Tropical Forest Science* **3**: 80-87.

APPANAH, S. and PUTZ, F.E. 1984 Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *The Malaysian Forester* **47**: 335-342.

BAKUNEETA, C., JOHNSON, K., PLUMPTRE, R. and REYNOLDS, V. 1995 Human uses of tree species whose seeds are dispersed by chimpanzees in the Budongo forest. *African Journal of Ecology* **33**: 276-278.

BAUR, K.S. and HADLEY, M. (eds.) 1990 *Reproductive ecology of tropical forest plants.* Man and the Biosphere series. UNESCO, Paris.

BAWA, K.S. and SEIDLER, R. 1998 Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology* **12**: 46-55.

BELLINGHAM, P.J., TANNER, E.V.J. and HEALEY, J.R. 1994 Sprouting of trees in Jamaican montane forests, after a hurricane. *Journal of Ecology* **82**: 747-758.

BERTHAULT, J.G. 1990 Comparaison d'ecosystemes forestiers naturels et modifies apres incendies en Côte d'Ivoire. *In*: PUIG, H. (ed.). Atelier sur L'amenagement et las conservation de l'ecosysteme forestier topicale humide. Cayenne, 1990. UNESCO, Paris.

BRANDANI, A., HARTSHORN, G.S. and ORIANS, G.H. 1988 Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *Journal of Tropical Ecology* **4**: 99-119.

BROKAW, N. 1987 Gap phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* **75**: 9-20.

BROWN, B.N. 1976 *Phytophthora cinnamomi* associated with patch death in tropical rain forests in Queensland. *APPS-Newsletter* **5**: 1-4.

BROWN, N.D. and JENNINGS, S. 1998 Gap-size niche differentiation by tropical rainforest trees: a testable hypothesis or a broken-down bandwagon? *In*: NEWBERY, D.M., PRINS, H.H.T. and BROWN, N.D. (eds.) *Dynamics of tropical communities. The 37th symposium of the British Ecological Society, Cambridge University 1996.* Blackwell Science, Oxford, pp. 79-94.

BUECHNER, H.K. and DAWKINS, H.C. 1961 Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* **42**: 752-766.

CAMPBELL, D.G. 1991 Gap formation in tropical forest canopy by elephants, Oveng, Gabon, Central Africa. *Biotropica* **23**: 195-96.

CANNON C.H., PEART, D.R. & LEIGHTON M. 1998 Tree species diversity in commercially logged Bornean rainforest. *Science* **281**:1366-1368.

CHAPMAN, C.A. and CHAPMAN, L.J. 1997 Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* **29**: 396-412.

CHUA, L.S, HAWTHORNE, W.D., GUAN, S.L. and SENG, Q.E. 1998 Biodiversity database and assessment of logging impacts. *In:* SEE, L.S. *et al.* (eds.) *Conservation, management and development of forest resources.* Proceedings of the Malaysia-United Kingdom Programme Workshop, 21-24 October 1996, Kuala Lumpur, Malaysia, pp. 30-40.

CLARK, D.A. 1994 Plant demography. *In*: McDade, L.A., Bawa, K.S., Hespenheide, B.H. and Hartshorn, G.S. (eds.) *La Selva: ecology and natural history of a neotropical rainforest.* University of Chicago Press, Chicago, Ill, pp. 90-105.

CLARK, D.B. 1990 The role of disturbance in the regeneration of neotropical moist forests. *In*: BAWA, K.S. and HADLEY, M. (eds.) *Reproductive ecology of tropical forest plants.* MAB series 7, UNESCO, Paris, pp. 291-315.

CRONK, Q.C.B. and FULLER, J.L. 1994 *Invasive plants: the threat to natural ecosystems worldwide.* A WWF Handbook. Chapman and Hall, London.

DAILY, G.C. and EHRLICH, P.R. 1996 Nocturnality and species survival. *P.N.A.S* **93** (21): 11709-11712.

DATTA, A. 1998 Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. *Oryx* **32**: 285-294.

DAWKINS, H.C. 1958 *The management of Natural Tropical High-Forest with special reference to Uganda.* Imperial Forestry Institute, University of Oxford, Oxford.

DAWKINS, H.C. and PHILIP, M.S. 1998 Tropical moist forest silviculture and management. A history of success and failure. CAB International, Oxon.

DE LA CRUZ, M. and DIRZO, R. 1987 A survey of the standing levels of herbivory in seedlings from a Mexican rain forest. *Biotropica* **19**: 98-106.

DENSLOW, J.S. 1987 Tropical rainforest gaps and tree species diversity. *Annual Review of Ecological Systematics* **18**: 431-451.

DENSLOW, J.S., GOMEZ DIAS, A.E. and SPIES, T.A. 1990 Seed rain to tree fall gaps in a neotropical rainforest. *Canadian Journal of Forest Research* **20**: 642-648.

EPP, G.A. 1987 The seed bank of *Eupatorium odoratum* along a successional gradient in a tropical rain forest in Ghana. *Journal of Tropical Ecology* **3**: 139-149.

FAVRICHON, V. 1998 Modelling the dynamics and species composition of a tropical mixed-species uneven-aged natural forest - effects of alternative cutting regimes. *Forest Science* **44**: 113-124.

GARTLAN, J.S., MCKEY, D.B., WATERMAN, P.G., MBI., C.N. and STRUHSAKER, T.T. 1980 A comparative study of the phytochemistry of two African rain forests. *Biochemical Systematics and Ecology* **8**: 401-422.

GASCON, C., WILLIMASON, G.B., & DA FONSECA, G.A.B. 2000 Receding forest edges and vanishing reserves. *Science*, **288**: 1356-1358.

GAUTIER-HION, A., DUPLANTIER, J.-M., QURIS, R., FEER, F., SOURD, C., DECOUX, J.P., EMMONS, L., DUBOST, G., ERARD, C., HECHESTWEILER, P., MOUNGAZI, A., ROUSSILHON, C. and THIOLLAY, J.-M. 1985 Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**: 324-337.

GHAZOUL, J., LISTON, K.A. and BOYLE, T.J.B. 1998 Disturbance-induced, density dependent seed selection in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *Journal of Ecology* **86**: 462-473.

GLENN-LEWIN, D.C. and VAN DER MAAREL, E. 1992 Patterns and processes of vegetation dynamics. *In*: GLENN-LEWIN, D.C., PEET, R.K. and VEBLEN, T.T. (eds.) *Plant succession: theory and prediction*. Chapman and Hall, London, pp. 11-59.

GORDON, W.F., VINSON, S.B., NEWSTROM, L.E., BARTHELL, J.F., HABER, W.A., and FRANKIE, J.K. 1990 Plant phenology, pollination ecology, pollinator behaviour and conservation of pollinators in Neotropical dry forest. *In*: BAWA, K.S. and HADLEY, M. (eds.) *Reproductive ecology of tropical forest plants*. MAB series 7, UNESCO, Paris, pp. 37-48.

GUEVARA, S.S. 1986 Plant species availability and regeneration in Mexican tropical rain forest. Acta Universitatis Upsaliensis, Comprehensive Summaries of Uppsala Dissertations for the Faculty of Science, 48.

HARTSHORN, G.S. 1978 Tree falls and tropical forest dynamics. *In*: TOMLINSON, P.B. and ZIMMERMAN, M.H. (eds.) *Tropical trees as living systems*. Cambridge University Press, New York, pp. 617-38.

HAWTHORNE, W.D. 1993 Forest regeneration after logging: findings of a study in the Bia South Game Production Reserve, Ghana. ODA Forestry Series. Natural Resources Institute, Chatham.

HAWTHORNE, W.D. 1994 *Fire damage and forest regeneration in Ghana*. ODA Forestry Series. Natural Resources Institute, Chatham.

HAWTHORNE, W.D. 1995 Ecological profiles of Ghanaian forest trees. Tropical Forestry Papers 29. Oxford Forestry Institute, UK.

HAWTHORNE, W.D. 1996 Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. *Proceedings of the Royal Society of Edinburgh*, **104B**: 75-176.

HAWTHORNE, W. D. AND ABU-JUAM, M. 1995. Forest protection in Ghana. IUCN,Gland, Switzerland and Cambridge, UK

HAWTHORNE, W.D., AGYEMAN, V. K., ABU JUAM, M., and FOLI, E. G. In press. Taking stock: An annotated bibliography of logging damage and recovery in tropical forests, and the results of new research in Ghana. Tropical Forestry Papers. Oxford Forestry Institute, UK.

HAWTHORNE, W.D. and PARREN M.P.E. 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology*. **16**: 133-150

HLADIK, A. and MIQUEL, S. 1990 Seedling types and plant establishment in an African rain forest. *In*: BAWA, K.S. and HADLEY, M. (eds.) *Reproductive ecology of tropical forest plants*. MAB series 7, UNESCO, Paris, pp. 37-47.

HOGBERG, P. and WESTER, J. 1998 Root biomass and symbioses in *Acacia mangium* replacing tropical forest after logging. *Forest Ecology and Management* **102**: 333-338.

HOWE, H.F. AND WESTLEY, L.C. 1988 *Ecological Relationships of Plants and Animals*. Oxford University Press, Oxford.

HUBBELL, S.P., FOSTER, R.B., O'BRIEN, S.T., HARMS, K.E., CONDIT, R., WECHSLER, B., WRIGHT, S.J. and LOO DE LAO, S. 1999 Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**: 554-557.

JANZEN, D.H. 1979 New horizons in the biology of plant defenses. *In*: Rosenthal, G.A. and Janzen, D.H. (eds.) *Herbivores: their interaction with secondary plant metabolites*. Academic Press, London, pp. 331-350.

JOHNS, A.D. 1988 Effects of "selective" timber extraction on rain forest structure and composition and some consequences for frugivores and foliovores. *Biotropica* **20**: 31-37

JOHNS, A.D. 1997 Timber production and biodiversity conservation in tropical rain forests. Cambridge University Press, Cambridge.

KASENENE, J.M. 1987 The influence of mechanized selective logging, felling intensity and gap-size on the regeneration of a tropical moist forest in the Kibale Forest, Uganda. *Tropical Ecology* **25**: 179-195.

KASENENE, J.M. and MURPHY, P.G. 1991 Post-logging tree mortality and major branch loss in Kibale forest reserve, Uganda. *Forest Ecology and Management* **46**: 295-307.

KERR, W.E., NASCIMENTO, V.A. and CARVALHO, G.A. 1994 Ha salvacao para os meliponineos? (Is there salvation for meliponine bees?) *In*: *Anais do 1 deg encontro sobro abelhas, de Ribeirao Preto,* 02 a 04 de Junho de 1994, USP-Campus de Ribeirao Preto, Brazil, pp. 60-65

KIGOMO, B.N., WOODELL, S.R. and SAVILL, P.S. 1994 Phenological patterns and some aspects of the reproductive biology of *Brachylaea huillensis* O. Hoffm. *African Journal of Ecology* **94**: 296-307.

KLAUS, G. KLAUS-HUGI, C. AND SCHMID, B. 1998 Geophagy by large mammals at natural licks in the rain forest of the Dzanga National Park, Central African Republic. *Journal of Tropical Ecology* **14**: 829-839.

LAURANCE, W.F. AND BIERREGAARD, R.O. (eds.) 1997. *Tropical Forest Remnants – ecology management and conservation of fragmented communities*. University of Chicago Press, Chicago and London.

LAWS, R.M., PARKER, I.S.C. and JOHNSTONE, R.C.B. 1975 *The ecology of elephants in North Bunyoro, Uganda.* Clarendon Press, Oxford.

LAWTON, R.M. 1955 The relationship between crown form and sex in (*Chlorophora excelsa*). *Empire Forestry Journal* **34**: 192-193.

LIEW, T.C. 1973 The practicability of climber cutting and tree marking prior to logging as a silvicultural tool in the management of dipterocarp forest in Sabah. *The Malaysian Forester* **36**: 80-122.

LOEHLE, C. 1988 Tree life history strategies: the role of defences. *Canadian Journal of Forest Research* **18**: 209-222.

LOISELLE, B.A., RIBBENS, E. and VARGAS, O. 1996 Spatial and temporal variation of seed rain in a tropical lowland wet forest. *Biotropica* **28**: 82-95.

LOWE, R.G. 1995 How can ecology contribute to the silviculture of natural tropical high forest and its regeneration? *Commonwealth Forestry Review* **74**: 162-163.

MALINGREAU, J.P., STEPHENS, G. and FELLOWS, L. 1985 Remote sensing of forest fires: Kalimantan and North Borneo in 1982-83. *Ambio* **14**: 314-321.

MARKHAM, A. (ed.) 1998 *Potential impacts of climate change on tropical forest ecosystems*. Kluwer Academic, Netherlands (reprinted from *Climatic Change* Volume 39, 1998)

MCNALLY, L.C. and SCHNEIDER, S.S. 1996 Spatial distribution and nesting biology of colonies of the African honey bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana, Africa. *Environmental Entomology* **25**: 643-652.

MOYERSOEN, B., FITTER, A.H. and ALEXANDER, I.J. 1998 Spatial distribution of ectomycorrhizas and arbuscular mycorrhizas in Korup national park rain forest, Cameroon, in relation to edaphic parameters. *New Phytologist* **139**: 311-320.

NASON, J.D. and HAMRICK, J.L. 1997 Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees. *Journal of Heredity* **88**: 264-276.

NEWMARK, W.D. 1991 Tropical forest fragmentation and the local extinction of understorey birds in the Eastern Usambara Mountains, Tanzania. *Conservation Biology* **5**: 67-78.

NG, F.S.P. 1983 Ecological principles of tropical lowland rain forest conservation. *In*: SUTTON, S.L., WHITMORE, T.C. and CHADWICK, A.C. (eds.) *Tropical rain forest ecology and management.* Special Publication Number 20 of the British Ecological Society. Blackwell Scientific Publications, Oxford, pp. 359-375.

O'BRIEN, T.G., KINNAIRD, M.F., DIERENFELD, E.S., CONKLIN-BRITTAIN, N.L., WRANGHAM, R.W. and SILVER, S.C. 1998 What's so special about figs? *Nature* **392**: 668.

OSMASTON, H. A. 1965 Pollen and seed dispersal in *Chlorophora excelsa* and other Moraceae, and in *Parkia filicoidea* (Mimosaceae) with special reference to the role of the fruit-bat, *Eidolon helvum. Commonwealth Forestry Rev*iew **44**: 96-103.

PARREN, M.E. 1991 Forest elephant (*Loxodonta africana cyclotis* Matschie) messenger-boy or bulldozer? The possible impact on the vegetation, with special reference to 41 tree species of Ghana. A.V. 90/51. Department of Forestry, Wageningen Agricultural University, The Netherlands.

PELISSIER, R., PASCAL, J.P., HOULLIER, F. and LABORDE, H. 1998 Impact of selective logging on the dynamics of a low elevation dense moist evergreen forest in the Western Ghats (South India). *Forest Ecology and Management* **105**: 107-119.

PHILLIPS, C. 1987 Preliminary observations on the effects of logging on a hill forest in Sabah. *In*: YUSUF HADI, KAMIS AWANG, NIK MUHAMAD MAJID and SHUKRI MOHAMED (eds.) *Impact of man's activities on tropical upland forest ecosystems*. Universiti Pertanian Malaysia, Serdang, Malaysia, pp. 187-215.

PHILLIPS, O.L. and SHEIL, D. 1997 Forest turnover, diversity and CO_2. *Trends in Ecology and Evolution* **12**: 404.

PLUMPTRE, A.J. 1995 The importance of "seed trees" for the natural regeneration of selectively logged tropical forest. *Commonwealth Forestry Review* **74**: 253-258.

PLUMPTRE, A.J. 1996 Changes following 60 years of selective timber harvesting in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* **89**: 101-113.

PLUMPTRE, R.A. 1996 Links between utilisation, product marketing and forest management in tropical moist forest. *Commonwealth Forestry Review* **75** (4): 316-325.

PUTZ, F.E. 1984 The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **65**: 1713-1724.

REDFORD, K.H. 1992. The empty forest. *BioScience* **42**: 412-422.

REJMANEK, M., REJMANKOVA, E. and KATENDE, T. 1996 Invasive plants in Ugandan protected areas. *Res Explor (in press).*

REJMANEK, M. 1999 Invasive plant species and invasible ecosystems. *In*: O.T. Sandlund (ed.) Invasive species and biodiversity management. Kluwer Academic, Netherlands, pp. 79-102.

ROBERTS, M.R. and GILLIAM, F.S. 1995 Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Modelling* **86**: 37-50.

ROBINSON, J.G., REDFORD, K.H., and BENNETT, E.L. 1999 Wildlife harvest in logged tropical forests. *Science* **284**: 595-596.

SCHUPP, E.W. 1990 Annual variation in seedfall, post-dispersal predation and recruitment of a neotropical tree. *Ecology* **71**: 504-515.

SHEIL, D. 1994 Naturalised and invasive plant species in the evergreen forests of the East Usambara Mountains Tanzania. *African Journal of Ecology* **32**: 66-71.

SHEIL, D. 1996 Species richness, forest dynamics and sampling: questioning cause and effect. *Oikos* **76**: 587-590.

SHEIL, D. 1998 A half century of permanent plot observation in Budongo Forest, Uganda: histories, highlights and hypotheses. *In*: DALLMEIER, F. and COMISKEY, J.A. (eds.) *Forest biodiversity research, monitoring and modelling: conceptual background and Old World case studies.* Proceedings from the 1995 Smithsonian MAB Washington Symposium. MAB, UNESCO, Paris, pp. 399-428.

SHEIL, D. and HAWTHORNE, W. 1995 How can ecology contribute to the silviculture of natural tropical high forest and its regeneration? A reply to Lowe. *Commonwealth Forestry Review* **74**: 181-182.

SHEIL, D., SAYER, J.A. and O'BRIEN, T. 1999 Tree diversity and conservation in logged rainforest.

SILVA, J.N.M., CARVALHO, J.O.P. DE, LOPES, J. DO C.A., OLIVEIRA, R.P. DE K. and OLIVEIRA, L.C. DE 1996 Growth and yield studies in the Tapajos region, Central Brazilian Amazon. *Commonwealth Forestry Review* **75**: 325-329, 350-352.

SKORUPA, J.P. 1988 The effects of selective timber harvesting on rain forest primates in Kibale Forest, Uganda. Ph.D. thesis, University of California, Davis.

SKORUPA, J.P. and KASENENE, J.M. 1984 Tropical forest management: Can rates of natural treefalls help guide us? *Oryx* **18**: 96-101.

SOUSA, W.P. 1984 The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**: 353-359.

STACY, E.A., HAMRICK, J.L., NASON, J.D., HUBBELL, S.P., FOSTER, R.B. AND CONDIT, R. 1996 Pollen dispersal in low-density populations of three neotropical tree species. The American Naturalist 148: 275-298.

STRUHSAKER, T.T. 1997 Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville.

STRUHSAKER, T.T., LWANGA, J.S. and KASENENE, J.M. 1996 Elephants, selective logging and forest regeneration in the Kibale forest, Uganda. *Journal of Tropical Ecology* **12**: 45-64.

SWAINE, M.D. (ed.) 1996. *The ecology of tropical forest tree seedlings*. Man and Biosphere Series, Volume 17. Unesco and Parthenon, Paris.

SWAINE, M.D. and HALL, J.B. 1983 Early succession on cleared forest land in Ghana. *Journal of Ecology* **71**: 601-627.

THOMAS, S.C. 1996 Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *Oikos* **76**: 145-154.

TURNER, I.M. 1996 Species loss in fragments of tropical rainforests: a review of evidence. *Journal of Applied Ecology* **33**: 200-209.

TURNER, I.M., CHUA, K.S., ONG, J.S.Y., SOONG, B.C. and TAN, H.T.W. 1996 A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conservation Biology* **10**: 1229-1244.

VAZQUEZ-YANES, C. and OROZCO-SEGOVIA, A. 1993 Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* **24**: 69-87.

WATERMAN, P.G. 1983 Distribution of secondary metabolites in rain forest plants; towards an understanding of cause and effect. *In*: SUTTON, S.L., WHITMORE, T.C. and CHADWICK, A.C. (eds.) *Tropical rain forest ecology and management.* Special Publication Number 20 of the British Ecological Society. Blackwell Scientific Publications, Oxford, pp. 167-179.

WATERMAN, P.G., ROSS, J.A.M., BENNETT, E.L. and DAVIES, E.G. 1988 A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biological Journal of the Linnean Society* **34**: 4-32.

WHITMORE, T.C. 1991 Invasive woody plants in perhumid tropical climates. *In*: RAMAKRISHNAN, P.S. (ed.) *Ecology of biological invasions in the tropics*. International Scientific Publications, New Delhi.

WHITMORE, T.C. and BROWN, N.D. 1996 Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **351**: 1195-1203.

WHITMORE, T.C. and BURSLEM, D.F.R.P. 1998 Major disturbances in tropical rainforests. *In*: NEWBERY, D.M., PRINS, H.H.T. and BROWN, N.D. (eds.) *Dynamics of tropical communities. The 37th symposium of the British Ecological Society, Cambridge University 1996*. Blackwell Science, Oxford, pp. 549-565.

WHITNEY, K.D. AND SMITH, T.B. 1998 Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. *Animal Conservation* **1**: 107-117.

WHITNEY, K.D., FOGIEL, M.K., LAMPERTI, A.M., HOLBROOK, K.M., STAUFFER, D.J., HARDESTY, B.D., PARKER, V.T. and SMITH, T.B. 1998 Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* **14**: 351-371.

ZAHNER, V. 1993 Hohlenbaume und Forstwirtschaft. (Hollow trees and forestry). *Allgemeine Forst Zeitschrift* **48**: 538-540.