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Forest Ecology and Management 154 (2001) 1–10

Forest Ecology  
and  
Management

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# Ecology provides a pragmatic solution to the maintenance of genetic diversity in sustainably managed tropical rain forests

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Received 17 January 2000; received in revised form 8 June 2000; accepted 26 September 2000

## Abstract

An important aspect of the sustainable management of tropical rain forests is the maintenance of genetic diversity within populations of commercial tree species. Logging may reduce genetic variation directly and may also affect genetic processes, leading possibly to genetic erosion and ultimately even species extinction. It is, however, impractical for the forest manager to make meaningful measurements of genetic variation and they are therefore inappropriate for use as indicators of sustainable forest management. We propose that the application of well-known silvicultural principles is the most practical way of preventing rapid loss of genetic diversity.

Most tropical rain forest tree species have many more individuals below the minimum size for commercial exploitation than above. The genetic diversity of these species will be little affected by logging, as the stems removed form only a small fraction of the total population. Similarly, for most species, disruption of normal mating patterns will either not occur or be transient, because reproduction commences at sizes well below felling limits, or because, after logging, juveniles will be recruited to the sexually mature size classes.

Strongly light-demanding species with a commercial value are most likely to suffer loss of genetic diversity from logging. Characteristically, these have populations in which only a small proportion of the total population lies in small size classes. In order to conserve genetic diversity, pre-felling silvicultural treatments will be required to increase the survival and growth of juveniles. Ecological and genetic research needs to focus on these light-demanding species. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Selective logging; Criteria and indicators; Sustainable management; Genetic diversity; Tropical rain forests; Genetic erosion

## 1. Introduction

A consistent area of concern in the vigorous debate on how to define and measure the sustainability of management practices in tropical rain forests, is the

maintenance of genetic diversity and processes within natural populations of trees. Almost all of the recently developed, international sets of standards against which the sustainability of tropical forest management is currently assessed include criteria and indicators relating to the conservation of genetic diversity. These include:

- The Amazon Co-operation Treaty (otherwise known as the Tarapoto Process), an international

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agreement subscribed to by eight South American countries in 1995 that seeks to ensure the long-term sustainability of forests in the Amazon. Criterion 4 (conservation of forest cover and of biological diversity) specifies ‘measures for the conservation of genetic resources’ as an indicator of sustainability.

- The International Tropical Timber Organisation criteria and indicators for sustainable management of natural tropical forests (ITTO, 1998). Criterion 5: biological diversity specifies a number of indicators including 5.6 ‘Existence and implementation of a strategy for in situ and/or ex situ conservation of the genetic variation within commercial, endangered, rare and threatened species of forest flora and fauna.’
- Forest Stewardship Council (1999) principles and criteria. Principle 6.3(b) requires that forest management shall maintain intact, enhance or restore genetic, species, and ecosystem diversity.
- CIFOR Criteria and Indicators Toolbox (CIFOR C&I Team, 1999). Criterion 2.3 requires conservation of processes that maintain genetic variation. Indicators include that there is no directional change in genotypic frequencies, that there are no changes in gene flow/migration, and that there are no changes in mating systems.

The function of criteria and indicators is to provide a practical means by which changes in forest condition, which occur as a consequence of management actions, can be monitored. They should, in principle, be defined so that they are clear, practical and easy to monitor, and be based, as far as possible, on available research knowledge and statistics (ITTO, 1998). All of these important requirements seem to have been forgotten in the case of genetic criteria and indicators. All 18 of the verifiers (sic) of the maintenance of genetic diversity proposed by Namkoong et al. (1996) require sophisticated laboratory-based analyses, lengthy field trials, or detailed monitoring of phenology, population structure, pollination and seed dispersal patterns. A number are based on the measurement of genetic parameters that are still the subject of scientific debate and whose values vary according to the measurement method (Hartl and Clark, 1997). Decisions on the baselines by which to gauge change are also problematic (Ledig, 1992).

Verification of many of these indicators requires extensive sampling. As a rule of thumb, for a diploid plant species with a population that is completely panmictic, 25 individuals should be sampled in order for there to be a 95% probability of detecting at least one copy of all alleles that occur with a frequency of greater than 5% (Frankel et al., 1995). The sampling frequency for polyploid species (many tropical tree species appear to be ancient polyploids) remains largely unresearched, but it is likely to be at least twice that for a diploid species. Adequate population estimates of most of the genetic parameters proposed by Namkoong et al. (1996), therefore require sampling of a minimum of 50 individuals per species. Those indicators that require field trials are impractical for most tropical tree species because appropriate planting and nursery techniques are not known. Very little is yet known about how juvenile characters predict those of mature trees and so trials would only yield meaningful results after decades. Our view is that it is impractical for forest managers to make meaningful measurements to monitor the conservation of genetic variation within managed tropical rain forest. In proposing that genetic parameters are incorporated as measures of the sustainability of forestry operations, academic geneticists and enthusiastic conservationists have risked making their criteria and indicators impossible for forest managers to apply. Instead, given the ways (outlined below) in which logging may effect genetic processes, we advocate a pragmatic assumption that, if post-logging regeneration of rare or commercial species is adequate, it is likely that their population genetic structure and diversity will not have been severely and permanently affected. We identify the circumstances and types of species for which this might not be the case, and which should form a focus for limited management and research resources. We also illustrate how this approach may be applied, by identifying those commercial species in a forest reserve (Moju, Pará state, Brazil) that may be genetically susceptible to selective logging.

## **2. The impact of selective logging on tree populations**

By far the most common form of natural forest management in the humid tropics involves the logging

of trees, of a limited number of species, that are larger than a specified diameter (rarely less than 45 cm and usually more). Pre- or post-felling silvicultural treatments that affect the density and species composition of natural regeneration are rarely applied because of the cost and labour that they entail. This type of logging is the subject of this paper. We do not consider the consequences of forest clearance that is clearly unsustainable at any level.

Selective logging removes timber trees and, at the same time, destroys non-commercial stems during felling and extraction. Only a handful of species in most tropical forests currently has commercial value for timber, constituting a tiny fraction of the tree flora of most forests. For example, Peninsular Malaysia has a total tree flora of approximately 3000 species, of which ca. 400 (16%) are commercial timber species, and only 30 (ca. 1%) are exploited in quantity (Whitmore, 1975). The number of commercial timber species in other parts of the tropics is generally smaller. As a result, only a small number of trees per unit area are removed from most forests. The FAO (1993) estimated that, between 1986 and 1990, an average of 33 m<sup>3</sup> ha<sup>-1</sup> of logs were extracted from natural forests in Asia and the Pacific region. The figure was lower in Africa (13 m<sup>3</sup> ha<sup>-1</sup>) and in Latin America and the Caribbean (8 m<sup>3</sup> ha<sup>-1</sup>). This is roughly equivalent to 7, 3 and 2 large trees ha<sup>-1</sup>, respectively.

Nevertheless, the trees that are felled often constitute a very high proportion of the large individuals of those commercial species. For example, Gullison et al. (1996) found that 91% of *Swietenia macrophylla* King stems above the felling limit had been felled in a Bolivian forest. Although the removal of large trees may have only slight effects on population demography (Hartshorn, 1975), a major concern is that logging may result in direct loss of genetic diversity and will increase the likelihood of further losses through impacts on one or more of the following processes:

1. *Population bottlenecks and genetic drift.* Reductions in population size may cause the random loss of alleles (with the rarest alleles at the greatest risk) and hence reduce genetic variation (a 'bottleneck effect'). Losses are likely to be greater if there is spatial genetic structure, with clumping of genetically similar individuals from limited seed dispersal or where particular species or genotypes are associated with areas of the forest that suffer disproportionately high levels of damage. The effects may also become important where stems of a rare species are killed.
2. *Dysgenic selection.* A selection system preferentially harvests the largest trees with the best form, such that poor quality trees constitute a larger proportion of the residual population. The impact of this dysgenic selection will be dependent on the intensity of logging, the relative contribution of residual trees to regeneration and, crucially, the extent to which undesirable traits are genotypic rather than phenotypic.
3. *Reproduction and mating systems.* Reduction in population size and increased distances between reproducing individuals can result in a suite of changes to the reproductive and mating processes, and may lead to reduced levels of seeding and/or undesirable levels of inbreeding with associated impacts on fitness (inbreeding depression). The long life span of most trees means that reproductively mature generations frequently overlap, with the potential for inter generation mating reducing the effective population size, compared to estimates from a forest inventory. Similarly the loss of incompatibility alleles, owing to severe reductions in population size, may also reduce seed production through a limitation of compatible pollination. Logging may also limit reproduction by affecting both the population size and behaviour of pollinator and dispersal agents.

### 3. Likelihood of population bottlenecks, genetic drift and dysgenic selection under selective logging

Where a tree species population is found to have few juveniles relative to the number of adults it is often inferred that the population is in decline. However, as Condit et al. (1998) have shown, there are a number of other factors which can affect species size distributions. For a population in equilibrium, the size distribution is determined by both growth and survival rates. In a review of studies of tropical rain forest tree dynamics Swaine et al. (1987) found that for most climax species, survival rates remained relatively constant as trees increased in size. This results in a size distribution in which each successive size class has fewer individuals. Most shade-tolerant tropical

rain forest tree species show this characteristic 'reverse J' size distribution (Hartshorn, 1978; Richards, 1952). As a consequence, within any forest, the vast majority of individuals of shade-bearing species are smaller than the commercially exploited size. Small trees will therefore contain most of the genetic diversity. Removal of only large, commercial-sized stems will cause little immediate loss of genetic variation amongst the shade-tolerant species.

In contrast to shade-tolerant species, survival of light-demanding species tends to increase with size, resulting in a much flatter (sensu Condit et al., 1998) size distribution in which the proportion of small sized individuals, in the population, is low. This pattern is exacerbated by differences in growth rates. Shade-tolerant species may accumulate large numbers of small, shade-suppressed individuals. In contrast, those seedlings of light-demanding species that are found in high illuminance conditions, grow quickly to large size, hence small individuals are relatively less abundant. This group of species includes both strict pioneers (sensu Swaine and Whitmore, 1988) and the most light-demanding of the climax species. Most pioneers are small trees and have no timber value, although a few are commercial (e.g. *Aucomea*, *Ochroma*, *Jacaranda copaia*). In the American tropics many long-lived pioneers are now beginning to receive considerable commercial attention (Guariguata and Finegan, 1998). There are some extremely valuable light-demanding climax species (e.g. *S. macrophylla*, *Entandrophragma* spp., light red meranti species of *Shorea*).

The species that are the most vulnerable to loss of genetic diversity caused by selective logging are those where the commercial-sized stems form a large proportion of the total population. In the absence of specific management, populations of these species might be vulnerable to substantial reductions in population size, dysgenic selection and subsequent genetic drift. This group includes any population that is in decline, and some pioneer or light-demanding climax species.

#### 4. Likely impacts on reproduction and mating systems under selective logging

The selective removal of large trees, most of which are reproductive (e.g. Plumptre, 1995) and highly

fecund (e.g. Gullison et al., 1996), reduces the reproductive population, and increases distances between reproducing individuals. It might be expected, therefore, that logging would cause a widespread increase in inbreeding and self-fertilisation (e.g. Murawski et al., 1994). However, the evidence currently available is equivocal on these matters. Many tropical tree species appear to be self-incompatible (Bawa, 1974; Zapata and Arroyo, 1978; Bawa et al., 1985a) and predominantly outcrossed (Murawski, 1995; Alvarez-Buylla et al., 1996). In these, inbreeding is only likely to occur if pollen flow is restricted to within groups of related individuals, that have resulted from limited seed dispersal. A large proportion of tropical rain forest trees are, however, animal-pollinated and some animal pollinators are able to carry pollen over large distances (e.g. carpenter bees, Janzen, 1971; bats, Heithaus et al., 1974).

The combination of mechanisms that promote outcrossing and the lability of pollinator behaviour appears to provide tropical rain forest trees with a degree of resilience to the potentially adverse effects of decreased population density. At a selectively logged forest in Thailand, a threefold decrease in density (when compared with an unlogged forest) of *Shorea siamensis* had little effect on the amount of fruit set, and a significant reduction in fruit set was observed only at a heavily disturbed site where tree density was reduced to one-tenth (Ghazoul et al., 1998). Other studies have shown either no effect of selective logging on outcrossing rates (Kitamura and Rahman, 1992) or a reduced (although still high) rate (Doligez and Joly, 1997). Differences between, and annual variation in, outcrossing rates for individual trees of several neotropical tree species have been reported to be consistent with changes in local flowering densities and the spatial patterns of flowering individuals (Murawski and Hamrick, 1991). Species occurring at low densities appeared to combine significant levels of correlated mating with long distance gene flow, whereas higher density species showed more random mating, generally over shorter distances. In three neotropical species (*Calophyllum longifolium*, *Spondias mombin*, *Turpinia occidentalis*) that occur naturally at low densities, mating patterns were strongly affected by the spatial distribution of reproductive trees. Where trees were clumped, the majority of matings were with near neighbours, whereas with

evenly spaced trees a large proportion of matings was over several hundred meters and well beyond the nearest reproductive neighbours, although still showing high levels of outcrossing (Stacy et al., 1996). Any increase in levels of inbreeding may, however, be unimportant in naturally regenerating forests, if, as is likely, selfed individuals are selected against through high mortality levels at various stages of regeneration.

The extent of any disruption to reproduction is likely to vary between ecological groups. Where big adult trees form a small proportion of the species' population, disruption will be temporary as smaller size classes will grow to reproductive size and augment the residual reproductive population. The increased light, reduced competition and possible increase in available nutrients resulting from logging may stimulate this recruitment, for a few years at least, and typically stimulates profuse regeneration of pioneer species from seed. The size at which reproduction commences is not known for most species but has been found to be highly correlated with the mean life span of a species (Harper and White, 1974) and thus pioneer species are likely to become reproductively mature more quickly than climax species (Whitmore, 1998). Plantation-grown trees may produce viable fruit at young ages and at small sizes, e.g., 7-year-old trees of ca. 20 cm diameter at breast height (dbh) by *Shorea leprosula* (Tang, 1978). There is little comparable information from natural forests. Plumptre (1995) investigated the proportion of individuals, in increasing diameter classes, that were capable of flowering, among 16 tree species (of which eight were commercial) in the Budongo forest, Uganda. Re-analysis of the graphs shows that 10 of these species had >20% of individuals in the 20–30 cm size class fruiting. In contrast, this proportion of fruiting individuals of three species of *Entandrophragma* was found only in the 80–90 cm dbh class and above. In Malaysia, 29% of dipterocarps <40 cm dbh fruited in a newly logged forest. Fruiting was judged to be more common in small trees in the newly logged forest than in nearby unlogged or old growth forests, as increased canopy exposure stimulates increased flower production (Appanah and Manaf, 1990). In Chimanes forest, Bolivia, seed production by *Swietenia macrophylla* started at 30 cm dbh, although maximum fecundity was found in trees well over 1 m dbh (Gullison et al., 1996).

Although there appears often to be a strong relationship between tree size and fecundity (e.g. Chapman et al., 1992), most importantly the limited data available suggest that reproduction may commence well below current felling limits. This means that trees too small for timber harvesting have the potential to contribute to the breeding population, and that many of the juveniles left after logging have only to make modest growth in order to join the reproductive population.

Temporary disruption of reproduction may cause behavioural and population changes in pollinators and seed dispersers. With a temporary reduction in the resources they require within the logged area, visitation from outside may be lower. This effect should again reduce with time, as the population of reproductive trees within the logged area increases. The effect will also be small if pollinators/dispersers are non-specialist feeders, as is commonly the case because oligophagy is uncommon in tropical rain forests among frugivores and nectivores (Whitmore, 1975; van der Pijl, 1982; Maberley, 1991; Mandujano et al., 1994; Chapman and Chapman, 1996; Tutin et al., 1997; Banack, 1998; Loiselle and Blake, 1999). For tree species with specialist pollinators successful pollination may become a limiting factor (Compton et al., 1994; Ghazoul et al., 1998). In contrast, species with unspecialised pollination syndromes are only likely to suffer problems when there is a general loss of fauna. Self-incompatible species that show highly asynchronous flowering within a population, may also be more susceptible to reductions in population size as a consequence of such an Allee effect (Allee, 1931).

In summary, for the majority of tropical rain forest trees, logging will disrupt sexual reproduction, but this disruption will be transient. The reproductive population remaining after logging will be progressively augmented by juveniles growing up from seed (in the case of pioneer species) or from the numerous individuals that were less than commercial size at the time of logging (shade-tolerant species). These species therefore appear to be genetically robust in the face of logging. Only in the most light-demanding climax species there is there a risk that recruitment to reproductively mature size classes will be insufficient to safeguard genetic diversity.

There appear, therefore, to be three conditions under which logging may disrupt reproduction for much longer:

1. Where a species does not maintain a soil seed-bank and has few individuals in size classes smaller than those that are harvested. Although many of the species that fall into this category are light-demanding and capable of rapid growth in disturbed conditions, recruitment may be insufficient to prevent a significant reduction in the size of the reproductively mature population.
2. Where most of the juvenile trees have been damaged during logging.
3. Where a species is naturally slow growing and therefore recruitment to reproductive size classes is slow. Many long-lived, slow-growing species may not reach reproductive maturity until they are relatively large.

### 5. Management strategies for maintaining genetic diversity

Carefully planned and executed low-impact logging will be the most effective way of maintaining the genetic diversity in harvested populations of the majority of tropical rain forest species with reverse J size class distributions. It is also the best way to ensure that other aspects of the forest ecosystem are maintained, e.g. nutrient cycling, hydrology and carbon storage.

Those species that do not have seedling banks and have little or no advanced regeneration may suffer a substantial reduction in population size as a consequence of even low-impact logging. Many of these species will be high light-demanding species that have seedlings that do not persist in forest shade. Practical and well-known silvicultural systems already exist for these species, viz. the so-called shelterwood systems. Under such systems the canopy is opened or 'lifted' prior to felling either as a silvicultural operation, or by logging other commercial species. This creates light levels at which dense stands of seedlings are able to establish and persist. An alternative is to restrict felling to those (short) periods after a fruiting event that has resulted in a good stand of seedlings. This was an essential tenet of the Malayan Uniform System (Wyatt-Smith, 1963), because the seedling bank of some dipterocarp species reduces almost to zero between mass, supra-annual fruiting events.

An important management question is the minimum stocking that is needed, before logging, in order to

minimise the risks of loss of genetic diversity when the large adults are felled. There should be sufficient juveniles to give a high probability that, given appropriate growing conditions, each felled adult will be replaced. Species belonging to different ecological guilds will differ in seed production, seedling establishment and average mortality between successive size classes. Most pioneer species produce large quantities of seed, but seedlings have high rates of mortality. In contrast, climax species typically have a lower rate of reproduction, but suffer lower juvenile mortality. However, these general patterns are likely to be significantly affected by disturbance. As yet there is very little information on the dynamics of seedling populations in logged forests which could be used to inform management decisions.

The '50/500 rule' (Franklin, 1980) for minimum viable population size can be used to identify populations of species which are likely to be at genetic risk. The 'rule' refers to a minimum population size (50) that theoretically reduces inbreeding depression to an acceptable level and a second minimum population size (500) that is theoretically sufficient for new variation arising due to mutation to replace that lost by genetic drift. Basic knowledge of species population densities from inventories can be used to determine species for which population sizes may be critically low, but must take account of reductions in effective population sizes owing to overlapping generations, dioecy, highly asynchronous flowering, etc. Particular care should be taken when a species is known to be regionally rare or endemic, and logging of such species should be suspended. However, for species that are ubiquitous both within and outside a concession, low population numbers within a concession itself do not in themselves imply a problem. Critical levels are only likely to occur in small isolated patches of forest, where stochastic threats are generally more immediate.

For species not at risk in these ways, the forest manager should guard against appreciable erosion of genetic diversity. Estimates of the population size required to conserve plant genetic diversity have been developed to give stringent yet pragmatic guidance for seed collection of rare species. These models vary in their genetic assumptions, the breeding systems they consider, the proportion of genetic variation they aim to capture and the certainty of achieving this (Frankel

et al., 1995). Consequently the population size varies between estimates. For these species that are not rare or endemic and where current populations are to be managed sustainably, we can therefore assume a large number of populations and relax some of the more stringent sufficiency requirements (cf. Krusche and Geburek, 1991). In general, a random sample of 50 individuals from a panmictic population will contain at least one copy of all alleles that occur at frequencies of >5% with a 95% degree of certainty (Marshall and Brown, 1975; Frankel et al., 1995). This is highly conservative where multiple populations are concerned (Marshall and Brown, 1975). Forest managers should therefore ensure that populations of logged species are sufficient to recuperate to a minimum of 50 reproductive individuals. This leaves two remaining issues. The first concerns the area within which these populations must occur. For three tropical rain forest tree species pollinated by diverse small insects, 95% of the pollen received by centrally located adults (the minimum area required to encompass a natural breeding unit) came from within 40–60 ha, depending on spatial distribution of the species (Stacy et al., 1996). Similarly, studies on other species pollinated by small to medium sized insects show that significant proportions of successful pollen movement occurs over several hundred metres (Hamrick and Murawski, 1990; Boshier et al., 1995). The minimum natural breeding unit area will vary according to pollination guild and requires further research (below). However, for trees pollinated by small, diverse insects it would be reasonable to suggest

that an average of at least 1 stem  $\text{ha}^{-1}$  (i.e. 50 individuals in a 50 ha natural breeding unit) be retained within each annual logging coupe. This may be conservative, as it ignores seed dispersal. The second issue concerns the size distribution of these remnant populations. The substantial literature on forest growth models will provide suitable techniques for the forest manager to estimate the number of stems in each size class required to produce the desired density of reproductive stems and the time-frame within which this will occur (e.g. Vanclay, 1994; Alder, 1995).

## 6. Research priorities

Three priorities emerge from this debate:

1. There is still little information on the regeneration ecology of most tropical trees. Many forest managers have an empirical understanding of the ecology of the major commercial species with which they work, but this information is rarely documented. Further study is needed on the dynamics of juvenile populations in order to determine the minimum stocking that is likely to result in the replacement of felled trees.
2. Those species potentially threatened by logging should be identified. A first attempt at predicting the species most at risk in the Brazilian Amazon has already been made (Martini et al., 1994). Using the criteria outlined in this paper, Table 1

Table 1

Types of species potentially under threat of genetic erosion from low-impact selective logging

Nature of species	Identification	Management solution
Commercial-sized stems form a large proportion of the total population	Forest inventory data	Silvicultural treatment and further population inventories to ensure adequate regeneration before logging of these species
Slow-growing species that reproduce only when large	Permanent sample plots and phenological studies	Discover minimum size at which trees become reproductive. Ensure that there are more than 50 trees greater than this size before next cut
Species with specific pollinators or seed dispersers	Published scientific literature. Studies of floral and fruit morphology, and animal vectors	Modify management to avoid/reduce habitat changes that will seriously affect pollinator/disperser populations
Rare or endemic species	Published floras and forest inventories	Do not log unless there are >500 reproductively mature individuals present in concession or contiguous forest area
Outcrossing species that are self-compatible	Reproductive biology research	Ensure that there are more than 50 reproductively mature trees before next cut

Table 2  
Pre-felling density of 10 commercial species in three size classes in two 4 ha plots in Moju forest, Pará, Brazil

Species <sup>a</sup>	Family	Density (ha <sup>-1</sup> )		
		≤300 cm height <sup>b</sup>	5–44.9 cm dbh	≥45 cm dbh <sup>c</sup>
<i>Anacardium giganteum</i> Loud. ex Steud.	Anacardiaceae	13	1.1	0.1
<i>Brosimum obovata</i> Ducke	Moraceae	52	1.0	0.3
<i>Couratari oblongifolia</i> Ducke et Knuth	Lecythidaceae	333	1.8	0.6
<i>Manilkara huberi</i> (Ducke) Standl.	Sapotaceae	511	6.4	2.4
<i>Manilkara paraensis</i> Standl.	Sapotaceae	28	1.4	0.4
<i>Piptadenia suaveolens</i> Miq.	Leguminosae	459	9.0	2.4
<i>Pithecelobium racemosum</i> Ducke	Leguminosae	82	3.9	0.0
<i>Sterculia pilosa</i> Ducke	Sterculiaceae	1073	15.1	0.9
<i>Terminalia argentea</i> Mart. et Eichl.	Combretaceae	121	2.4	0.3
<i>Vouacapoua americana</i> Aubl.	Leguminosae	213	18.6	2.8

<sup>a</sup> Only those species with at least 10 individuals ≥5 cm dbh, in the two sample plots, are included in this analysis.

<sup>b</sup> Mean density from annual measurements 1994–1997 from sixty 5 × 5 m<sup>2</sup> subplots in each sample plot.

<sup>c</sup> The minimum diameter of trees that may be felled in Pará is 45 cm dbh.

describes how to identify species that may be at risk and possible management solutions. Table 2 applies these to data from Moju forest in the Brazilian Amazon. This illustrates the size distributions of the commercial species: a further 14 species were logged but had too few stems ≥5 cm dbh within the two sample plots to generate meaningful size distributions. None of the species fall into the first criterion of Table 1, i.e. commercial-sized stems (≥45 cm dbh) are a large proportion of their populations. Research should investigate the effect of logging on the ecology and genetics of such species, with a view of developing particular management strategies.

3. More information is required on the size at which trees of commercial species become reproductive in natural forests. This is needed in order to set acceptable lower size limits for felling. The minimum size at first flowering may not be the same in plantations and arboreta.
4. More estimates of the minimum area required to encompass natural breeding units are required for trees belonging to different pollination guilds and at various population densities from natural forests. This should be used in conjunction with the results on stem replacement and size of reproduction (points (1) and (3) above) to set the minimum stocking densities that must be present after logging.

As Ledig (1992) pointed out, the paucity of baseline data on the levels and dynamics of genetic diversity within tree populations makes it difficult to quantify the effects of selective logging. It is salutary to note that despite the recent enthusiasm for including genetic criteria and indicators of sustainable forest management this baseline data is still lacking.

## 7. Conclusions

It is impractical for the forest manager to make meaningful measurements of genetic variation and they are inappropriate for use as indicators of sustainable forest management. We propose, instead, that implementation of simple silvicultural rules that require adequate natural regeneration to be present before felling is permitted, will ensure that the impacts on genetic diversity are small. We agree with Ledig's (1992) assertion for selective logging, that 'Local genetic structure may be altered by selection and by changes in demography and in the mating system, but, in all probability, gene diversity and geographic structure will be little affected.'

Given contemporary extensive and intensive human intervention in the tropics, we must ensure that managed tree populations are left with sufficient genetic diversity that they can continue to adapt to whatever future conditions may develop. By dint of their



population structure, the genetic diversity of the majority of tropical rain forest trees is unlikely to be significantly affected by low-impact selective logging. The fact that only a small fraction of their populations will be killed mitigates against genetic drift, dysgenic selection and all but a temporary disruption to reproductive processes. By the same argument, we highlight those species likely to be most vulnerable, viz. the light-demanding climax species, for which a standard shelterwood system should be used.

We are concerned that criteria and indicators for the conservation of genetic diversity such as those proposed by CIFOR C&I Team (1999) are impractical and will deter forest managers from making any meaningful attempt to maintain genetic diversity in production forests. Instead, we propose that forest managers use a list of simple ecological criteria to assess which species may be at risk from logging and then target management so as to alleviate any possible problems.

### Acknowledgements

Thanks to Milton Kanashiro for inviting one of us (SBJ) to attend the DENDROGENE workshop held in Belém, Brazil in May 1998, which inspired this review. SBJ, TCW and DHB were supported by the British Government's Department for International Development when this review was written. Thanks to Stephen Harris, Bryan Finegan, Jeff Burley and Mark Sandiford for constructive criticism and discussion.

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