ORIGINAL PAPER

Ecological considerations for using dipterocarps for restoration of lowland rainforest in Southeast Asia

Chris J. Kettle

Abstract The lowland dipterocarp forests of Southeast Asia support a substantial proportion of the world's biodiversity. They are of considerable environmental and economic value at the local, regional and global scale, providing many goods and services to a growing population. The forests of this region are among the fastest disappearing in the world and restoration is urgently required. This paper provides a review of the ecological constraints to restoration of lowland dipterocarp forest in Southeast Asia. It focuses on the production of planting stock, the significance of site-species matching and post-planting site maintenance. It identifies gaps in our knowledge and highlights priority areas of research. Adopting a long-term view is essential for restoring as well as conserving the dipterocarp forests of Southeast Asia. An immediate strategy for the conservation and management of dwindling genetic resources of these important timber species is essential. This will provide the foundations for sourcing seed and production of planting material for longer term restoration. The importance of species-site matching, mycorrhizal fungi and post-planting maintenance for restoration are apparent. Financing is a major limiting factor to dipterocarp forest restoration. Trading in carbon, private finance and environmental markets afford considerable opportunities for restoring these forests providing their total value is recognised. Despite the wealth of ecological knowledge we already have for scientifically-informed forest restoration, without the backing of governments and corporate stakeholders, forest restoration will not gain the urgently required momentum.

Keywords Conservation · Restoration · Rehabilitation · Tropical rainforest · Dipterocarpaceae · Enrichment planting

C. J. Kettle (✉)
Institute of Terrestrial Ecosystems, Ecosystem Management, ETH Zurich, CHN G73.2,
Universitaetstrasse 16, 8092 Zurich, Switzerland
e-mail: chris.kettle@env.ethz.ch

Introduction

The lowland rainforests of Southeast Asia are globally significant and among the most diverse forests in the world supporting a sizeable proportion of the world's biodiversity (Myers et al. 2000; Davies et al. 2005). These forests provide numerous ecosystem services including fresh water management, soil protection and pollination services. From a global perspective, perhaps the most significant is the storage of carbon. Deforestation accounts for 18% of global greenhouse gas emissions (Angelsen et al. 2009). Moreover, Southeast Asia is estimated to contribute 29% of the global total from deforestation (Phat et al. 2004). Recent reports indicate that the rate of tropical forest loss in the region is greater than all other tropical regions (Bradshaw et al. 2009). The rapid degradation of tropical forests and its conversion to alternative land use is predicted to have catastrophic implications for biodiversity (Wilcove and Koh 2010), and the resilience of these regions.

Substantial areas of forest in Southeast Asia are dominated by the single family of trees the Dipterocarpaceae, with 13 of the 16 genera and 92% of the 510 species restricted to Asia (Bawa 1998). The family is ecologically dominant and also economically significant. The dipterocarps account for 80% of timber exports from the region providing a major source of revenue for many developing nations. Round-wood logs of dipterocarp species formed 25% of global consumption of tropical hardwoods, valued at almost half a billion US$ between 2006 and 2007 (ITTO 2008). The long-term resilience and resistance of these lowland dipterocarp forests and the conservation of the supported biodiversity depends on a myriad of factors, including economics, political will and scientifically-informed management.

There is an urgent need not only to arrest current rates of deforestation (Koh 2007a) but to reverse the trend in declining native forest cover in Southeast Asia. This paper provides a review of the ecological constraints to lowland dipterocarp forest restoration. It identifies major gaps in our knowledge and highlights areas of research that should be a priority. It is recognised that other tree families such as the Burseraceae, Lauraceae, Fabaceae and Moraceae are important in restoration, but this manuscript focuses specifically on the Dipterocarpaceae as one of ecologically and economically dominant groups within the region. Specifically it focuses on the production of planting stock of dipterocarp species for restoration, the significance of site-species matching, and post-planting site maintenance for successful restoration.

Current situation

Secondary forest constituted 63% of the total forest cover in Southeast Asia in 2005 (data extracted from Koh 2007a). Secondary forests have an important role in sustaining the region's biodiversity (Barlow et al. 2007; Meijaard and Sheil 2007) and providing other ecosystem services such as carbon storage (Berry et al. 2010). However, due to declining timber stocks (FAO 2007) and reduction in timber concessions (Dennis et al. 2008) such forests become increasingly at risk of conversion. Rural poverty and shifting cultivation (Lawrence 2004) conversion to biofuels (Koh 2007b; Wilcove and Koh 2010), as well as increasing fire frequency (Langner and Siegert 2009) all jeopardise the resilience of forest landscapes in Southeast Asia. Meeting international targets to prevent biodiversity loss (Convention on Biological Diversity) and mitigate climate change (Kyoto Protocol) require a radical shift in strategy to increase the ecological and economic value of degraded forest lands. There are a number of ecological reasons why dipterocarp forests may be

especially sensitive to habitat degradation and fragmentation. Briefly, many species have a low density of reproductive adults, they are insect pollinated, have poor seed dispersal, and recalcitrant seeds, traits which are likely to reduce the resilience of dipterocarp forest to fragmentation (Aguilar et al. 2006). A more holistic approach to Sustainable Forest Management which incorporates these factors is urgently needed to prevent future degradation (de Freitas and Pinard 2008; Sist et al. 2008). However, for the large areas of already degraded forest land, planting of nursery-reared native tree seedlings can increase their economic and ecological value (Edwards et al. 2009).

Challenges to restoration of dipterocarp forest

When and where is planting necessary?

Nearly two decades ago it was estimated that there were at least 70 million hectors of seriously depleted forest which has been over-logged and subject to shifting cultivation in Southeast Asia (ITTO 1990 in Adjers et al. 1995). In order to gain an up-to-date, albeit coarse, picture of the extent of land that might be amenable for planting, the following simple analysis was conducted. I calculated two estimates of degradation based upon area of forest with (i) canopy cover >10 and <25% and (ii) canopy cover >10 and <50%. These data are derived from automated algorithms run on data gathered by the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument during 2000 (WRI 2009). To these estimates I added land area dominated by the invasive grass *Imperata cylindrica* taken directly from Garrity et al. (1997). Based upon these assumptions it is predicted that as much as 15–30% of total land cover (50–130 million hectors) in Southeast Asia may be amenable to reforestation or restoration (Fig. 1). The resolution of current data sets to estimate land amenable for forest restoration is limited. Developing new data sets based on landscape indicators, such as forest canopy gap fraction (Asner et al. 2006), cropland expansion (Morton et al. 2006), and fire damage (Langner and Siegert 2009) which can be determined using remote sensing should provide greater resolution.

The strategies which can be employed to restore tropical forests have been reviewed by Lamb et al. (2005). Decisions on which strategies to adopt are based upon weighing the cost and benefits associated with the specific objectives of restoration, and especially the extent to which processes of natural regeneration are severed. Restoration of dipterocarp forest and degraded land are most likely to be via two main pathways: (a) enrichment planting: planting seedlings of the most economically desirable dipterocarp seedlings in degraded forest in order to increase its timber productivity; (b) complete forest restoration, which involves establishing a nurse canopy of fast-growing light-demanding species followed by under-planting with dipterocarps. Table 1 summarises the main strategies and highlights the (hypothetical) optima where the greatest benefit is gained at the least cost. In reality such decisions will be made on a case by case basis and will often be driven by other social and political factors. To prevent further conversion of secondary or primary forest to croplands, conservationists are calling for completely degraded land to be used for the expansion of crops, such as oil palm plantations, as a matter of priority (Wilcove and Koh 2010).

There have recently been a number of major initiatives to rehabilitate forests via planting. These include international initiatives, such as the UNEP billion trees campaign, and more regional projects, such as the 5MHRP in Vietnam (McNamara et al. 2005), the Sow a Seed program funded by IKEA and the FACE Foundation Innoprise project which respectively aim to restore 8000 and 30000 ha of degraded dipterocarp forest in Borneo (www.searrp.org,
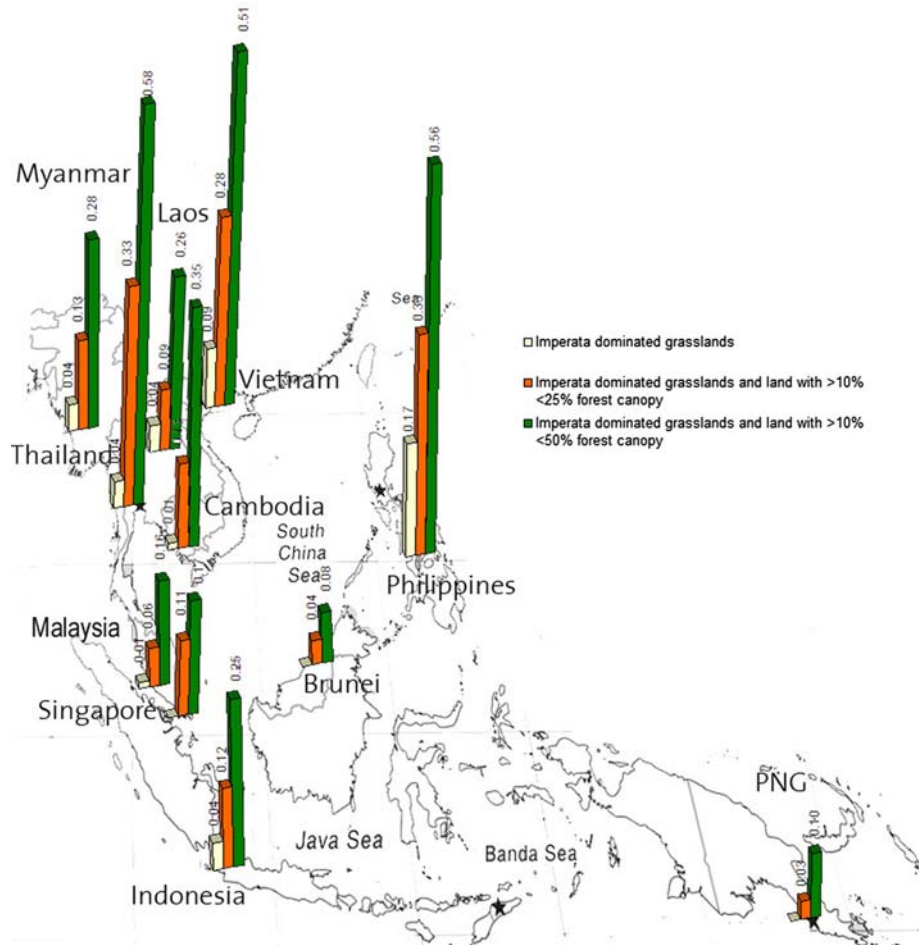
Fig. 1 Illustration of the proportion of total land area per Southeast Asian country which may be amenable to forest restoration and rehabilitation, based on extent of *Imperata* grasslands and forests with less than 25% or less than 50% canopy cover

2009) by enrichment planting (Moura-Costa et al. 1994). The real biodiversity benefits of these projects will depend on their ability to restore ecological function. Plantations of exotic species which are destined to be clear felled should not be accepted as forms of forest rehabilitation. Enrichment planting of native tree species on logged dipterocarp forest has recently been reported to increase the landscape scale diversity of avian assemblages (Edwards et al. 2009) clearly enhancing biodiversity value. There is an urgent need for internationally recognised criteria for what constitutes forest rehabilitation to ensure that such projects have a genuine biodiversity and environmental benefit. Enrichment planting of commercially logged dipterocarp forest has been extensively established in Indonesia, while Malaysia has only more recently begun to investigate this as a management strategy (Weinland 1998). Establishment of commercial plantations of valuable dipterocarp species has been the focus of research in Southeast Asia for nearly a century. To date, juvenile

Table 1 Matrix of forest degradation and different strategies of forest restoration scored for their associated financial costs and benefits (ecological, social and economic)

The shaded cells indicate those scenarios where the benefits are greater than the costs. The ellipse indicates a hypothetical window of optimal decisions

dipterocarps have been considered too sensitive for even age plantations (Weinland 1998). Although plantation forest is increasingly being recognised for its biodiversity benefits in temperate regions (Brockerhoff et al. 2008) plantations of exotic species in the tropics have considerably lower biodiversity value than secondary forest (Barlow et al. 2007) and conversion of secondary forest to exotic plantation will lead to further biodiversity losses. The use of native species for plantations is likely to have far greater biodiversity benefits than either exotic plantations or conversion to other land uses such as oil palm. Of course, these management strategies fundamentally depend on the ability to produce sufficient numbers of viable seedlings of appropriate native tree species for planting.

Challenges to large scale production of dipterocarp planting material

Seed collection

The technical knowledge to propagate dipterocarps on a relatively large scale exists (Weinland 1998) although at the national level capacity may be limited. Dipterocarp reproductive ecology however, provides considerable challenges for the forest nurseries, which may in part explain why enrichment planting and restoration have not been highly successfully in the past (Appanah 1998). Firstly, seed production in dipterocarps is unpredictable (Bawa 1998; Paquette et al. 2009) and mast-fruiting is often super-annual

with trees producing fruits at the same time with overlapping windows between species (Ashton et al. 1988; Maycock et al. 2005; Brearley et al. 2007a). This challenge is exacerbated by the fact that diptercarp seeds are recalcitrant and cannot be stored for long periods of time (Adjers and Otsamo 1996). Secondly, most dipterocarps are huge trees, many ranging in height from 30 to 60 m and with dbh > 3 m. Climbing trees to collect seeds is an extremely technical and often dangerous task, meaning that it is not easy to collect seeds before they fall. From a practical perspective, collecting seeds has to be done over relatively short intensive periods of a few weeks, with regular phenological monitoring. Knowledge on dipterocarp seed handling and storage, as well as germination and potting, has been established for the major commercial species (Adjers and Otsamo 1996). Seeds need to be collected as quickly as possible, protected from fungal infection, overheating, physiological breakdown and germinated as soon as possible. This makes the collection of rare species of dipterocarp very difficult, given that many only survive in remote forest locations.

Genetic constraints

The genetic quality of dipterocarp seed collections has received little research attention. Recent studies of gene flow and genetic diversity in adult populations (Konuma et al. 2000; Kenta et al. 2002, 2004; Ng et al. 2004; Lee et al. 2006; Fukue et al. 2007) enable us to make some generalisations. Habitat fragmentation is likely to lead to a reduction in the effective population size of many dipterocarp species, especially small-flowered species which may have more restricted gene flow (Kettle et al., submitted-b). A reduction in stand density and isolation of individuals may lead to elevated inbreeding. Seed collections for restoration, which constitute a high proportion of inbred individuals, have been reported in tropical conifers (Kettle et al. 2008). Ideally seed collections should be made from primary forest stands with a good density of reproductive adults. Unfortunately, due to the extent of forest degradation this may not always be an option. Seed production in logged forest has been recorded as low as 23% compared to primary forest for dipterocarps (Curran and Webb 2000). There is a major gap in our knowledge of seed yields for commercial dipterocarp species. Such data will be especially important for developing sustainable seed harvesting strategies. Recent studies indicate that species of dipterocarp are likely to be differentially susceptible to the negative genetic consequence of fragmentation (Kettle et al., submitted-a, submitted-b) and selective logging (Ng et al. 2009).

Wildling collection

An alternative and favoured approach is to collect wildlings (wild seedlings) from the forest floor. This may result in better genetic quality of the planting stock because these seedlings have already been through a selection process on the forest floor (Kettle et al. 2008). Wild seedlings are likely to have been the result of several reproductive seasons and thus be more genetically diverse than a single seed collection. Collection of wildings is not without its challenges, they often suffer from rapid and high mortality post-germination on the forest floor, and collection and transport can be logistically difficult, together with slow hardening off periods before planting (Weinland 1998). The extent to which wilding collections may negatively impact on natural regeneration in remnant forest is not well understood and seedling banks in some reserve forests of Borneo have been devastated by wildling collecting (Nilus, Pers. Commun.).

Vegetative propagation

The large majority of enrichment planting in Indonesia uses plants propagated using vegetative stem cutting from wildlings (Weinland 1998). In Malaysia vegetative propagation has remained largely experimental, although bulk clones of seedlings from collected wildings for a number of commercial species (*Shorea parvifolia*, *S. leprosula*, *S. acuminata*, *S. bracteolata*, *S. roxburgii* and *Hopea odorata*) have been established (Ahmad 2006). Vegetative propagation has a number of practical and economic advantages over sexual propagation. It saves time and can produce uniform planting stock continuously throughout the year from selected parental stock. There are obvious disadvantages; by definition this leads to the homogenisation of the planting material which could increase vulnerability of planting material to both existing and novel pests and pathogens, as illustrated in crop species (Zhu et al. 2000). This could also have serious implications for future reproduction of restored forest and their long-term viability. If species are highly self-incompatible then breeding between ramets of the same clone is likely to fail. Furthermore, if restored forests are made up of a high proportion of clonal ramets of specific genotypes, this could lead to the loss of genetic variation in remnant natural forest stands through genetic swamping of remnant population with maladaptive genes (Hedrick 2005). The constraints on seed and wildling collections are significant, but the use of vegetative propagation should not be viewed as a panacea.

Scientifically-informed seed and wildling collections, coupled with a long-term commitment to establish in-situ and ex-situ seed orchards and genetic reserves, should be high on the agenda of the forestry sector. Such seed orchards represent a win–win situation in the long term, as these can be established from selected genotypes of mother trees which show adaptation to given sites, have desirable form and ensure the maintenance of species genetic diversity. Seed orchards could be established alongside areas in need of restoration and could increase connectivity within the forested landscape as well as more accessible seed and/or seedlings. Selection of progeny from a sufficiently large number of Plus trees (trees selected for superior form and value) to establish seed orchards should ensure the minimum of inbreeding (Lee 2000). Theoretically collecting from 30 to 50 adult trees should be sufficient, assuming that viability is equivalent across individuals. Seed orchards not only provide a means of seed production and ex-situ conservation, but also the opportunity to explore levels of local adaptation, site specificity and a means of certification of provenance in addition to providing employment in rural locations. Seed orchards could be integrated into other agroforestry systems (Erdmann 2005) or even in oil palm plantations, under new initiatives such as POTICO described by Wilcove and Koh (2010). These would not only increase the biodiversity value of such lands but increase the landscape connectivity for many forest species (Brockerhoff et al. 2008).

What to plant and where

Site conditions can provide major constraints to survival of seedlings whether in enrichment planting of logged forest, secondary forest or totally degraded land. These constraints can be separated into abiotic effects associated with limited resource availability (soil nutrients, moisture and light) and biotic effects, such as herbivory, pathogens, competition and microbial symbiosis. This necessitates the careful selection of appropriate site and species. Soil compaction is a major constraint to the survival of naturally regenerating and planted dipterocarp seedlings (Nussbaum et al. 1995; Nussbaum 1996). Loss of the surface soil, which contains much of the nutrients for plant growth, limits seedling establishment.

Restoration of degraded lands

The natural succession pathways for forest recovery following anthropogenic disturbance can be very slow or even completely blocked. Many studies have demonstrated that planting native species can reverse this process (Lamb et al. 2005). In Southeast Asia, nitrogen fixing exotic pioneer species such as *Acacia mangium* have been favoured as plantation species and as a nurse species for restoration of native forest on degraded sandy soils (Norisada et al. 2005). However, given the increasing reports of invasion by exotic species, including *A. mangium* in Brunei (Osunkoya et al. 2005) native species should be used as a preference for establishing nurse canopies for reforestation. A recent study (Shono et al. 2007) using 45 native tree species to restore degraded land in Singapore, revealed survival rates over a period of five years greater than 90% across species. Among the seven dipterocarp species planted, four showed good performance, emphasising the variation between species exposure tolerance during early establishment (Shono et al. 2007). *Shorea leprosula,* for example, is known to benefit from open conditions. In contrast *S. ovalis* and *S. macroptera* have consistently been shown to perform poorly in open sites (Shono et al. 2007). These findings emphasise the importance of research to enable site-species matching for restoration of dipterocarp forest, and the potential for native species to be used to establish a nurse canopy.

Dipterocarp species have been shown to have habitat associations with both topography and edaphic factors in a number of studies (Paoli et al. 2006; Russo et al. 2008; Suzuki et al. 2009). Paoli et al. (2006) showed that 18 of 22 species of dipterocarp at a site in Borneo showed negative or positive associations with either granitic or alluvial soils, similar observations were also made with soil nutrients. These associations are thought to reflect trade-offs between fast growth and low mortality (Russo et al. 2008). In a study of eleven species of dipterocarp at a site in Peninsular Malaysia, *Shorea maxwelliana* was associated with well-drained alluvial soils on flat lands, while *S. leprosula* favoured less well-drained valley soils (Suzuki et al. 2009). Many of these habitat associations were significant at early life stages, emphasising the importance of these factors for site-species matching in the early establishment phase of forest restoration. There is a substantial body of knowledge on the floristic variation in dipterocarp forest over relatively large geographic scales, for example over the whole of Sarawak (Potts et al. 2002). However, such information may not always be adopted or in a form accessible to forestry practitioners. Research investigating levels of local adaptation in dipterocarps, including provenance trials, will not only improve our ability for site-species matching, but also the extent to which generalisations can be made across regions.

Taxonomy

The high diversity and lack of specialist taxonomists able to determine species of dipterocarp presents a considerable constraint for their management. While identification of some of the most widespread and common species is less problematic, identification of rare species, and especially wildlings collected for either ex-situ conservation or restoration, can be a problem. Given the importance of site-species matching for the success of restoration programmes, correct determination of seedlings to the species level is relevant. Recent advances in DNA barcoding of land plants (CBOL 2009) are likely to revolutionise species delimitation in the future. This will be especially useful for seedling discrimination of taxonomically cryptic species but, only when such methods are relatively routine and inexpensive.

Mycorrhizae

The Dipterocarpaceae are largely ectomycorrhizal in their associations, although a few species are thought to form both ecto- and arbuscular mycorrhizas (Lee 2006). The main groups of fungi involved in dipterocarp symbiotic associations include: Russulales, Amanitales, Botetales, Cantharellales and some hypogeous taxa (Lee et al. 2008). Molecular evidence indicates that the Thelephoraceae are commonly associated with the Dipterocarpaceae (Sirikantaramas et al. 2003). In Sabah, the diversity of morphospecies found on seedlings of *Hopea nervosa* was 40% greater in unlogged than logged forest (Alexander and Lee 2005). The potential for improved establishment of dipterocarp seedlings with the inoculation of mycorrhiza has been demonstrated for several species (Brearley et al. 2007b; Lee et al. 2008). This work has demonstrated that species of dipterocarp and their mycorrhizal symbionts can be partitioned along contrasting abiotic axes (Brearley et al. 2007b). On a more practical level, inocula isolated from one species can be successfully inoculated into other species and even genera, leading to improved mineral nutrition and drought tolerance (Lee et al. 2008). Dipterocarp seedlings inoculated with ectomycorrhizal fungi do not always successfully develop ectomycorrhizas, but inoculation of unidentified fungi improves phosphorus uptake and growth of some dipterocarp seedlings in the nursery. A native species isolated from *Shorea parvifolia* has shown to persist on roots up to 6 months after planting in degraded sites (Lee et al. 2008).

Isolating ectomycorrhiza inoculum that persist on hosts dipterocarp seedlings both in nursery and field conditions, show signs of improving seedling growth and survival in the early stages of establishment (Lee et al. 2008). However, a clear gap in our knowledge is the extent to which inocula are adapted to certain host species and site conditions. Advances in molecular techniques used to refine our knowledge of the taxonomy, inter and intra-specific genetic variation within mycorrhiza will help with this endeavor (van der Heijden et al. 2008).

Herbivory and pathogens

Changes in the herbivore community as a consequence of habitat degradation have consequences for seedling communities, whether natural or planted. A reduction in herbivores can lead to an increase in seedling density but a substantial loss of species diversity (Dalling and Burslem 2008). Fragmentation can often have similar and synergistic effects where trophic cascade effects on the herbivore community have resulted in increased seedling herbivory (Dalling and Burslem 2008). Evidence of density dependent mortality and pathogen outbreaks can impact on adult tree density (Augspurger and Kelly 1984). This has implications for the patterns and densities under which seedlings should be planted. For example, high densities of conspecific seedlings could suffer greater mortality. Planting a high species diversity of seedlings is likely to minimise the effects of density dependent mortality. Moreover, planting seedlings at a distance from adult conspecifics which may harbour pests or pathogens may also reduce mortality (Okuda et al. 1997).

Planted and not forgotten

Tending and site maintenance

Understanding the regeneration niche of dipterocarps and how they partition along axes associated with light as well as edaphic factors (Matsune et al. 2006; Romell et al. 2008; Dent and Burslem 2009; Romell et al. 2009) is not only important for site selection, but for

determining their requirements post-planting. Although low light intensity is important during germination and early establishment, there is considerable variation between species survival and growth rates in response to tending, weeding and gap management, such as by girdling or thinning of fast growing pioneer species (Adjers et al. 1995; Matsune et al. 2006). Research on the effects of gap creation and its shape has provided insight into the importance of light environment for regeneration of dipterocarp forest (Romell et al. 2008, 2009). Survival rates for planted dipterocarps in gap or line planting have been recorded ranging from 40 to 86%. Artificial shade house experiments (Ashton et al. 2006) recorded survival between 67 and 97% in seedlings of two *Dipterocarpus* species for two years, with the highest mortality under deep shade. Reduction in the density of the subcanopy has shown to increase seedling survival in three out of four study species (Romell et al. 2008). *Shorea pauciflora*, the one exception, has high survival rate irrespective of subcanopy treatment, indicating differential capability to respond to low light levels. Canopy openness appears to have clear effects on growth, with dipterocarp seedlings growing faster under wider gaps (Adjers et al. 1995; Otsamo 2000; Bebber et al. 2002; Romell et al. 2008). Interestingly, girdling of canopy trees led to increased relative height growth (Romell et al. 2008) despite having no effect on light availability (Romell et al. 2009), suggestive of the potential effects of below ground competition. In summary, once planted, dipterocarp seedlings are likely to require considerable tending to maintain optimal light environments for growth and survival, especially during restoration of completely degraded lands. Such tending is species and site specific, and will add considerable cost to any restoration project.

Financial constraints

The economic, social and environmental values of forests are widely recognised. Some 1.6 billion people depend on forests for food, fuel and livelihoods (UN-DESA 2009). The importance of sustaining forest landscapes for poverty alleviation is becoming increasingly clear (MDG 2009). However, immediate local needs often drive decisions for land use change. Restoration of forest landscapes is a long-term process which requires sustained sources of funding as well as substantial political will. Opportunities for long-term funding are available across the private, public, international and NGO sectors, including payment for environmental services, such as watershed protection or carbon storage, taxes, subsidies, multilateral donors as well as private for-profit sources such as socially and environmentally responsible investment companies and certified forest goods such as the Forest Stewardship Council (FSC). Access to such financing requires unification of the economic, social and environmental objectives of forest restoration so as to demonstrate the significance of restoration for poverty alleviation (Schuyt 2005). Accurate estimates of the full economic value of a forest restoration will enable this to be weighted realistically against other land uses. Reforestation projects are increasingly being financed under the auspices of the Clean Development Mechanism (CDM) ratified by the Kyoto Protocols scheme for trading "Certified Emissions Reductions" CER's (UNFCCC 2009; Paquette et al. 2009). Currently afforestation/reforestation accounts for a tiny fraction of registered CDM's (0.03%) (UNFCCC 2009). Such schemes have the potential to provide low-income communities with a source of income and other ecological and social benefits. However, the feasibility of small scale reforestation projects has been questioned (Coomes et al. 2008). Currently, to be eligible for financing under the CDM, sites must have been devoid of forest as of the end of 1989. In effect this excludes schemes which employ enrichment planting of existing but degraded forest, from being financed under the CDM, despite the

major economic and ecological advantages they may offer (Paquette et al. 2009). For example, enrichment planting of dipterocarp forest in Malaysian Borneo is estimated to cost between 10 and 30% of the costs for restoration of completely degraded land (Maycock, Pers. Commun.)

Outlook and conclusion

Rates of deforestation in Southeast Asia remain among the fastest in the world. Degradation of secondary forest and subsequent land conversion has global consequences. Establishment of strategies for restoration and regeneration of degraded lowland rainforest is of paramount importance. There are a number of circumstances where the recovery of lowland rainforest will only be realised by planting native species. Enrichment planting and complete restoration can increase the biodiversity and long-term economic value of large areas of Southeast Asia. When weighting the fundamental cost-benefits of these alternative approaches, enrichment planting is likely to be the preferable option. However, the visibility of complete forest restoration may raise community environmental consciousness with additional societal and political benefits. Such aims require great political will and considerable economic incentives which may be facilitated by international agreements based upon the Kyoto protocol. However, ecological constraints to restoration and regeneration associated with the Dipterocarpaceae need to be addressed by scientific research and local capacity building. Establishment of ex-situ conservation units, seed orchards and research on the genetic resources of major dipterocarp species are urgently required. Increasing our knowledge and capacity to generate large volumes of appropriate and genetically diverse planting stock from a range of species is fundamental to successful forest recovery. In the long-term these initiatives could have major ecological and economic benefits but action is needed now to ensure that the vital genetic resources of many important species are not lost forever. Although much of the ecological knowledge to achieve successful forest restoration already exists, without the backing of governments and corporate stakeholders, scientifically-informed forest restoration action will not gain the urgently required momentum.

References

Adjers G, Otsamo A (1996) Seedling production methods of dipterocarps. In Schulte A, Schone D (eds) Dipterocarp forest ecosystems towards sustainable management. World Publishing Co. Pte. Ltd., Singapore, pp 391–410

Adjers G, Hadengganan S, Kuusipalo J, Nuryanto K, Vesa L (1995) Enrichment planting of dipterocarps in logged-over secondary forests—effect of width, direction and maintenance method of planting line on selected *Shorea* species. For Ecol Manag 73:259–270

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980

Ahmad DH (2006) Vegetative propagation of dipterocarp species by stem cuttings using a very simple technique. In: Suzuki K, Ishii K, Sakurai SSS (eds) Plantation technology in tropical forest science. Springer, Tokyo, pp 69–77

Alexander IJ, Lee SS (2005) Mycorrhizas and ecosystem processes in tropical rain forest: implications for diversity. In: Burslem DFRP, Pinard MA, Hartley SE (eds) In biotic interactions in the tropics. Cambridge University Press, Cambridge, pp 165–203

Angelsen A, Brown S, Loisel C, Pwekett L, Streck C, Zarin D (2009) Reducing emissions from deforestation and forest degradation (REDD): an options assessment report

Appanah S (1998) Management of natural forests. In: Appanah S, Turnbull JM (eds) A review of dipterocarps taxonomy, ecology, silviculture. Centre for International Forestry Research, Bogor, pp 133–149

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae—new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132:44–66

Ashton MS, Singhakumara BMP, Gamage HK (2006) Interaction between light and drought affect performance of Asian tropical tree species that have differing topographic affinities. For Ecol Manag 221:42–51

Asner GP, Broadbent EN, Oliveira PJC, Keller M, Knapp DE, Silva JNM (2006) Condition and fate of logged forests in the Brazilian Amazon. Proc Natl Acad Sci USA 103:12947–12950

Augspurger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings—experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61:211–217

Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, Motta CD, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci USA 104:18555–18560

Bawa KS (1998) Conservation of genetic resources in the Dipterocarpaceae. In: Appanah S, Turnbull JM (eds) Review of the dipterocarps: taxonomy, ecology, silviculture. CIFOR, Bogor

Bebber D, Brown N, Speight M, Moura-Costa P, Wai YS (2002) Spatial structure of light and dipterocarp seedling growth in a tropical secondary forest. For Ecol Manag 157:65–75

Berry NJ, Phillips OL, Lewis SL, Hill JK, Edwards DP, Tawatao N, Ahmad N, Magintan D, Khen CV, Mohammed M, Ong R, Hamer K (2010) The value of logged tropical forests: lessons from northern Borneo. Biodivers Conserv (this issue)

Bradshaw CJA, Sodhi NS, Brook BW (2009) Tropical turmoil: a biodiversity tragedy in progress. Front Ecol Environ 7:79–87

Brearley FQ, Proctor J, Suriantata, Nagy L, Dalrymple G, Voysey BC (2007a) Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo. J Ecol 95:828–839

Brearley FQ, Scholes JD, Press MC, Palfner G (2007b) How does light and phosphorus fertilisation affect the growth and ectomycorrhizal community of two contrasting dipterocarp species? Plant Ecol 192:237–249

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

CBOL PWG (2009) A DNA barcode for land plants. PNAS 106:12794–12797

Coomes OT, Grimard F, Potvin C, Sima P (2008) The fate of the tropical forest: carbon or cattle? Ecol Econ 65:207–212

Curran LM, Webb CO (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. Ecol Monogr 70:129–148

Dalling JW, Burslem DFRP (2008) Anthropogenic disturbance in tropical forests: toward a functional understanding of seedling responses. In: Leck MA, Parker VT, Simpson RL (eds) Seedling ecology and evolution. Cambridge University Press, Cambridge, pp 332–351

Davies SJ, Tan S, LaFrankie JV, Potts MD (2005) Soil-related floristic variation in a hyperdiverse dipterocarp forest. In: Roubik DW, Sakai S, Hamid Karim AA (eds) Pollination ecology and rain forest. Springer, New York

de Freitas JV, Pinard MA (2008) Applying ecological knowledge to decisions about seed tree retention in selective logging in tropical forests. For Ecol Manag 256:1434–1442

Dennis RA, Meijaard E, Nasi R, Gustafsson L (2008) Biodiversity conservation in Southeast Asian timber concessions: a critical evaluation of policy mechanisms and guidelines. Ecol Soc 13(1):25

Dent DH, Burslem D (2009) Performance trade-offs driven by morphological plasticity contribute to habitat specialization of Bornean tree species. Biotropica 41:424–434

Edwards DP, Ansell FA, Ahmad AH, Nilus R, Hamer KC (2009) The value of rehabilitating logged rainforest for birds. Conserv Biol 23:1628–1633

Erdmann TK (2005) Agroforestry as a tool for restoring forest landscapes. In: Mansourian S, Vallauri D, Dudley N (eds) Forest restoration in landscapes: beyond planting trees. Springer, New York, pp 274–279

FAO (2007) State of the worlds forests. Food and Agriculture Organisation of the United Nations, Rome

Fukue Y, Kado T, Lee SL, Ng KKS, Muhammad N, Tsumura Y (2007) Effects of flowering tree density on the mating system and gene flow in *Shorea leprosula* (Dipterocarpaceae) in Peninsular Malaysia. J Plant Res 120:413–420

Garrity DP, Soekardi M, VanNoordwijk M, DelaCruz R, Pathak PS, Gunasena HPM, VanSo N, Huijun G, Majid NM (1997) The Imperata grasslands of tropical Asia: area, distribution, and typology. Agrofor Syst 36:3–29

Hedrick P (2005) 'Genetic restoration': a more comprehensive perspective than 'genetic rescue'. Trends Ecol Evol 20:109

ITTO (1990) Annual review and assessment of the world timber situation. International Tropical Timber Organisation, Yokohama

ITTO (2008) Annual review and assessment of the worlds timber situation. International Tropical Timber Organisation, Yokohama

Kenta T, Shimizu KK, Nakagawa M, Okada K, Hamid AA, Nakashizuka T (2002) Multiple factors contribute to outcrossing in a tropical emergent *Dipterocarpus tempehes*, including a new pollen-tube guidance mechanism for self-incompatibility. Am J Bot 89:60–66

Kenta T, Isagi Y, Nakagawa M, Yamashita M, Nakashizuka T (2004) Variation in pollen dispersal between years with different pollination conditions in a tropical emergent tree. Mol Ecol 13:3575–3584

Kettle CJ, Ennos RA, Jaffre T, Gardner M, Hollingsworth PM (2008) Cryptic genetic bottlenecks during restoration of an endangered tropical conifer. Biol Conserv 141:1953–1961

Kettle CJ, Hollingsworth PM, Burslem DFRP, Maycock C, Khoo E, Ghazoul J (submitted-a) Fine-scale spatial genetic structure and genetic diversity in three dipterocarp tree species with contrasting flower size

Kettle CJ, Maycock C, Ghazoul J, Hollingsworth PM, Khoo E, Burslem DFRP (submitted-b) Flower size and differential pollination success in tropical forest trees

Koh LP (2007a) Impending disaster or sliver of hope for Southeast Asian forests? The devil may lie in the details. Biodivers Conserv 16:3935–3938

Koh LP (2007b) Potential habitat and biodiversity losses from intensified biodiesel feedstock production. Conserv Biol 21:1373–1375

Konuma A, Tsumura Y, Lee CT, Lee SL, Okuda T (2000) Estimation of gene flow in the tropical-rainforest tree *Neobalanocarpus heimii* (Dipterocarpaceae), inferred from paternity analysis. Mol Ecol 9:1843–1852

Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1632

Langner A, Siegert F (2009) Spatiotemporal fire occurrence in Borneo over a period of 10 years. Glob Chang Biol 15:48–62

Lawrence D (2004) Erosion of tree diversity during 200 years of shifting cultivation in Bornean rain forest. Ecol Appl 14:1855–1869

Lee SL (2000) Mating system parameters of *Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae) in three different forest types and a seed orchard. Heredity 85:338–345

Lee S-S (2006) Mycorrhizal research in Malaysian plantation forestry. In: Suzuki K, Ishii K, Sakurai S, Sasaki S (eds) Plantation technology in tropical forest science. Springer, Tokyo, pp 157–166

Lee SL, Ng KKS, Saw LG, Lee CT, Muhammad N, Tani N, Tsumura Y, Koskela J (2006) Linking the gaps between conservation research and conservation management of rare dipterocarps: a case study of *Shorea lumutensis*. Biol Conserv 131:72–92

Lee SS, Patahayah M, Chong WS, Lapeyrie F (2008) Successful ectomycorrhizal inoculation of two dipterocarp species with a locally isolated fungus in Peninsular Malaysia. J Trop For Sci 20:237–247

Matsune K, Soda R, Sunyoto, Tange T, Sasaki S, Suparno (2006) Planting techniques and growth of dipterocarps in abandoned secondary forest in East Kalimantan, Indonesia. In: Suzuki IKK, Sakurai S, Sasaki S (eds) Plantation technology in tropical forest science. Springer, Tokyo

Maycock CR, Thewlis RN, Ghazoul J, Nilus R, Burslem D (2005) Reproduction of dipterocarps during low intensity masting events in a Bornean rain forest. J Veg Sci 16:635–646

McNamara S, Tinh DV, Erskine PD, Lamb D, Yates D, Brown S (2005) Rehabilitating degraded forest land in central Vietnam with mixed native species plantings. In: Workshop on improving productivity in mixed-species plantations. Ballina, Australia, pp. 358–365

MDG (2009) Millenium Development Goals report, 2009. MDG, New York

Meijaard E, Sheil D (2007) A logged forest in Borneo is better than none at all. Nature 446:974–974

Morton DC, DeFries RS, Shimabukuro YE, Anderson LO, Arai E, Espirito-Santo FD, Freitas R, Morisette J (2006) Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. Proc Natl Acad Sci USA 103:14637–14641

Moura-Costa P, Sau Wai Y, Chye Lye O, Ganing A (1994) Large scale enrichment planting with dipterocarps as an alternative for carbon offset—methods and preliminary results. In: Proceedings of the 5th round table conference on dipteocarps. J Trop For Sci, FRIM, Kuala Lumpur

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Ng KKS, Lee SL, Koh CL (2004) Spatial structure and genetic diversity of two tropical tree species with contrasting breeding systems and different ploidy levels. Mol Ecol 13:657–669

Ng KKS, Lee SL, Ueno S (2009) Impact of selective logging on genetic diversity of two tropical tree species with contrasting breeding systems using direct comparison and simulation methods. For Ecol Manag 257:107–116

Norisada M, Hitsuma G, Kuroda K, Yamanoshita T, Masumori M, Tange T, Yagi H, Nuyim T, Sasaki S, Kojima K (2005) *Acacia mangium*, a nurse tree candidate for reforestation on degraded sandy soils in the Malay Peninsula. For Sci 51:498–510

Nussbaum RHAL (1996) Rehabilitation of degraded sites in logged-over forest using dipterocarps. In: Schulte A, Shöne D (eds) Dipterocarp forest ecosystems: toward sustainable management. World Scientific, Singapore

Nussbaum R, Anderson J, Spencer T (1995) Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. For Ecol Manag 74:149–159

Okuda T, Kachi N, Yap SK, Manokaran N (1997) Tree distribution pattern and fate of juveniles in a lowland tropical rain forest—implications for regeneration and maintenance of species diversity. Plant Ecol 131:155–171

Osunkoya OO, Othman FE, Kahar RS (2005) Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium*, and those of a native Borneo heath-forest species, *Nelastoma beccarianum*. Ecol Res 20:205–214

Otsamo R (2000) Early development of three planted indigenous tree species and natural understorey vegetation in artificial gaps in an *Acacia mangium* stand on an *Imperata cylindrica* grassland site in South Kalimantan, Indonesia. New For 19:51–68

Paoli GD, Curran LM, Zak DR (2006) Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. J Ecol 94:157–170

Paquette A, Hawryshyn J, Senikas AV, Potvin C (2009) Enrichment planting in secondary forests: a promising clean development mechanism to increase terrestrial carbon sinks. Ecol Soc 14:15

Phat NK, Knorr W, Kim S (2004) Appropriate measures for conservation of terrestrial carbon stocks—analysis of trends of forest management in Southeast Asia. For Ecol Manag 191:283–299

Potts MD, Ashton PS, Kaufman LS, Plotkin JB (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in Northwest Borneo. Ecology 83:2782–2797

Romell E, Hallsby G, Karlsson A, Garcia C (2008) Artificial canopy gaps in a *Macaranga* spp. dominated secondary tropical rain forest—effects on survival and above ground increment of four under-planted dipterocarp species. For Ecol Manag 255:1452–1460

Romell E, Hallsby G, Karlsson A (2009) Forest floor light conditions in a secondary tropical rain forest: after artificial gap creation in northern Borneo. Agric For Meteorol 149:929–937

Russo SE, Brown P, Davies SJ (2008) Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients (vol 96, pg 192, 2008). J Ecol 96:1330–1330

Schuyt K (2005) Opportunities for long-term financing of forest restoration in landscapes. In: Mansourian S, Vallauri D, Dudley N (eds) Forest restoration in landscapes: beyond planting trees. Springer, New York, pp 161–165

Shono K, Davies SJ, Chua YK (2007) Performance of 45 native tree species on degraded lands in Singapore. J Trop For Sci 19:25–34

Sirikantaramas S, Sugioka N, Lee S-S, Ibrahim FH, Lee H-S, Szmidt A, Yamazaki T (2003) Molecular identification of ectomycorrhizal fungi associated with Dipterocarpaceae. Tropics 13:69–77

Sist P, Garcia-Fernandez C, Fredericksen TS (2008) Moving beyond reduced-impact logging towards a more holistic management of tropical forests. For Ecol Manag 256:VII–IX

Suzuki R, Numata S, Okuda T, Supardi MN, Kachi N (2009) Growth strategies differentiate the spatial patterns of 11 dipterocarp species coexisting in a Malaysian tropical rain forest. J Plant Res 122:81–93

UN-DESA (2009) Forests: the Green and REDD of Climate Change. In: UN-DESA Policy Brief No. 16. United Nations Department of Economic and Social Affairs, New York

UNFCCC (2009) CDM registration. United Nations Framework Convention on Climate Change

van der Heijden MGA, Bardgett RD, van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11:296–310

Weinland G (1998) Plantations. In: Appanah S, Turnbull JM (eds) Review of the dipterocarps: taxonomy, ecology and silviculture. CIFOR, Bogor, pp 151–185

Wilcove D, Koh LP (2010) Addressing the threats to biodiversity from oil palm agriculture. Biodivers Conserv (this issue)

WRI (2009) Earth trends: the environmental information portal. World Resource Institute, Washington, DC

Zhu YY, Chen HR, Fan JH, Wang YY, Li Y, Chen JB, Fan JX, Yang SS, Hu LP, Leung H, Mew TW, Teng PS, Wang ZH, Mundt CC (2000) Genetic diversity and disease control in rice. Nature 406:718–722