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Research needs for restoring seasonal tropical forests in Thailand: accelerated natural regeneration

KATE HARDWICK[1], JOHN R. HEALEY[2], STEPHEN ELLIOTT[3] and DAVID BLAKESLEY[4,*]
*[1]Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK; [2]School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, UK; [3]Forest Restoration Research Unit, Biology Department, Science Faculty, Chiang Mai University, Thailand 50200; [4]Horticulture Research International, East Malling, West Malling, Kent ME19 6BJ, UK; *Author for correspondence e-mail: david.blakesley@hri.ac.uk; phone: +44 1732 843833; fax: +44 1732 849067*

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Abstract. Accelerated natural regeneration (ANR) is a relatively cheap method of reforestation, which encourages natural establishment of indigenous trees and shrubs. It requires a low input of labour, but a high input of ecological information. In this paper, the knowledge required to predict and manipulate the natural regeneration of seasonal tropical forest is reviewed and areas in need of further research are identified. Regeneration will be influenced by five groups of potentially limiting factors; site resources (soil and microclimate); competition with weeds; site disturbance; occurrence of established woody plants or their propagules; seed dispersal by wild animals and birds. This paper considers each of these, their interactions with seasons, and each other. Collation of existing information on these topics, combined with the suggested further research, should facilitate the creation of tools that will enable practitioners to judge the regeneration potential of sites and to select the most appropriate ANR techniques.

Introduction

The destruction of southeast Asia's seasonally dry tropical forests is widely acknowledged to be a serious problem, worsening rural poverty and causing degradation of water catchments and losses of biodiversity. Although countries such as Thailand are now addressing this problem by protecting remaining forests, these are often too degraded to meet the need for sustainable forest ecosystems. In order to meet local as well as national objectives, such as obligations under Agenda 21 of the United Nations Conference on Environment and Development and carbon-offset goals for reabsorption of CO_2, there is increasing demand for degraded forest lands to be restored to a condition that closely matches the previous forest ecosystems. In Thailand, for example, the Government has identified deforestation as the greatest threat to biodiversity and plans to restore forest cover using idigenous tree species, from the present level of less than 20% of the Kingdom's area to 40%, with 25% earmarked for biodiversity conservation. In this paper we are primarily concerned with the restoration of forests for biodiversity conservation, using indigenous tree species.

In attempting to restore a forest to its previous condition, consideration must be given to both physical structure and species composition. Recent studies have shown that the species richness of seasonally dry tropical forests, which experience a distinct dry season, can be as high as that of many tropical rain forests (Maxwell and Elliott 2001). At elevations of 700–1600 m ASL, our research in Doi Suthep-Pui National Park, Chiang Mai Province, includes both the low stature open deciduous forest associations of the lowlands (deciduous dipterocarp-oak, bamboo deciduous forest and mixed evergreen deciduous forest) and the dense, multi-layered evergreen forest of the uplands (*sensu* Maxwell and Elliott 2001), comprising at least 493 tree species.

The restoration of complex tropical forests on a large scale is a comparatively modern need, which has been approached in a variety of ways (Table 1). Each approach involves introducing woody plants to degraded sites, or accelerating their natural regeneration, or a combination of both activities. Planting tree seedlings is the most labour- and capital-intensive option, as it involves human input in seed collection, propagation, planting out on degraded sites and subsequent management until the trees can survive and grow independently. Accelerating the natural regeneration of tree and shrub species requires less human input, compared with tree planting (Goosem and Tucker 1995; Knowles and Parrotta 1995; FORRU 2000; Blakesley et al. 2002a,b), and is thus a cheaper alternative. However, it requires advanced knowledge of forest ecosystem dynamics, which at present is scarce, and it is only feasible on sites where there exists, or there is the potential for, sufficient woody regeneration to be accelerated. Naturally regenerated sites often support only a small fraction of the full range of forest tree and shrub species that are normally present in diverse primary forest ecosystems, so ANR may need to be supplemented with enrichment tree planting to achieve the desired species composition (Table 1).

This paper focuses on research needs for accelerating natural regeneration for forest restoration (ANR). Some successful ANR techniques include protection of regenerating areas from fire and digging out, cutting or flattening weeds around naturally established trees or shrubs (Dugan 2000). Domestic cattle have also been used to trample and eat weeds, while dispersing seeds in their faeces (Janzen 1988). Techniques that have been tested, but not implemented on a large scale, include erecting perches to encourage seed dispersal by birds (McClanahan and Wolfe 1993; Holl 1998; Scott et al. 2000) and scattering tree seeds ('direct seeding') (Sun and Dickinson 1995). A considerable amount of research is still needed to address many aspects of ANR. This was highlighted at a recent international meeting in Thailand, devoted to forest restoration for wildlife conservation (Elliott et al. 2000), during which the 'Chiang Mai Research Agenda for the Restoration of Degraded Forest Lands for Wildlife Conservation in Southeast Asia' (Elliott 2000) was formulated by a quorum of regional experts. In the paper presented here, we highlight areas of the Research Agenda of most importance to ANR.

Table 1. Various approaches to forest restoration. The approaches are ordered from that with the greatest requirement for human-input to that with the least (i.e. from the least to the greatest reliance on natural regeneration)

Restoration approach	Stage 1 (site capture)	Stage 2 (species enrichment)	Examples
Staggered planting of primary forest species	Plant a mixture of exposure-tolerant species	Plant a mixture of 'shade-demanding' species	Knowles and Parrotta (1995)
Framework species method	Plant a mixture of 'framework' species	Encourage subsequent natural regeneration	Goosem and Tucker (1995)
Catalytic monoculture	Plant a catalytic monoculture	Encourage subsequent natural regeneration	Parrotta (1993) Lugo (1997)
ANR[a] with enrichment planting	Encourage natural regeneration	Plant missing primary species	Dalmacio (1987)
ANR without enrichment planting	Encourage natural regeneration	Encourage natural regeneration	Dugan (2000)

[a]ANR = accelerated natural regeneration.

Is accelerated natural regeneration appropriate?

The first step of any forest restoration project must be a site assessment, first of all to determine whether restoration is actually feasible within the wider landscape and if so, to quantify actual and potential levels of natural regeneration, and to decide the most appropriate methods to adopt. The whole restoration site must be carefully surveyed as regeneration is often heterogeneous, depending on distances from seed sources, aspect, topography, soil type, the duration and intensity of past land-use and subsequent disturbances, and the time elapsed since the last major disturbance event. The most appropriate restoration approach may vary considerably within a heterogeneous site. For example, it may be necessary to confine ANR to actively regenerating parts of the site, such as edges or isolated islands around fruiting trees, while planting framework tree species (Table 1) in areas further from seed sources, where the density of seed rain is insufficient for ANR.

To improve site assessment techniques, further research must address the following crucial questions:

1. Which soil and vegetation variables best predict the potential of sites to be successfully restored by ANR?
2. What is the distribution of the density of seeds dispersed with distance from forest seed sources, for different categories of tree species and site environments?
3. What is the minimum density of *in situ* woody plant propagules (soil seed bank, seedling bank, sprouting tree stumps, etc.) or seed rain needed to allow the establishment of an adequate density of trees by ANR?

As a result of a long tradition of managing natural forests for timber in southeast Asia, much information relating to Question 3 already exists for timber tree species (e.g. Wyatt-Smith and Panton 1995). This knowledge base needs to be widened to include non-timber species, and there is much scope for collaboration between the timber industry and conservation organisations in this field.

Research based on the above questions will provide the information needed to develop site assessment indices to evaluate the potential for using ANR and the need for any supplementary tree planting. If ANR is considered appropriate for parts or all of the site, the next decision is to select the most effective management techniques. The aim of any intervention in natural forest regeneration is to overcome limiting factors that slow succession. These factors can be divided into five groups:

1. Site resources (soil and microclimate),
2. Competition with weeds,
3. Site disturbance,
4. Occurrence of established woody plants or their propagules,
5. Seed dispersal by wild animals and birds.

It is important to consider the limiting factors operating at all stages of the regeneration process, namely seed production and dispersal, and seedling recruitment, establishment and growth (Hardwick et al. 1997). A technique to overcome a factor limiting an early stage in the process would be useless if another factor limiting a later stage were ignored, and vice versa.

Site resources

Tree species vary widely in their survival and growth responses to site resources such as nutrients, moisture and light (Bongers et al. 1999; Poorter 1999; Kitajima 2002). A species' tolerated range of resource levels is often narrower for growth than for survival, and these tolerance limits may vary during the life cycle of the species (Grubb 1998). In moist regions, light is usually the most critical factor limiting regeneration of tree species, but in dry regions, water will be most limiting and too much sunlight could be detrimental, causing damagingly high leaf temperatures that cannot be ameliorated by cooling through transpiration. Thus, in seasonal climates, the key limiting factor is likely to fluctuate from light to water, depending on season. It also follows that the effect of 'nurse trees' (whether naturally established or planted) on woody regeneration may be related to site moisture availability (Parrotta et al. 1997). On drier sites, established trees would compete for water with regenerating seedlings, whilst simultaneously providing beneficial shade and higher air humidity. Anecdotal evidence suggests that the net effect varies between positive and negative in different situations, but there is a lack of quantitative data on this.

In a site assessment, direct measurement of resources such as soil nutrients, soil moisture, temperature, light and humidity would be time consuming, costly and require the use of equipment that may be unavailable to the site manager. It is thus more practical to infer levels of resources from widely available climatic data and from easily observable site factors that regulate and/or indicate resource levels, for example, soil structure and composition, and the presence or absence of indicator plant species.

Nutrient availability is a key factor in the restoration of post-industrial and primary successional land, but its importance in secondary succession, where soil is intact, is less clear (Jordan 1989). It has been assumed that the incorporation of ash into the topsoil following slash and burn clearing of forests for agriculture brings about a short-term increase in nutrient availability. However, burning results in a far more complex flux and loss of nutrients to the soil of which the release of nutrients due to heating from non-plant available to plant available forms in the soil may make a substantial contribution (Giardina et al. 2000a,b). The availability of these nutrients for forest restoration will depend on the subsequent use of the land before it becomes available for restoration.

Nutrient cycling in tropical secondary forests can rapidly recover to levels in undisturbed forests (McDonald and Healey 2000). The ability of trees to absorb nutrients is improved by symbiotic relationships with mycorrhizal fungi (Harley and Smith 1983; Read et al. 1992), which are often specific to particular tree species. However, the importance of the availability of mycorrhizal fungi as a limiting factor in tree regeneration, has not been fully investigated, due partly to the difficulty of isolating and identifying them. Abandoned agricultural sites are unlikely to lack mycorrhizal fungi completely, although the number of fungus species capable of infecting forest tree roots may be greatly depleted (Musoko et al. 1994). Severely degraded sites, such as abandoned mines, are often very deficient in mycorrhizal fungi. On such sites, artificially inoculating trees with appropriate fungus species has effectively promoted tree establishment in both dry and wet tropical environments (Wilson et al. 1991; Setiadi 2000).

Research needs. More research is needed to compare the efficacy of different ANR techniques in relation to season and site moisture availability, with particular emphasis on the 'catalytic' effect of nurse trees. Also, the level of depletion of mycorrhizal fungi populations, following different intensities of disturbance, warrants further attention and research into inoculation methods for mycorrhiza-deficient soils would be of particular value. Basic research on the range of resource needs for individual species should also be undertaken. Where possible, functional groups should be defined to facilitate the matching of species to a site's resource levels.

Competition with weeds

In sites identified for forest restoration, our definition of a weed is any plant that is either alien to the natural forest ecosystem, or inhibits the establishment and growth of tree seedlings. Competition with weeds often regulates the level of site resources that are available to individual tree seedlings in early successional stages. Although, in temperate climates, shrub or herb cover has been found to be a barrier to tree colonization (Hill et al. 1995), in the seasonal tropics, the effect varies according to season, due to seasonal fluctuations in site resources. For example, in northern Thailand, during the rainy season weeds compete with young tree seedlings for light and retard growth, but in the hot dry season they often facilitate survival by protecting seedlings from damagingly high levels of solar radiation (Hardwick 1999).

Different weed communities have different levels of resistance to colonization by tree species. In a study in temperate North America, Hill et al. (1995) found that weed canopy height was the crucial factor. The growth rate of newly established seedlings was equally inhibited by different weed communities, but growth increased dramatically once seedlings emerged above the weed canopy. Thus the higher the weed canopy, the slower the rate of tree colonization: shrub communities with a high canopy were more resistant to tree colonization than low growing grass communities. By contrast, in tropical Amazonia, the shrub *Cordia multispicata* was more favourable for tree seedling growth than the grass *Panicum maximum*, as it increased soil nutrient availability, litter nutrient concentrations and light availability (Vieira et al. 1994). Thus, in the tropics, characteristics of the weed community other than canopy height may most affect tree colonization, but data is scant on this subject.

Research needs. Research is needed to grade the common weed communities in seasonal southeast Asia according to their 'resistance' to tree colonization. To this end, two indices devised by Hill et al. (1995) could be adapted to tropical environments. They are the establishment/emergence ratio (the ratio of the number of seedlings established in a given year to the number of those seedlings that survive to reach 2 m in height) and the time to first emergence (the time taken for the fastest growing seedling in a cohort to emerge above the weed canopy). More research is also needed to clarify the protective/competitive role of different weed species according to season, so that weed removal can be timed for optimum benefit.

Site disturbance

The level of site resources, in particular its mediation through weed competition, will be strongly influenced by both the past and present disturbance regimes. Disturbance regimes are characterized by four or more dimensions (frequency, intensity, timing and extent), which presents a challenge to their characterization (Grubb 1985). Fire is the most serious form of disturbance in seasonal tropical forests. Infrequent, natural fires have probably always been a feature of the ecology of deciduous forests (Stott 1986), but now fires are mostly started by humans and consequently they have become more frequent, widespread and damaging. In montane evergreen forests, fires are invariably started by humans and lead to forest degradation. The risks from such fires can be exacerbated by climatic changes. In the tropical rainforest of East Kalimantan, Borneo for example, an increased frequency of forest fires in 1997–1998 was associated with drought caused by the El Nino/Southern Oscillation (Siegert et al. 2001). The effects of these fires on seed banks, sprouting and post fire dynamics of different plant groups has recently been reviewed (van Nieuwstadt et al. 2001).

Controlled burning at the start of the restoration process has been used as an ANR tool in Amazonia (Nepstad et al. 1990) to reduce populations of weeds and leaf-cutter ants, which are severe limiting factors there. However, Kennard et al. (2002) reported that high intensity burns in tropical dry forests of lowland Bolivia can alter community structure and composition more drastically than the other treatments. Its suitability for southeast Asia is also questionable: uncontrolled annual burning is the most common cause of forest restoration failure in northern Thailand (Svasti 2000). Fire could potentially be used to open the dominant weed canopy (e.g. of ferns) in sites with poor tree regeneration, but the destruction of susceptible woody plants, and the risk of fire spreading to surrounding areas, are likely to outweigh any potential benefits. The risk of accidental fire is highest in highly degraded, grass-dominated sites and decreases as tree regeneration proceeds and the grass is shaded out.

When the trees reach a certain size they may be able to withstand low intensity fires. For example in northern Thailand Elliott et al. (in press) showed that, as rapidly as 21 months after establishment, many tree species were able to survive a moderate litter burn, mostly unharmed, or to rapidly recover afterwards. *Acrocarpus fraxinifolius*, *Ficus hispida* var. *hispida*, *Ficus racemosa* var. *racemosa*, *Glochidion kerrii*, *Gmelina arborea*, *Hovenia dulcis*, *Machilus bombycina*, *Melia toosendan*, *Michelia baillonii*, *Rhus rhetsoides*, *Sapindus rarak*, *Sarcosperma arboreum* and *Spondias axillaris* all showed exceptional resistance to fire, with survival rates of 70% or higher after burning. However, response to fire was highly variable among species. Such observations can help to determine how long fire prevention measures must continue, after ANR techniques have been implemented.

Domestic animals influence regeneration of woody plants on ANR sites through their effect on weeds, established woody plants and propagule availability. The overall effect may be positive or negative. In Costa Rica browsing severely reduced regeneration of trees and shrubs in plantations (Haggar et al. 1997). By contrast, cattle have been used elsewhere to promote regeneration, by suppressing grass and dispersing heavy seeds through their faeces (Janzen 1988).

Other disturbance factors that may influence forest regeneration include catastrophic wind and other wind generated canopy disturbances (Whigham et al. 1999), logging, flooding, insect and wild animal herbivory and plant pathogens.

Research needs. The potential for controlled burning in ANR could be further investigated, but only if it is judged to be socially and politically acceptable. There has been very little research undertaken to investigate how prescribed burning might be used most effectively. The timing of fire susceptibility in relation to successional stage is poorly understood, but needs to be more clearly defined, so that managers can plan long-term maintenance and protection. To lower the risk of uncontrolled spread of fires, should fire breaks be created around sites, and for how long must such protection be maintained? Should the strategy be switched to the use of controlled burns to reduce fuel loads once trees have reached a certain size? In fire-prone grasslands, it is particularly important to identify fast growing species that can regenerate after burning – they may be the only species able to establish.

The effectiveness and practicality of using domestic animals as an ANR tool in seasonal southeast Asia warrants further attention. Where browsing limits natural regeneration, unpalatable tree or shrub species should be identified, encouraged or planted for initial site capture (see Table 1).

Established woody plants or their propagules

Regeneration of forest tree species may arise from either existing on-site sources (tree stumps, seedlings or the soil seed bank) or from the incoming seed rain.

Soil seed bank

The pre-existing soil seed bank is unlikely to contribute much to natural regeneration after periods of disturbance lasting longer than a year (Nepstad et al. 1996). This is because most tropical tree seeds have short dormancy periods, after which they either germinate or die. A survey of 353 tree species in northern Thailand (Elliott et al., unpublished data) found that 39% had median dormancy periods of less than 30 days. Less than 8% of the species examined produced seeds that remained viable for more than 6 months, whilst after 1 year less than 2% of the species remained viable. For slash and burn areas that are cultivated for 2–3 years or longer, it is probable that no viable tree seeds from the original soil seed bank will remain, and instead, the seed bank will be dominated by the seeds of herbaceous weed species which have arrived through recent dispersal.

Research needs. Because of the technical difficulties involved there has been a paucity of studies of the soil seed bank composition in degraded forest sites in southeast Asia. However, Cheke et al. (1979) found that in the soil of primary rain forest in northern Thailand there was an abundance of seeds of pioneer tree species, such as *Macaranga denticulata* and *Trema orientalis*, even up to 175 m from their nearest seed parent tree and at up to 20 cm soil depth. Future research should assess the occurrence of both pioneer and climax tree species' seeds in the soil seed bank of degraded sites that have been subject to different disturbance regimes.

Stumps

The most rapid establishment of forest cover is generally agreed to be from the sprouting of tree stumps (coppicing), (e.g. de Rouw 1993). Primary forest species are as likely as secondary species to regenerate from stumps or roots (de Rouw 1993; Kammesheidt 1998; van Nieuwstadt et al. 2001) and, when they exist in disturbed areas, they should be the focus of initial ANR efforts. Coppicing stumps have greater resistance to fire and browsing than young seedlings and their faster initial growth rate enables them to grow above the weed canopy more quickly.

There is much variation between species in their ability to resprout after repeated cutting and in particular after burning (de Rouw 1993; Miller and Kauffman 1998). However, at present, there is little established basis to predict the relative coppicing ability of different species. Physical characteristics of individual stumps may help to predict their sprout production. Many studies have found that stump height is a key factor influencing the occurrence and vigour of sprouting (e.g. Khan and Tripathi 1989; Johansson 1992; Misra et al. 1995). Negreros-Castillo and Hall (2000) found that the number and height of sprouts was related to parent tree diameter and Rijks et al. (1998) found that sprout production from *Chlorocardium rodiei* (Lauraceae) stumps in Guyana was less likely for hollow stumps than for intact ones. Sprout number may not be the best indicator of establishment success from stumps; in many circumstances the growth rate of the largest sprout is more significant and in some cases this is negatively correlated with sprout number. However, sprout number becomes more important if sprouts suffer significant mortality (e.g. due to fire or herbivory). Tall stumps have a better chance of surviving fire, browsing and weed competition as the vulnerable sprouts are produced above the height of disturbance. They may, however, be more susceptible to stem rot and windthrow.

Influencing the nature of the initial disturbance to maximise the density and height of live stumps can greatly reduce the time needed for regeneration. This may be feasible when the forest is being cut for timber or short-term, slash-and-burn agriculture.

Research needs. Much of our knowledge of coppicing comes from dry, naturally fire-prone areas of the world (such as African miombo, Australian savanna and American chaparral), where resprouting is an important natural regeneration mechanism. The information presented above needs to be tested in moister areas of the seasonal tropics (such as montane northern Thailand and Indo-China) where fire has become more prevalent due to human activities and where the native species may be less able to coppice, or may suffer higher rates of mortality following coppicing, for example, due to fungal infection. An assessment of the ability of evergreen forest species to coppice after fire is particularly important. Also, we need to know the length of time that stumps can remain viable before sprouting and how techniques such as weeding, re-cutting or application of hormones can be used to stimulate sprout production from stumps.

Seedlings

Seedling density alone is not a good indicator of regeneration potential, because the probability of establishment of an individual seedling is closely related to its size (Harcombe 1987): a seedling 1.2 m tall is much more likely to survive and grow than one that is 20 cm tall, however potential for successful regeneration cannot simply be predicted from measurement of the absolute size of seedlings as the nature of the size-survivorship relationship varies between species (Condit et al. 1998). Because the probability of a seedling successfully developing into an adult tree may be much greater once it has grown above the weed canopy, it may be more useful to record seedling height relative to the top of the weed canopy, that is, the distance above or below it, or simply whether it is taller or shorter.

An alternative indicator of site regeneration potential is seedling frequency, which here refers to the percentage of sample plots of a given size in which seedlings of woody species are present. In the Philippines, a unit area of 1 m^2 has been used (Sajise et al. 1989). Seedling frequency may be more important than average density across a whole site, as seedling distribution can be very clumped. A site is more likely to be successfully colonized when seedlings are widely dispersed because mortality is often high in dense seedling clumps (Connell et al. 1984) and 'safe sites' for seedling establishment are generally few and far between.

Research needs. Seedling data can help to predict the ANR potential of a site and more research is required to develop simple and effective survey protocols and site assessment indices. For example there is no consensus about what minimum size should be set for inclusion of seedlings in a survey. Sajise et al. (1989) recommended a minimum height of 15 cm in the Philippines, but is this limit appropriate in other locations and across a range of species?

In order to address such practical questions, there is a need for long-term monitoring of permanent plots, where the initial condition of seedlings of regenerating tree and shrub species is assessed by numerous variables (e.g.

density, frequency, species, absolute height, height relative to the top of the weed canopy, diameter) and the subsequent course of regeneration is then monitored. After a few years, information on the successfully established seedlings should be compared with the initial state data to see which index (single variable or combination of variables) best predicted the outcome (Ndam 1998). Tools for seedling identification are also seriously lacking and this need is explored further in the final section.

Seed rain

After severe and prolonged disturbance, remnant stumps, seedlings and the soil seed bank will be sparse or absent, so the potential for natural regeneration will depend entirely on seeds dispersed into the area. An understanding of seed shadows (i.e. patterns of seed dispersal) is crucial for predicting which potential parent trees will contribute seed to an open site – an important step in assessing its regeneration potential. A two-curve model has been proposed to describe an individual tree's seed shadow and applies equally to both wind and animal dispersed species (Clark 1998). According to this model, most seeds produced by a tree are locally dispersed and their density declines exponentially with distance from the tree. Around 10% of the seeds are dispersed across greater distances and their seed shadow is described with a 'fat-tailed' curve, where seed density falls off very gradually and extends over a distance of 1–10 km. Little is known about the long-distance component of the seed rain, because it is difficult to measure, due to the very low density of seeds. However, this component is essential for regeneration of isolated sites.

Tall, fruiting trees, located in and adjacent to a site, make the greatest contribution to the seed rain, irrespective of the overall species composition of surrounding forest (Hardwick 1999). Therefore, it may be possible to predict the species composition of the seed rain by surveying these potential parent trees. Caution is needed in interpreting seed rain data, because species differ in the number of seeds expected to produce a single seedling (Hardwick 1999). However, spatial distribution of seedling recruitment in the forest understorey can be predicted from adult tree distributions (Ribbens et al. 1994) and there is scope for further research to help predict recruitment in clearings.

Research needs. We need to be able to predict more precisely the seed-shadow dimensions of the locally dispersed component of the seed rain and in particular to know how this is related to tree size and seed dispersal mode and how it is affected by whether dispersal is through forest or across degraded areas. Innovative research methods are required to quantify the long-distance dispersal component of the seed rain. Long-distance dispersal curves should be characterised for species representing a range of dispersal mechanisms (i.e. by wind, birds, bats or terrestrial mammals) under a range of local conditions, representing variations in forest cover and the presence of animal dispersers.

Seed dispersal by wild animals and birds

Like domestic stock, wild animals can have a range of impacts on plant regeneration: negative impacts include browsing and seed predation, but seed dispersal and the influence of seed predation on community diversity can be important positive effects. Rate of seed input by wild animals will be influenced by the local population size of each species (in many cases this may have been reduced by hunting and habitat loss) and by the attractiveness of the site to them. Where populations of large vertebrate species are rare, this seriously limits dispersal into degraded areas of large-seeded tree species, which represent a major component of the tree community especially in evergreen forests. In her study in northern Thailand, Hardwick (1999) found tree seeds longer than 14 mm in seed traps placed under the canopy of adjacent forest but none in seed traps placed in the centres of three abandoned agricultural clearings. This result explains the observed rarity of large-seeded animal-dispersed tree species in the regenerating tree communities on degraded sites.

Some frugivorous birds are highly effective dispersers of tropical forest tree seeds, in some cases over considerable distances (Sun et al. 1997; Whitney et al. 1998), although there is wide variation in the effectiveness of different species at dispersing seeds into degraded sites (Corlett and Hau 2000). Structural diversity of vegetation encourages overall bird diversity (MacArthur and MacArthur 1961) and thus increases the likelihood of visits from seed dispersing species. Therefore, to encourage seed input into ANR sites specialized resources can be provided that are selected to attract the bird and mammal species that are most likely to disperse seeds from intact forest. Toh et al. (1999) observed that birds use scattered, isolated trees in abandoned farmlands in southern Queensland as perches and so they become the main focus for the input of bird-dispersed seeds. Artificial bird perches can be constructed as a substitute for trees. For example, in degraded forest plots in northern Thailand, Scott et al. (2000) reported that the species richness and density of bird-dispersed seeds were significantly higher beneath bamboo bird perches than in control areas. Holl (1998) found natural branches (alive or dead) to be more effective than straight bars.

Vegetation bearing edible fruit attracts birds into clearings and thus further increases seed rain (Scott et al. 2000), although not necessarily beneath the food supply itself (Wilson and Crome 1989; Holl 1998), possibly because birds do not always eat and defecate in the same place. Thus, providing that some trees and shrubs bearing edible fruits are present to attract birds into the general area, species that do not bear such fruit may still improve seed dispersal, by providing perches (Toh et al. 1999). The effectiveness of perch trees is even greater if they occur in clumps.

The effectiveness of bird perches in accelerating natural regeneration will depend on the severity of limiting factors operating at later stages of the regeneration process. For example, in denuded ex-mine sites in North America, perches increased both seed rain and seedling establishment (McClanahan and

Wolfe 1993). By contrast, in weedy clearings in Costa Rica, the seed rain was increased by perches, but seed predation and weed competition severely limited recruitment and establishment, resulting in only a small increase in the established seedling population (Holl 1998). Where weed competition limits seedling establishment, tree planting would have the double advantage of attracting seed dispersers and shading out weeds (Parrotta 1993), although this shade may also limit seedling establishment of more light-demanding tree species.

Most studies agree that post-dispersal seed predation in weedy areas (especially by rodents) is a significant factor limiting seed availability (Hardwick 1999), with mortality levels ranging from ca. 20% (Osunkoya 1994) to at least 80% (Uhl 1987; Hammond 1995; Hau 1997) of all seeds. The density of seed consuming rodents in these sites will be regulated by the activity of their predators, such as birds of prey. Reducing the weed cover and providing bird perches may increase this predation and make the site less attractive to rodents. As well as birds, bats are important dispersers of tropical tree seeds. Therefore provision of a range of habitat features, such as refuges, nesting sites for birds and bat boxes, may all contribute to the rapid colonization of target sites by a diversity of animals and consequently of plant species.

Research needs. Research should focus on the identification of target wildlife species (those most likely to disperse seed from forest to regenerating sites) and the habitat features that should be enhanced or introduced to attract these species into ANR sites. Further work would then be necessary to determine the optimum design and location of such features and to monitor their effectiveness at attracting wildlife. Specifically, research should test the effect of bird perches in southeast Asian forest environments and how their efficacy is influenced by distance from a forest seed source. Where large mammals or birds are no longer present in an area, large tree seeds may still need to be directly sown. In North Wales, Shaw (1968) found that burying large seeds significantly reduced the risk of predation, but new research is needed to determine whether this is the most effective method in tropical environments.

Information interpretation and output

There is a pressing need for more and better identification manuals for seedlings and stumps to enable accurate site surveys (FORRU 2000). In most of southeast Asia, tools for seedling identification are severely lacking and this is a major obstacle to regeneration surveys. If it is not possible to identify to the species level, the most useful identifiable group should be determined. This may be genus or family, or it may be sufficient to classify seedlings according to a morphological trait, such as the size or dispersal mechanism of seeds, or the gross shoot architecture or leaf-form of seedlings. Whilst the bark of stumps will correspond to that of intact trees, the morphology of epicormic shoots may differ from that of adults, and these characters might usefully be included in new identification manuals.

A broad research project is needed in the region, to determine whether the rate and path of succession is predictable from an assessment of the limiting site factors described above and, if so, to develop a model to predict the pattern of succession under given site conditions. The research should establish which site variables (e.g. rainfall, frequency of disturbance, type and intensity of disturbance, weed cover, distance from nearest seed source) most determine the rate of recovery. The results could be used to develop indices for rapid site assessments, to determine the potential for ANR and the most appropriate ANR techniques to employ.

In developing countries, much ecological knowledge is held by local people and has not yet been adequately integrated with formal scientific knowledge (Sinclair and Walker 1999). Many farmers, carrying out slash-and-burn agriculture, manage regenerating forests as fallows, before another cycle of cultivation. It is, therefore, likely that, in some environments, local knowledge could substantially improve forest restoration methods. Therefore, recording local ecological knowledge, testing it and combining it with existing scientific knowledge of forest regeneration should be a priority. This may well lead to an adjustment in the priorities identified for new scientific research (e.g. Paudel et al. 1997).

Ultimately, all relevant information should be collated to create a decision support system for practitioners. This may take the form of a handbook, interactive software or other methods appropriate for particular user groups. A computer programme has already been created in the UK to aid the restoration of ecosystems such as wetlands and grasslands (Pywell and Cox 1998) and it raises exciting possibilities for the use and interpretation of ecological information for the restoration of tropical forests.

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