# RESEARCH NEEDS FOR THE ECOLOGY OF NATURAL REGENERATION OF SEASONALLY DRY TROPICAL FORESTS IN SOUTHEAST ASIA

# K. A. Hardwick<sup>1</sup>, J. R. Healey<sup>1</sup> and D. Blakesley<sup>2</sup>

## ABSTRACT

Widespread forest restoration on degraded lands is needed to meet local and national targets for natural forest cover. Accelerated natural regeneration (ANR) is a relatively cheap method of reforestation, which encourages natural establishment of 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 natural regeneration of seasonal tropical forest is reviewed and areas in need of further research are identified.

Forest regeneration is influenced by four groups of potentially limiting factors. (1) Disturbance: how can we minimise the negative and maximise the positive effects of fire and grazing? (2) Site resources: how do spatial and seasonal variations in moisture availability affect regeneration and how do they interact with other limiting factors? Under what circumstances are low levels of mycorrhizal inoculum limiting and how can they be increased? (3) Weed competition: how do competition and facilitation vary with season, weed species and the size and species of tree seedling? (4) Plant and propagule availability: how can stumps, seedlings and the seed rain be quantified and plant establishment from them predicted? How can the seed rain be increased?

We should collate all available information to create tools that will enable managers to judge the regeneration potential of sites and to select the most appropriate ANR techniques.

*Key words:* accelerated natural regeneration; succession; forest restoration; monsoon forest

#### **INTRODUCTION**

Destruction of Southeast Asia's seasonally dry tropical forests is widely acknowledged to be a serious problem, causing degradation of water catchments, losses of biodiversity and exacerbating rural poverty. Most countries are now attempting to solve the problem by protecting remaining forest. However such forest is often too degraded to meet the need for

<sup>&</sup>lt;sup>1</sup> School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd, LL57 2UW, U.K.

<sup>&</sup>lt;sup>2</sup> Horticulture Research International, East Malling, West Malling, Maidstone, Kent, ME19 6BJ, U.K.

healthy, natural forest. For example, in Thailand government policy is for 25% of the total land area to be covered with conservation forests (LEUNGARAMSRI & RAJESH, 1992), but at present less than 23% is forested (FAO, 1997) and much of the forested area is made up of commercial plantations and severely degraded natural forest. There is a need to restore original forest ecosystems, where they have been partially or totally destroyed, to meet local and national objectives, including countries' international obligations following the United Nations Conference on Environment and Development.

Large-scale restoration of complex tropical forests is a comparatively modern dilemma, which has been approached in a variety of ways in recent years (Table 1). Each approach involves either introducing plant material to the site or encouraging natural regeneration of woody plants or a combination of the two. Planting seedlings is the most labour- and capital-intensive option, as it involves human input at all stages of the regeneration process: collecting seed, raising seedlings in a nursery, planting and maintaining the seedlings until they can survive and grow without further attention. Encouraging natural regeneration requires less human input and is thus a cheaper alternative, but it demands a higher input of ecological information about each site. Furthermore, it can only be used on sites where there exists, or there is the potential for, sufficient woody regeneration to be accelerated (Fig. 1).

Restoration approach	Stage 1 (site capture)	Stage 2 (species enrichment)	Examples
Staggered planting of primary forest spp.	Plant a mixture of exposure-tolerant spp.	Plant a mixture of "shade- demanding" spp.	Knowles & Parrotta, 1995
Framework spp. method	Plant a mixture of "framework" spp.	Encourage subsequent natural regeneration	Goosem & Tucker, 1995
Catalytic monoculture	Plant a catalytic monoculture	Encourage subsequent natural regeneration	Parrotta, 1993 Lugo, 1997
ANR <sup>a</sup> with enrichment planting	Encourage natural regeneration	Plant missing primary spp.	DALMACIO, 1987 (unpublished)
ANR without enrichment planting	Encourage natural regeneration	Encourage natural regeneration	

Table 1. Various approaches to forest restoration.

<sup>a</sup>ANR = accelerated natural regeneration

This paper focuses on research needs for accelerated natural regeneration (ANR). In ANR, natural establishment of tree and shrub species is promoted and any missing, but desired, species are subsequently introduced by enrichment planting. Enrichment planting will not be included here, since the methods involved are covered in other parts of this volume. Some successful ANR techniques include fire prevention, weeding around naturally established trees and shrubs by cutting or pressing (DUGAN, 2000) and using domestic cattle to trample and eat weeds, while dispersing seeds through 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 & WOLFE, 1993; HOLL, 1998) and scattering tree seeds (SUN & DICKINSON, 1995).



Figure 1. A summary of the range of approaches to forest restoration, showing relative levels of human input involved and the role of planted material and natural regeneration in each. The level of human input declines with decreasing emphasis on planting, although the columns are not to scale or based directly on actual economic data. From left to right, the use of natural regeneration increases with the level of natural regeneration already present on site.

Research priorities are identified from the perspective of managers or landowners faced with restoring degraded land for conservation. Managers will have to make certain decisions and will need ecological information to do so. The decision-making process will be briefly outlined and relevant ecological knowledge reviewed. Gaps in the present knowledge base will be highlighted and suggestions made for further research and for collation and distribution of research results.

# MANAGEMENT DECISIONS

To select an appropriate approach to forest restoration, a manager must first assess actual and potential levels of natural regeneration. It is important that the whole area for

restoration is carefully observed, since the level of regeneration may be highly heterogeneous, depending on distances from nearest seed sources, aspect, topography, soil type, duration and intensity of past use and time since last disturbance. The most appropriate restoration approach may vary considerably within a heterogeneous site. For example, it may be best to confine ANR to certain actively regenerating parts of the site, such as edges or isolated islands around fruiting trees, while planting framework species in central areas, further from seed sources. If ANR is considered appropriate for a site, the next decision will be what site management techniques to use to accelerate regeneration most effectively. The aim of the techniques will be to overcome factors limiting succession. These factors can be divided into four groups:

- 1) disturbance,
- 2) resources (too high or too low),
- 3) weed competition and
- 4) lack of established plants or propagules.

Any single technique may overcome one or several limiting factors (Table 2). Managers must not only choose the most appropriate techniques for each site, but also plan the timing of application of each technique. The latter is an important consideration in a seasonal climate and requires an understanding of the changing nature of limiting factors with the seasons. The choice of restoration approach and specific management techniques will be dictated by the particular limiting factors operating at each site and the levels of these should be assessed.

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. It is notable that those techniques that affect the existing vegetation influence all limiting factors, in either a positive or negative way (Table 2).

# EXISTING KNOWLEDGE BASE AND RESEARCH NEEDS

Qualitative indices of both existing regeneration and of the severity of limitations should be developed to help the manager interpret the results from the site assessment. The ecological information needed to establish data-collection protocols and to develop indices to help interpret the site data will be explored in this section<sup>3</sup>. Each group of limiting factors will be considered in turn.

<sup>&</sup>lt;sup>3</sup> See Part 7, research proposal 1.1.

Techniques	Limiting factor					
	Disturbance	Site resources		Weed	Plant/propagule	
		Soil	Micro-climate	competition	Availability	
Guarding	Х					
Fire-breaks	X					
Fencing	Х					
Cultivation	$(\downarrow fuel)$	$\stackrel{X}{(\downarrow \text{ compaction})}$	x (↓ plant cover so ↑ light)	X	x (↑ germination?)	
Weed control	x (trash ↑ fuel)	x (trash = mulch)	x (↑ light, ↓ humidity, but trash shades soil)	Х	x (↑ germination?)	
Thinning woody growth	x (trash ↑ fuel)	x (trash = mulch)	x († light, but trash shades soil)	Х	x (↑ germination & coppicing?)	
Controlled burning	x (↓ fuel)	х	x (↑ light, ↓ humidity)	X	x (↑ germination & coppicing?)	
Grazing	x (↓ fuel)	x (manure ↑ nutrients)	x (↑ light, ↓ humidity)	x (weeds eaten & trampled)	x (seeds eaten & dispersed by animals)	
Bird perches		x (bird droppings ↑ nutrients)			x	
Tree seed scattering					X	
Tree seed planting <sup>a</sup>					x (protects from predation)	

Table. 2. Factors limiting forest regeneration and the techniques to overcome them. An"x" indicates which limiting factors are affected by each technique.

<sup>a</sup> Seedling planting techniques have been omitted as they are covered in other papers.

# 1. Site disturbance regime

Fire is the predominant form of disturbance in seasonal tropical forests. Although rare fires are arguably a natural part of the ecosystem in deciduous forests (STOTT, 1986), fire in the montane evergreen forests are invariably started by man and lead to forest degradation.

Controlled burning at the start of the restoration process has been used as an ANR tool in Amazonia (NEPSTAD *ET AL.*, 1990) to reduce weeds and leaf-cutter ants, which are severe limiting factors there. However, its suitability for Southeast Asia is questionable: uncontrolled annual burning is one of the key causes of forest restoration failure in northern Thailand (pers. obs.). Fire could potentially be useful for opening up poorly regenerated sites dominated by colonisation-resistant weeds, such as ferns. In addition, it stimulates root suckering in *Rhus chinensis* (pers. obs.) and may have a similar effect on other tree species. However, the risk of fire spreading to surrounding areas may outweigh any potential benefits. The risk of accidental fire is highest in highly degraded, grass-dominated sites and decreases as regeneration proceeds and the grass is shaded out. When the trees reach a certain height they may be able to withstand occasional low intensity fires.

Like fire, grazing has both positive and negative effects and needs to be strictly controlled. In Costa Rica, grazing severely reduces woody regeneration in plantations (HAGGAR *et al.*, 1997), but cattle have been used to promote regeneration by suppressing grass and dispersing heavy seeds through their faeces (JANZEN, 1988).

#### **Research needs**

The potential for controlled burning in ANR should be further investigated<sup>4</sup>, if it is judged to be socially and politically acceptable. The timing of fire susceptibility in relation to successional stage is loosely understood but needs to be more clearly defined so that managers can plan long-term maintenance and protection. For how long should sites be protected from fire? Should controlled burns be used when the trees reach a certain height to reduce fuel loads and thus lower the risk of accidental fire and uncontrolled spread of intentional fires? Is it practical and economic to plant tall, more fire- and grazing-resistant saplings or cuttings in areas where disturbance is unavoidable? 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. In heavily grazed areas, where grazing clearly limits natural regeneration, the priority should be to identify unpalatable species to be planted or encouraged in the initial site capture stage.

# 2. Site resources

In moist areas, light is the critical limiting factor for the regeneration of most tree species (i.e. the more the better). In dry areas, water is most limiting and too much sunlight can be detrimental, causing damagingly high leaf temperatures that cannot be ameliorated by the cooling caused by transpiration. Thus in seasonal climates, the key limiting factors



<sup>&</sup>lt;sup>4</sup> See Part 7, research proposal 3.2.

are likely to fluctuate from light to water according to 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 the regenerating seedlings, while simultaneously providing beneficial shade and higher air humidity. The net effect is likely to vary between positive and negative in different situations, but most of the evidence is still anecdotal.

Direct measurement of site resources, such as soil nutrients, soil moisture, temperature, light and humidity are time consuming, costly and require the use of equipment which may be unavailable to the manager. It is thus more practical to infer the level of resources from widely available climatic data and from easily observable on-site factors that regulate and/or indicate the level of resources, e.g. the structure and composition of the soil and dominant vegetation.

Nutrient availability is a key factor in the restoration of post-industrial and primary successional land, but its importance in secondary succession, where there is an intact soil, is much less clear. It is believed that the ability of trees to take up available soil nutrients is improved by symbiotic mycorrhizal associations (HARLEY & SMITH, 1983; READ *ET AL.*, 1992), which are often specific to particular tree species. However, again there is a severe lack of knowledge concerning the importance of mycorrhizal fungi availability as a limiting factor in tree regeneration. This is partly due to the difficulty of identifying the different species. Abandoned agricultural sites are unlikely to lack mycorrhizal fungi, although the number of species of fungi that form symbioses with forest trees may be greatly depleted (MUSOKO *ET AL.*, 1994). Primary successional sites, such as abandoned mine sites, are often severely deficient in mycorrhizal fungi, and fungal inoculation has been found to be an effective intervention to promote tree establishment in a dry tropical environment (WILSON *ET AL.*, 1991).

# **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 depletion of mycorrhizal fungi populations, after different intensities of disturbance, warrants further attention. Research into inoculation methods for mycorrhiza-deficient soils would be of particular value.

#### 3. Weed competition

Although in temperate climates any vegetative cover is seen as a barrier to tree colonisation (HILL *ET AL.*, 1995), in the seasonal tropics the effect varies according to season, due to the seasonal fluctuations in site resources mentioned above. 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 can protect seedlings from damagingly high levels of solar radiation (HARDWICK 1999).

Different weed communities have different levels of resistance to colonisation by tree species. In a study in temperate North America, HILL *ET AL*. (1995) found that weed canopy height was the crucial factor. Different weed communities equally inhibited the growth rate

of newly established seedlings, but growth increased dramatically once seedlings emerged above the weed canopy. Thus the higher the weed canopy, the slower the rate of tree colonisation: shrub communities with a high canopy were more resistant to colonisation by trees 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).

HILL *ET AL.* (1995) devised two measurements for comparing the invasibility of different weed communities: 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). This approach could usefully be adapted to tropical environments

#### **Research needs**

Research is needed to grade the common weed communities in seasonal Southeast Asia according to their "resistance" to tree colonisation, possibly using the indices of HILL *ET AL*. (1995). Also more research is needed to clarify the protective or competitive roles of different weed species according to season, so that weed removal can be timed for optimum benefit.

#### 4. Established plant / propagule availability

Regeneration of forest tree species may arise either from existing on-site sources (tree stumps, seedlings or a soil seed bank) or from incoming seed rain. The soil seed bank will not be considered here as after long-term disturbance it is likely that any seeds deposited during the time of forest cover will have died or germinated (NEPSTAD *ET AL.*, 1996) and the soil seed bank is likely to be dominated by weed seeds.

### a) Stumps

Researchers agree that the most rapid establishment of forest cover is from sprouting tree stumps (coppicing), (DE ROUW, 1993). Primary forest species are as likely as secondary species to regenerate from stumps (DE ROUW, 1993; KAMMESHEIDT, 1998) 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.

The manager will need to know which stumps are likely to produce sprouts. There is much variation between species in their ability to resprout after repeated cutting and in particular after burning (DE ROUW, 1993; MILLER & KAUFFMAN, 1998) but as yet, no satisfactory functional grouping has been developed to explain and predict differences in coppicing ability. Physical characteristics of stumps may help to predict sprout production. Many studies have found that stump height is a key factor influencing the occurrence and vigour of sprouting (e.g. KHAN & TRIPATHI, 1989; JOHANSSON, 1992; MISRA *ET AL.*, 1995). NEGREROS-CASTILLO & HALL (2000) found that the number and height of sprouts was

related to the 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) and the maintenance of a large "sprout bank" may then be important. Tall stumps have a better chance of surviving fire, browsing and weed competition as the vulnerable sprouts are produced above the height of disturbance.

Where possible, there is enormous value in influencing the nature of the initial disturbance to maximise the density and height of live stumps. This may be feasible when the forest is being cut for timber or short-term, shifting-cultivation agriculture.

## **Research needs**

Much of our knowledge of coppicing comes from dry, naturally fire-prone areas of the world (such as African miombo, Australian savannah 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 the impact of human beings and where the native species may be less able to coppice, or may suffer higher rates of mortality following coppicing, e.g. 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 what can be done to stimulate sprout production from stumps, for example weeding, recutting or application of hormones. Is there such a thing as stump dormancy or is a non-sprouting stump a lost cause? Identification of stumps is a valuable management activity, which will be examined further in the final section.

#### b) Seedlings

A protocol is needed for the survey of seedling regeneration, so managers may gather relevant data that will enable them to predict the regeneration potential of the site. 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): the probability of success of a seedling 1.2 m tall is much greater than one that is 20 cm tall. Although the nature of the size-survivorship relationship varies between species (CONDIT ET AL., 1998), it would be practical to identify a minimum size for inclusion in the seedling survey, which can be applied to all species. SAJISE ET AL. (1989) have recommended a minimum height of 15 cm in the Philippines, but this limit needs further testing in other locations and across a range of species. Rather than measure the size of each individual seedling it may be more efficient to count seedlings in a number of rough and ready size classes, e.g. knee to waist, waist to chest, and above (for a standard-sized forester!). As 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 the seedlings' height relative to the top of the weed canopy, i.e. the distance above or below it, or simply whether they are 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  $1 \text{ m}^2$  has been used (SAJISE *ET AL.*, 1989). Seedling frequency may be more important than the average density across a whole site, as seedling distribution can be very clumped. A site is more likely to be successfully colonised when seedlings are widely dispersed because mortality is usually high in dense seedling clumps and "safe sites" for seedling establishment are often few and far between.

#### **Research needs**

There is a need for long-term monitoring studies, to assess the initial condition of tree and shrub seedlings using several variables (e.g. density, frequency, species, absolute height, diameter, relative height below or above the top of the weed canopy) and the subsequent course of regeneration. After a few years, information on successfully established seedlings should be compared with the initial site data to see which index (single variable or combination of variables) best predicted the outcome (NDAM, 1998). A long-term study is needed. Tools for seedling identification are also seriously lacking and this need is explored further in the final section.

### c) 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 incoming seed rain. An understanding of seed shadows (i.e. patterns of seed dispersal) is crucial for predicting which potential parent trees will contribute seed to a clearing - an important step in assessing the regeneration potential of sites. A two-curve model has been proposed to describe an individual tree's seed shadow (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, i.e. density falls off steeply with distance. Approximately 10% of the seeds are dispersed over long distances. Their seed shadow is described with a "fat-tailed" curve. Seed density gradually diminishes and extends over great distances of 1 to 10 km. Little is know about the long-distance component of the seed rain, as it is difficult to measure due to the very low density of seeds. However, this component is essential for the regeneration of isolated sites.

Tall, fruiting trees located in and adjacent to a site make the biggest contribution to the seed rain irrespective of the overall species composition of surrounding forest (HARDWICK, 1999), so managers may be able 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, it has already been shown that the 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 along these lines to predict recruitment in clearings.

Bird species have been found to be highly effective in seed dispersal of tropical forest trees, in some cases over long distances from the seed parent tree (SUN *ET AL.*, 1997; WHITNEY *et al.*, 1998). Structural diversity of vegetation encourages bird diversity

(MACARTHUR & MACARTHUR, 1961). The presence of "bird perches" generally increases bird-dispersed seed rain compared to open areas, although natural branches (alive or dead) are more effective than straight bars (HOLL, 1998). The presence of fruit on bushes or bait on artificial perches in clearings does not necessarily improve seed dispersal at that spot (WILSON & CROME, 1989; HOLL, 1998), possibly because birds do not always eat and defecate in the same place. Thus, providing that fruiting trees and shrubs are present to attract birds into the general area, species bearing wind-dispersed seeds may also improve seed dispersal by providing perches, even though they do not provide the birds with food.

Perches increase seed rain and seedling establishment in denuded ex-mine sites in North America, (MCCLANAHAN & WOLFE, 1993). However, the effectiveness of perches may depend on the severity of limiting factors operating at later stages of regeneration. For example, in weedy clearings in Costa Rica, seed rain was increased by perches, but seed predation and weed competition severely limited recruitment and establishment, so the established seedling population was not greatly increased (HOLL, 1998). In such cases where weed competition limits seedling establishment, the nurse trees planted in the "framework" or "catalytic monoculture" approaches to ANR would have the double advantage of attracting seed dispersers and shading out weed competition (PARROTTA, 1993), although their shade may also limit tree seedling establishment. Most studies agree that seed predation in cleared areas is a significantly limits seed availability, with mortality levels ranging from c. 20% (OSUNKOYA, 1994) to at least 80% (UHL, 1987; HAMMOND, 1995) of all seeds. Burying seeds may reduce the risk of predation (SHAW, 1968).

#### **Research needs**

We need to be able to predict more precisely the seed-shadow dimensions of the locally dispersed component of the seed rain. In particular we need 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. wind, bird, bat and mammal) under a range of local conditions representing variations in forest cover and the presence of animal dispersers.

Confirmation of the above results on the effect of perches would be valuable and we also need to know how distance from a forest seed source affects the efficacy of perches<sup>5</sup>. More research is needed on methods of avoiding predation of direct-sown seeds<sup>6</sup>.

# INFORMATION INTERPRETATION AND OUTPUT

It is clear that there is a pressing need for more and better identification manuals for seedlings and stumps to enable the manager to carry out accurate site surveys. In most of Southeast Asia tools for seedling identification, in particular, are severely lacking and this is a major obstacle to regeneration surveys. If it is not possible to identify to species level,



<sup>&</sup>lt;sup>5</sup> See Part 7, research proposal 2.2.

<sup>&</sup>lt;sup>6</sup> See Part 7, research proposal 4.3.

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 size or dispersal mechanism of seeds, or gross shoot architecture or leaf-form. Whilst the bark of stumps will correspond to that of intact trees, the morphology of epicormic shoots may differ from that of adults. Such characteristics 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<sup>7</sup>. 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) were most relevant to 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, a large amount of ecological knowledge is held by local people and has not yet been adequately integrated with formal scientific knowledge (SINCLAIR & WALKER, 1999). Many farmers carrying out slash-and-burn agriculture manage regenerating forest as fallows before another cycle of cultivation. It is therefore likely, in some environments, that local people's knowledge could make a major contribution to the information needed for improved methods of forest restoration. Therefore one priority should be the recording of relevant local knowledge of forest regeneration and its integration with scientific knowledge. 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 managers. 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 for the restoration of ecosystems such as wetlands and grasslands (PYWELL & COX, 1998) and it demonstrates the exciting possibilities for the use and interpretation of ecological information for the restoration of tropical forests.

#### REFERENCES

- CLARK, J. S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.* 152 (2): 204-224.
- CONDIT, R., R. SUKUMAR, S. P. HUBBELL and R. B. FOSTER, 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. *Am. Nat.* 152 (4): 495-509.
- DALMACIO, M., 1987. Assisted Natural Regeneration: A Strategy for Cheap, Fast and Effective Regeneration of Denuded Forest Lands (unpublished). Philippines Department of Environment and Natural Resources, Region 8, Tacloban City, Philippines.

<sup>&</sup>lt;sup>7</sup> See Part 7, research proposal 1.1.

- DE ROUW, A., 1993. Regeneration by sprouting in slash and burn rice cultivation, Tai rain forest, Cote d'Ivoire. J. Trop. Ecol. 9: 387-408.
- DUGAN, P., 2000. Assisted natural regeneration: methods, results and issues relevant to sustained participation by communities. In ELLIOTT S., J. KERBY, D. BLAKESLEY, K. HARDWICK, K. WOODS and V. ANUSARNSUNTHORN (Eds). Forest Restoration for Wildlife Conservation, Chiang Mai University.
- FAO, 1997. State of the World's Forests 1997. Food and Agriculture Organisation.
- GOOSEM, S. and N. I. J. TUCKER, 1995. *Repairing the Rainforest.* Wet Tropics Management Authority, Cairns, 72 pp.
- HAGGAR, J., K. WIGHTMAN and R. FISHER, 1997. The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. *For. Ecol. Manage*. 99: 55-64.
- HAMMOND, D. S., 1995. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. J. Trop. Ecol. 11: 295-313.
- HARCOMBE, P. A., 1987. Tree Life Tables. BioSci. 37: 557-568.
- HARDWICK, K., J. HEALEY, S. ELLIOTT, N. GARWOOD and V. ANUSARNSUNTHORN, 1997. Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand. *For. Ecol. Manage*. 99: 203-214.
- HARDWICK, K. A., 1999. Tree colonization of abandoned agricultural clearings in seasonal tropical montane forest in northern Thailand. Ph.D. thesis, University of Wales, Bangor, UK. 165 pp.
- HARLEY, J. L. and S. E. SMITH, 1983. *Mycorrhizal symbiosis*. Academic Press, London, 483 pp.
- HILL, J. D., C. D. CANHAM and D. M. WOOD, 1995. Patterns and causes of resistance to tree invasion in rights-of-way. *Ecol. Appl.* 5(2): 459-470.
- HOLL, K. D., 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restor. Ecol.* 6(3): 253-261.
- JANZEN, D. H., 1988. Tropical ecological and biocultural restoration. Science 239: 243-44.
- JOHANSSON, T., 1992. Sprouting of 2- to 5-year-old birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth) in relation to stump height and felling time. For. Ecol. Manage. 53: 263-281.
- KAMMESHEIDT, L., 1998. The role of tree sprouts in the restoration of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay. *Plant Ecol.* 139(2): 155-165.
- KHAN, M. L. and R. S. TRIPATHI, 1989. Effects of stump diameter, stump height and sprout density on the sprout growth of four tree species in burnt and unburnt forest plots. *Acta Oecol.*, 10: 303-316.
- KNOWLES, O. H. and J. A. PARROTTA, 1995. Amazonian forest restoration: an innovative system for native species selection based on phenological data and field performance indices. *Comm. For. Rev.* 74: 230-243.
- LEUNGARAMSRI, P. and N. RAJESH, 1992. *The Future of People and Forests in Thailand After the Logging Ban.* Project for Ecological Recovery, Bangkok, Thailand, 202 pp.

- LUGO, A. E., 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *For. Ecol. Manage*. 99: 9-19.
- MACARTHUR R. H. and J. M. MACARTHUR, 1961. On bird species diversity. *Ecology* 42: 594-598.
- MCCLANAHAN, T. R. and R. W. WOLFE, 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Cons. Biol.* 7(2): 279-288.
- MILLER, P. M. and J. B. KAUFFMAN, 1998. Effects of slash and burn agriculture on species abundance and compositions of a tropical deciduous forest. *For. Ecol. Manage*. 103: 191-201.
- MISRA, P. N., S. K. TEWARI, R. S. KATIYAR and D. SINGH, 1995. Effect of coppicing height on the regeneration and productivity of certain firewood shrubs in alkaline soils of North Indian plains. *Biomass and Bioenergy* 9: 459-463
- MUSOKO, M., F. T. LAST and P. A. MASON, 1994. Populations of spores of vesiculararbuscular mycorrhizal fungi in undisturbed soils of secondary semideciduous moist-tropical forest in Cameroon. *For. Ecol. Manage*. 63: 359-377.
- NEGREROS-CASTILLO, P and R. B. HALL, 2000. Sprouting capability of 17 tropical tree species after overstory removal in Quintana Roo, Mexico. *For. Ecol. Manage.* 126: 399-403.
- NEPSTAD, D., C. UHL and E. A. SERRAO, 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. In: A. Andersson (Ed.), *Alternatives to deforestation: steps towards sustainable use of the Amazon rain forest.* Columbia University Press, New York, 215-229.
- NEPSTAD, D.C., C. UHL, C. A. PEREIRA and J. M. C. DA SILVA, 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos* 76 (1): 25-39.
- NDAM, N., 1998. Tree regeneration, vegetation dynamics and the maintenance of biodiversity on Mount Cameroon: the relative impact of natural and human disturbance. Ph.D. thesis, University of Wales, Bangor, UK, 278 pp.
- OSUNKOYA, O., 1994. Postdispersal survivorship of north Queensland rainforest seeds and fruits: effects of forest, habitat and species. *Aust. J. Ecol.* 19: 52-64.
- PARROTTA, J. A., 1993. Secondary forest regeneration on degraded tropical lands. The role of plantations as "foster ecosystems". In: H. Leith and M. Lohmann (Eds), *Restoration of Tropical Forest Ecosystems*. Kluwer Academic Publishers, Dordrecht, The Netherland, 63-73.
- PARROTTA, J. A., J. W. TURNBULL and N. JONES, 1997. Catalyzing native forest regeneration on degraded tropical lands. *For. Ecol. Manage*. 99: 1-7.
- PAUDEL, K. C., R. PANDIT, L. K. AMATYA, D. B. GURUNG, H. S. BHANDARI, A. H. HARDING, and S. P. BHATTARAI, 1997. Agroforestry research strategy for Lumle Agricultural Research Centre, 1997-2001. 37 pp.
- PYWELL, R. F. and R. Cox, 1998. The decision support system for habitat restoration. NERC / MAFF, U.K.
- READ, D. J., D. H. LEWIS, A. H. FITTER, and I. J. ALEXANDER, 1992. *Mycorrhizas in ecosystems*. CAB International, Wallingford, England.

- RIBBENS, E., J. A. SILANDER, and S. W. PACALA, 1994. Seedling recruitment in forests calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75, 1794-1806.
- RIJKS, M. H., E. J. MALTA and R. J. ZAGT, 1998. Regeneration through sprout formation in *Chlorocardium rodiei* (Lauraceae) in Guyana. *J. Trop. Ecol.* 14: 463-475.
- SAJISE, P. E., C. V. ARENAS, J. C. DUMA, L. M. FLORECE, W. S. GRUEZO and F. P. LANSIGAN, 1989. Assisted natural regeneration: working with nature reforestation strategy. Unpublished memo circular #17, Department of Environment and Natural Resources, Philippines.
- SHAW, M. W. L., 1968. Factors affecting the natural regeneration of Sessile Oak (*Quercus petraea*) in North Wales. II. Acorn losses and germination under field conditions. J. Ecol. 56, 647-60.
- SINCLAIR, F. L. and D. L. WALKER, 1999. A utilitarian approach to the incorporation of local knowledge in agroforestry research and extension. In: L. E. Buck, J. P. Lassoie and E. C. N. Fernandes (Eds), *Agroforestry in sustainable agricultural* systems. CRC Press, Boca Raton, Florida, USA, 245-275.
- STOTT, P., 1986. The spatial pattern of dry season fires in the savanna forests of Thailand. *J. Biogeog.* 13: 345-358.
- SUN, D. and G. DICKINSON, 1995. Direct seeding for rehabilitation of degraded lands in north-east Queensland. *Aust. J. Soil Water Cons.* 8(4): 14-17.
- SUN, C., A. R. IVES, H. J. KRAEUTER, and T. C. MOERMOND, 1997. Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* 112, 94-103.
- UHL, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75: 377-407.
- VIEIRA, I. C. G., C. UHL and D. NEPSTAD, 1994. The role of the shrub Cordia multispicata Cham. as a succession facilitator in an abandoned pasture, Paragominas, Amazonia. Vegetatio 115 (2): 91-99.
- WHITNEY, K. D., M. K. FOGIEL, A. M. LAMPERTI, K. M. HOLBROOK, D. J. STAUFFER, B. D. HARDESTY, V. T. PARKER and T. B. SMITH, 1998. Seed dispersal by Ceratogymna hornbills in the Dja Reserve, Cameroon. J. Trop. Ecol. 14, 351-371.
- WILLSON, M. F. and F. H. J. CROME, 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. J. Trop. Ecol. 5: 301-308.
- WILSON, J., R. C. MUNRO, K. INGLEBY, P. A. MASON, J. JEFWA, P. N. MUTHODKA, J. M. DICK, R. R. B. LEAKEY and P. G. JARVIS, 1991. Tree establishment in semi-arid lands of Kenya role of mycorrhizal inoculation and water-retaining polymer. *For. Ecol. Manage*. 45: 153-162.

## QUESTIONS AND COMMENTS

### M.R. Smansnid Svasti

Regarding fire-tolerant species, we have indeed been monitoring species to see which can coppice and sucker after fire. Gymnosperms had the best survival, because their leaf buds are tightly enclosed and do not burn, so after the fires they can still produce new growth. However, after the last fire, everything except the Gymnosperms burnt to the ground and died. Every year we get fire and we do not think that selecting fire-tolerant species is enough to combat the problem, so this year we have undertaken a very intensive fire-protection programme.

### Kate Hardwick

It is very interesting and useful to look at which species can survive fire and why. However, I agree that, when a site is burnt every year, just planting fire-tolerant species cannot solve the problem. We also need to explore other techniques such as controlled burning to reduce the fuel load on the site.

# David Lamb

Not all fires are the same and variations in intensity, time of year etc. may well give us opportunities to manipulate fires through controlled burning. Also there are great differences between species in how they respond to different intensities of fire. Coppicing is probably much more common than we think and we do see it in a lot of species in moist areas. Instead of asking which species coppice, we should be asking questions such as: what is the upper limit to stump size? Will regrowth be unstable and snap off in high winds?

### Kate Hardwick

I would agree with that, but would add that the answers to these valuable questions will vary between species and that should be taken into consideration in any further research.

### **Ulfah Siregar**

With so many species in native forest, how do you choose which species should be assisted in their regeneration? Secondly, regarding long distance seed dispersal, one method would be to use genetic markers to see where seeds are coming from.

#### Kate Hardwick

It is an interesting idea to use genetic markers. The choice of species to assist is an important consideration which would be governed by many of the same factors which determine the choice of species to plant, and these will be covered in the next session.