Ecology and other biological fields are also needed, particularly in studying more closely the mechanisms of resilience of forest ecosystems, but they are more favoured in the themes C and E of ETFRN focusing on natural regeneration and management of natural forests.

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Group 3: Natural Regeneration of Natural and Semi-natural Forest Ecosystems

(written by Dr. F. Bongers, Wageningen Agricultural University, The Netherlands)

INTRODUCTION

The concept of natural regeneration is generally used at two levels. At the species level natural regeneration is part of the life cycle between flowering and seed set, through dispersal, germination, seedling establishment and growth to the sapling stages. "Natural" refers to the absence of direct human influence (e.g. pollination, seed introduction, tree planting). At the community and ecosystem level natural regeneration is part of the forest growth cycle and refers to the initial phases of forest establishment and forest development. The same processes as mentioned above are of prime importance in this respect. The closely related term of reforestation is mostly used for the human-managed forest recovery processes, in many cases connected with land rehabilitation.

In this paper we would like to indicate the aspects of natural regeneration on which new research should be focused. Before listing some important fields of research we would like to draw attention to some general aspects:

1. In regeneration studies by far the most attention is put to moist forests. Studies from montane and dryland areas (arid and semi-arid zones, with seasonal rainfall in most cases) are almost completely absent. This is remarkable in view of the great proportion of the world covered by these climates, the great proportion of the population living in these zones, and the environmental problems in these areas.
2. There is a wide gap between the studies performed by ecologists, and those by foresters. In most cases ecologists focus on natural ecosystems with little or no practical follow-up. Foresters have put much attention to exotic species, especially in the dryland areas. Ongoing discussions on burning, grazing and cutting management in dryland areas demonstrate this: many foresters still see these processes as undesirable, whereas most ecologists know for long that these are natural processes, which, provided a certain limited frequency and intensity, are essential for maintenance of proper ecosystem functioning. We share the opinion that both ecological and forestry principles should be integrated at the field level.

3. In natural regeneration studies the processes and their underlying factors are essential. Not only the driving forces of the physical environment (e.g. light, water, nutrients) but also the biological ones (plant-animal, plant-plant and animal-animal interactions) are of prime importance. Humans should be taken into account as part of the environment, not as a separate entity.
4. Species-oriented studies should focus on abundant species at different sites, and not on the many ubiquitously rare ones, because abundant species (i) determine the community structure and dynamics, (ii) contribute the most to the biomass and the cycling of nutrients and water balance, (iii) are in general better known taxonomically, (iv) have large statistically reliable sample sizes, (v) will be more widespread and allow site-site comparisons, (vi) are of more potential interest to silviculture (vii) with limited manpower, time and effort they present better scientific return per tree sought and measured.
5. To understand the natural regeneration of the abundant and important species the following should be held in mind:(i) forests are very variable in time and space (decades, km), (ii) many tropical tree species have wide tolerances of site conditions, (iii) history (10 to 1000 y) plays a major role in understanding the present situation, (iv) the rates of change from competitive interactions and selection can be very slow, over centuries (however, objective, realistic and testable predictions are needed for the next two decades).
6. A major difficulty is the lack of generality in tropical forest regeneration studies, a synthesis of the main factors and processes and a flexible predictive model for forest dynamics. A priority should be to draw up a data base of known sites for long time-lines and abundant species to allow regional comparisons. Basic quantitative data are lacking and more researchers should be aware of valid sampling designs, asked to permanently label plots for remeasurement and try to attain the highest level of taxonomic support. Currently, much forest inventory data is of little use for ecological analysis because sampling and identification are often inadequate.

IMPORTANT TOPICS FOR RESEARCH

In this section some major research questions and research topic will be listed, and some background information given. The listed items are not presented in order of importance.

Why are some forests dominated by only a few species?

In view of the worldwide biodiversity debate this question is crucial for the understanding of forest regeneration. Two important questions to be addressed by natural regeneration studies are: (i) Is species composition constant, and within what spatial and temporal limits, or are forests changing gradually in time and space? (ii) what factors determine where a forest is placed on the scale between monodominant, through co-dominant to mixed forest (lack of domi-

nance, but species-rich forest). Answering these questions, with a focus on the processes involved, will enlarge our understanding of species richness.

Effects of disturbances, human and natural, on diversity and structure

What are the effects of different natural (e.g. droughts, landslides, pests) and human-induced (e.g. logging, burning, hunting, grazing) disturbances and types of intensities on regeneration? What are the consequences in terms of diversity and structure? In what sense does recovery lead to a return to the predisturbance situation (resilience)?

It is well known that tropical forest regeneration after disturbance depends on the kind of disturbance and its intensity. In the case of regeneration after agriculture (fallowlands or 'old fields') the type of land use, the accompanying agronomic practices, and the time the land has been used are crucial. Studies should focus on the relationship between the initial situation (in terms of available root stocks and seeds, nearby presence of trees as seed sources, soil and water conditions etc.), the anthropogenic stress factors during regeneration (eg. grazing, burning, wood collection) and the transition process. There are certainly some initial situations that do not show any substantial form of natural regeneration (i.e. a threshold has been surpassed - irreversible degradation called regression takes place). It is of utmost importance to define such thresholds. There may be relatively simple methods that can support the system to overcome such thresholds (eg. breaking the soil crust, reseeding, enrichment with certain key species).

Similar processes and problems occur in forests which suffered from different intensities and frequencies of selective logging. In order to develop recommendations for managing disturbed sites, it is necessary to evaluate the consequences of the presently large array of disturbances and land use systems on the diversity and structure of tropical forests. This is especially relevant for regenerating forests. Therefore, comparative studies should be conducted: (i) long chronosequences (up to e.g. 100 years); (ii) effects of fragmentation on forest structure and diversity recovery; and (iii) long-term monitoring of permanent plots sustaining regenerating forests after different kinds of disturbances and land use systems.

In order to get reliable data, answering these questions should imply conducting studies along a gradient of habitats. Especially a disturbance gradient is important in this respect. Basic field observations at the community level are a good start to analyze the effects of disturbances, but replicated experiments at a species level also allow the improvement of conclusions and predictions that can be drawn at the first sight.

Not only the arborescent population should be studied, but also lianas and epiphytes who merit special attention as lianas may strongly retard or impede succession, while the presence of epiphytes may indicate

specific levels of recovery. Also, studies of the development and/or recovery of soil humus profiles along differing successional gradients are needed, especially in areas where the ecological function of the top- and subsoil has to be restored for the sake of natural regeneration and forest recovery.

In dryland areas emphasis should be laid on the relationship between variable frequency and intensity of the human interventions, in relation to natural disturbances (the severity of which decreases with increasing rainfall), on forest biodiversity, biomass and productivity. The process of bush encroachment in grazing lands is very important. This process is still little understood, particularly in terms of resilience and thresholds. Attention may be focused on key species (e.g. species dominating the bush encroachment stage).

A major question is to what extent the structure and floristic composition recovers after human intervention. In order to stimulate the process of recovery in e.g. abandoned forest lands, selectively-logged forest areas, it is of fundamental importance to know if and how the regeneration process leads to partial or complete resilience, i.e. to an ecological return of the predisturbance situation. This question is inevitable if we want to predict recovery rates and, if possible, the time needed for an 'acceptable' level of forest recovery following human intervention. The modelling of recovery trends using different scenarios through varying parameters in a simplified forest ecosystem may be useful to predict the potential resilience of the ecosystem under study.

Importance of recent climatic change (e.g. desertification, intensification of dry periods) on regeneration processes

All forest ecosystems are strongly controlled by climatic factors and evidence suggests that seasonality and rainfall are much more important than soil type and nutrients, though these interact at local scales. Global climate is changing. Priority should be given to climatic effects on natural regeneration in tropical forests.

The desertification debate has unfortunately focused for a long time on the energy crisis, supposed to be the main cause. This has led to the focus on rapidly growing wood producing exotics. Because of the "crisis nature" of the problems, virtually no fundamental studies have taken place in this field (all trial and error work). It is still commonly held among foresters that local people have no indigenous knowledge on tree or forest management.

In dry areas the period and depth of soil wetting is fundamental for natural regeneration (NB. germination is not a problem, seedling survival during a one-year cycle including the dry season is the major bottleneck). Climatic change has certainly influenced seedling survival, but the additional influence of soil degradation on water availability should be integrated in the analysis. Of several species, it is clear that their area of distribution is decreasing towards zones with higher rainfall. Decreasing groundwater levels may play a role as well.

This calls for detailed ecophysiological studies on response to drought, seasonal water balance and intense leaching in wet

seasons. Studies on the relationship between water availability and seedling survival should provide clues on the underlying dynamics, and should be carried out for several years. This in relation to rooting dynamics and the physiology of water uptake and use. Practical implications may be selection for species and individual plants that are best adapted to survival of the dry season (nowadays, selection always takes place on the most rapidly above-ground growing plants). An understanding is required of how climate affects phenology, especially fruiting in most years. Transplant experiments with seedlings are very useful. Two overall approaches are essential: (i) long-term measurements on key abundant species in permanent plots (especially those identified by hypotheses), (ii) comparative studies in plots over rainfall gradients, locally and regionally.

Studies of these factors are probably best conducted in Africa where gradients are well established, change is fast, there is a range of seasonality, the flora is well-known and soils are variable.

Reliable predicts from regional-climate based models are required. The most urgent question is whether there is a consistent transitional change of species composition in time.

Comparative studies of different bottle-neck phases in life history, with emphasis on seed, seedling and sapling dynamics in space and time

The natural regeneration of forests requires information on the controlling or limiting stages to recruitment. Some phases in the life history of plant species may affect population size and vitality more than other. In many cases the seedling stage is the most vulnerable stage in a plant's life. In other species the sapling stage or even the seed itself forms the bottle-neck for a healthy population.

The role of animals in dispersal, predation of seeds and fruits and grazing of seedlings and saplings should be quantified, taking into account the tree-to-tree variation. What controlling roles do animals have on the relative survival of different species? The impact of high levels of hunting in forests, leading to a strong decline of animal densities, on future forest composition should be addressed.

All plants respond to more light but some are more tolerant to shade than others. Studies should concentrate on species' light threshold levels and their consequences for survival of seedlings in the forest. Similarly, all species respond to added nutrients, but most are intolerant to low nutrient levels. Mycorrhizas play a role in this respect. As tropical forest systems globally become more and more phosphorus depleted, more effort is needed on studying light-phosphorus interactions at low threshold levels. These tolerant species are the new silvicultural species of the future.

Research on the competition among close-packed saplings of similar and different canopy and subcanopy species merits attention.

At the canopy level more ecophysiological work is needed to understand the control of seed production, its timing and amount: is it nutrient limited, water controlled, or animal dependent?

Vegetative reproduction of major species
Regeneration and reproduction ecological studies of tropical forests have mainly focused on generative mechanisms. Recent studies have proven the importance of coppice shoots for regeneration following disturbance. For instance, Costa Rican montane oak forests are locally managed through coppicing techniques, Central American lowland rain forests recover from hurricanes through a process of resprouting. In dryland areas many species regenerate vegetatively. These species might be propagated in particular for land rehabilitation and soil protection purposes.

Forest gaps and their role in species regeneration
The natural forest is a structurally complex mosaic in time and space. Openings in the forest occur as canopy trees fall down. Most species profit from canopy openings, but the effects depend on the changed conditons and on plant development phase. Gaps at different heights in the canopy profile enable further growth of pole trees of different sizes. Gap creation is a stochastic process.

Seed release from adults may lead to clumped distributions in the forest. When gap creation and seed availability coincide recruitment may occur. Much more effort is needed in mapping trees and gaps and the spatial patterns of small trees. Models can indicate how some forests become monodominant or mixed.

Very little is known of the importance (intensity, frequency) of competition between neighbouring trees for light and nutrients, especially when gaps are created above small trees. How does neighbourhood composition affect the outcome? At the pole stage, competition would be expected to be most intense, showing the adaptive characteristics of species to the site. These questions can only be answered by detailed field data from permanent plots studied over long periods of time. Models of forest regeneration need to account for spatial variation in regeneration. The importance of competition is central to understanding why at some sites monodominance of some species prevails, while at others a mixed forest composition dominates.

CONCLUDING REMARKS

In general we feel that more attention should be paid to long-term studies as regeneration processes take a long time. At the same time modelling tools for the complex multispecies tropical forests should be (further) developed, especially the ones with prediction values. We plea for quantification, formalization and standardization.

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Natural regeneration means regrowth of the forest without intervention by man. Identification of forest and tree stages with limited recruitment may provide valuable insights into new silvicultural techniques. These data are needed to build simple, powerful and predictive models of forest regeneration to predict canopy composition and explain site-to-site differences.

Studies of natural regeneration of specific species must be put in the context of the whole forest community and the ecosystem, and also in the context of the human landuse systems in the area.

Studies should lead to conclusions with at least a minimal application value (restoration, conservation, interventions). The alarming state of the environment in many dryland areas warrants a focus on natural regeneration processes for ecosystem rehabilitation. To contribute to future sustainability of the activities, such studies should be as much as possible participatory, i.e. involving not only governmental and non-governmental (forestry) agencies, but also local communities, especially as there is quite some knowledge among local people on natural regeneration of some desirable tree species.

Group 4: Genetic Diversity Studies

(written by Prof. Olavi Luukkanen, University of Helsinki, Finland)

INTRODUCTION

Tropical forest genetics has two major goals which have to be considered both in research and in the application of research results in development: conservation and domestication. The present report focuses on research needs.