MANIPULATION OF LIGHT IN TROPICAL RAIN FOREST

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1. ABSTRACT

The manipulation of tropical forest is directed towards transforming the forest, or its components, in such a way that the forest delivers more products. In tropical silvicultural systems, manipulating the structure of the forest is what is important, and in nearly all cases this is aimed at influencing the competition among individuals - competition mainly for light. To be able to manipulate rationally and functionally, we need to know whether species react to changes in light, and how they react to these changes.

The ecological research of our group is dedicated mainly to the biological aspects of the relationship between light and (1) the structure of the forest, (2) the dynamics of the populations of selected species, and (3) the growth and development of trees.

Light in the forest is mainly determined by the openness of the forest canopy. Gaps in the canopy that result from falling trees and branches are crucial in this respect. Their dynamics in space and time determine the dynamics of light in the forest. The survival probability of a tree increases with tree size, and light has a positive influence on tree size. At high light, trees grow better, seedlings as well as large trees, but the trees' reactions are related to the ontogenetic tree phase. Pioneer trees grow faster than shade-tolerants do, and profit more from higher light levels.

A manipulative increase in light level is only worth the effort when desired species and individuals profit more from it than do undesired species and individuals. Manipulations aimed at small individuals also pay off, as a small increase in survival directly leads to a higher density of desired individuals. Manipulations directed at large individuals only lead to higher production on the individuals already present. Research on reactions of individuals and species to light and changes in light can lead to predictions of the effects of manipulations, which we need for sound manipulation. New analyses of old data using modern knowledge and techniques could be rewarding. Experiments directed to answering specific questions could also increase our understanding. This could improve the predictions as well as the results of manipulations.

Diversification, small-scale use, and spatial stratification of manipulations, focused on species and individuals, deserve more attention. For that, we should also look more at systems that local people use. Studies need to be positioned into a general frame of manipulations aimed at specific products from, and functions of, tropical forest.

2. INTRODUCTION

Tropical rain forests have many uses. One group of uses is the extraction of forest products (e.g. fruit, latex, bush meat, medicines, and wood). Most tropical rain forests are very rich in species. On the one hand, this leads to a high probability that at least some of the species provide products wanted by humans, but on the other hand it implies that typically the number of individuals of one species is low.

This also means that the natural production per species may be badly reduced, when expressed per unit of area. The extraction of forest products, thus, is nearly always hampered by the low availability of the individuals that provide the products. For some species, however, individuals tend to grow together, and thus, on a local scale, the availability of products can be high.

Ever since people have used products from the forest, they have, in one way or another, been influencing the production of the goods (Wiersum, 1997). Nowadays, it is beyond dispute that nearly all tropical forests are influenced by man. Such influence may range from picking fruits, via cutting down scattered trees for honey collection, tending individual trees in forest gardens near a village, to operating large-scale logging concessions.

Silvicultural systems in the tropics are focused on transforming the natural forest into a forest with a higher abundance and production capacity of one or more species that are wanted for their products (cf. Lamprecht, 1989). These transformations vary in intensity:

- A low-intensity transformation does not change the system or its constituent parts very much and thus has a low impact. In most cases, the result is only a slight change in the production capacity of the system;
- Low-to-medium intensity transformation. The near-to-nature or nature-analogous systems generally cause only mild transformations. The yield of products in such systems is typically low, at least the short-term yield is;
- Medium-to-high intensity transformation. Most sustained-yield silvicultural systems have a medium-to-heavy impact on the forest ecosystem. In many cases, the forest is opened up drastically (basal area reductions up to 75%), leading to a completely different forest;
- A high-intensity transformation is a transformation that drastically changes the system (e.g. into a plantation designed for one special product only). The original system then ceases to exist.

Most silvicultural systems have in common that they are designed to stimulate the growth and production of desired species by changing the environment of individuals of these species. In most cases, this boils down to killing individuals of undesired species. The central idea is that the desired individuals grow or produce better when competition from others, mainly for abiotic environmental resources, is reduced. In many forests, light is the most important limiting abiotic resource for plant growth, constituting a bottleneck for growth and development of individuals, especially in the young phases. Water and nutrients come in the second place, but this, of course, depends on local conditions (e.g. in forests on poor white sand soils, the importance of resources may be reversed).

In this paper, I will discuss the role of light in forests, and the way in which knowledge of the light environment and the light requirements of trees can be applied in silviculture. First, I will treat in detail the manipulation of light in silviculture. Second, I will summarise some major results of research work on the role of light in the tropical rain forest in French Guiana. Third, I will discuss the importance of these findings for silvicultural manipulation of the forest. I will conclude with promising new directions for research in the near future in the field of light and the manipulation of tropical rain forest.

3. SILVICULTURE AND MANIPULATION OF THE LIGHT ENVIRONMENT

In silvicultural systems, manipulation of the forest is mostly aimed at one desired species, or a group of such species: species that provide desired products. Three general types of intervention are possible in forest manipulation:

- A change in abiotic resource availability (e.g. light, water, nutrients), aiming at a reduction of competition (for light, water, nutrients, physical space);
- A change in the intensity of interactions: plant-plant, plant-animal, animal-animal (e.g. hunting seed-dispersing animals);
- A reduction or elimination of 'bad' individuals (e.g. bad stem, little fruit, high disease susceptibility), or a specific stimulation of 'good' individuals (e.g. leading to genetic selection).

Most types of interventions used in silvicultural systems lead to a change in the light conditions in the forest (Lamprecht, 1989; 1993). The most commonly used intervention is refinement thinning, which is a general stimulation of all individuals of desired species by an overall, systematic reduction of competition by individuals of undesired species. In those cases, all or most undesired trees are cut or poison-girdled in order to promote the growth of desired trees. The second intervention is liberation thinning, which is the stimulation of selected individuals by a strong reduction in competition from nearby individuals. Both are mainly focused on the desired individuals already present. An example is the CELOS Silvicultural System, which uses both general refinement thinning and specific liberation thinning (de Graaf, 1986; Jonkers, 1987). A third intervention is the creation of gaps in the canopy (e.g. the Kintap System; Sagala, 1994), or the cutting of small strips (e.g. the Palcazu System: Hartshorn, 1989; Stocks and Hartshorn, 1993). On the one hand, this is a way of logging; on the other, it is a manipulation aimed at an increased recruitment of a specific group of species.

Table 1 Forest manipulation: some of the questions to be asked

Forest manipulation: questions to be asked
• Which species and which individuals to focus on? Which criteria?
• Where should individuals be eliminated? Which criteria?
• How to eliminate individuals?
• How do species react? What do species need?
• Biological and physiological background: how does it work?

Ideally, these interventions are based on ecological knowledge of the targeted species. Only in a very few cases, however, and only for a very few species is this ecological knowledge sufficiently available. In fact, what do we need to know for each of these manipulation types (Table 1)?

1. Refinement: stimulation of all individuals of desired species by an overall systematic reduction of competition by individuals of undesired species (all or most undesired trees are cut or poison-girdled to promote the growth of desired trees).
    - On which (group of) species should the measures be focused, and which species should be eliminated? What criteria should be used for selecting desired species? Especially the undesired species deserve attention. Which individuals should be eliminated? Lower- diameter limits of cutting are very important in this respect (e.g. in relation to tree size at maturity);

   - Where should undesired individuals be eliminated? Is this everywhere, or on specific locations (e.g. depending on the competitive influence on desired individuals)?
   - By what method should individuals be eliminated? Cutting, for instance, leads to high damage levels, while poisoning and poison-girdling is slower, but less damaging;
   - Is it possible to use the same elimination techniques for all these species? Do all desired species respond in the same way to treatment?
2. Creating gaps or cutting strips in the canopy, aimed at an increased recruitment of a specific species or group of species.
   - Which species should be targeted? Which criteria are to be used?
   - What kind and sizes of gaps or strips are needed for these species?
   - Do light levels in the gap and light requirements of the species change in the same direction with increasing gap age and tree development?
3. Liberation: stimulation of selected individuals by a severe reduction in competition from nearby individuals;
   - Which species (and which individuals of these species) should be targeted? Which criteria are to be used?
   - What is the hierarchy in desirability of the species, and of the individuals? (Is Species A favoured over Species B, both being desired species?);

   C Is this hierarchy location-specific? (Species A is favoured here; Species B is favoured there.);

   - How does a species respond to liberation? How much liberation is needed? When is liberation needed? When is liberation most effective? What are the effects on, for instance, wood quality?
   - What is the biological and physiological background of liberation? How does it work? What biological mechanisms are important? How can we understand these mechanisms? What is the variation that exists among and within species?

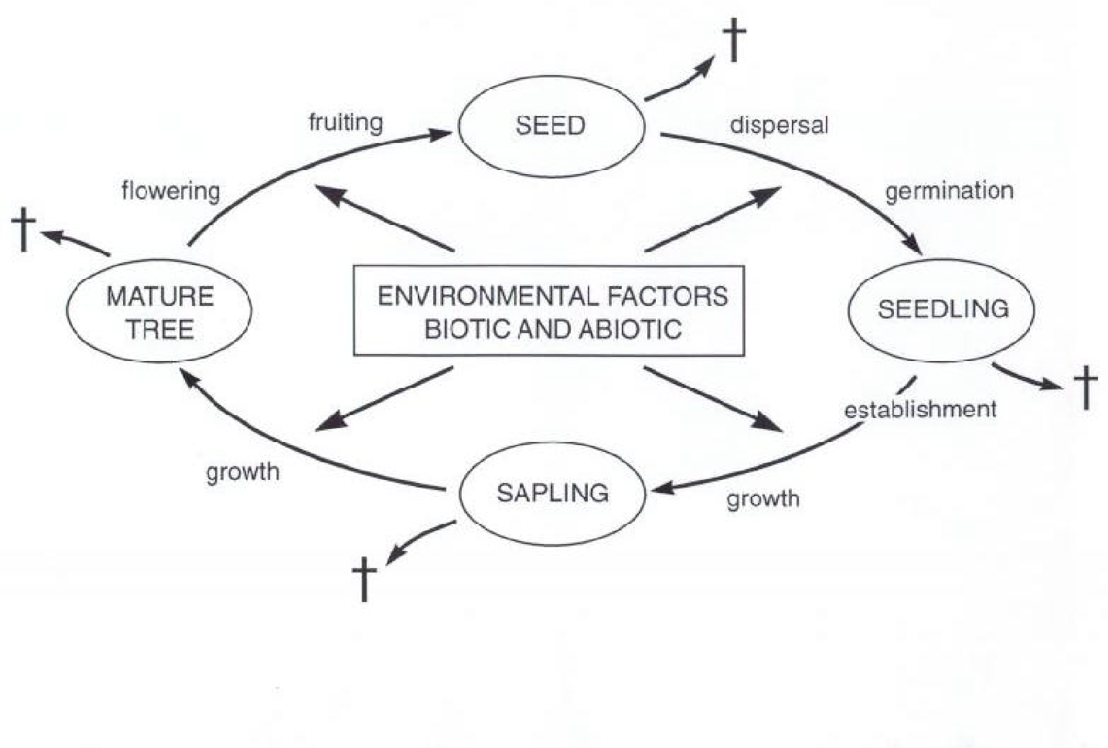

Figure 1 Life cycle diagram of a tree. Light is an important abiotic factor influencing all processes involved.

From the ecological point of view, it is central that we know as much as possible about the effect of light on the life history of species. Figure 1 schematises the life history of a tree, and the role of the environment. Mature trees produce seeds that are dispersed and germinate to produce seedlings. These grow into saplings and further to mature trees. Individuals may die in all stages. The processes involved in the transition from one phase to another (e.g. pollination, germination, growth) are influenced by environmental factors, biotic as well as abiotic. Here I will concentrate on the role of light.

4. CANOPY DYNAMICS, LIGHT, AND TREE-LIFE HISTORY RESEARCH IN FRENCH GUIANA

In the rain forest of French Guiana, we are studying some of the processes mentioned (Figure 1), and how light shapes the outcome of these processes. Our main research area is the forest of the Biological Station, Les Nouragues, approximately 100 km south of Cayenne. The forest is tropical lowland rain forest and is typical of a large part of the area. Recent human influence (over the last 200 years) is virtually nil. We are concentrating our efforts on 12 ha of forest, where we started our research in 1990. The concentration in that area gives us the opportunity to integrate data from several sub-studies. Figure 2 indicates the main research lines.

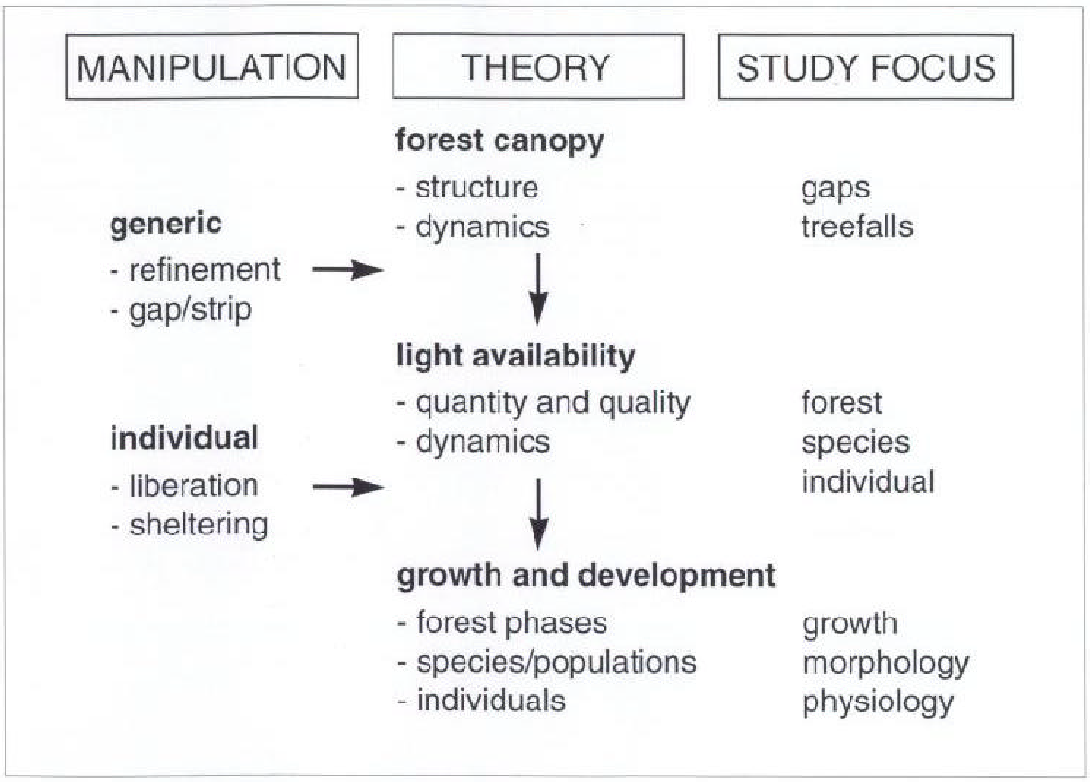

Figure 2 Conceptual scheme of our studies in French Guiana

In forests, light and variations in light are mainly determined by the above-ground structure of the forest and by changes in it. Openings in the canopy of the forest, mostly caused by falling trees or large branches, are of primary importance for the light climate. We analyse the effect of canopy dynamics on the light environment, using a forest patch perspective as well as an individual tree perspective. We focus on both the temporal and the spatial dynamics of light, mainly the quantity of light but also its quality. As the next step in the chain, we study the effects of light on some selected species. We look at the responses of the trees to variations in the availability of light, in terms of recruitment, mortality, growth, and development. Crown development is studied at various scales: the whole crown, branches, shoots, internodes, and individual leaves. We try to understand the processes and resulting patterns, using detailed studies of morphology and ecophysiology.

The results of these studies can be directly related to intervention and manipulation techniques. Generic treatments such as general refinements affect the general light climate at the level of tree canopies. Refinement will lead to an overall increase in light availability. Gap and strip-cutting techniques will do the same, but on a relatively small scale. In contrast, liberation thinning directly influences the light availability at the scale of individuals. Our studies address most of these aspects.

4.1 Canopy dynamics and light availability

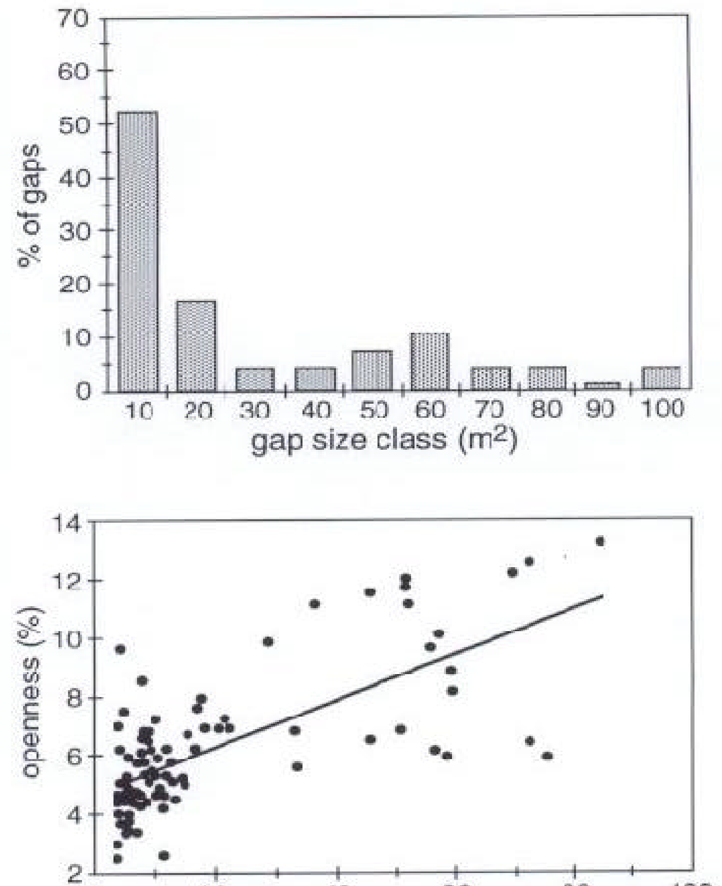

Figure 3 (A) Frequency distribution of sizes of canopy gaps that occurred between 1990 and 1993 in 12 ha of forest (n=42, sizes according to the Brokaw method)
(B) Gap size and canopy openness, Les Nouragues forest. Openness = 4.70 + 0.077 * gap size. R^2 = 0.47 (after van der Meer and Bongers, 1996b)

The results of our studies on canopy dynamics show that in the natural forest of Nouragues (van der Meer, 1995; van der Meer and Bongers, 1996a and b):

- The number of gaps per year is highly variable, both in time and in space;
- Most gaps are very small, and the number of large gaps is very low;

- The total forest area in gap phase at any moment is small (1-2%);
- It takes 10-15 years for a gap to close, depending on the original gap size;
- About 1-2% of the trees >10 cm DBH fall each year;
- Most falling trees do not result in canopy gaps;
- Most trees die because other trees knock them over.

These canopy dynamics result in great changes in the availability of light in the forest. Because of the different sizes of canopy openings and the changes therein, light availability is highly variable, on all scales, in space as well as in time. Figure 3 shows some of this variability in frequencies of gap size and light levels in the centre of gaps of different sizes. Because most gaps are small, the light levels are generally low, compared with the light levels in the open. As large gaps are scarce, high light levels are also scarce. A direct result of the scarcity of large gaps is that, in this forest, the proportion of light-demanding species (the species that require high light levels throughout their life history) and individuals is low.

We are currently analysing the dynamics of changes in gaps: closure in terms of vegetation, and changes in terms of light. These studies include the transition zones towards the closed forest, and the closed forest itself.

4.2 Light and performance of species and individuals

Our studies on the effect of light and changes therein on individual trees of four selected species (Sterck, 1997; Bongers and Sterck, 1998) show that:

- Individuals of all size classes may be found under all light conditions, except for the largest individuals;
- The proportion of individuals in high light increases with height;
- Pioneer trees grow under higher light levels than shade-tolerants, but
- Pioneer trees are also found in the shade, and shade-tolerants are also found in high light;
- For many trees, light levels changed during the 5 years of study: some received more light, others received less;
- Small individuals experience greater changes in light than large individuals.

These light levels, and the changes therein, have great effects on population dynamics and on the growth and development of individual trees. To be able to quantify these influences, we are studying these aspects for some selected species. The leading questions here are:

- What is the relationship between light and the probability of survival? What is the relationship between light and the growth and development of individuals?
- What are the differences between species in this respect?

We monitor individuals in the field in a range of light conditions, and we also analyse experimental liberation of individual trees, taking into account possible differences between size classes. We do not merely confine ourselves to growth in size (diameter, height), but look more closely at an individual’s response in terms of shoot development, leaf and branch turnover, leaf area development, branching patterns, and leaf characteristics.

Figure 4 gives an example of the development over three years of two individuals of *Dicorynia guianensis*, one in a gap, and the other in the understorey. These individuals were equal in size and development phase at the start of the study. After three years, the individual in the gap had more leaves, a higher LAI, more branches, was higher, and had a thicker stem. The crown was larger and more elongated because the top shoots grew relatively faster than the lateral crown shoots (Sterck, 1997).

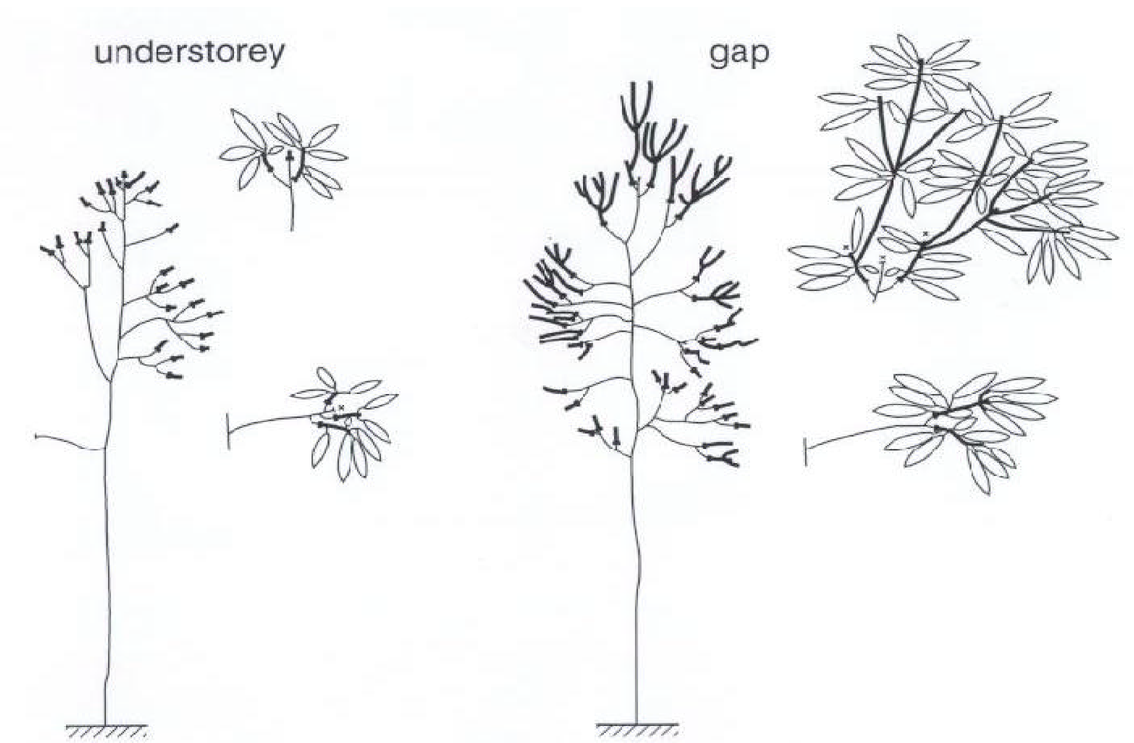

Figure 4 Tree development of *Dicorynia guianensis* (1991-1994) in two contrasting environments, Les Nouragues forest, French Guiana. Trees were 9 m high at the start of the measurements. For each tree the development at the top and halfway into the crown is depicted in detail. (from Bongers and Sterck, 1998).

4.3 What did we learn about the influence of light on individual and species performance?

The results on the population dynamics of several species (van der Meer, 1995; van der Meer, Sterck and Bongers, 1998; Bongers *et al*., unpublished data) show that:

- All species studied perform better in high light than in low light. Pioneer species do very badly in very low light, but benefit more from high light than shade-tolerant species;
- Germination and seedling survival are higher in high light than in low light, leading to more established individuals;
- Growth in high light (in terms of biomass, height, diameter) is faster, but may be at the cost of flexibility and efficiency of light interception (needed when overshaded);
- Seedlings and small saplings contribute more to population size than pre-mature individuals.

The results of research on the tree architecture of *Dicorynia guianensis* and *Vouacapoua americana* (Sterck, 1997; Bongers and Sterck, 1998; Sterck and Bongers, 1998) show that:

- Light limitation plays a crucial role in trees up to a height of at least 20 m;
- Trees of both species respond to increased light levels with accelerated crown expansion;
- Trees respond to decreased light levels with more efficient light interception (reduced self-shading, reduced crown elongation, lower costs of producing leaf area, lower investment in stability);
- Responses to light occur at all levels within the crown hierarchy (i.e. the leaf, metamer, extension unit, sympodial unit, and whole crown level), when comparing trees from contrasting light environments;
- In natural populations, responses to light occur at some, but not all, crown light levels. Probably, this reflects the rarity of extremely high light levels in the forest, rather than the inability to respond;
- Trees shorter than 20 m show similar responses to light, irrespective of their height;
- Trees taller than 20 m may show different responses to light than shorter trees, because of

ontogenetic constraints or the high light levels in the upper canopy;
- The mechanical stability of trees decreases with size in early life phases, but increases in later life phases;
- Tall stature species are more slender than shorter stature species because they support narrower crowns;
- Tropical trees are more slender than temperate trees. This may be due to lower light levels and/or wind speeds in the tropics;
- The architecture of trees is of great importance for the interception of light, and for competition for light with neighbours.

Currently, we are studying the ecophysiological background of these light adaptations in trees of these and other species in the Les Nouragues forest (Rijkers *et al. unpublished data*). In current and future studies, the results of the single studies mentioned here will be integrated, and the processes and results (e.g. those on leaf, shoot, branch, crown, and trees of different sizes) will be up-scaled and down-scaled, which will lead to predictions of the influence of light on the development of the species.

Also, to find the influence of light on the seed-to-seedling transition, studies are being performed on the interactions between light and animals (as seed dispersers and seed destroyers, and seed and seedling herbivores). Especially the interaction between light, canopy gaps, and the scatter-hoarding of large seeds of selected species (e.g. *Carapa guianensis*, *Vouacapoua americana*, *Licania albida*) by the ground-dwelling rodents Agouti (*Dasyprocta agouti*) and Acouchi (*Myoprocta acouchi*) is receiving detailed study (Jansen *et al*. unpublished data). By following the fate of the seeds of these species, we quantify the effects of this interaction on the regeneration of these species. One important preliminary result is that some of the large seeds are dispersed preferentially into treefall gaps. This, however, is not for the light conditions, but mainly for the shelter that the treefall debris supplies. Another example of an interaction between treefall gaps and animals is the dispersal, by Manakin birds, of Melastome plants away from treefall gaps. The birds disperse the seeds of these gap pioneer plants preferentially out of the gaps towards the lek, the display ground of these birds (Krijger *et al.*, 1997).

5. IMPLICATIONS FOR SILVICULTURE

What can we learn from our studies, and other comparable studies, for application in silviculture? Figure 5 shows applied aspects for the components of the life history of trees and for the processes involved therein. It shows three applications dealing with the influence of light on the main processes occurring in each component of the life history. I will briefly expand on a few of them.

Many seeds need safe sites (*sensu* Harper, 1977) to be able to germinate. The high light environment of a large canopy gap and its importance for some pioneer trees (e.g. *Cecropia* species; see e.g. Alvarez-Buylla and Martinez-Ramos, 1992) is just one example. To reach a safe site, directional dispersal is an advantage and animals play a crucial role therein. The interaction between light environment and animal dispersal has a direct influence on seed survival and seed germination. The results of the studies we are performing on Agoutis and their role in seed dispersal and seedling establishment of *Carapa guianensis* and *Vouacapoua americana* clearly indicate the extreme importance of such animals (see also Forget *et al.*, 1998). The direct effect of man on such animals (e.g. by hunting, which increases after the forest is opened up in logging concessions) may have a cascade of effects on various tree species that depend on these animals for their regeneration.

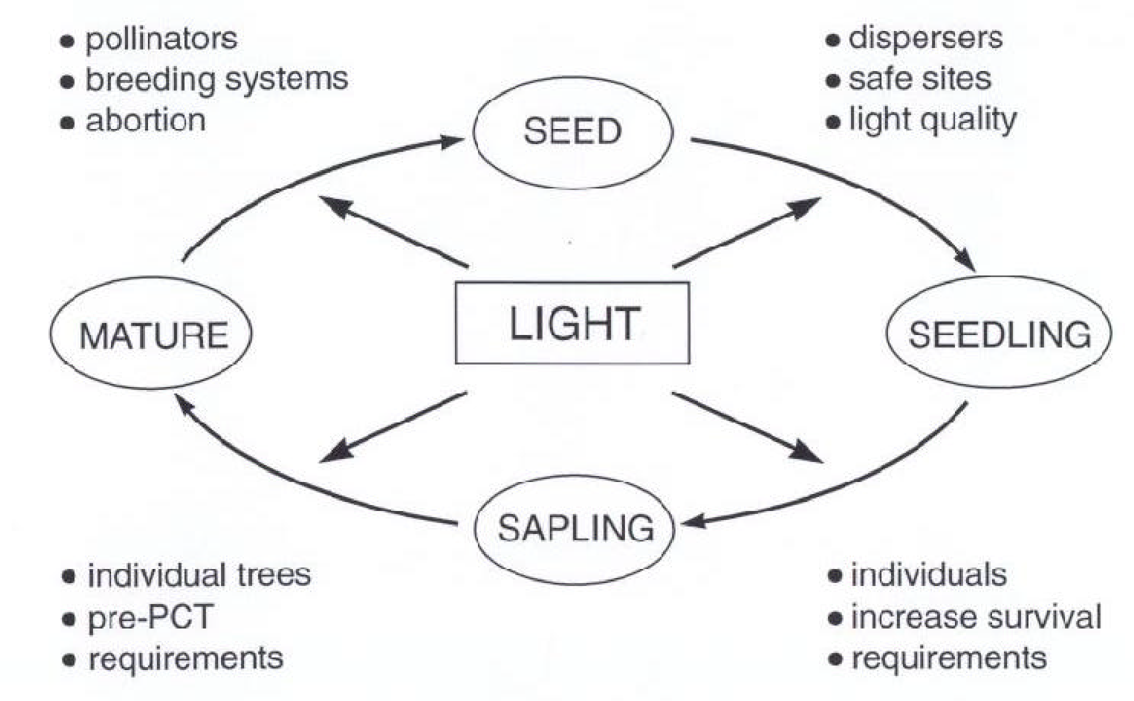

Figure 5 Application in silviculture of research on the effects of light on tree life history aspects (see text)

Light clearly improves the establishment probabilities of seedlings, and also the growth of seedlings, saplings, and large individuals (Swaine, 1996). The fact that secondary species benefit most from high light indicates that light manipulation should not be general, but should be specifically directed towards desired species and individuals. Too much light will have a negative effect, both in terms of a shift in species composition and in tree allometry (heavy branching early in life).

The relatively high importance of small individuals for the overall population size (see also Zagt, 1997) asks for manipulations directed towards individuals with high reproductive output and towards seedlings and saplings. As light increases the survival of small plants that grow in the dark understorey (see e.g. Zagt, 1997), a specific manipulation will directly lead to a higher stock of desired individuals. Especially in the cases where highly valued species hardly regenerate (like some of the African mahogany species; see e.g. Poorter *et al.*, 1996), specific treatment of the few individuals is worth the effort. Manipulations directed only at larger individuals, like all manipulations directed at potential crop trees (which in most cases have a diameter of between 30 and 50 cm), will increase growth only on presently available larger trees. Manipulation of potential crop trees will thus give results in the silviculturally short term only, while manipulation of smaller individuals will give results in the long term. This clearly calls for a broadening of the scope and purpose of light manipulations.

For most species, including many commercially interesting ones, we know little about the specific requirements for germination, establishment, growth, and development. In the scientific literature, information is available about specific components of the life cycle of several species (see e.g. Swaine, 1996, for seedlings), but in many cases these are not commercially interesting species. Also, the translation of scientific information on species requirements towards the community of users of the information (e.g. foresters working for large forestry enterprises) should be improved. The production of monographs in which the current knowledge on specific tree species or specific genera is presented should be stimulated. Such monographs could be valuable for the scientific community as well as for user groups (but in the latter case the information should be transformed and translated).

Studies on actual light levels to which individuals are subjected and how these change with time are important. They give us information about the natural conditions under which species live. Manipulation enables us to benefit from that natural variation. Manipulation of forest structure can be translated directly into manipulation of light levels. It is clear that manipulations should at least extend the period of high light over a longer time than under natural conditions.

What has clearly emerged from our studies is that light influences various parts of the plant in different ways. High or low light levels cause trees to change their growth and investment patterns in such a way that it is profitable for the tree - now, or in the near or distant future. Growth responses depend much on the tree species, and any manipulation directed towards an increase in growth should be attuned to the natural response pattern of the species. To be able to do this, we need to have detailed knowledge of the ecological requirements of a species. What is also important is the individual=s developmental phase: ontogenetic effects need to be separated from light effects (Coleman *et al.*, 1994). It should be noted that light requirements are not constant during the lifetime of a tree, and that relative light requirements among species also change (Oldeman and van Dijk, 1991; Grubb, 1996).

Table 2 Effects of forest intervention on mortality rate, gap area, and individuals of heliophilous species, Paracou, French Guiana. All values are percentages. Data from Durrieu de Madron (1993, 1994).

	Control	**Logging**	**Logging + refinement**	**Logging + refinement + extraction**
Mortality	11	20	29	26
Gap area	13	50	64	83
Heliophilous	11	34	41	47

Most manipulations in tropical forestry systems are not species-specific, but are directed towards a whole group of species. Species, however, are not usually grouped on the basis of ecological requirements, but on their usefulness and value. There is, however, no *a priori* reason why species from such value groups should respond similarly to manipulations. In most cases, manipulations are aimed at the group of commercial species, species that have a relatively high value and can be sold on the market. The non-commercial species are then classified into a secondary species group. Examples from the Guianas region are the studies underlying the CELOS Silvicultural System in Suriname (de Graaf, 1986; Jonkers, 1987; Jonkers and Schmidt, 1984; Poels, 1987) and the studies done at Paracou, French

Guiana (Durrieu de Madron, 1993; 1994; Favrichon, 1997). In these studies, various logging intensities and refinement thinning regimes are being tested. Table 2 shows some of the results of the Paracou experiments.

Three levels of manipulations were compared with a control. In the first treatment, individuals of first-class timber species with a diameter above 50 or 60 cm were cut. In the second treatment, this logging intensity was combined with a refinement in which all individuals of secondary species above 40 cm diameter were poison-girdled. In the third treatment, all individuals of secondary species between 40 and 50 cm were exploited, and individuals over 50 cm were poison-girdled. In the heavier treatments, the mortality of the remaining trees was considerably higher than in the control. Also the total area classified as gap was drastically increased, from 1.3% in the control to over 80% in the heaviest treatment. This high percentage indicates that, in fact, the remaining area no longer consists of a matrix of high forest with gaps in it, but of a matrix of open area with scattered patches of high forest. The gap concept (the area opened up by the fall of one or more canopy trees) can no longer describe the situation after such heavy treatments. The damage to remaining trees was high (ranging from 8-9% in Treatment 1 to 15-17% in Treatment 3; Durrieu de Madron, 1993, p. 127). It is striking that the percentage of individuals of secondary species (undesired species) was very high three to four years after the treatment. The secondary species almost dominates the vegetation. This means that the increase in the undesired species is much higher than the increase in desired species.

This result is comparable with results obtained in the CELOS experiments: the desired species do increase, but the undesired species profit much more from the manipulation (de Graaf, unpublished data; Poels *et al.*, 1997). The same accounts for the SODEFOR experiments in Côte d=Ivoire (Dupuy *et al.*, 1997). This leads to the question of the effectiveness of the interventions. Only a regularly repeated intervention in which the secondary species are killed will lead to a higher density of individuals of desired species. But, what will be the effect when the number of secondary individuals is drastically reduced? This will depend greatly on the interactions and dependence of the desired species on animals which, in their turn, may depend heavily on secondary species for their survival. In the end, this may lead to a severe impoverishment of the system and a decrease in the number of desired species as well. Also important is the loss of nutrients after several heavy interventions.

6. CONCLUSIONS

Manipulation of the structure of the forest aimed at increasing the light levels on species and individuals leads to an increase in growth and production of the trees involved. Generic treatments aimed at the general group of commercially interesting species may stimulate the growth and development of undesired species at the cost of the desired ones. This calls for regular treatments favouring the desired species.

Many studies on species distribution and species composition of tropical forest show that the tropical rain forest is spatially strongly stratified. Some species are abundant here; others are abundant there. Our studies also show that the requirements for light depend strongly on the species and on the developmental phase of the individuals, and that the same accounts for the responses of species to light and changes therein. Manipulations should thus be directed towards species and what these species need, instead of directing it to large, ecologically very vaguely defined groups of species. Give species and individuals what they need (e.g. to assist them to deliver what we need from them). This calls for highly stratified manipulations: treatments that are different from place to place, from species to species, and to some extent, from individual to individual.

Scientifically sound data are needed to enable us to use specific treatments. Relatively little is known about the requirements of species with respect to light, other than very general notions of shade tolerance. As studies on manipulations at the species level and at the individual level are scarce, we can do two things: First, reanalyse already collected data but with an individual focus, using new techniques and new insights. Second, design new experiments directed at specific questions. The experiments performed by the German Technical Development Agency, GTZ, in Côte d=Ivoire, where the effects of individual treatments were studied, are a nice example of this approach (Waitkuwait, pers. comm.; Parren and de Graaf, 1995).
Deserving more attention are the inventory and monitoring of the present situation in the forest, and the effects of logging and silvicultural treatments on the forest, not only in research, but especially in forest enterprises. For long-term forest enterprises, such investments will soon pay off. The methods and the details should depend on the local variability in the area in question. Hierarchically stratified approaches are needed.

Because we know that species respond in different ways, we ourselves should refrain from general manipulations to increase light availability. In many cases, the wrong species have the highest benefit. Modern information technology, together with information on species-specific requirements, make highly stratified manipulations possible. In this respect, we could look at recent developments in forestry and agriculture. What could tropical forestry learn from recent developments in ecology-based forestry and agriculture? And also, what could tropical forestry learn from the sheer endless ways in which local people influence and manipulate their forests (Wiersum, 1997)?

An often heard argument against specific manipulations is that they are too expensive. But, activities in the forest generally make up a relatively small part of the total costs (de Graaf, pers. comm.), and by far the highest cost is the use of heavy machinery (van Leersum, pers. comm.). I predict that, at least for the higher-valued species, specific manipulations will pay off very soon. The question is not: can we afford specific manipulations? The question should be: under what conditions are such manipulations worth the effort? Scenario studies are needed: scenario studies in which many aspects of the manipulation of light in the forest are taken into account.

7. ACKNOWLEDGEMENTS

The research work in French Guiana is, for a large part, being done in cooperation with researchers working for their PhD or MSc theses, notably P.J. van der Meer, F.J. Sterck, A.J.M. Rijkers, and P.J. Jansen. Constructive comments on an earlier version of this paper were received from N.R. de Graaf, F.J. Sterck, and K.F. Wiersum.

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MANIPULATION OF LIGHT IN TROPICAL RAIN FOREST

Achievements

- Insight has been achieved in the significance of gap and light dynamics in tropical rain forest.
- Understanding of variation in response to light between species belonging to different regeneration strategies.

Challenges and Problems; Information Needs

- Still limited knowledge concerning the biological mechanisms that govern tree growth and variation therein between species and life cycle stage.
- Manipulations in tropical forestry are not species-specific, but directed towards biologically ill-defined groups of species.
- Application of silvicultural intervention may lead to an increase of undesired species that is much higher than the increase of desired species.

Points for Future Research

- Design of refinement treatments: species choice; lower cutting limits; spatial aspects of tree elimination; method of elimination.
- Design of gap and strip cutting treatments: species choice; gap sizes to be created.
- Design of liberation treatments: species choice; timing and efficiency of liberation; effects on wood quality; biological mechanism of liberation.
- Relation between light and growth, survival of species; and species-specific differences therein.
- Re-analysis of existing datasets, focusing on tree individuals
- Development of forest models in order to carry out scenario studies.

Conclusions

- Silvicultural manipulation of forests should be attuned to the natural response pattern of the species, rather than to commercially defined groups of species.