



REVIEW ARTICLE

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Natural regeneration in tropical forests

Regeneração natural em florestas tropicais

ABSTRACT: The sustainability of forest management is supported by the natural regeneration of species, whose mechanisms have been investigated by foresters and ecologists. Numerous studies have addressed the dynamics of tropical forests, always based on a previously existing vegetation and floristic composition. However, in assessing the population dynamics of isolated species, concepts such as recruitment and ingrowth, generally taken as synonyms, can express distinct principles that will be discussed in this review, whose aim is to analyze the strategies of natural regeneration of tree species in tropical forests and models used to evaluate its dynamics, some of which show mathematical indeterminacy in evaluating recruitment and ingrowth. The Rate of Natural Regeneration (NR) proposed in this study represents an approach that eliminates this problem of mathematical indeterminacy. Strategies for natural regeneration of tree species include concepts such as seed or seedling banks, and classification in ecological groups as pioneer and climax species based on seed size, germination, seedling establishment, demand for gaps, etc. The classification based on the diameter distribution of tree species considers that this structure expresses their life story, as the result of the interaction of genetic factors with biotic and abiotic factors of the ecosystem. Therefore, many timber species whose static natural regeneration does not exist in the primary forest, but present mature trees, have as regeneration strategy a strong dependence on disturbances to regenerate and grow. Thereat, the lack of continuous and decreasing distribution cannot prevent their use via forest management.

RESUMO: A sustentabilidade do manejo florestal está apoiada na regeneração natural das espécies, cujos mecanismos têm sido investigados por silvicultores e ecologistas. Inúmeros trabalhos têm tratado da dinâmica das florestas tropicais, sempre partindo de uma vegetação e composição florística previamente existente. Todavia, na avaliação da dinâmica populacional de espécies isoladas, conceitos como recrutamento e ingresso, em geral tomados como sinônimos, podem expressar princípios distintos que serão discutidos nesta revisão, cujo objetivo é analisar as estratégias de regeneração natural das espécies arbóreas em florestas tropicais e os modelos utilizados para avaliar a sua dinâmica, alguns dos quais apresentam indeterminação matemática ao avaliar recrutamento e ingresso. A Taxa de Regeneração Natural (TR) proposta neste estudo representa uma abordagem que elimina esse problema da indeterminação matemática. As estratégias de regeneração natural das espécies arbóreas incluem conceitos como banco de sementes ou de plântulas e a classificação em grupos ecológicos como espécies pioneiras e de clímax, com base no tamanho de sementes, germinação, estabelecimento de plântulas, demanda por clareiras, etc. A classificação baseada na estrutura diamétrica das espécies arbóreas considera que essa estrutura expressa a história de suas vidas, sendo o resultado da interação de fatores genéticos com os fatores bióticos e abióticos do ecossistema. Portanto, muitas espécies madeireiras, cuja regeneração natural estática não existe na floresta primária, mas apresenta árvores adultas, têm como estratégia de regeneração uma forte dependência de distúrbios para regenerar e crescer. Logo, a falta de distribuição contínua e decrescente não pode impedir seu aproveitamento via manejo florestal.

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1 Introduction

The equatorial or tropical rain forests contain a large potential of natural resources, both physical (wood and non-wood products) and non-physical, such as environmental services (e.g., recreation, fertility and soil conservation, regulation of the hydrological cycle, landscape, shelter for wildlife, and carbon stocking). However, there has been much controversy about the best use for these resources. At one extreme are preservationists who defend the untouchability of the forest as a reservoir of biodiversity and environmental cleaning. On the other side are those who regard the forest as an obstacle to development and conversion to agricultural uses, urbanization or even mining. Additionally, some conservationists argue for the rational use of these forests through forest management techniques based on principles of sustainability, which means using forest resources while ensuring that future generations can enjoy them in the same current state. The basis for this sustainability is the assurance of renewability of resources extracted from the forest or its regeneration.

Natural species regeneration in tropical forests has been presented in many papers in the scientific literature, either as forest inventories, phytosociological and demographic studies, or in terms of population dynamics of the species or communities. In the latter case, it is interesting to evaluate the basic processes of recruitment, growth and mortality that in tropical forests are influenced by natural disturbances such as the gap formation. In this context, the aim of the present review is to provide a silvicultural approach to natural regeneration through gaps with a critical analysis of the methods of study proposed, some of which have mathematical inconsistencies.

2 Development

1.1 2.1 *Concept of natural regeneration*

Etymologically, regeneration means the action of generating, reproducing, reconstructing, restoring, recovering, and renewing, among other actions. These terms apply to vegetation and are understood as regeneration that may be natural or artificial, depending on human involvement.

The term natural regeneration (NR) in forestry terminology has two meanings, which must be understood within the context in which they are applied: 1) NR can refer to the characterization of a current state of vegetation (static concept) being expressed as “the number of young individuals of a population”, “number of individuals below a certain size”, or, in physiological terms, “individuals who have not reached reproductive age”; and 2) NR can also refer to the process of renewal of quotas of a population or stand (dynamic concept).

Within a species population in natural forest, one can consider an individual of a size category to be natural regeneration from the size category immediately preceding it. Therefore, the current state from the static point of view is the result of the dynamic process.

2.2 *The numbers issue in assessing natural regeneration*

In forestry terms, depending on the concept of RN with which one is discussing – static or dynamic – the purpose of the assessment of natural regeneration is to determine whether

stocks or the regeneration process are able to ensure that an exploited species can replenish the harvested material. The concept of sustainable forest management is based on this ability to replenish harvested forest products, whether timber or non-timber. The evaluation of this capability is realized using sampling vegetation either with one approach – evaluation of the static point of view – or by two or more static samplings at different times – evaluation of the dynamic point of view.

The evaluation of the NR by the static approach involves the quantification of stocks of a stand or population in a considered moment according to criteria or pre-established concepts. Several studies have used this quantification of the entire world’s rainforests (Jardim & Hosokawa, 1986; Holmgren; Persson, 2002; Grogan et al., 2008; Assis & Wittmann, 2011; Gómez, 2011; Mendes et al., 2013). In this sense, the size limit of the NR is very arbitrary and depends on the objectives of the evaluation. Jardim & Hosokawa (1986) considered all plants smaller than 20 cm diameter at breast height (DBH) to be NR. In terms of forest management for timber production in general, those plants with DBH below the minimum cutting diameter (MCD) are considered to be NR.

The evaluation of the forest NR’s from a dynamic viewpoint means to quantify the balance between the processes of recruitment (or ingress), mortality and growth. This evaluation requires two static samples spaced in time, which can be conducted using permanent or temporary plots. In permanent plots, it is possible to evaluate species mortality and ingress/recruitment, dynamics of individual plant attributes (e.g., DBH, height, and trunk volume) and average individual and group attributes (e.g., basal area, abundance, and stand volume). In temporary plots, it is only possible to evaluate the dynamics of average attributes, i.e., it is not possible to assess the ingress/recruitment, mortality or growth of an individual tree.

The scientific literature (Silva & Araújo, 2009; Colpini et al., 2010) considers the terms ingress and recruitment to be synonymous, defining them as the input of a new individual within the limits defined for inclusion in the sampling process, compared to those that were already present in the previous measurement. However, this new individual may belong to a species already represented in the area in the first sample measured or a new species in the sample. To differentiate these two conditions, here we adopt the following criterion: the ingress will refer to the set of individuals of a new species in the area and the recruitment to the set of new individuals of a species already present in the area since the first static sampling.

In studies of communities or populations dynamics, several models have been proposed to assess recruitment or ingress (Swaine & Lieberman, 1987; Korning & Balslev, 1994; Sheil; May, 1996; Mews et al., 2011; Ribeiro et al., 2012). Other approaches consider the direct ratio between the number of recruits and density before the study commencement (Condit et al., 1995; Colpini et al., 2010; Souza et al., 2012). Regarding the recruitment of individuals of a species present at baseline, all of the above methods may be used. However, regarding the ingress of a new species in the community, in which the initial density of the species is nil, some of these approaches, such as those based on the ratio between the number of recruits and the initial density of the species (Condit et al., 1995; Sheil & May, 1996; Colpini et al., 2010; Souza et al., 2012) or the model

$(m(r) = \{100[\ln(n_0) - \ln(n_i)]\} \cdot T^{-1})$ (Swaine; Lieberman, 1987), may present inconsistencies as a mathematical indeterminacy due to a division by 0 (zero) or the logarithm of 0. Therefore, valid models such as those of Mews et al. (2011) and Mory & Jardim (2001) have been developed to register the ingress of a new species.

Mortality, which is different from ingress or recruitment, is distributed over the entire size range of vegetation or population of species and refers to the number of plants that have died, between two static samples, by natural causes such as pests, diseases, natural fall, or competition or by artificial causes such as logging. Mortality evaluation is simpler than recruitment because it does not involve mathematical problems in the models as the ingress of a species.

The balance between mortality and recruitment/ingress indicates the fluctuation in population density of the species and is the main information obtained in the study of dynamics of populations or communities, because it results from the interaction of all biotic and abiotic factors. It can be stated that the life history or the population dynamics of a species in a community or forest, expressed in terms of diameter distribution (Engone Obiang et al., 2014) or size distribution, is the result of this balance over time. Any consistent method of evaluation will produce a dynamic balance between mortality and recruitment when a sufficiently long period of time is considered (Sheil & May, 1996). Obviously, in practice, seasonal imbalances are expected and verified (Colpini et al., 2010; Santos & Jardim, 2012; Viana & Jardim, 2013; Sundarapandian; Swamy, 2013), but in the long term the assumption of Sheil & May (1996) should be confirmed.

Several methodologies have been proposed for the assessment of balance (Korning & Balslev, 1994; Mory & Jardim, 2001; Ruschel et al., 2009; Ribeiro et al., 2012). However, any methodology or model to assess this balance that considers the ratio between the final density and initial density, as in the Natural Regeneration Rate (NRR%) (Jardim, 1986) or Ruschel et al. (2009), or even the logarithm of the initial density (Ribeiro et al., 2012), will result in a mathematical indeterminacy in the case of ingress of a new species in the sample.

NRR% is an expression that allows the analysis of the dynamic behavior of a species, group of species or a forest as a whole at the end of a period of study or monitoring. NRR% is generally calculated using the values of abundance, but one can use basal area, volume or other variables that express density. Calculation expresses the result of the interaction of the processes of mortality, ingress or recruitment and growth.

The preliminary model of NRR ($NRR\% = [(A_1 A_0^{-1}) - 1] * 100$, where A_1 = absolute abundance at study end; $A_0 = n_c + n_i$, n_c = output of individuals by death or growth and n_i = input of individuals who enter the sample; and A_0 = absolute abundance at baseline) had this mathematical indeterminacy (Jardim, 1986) when referring to the appearance of a new species in the sample, i.e., $A_0 = 0$. For this reason, Mory and Jardim (2001) proposed a new expression for NRR (%) ($NRR = [(A_1 - A_0) \cdot (A_0 + A_1)^{-1}] * 100$) that eliminated the mathematical indeterminacy of the previous model of Jardim (1986).

The interpretation of the values of NRR, considering the balance between recruitment and mortality dynamics of the forest, can express the following variation: $NRR (\%) = 100\%$

means the ingress of a new species in the sampled area; $NRR (\%) = -100\%$ means the death of all individuals of the species and their elimination in the sampling area; $NRR (\%) > 0$ means recruitment > mortality, soon resulting in an increased density in the sampled population of the species; $NRR (\%) < 0$ means recruitment < mortality, resulting in thinning in the sampled population of the species; and $NRR (\%) = 0$ means recruitment = mortality, soon resulting in equilibrium in the population.

The graphical representation of the balance between recruitment and mortality as a function of time can take various forms, but in general it can be represented by a sigmoid curve, called a logistic growth curve by the French mathematician Verhulst in 1845. This curve is the result of resistance that environmental factors impose on the intrinsic rate of natural increase or biotic potential (Figure 1).

Growth is the gradual increase in the size of measurable variables (diameter, height, basal area and volume) of a plant or stand. The growth of individual trees is the sum of the division, elongation and thickening of their cells, which are influenced by the interaction of genetic characteristics of the species with biotic and abiotic factors of growth.

Although growth rates vary substantially among species, the general growth pattern is remarkably consistent. Thus, any dendrometric variable of a plant (diameter, height, basal area, or volume), when plotted as a function of age, will also result in the logistic growth curve of Figure 1.

In this case, the curve shows that growth is accelerated at the beginning when environmental resources are abundant, but tends to reduce in intensity as age advances and as competition for these resources increases.

The gradual increase in plant size per unit time is called an increment. The difference between tree dimensions, measured at the end and the beginning of a year of growth, is called

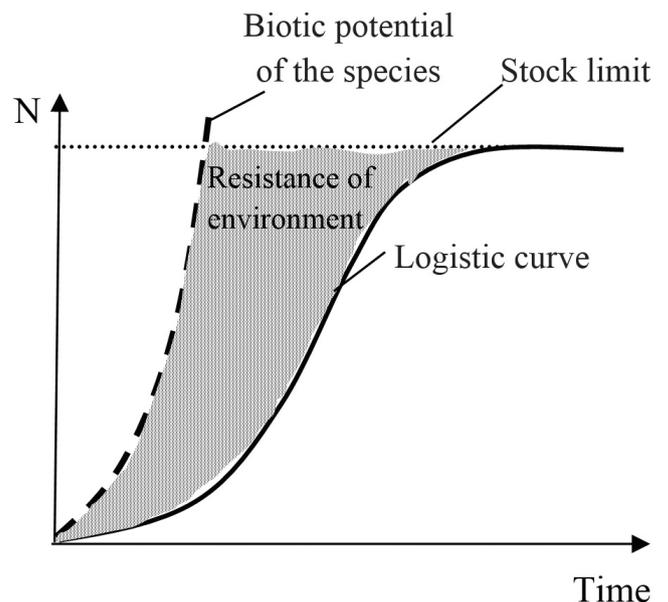


Figure 1. Theoretical curves of population growth. The environmental resistance is represented by shaded area. Adapted from Dajoz (1983).

Figura 1. Curvas teóricas de crescimento de uma população. A resistência do meio está representada pela faixa sombreada. Adaptado de Dajoz (1983).

Current Annual Increment (CAI). The difference between the tree dimensions, measured at the end and the beginning of any period of years of growth, divided by the number of years of the period is called Periodic Annual Increment (PAI). As it is difficult to accurately measure the CAI, it is usually replaced by PAI. The average growth at any age is called the Mean Annual Increment (MAI), which is obtained by dividing the cumulative size of the plant dimensions by its age. In the evaluation of natural forests, is difficult to know the plants' ages, making it difficult to determine the MAI of a tree if it is not planted or of known origin.

2.3 Mechanisms of natural regeneration

2.3.1 Natural regeneration dynamics through succession in gaps

In many forest inventories that cover the entire size range of a species, as in Jardim & Hosokawa (1986), it has been verified that the forest as a whole always has a diametric distribution in continuous and decreasing shape. However, when analyzing a species alone, it is found that only a few exhibit this regularity. In most species, when a sampling is in the closed canopy, large discontinuities or flattening in the distribution are observed, reaching a total absence of young individuals in some species. In samples that reach gap areas, the appearance of juveniles of species that are absent in areas with closed canopy is usually observed.

Aubreville's theory of natural regeneration in mosaics was developed to explain the lack of natural regeneration of species in the forest canopy. He found that the climax stage of the African rainforest was spatially dynamic, making it difficult to predict the dominant species in a climax community in particular. For example, a species might dominate a specific community today, but no natural regeneration indicates that the species will be replaced by another and that it may be regenerating in a new area dominated by another species, which will eventually be replaced.

The dynamics of tropical rainforests have been studied for many years. Although the fact that this process fundamentally depends on these gaps is accepted by almost all researchers, little is known about the behavior of isolated species relative to different microenvironments created in the gaps. Whether these microenvironments that favor the development of these species in the forest are changing the level of resources available and the efficiency of recruitment or ingress is unknown.

Many timber species do not exhibit continuous and decreasing (J-inverted) diameter distribution in undisturbed forest because this regeneration is totally dependent of the gaps. Approximately 75% of the 105 canopy trees species of the stand studied by Hartshorn (1978) depend on the light of the gaps to regenerate successfully. The self-elimination of *Tachigalia sp.* trees, one year after a single fruiting, seems to be a particular mechanism of gap-creation, which favors its own regeneration. Of 63 timber species seedlings per hectare found in gaps of medium size (333 m²) and 15 months of age, three-quarters appeared after selective logging (Verissimo et al., 1989). Previous results reinforce the idea that some type of disturbance should exist for conserving *Aucoumea klaineana* (Engone Obiang et al., 2014).

Within this context, to imagine that certain tree species exhibiting no young individuals in their diameter structure are species at risk of extinction is to deny that their adult individuals were seedlings in the not too distant past, depending on the growth rate. This notion ignores the fact that some mechanism allowed the regeneration of this species. Research has shown that species with this type of diametric distribution – the so-called shade-intolerant or heliophile, as they are better known – use a regeneration strategy dependent on gaps as a consequence of the death of one or more forest canopy trees (Jardim et al., 1993; Santos & Jardim, 2012; Viana & Jardim, 2013). For some species, such as *Swietenia macrophylla* and others, only the disturbance caused by large gaps, such as those produced in forestry, provides substrate for natural regeneration.

Thus, the idea that has been consolidated to only allow exploitation of timber species with continuous and decreasing diameter distributions (J-reverse) to ensure their sustainability lacks a technical and scientific foundation, because it has been shown at experimental scales that forestry, even reduced impact logging, promotes the formation of gaps of varying sizes that stimulate the natural regeneration of most timber species harvested, such as *S. macrophylla*, *Tabebuia serratifolia*, and *Dinizia excelsa*, among other shade-intolerant species.

Understanding the forest composition and structure dynamics requires the measurement of changes in these characteristics over time; these changes are usually activated by gaps created when a tree falls, causing the start of a new age class and the rapid growth of previously suppressed individuals.

Gap is the term used to designate the existing discontinuities in the structure of a forest canopy caused by a falling tree or a part thereof. There are several gap concepts in the literature, all of which express the idea of an opening or hole in the forest canopy. It is important to realize that within a gap, microclimatic conditions are completely changed from the surrounding closed forest. Some concepts are approaching this idea. Popma et al. (1988) suggested that a gap encompasses a zone of influence, which extends as far as there are pioneer species regenerating.

One can define a gap as a discontinuity of canopy of varying sizes that protrudes from the canopy to the forest floor, encompassing a zone of influence until where secondary species are regenerating (Figure 2).

Succession varies in the humid tropics because of differences in floristic composition, soil type and the nature and extent of disturbance (Bazzaz & Pickett, 1980). The presence of large numbers of species that require light for their establishment, when spread throughout the canopy of a native forest, indicates the former existence of a gap. For many species, the main factor that regulates population structure is the chance of occurrence of a gap on seedlings that will allow them to grow. Even small holes in the canopy (sunflecks) allowing no more than 40 minutes of daily insolation can stimulate the growth of seedlings on the forest floor (Bazzaz & Pickett, 1980).

The existence of a seedling and sapling bank waiting long periods for conditions that favor their growth has been recognized. This concept presupposes a state of quiescence of seedlings, where they maintain a minimum metabolism of survival without growth, but has been mistaken for tolerant species, whose continuous and decreasing diameter distribution contains plants that, although very slowly, usually grow in the

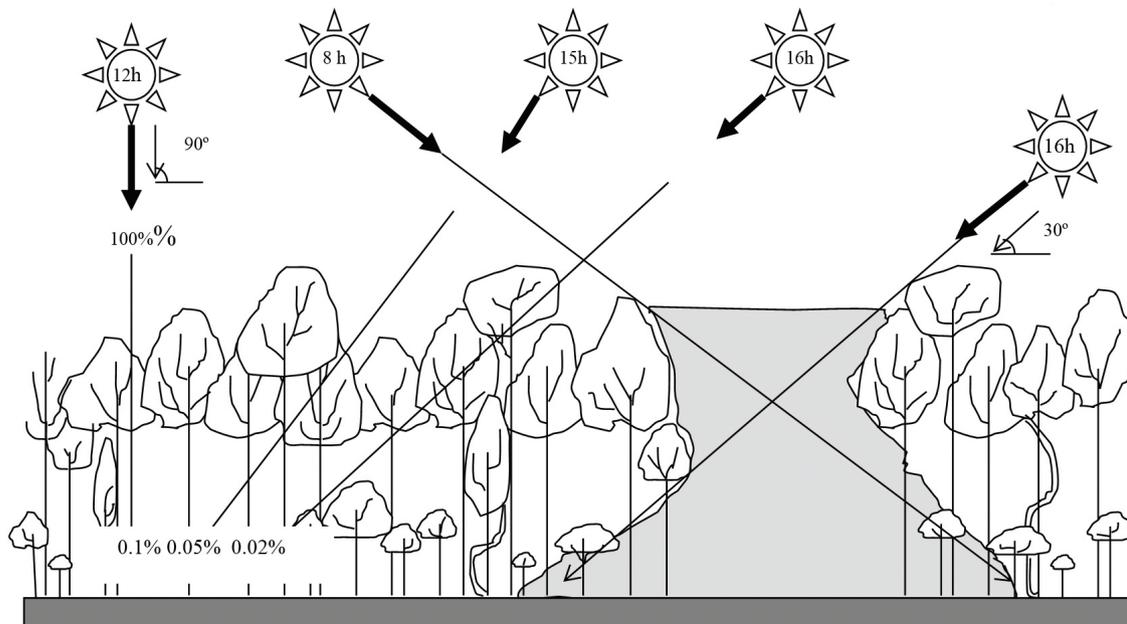


Figure 2. Schematic drawing of a gap showing the sunlight passing through it. Adapted from Longman and Jenik (1981).

Figura 2. Desenho esquemático de uma clareira ilustrando a incidência dos raios solares através da mesma. Adaptado de Longman e Jenik (1981).

forest. Without gaps, it is possible that all seedlings except those species of the understory, which spend their entire life in dense shade, may eventually die (Whitmore, 1978).

The literature on the process of natural succession in tropical forests is already quite large, as shown in the review of Jardim et al. (1993). The disturbance theory, whose successional model links community richness to the age, size and frequency of disturbance, suggests that natural succession in tropical forests starts with gap formation. This theory is widely accepted and divides succession into three phases: (1) gap phase, (2) forest growing and (3) mature forest. The duration of each phase depends on factors such as the magnitude of the disturbance, especially in terms of the size of the opening in the forest canopy.

Successional dynamics in the forest as a whole can be represented by a long and continuous process of opening⇒covering⇒closure⇒opening gaps. After its formation, a gap goes by a more or less long period of recovery or covering (succession), culminating in its closure.

The time period between the gap formation and its closure depends on the size of the gap. If the gap is caused by a falling branch or a small tree, its closure may be completed through the lateral expansion of branches of the surrounding trees or by the rapid vertical growth of preexisting advanced natural regeneration. Therefore, if it appears that succession begins in an advanced stage, the recovery will be rapid, favoring species opportunistic of small gaps.

When a gap is formed by the felling of large trees, its closure is more time-consuming, because the succession is restarted from a far less advanced stage. In this case, a certain degree of colonization will be needed for the covering in addition to the growth of advanced regeneration, resulting in a more or less intense competition until the predominance of some canopy species. This process favors opportunistic species of large gaps

or late secondary, which are normally emergent species that develop large biomass.

In large gaps formed by the fall of several trees, succession is activated in its earliest stages, with extensive colonization by invaders and pioneers that will compete strongly with the existing regeneration. However, because the colonizers are relatively short-lived, they will gradually be replaced by more persistent vegetation and higher biomass until complete canopy closure.

Three gap characteristics are considered to be important in the study of vegetation dynamics: the physical environment of the gap, the gap size and the gap turnover rate. In relation to the physical environment, it is clear that for each gap size there are corresponding microclimate conditions. Due to the influence that the gap size exercises, physical factors such as size can be important variables affecting seed germination and seedling survival.

Different species are successful in gaps of different sizes, which means that the gap size strongly influences the floristic composition and distribution of plant species in the forest. The higher the gap, the more varied is the microclimate inside it compared with undisturbed forest. Therefore, the gap size can determine which species colonize a gap, because it can cause major changes in microclimate and root competition, which may temporarily lessen in the gap center. Small gaps favor the growth of advanced regeneration, as is the case with seedlings and young plants already established before the formation of a gap. In contrast, in very large gaps, these individuals can grow little bit or die due to high radiation load (Whitmore, 1978).

According to Whitmore (1978), the main differences between the environment in gaps and under closed canopy are an increase in light and changes in its quality, as well as increases in temperature and saturation deficit. An increased availability of nutrients may also occur when dead plants

decompose. These changes in the physical environment alter the biocenosis; as established seedlings die as a result of their sensitivity to light, plants of pioneer species appear and experience growth maximization.

Under natural conditions (undisturbed forest), the interaction of the physical environment, the size and turnover rate of gaps results from a stochastic process (Bazzaz & Pickett, 1980) in which gap formation is random in space and time, although there is a higher probability of falling trees during the rainy season. In this case, the behavior of the species follows its natural course, according to competitive hierarchy (Swaine & Hall, 1983).

In managed forests, the interaction of the three factors is influenced by logging intensity and the composition of exploited species. The presence of gaps is spatially random because it depends on the spatial distribution of trees. However, from a temporal point of view, there is a tendency to change the time of gap formation to seasons of drought, when the logging operation is made more efficient. However, the phenology of species is adjusted to the natural process of gaps formation. Therefore, it is possible that changes in the magnitude and the temporal order of gaps formation can change the probabilities of a species or any ecological group being more or less successful.

The covering capacity of timber species, many of which are late successional or opportunistic and shade-intolerant, may be reduced by the removal of mother trees and maintenance of individuals of non-commercial species. However, with logging, this phenomenon can be offset by the creation of more favorable environments for the recruitment and growth of the most intolerant species. The mortality of tolerant species may be increased due to the higher intensity of radiation on seedlings in the understory, which are not adapted to high levels of brightness resulting from the opening of the canopy by exploitation. Therefore, we should consider that the large gradient of gap sizes is an important factor in determining the high heterogeneity of tropical forests. Many canopy species, which in the seedling and sapling stages are absent in the forest floor, depend on gaps for regeneration and therefore should be considered normal components of the mature forest rather than successional species that should die as the forest matures (Hartshorn, 1978).

2.3.2 Interaction with ecological groups

The vegetation of a rainforest is composed of a very large number of life forms. However, it has been found that there are great differences between the floristic compositions of the upper canopy and understory of the rainforest (Jardim & Hosokawa, 1986; Mendes et al., 2012). For this reason, dynamics studies inevitably require the division into classes or smaller groups of vegetation. However, the classification of species into ecological groups is very controversial in the literature. Numerous attempts have been made to classify the species in terms of their ecological behavior.

Up to four species groups have been established due to the need for gap development (Whitmore, 1984): 1) Species that establish and grow under closed canopy; 2) species that establish and grow under closed canopy but benefit from the gap; 3) species that are established under closed canopy but require gaps to mature and reproduce; and 4) species that are

established, grow and reproduce only in gaps. These features are merely points on the large gradient of light conditions that species demand, and each species may be unique in their requirements. Another classification (Swaine & Whitmore, 1988) proposed a division of the species into pioneers and non-pioneers, based on germination and seedling establishment. In each group, based on the height at which maturity is reached, Swaine and Whitmore proposed a subdivision into the following: dwarf, small, medium and large trees.

Based on the combination of biological forms (herbaceous or woody) and origins (secondary or forest areas), another classification of the species into four groups was proposed by Mitja et al. (2008): forest woody species, pioneer/secondary woody species, forest herbaceous species and secondary herbaceous species. This classification is controversial when considering pioneer or secondary woody species as non-forest species, as there exist dozens of species, mainly of timber, with a secondary characteristic.

In general, classifications are based on the light demands of the species. Shade tolerant species can regenerate and grow independent of gaps and are very efficient in their use of the diffuse radiation that exists within the forest. Intermediary species regenerate and grow in varying degrees of light that are available in medium to small gaps. Shade intolerant species only regenerate and grow in environments with much direct light afforded by large gaps, because they are inefficient in their use of light radiation.

Some classifications incorporate other factors, such as selection strategy or the seed size and means of dispersal (Table 1). However, there is generally consensus that the process of natural regeneration of tree species in a tropical forest is strongly dependent on the presence of gaps that provide the conditions, especially in terms of light, for the establishment of regeneration.

These dichotomic classifications that categorize species as light- or shadow- preferring or in terms of pioneer, early secondary, late secondary and climax species (Budowski, 1965), represent a great simplification of a large and complex ecophysiological behavior gradient existing in equatorial forests species. Despite the fact that any plant, in principle, is heliophilic, as it needs light to perform photosynthesis, plants require varying degrees of radiation intensity.

The changing light requirements of a tree species throughout its life history can be preliminarily inferred from the analysis of diameter distribution of their stems (Jardim et al., 1996), as suggested in Table 2.

If a species has a continuous and decreasing diameter distribution, such as the “J-inverted” distribution, this characteristic indicates that, in terms of light, the species has no restrictions for natural regeneration process (i.e., seedling recruitment in natural regeneration is regular and constant and offset by high mortality). Species with this ecological characteristic are classified as shade tolerant, i.e., they regenerate and grow under diffuse light within the forest environment.

If a species has discontinuities in its diameter distribution or even an absence of individuals in the lower DBH classes, this characteristic reflects trouble in natural regeneration, often due to the dependence of light for germination. These species are called intolerant to shade or diffused light, are considered to be

Table 1. Morphological and physiological characteristics for populations with opportunistic (r) and equilibrium (K) strategies for rainforest species. Excerpted from O'Brien & O'Brien (1995).

Tabela 1. Características morfofisiológicas para populações com estratégias oportunistas(r) e em equilíbrio(K) para espécies da floresta tropical. Extraído de O'Brien & O'Brien (1995).

	Selection r (Opportunistic)	Selecting K (Tolerant)
Succession stage	Initiation	Final
Size population	Without balance, usually below the support capacity, periodic recolonization	Constant over time, near the support capacity, without colonization
Mortality	Density-independent, undirected or catastrophic	Density-dependent, more directed
Competition	Variable, usually loose	Usually strong
Dispersion	Long distance	Local
Longevity	Short, a few years	Long, over 20 years
Aims to	Productivity	Efficiency

Table 2. Shape and amplitude of the diameter distribution of stems (for trees in unlogged forest).

Tabela 2. Forma e amplitude da distribuição diamétrica (para árvores em floresta não explorada).

Shade Tolerant	Intermediate	Shade Intolerant
Continuous and decreasing (J-inverted) diameter distribution with great number of individuals in the lower size classes	Continuous or not diameter distribution, flatter than the tolerant	Discontinuous diameter distribution, lack of young individuals and many individuals in the higher diameter classes
Diameter amplitude reduced, smaller than the others, below 60-70 cm	Diameter amplitude very variable (usually above 60-70 cm)	Large diameter range, above 70-80 cm

“extravagant” in their use of photosynthetically active radiation (PAR), and therefore demand strong light. The presence of gaps in the forest canopy is the factor that sets light conditions for the seed germination of these species.

Species whose diameter distribution has an intermediate shape between these two extremes are called intermediate or opportunistic of large or small gaps, according to their demand for more or less light for establishment.

3 Final Remarks

The term natural regeneration refers to the number of young plants of a population, settlement or forest or to the process of establishment of these young plants, (i.e., the processes of recruitment or ingress, mortality and growth). Recruitment and ingress, although signifying the entry of new individuals in the sample, may represent different situations; these terms can refer to the entry of an individual of a species already present in the area (recruitment) or to the input of an individual of a new species in the sample (ingress).

The models that assess recruitment or ingress often exhibit inconsistencies when evaluating the entry of a new species in the sample, which can present a mathematical indeterminacy represented by a division by zero (0) or one logarithm of zero (ln 0). The model called Natural Regeneration Rate eliminates this indeterminacy of mathematics to assess the entry of a new species in the community or forest. The model needs to be tested with other variables, such as basal area and volume, used to evaluate the dynamics of managed forests.

Many timber species have very low or no natural regeneration in the static sense of the term because of their dependence on the presence of gaps. However, this cannot be considered a valid argument to suggest the impediment of their commercial

exploitation, because if adults exist in a large proportion, there is some mechanism for regeneration (the gap formation).

Gap size varies over a continuum in which environmental conditions follow the same continuous pattern of variation. In terms of light, for example, gaps can be said to vary from a single “sunfleck” (small areas on the forest floor reached by direct solar radiation that gets through the canopy) to high levels of radiation from large gaps. Within this range of variation, the interactions between environmental factors and between plants and these factors are so numerous and so complex that any simplification will result in many exceptions and difficulties of ecological classification of species.

The strategy of the seed bank is a method to maintain coverage of an area. However, this is also a strategy characteristic of invaders and pioneer species, because no large dormancies for timber species seeds have been identified. Moreover, the concept of a seedling bank has been considered important in management, which would solve the stock problem in the natural regeneration of timber species. This concept seems to be reasonable; if there is a marketable stock of these species and very little regeneration by current criteria of minimum stock, then there must be a method by which the few seedlings survive to reach the canopy. An interesting hypothetical mechanism is the so-called seedling quiescence, which allows seedlings to wait long periods for conditions favorable to their development.

Knowledge of this successional process, although empirical, has been employed in silvicultural systems based on natural regeneration. However, their functioning remains to be scientifically determined to ensure maximum use of the productive potential of tropical forests, because under natural conditions, this function only restores the losses from death or natural fall.

Although foresters have for centuries created gaps of various sizes to control trees' growth and floristic composition of forest stands, only when the processes of regeneration of tree species in tropical forests, especially those in and around gaps, is understood will real progress have been made in solving problems such as the maintenance of species richness in such systems and the development of non-empirical silvicultural systems for the sustainable management of tropical forest resources.

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