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FORICO: Gap Dynamics Model of the Lower Montane Rain Forest in Puerto Rico

T. W. Doyle
H. H. Shugart
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FORICO: GAP DYNAMICS MODEL OF THE LOWER MONTANE RAIN FOREST IN PUERTO RICO*

T. W. Doyle, H. H. Shugart, and D. C. West

ENVIRONMENTAL SCIENCES DIVISION
Publication No. 1879

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*Submitted as a thesis by T. W. Doyle to the Graduate Council of the University of Tennessee in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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A model, FORICO, was developed to simulate the natural gap succession of the lower montane rain forest in Puerto Rico. The FORICO model stochastically simulates a 1/30-ha stand, and determines, on a yearly basis, the establishment, growth, and death of individual trees. Hurricane frequency and stand damage probabilities are included to mimic storm effects common to forests of the West Indies. Validation of the model was achieved by correlating diameter distributions and species ranking of model results to field data. Comparison of hurricane and nonhurricane simulations indicate that disturbance plays an important role in maintaining the composition and species diversity of the Puerto Rican rain forest.

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INTRODUCTION

Over the past 10 years, systems modeling has been particularly useful in studying the long-term dynamics of forest succession. As a result, a number of forest simulation models were constructed to mimic the successional dynamics of mixed species forests, mainly temperate types. The purpose of this study was to develop a forest model, FORICO, of gap formation and replacement in the tropical rain forest of Puerto Rico. The model was constructed by modifying the FORET model developed by Shugart and West (1977) to conform with the tree species and forest characteristics of the lower montane rain forest on the lower slopes and ridges below 600 m in the Luquillo Experimental Forest in northeastern Puerto Rico.

Recent studies (Whitmore 1978, Hartshorn 1978) emphasized the impact and importance of canopy gaps and tree-falls in the structural and compositional dynamics of tropical rain forests. Findings indicate that many rain-forest species are dependent on gaps for regeneration as well as their continued persistence in mature forest. Furthermore, current diversity theory suggests that forest systems subject to frequent gap occurrence, or other chronic disturbance, tend to support a comparatively richer species assemblage. Connell (1978) used this argument to explain the high tree diversity of tropical rain forests. Tropical storms and hurricanes are noted to cause recurring tree-falls and landslides in forests of the West Indies (Wadsworth and Englerth 1959).

Models of tropical forests are scarce, partially because of insufficient data and limited knowledge of these forest systems. The Luquillo Experimental Forest in Puerto Rico has a long ecological research history (Wadsworth 1970), having been protected since 1903 for resource management and scientific purposes. Within this forest reserve near El Verde, Puerto Rico, an intensive and comprehensive ecological endeavor was performed during the AEC-PRNC Rain Forest project (Odum and Pigeon 1970). Moreover, the U.S. Forest Service Institute of Tropical Forestry has been conducting long-term forest inventories and remeasurement studies for over 30 years. This extensive research base of the forest is unique in the tropics and thus provides an ideal study opportunity to develop a forest model of a tropical rain forest.

CHAPTER I

THE STUDY FOREST

Location and Climate

The study forest covers the lower slopes and ridges of the mountains in the Luquillo Experimental Forest in northeastern Puerto Rico (18 20'N, 65 45'W) (Fig. 1). The area supports a single-dominant forest restricted to Puerto Rico and the Lesser Antilles at lower elevations between 150 and 600 m. This evergreen forest was described by Murphy (1916) and later by Gleason and Cook (1926) as "Rain Forest." Based on its attributes and nonseasonal climate, Richards (1952), included this forest type of the West Indies within the "Tropical Rain Forest" classification. Lacking the overall stature and multiple synusiae of true rain forests, Beard (1944) more specifically defines this forest system as "lower montane rain forest."

The climate experienced by the Luquillo Mountains, as the first orographic barrier to the easterly blowing trade winds, is classified in the Af type or tropical rain forest climate of the Koppen classification scheme (Haurwitz and Austin 1944). An extensive climatic study at El Verde, Puerto Rico (Odum et al. 1970) further revealed a relatively constant and uniform climate characteristic of rain forest regimes. The nonseasonality of this forest environment is reflected in the narrow, mean temperature ranges, both monthly and daily, varying less than 4°C (Odum et al. 1970). Rainfall records show an annual precipitation range of 3000 to 4000 mm (Briscoe 1966, Wadsworth 1948). From July to November, tropical storms and hurricanes are prevalent,

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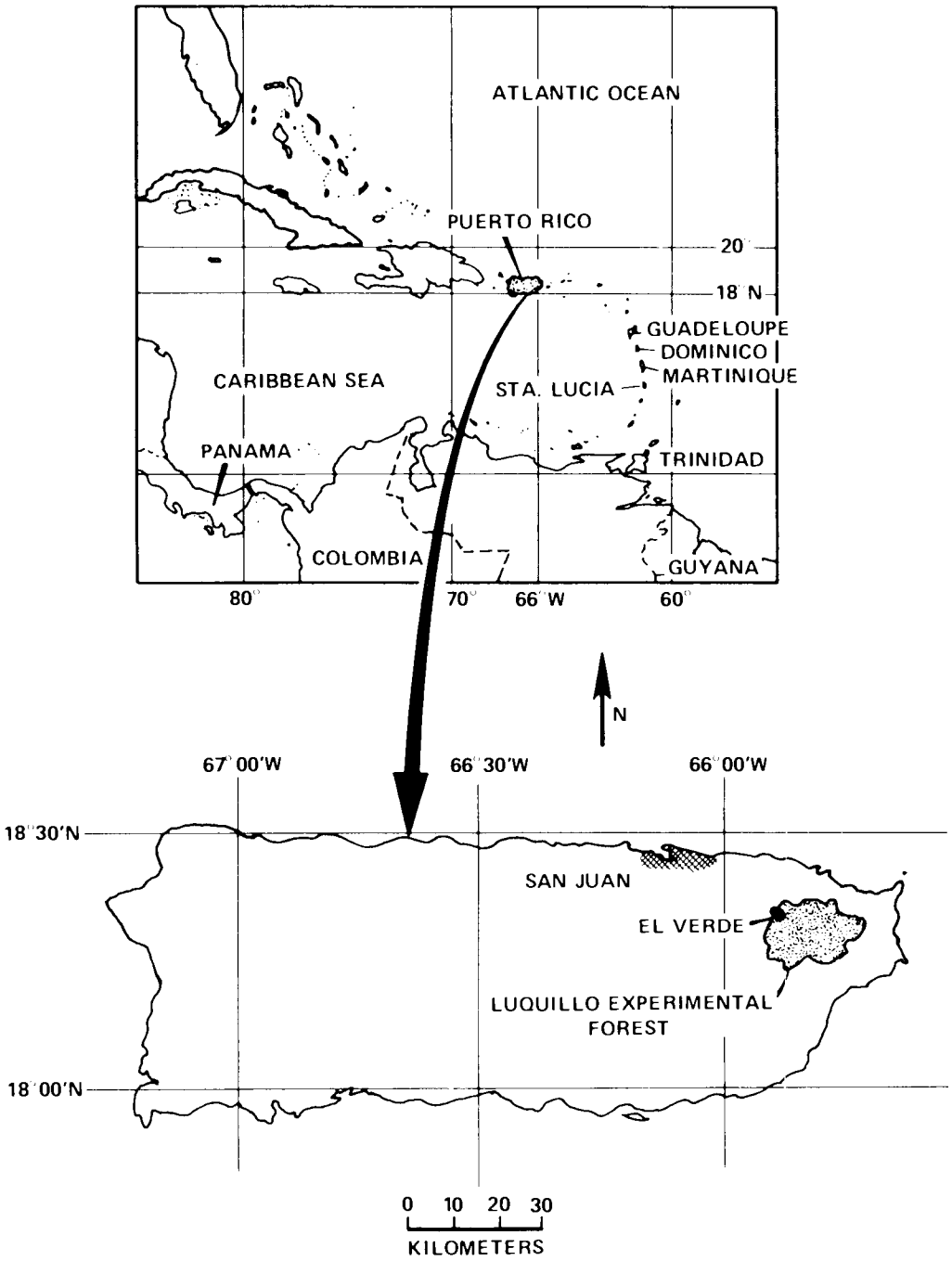

Fig. 1. Map of Puerto Rico and West Indies including an enlargement of Puerto Rico and the location of the study forest.

bringing heavy winds and torrential rains responsible for considerable damage both to personal holdings and the forest.

Geology, Soils, and Topography

The geology of the study area consists primarily of igneous formations of andesitic and basaltic composition (Beinroth 1969, Mitchell 1954). Mountain soils are acid clayey types from heavily leached inceptisols (Buol 1973, Edminsten 1970, Roberts 1942). Topography is rugged and steep with large boulders covering much of the soil surface. Slopes in most places exceed 45%.

Floristic Classification and Description

Floristically, this lower mountain forest of Puerto Rico is labeled the "*Dacryodes-Sloanea*" association (Beard 1944) throughout the Lesser Antilles and locally is called the "tabonuco" forest type (Wadsworth 1951, 1957), after the dominant tabonuco tree (*Dacryodes excelsa* Vahl). Beard's (1944, 1955) physiognomic classification of tropical vegetation designated this forest as "lower montane rain forest," having only two tree strata, a canopy at 20 to 30 m and a subcanopy at 3 to 15 m. Even more general is Holdridge's (1947) life zone system, which, based on climatic input, classifies this same forest as "subtropical wet forest" (Holdridge 1970, Ewel and Whitmore 1973).

Wadsworth (1950, 1951, 1970) provided a thorough description of the tabonuco forest and its research history. He noted that this forest was likely the climax vegetation for a one-third of Puerto Rico before it became a Spanish colony. This forest type is now restricted

to less than 4000 ha (10,000 acres) of protected forest lands. Nearly 200 arborescent species have been identified, 60% of which are considered rare or uncommon (Little 1970). Tree species diversity of "virgin" tabonuco forest has been estimated at 33 species per acre (~13/ha) from a 10 acre (4-ha) sample which tallied 73 arborescent species in total (Wadsworth 1951).

The lower montane rain forest or tabonuco forest displays many of the forest characteristics typical of tropical wet vegetation. Thick-stemmed lianes, stranglers, climbers, arborescent ferns, and palm trees are present in abundance. Buttressed and stilted roots are also conspicuous. Tree bark is generally thin and smooth, often covered with mats of lichenous and algal growth. Bromeliads, mosses, and orchids are common, drawing support from tree trunks and branches. Thick, leathery mesophyllic leaves are also typical of this predominantly evergreen rain forest.

Structure and Composition

The vegetation structure and species composition of the tabonuco forest was investigated extensively in several studies which identified the kinds of species and number of trees with regard to their position and relative importance in the forest community. Wadsworth (1951, 1957) distinguished three tree strata; a discontinuous emergent layer at 30 m, a continuous canopy layer at 20 m, and a discontinuous understory from 3 to 15 m in height. An average leaf area index of 6.4 m^2/m^2, and a maximum of 12.0 m^2/m^2, in pure tabonuco stands was recorded (Odum et al. 1963). The density diameter distribution of

canopy species in this forest exhibits the "classical L-shaped curve, with less than 4% of the stems larger than 60 cm" (Briscoe and Wadsworth 1970). In a comprehensive vegetation survey of the tabonuco forest near El Verde, Puerto Rico, Smith (1970) determined the relative density, seedling density, and successional status of the various plant species in each of several forest synusiae classes, namely canopy, understory, climbers, herbs, and saprophytes.

Tree Growth and Stand Development

Most tropical tree species, unlike most temperate trees, apparently do not produce annual growth rings from which to determine tree age and growth rate. This is especially true of tropical, moist aseasonal forests, emphasizing the importance of the forest remeasurement studies conducted in Puerto Rico. Long-term study results of growth rates for tree species from the tabonuco forest type were published by Wadsworth (1947, 1953, 1970), Murphy (1970), and Crow and Weaver (1977). Although tropical rain forests are believed to produce rapid plant growth, these studies indicate slow growth as have others (Baur 1964, Keay 1961, Mervart 1970, Whitmore 1974) elsewhere in the tropics. Not only was growth found typically to be slow, but it also varied widely within and between species and from site to site.

Growth studies by Murphy (1970) and Crow and Weaver (1977) attempted to correlate tree growth with various environmental and tree-specific factors. As expected, the strongest relation to tree growth was found with crown position, the larger dominant trees having the fastest growth rates and the smaller suppressed individuals showing the slowest rates. Microtopography apparently influences differential

drainage and species distribution (Smith 1970, Wadsworth 1953, 1970), and probably contributes greatly to the variability in species growth rates (Crow and Weaver 1977).

With the records from remeasurement studies such as those done in the Puerto Rican forests, a considerable amount of insight was gained on the temporal dynamics of this tropical moist forest. Analyzing a thirty-year forest chronicle, Crow (1980) distinguished two phases of developmental change in both the structure and composition of a 0.75-ha tabonuco forest stand. The first phase reflected a recovery trend or building response to earlier hurricane disturbance, wherein secondary species, stem density, and stand biomass were sharply increasing. By the end of the 30-year period, species diversity and stem density had declined, while biomass and basal area accumulations were leveling, indicating the oncoming of a "mature phase" forest dominated by primary species. Stand ingrowth and mortality were monitored over the study period; the results revealed a rapid turnover rate of 50%, mostly of stems in the lower size classes. Also, Crow (1980) found the tree height profile of this stand to change considerably over the 30 years from a well-defined canopy layer of smaller trees to a less-stratified distribution of trees much taller in overall stature. In a similar study of related data, Briscoe and Wadsworth (1970) examined the stand dynamics and yield differences between thinned and nonthinned plots.

Succession

Despite the intensive forest surveys that were conducted in the tabonuco forest, only brief, classical descriptions (Gleason and Cook 1926, Wadsworth 1957) of the natural forest succession were published.

However, several recent studies quantified the regrowth of early succession and determined the principal role of native species in the recovery of disturbed tabonuco forest. In a succession experiment following cutting and herbicidal treatments, Ewel (1971) calculated heights, stem density, biomass, leaf area, and optical density as well as compositional characteristics of first-year regrowth. To investigate the successional strategy of *Palicourea riparia* Bentham, Lebron (1977) sampled canopy gaps, roadside areas, permanent seedling quadrats (McCormick 1970), and the three Rain Forest Project study centers (Odum and Pigeon 1970) for sites variable in age, environment, and disturbance history. Other autecological studies (Bannister 1970, Muniz 1978, Sastre 1979, Silander 1979) also shed considerable light on the population dynamics and successional role of key species. Although extensive background information is available on the ecology of the tabonuco forest and its component species, a comprehensive study of succession and gap dynamics is yet needed to synthesize these data and to identify the successional aspects and patterns of this forest system.

CHAPTER II

GAP PHASE DYNAMICS

Gap Phase Theory

Tropical forest communities are frequently noted for their patchiness and pattern of continual forest renewal (Whitmore 1975). Evidence of patchy or "mosiac phenomena" emphasizes the impact and importance of a single canopy tree death in the structural and compositional dynamics of the rejuvenating mature forest (Whittaker and Levin 1977). Disruption of the canopy strata from a localized disturbance (e.g., tree fall) constitutes a gap wherein the forest environment is altered and subsequent vegetative growth and establishment is induced (Runkle 1979). Watt (1947) coined this gap formation and replacement process "gap phase." The intercommunity patterning of gap phase involves the many different processes and fortuitous events acting on the individual, species, and community level.

Mosaic Phenomena

Observations in the wet tropics suggest that dominant climax canopy species do not replace themselves in space or in time. Richard's (1952) support and account of Aubreville's (1938) 'mosaic or cyclical theory of regeneration' states that primary tropical rain forest floristically composes a 'mosaic' of dominant species whose understory differs in composition, and the replacement process of which occurs in a 'cyclic' fashion of fluctuating species composition. Watt (1947) likewise acknowledged this mosaic phenomenon, though consisting of patches, or "phases" as he called them, dynamically related in a

"space-time pattern" of regular cyclic changes in any given locale. In his "Biological Nomad theory," van Steenis (1958) detailed the role, prevalence, and patchiness of nonclimax secondary species in colonizing the 'eyes' or canopy gaps in tropical climax rain forest. These mosaic patterns are thought to reflect the type and frequency of disturbances and microsite differences of gap formation in the natural growth cycle of mature forest (Whitmore 1978, Hartshorn 1978). Chance establishment, specialized species attributes, and high species-richness are also thought to contribute to this patchy phenomenon and the dynamic nature of tropical rain forests.

Gap Formation

Inherent to gap formation and recolonization are the patterns of disturbance. Disturbance can be defined as any consequence upsetting the structure and equilibrium of a forest locale (Runkle 1979). The type, frequency, and extent of the disturbance are somewhat determined by the nature of the forest system, its component species, and its environment. Old age, suppression, wind, disease, and damage by animals or other tree-falls are the principal elements contributing to tree death and gap occurrence. Strong (1977) proposed "epiphyte-loads" as a major determinant of tree-fall and diversity in equatorial tropical forests. Superficial root systems, as are common in tropical wet forests, along with unstable soils, impeded drainage, and mountainous slopes foster the events of landslide and tree-fall. Although a single tree-fall can initiate a domino effect, creating a rather large canopy opening, such consecutions are considered rare and likely the result of external forces.

Natural extrinsic disturbances including cyclonic storms (Webb 1958, Whitmore 1974), wildfires (Budowski 1959, 1965), and geophysical eruptions (Beard 1945, 1976) have been observed as formidable forces responsible for gap openings as well as larger clearings sometimes covering square kilometers. In Puerto Rico, heavy winds and rainfall associated with tropical storms and hurricanes have been noted to cause considerable limb damage and treefalls (Wadsworth and Englerth 1959). Records show that 50 hurricanes in the past 450 years have passed directly over Puerto Rico, about one every nine years. Although the regularity and severity of these events cannot be accurately assessed, the evidence of their impact can be readily inferred from observation, long-term forest data, and the high density of early successional species represented in the tabonuco forest.

Forest turnover rates give some indication of the forest dynamics in terms of the area in gaps formed each year and the total years at this rate before a new forest would replace an old one. Hartshorn's (1978) study of gap dynamics in Costa Rica disclosed for a tropical wet forest, an average gap size of 90 m^2 and a mean turnover rate of 118 ± 27 years. This rate of gap formation by his calculation is faster and more dynamic than either dry tropical or extratropical forests. A comparable estimate from a UNESCO/UNEP/FAO report (1978) documented a turnover rate ranging 40 to 100 years for tropical rain forest.

Gap Recolonization

Many tropical species are "gap opportunists" whose permanence in the mature forest is dependent on gap occurrences and adaptations for

successful regeneration. As much as 75% of the canopy tree species in the La Selva forest of Costa Rica may be within this category (Hartshorn 1978). The success of these species in colonizing a gap opening largely depends on gap size and environment; proximity of seed source, dispersal, and dormancy mechanisms; biotic interactions; and chance gap occurrence both in space and time.

Gap size, position, and shape influences the gap environment and the subsequent replacement process. The vacant canopy and disrupted rhizophere caused by a fallen tree introduces an important change in the microclimatic and substrate conditions. Soil and air temperature, light quantity and quality, and mineral soil exposure increase, while soil moisture and root competition are reduced. In small gaps, long and narrow, the stimulus for growth may not be as significant in the establishment of new seedlings as in the surrounding intact forest. As gap size increases, though, regeneration plays a greater role in canopy replacement. Acevedo and Marquis (1978) and Brokaw (1979) independently established that gap openings larger than 150 m^2 were colonized by pioneer and gap species, while gaps less than 150 m^2 in size were dominated by late successional species.

Seed source, dormancy, and dispersal can determine the success with which species colonize gap openings. Seed-bearing adults in close proximity to a gap may improve their species representation except where seed dormancy and dispersal mechanisms compensate. Several studies in the tropics (Guevara and Gomez-Pompa 1972, Symington 1933, Vasquez-Yanes 1974) revealed the dormancy of seeds of secondary species which may remain viable between disturbances. Pioneer species, more so than primary species, generally have smaller, lighter seeds with

long-distance wind-dispersal capabilities as well as the tendency to flower more continuously throughout the year (Frankie et al. 1974). However, this does not preclude the effectiveness of biotic dispersal of pioneer species by birds and bats which appears extremely important in tropical forests (Hartshorn 1978). Whatever advantage "gap" species gain from efficient seeding mechanisms and fast growth is compensated for by primary species in their physiological ability to regenerate and persist under a closed canopy.

Plant herbivory and allelopathic responses may also affect the presence or proportion of certain species in gap recolonization. Seed predation (Janzen 1970, 1971, Sarukhan 1978) was studied to explain the diversity, spatial patterning, and reproductive success of tropical tree species due to selective grazing by herbivores on palatable species. Plant defenses of physical, chemical, and/or mutualistic origin were identified as mechanisms in which to escape predation from grazers or to reduce competition from neighboring plants.

The chance occurrence of gaps temporally as well as spatially is all important as to which species successfully colonize a gap. It is unknown, however, to what degree the timing of probabilistic events (e.g., tree death, tree-fall, hurricane, other gap-causing forces) may play in gap replacement. Seed production, predation, and dormancy periods coinciding with seasons of high gap incidents can enhance or reduce the relative numbers of certain species in the recolonization process. Even gap size and proximity from seeding adults is fortuitous, emphasizing the spatial influence of gap occurrence. Many factors affect gap composition, but the end result appears largely to be a matter of chance (Webb et al. 1972).

CHAPTER III

FOREST MODELING

Over the past 10 years, systems modeling has been particularly important in studying the long-term dynamics of forest succession which otherwise might require several human generations to observe directly. Because of the utility of the systems approach for this purpose, a myriad of forest succession models were constructed to simulate the successional dynamics of forest types ranging from northern hardwood forest to tropical rain forest. A review of these forest succession models was published by Shugart and West (1980).

Forest Succession Models

Forest succession models can be categorized according to whether an individual-by-individual or a community-by-community succession process represents the basic unit of change. Shugart and West (1980) on this distinction and spatial constraint, defined three model types; tree, gap, and forest. Tree and gap models are similar in appropriating change on the individual tree level but vary in parameter input and spatial detail. Though not restricted in stand size, tree models do require detailed data input designating tree replacement probabilities by trees of the same or other species. Gap models and functional stand models employ a more empirical approach to simulate the differential establishment, growth, and survival of individual trees on a specified spatial unit, approximating a large gap opening. The third model type, forest models, predicts forest succession on a regional

scale from derived transitional probabilities or rates determining the replacement and displacement of defined cover-states or successional communities through time. As an introduction to the development, results, and discussion of the FORICO model, this literature review focuses exclusively on gap models, their functional design, validation, and utility.

Gap Models

JABOWA (Botkin et al. 1972) was the first of many gap models (Mielke et al. 1978, Tharp 1978, Shugart and Noble 1980, Shugart and West 1977, Shugart et al. 1980) developed to simulate the forest dynamics and competitive interrelations among individual trees on a specified spatial unit. Parameter derivations are less dependent on actual field data than on the biological and physical characteristics of the represented species and forest environment. These models use functional relationships of tree establishment, growth, and survival computed on a per annum basis. Regenerative input of new seedlings varies between models, but considers such species-specific factors as dispersal mechanisms, dormancy periods, grazing palatability, light conditions, leaf litter and mineral soil requirements, and site evaluation. Tree growth is incremented by diameter as a function of tree size, climate, available light, soil moisture, and competition. Death of an individual tree is largely a chance event either age-related or the result of disturbance. Several models include an additional mortality factor to eliminate suppressed trees after an extended period of nongrowth.

Other major assumptions are prominent in the conceptual scheme of these gap models, especially concerning gap dynamics and tree ontogeny. Gaps are the result of canopy tree(s) death and disturbance. These gaps occur within an intact forest providing an adequate and equitable seed source from all species. Natural succession or gap recolonization is modeled as a stochastic tree-by-tree replacement process. Under optimum conditions, annual tree growth is proportional to the amount of sunlight received. The distribution of available light through a vertical profile of a forest is a negative exponential function of leaf area and light extinction. The age-related death function assumes that only 1 to 2% of all tree seedlings survive to reach their maximum age. Gaps are spatially homogeneous areas in which competitive effects from shading and crowding are evenly distributed for all trees over the entire stand.

An important component of the functional design in gap models is the simulated gap size. This spatial dimension ranges from 1/100 to 1/12 ha, depending on the particular model or forest system. Shugart and West (1979) found that stand sizes above or below certain limits introduced erroneous model behavior and results. Their study concluded that the ideal gap size for modeling purposes approximated the canopy spread of the largest tree specimen recorded for the forest being modeled.

Model validation serves to evaluate the veritability and reliability of model performance and results. Shugart and West (1980) outlined several validation techniques, including the following: direct comparison of model results and actual field observations,

predicting environmental gradient responses, reproducing the effects of historical events, and accidental occurrences. The validity and veracity of these tests is strengthened by the degree of data independence between model parameters and inputs from the testing data.

Because gap models depend on their conceptual design and less on actual forest data for model development and simulation, they are more amenable to validation and application. Shugart and Noble (1980) tested their simulation model, BRIND, of an Australian Eucalyptus forest against independent data, matching closely the mean diameter, basal area, and stocking density measurements of a forest dominant. Botkin et al. (1972) successfully predicted the elevational transition between two northeastern forest types by entering conditions which defined an environmental gradient. Shugart and Noble (1980) applied similar gradient response tests by varying both elevation and wildfire disturbance frequencies. Employing a hindcast procedure, Shugart and West (1977) validated their FORET model of a mixed-deciduous forest in East Tennessee by including chestnut as a viable species and predicting preblight chestnut forests based on historical data. These models are also tested in their ability to project the structural and compositional characteristics of mature forests.

Forest succession models, particularly gap models, have demonstrated their utility to tackle applied problems concerning environmental impacts and management strategies. Modifying the FORET model, West et al. (1980) investigated pollutant stress from sulfur dioxide on the long-term dynamics of forests in East Tennessee. The KIAMBRAM model (Shugart et al. 1980) of a subtropical rain forest in

Australia was altered to assess the impact from different commercial tree harvest practices. FORAR, a forest simulator for Southern Arkansas, was developed by Mielke (1977) to determine the effects of various timber management schemes on red-cockaded woodpecker habitat. Shugart and West (1980) outlined other important applications in the future, including large-scale and long-term forest changes resulting from global environmental effects.

Tropical Forest Models

Forest modeling of tropical American forests has been limited to only a few systems where sufficient data and research on a forest and its species are available. Ecosystem models of energy flow and elemental cycling were among the first efforts to capture the dynamics of tropical forests. Ewel (1971) developed an energy model of early successional regrowth for the tabonuco forest in Puerto Rico. Using a projection matrix model, Hartshorn (1972) described the population dynamics of a single tropical tree species, *Pentaclethra macroloba* (Willd.) Ktze. Wadsworth (1977) employed a transition matrix approach to investigate the distribution of tree diameters through time in the tabonuco forest of Puerto Rico. Considering gap formation rates and the colonizing ability of shade-tolerant and shade-intolerant species, Acevedo (1978) tested a Markov model to simulate the dynamics and mosaic composition of a tropical rain forest. The emphasis of this paper focuses on the results and application of the FORICO model designed to simulate gap dynamics and succession of the lower montane rain forest in Puerto Rico.

The FORICO Model

The FORICO model was constructed by modifying the FORET model developed for southern Appalachia by Shugart and West (1977) to conform to the characteristics of the tabonuco forest and its represented species. This is one of many gap models already discussed, designed to simulate the successional dynamics and competitive interrelations among individual trees on a spatial scale that approximates a large canopy gap (ca. 0.01-0.1 ha). The simulated gap of the FORICO model represents a 1/30-ha circular area (Fig. 2). Key autecological parameters of 36 common tree species are used as input for the model (Table 1). Model processes, mainly tree birth, growth, and death, are expressed as functional relationships computed in yearly intervals. A flow diagram of model subroutines illustrates the order and function of these processes and support programs (Fig. 3). A general summary of the design and mechanics of FORICO by major subroutines follows. A more complete description of FORICO can be found in Doyle (1982).

The BIRTH subroutine (Fig. 3) determines the species and number of new seedlings that are established on the plot each year. Eligibility of model species for recruitment is based on their silvicultural characteristics and regenerative requirements for successful establishment. Selection of eligible species and seedling numbers for planting is modeled as a stochastic process. Each new tree is assigned a randomly determined seedling size. At the initiation of a simulation trial or following a significant turnover or disturbance, the model continues to seed in new trees until a minimum leaf area or biomass level is attained.

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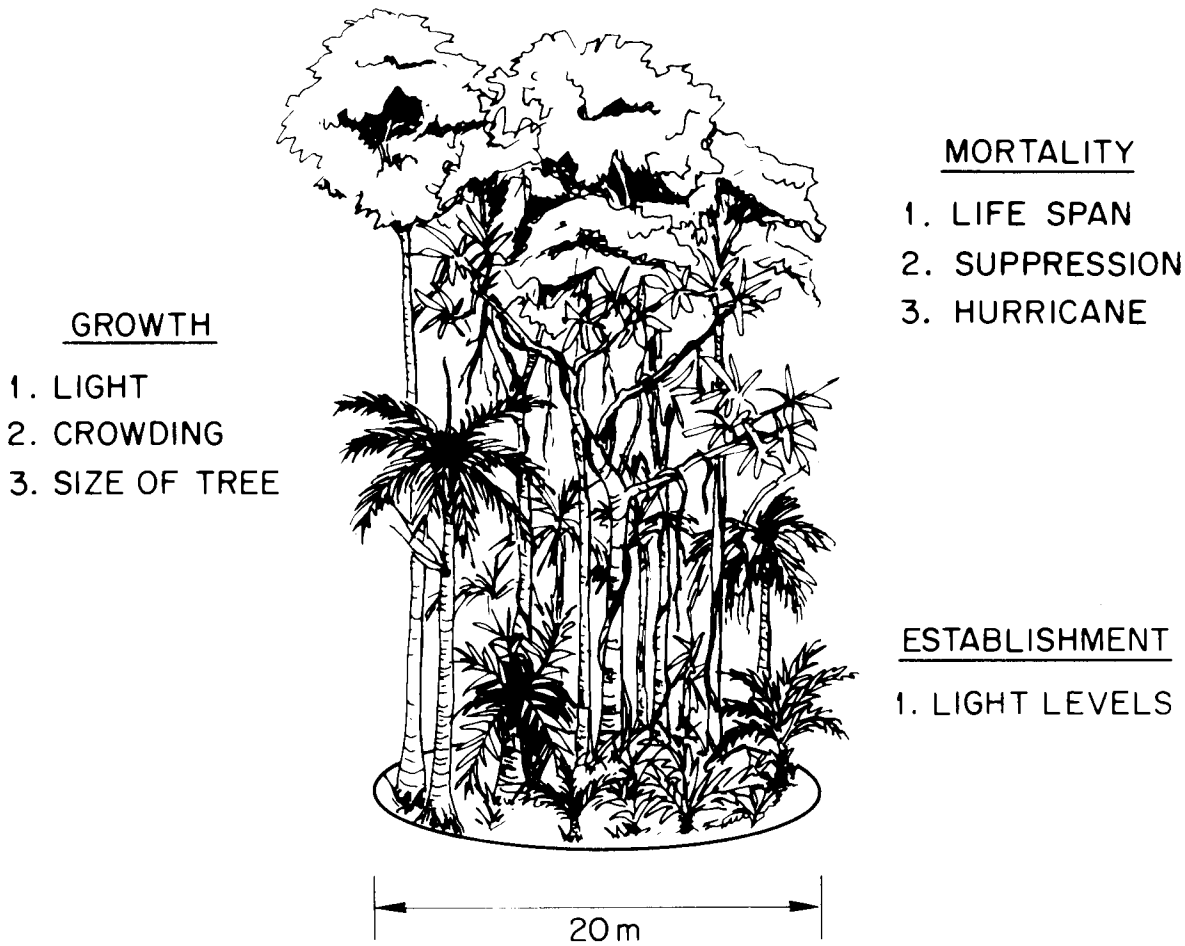

Fig. 2. Illustration of the simulated 1/30-ha forest stand, a circular plot 20 m in diameter, and the major model processes and factors affecting individual tree establishment, growth, and mortality.

Table 1. Species list and autecological parameters used in the FORICO model

Species name[a]	Dmax[a]	Hmax[a]	B_2	B_3	TOL[b]	AGE[c]	G[d]	Smin	Smax
Alchomea latifolia	46	1524	60.30	0.6554	2	58	240.19	0.05	0.12
Alchorneopsis portoricensis	46	1524	60.30	0.6554	2	56	246.40	0.05	0.12
Buchenavia capitata	122	2438	37.72	0.1545	2	120	182.85	0.05	0.12
Byrsonima coriacea	46	1829	73.56	0.7996	3	46	202.78	0.12	1.00
Casearia arborea	15	914	103.60	3.4533	3	47	175.37	0.12	1.00
Casearia sylvestris	10	457	64.00	3.2000	2	44	99.00	0.05	0.12
Cecropia peltata	61	2134	65.47	0.5366	3	50	271.12	0.12	1.00
Cordia borinquensis	13	610	72.76	2.7988	1	43	131.99	0.004	0.75
Cyathea arborea	13	914	119.53	4.5976	3	17	461.89	0.12	1.00
Dacryodes excelsa	152	3048	38.30	0.1259	1	205	132.34	0.004	0.05
Didymopanax morototoni	46	1829	73.56	0.7996	3	52	267.65	0.12	1.00
Drypetes glauca	15	914	103.60	3.4533	1	56	147.19	0.004	0.05
Eugenia stahlii	30	1829	112.80	1.8800	1	103	154.85	0.004	0.05
Euterpe globosa	20	1524	138.70	3.4675	1	22	587.34	0.004	1.00
Guarea rumiflora	15	762	83.33	2.7777	1	41	169.56	0.05	0.12
Guarea trichiloides	91	2286	47.23	1.2095	2	121	169.56	0.004	0.05
Hirtella rugosa	8	610	118.25	7.3906	1	32	164.62	0.004	0.05
Homalium racemosum	61	2134	65.47	0.5366	2	107	178.41	0.05	0.12
Inga laurina	46	2134	86.82	0.9437	1	75	229.10	0.05	0.12
Inga vera	46	1524	60.30	0.6554	2	65	271.38	0.05	0.12
Laetia procera	30	2286	143.26	2.3877	3	86	228.60	0.05	0.12
Linociera domingensis	30	1829	112.80	1.8800	1	65	247.67	0.05	0.12
Manilkara bidentata	122	3048	47.72	0.1955	1	157	171.76	0.004	0.05
Matayba dorningensis	46	1829	73.56	0.7996	1	70	232.60	0.004	0.05
Miconia prasina	10	762	125.00	6.2500	2	26	257.17	0.05	1.00
Miconia tetrandra	30	614	92.46	1.5411	1	53	257.17	0.05	0.12
Ocotea leudoxylon	25	1524	110.96	2.2192	2	35	387.09	0.05	0.12
Ocotea moschata	76	2438	60.55	0.3983	1	76	57.03	0.004	0.05
Ormosia krugii	61	1829	55.47	0.4547	2	84	197.89	0.05	0.12
Palicourea riparia	8	457	80.00	5.0000	2	29	142.81	0.05	1.00
Psychotria berteriana	10	610	94.60	4.7300	3	28	195.68	0.05	1.00
Sapiura laurocerasus	61	1829	55.47	0.4547	2	167	99.00	0.05	0.12
Sloanea berteriana	91	3048	63.97	0.3515	1	118	226.08	0.04	0.05
Tabebuia heterohylla	46	1524	73.56	0.7996	3	79	206.75	0.05	0.12
Tetragastris balsamifera	46	2438	100.04	1.0874	1	169	125.87	0.004	0.05
Trichilia pallida	15	914	103.60	3.4533	1	254	32.23	0.004	0.05

[a]Taken from Little and Wadsworth (1964).

[b]Tolerance classes for each species drawn from Smith (1970).

[c]Computed from a supplemental program in Appendix A-1 using the G constant and maximum size figures.

[d]Derived from tree growth data provided by the U.S. Forest Service Institute of Tropical Forestry (see Crow and Weaver 1977).

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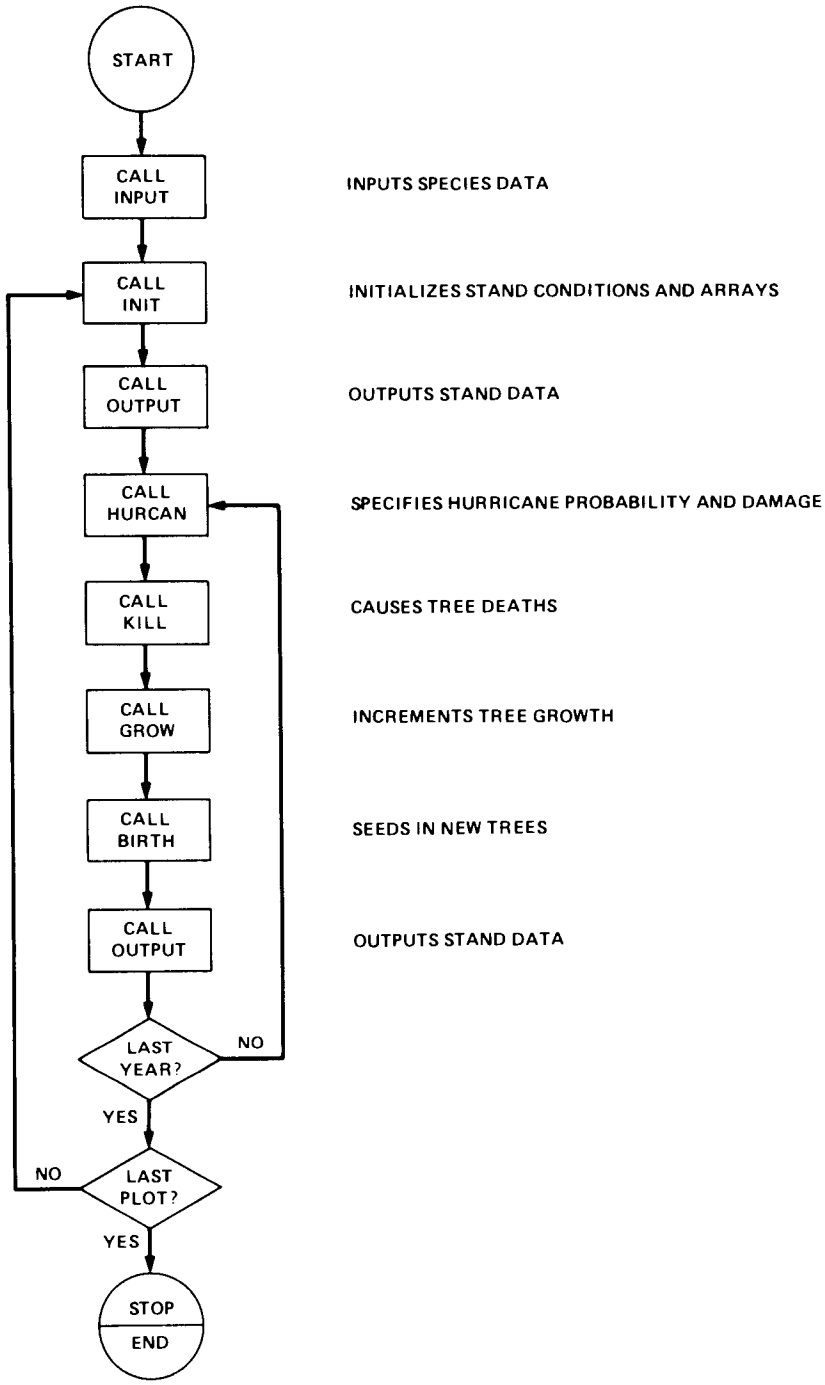

Fig. 3. Flow diagram of calls to subroutines in the FORICO model. The general function of each subroutine is listed beside the subroutine named in the box.

The GROW subroutine (Fig. 3) calculates and increments the predicted annual diameter growth of each tree. Under optimum conditions, annual tree growth is directly related to the amount of sunlight the tree receives in leaf area times the energetic cost of maintaining its size. Species' maximum diameter and height figures are used to derive coefficients B_2 and B_3 (Table 1) from a parabolic expression (Ker and Smith 1955) for estimating tree height from tree diameter. Tree size, B_2 and B_3, and the growth parameter G (Table 1) are used to calculate the maximum expected diameter increment for each tree. The species growth constant, G, is approximated for each species as a function of its maximum known growth rate (see Appendix of Botkin et al. 1972). Maximum annual growth figures of native species were readily available from forest remeasurement data collected and provided by the U.S. Forest Service Institute of Tropical Forestry in Rio Piedros, Puerto Rico. This optimum growth increment is then reduced by growth inhibiting factors, namely shading, competition, climate, and other environmental stresses as they apply. Taking into account the stand structural profile, the model determines the vertical distribution of tree heights in 0.1-m units and the leaf area of each tree. The sum leaf area above each tree, obtained from adding the leaf area of all taller trees, is then used to estimate the amount of light available to each tree for growth due to shading. The distribution of photosynthetic light through the stand canopy is determined from a negative exponential function defining the relationship between leaf area and light extinction. After determining the amount of light available to each tree, the model computes the growth reduction associated with the

decreased photosynthetic potential under shaded conditions. Light saturation and compensation values for species in general tolerance classes, TOL (Table 1), are used to generate photosynthesis curves which define the shade effect on tree growth. Competition for space and nutrients also limits potential tree growth. The model employs a linear function that proportionally reduces tree growth due to crowding as the total stand biomass approaches a maximum biomass level recorded for the model forest. Climate is another important factor influencing tree growth. Because the G parameter value was calculated from actual field measurements of species growth, climate is intrinsically incorporated in the derivation of the optimal growth increment.

The KILL subroutine (Fig. 3) eliminates trees from the simulated stand as a stochastic function of age- and growth-related deaths. Each tree is assumed to have an intrinsic mortality rate such that under normal conditions only 1 to 2% of all seedlings in a cohort ever live to reach their life expectancy. The probability of a tree dying in any one year is expressed as a negative exponential of the above survival percentage and the species' maximum age. A random number is generated and compared with this probability to determine whether each particular tree survives or dies in that year. Suppressed individuals that fail to maintain a minimal growth rate are subjected to an additional probability of dying. This additional mortality factor has the effect of allowing only 1% of a suppressed cohort to survive 10 years.

Subroutine HURCAN (Fig. 3) of the model stochastically mimics cyclone storm effects common to forests of the West Indies. Wadsworth and Englerth (1959) reported from historical records that 50 hurricanes

have passed over Puerto Rico over the last 450 years. This indicates a return frequency of one hurricane every nine years, and thus the model uses 0.111 as the probability that a hurricane will occur in any one year of simulation. Quantitative data do not exist on the impact of historic storms in the study area. In the simulations reported here, it was assumed that hurricanes removed, on the average, 0 to 10% of stand density. In each hurricane year, a random number between 0 and 0.1 was used as the probability of stem removal for that year. Individual stems were then stochastically selected for removals, based on that probability.

CHAPTER IV

MODEL RESULTS AND DISCUSSION

Trends in vegetation change and development as indicated by stand leaf area, aboveground biomass, and stem density are duplicated successfully by the FORICO model. Similarity of structural and compositional aspects between model stands and actual forest plots of varying successional maturity further verified the performance of the model. In addition, comparison of hurricane and nonhurricane simulations substantiate the importance of natural disturbances in maintaining the overall forest composition and species diversity of the tabonuco forest.

The FORICO model is programmed to yield simulated results that can be readily compared with standard forest measurements. Model results were obtained from a composite simulation of 120 stands, projected for a time scale of 500 years. Initial stand conditions constituted an open gap with no standing trees present.

Model Validation

Structural and compositional agreement between simulated results and actual field observations provided the basis for model validation. The FORICO model was initially tested for its ability to simulate the stand density characteristics of young and mature aged stands. This test involved the statistical comparison of density-diameter distributions between modeled stands and actual forest plots of similar successional age. Secondly, the model's ability to predict the species

composition of mature-state tabonuco forest was evaluated. A rank correlation of species ranking by abundance was used to validate model performance in this respect.

Model Performance

Model simulation of the temporal changes in stand leaf area, aboveground biomass and stem density is shown in Fig. 4. Leaf area sharply increases through the first 30 years of gap recolonization to its highest level of 7.8 m^2/m^2 (Fig. 4a). A natural thinning and canopy stratification becomes evident as the average leaf area declines about a stand equilibrium averaging 6.5 m^2/m^2. Several studies conducted in the tabonuco forest reported leaf area averages of 6.4 m^2/m^2 (Odum et al. 1963) and 7.3 m^2/m^2 and 6.6 m^2/m^2 (Jordan 1969). These estimates are comparable to the figures stated above and the range in model output.

The general pattern in model simulation of aboveground biomass (Mg/ha) displays a developing trend through year 125 when biomass accumulation reaches its maximum of 260 Mg/ha (Fig. 4b). After year 100, the stand biomass tends to fluctuate between 200 and 250 Mg/ha within a relatively steady-state condition. This range is compatible with aboveground biomass figures (150, 200, and 245 Mg/ha) calculated by Ovington and Olson (1970) for three study sites in the tabonuco forest.

The total number of stems above 1.3 cm dbh on the 1/30-ha stand decreases rapidly until year 50 at which point an equilibrium condition appears to develop (Fig. 4c). Stem density remains relatively constant

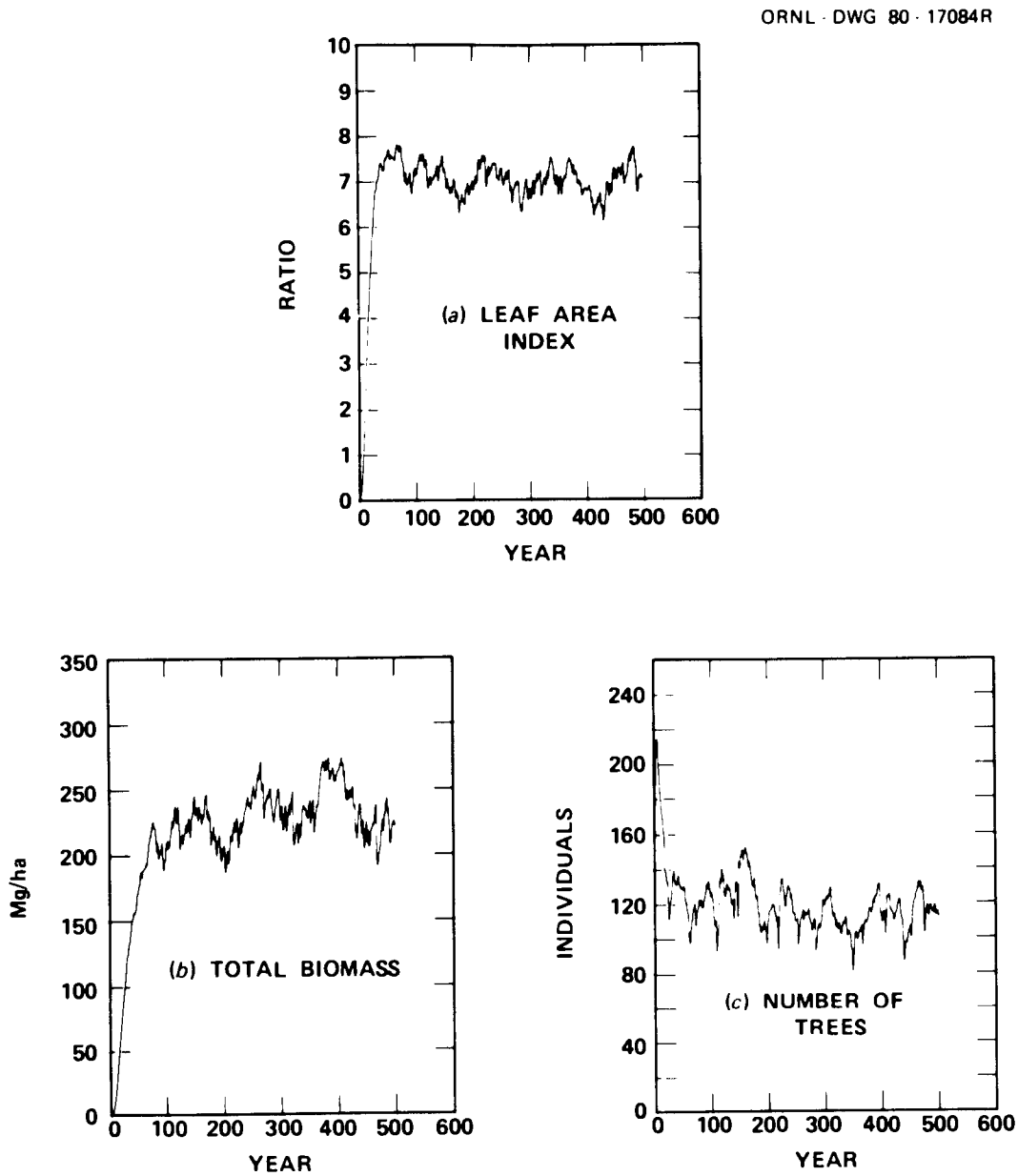

Fig. 4. Mean values for 120 simulated 1/30-ha plots through 500 years of model simulation: (a) leaf area index (m^2 leaves/m^2 land area); (b) total aboveground biomass (Mg/ha); and (c) total number of trees (individual trees greater than 1.3 cm).

to the end of the simulation averaging about 110 trees per plot. The cyclical pattern of these simulations reflect the normal canopy displacement trends of gap formation and replacement.

Little can be determined of the model's ability to simulate the structural dynamics of the tabonuco forest from tree density figures without consideration of the distribution of tree sizes. Comparisons of density-diameter distributions of simulated stands and actual forest plots tested and confirmed the validity of the FORICO model to reproduce forest structure. This test also included the predictability of the model to duplicate the stem density characteristics of stands in early and late successional stages.

Density-diameter distributions represent the number of trees apportioned in defined diameter size classes over the diameter range of a stand. Table 2 lists the density and cumulative percentage of stems in each diameter class for model-predicted and forest-observed stands of variable age. From one year to the next, individual trees may grow into larger size classes or remain in the same one, provided tree death or disturbance does not occur. Therefore, these distributions are not static and are subject to continual change as governed by the rates of growth and mortality. There is additional reason for the shape of diameter distribution curves giving some indication of the successional maturity and dynamics of a stand. Figure 5 shows the observed and predicted density-diameter distributions of 9-, 14-, and 150-year-old stands, respectively, derived from stem densities and cumulative percentages in each size class as presented in Table 2.

Table 2. List of cumulative percentages and stem densities by size-class for observed forest stands 9, 14, and 150 years of age and predicted model results 9, 14, and 150 years into simulation

			Stand age - 9 year				Stand age - 14 year				Mature stand 150 year				
Size-class	Size-class range (cm)	Size-class midpoints (cm)	Observed cumulative frequency	Predicted cumulative frequency	Observed stem number per 1/30 ha	Predicted stem number per 1/30 ha	Observed cumulative frequency	Predicted cumulative frequency	Observed stem number per 1/30 ha	Predicted stem number per 1/30 ha	Observed cumulative frequency	Predicted cumulative frequency	Observed stem number per 1 ha	Predicted stem number	Size-class
1	13-40	2	77.1	77.6	471	251	50.0	56.6	49	169					1
2	4-8	6	91.3	93.6	87	52	79.6	66.3	29	29	49.3	45.7	878	846	2
3	8-12	10	98.9	99.6	47	19	90.8	87.9	11	65	66.6	64.8	307	353	3
4	12-16	14	100.0	100.0	7	2	98.9	99.4	8	34	79.5	75.4	230	195	4
5	16-20	18					100.0	100.0	1	2	86.2	82.0	120	122	5
6	20-24	22									89.7	86.5	63	83	6
7	24-28	26									91.9	89.9	40	62	7
8	28-32	30									93.2	92.2	23	43	8
9	32-36	34									93.9	94.1	13	35	9
10	36-40	38									94.7	95.4	15	22	10
11	40-44	42									95.7	96.5	18	20	11
12	44-48	46									96.5	97.2	15	15	12
13	48-52	50									97.1	97.9	10	13	13
14	52-56	54									97.8	98.5	13	10	14
15	56-60	58									98.5	98.9	13	9	15
16	60-64	62									98.8	99.3	5	6	16
17	64-68	66									98.9	99.5	3	5	17
18	68-72	70									99.2	99.7	5	4	18
19	72-76	74									99.5	99.8	5	2	19
20	76-80	78									99.5	99.8	0	1	20
21	80-84	82									99.6	99.8	3	0	21
22	84-88	86									99.7	99.9	3	1	22
23	88-92	90									99.7	99.9	0	0	23
24	92-96	94									99.7	100.0	0	1	24
25	96-100	98									99.7		3		25
26	100-104	102									100.0				26
27	104-108	106													27
28	108-112	110													28

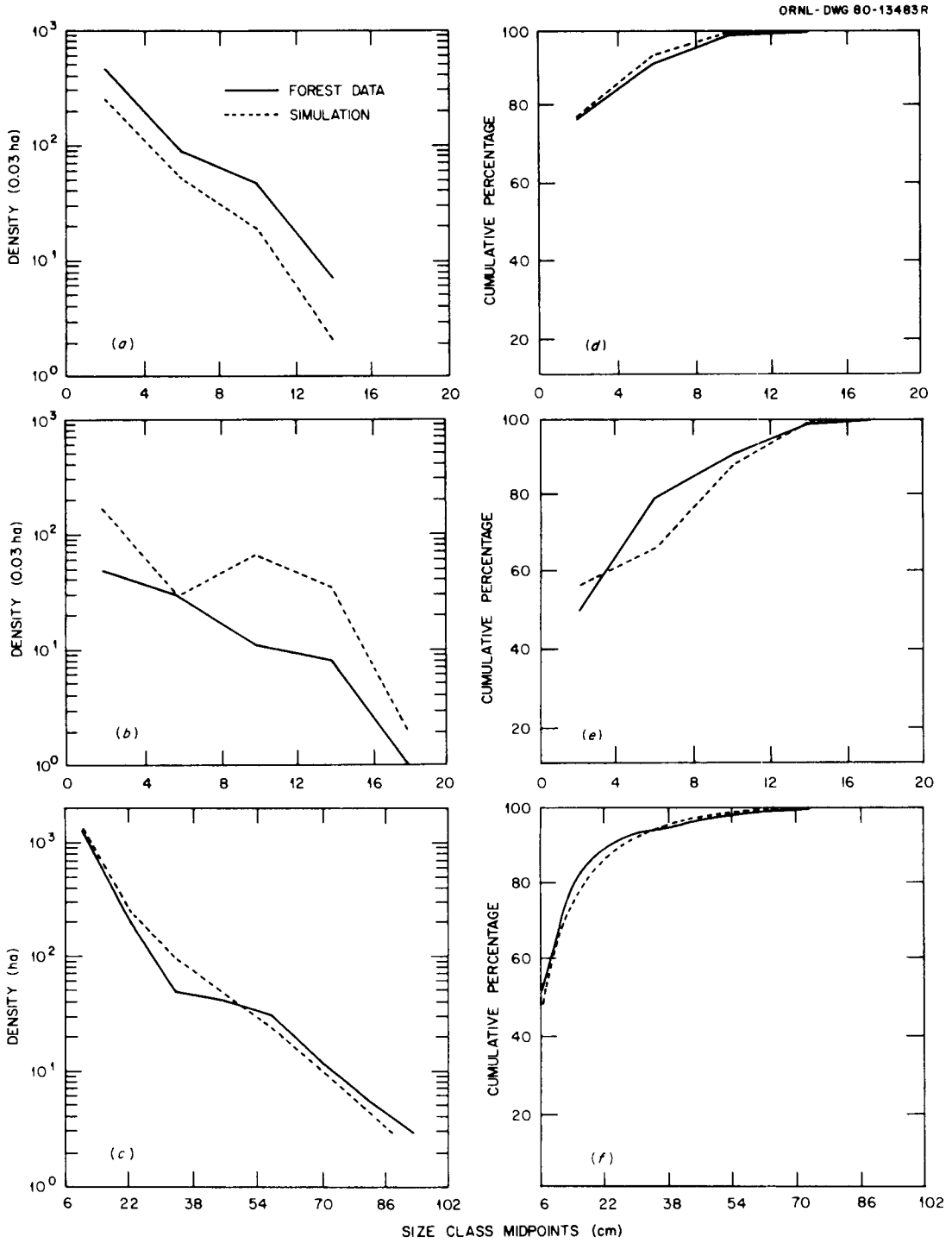

Fig. 5. Density-diameter distributions for simulated results and field data from stands of different ages: (a) 9-year-old stand; (c) 14-year-old stand; (e) 150-year-old stand. Cumulative frequency distributions for simulated results and field data from stands of different ages: (b) 9-year-old stand; (d) 14-year-old stand; (f) 150-year-old stand.

The stem density values from both simulated and actual independent data were converted into cumulative percentages of the total stand density for successive diameter classes from smallest to largest (Table 2). This results in cumulative frequency distributions (Fig. 5) that can be statistically compared by using the Kolmogorov-Smirnov two-sample test (Siegel 1956). The diameter distributions for all three stand comparisons were found not significantly different at the 0.01 level. This proves to be a powerful validation test. It indicates that the model adequately predicts ingrowth and mortality rates for each size class and compensates for the differences in these rates for young and mature aged stands. Not only that, but it simulates tree densities for diameter classes differentiated by only 4 cm. The larger the size classes, the less significance this test would hold. This structural agreement in tree size and number for variable-aged stands verifies the model's ability to mimic the successional dynamics of forest structure in the tabonuco forest.

It has been shown that the floristic composition in the tabonuco forest varies greatly from site to site, attributed mostly to topography and disturbance history (Crow and Grigal 1980). To account for this compositional variation, model results of species composition were validated against a 2-ha sample of tabonuco forest (see Table 2 in Wadsworth 1970) by correlating a numerical ranking of species abundance. Table 3 lists each of the model species according to their observed and predicted ranking and abundance. Using a Spearman rank correlation test (Siegel 1956), an r_s value of 0.66 indicated that the forest and model samples of species ranking were significantly correlated to the 0.05 level.

Table 3. Species, rank, and abundance of field observations and predicted model results

Species name	Observed		Predicted	
	Rank	Stem number	Rank	Stem number
Dacryodes excelsa	1	403	1	442
Euterpe globosa	2	348	9	408
Sloanea berteriana	3	225	3	224
Cordia boringuensis	4	133	29	9
Manilkara bidentata	5	130	2	406
Didymopanax morototoni	6	126	5	151
Cecropia peltata	7	119	4	203
Miconia prasina	8	86	21	25
Ormosia krugii	9	73	14	39
Psychotria berteriana	10	71	15	39
Ocotea moskhata	11	63	7	132
Mateyba domingensis	12	59	6	140
Tetragastris balsamifera	13	50	8	110
Alchornea latifolia	14	48	23	20
Alchorneopsis portoricensis	15	45	17	36
Inga vera	16	33	16	37
Guarea trichiloides	17	33	12	66
Tabebuis heterophylla	18	30	33	3
Drypetes glauca	19	26	25	17
Buchenavia capitata	20	23	31	7
Inga laresina	21	19	13	63
Byrsonima coriacea	22	19	11	69
Sapium laurocerasus	23	19	22	21
Laetia procus	24	12	30	8
Ocotea leucorylon	25	12	19	28
Casearia sylvestris	26	9	34	3
Homaluim racemosum	27	8	20	27
Cyatrea arborea	28	8	27	13
Guarea ramifeora	29	8	18	31
Eugenia starlii	30	6	10	71
Casearia arborea	31	6	32	6
Linociera domingensis	32	5	24	19
Hertella rugara	33	2	35	0
Trichilia pallida	34	1	36	0
Miconia tetrandra	35	0	26	17
Palicourea rigaria	36	0	28	10

Conformity of species composition by ranking can be further discussed by comparing the abundance values of the seven most important species which comprise more than 65% of the stem density in this forest. Model output shows fairly accurate figures for abundance among the forest dominants, Dacryodes excelsa and Sloanea berteriana, as well as the common pioneer species, Didymopanax morototoni and Cecropia peltata. Some anomalies, however, include the relatively poor representation of Cordia borinquensis and Euterpe globosa, and the over representation of Manilkara bidentata. Cordia borinquensis is an abundant understory species capable of surviving beneath the canopy for relatively long periods with little measurable growth. Adjusting the function which eliminates suppressed trees would allow for its persistence and improve their position in the species ranking. Sierra palm, Euterpe globosa, is well represented in the forest on poorly drained, unstable soils where its specialized root system allows it a competitive advantage over the other species (Bannister 1970). The FORICO model does not include a site index or edaphic parameter to account for site quality or differences, which could be included to help improve the standing of this species. The overabundance of Manilkara bidentata can be explained in both its historical record and autecology. Because its wood is one of the finest and hardest of all Puerto Rican trees, it has also been the one most selected for harvesting. This selective influence does not show in the forest data nor in the loss of its regenerative potential. In addition, this species has the growth characteristics of a secondary species, but the tolerance and longevity of a primary species. As for the remaining species, the model

demonstrates relative agreement in species abundance. These model results reflect a slight favoring of pioneer and primary species, while underestimating the numbers of late secondary species. This model response appears to be related to the disturbance pattern used in the simulation.

Current diversity theory suggests that forest systems subject to chronic disturbance tend to support a comparatively richer species assemblage. Connell (1978) used this argument to explain the high tree diversity of tropical rain forests. Comparison of hurricane and nonhurricane simulations indicate that disturbance plays an important role in maintaining the compositional variation and species diversity of the tabonuco forest in Puerto Rico. Figure 6 compares dominance-diversity curves from field observations and model simulations with and without hurricane effects. Dominance-diversity relationships associate the importance of a species with its ranking from most to least dominant. The dominance-diversity curve including hurricane effects converges and overlays with the curve for the tabonuco forest, while the curve without hurricane effects differs considerably. In the absence of disturbance, the model predicts a forest community low in diversity and dominated mostly by late successional species. It also becomes apparent that without gap occurrence, gap-dependent species risk local extinction.

The change in community composition and diversity between the hurricane and nonhurricane simulations further suggests that certain floristic associations are likely to predominate under particular disturbance patterns. Horn (1975) found that diversity is greater at

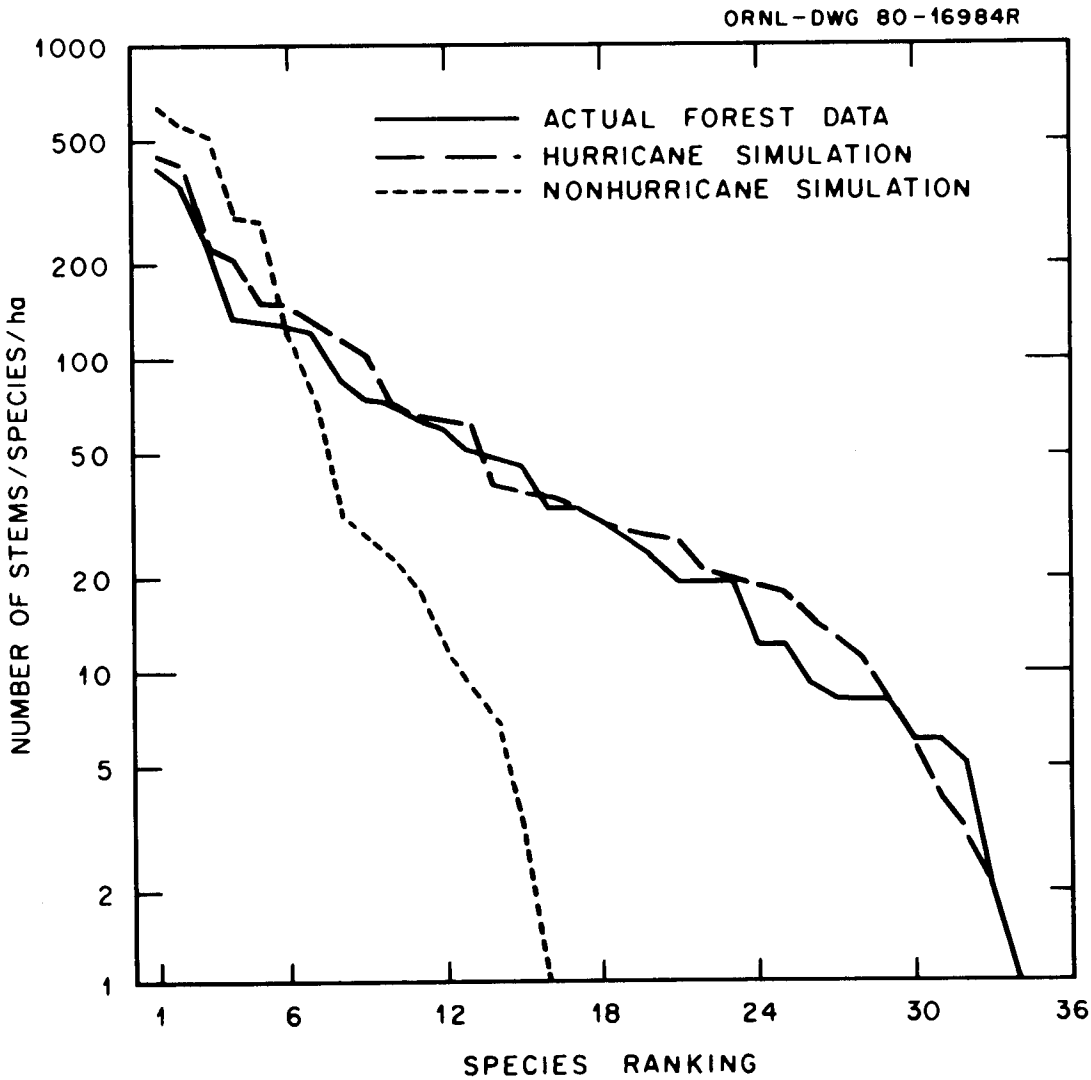

Fig. 6. Dominance-diversity curves for model simulation with and without hurricane effects and tabonuco forest data. Species rank ranges from most abundant (1) to least abundant (36). Species abundance is represented as the total number of stems (above 4 cm dbh) per hectare.

intermediate levels of disturbance than high or low disturbance extremes. Crow and Grigal (1980) identified eight major floristic groupings in the tabonuco forest that correlated well with topographic position and disturbance history.

This general theory and model result also applies to the structural aspects of forest stands affected differentially by disturbance. Forest sites incurring frequent tree-falls commonly have many more trees in lower size-classes than in the upper size-class range. On the other hand, stands less prone to wind-throw or other destruction consequently support fewer stems of larger stature. Hartshorn (1978) explained the low density of large trees in tropical wet forests based on their dynamic nature and frequent gap occurrence. Model behavior and output from hurricane and nonhurricane simulations similarly substantiate these trends in stand density changes with the variation in disturbance.

CHAPTER V

CONCLUSIONS

The FORICO model demonstrates the applicability of employing the functional modeling design of gap models to simulate the forest gap succession of a diverse tropical rain forest. Although the model was adapted from a conceptual approach originating from temperate applied models, the underlying principles of forest growth and development appear to be similar for both temperate and tropical forest systems.

The model duplicated the dynamics of gap formation and replacement process by considering the birth, growth, and death of individual trees on a 1/30-ha stand. Simulations of stand biomass and leaf area values followed the classic successional trend of increasing in early years until reaching and maintaining a steady-state condition. Comparison of average leaf area and stand biomass results from simulation and field observations were remarkably similar. The model also exhibited the ability to predict the stand density and compositional characteristics of the tabonuco forest. Density-diameter distributions from simulated stands significantly correlated with actual forest plots for young and mature aged stands. A correlation of species rank by abundance indicated no significant difference between model results and field observations with respect to the species composition of a mature-state forest.

Comparison of hurricane and nonhurricane simulations indicate that disturbance plays an important role in maintaining the compositional variation and species diversity of the lower montane rain forest in

Puerto Rico. This result substantiates the importance of gap occurrences for the continued persistence of gap-dependent species. It also supports recent evidence of diversity theory showing that diversity increases with disturbance.

One of the potential applications of the FORICO model includes further investigation of the ecological role of disturbance, both natural and man-induced. By varying the frequency and intensity of a perturbation, trends in system diversity, stability, and evolution may be examined. The role and position of key species in the successional dynamics of a forest system can also be evaluated. Simulated introductions of exotic species and superior genetic traits could be studied with regard to the theoretical and practical considerations of species success. Modeling the large-scale effects of rapid deforestation of tropical rain forests may provide a more accurate estimate of the true environmental impact as well as a supplement to management strategies and decisions.

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