To the Graduate Council:

I am submitting herewith a dissertation written by Chengxia You entitled "Population dynamics of Manilkara bidentata (A.DC.) Cher. in the Luquillo Experimental Forest, Puerto Rico." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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and Dean of The Graduate School

POPULATION DYNAMICS OF *Manilkara bidentata* (A.DC.) Cher. IN THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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ABSTRACT

Objectives of this ecological life cycle study are to identify population properties and environmental factors which influence population dynamics of Manilkara bidentata, a primary canopy tree species in the Luquillo Experimental Forest (LEF) of Puerto Rico. Factors which most strongly influence Manilkara population distribution and abundance are: 1) long range seed dispersal (> 100 meters) by bats to favorable habitats, 2) long term (40 yrs) persistence of seedlings in closed canopy forests, and 3) rapid and effective acclimatization of seedlings to increased light following forest disturbances (4x and 24x increase in seedling height growth rates in small and large gaps respectively). All these factors contribute to relatively high survival rates from seedling to sapling size classes. The transition from seedling to sapling size class is the most critical stage in the life cycle. Hurricane disturbance is the most important exogenous event influencing Manilkara population dynamics. Fluctuations of age-classified density, biomass, and nutrient distribution of Manilkara populations are "stamped with the brand" of hurricane cycles. A population matrix simulation model supports interpretations of field data which indicate that one consequence of hurricane disturbance is a reduction of seedling mortality rates. This reduction is probably a

consequence of the release of seedling growth from suppression under forest shade conditions.

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CHAPTER I

INTRODUCTION

This is a study of the population dynamics of Manilkara bidentata (A. DC.) Cher. near the El Verde field station in the Luquillo Experimental Forest (LEF) of Puerto Rico. Manilkara is one of most important tree species in the Tabonuco Forest which is a major forest type in the Subtropical Wet Forest Life Zone in Puerto Rico (Holdridge, 1970; Ewel and Whitmore, 1973). This forest is composed of over one hundred tree species with three obvious tree strata: a discontinuous upper stratum, a second continuous canopy at 20 m, and an understory (Brown, et al. 1983). Previous studies in the Tabonuco Forest indicate that Manilkara bidentata is a primary tree species (sensu Brokaw, 1985) based upon its life form, synusial position, climatic preference, and successional status (Little and Wadsworth, 1964; Smith, 1970). Results of physiological-ecological studies (Odum, Lugo, et al., 1970; Lugo, 1970) also demonstrated that Manilkara bidentata is a primary or "climax" species. Reported densities and importance values indicate that Manilkara bidentata is one of the most important primary canopy tree species in the LEF (Wadsworth, F. H. 1951; Briscoe and Wadsworth, 1970; Wadsworth, R. K. 1970; Smith, 1970; Crow, 1980).

I-1. Objectives

Objectives of this study are:

A. To describe the ecological life cycle of Manilkara bidentata and to investigate demographic characteristics throughout its life cycle in the Tabonuco Forest of the LEF of Puerto Rico.

B. To determine ecological factors and events which have significant influences on the population dynamics of Manilkara bidentata.

C. To develop a projection model for Manilkara bidentata population dynamics. This model may serve as one component of a comprehensive model of the LEF.

I-2. Studies of tree population dynamics

Studies of tree population dynamics are a foundation for understanding processes of forest dynamics, whether from a succession, regeneration, disturbance ecology, species evolution, or forest management perspective (Stearns, 1949; Davis, 1966; Holland, 1969; Henry and Swan, 1974; Harper and White, 1974; Harper, 1977). Comprehensive studies which attempt to incorporate all components of the life cycle of tree species are very limited, even though the importance of this subject was emphasized in Harper's very influential publication, Population Biology of Plants

(1977). Perhaps the reason for this limitation lies in the difficulty of dealing with the long ecological time scale of tree life spans. As a result, most studies of population dynamics of plant species have been focused on herbaceous species (Greig-Smith, 1957; Selman, 1970; Sharitz and McCormick, 1972; Holt, 1972; Naylor, 1972; Mack, 1976). Studies of temperate tree population dynamics provide an understanding of the structural patterns and dynamics of temperate forests, although many are limited to partial life cycles (Ghent, 1958; Spurr, 1964; Peterken, 1966; Davis, 1966; Holland, 1969; Hett and Loucks, 1968; Blackburn and Tueller, 1970; Auclair and Cottam, 1971; Heinselman, 1971; Hett, 1971; Henry and Swan, 1974; Spring et al., 1974; Harper, 1977).

I-3. Studies of tropical tree population dynamics

Beginning in the 1970s, studies on tropical tree population dynamics became more abundant (Bannister, 1970; Lebron, 1977; Muniz-Melendez, 1978; Silander, 1979; Sastre-DeJesus, 1979; Nieves, 1979; Sarukhan, 1978; Wyatt-Smith, 1987; Swaine, Lieberman, et al., 1987; Schupp, 1990). However, very little attention has been paid to flowering and fruiting, seed production, and seedling and sapling recruitment. Most studies focus on later life cycle stages ignoring critical ecological events which influenced

distribution and abundance of terminal life cycle stages. The 1984 symposium entitled "The Dynamics of Tree Populations in Tropical Forest" (Swaine and Lieberman, 1987) is a landmark contribution to our understanding of tree population dynamics in tropical forests. Comparisons of periodic demographic data of tree populations in permanent plots from three continents (Manokaran and Kochummen, 1987; Okali and Ola-Adams, 1987; Swaine, Hall, et al., 1987; Lieberman and Lieberman, 1987) provides a general picture of tropical tree population dynamics. These forests were considered to be in a dynamic steady state. It is assumed that species mortality is balanced by recruitment and forest productivity is approaching carrying capacity.

It is generally believed that tropical rain forests have high species diversities as well as high ecological and functional diversities. Most tropical forest ecosystems may never stay in a state of equilibrium such as do those reported in the 1984 symposium. For example, in Puerto Rico, on average, hurricanes pass the island every 10 years and produce significant damage once every 62 years (Wadsworth, 1951; Wadsworth and Englerth, 1959; Scatena, 1989). One question being addressed in the Long Term Ecological Research (LTER) project in the LEF of Puerto Rico is how forest ecosystems respond to such periodic disturbances. The behavior of a forest ecosystem depends on behaviors of its components, especially of primary tree

species. Are ecological life cycles of primary species adapted to hurricane disturbance? Results of this study indicate the answer to this hypothesis is, "yes." A question that remains is, "how?"

I-4. Studies of tree population dynamics in the LEF

The Tabonuco Forest in the LEF of Puerto Rico may be the most intensively studied montane tropical rain forest of in the world. McCormick (in press) and his students have conducted population studies of six woody species in this forest since 1964, trying to gain insight into forest dynamics by understanding life cycle processes of key species. Species which have been studied include: a palm, Prestoea montana (R. Grah.) Nichols. (= Euterpe globosa) (Bannister, 1970); a shrub, Palicourea riparia Benth. (Lebron, 1977); and canopy tree species, Inga vera (Willd.) subsp. vera (Muniz-Melendez 1978), Cecropia peltata L. (Silander, 1979), Buchenavia capitata (Vahl) Eichl. (Sastre-DeJesus, 1979). An additional study of Didymopanax morototoni (Aubl.) Decne. & Planch. was conducted by Nieves (1979). Both Didymopanax morototoni and Cecropia peltata are pioneer or early successional species, whereas Inga vera and Buchenavia capitata have characteristics more similar to those of primary or late successional species. Studies of individual species population dynamics have provided a basis

to understand and predict forest dynamics. Based on past studies of tree population dynamics in the LEF, McCormick (in press) developed a conceptual model which included five life stages, 16 ecological-biological processes, and three regulators (Figure 1)[1]. This model has been used as an organizational framework for research conducted in this study.

I-5. Past studies of Manilkara bidentata

Manilkara bidentata exhibited a trend of increasing dominance following forest disturbance by a severe hurricane in 1932. It ranked 5th in density and 10th in basal-area among tree species (only for DBH > 4 cm) in the Tabonuco Forest by 1946 (Briscoe and Wadsworth, 1970). It increased in dominance from 1946 to 1976: raising its proportion of density from 9.0% to 14.5% and its proportion of basal-area from 5.6% to 10.7% (Crow, 1980).

In the Rain Forest Project of the U.S. Atomic Energy Commission (Odum and Pigeon, 1970), several investigations were conducted on many aspects of Manilkara bidentata. Significant reports are identified in Table 1. Few of these investigations were concerned with the ecological life cycle. Almost nothing about the ecological life cycle of

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[1] All figures and tables are displayed in APPENDIX.

Manilkara bidentata was found in other reports. Therefore, reproductive strategies, mortality and recruitment characteristics of early life stages (which may be the most critical life stages in population dynamics of tropical tree species), and population responses to disturbances are virtually unknown.

I-6. Period of field studies

Field studies were conducted from September of 1986 to June of 1989. Data were collected in September of 1986, January through March of 1987, October of 1987, March of 1988, and May through June of 1989. Hurricane Hugo struck Puerto Rico on September 19, 1989. The Tabonuco Forest suffered considerable damage (Scatena and Lugo, in preparation), 57 years after the severe hurricane in 1932. Brown et al. (1983) estimated that it requires approximately 40 years for the Tabonuco Forest to recover structurally from severe damage by hurricanes. Therefore, it may be assumed that the Tabonuco Forest was in a dynamic equilibrium (pre-hurricane) state during the period of field studies. Studies of pre-hurricane population dynamics provide a baseline against which to compare post-hurricane population dynamics.

I-7. Data analysis

Data are analyzed by using STATGRAPHICS (STSC, Inc. 1985). The major statistic reference was Applied Regression Analysis and Other Multivariable Methods written by Kleinbaum, Kupper, and Muller (1988).

CHAPTER II

THE SPECIES

II-1. Taxonomy and description

Manilkara bidentata (A. DC.) Cher. belongs to the Sapotaceae (Sapodilla family). Its botanical synonym, Manilkara nitida (Sesse and Moc.) Dubard, was used widely before the 1960s. Its common spanish name is AUSUBO and the commercial name is BALATA. Throughout this document the short name Manilkara is used to represent the full name Manilkara bidentata. Manilkara is one of the most desirable commercial timber species in Puerto Rico. The wood is very strong, hard and heavy. Specific gravity averages 0.82 (Little and Wadsworth, 1964).

Manilkara is evergreen. Mature trees are characterized by a dense crown of horizontal branches with layered foliage. Alternate leaves with many faint, parallel veins are large (9 - 25 cm long and 4 - 11 cm broad), elliptic and dark green. White milky latexes appear in droplets from cut leaves and incisions in the trunk and stems. Large straight trunks have broad, rounded buttresses spreading at the base. In Puerto Rico, Manilkara may attain a height of 30 m and a diameter of 1.3 m (Little and Wadsworth, 1964).

There are 3 - 10 small whitish fragrant bell-shaped flowers (corolla about 7 mm in diameter) in lateral clusters at leaf bases. After flowering, most fruits wither and usually only one or two remain to ripen. Smooth, round to oval berries are approximately 2.5 - 3.2 cm long and have an edible sweet pulp when ripe. Each fruit usually contains a single shiny black seed 1.8 - 2.5 cm long, 1 - 1.5 cm broad, and 0.7 - 0.9 cm thick. It is extremely difficult to observe these scattered flowers and fruits from ground level.

II-2. Geographic distribution of the species

Manilkara can be found throughout the West Indies. It also ranges from Mexico through Panama to northern South America, including the Guianas, Venezuela, and northern Brazil and Peru (Little and Wadsworth, 1964; Murphy, 1970).

II-3. Ecological relationships

Manilkara is a constituent of several different forest types (Table 2), attaining its best development in the Lower Mountain Rain Forest, the Lowland Rain Forest (Beard, 1944, 1946a, 1946b, 1949, 1955), or in the Subtropical Wet Forest Life Zone (Holdridge, 1970; Ewel and Whitmore, 1973). Throughout the West Indies, it occurs in areas where

rainfall varies from 1500-4000 mm/yr (Table 2). In South America, it is possible that many areas receive in excess of that amount. All sites are frost-free.

Physiographically, Manilkara is found on slopes, on plateaus, and in coves. In Puerto Rico it attains its best development on alluvial plains and it also occurs in the moist coastal and limestone forests (Little and Wadsworth, 1964). Altitude distribution ranges from near sea level to 600 m. In Trinidad it is common on hills and in Surinam it is common along river banks (Schulz, 1960). Manilkara is well adapted to acid and clay soils derived in situ or deposited by alluvial or colluvial processes. In Trinidad it thrives on a variety of soils ranging from clays to sands, including rocky soils, and on several different geologic formations (Marshall, 1939).

In the Tabonuco Forest, Manilkara is mainly associated with Dacryodes excelsa Vahl, Sloanea berteriana Choisy and Buchenavia capitata (Beard, 1944, 1946a, 1946b, 1949, 1955), which dominate the upper stratum of the Tabonuco Forest. Species assemblages produced by using statistical clustering techniques indicate that it occurs most often on upper slopes with Buchenavia capitata (Crow and Grigal, 1979). Manilkara is very shade tolerant, especially during seedling and sapling stages. It grows slowly in forest shade (Murphy, 1970; Crow, 1980).

CHAPTER III

THE STUDY AREA

The study area was described in great detail in several extensive research projects including "The Rain Forest Project " (Odum and Pigeon, 1970) and "US Man and the Biosphere (MAB) Program" (Brown et al., 1983).

III-1. Geographic location

Puerto Rico, an eastern and small island of the Greater Antilles island chain, is located within the "hurricane belt" (Anthes, 1982, Figure 2). The Luquillo Mountains, with a highest peak 1075 m above sea level, rise at the northeastern corner of Puerto Rico. The Luquillo Experimental Forest, formerly called the Caribbean National Forest, occupies most of the area of the Luquillo Mountains. The study area is situated in the northwestern section of the Luquillo Mountains (Figure 3) at an elevation ranging from 350 m to 500 m. The El Verde field station is located at 18°19'N, 65°45'W.

III-2. Macroclimate of the study area

Located in the tropical zone and rising into the prevailing trade winds, most areas of the Luquillo Mountains are located in the Subtropical Wet Forest Life Zone or in the Tropical Moist Forest Life Zone (Holdridge, 1967). McDowell and Estrada-Pinto (1988) calculated a mean annual precipitation of 3561 mm from records kept between 1975 to 1986 at the El Verde station. There is distinct seasonality in rainfall in this area. A dry period extending from January or February to April was reported by Smith (1970), Lebron (1977), Silander (1979), and Sastre-DeJesus (1979). Brown, et al. (1983) described water as a possible stressor on LEF ecosystems. A high peak of rainfall usually occurs in May. Excessive water during the peak rain period may have a negative influence on tree growth.

Annual temperature was calculated as 21°C - 25°C at El Verde by different researchers (Odum, Drewry, et al. 1970; Silander, 1979). Annual variation in mean monthly temperatures is small, approximately 3.5°C; mean daily fluctuation is greater, up to 7.9°C (Silander, 1979).

Odum, Drewry, et al (1970) reported typical total solar insolation to be 383 g-cal/cm^2/day, with a relative humidity of 91%, an absolute humidity of 18.7 g/m^3, a pan evaporation of 1.84 mm/day, and an average wind travel of

2.6 mph above the forest canopy at the El Verde field station.

III-3. Microenvironment of Manilkara populations

Most Manilkara seedlings, saplings and small trees developed in forest shade prior to Hurricane Hugo. According to results of "The Rain Forest Project," plants 13 m or more in height composed about 70% of the closed canopy (Desmarais and Vazquez, 1970). Microclimate near the forest floor was relatively stable (Odum, Drewry, et al 1970): diurnal temperature ranged from 21°C to 24°C. Daily insolation was about 20 g-cal/cm²/day, 3% to 8% of that above the canopy. The diurnal range of relative humidity was 89 to 97%. Pan evaporation was 9% of that above the forest canopy. Winds were 0.74 mph (28% of that above the canopy).

Treefall gaps can be expected to provide different microenvironments from those in forest shade. Scatena and Lugo (in preparation) reported that large gaps (canopy openings > 250 m²) are rare in the Tabonuco Forest except following hurricanes. Treefalls usually create small gaps (60 - 100 m² of canopy openings). Within gaps, significantly more light (compared to in forest shade) becomes available to plants but other environmental parameters are only slightly different from those under

closed canopy (Lebron, 1977; Silander 1979). Large canopy openings created by hurricanes provide a considerably different microenvironment for Manilkara seedlings and young trees, but there were no data available for this case in the Tabonuco Forest prior to Hurricane Hugo.

Because of a completely faulted and folded terrain (Seiders, 1971), the study area is composed of many valleys, ridges, and narrow slopes. Large boulders cover as much as 60% of the surface (Edmisten, 1970). Forest-floor micro topography is very complex and micro habitats for seedlings are very diverse.

According to Edmisten (1970), Soriano-Ressy et al. (1970), and Brown, et al. (1983), soils of the El Verde area are highly variable. In general the soil parent material was marine-deposited basalt and tuff breccia. The most common soils are associated with the Los Guineos clays and clay loams. Small rocks (up to 0.5 m in diameter) are found throughout the soil profile. Despite a composition of as much as 42% - 65% clay, the soil has an excellent crumbly structure that results in good internal drainage. Selected physical and chemical properties of the soil in the study area are listed in Tables 3 and 4.

CHAPTER IV

PHENOLOGY AND REPRODUCTIVE SUCCESS

IV-1. Phenology

Phenology is the study of the seasonal timing of life cycle events. For plants the seasonal timing of such events as leaf production, leaf fall, flowering, and fruit production are critical to survival and reproduction (Rathcke and Lacey 1985). Unlike most tree species in temperate zones, some tropical trees may have significant variations in phenological phenomena (Croat, 1975; Rathcke and Lacey, 1985), which mask distinct seasonal rhythms (Putz, 1979). Manilkara was reported to exhibit variable timing of occurrence of peak flowers and fruit drop on several different islands in the West Indians (Marshall, 1939; Estrada-Pinto, 1970).

Methods

Within the study area, 30 mature canopy trees were selected for phenological observations. These trees were tagged and phenological data were collected in September of 1986; January, February, March, and October of 1987; March of 1988; and May of 1989. Frequency of trees with flowers and/or fruits is expressed as a percent of the 30 trees.

Timing of leaf production and loss was also recorded. Flowering durations (the time from starting date to dropping date) were recorded to 50 position-recorded flowers on branches of tree No.7 which was conveniently designated beside a canopy observation tower. Fruiting durations were recorded for 20 marked fruits on tree No.7. Fruiting of four other trees were observed by using binoculars from the forest floor. Time required for fruit development was also recorded.

Preliminary observations revealed that flowering takes place on only a part of a tree's branches. The solar orientation of branches with flowers and/or fruits was recorded on 9 trees in September of 1986 and February of 1987 to determine if there is a correlation between reproduction and sunlight exposure.

Results

Manilkara, as a literal evergreen species, showed no evidence of a seasonal flush in leaf production or leaf loss. In observations from January to March of 1987, 50% of the 30 marked trees were either flowering, fruiting, or both (Table 5). Percent flowering or fruiting in October 1987, March 1988, and June 1989 were 50%, 57%, and 50%, respectively. A light fruit drop was found at all observation periods. There was no apparent rhythm in sexual reproduction during the study period.

Although flowering of some trees may last throughout the year, a single flower lasts for approximately 5 days. A single fruit develops over approximately 11 months.

Earlier observations that flowers occurred on only a portion of branches or on a certain branch during a season were confirmed. Records of solar orientation of branches with flowers and/or fruits are presented in Table 6. There was no relationship between reproductive branches and orientation to sunlight. However, most flowering branches were at least partially exposed to direct sunlight.

IV-2. Annual reproductive potential and success

Asexual reproduction of Manilkara is negligible. Only two root-sprouts were found in the study area during the entire study period. Sexual reproduction is primarily responsible for the abundance of seedling populations of Manilkara. Investigations of reproduction of Manilkara trees included annual reproductive potential and actual reproductive performance in 1987.

Annual reproductive potential is defined the occurrence of the average number of flower-buds per square meter of forest floor area, which represents maximum seed potential production per season. However, many flower-buds failed to bloom and most fruits aborted before maturity. The number of successful ripe fruits (one fruit has one

seed) among all flower-buds was expressed as the actual reproductive performance. A reproductive-twig is defined as a twig with at least one flower-bud, flower or fruit. In the Tabonuco Forest only a portion of the canopy-twigs are reproductively active each season. Methods used to estimate annual reproductive potential and actual reproductive performance are described as follows.

Methods

Crown-size (crown projection area in m^2) per square meter of forest-floor was measured for canopy trees in permanent transects. The average number of canopy-twigs per square meter crown-size was measured for six harvested trees. Canopy-twigs per square meter forest floor area were calculated by converting crown cover to forest floor area.

The number of reproductive-twigs was counted for 11 trees, 6 of which were harvested. For each tree, the average reproductive-twigs per square meter crown was calculated by dividing the number of reproductive-twigs by crown-size (m^2) of the tree. The average canopy-twigs (including non-reproductive-twigs) per square meter crown was calculated by dividing the total number of canopy-twigs by crown-size for the 6 harvested tree. The ratio (%) of reproductive-twigs to canopy twigs per square meter was calculated by dividing reproductive-twigs/m^2 by canopy-twigs/m^2 crown-size. Then reproductive-twigs per square

meter forest floor area was calculated by multiplying the above ratio times canopy-twigs per square meter of forest floor area.

A total of 274 reproductive-twigs were collected from 15 trees (including the six harvested trees). Samples included not only reproductive-twigs with flower-buds, blooming flowers and/or fruits, but also old twigs with scars of flower-buds, flowers or ripe fruits. Numbers of flower- buds, flowers and ripe fruits (or scars of equivalent categories) were counted for each inflorescence and summed for each twig. The average number of flower-buds, flowers, and ripe fruits per reproductive-twig was then calculated.

Annual reproductive potential in the forest (flower-buds per square meter forest floor area) was estimated by multiplying the average number of flower-buds per reproductive-twig times reproductive-twigs per square meter of forest floor area. Actual reproductive performance in the forest (ripe fruits or seeds per square meter forest floor area) was estimated by multiplying the average number of ripe fruits per reproductive-twig times reproductive-twigs per square meter of forest floor area. Percentages of flowers and ripe fruits per number of flower-buds were also calculated.

Results

There were 0.1244 m^2 of Manilkara crown per square meter of forest floor area. Average number of canopy-twigs per square meter of crown was 53/m^2. There were approximately 6.6 canopy-twigs/m^2 forest floor area.

Numbers of reproductive-twigs were variable among sample trees (Table 7, n = 11, CV = 1.14). The average ratio of reproductive-twigs to canopy-twigs was 1.8%. There was an average of 0.12 reproductive-twigs per square meter of forest floor area.

There was an average of 7.9 flower-buds per square meter of forest floor area (Table 8). Among 274 collected reproductive-twigs, 93 twigs had ripe fruits or scars of ripe fruits and 109 twigs had flowers or flower scars. Results indicate that 25% of the flower-buds bloomed and only 4% of the flower-buds successfully developed into ripe fruits (Table 8). An average of 0.3 seeds/m^2 were produced in the forest in 1987 (Table 8).

IV-3. Discussion

According to different researchers, Manilkara was reported to have different phenological patterns in various locations of the West Indies. In Puerto Rico, based on his observations at El Verde from 1963 to 1967, Estrada-Pinto (1970) reported that flowering of Manilkara occurred mainly

from May through August. Flowers also occasionally occurred in late autumn. Fruits developed through the autumn. Principal fruit drop time was winter and early spring. In Trinidad Manilkara flowered at the beginning of the dry season, January to February, and fruits were ripe by April-May (Marshall 1939). In both regions, good flowering and fruiting occurred at intervals of 3-4 years.

In this study, high variations in flowering phenology were found among marked Manilkara trees at El Verde. There was no evidence of flowering synchrony. Some trees (e.g. No.3, No.5 and No.7) flowered throughout the year and flowers, young fruits and ripe fruits were present on the same branches. Some trees (e.g. No.8, No.12 and No.29) had no sexual reproductive activity during the entire study period. Percentages of trees with flowers and fruits was 50% - 60% at any time during the study period.

A fruit drop peak was not found in this study. However, fruit dispersal by animals might conceal a minor peak. During the study period, fruit production was apparently sparse. However, it is assumed that there was a high production of seeds in 1986. In that year newly established seedlings were found under 73% of parent trees (Table 5) and the new seedling population was large in September. The fruit drop peak was estimated to have occurred in June or July of 1986. After 1986, individual trees flowered sporadically and seed production was light

and variable throughout the year, although 50% - 60% of marked trees had reproductive activity over three years.

In this study, reproduction of Manilkara was analyzed by using quantitative methods to determine survival from flower-buds to ripe fruits in the 1987 season. Data were collected directly from parent trees instead of using screen baskets to collect fruits (Estrada-Pinto, 1970). Bats are a major dispersal agent for Manilkara seeds (the next chapter POLLINATION AND DISPERSAL). Seed dropping patterns and amounts noted were highly related to bat habitats and behavior. In addition Manilkara populations have a clumped distribution pattern (page 73). Therefore, direct measurements are preferable to indirect estimates based upon screen baskets.

According to earlier estimates, Manilkara's actual reproductive performance in early 1987 should have yielded an average of 0.3 seeds/m^2 from a cohort of flower-buds. Estrada-Pinto (1970) reported very similar fruit production (0.8/m^2/yr) at El Verde. The difference may be due to three factors: 1) variations in phenological patterns year to year and in the occurrence of reproductive-twigs among trees (coefficient of variation was 1.14 in 1987's samples, see Table 7.) must lead to variation in seed production; 2) as discussed above, Manilkara's clumped distribution and seed dispersal by bats may lead to errors when a limited number of screen baskets (method of Estrada-Pinto) are used to

collect seeds; and 3) it is not clear whether the 0.8 fruit/m^2 was ripe fruit. Many fruits abort before becoming mature. In spite of these sources of variability, the two independent estimates are very similar.

Sexual reproduction in Manilkara occurs only in canopy trees. When sample trees were harvested in February 1987, tree M-23 (with DBH = 18.6 cm and height = 18.5 m) was found to be in its first year flowering. Its crown had just emerged at the top of canopy. Only two reproductive-twigs with blooming flowers were found. Flower scars were not found on any other twigs.

It was observed that only 50 - 60% of canopy trees produced flowers in one season, and among these trees only a portion of the branches had flowers and/or fruits. In 1987, the annual reproductive potential was very different from actual reproductive performance. There were approximately 8 emerged flower-buds/m^2, but only 0.3 seeds/m^2 were produced due to abortion of flower-buds, flowers, and young fruits. Actual reproductive success is only 4% of the reproductive potential. Abortion may be caused by microenvironmental stressors, such as inadequate water supply in the dry period, inadequate nutrients available due to competition with other plants, or grazing by herbivores. Absence of seasonal rhythms suggests that phenological and reproductive patterns may be influenced more by microenvironment conditions than by macroclimate.

Compared to pioneer tree species such as Cecropia peltata, Manilkara bidentata has very low seed production. Of all tree species in the Tabonuco Forest at El Verde, Cecropia may represent the r-selected extreme and Manilkara may represent the K-selected extreme in terms of the r- and K- selection continuum concept (Silvertown, 1982).

Continuous seed production, however light, might favor seed dispersal which depends upon animal vectors of low population density. Continuous seed production also encourages animal vectors with a continuous food resource. Continuous seed production might also assure propagule availability at a time when temporal and spatial microenvironmental conditions favor seedling establishment.

CHAPTER V

POLLINATION AND DISPERSAL

V-1. Methods

Possible pollinators of Manilkara were observed for tree No.7 which was located next to an observation tower. From the forest floor pollinators were also observed for trees No.1, 3, 5, and 17. On five cloudless days in February 1987 and March 1988, observations over five minute periods were conducted at twenty-five minute intervals from 6 am to 7:30 pm.

Fruit dispersal vectors were also observed for trees No.7, 5, and 4. Positions of 9 ripe fruits (yellow color) on tree No.7 and of 10 ripe fruits on trees No.4 and 5 (5 fruits each tree) were recorded on January 26 1987. Presence of these fruits on parent trees or on the forest floor under parent trees was checked daily for 15 days. Animal tooth-marks were identified on fruits found under parent trees.

In order to estimate the frequency of fruit dispersal by animals, an effort was made to collect fruits on the forest floor in the entire study area. Animal tooth-marks on these fruits were also identified.

Gravity and wind are additional dispersal vectors.

Dispersal range by gravity and wind was investigated in 6 transects under 3 parent trees in September 1986. Parent trees were selected on slopes without steep topographic changes. Under each parent tree, 2 transects were established radiating from the base of the tree, in which one was towards the up-slope and the other was towards the down-slope. Each transect was one meter in width and was divided into one square meter plots extending outward from the base of the tree. Seedling density in each plot was measured. Density distribution pattern of seedlings under parent trees was used to indicate the seed dispersal pattern by gravity and wind.

V-2. Results

Bees were observed to be the major pollinators. They were present during 90% of the observations. Other tiny insects were found within flowers and they may also play a role in pollination.

Two significant dispersal agents were observed: 1) bats and 2) gravity combined with other physical factors. During an observation from the canopy level tower at 8:25 pm on 1 February 1987, a bat flew around the crown of tree No.7 and remained on a twig with ripe fruits. Most ripe fruits collected under parent trees and in other places on the forest floor had been sucked by bats and had distinct bat-

tooth-marks on fruit skins. Over the observation period, all position-recorded fruits disappeared in the evening or at night. Of 9 ripe fruits on tree No.7, none were found under the tree. They are assumed to have been removed by bats. Of 10 position-recorded fruits on trees No.4 and 5, one fruit with bat-tooth-marks was found under tree No.4 and one fruit with bat-tooth-marks and one seed without fruit pulp was found under tree No.5. All other fruits were missing.

During reconnaissance trips throughout the Tabonuco Forest at El Verde, a total of 84 ripe fruits were collected. Among the 84 fruits 80 (95%) had been bitten by bats. Nineteen out of 84 (23%) were found under trees which could have been parent trees. There were an additional 28 seeds and some fruit skins (with bat-tooth-marks) found within an area of less than two square meters under one big tree. It appears that some bat(s) ate fruits and dropped seeds from the same location on a parent tree over a period of several days.

Most seedlings were distributed within a radius of 10 m around the tree base (Figure 4). Seedling density decreased with increasing distance from the tree. In some locations where trees were on steep slopes or close to drainage pathways, fruits rolled or were transported by water 20 m - 30 m away from parent trees.

V-3. Discussion

Manilkara's flowers are fragrant and attract insects but they are probably too small to attract birds. Insects, especially bees, play a major role in the pollination of this tree species. Although flowers exhibit none of the typical adaptations to wind pollination, wind pollination can not be ruled out.

A large number of young seedlings are distributed beyond the range of gravity dispersal. Some seedlings were found on ridge tops where there were no parent trees. It was assumed that Manilkara's seeds were carried there by animals. Many Manilkara seedlings were also found in a mahogany plantation, devoid of parent trees. It is not likely that rats transported seeds across a road for such a long distance as 50 - 500 m from the Tabonuco Forest to the plantation site (rats have a home range of 20 m, see Weinbren et al., 1970). It most probable that Manilkara seeds were dispersed by bats. This is further supported by the observation that 95% of ripe fruits were dispersed by bats (e.g. this percentage contained bat-tooth-marks). Birds may also play a minor role in Manilkara's seed dispersal (unpublished documents from the Institute of Tropical Forestry, Puerto Rico), but in this study there is no evidence to support this hypothesis. Frugivore birds large enough to take Manilkara fruits were not observed to be

active in the evening or at night, the period when ripe fruits are removed by animal vectors.

Four species of frugivore bat, Artibeus jamaicensis, Stenoderma rufum, Erophylla sezekorni, and Brachyphylla cavernarum, have been reported at El Verde, of which A. jamaicensis is most abundant (Tamsitt and Valdivieso, 1970; Willig and Bauman, 1984). S. rufum may be a major consumer of Manilkara fruits. Digestive tracts of 23% of captured S. rufum and of 3% of captured A. jamaicensis contained Manilkara fruit pulp (Willig, in press). S. rufum is endemic to Puerto Rico and nearby islands (Willig, in press) and was generally reported to be rare and to have seasonal fluctuations of abundance (Tamsitt and Valdivieso, 1970; Willig, in press).

Bats are attracted by the sweet pulp of Manilkara fruits, but there is no evidence that bats eat or swallow the seeds. Frugivore bats may prefer to stay on large trees which have sparse crowns. Several patches of numerous Manilkara seedlings were also found under large trees with sparse crowns such as Buchenavia capitata. Crow and Grigal (1979) reported that Manilkara frequently occurred on upper slopes along with Buchenavia. This association appears to be related to seed dispersal by bats. The advantages of seed dispersal to relatively sparse canopy cover locations are obvious: seedlings survive and grow better under higher light conditions. This dispersal pattern adds to the

evenness component of the species diversity equation, and thereby contributes to the rich species diversity of this forest.

Gravity and normal wind probably can not disperse seeds (fruits) further than 10 m from parent trees. Seedlings survival under parent trees is very poor (page 78), probably due to predation and competition with parent trees (Janzen, 1970). Bats may provide the means for seedlings to escape predators, to minimize intra- specific competition, (Janzen, 1970) and to reach habitats with better light conditions.

Manilkara flowers sporadically and fruit production is light and continuous throughout the year. This may benefit both Manilkara and bats. Bats can gain some food from Manilkara throughout the year. Manilkara seedlings grow better, and in turn, may have higher recruitment rates in habitats with relatively sparse canopy cover (page 54). With the assistance of bats, it may not be necessary for Manilkara to have a heavy reproductive effort in order to achieve successful regeneration. It is clear that seed dispersal by bats is one of the most important factors influencing Manilkara's distribution, abundance, and population recruitment in the Tabonuco Forest.

CHAPTER VI

GERMINATION AND SEEDLING ESTABLISHMENT

Germination is viewed (in this study) as a starting point in the life cycle, a point when an individual plant relinquishes the protection of the seed coat and interacts independently with the environment in which it lives. Each plant species has evolved a pattern of timing, synchrony, and duration required for germination under the influence of abiotic and biotic selective factors (Rathcke and Lacey, 1985). Located in a tropical area, the Tabonuco Forest experiences considerably less seasonality of macroclimate than temperate forests. If the stability of microenvironments in the Tabonuco Forest is similar to that in tropical forests of Malaysia, seeds do not necessarily enter dormancy and they germinate throughout the year (Ng, 1978).

VI-1. Methods

Germination

In September 1986, a total of 75 Manilkara seeds were collected from the forest and brought to the ecology laboratory at the University of Tennessee at Knoxville (UTK). Seeds were sown in a terrarium. Temperature,

relative humidity, and solar radiation in the terrarium were controlled (21°- 23°C, 85% -90%, and less than 25 cal/cm²/day). These conditions are similar to those in the Tabonuco Forest at El Verde. Time of hypocotyl emergence was recorded and results were expressed as percent germination.

In March 1987, another cohort of 53 seeds was transported from El Verde to UTK. They had been collected from fruits that bats had eaten. They were sown under the same conditions as above and percent germination was determined.

Percent seed germination was also estimated under natural conditions in the Tabonuco Forest. In September 1986, 12 one square meter plots were established under 3 parent trees (4 plots under each tree). Newly established seedlings in all plots were counted. Seeds that had failed to germinate were collected. Percent germination was expressed as a percent of newly established seedlings relative to the sum of those seedlings and non-viable seeds.

Seedling establishment

Seedling establishment was observed in the forest in September 1986. Initial morphology of seedlings (sensu Ng, 1978) was observed. Height of hypocotyls (initial height of seedlings) was measured for 116 newly germinated seedlings before roots were established in the soil. Surface area of

the two cotyledons (for each seedling) was measured for 30 seedlings using a LI-3050A Area Meter (LI-COR, Inc., P.O.Box 4425, Lincoln Nebraska 60504 USA). Root length and development were also recorded.

To examine the survival potential of seedlings before they are established, 30 recently germinated seedlings were put on dry litter in forest shade with roots covered by one piece of leaf litter for 10 days in February 1987. These seedlings were then transplanted into two plots. They were inventoried 3, 7, 14, and 20 days after transplantation to determine survival.

VI-2. Results

Germination

Manilkara seeds germinated immediately after fruit flesh decay was complete. From field observations fruit flesh decay required approximately one month. In the germination experiment in 1986, 40 - 45 days were required for all seeds to germinate (Table 9). In the germination experiment in 1987, three seedlings emerged 28 days after seed sowing. The peak of seedling emergence occurred 35 - 42 days after seed sowing. None of the ungerminated seeds were viable two months after the sowing dates. Most of them were apparently destroyed by fungi or other pathogens.

At the laboratory at UTK, 7 out of 75 (9%) seeds sown

in September 1986 and 22 out of 53 (42%) seeds sown in March 1987 germinated (Table 9). Under parent trees in the Tabonuco Forest, a total of 552 newly established seedlings (probably germinated by August and September 1986) and 625 non-viable seeds were found in 12 plots. Percent germination in the field was 47%.

Seedling establishment.

Manilkara seedlings exhibited typical epigeal germination. Cotyledons started turning green as soon as the seed shell cracked open. Average surface area of the cotyledon was 8.2 cm^2 (SD=0.9, n=30). Average hypocotyl height was 8 cm (SD=1.6, n=116). There was no epicotyl. The primary root extended as long as 10 cm in the litter layer. Many seedlings developed second order roots and root hairs on primary roots before roots penetrated the soil. None of the 30 seedlings that were put on dry litter in forest shade died during the first 10 days. None of them died during the first 20 days after subsequent transplantation.

VI-3. Discussion

Unfortunately, there were never enough seeds available at any time to conduct additional experiments, such as examining the relation of germination to light conditions or

duration of seed viability. Because of the limited supply of seeds, an indirect method was used to estimate percent germination in the forest. This method may have produced an over-estimation of percent germination. It was possible to miss some non-viable seeds while searching for them in litter. Also rapid decomposition in the forest may have destroyed some non-viable seeds, especially some seeds in immature fruits. Therefore, the under-estimation of non-viable seeds could lead to an over-estimation of percent germination.

An interesting aspect of seed germination is that there is a high percent of germination of seeds which are dispersed by bats. All of the 53 seeds collected in March 1987 were bat-dispersed. The percent germination (42%) was considerably higher than that of seeds collected under parent trees (9%). Seeds collected under parent trees might be either undeveloped or severely infected by pathogens during decay of fruit flesh. It is apparent that bats can identify ripe fruits very well and therefore unconsciously select good seeds from parent trees. As the actual reproductive performance was defined on the basis of ripe fruits (page 17), percent germination estimated from bat-dispersed ripe seeds (42%) should be the most useful and appropriate ratio.

Ng (1978) defined germination within 12 weeks as "rapid germination." Using this definition, Manilkara seeds

did not exhibit dormancy. All viable seeds germinated within 7 weeks. Rapid germination should reduce exposure to predation by insects and pathogens.

Manilkara seeds are approximately 1.8 - 2.5 cm long, 1 - 1.5 cm broad, and 0.7 - 0.9 cm thick. Cotyledons have an area of approximately 8 cm^2 and are as thin as true leaves. Manilkara cotyledons were recorded to persist for over three years before true leaves developed (page 51). The function of cotyledons is not only the storage of energy and nutrients. They also serve as photosynthetic organs immediately after germination. Seedlings appear to be unusually dependent upon cotyledon photosynthetic products for survival. Because most viable seeds are dispersed by bats, many have an opportunity to reach areas where photosynthetic cotyledons have sufficient light to produce energy needed during establishment. Morphological and functional characteristics of cotyledons are probably the reason that young seedlings of Manilkara have such high survival (page 83).

Epigeal seedlings of Manilkara have an average initial height of 8 cm. Many seedling hypocotyls reached 12 cm. The 2 - 2.5 mm thick hypocotyl, supported by a vigorous root system, is strong enough to avoid burial by subsequent litter fall. Another advantage of Manilkara's robust seedlings is that they may not be easily overwhelmed by fungal infection under dark and humid conditions on the

forest floor (e.g. Ng, 1978). In studies of establishment strategies of 180 tree species in tropical rain forests of Malaysia, Ng (1978) concluded that the mainstream of evolution appears to favor large seeds and seedlings and germination that is rapid and epigeal.

In summary, the success of seedling establishment of Manilkara may be attributed to the following factors: 1) light and continuous production of bat-dispersed seeds throughout the year; 2) rapid germination of non-dormant seeds; 3) large epigeal seedlings with persistent photosynthetic cotyledons; 4) rapid development of seedling roots which withstand desiccation; and 5) seed dispersal by bats to relatively high light microhabitats.

CHAPTER VII

AGE ESTIMATION

VII-1. Methods

Age estimation of seedlings

There have been no previous age estimates of Manilkara seedlings. In this study, seedlings were divided into two categories: young seedlings less than 15 cm in height and old seedlings with a height of 15 cm - 50 cm. Age and height of 27 young seedlings were directly measured over a period of 2.5 years following germination. An indirect method, the number of clear leaf scars, was used to estimate the age of old seedlings. In the understory of the closed canopy forest, 34 old seedlings were randomly chosen for study. Leaves were marked in October 1987. Increments of leaf number were recorded in May 1989. Annual increment in numbers of leaves (AIL) was calculated by the leaf increment from October 1987 to May 1989 divided by 1.583 (one year and seven months). AIL was expressed as #/yr. The total number of leaf scars on each of 34 seedlings was counted and seedling height was measured in May 1989. Age was estimated by the total number of leaf scars divided by the AIL for each seedling. Age-height relationships for young and old seedlings were determined by regression analysis and a

regression equation was established.

Age estimation of trees

It was determined in this study that Manilkara trees in Puerto Rico have annual growth rings (see discussion). A growth ring is composed of periodically alternating bands of fibre and parenchyma cells (sensu Fahn et al., 1981). Boundaries of growth rings are marked by one or several very large parenchyma bands. Age estimation of trees (height > 130 cm^2) is based upon analysis of annual growth rings.

A U.S. Department of Agriculture, Forest Service handbook (Graves and Ziegler, 1912) prescribed a method to estimate the total age of trees: the total number of "annual rings" at DBH plus the number of years required to grow as high as the DBH measurement. For Manilkara trees in this study, the total age of the tree was estimated by the sum of three life periods: 1) the seedling life period, 2) the sapling life period, and 3) the tree life period.

The phrase "life period" refers to the time (yrs) required for an individual to grow from one size class to the next larger size class. The seedling life period refers to years required for seedlings to reach 50 cm in height. The average seedling life period is estimated by a regression equation which describes height-age relationships

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[2] In this study, 130 cm = height of DBH measurements.

for all seedling samples (according to the above section).

The sapling life period refers to years required for height growth from 50 cm to the DBH measurement. The tree life period refers to years following attainment of 130 cm height until the time of analysis. Sapling life period and tree life period were estimated by analysis of growth rings. A total of 17 trees were harvested in the El Verde forest. Cross sections were taken from each tree at DBH. Additional cross sections were taken from 5 small trees of the 17 trees at 50 cm above ground (it is not practicable to take the entire cross section for larger trees because of buttresses). To prevent mold, all cross sections were oven-dried at the field station on the day they were collected. At the University of Tennessee, cross sections were smoothed on one surface and were analyzed with a microcomputer-based tree-ring measuring system (Robinson and Evens, 1980) at a maximum magnification of 135x.

The sapling life period of the 5 small trees was estimated by the difference between growth ring numbers on cross sections at heights of 50 cm and DBH. The average sapling life period of the 5 small trees was used as an estimation of the sapling life period for other 12 larger trees. Numbers of growth rings on cross sections at height of DBH were also counted for the 12 larger trees. The tree life period (in years) for 17 trees was expressed as the number of growth rings at DBH. Then correlationships

between DBH and the tree life period were determined by regression analysis and a regression equation was established.

Age estimation of saplings

Regression analysis was used to estimate age-height relationships. The analysis was based upon 34 old seedlings and 5 small trees harvested from the Tabonuco Forest at El Verde.

VII-2. Results

Age estimation of seedlings

After 2.5 years growth, young seedlings only attained an average height of 10 cm (Table 10). Although heights and total numbers of leaf scars of old seedlings varied from each other, AILs were very similar, ranging from 1.59 - 2.53 pieces per year (Table 11). There is a high correlation (R^2 = 0.911) between height and age for all seedling samples (Figure 5). Therefore, the regression equation

$$As = -4.389 + 0.836\ Hs \quad (R^2 = 0.911),$$

where As = seedling age (in years); Hs = seedling height (in cm), is used for age estimation of seedlings in permanent transects based upon measurements of seedling

height. The average time required for a seedling to reach 50 cm in height is approximately 37 years, estimated by this equation.

Age estimation of trees

The average sapling life period of Manilkara trees is 13 years (Table 12). The average transition time to attain a height of 130 cm (following germination) is 50 years (13 + 37 = 50 yrs). A period over than 100 years is required for a tree to attain the forest canopy (approximately 20 m height) (Table 13). Of harvested trees, tree M-23 was 116 years old (Table 13) when it was in its first year flowering.

The regression equation for relationships between DBH and the tree life period (equivalent of growth ring number on DBH cross section) (Figure 6) is

$$At = 8.487 + 2.912\ DBH \quad (R^2 = 0.984),$$

where At = tree life period in years. This regression equation is used to estimate the tree life period of Manilkara populations in the LEF.

Age estimation of saplings

The regression equation for height-age relationships of Manilkara saplings (Figure 7) is

$$Asap = -57.465 + 54.298 (\log Hsap) \quad (R^2 = 0.981),$$

where Asap = age (in years) of saplings and Hsap = height (in cm) of saplings. Because the logarithmic correlationship is very significant, this equation is used for age estimation of intermediate size classes between old seedlings and small trees.

VII-3. Discussion

The purpose of this chapter is to estimate size-age relationships of all size classes of Manilkara populations. Age determination of tropical trees is typically very difficult (Ashton, 1981; Mariaux, 1981; McCormick, in press). Manilkara trees have growth rings and the ring number has a high correlation with size (Figure 6). Manilkara seedlings have distinct leaf scars. These facts support the use of growth ring analysis and leaf scar methods to estimate age for Manilkara populations.

Use of growth rings to estimate age for tropical trees has been the subject of much controversy (Bormann and Berlyn, 1981). Factors responsible for growth ring formation in Manilkara are uncertain. Most tropical trees do not have growth rings or the growth ring is not annual. However, a few tree species in the tropics have been

reported to have annual rings (Fahn et al., 1981; Eckstein et al., 1981). Growth rings may be caused by genetic factors. For example, teak (Tectona grandis) is an introduced tree species to Puerto Rico. It has annual growth rings (Odum, Murphy, et al., 1970). Alternating wet-dry periods may also cause growth marks. Sloanea is a native to Puerto Rico and its growth rings are probably a response to alternating wet-dry seasons (Odum, Murphy, et al., 1970). A "wetter than average wet period" may be another factor responsible for the growth mark (Eckstein et al., 1981). Xia and McCormick (in preparation) found a correlation between annual rainfall and ring width in Manilkara trees at El Verde (Figure 8).

Several sources of evidence support the assumption that growth rings of Manilkara represent annual growth. This evidence includes 1) continuation of rings around the tree, 2) continuation of rings vertically, 3) occurrence of distinct wet-dry seasons, 4) significant relationships between width of rings and precipitation incidence, 5) significant relationships between number of rings and DBH, 6) significant similarity of estimation of DBH growth rates by methods of "annual ring" analysis and by methods of long-term periodic tape measurements of DBH (page 61).

Height-age relationships of old seedlings and saplings (Figure 7) is somewhat unusual and interesting. The logarithmic relationship is very significant ($R^2 = 0.981$).

Height of saplings sharply increased 50 - 60 years ago. This sharp change is probably a response to disturbance resulting from the 1932 hurricane.

CHAPTER VIII

SEEDLING GROWTH

Seedling height growth was determined under three kinds of microenvironments: A) in the "normal microenvironment" of the closed canopy forest, B) under small gap microenvironments which were created by treefalls, and C) under large gap microenvironments which are an approximation to canopy openings typical of hurricane damage.

Disturbances favor pioneer species in tropical forests (Hartshorn, 1980; Brokaw, 1985; Denslow, 1987). Effects of disturbance on primary (shade-tolerant) tree species may vary depending on the species and disturbance regime. Most primary species depend on some period of exposure in gaps to reach maturity (Brokaw, 1985). However, very large gaps may not favor regeneration of primary tree species. Regeneration of many primary species is hindered by excessive exposure to sunlight in very large gaps of rainforests, for example, in the Solomon Islands and the Far East (Whitmore, 1974; 1975). Based on this information, two hypotheses were developed to explain the relationship of disturbance to regeneration of Manilkara seedling populations: 1) small gaps created by treefalls will promote growth and recruitment of Manilkara seedlings, and 2) strong solar radiation in very large gaps

(which could be created by hurricanes) is harmful to shade-tolerant seedlings.

VIII-1. Methods

Criteria measured

The base of a cotyledon or the cotyledon stem scar was used as the initial point of measurement for determination of increment of height growth of young seedlings. Height growth increments of old seedlings were measured as the distance between the petiole base of the marked leaf and the terminal bud. Height growth rates were estimated by dividing the height increment by the time interval. It was expressed as mean monthly increment (MMI) (cm/month).

Height growth of young seedlings

In February 1987, a total of 13 permanent plots (ranging from 2 m^2 to 6 m^2 each) were established within five different microenvironments. Microenvironment #1 was in the understory of the closed canopy forest but not under parent trees. Herbaceous plants and other tree seedlings in the plots were left intact to maintain the established state of competition for light and other resources. This condition represents an undisturbed closed canopy microenvironment in the forest. Fifteen young tagged seedlings (those with only two cotyledons) were transplanted to each of 3 plots (4 m^2

each) for a total of 45 seedlings.

Microenvironment #2 was similar to microenvironment #1 except that herbaceous plants and other tree seedlings were removed to reduce competition for light or other resources. Two microenvironment #2 plots (4 m^2 each) were established near microenvironment #1 plots. A total of 30 young seedlings, 15 seedlings per plot, were transplanted, tagged and studied under "reduced-competition" conditions.

Microenvironment #3 was under parent trees in the closed canopy forest with understory plants left intact. A total of 54 young seedlings were tagged in 6 plots (2 m^2 each) under three parent trees.

Microenvironment #4 was in a small treefall gap (approximately 50 m^2) with understory plants left intact. A total of 15 young seedlings were transplanted to a plot (6 m^2) within microenvironment #4.

Microenvironment #5 was in an open area of the El Verde field station (approximately 25 m x 100 m), simulating the light conditions of a large post-hurricane gap. A total of 100 young seedlings were transplanted into a plot (5 m^2) that was located at the north side of the open area. In December of 1987, a landslide destroyed the plot and left only sixteen seedlings.

For all plots, measurements of growth increments in height were conducted in October, 1987 (after a growth period of 8 months), in March, 1988 (after 13 months), and

in May, 1989 (after 27 months). Within plots, sample numbers declined over time due to mortality. Height growth rates were estimated as an average of the MMI of survivors at each time of measurement.

To understand the relationship of seedling height growth to light conditions, incoming solar radiation was measured in microenvironments #1, #4, and #5. Two Mechanical Pyranographs (Model 3010) (QUALIMETRICS, Inc., 1985) with seven-day charts (QUALIMETRICS, Inc., 1985) were used to measure g-cal./cm^2/day. Pyranogaphs were placed 30 cm above the ground in each study site and left to record for at least one week in May, 1989. Additional Pyranographic measurements were conducted on the roof of a building in the El Verde field station for two weeks in June 1990. Data from the roof station was used as an estimate of the full solar radiation above the canopy of forest. Daily potential solar radiation for each site was calculated from the maximum hourly values on cloudless days using the method described in the QUALIMETRICS Mechanical Pyranograph manual (QUALIMETRICS, Inc., 1985). The solar radiation factor (SRF) for each microenvironment was expressed as a percentage of full solar radiation. SRFs were used as indicators of light conditions at each microenvironment. Absolute light values are variable and of limited significance to this study.

Height growth of old seedlings

Forty seedlings were randomly selected in the understory of the closed canopy forest and marked in October 1987. Their height increments were measured in March 1988 and May 1989. By October 1987, young seedlings in microenvironment #5 had grown into the old seedling stage. Height increments were measured again in March 1988 and May 1989. The average MMI of height after October 1987 was used as the estimate of the growth rate of old seedlings.

Transplant experiments

Old seedlings have persisted in forest shade for many years (10 - 40 years). To determine the influence of "canopy openings" on height growth of old seedlings, 44 seedlings were transplanted from forest shade into pots and put in the large gap microenvironment (#5). The 34 remaining old seedlings were transplanted into pots and returned to the forest shade microenvironment (#1). Seedlings were transplanted in March 1988. Height growth was measured in May 1989.

VIII-2. Results

Height growth of young seedlings

Seedling growth rates were significantly ($P<0.001$) different under all microenvironmental conditions, except

between plots with and without "reduced-competition" (P>0.05) (Table 14). However, within each microenvironment, except the large gap, height growth rates were statistically similar to one another during three measurement intervals (two P values greater than 0.01 and the others greater than 0.05) (Table 14). Seedlings in microenvironments #1 - #4 exhibited a nearly linear increment of height growth over time (Figure 9).

Young seedlings grew most slowly under parent trees. The average MMI was 0.023 (SD = 0.025) cm/mo or 0.28 cm/yr from Feb. 1987 to March 1988. Young seedlings also grew slowly in the closed canopy forest when not under parent trees. The average MMI was 0.048 (SD = 0.029) cm/mo or 0.58 cm/yr from Feb. 1987 to May 1989. Some seedlings survived under parent trees and in forest shade for over three years with only two cotyledons. During the first eight months young seedling height growth rates under small and large gap conditions were respectively 4x and 24x faster than under forest shade.

Height growth of old seedlings

Old seedlings also grew slowly in understory shade of the closed canopy forest. Height growth rate was 0.115 (SD = 0.055) cm/mo or 1.38 cm/yr, which is statistically significantly different ($P < 0.001$) from young seedlings

under similar shade conditions (Table 14). This rate is 2.4x faster than that of young seedlings under the same microenvironmental condition. Old seedlings under the large gap microenvironment grew 17x faster than those in forest shade.

Acclimatization of old seedling growth to different light conditions

In the transplant experiments, old seedlings that were transplanted from forest shade into pots and returned to forest shade grew an average of 0.118 (SD = 0.038) cm/mo in height (Table 14). This rate was very similar to that of non-transplanted old seedlings under the same condition ($P > 0.5$). Thus, transplantation had no detectable effects on the height growth. But old seedlings which were transplanted from forest shade to the large gap microenvironment grew significantly ($P < 0.001$) faster (11x) than old seedlings under forest shade.

Maximum potential solar radiation above the forest canopy was approximately 366 cal./cm^2/day. This value is close to that (382 cal./cm^2/day) of Odum, Drewry, et al., (1970). Radiation in the closed canopy forest, in the small gap, and in the large gap were estimated to be approximately 5%, 15%, and 58% of the solar radiation above the forest canopy, respectively. Comparisons of seedling growth under various light environments reveal the capability of

seedlings to acclimatize to increasing light conditions (Figure 10).

VIII-3. Discussion

Height growth rates of plants are reported to have a positive correlation with initial heights when grown in a non-constrained state (Hunt, 1978). The taller a seedling is initially, the greater the net height increment the seedling should produce. In this study, there was no significant correlation ($R^2 = 0.14$) between initial heights and MMIs (Figure 11). It is clear that seedlings of Manilkara which survived in the closed canopy forest grew in a constrained state. The major constraint was light. A young seedling was able to grow faster under increased light conditions (e.g. a large or small gap) than a taller old seedling under the forest shade.

Both young and old Manilkara seedlings have the intrinsic ability to survive and grow slowly under high shade conditions and to acclimatize to high light conditions following disturbance. Seedlings grew considerably faster under the very large gap microenvironment. Old seedlings that had lived in a high shade understory for many (10 -40 years were still able to acclimatize quickly and to grow rapidly under increased light. Height growth of seedlings was promoted by as little as a 10% increase in light at the forest floor.

The height growth rate of young seedlings under the state of competition with understory plants was similar to that under the "reduced-competition" state. This similarity suggests that competition with understory plants was not a major factor affecting growth of seedlings, or that factors other than light were not limiting during the period of study.

Results of transplant experiments support hypothesis one: microenvironmental conditions in a small gap created by treefalls promoted height growth of Manilkara seedlings. Interestingly, strong solar radiation under large gap conditions was not harmful. In fact seedlings grew considerably faster under the large gap microenvironment than under other microenvironments (Figures 9 and 10). Accordingly, the second hypothesis, strong solar radiation is harmful, is rejected. This result also suggests that canopy openings created by hurricane disturbances should favor regeneration of Manilkara by promoting rapid growth of young and old seedlings.

As discussed on page 29, bats often disperse Manilkara seeds away from parent trees to relatively sparse canopy microhabitats. Young seedlings clearly grow faster under better light conditions than those which occur under parent trees. This illustrates the importance of seed dispersal by bats. Distribution and abundance of Manilkara populations in the Luquillo forest are strongly influenced, if not

dependent, upon bats and forest disturbance, especially large scale (24x vs 4x increase in height growth rates in large vs in small gaps) disturbances such as hurricanes.

CHAPTER IX

SAPLING AND TREE GROWTH

IX-1. Methods

Manilkara trees and saplings grow very slowly in the forest. It was very difficult to get accurate data for tree growth (in height, DBH, crown-size, etc.) during the constrained study period. Indirect methods were used to estimate tree and sapling growth rates.

Correlations between tree growth parameters

Manilkara trees have an efficient form: a straight trunk and dense crown. High correlations of DBH with height and crown-size (crown projective area) were assumed. High correlations of DBH with trunk volume as well as height with basal area were expected. In the Tabonuco Forest at El Verde 103 trees were randomly selected in February 1987. Tree height was measured by using a Suunto Clinometer. Tree DBH was measured on trunks at 130 cm height above ground using a diameter tape. Crown-size was usually estimated and expressed as the long-dimension x the short-dimension. Regression analysis was used to determine correlations of DBH with height, crown-size and trunk volume, as well as height with basal area.

Height growth rate of saplings

Height growth rate of saplings was expressed as mean annual increment (MAI) of height (m/yr) during the period that a sapling grew from 0.5 m to 1.3 m. Sapling growth rate was estimated by dividing 0.8 m (1.3 m minus 0.5 m) by average duration of the sapling life period (13 yrs, see Table 12).

Tree growth rates

Tree growth rates were expressed as MAI of DBH (cm/yr), basal-area (BA, cm^2/yr), and height (m/yr). MAI of DBH is estimated by dividing the DBH (cm) by the number of tree rings at DBH position (Table 13, column 6). MAI of BA can be converted from MAI of DBH by using the equation $BA = 1/4 (\pi D^2)$, where BA = basal-area (cm^2), $\pi = 3.1416$, and D = DBH. MAI of height was estimated by dividing the increment of height growth by the number of tree rings at DBH (1.3 m). Average MAIs of DBH, BA, and height were calculated from 17 trees. These MAIs were used to represent growth rates of populations and used to compare with growth rates reported in previous studies.

Leaf area

Leaf area is one of the most important factors which influences growth rates. Leaves of 31 Manilkara individuals which ranged from old seedlings to canopy trees were

harvested for leaf area measurements. All leaves of seedlings and saplings were put in plastic bags immediately following harvesting and weighing. Tree leaf samples were selected from three branches at the top, middle and lower positions of crowns. Leaf area was measured using a LI-3050A Area Meter at the El Verde field station on the days of harvest. Total leaf area was calculated as the ratio of leaf-area/wet-weight of samples multiplied by the total wet-weight of leaves for each tree. A leaf index was calculated for tree samples. A regression analysis was used to determine correlations of leaf area with plant size (height and DBH).

IX-3. Results

Correlations between tree growth parameters

As expected, logarithmic correlations of DBH with height and with HD^2 are very high (Figure 12, a and c). HD^2 represents the square of DBH (Table 15) multiplied by height (Table 15) and it is a function of trunk volume. The correlation between height and basal-area (Figure 12, d) is similar to that of DBH with height. The correlation between DBH and crown-size (Table 15 and Figure 12, b) is not as significant as that between DBH and height. Relevant regression equations are presented in Table 16.

Height growth rate of saplings

Based on results presented on page 43, the average duration of the sapling life period was 13 years. Therefore, MAI of height during this period is 0.06 m/yr (0.8/13).

Tree growth rates

The average MAI of DBH and height were 0.24 cm/yr (ranging 0.16 - 0.34 cm/yr) and 0.21 m/yr (ranging 0.10 - 0.33 m/yr), respectively (Table 17). The average MAI for BA was 2.77 cm^2/yr (ranging 0.26 - 8.56 cm^2/yr) (Table 17).

Leaf area

There were high logarithmic correlations of leaf area (Table 18) with plant size (to DBH, $R^2 = 0.968$ and to height, $R^2 = 0.984$) (Figure 13). However, some variations of leaf area may indicate damage to tree crowns by strong winds. For example, the leaf area of tree No. M-26 (93.95 m^2, Table 18) was considerably less than that of trees No. M-24 and No. M-30 which had a smaller DBH (Table 18). Tree No. M-26 was locate on a slope more exposed to wind and was observed to have excessive damage to large limbs.

IX-3 Discussion

At El Verde, the "predominant height" (Spurr, 1964) of Manilkara tree populations is 22 - 24 m. As a tree reaches

the "predominant height", height growth nearly ceases but DBH growth continues until death. Many factors may contribute to limit "predominant height." The high correlation of tree height with DBH or basal-area (Figure 12, a and d) is attributed to the fact that most samples had a DBH less than 50 cm and 68% of them were subcanopy trees. The relatively low correlation between DBH and crown-size (Figure 12, b) is probably due to wind damage on crowns of large trees by hurricanes.

There are no previous reports of Manilkara height growth rates in undisturbed Tabonuco Forests. Marrero (1947) reported Manilkara height growth rates in plantations of Puerto Rico. The average height growth rates of young trees (the average age was 9 years) in plantations was approximately 0.24 m/yr. This rate is considerably higher than the average height growth rate of saplings in this study (0.06 m/yr) but is very similar to the average height growth rate of trees (0.21 m/yr) of this study.

High correlations between DBH and other growth parameters allow the use of DBH as a key parameter of tree growth. Compared to DBH growth rates of previous studies (Table 19), the DBH growth rate of 0.24 cm/yr (mean DBH = 12.2 cm, n = 17) in this study is as same as that (0.24 cm/yr, mean DBH = 11.6 cm, n = 135) of Murphy (1970) who used periodic tape measurements at the same study area. Taking our samples with a DBH greater than 9 cm (the minimum

size of Murphy's samples for another investigation) the average MAI of DBH was 0.29 cm/yr (SD = 0.03, n = 9), which is only 10% lower than Murphy's result (0.32 cm/yr, n = 25) reported for 1970.

Weaver (1983) estimated the lowest growth rates in DBH (0.10 or 0.16 cm/yr). His data were from a small number of samples and most sample trees were small. These small trees might have grown under suppressed conditions. Crow and Weaver (1977) estimated the highest growth rates in DBH: 0.51 - 0.58 cm/yr. Their data were taken from thinned secondary forests and the sample trees were purposely selected as "crop trees" which could grow under much less suppressed conditions.

In summary, Manilkara tree growth rates estimated in this study are similar to those of previous studies. Especially the average MAI of DBH in this study is as same as that from periodic tape measurements of DBH in previous studies. As tree growth rates in this study were estimated by growth ring numbers, it further supports the assumption that growth rings are annual rings.

CHAPTER X

STANDING CROP BIOMASS AND NUTRIENT CONTENTS

To understand accumulation and movement of biomass and nutrient elements throughout the life cycle of Manilkara, above ground standing crop biomass and four nutrient elements: P, K, Ca and Mg were investigated. Studies of underground biomass and nutrient elements were not included because it was not practicable to harvest roots during this study. In a practical sense, above ground measurements are most instructive to forest managers. Another group of scientists have been studying underground processes with the LTER project in the LEF. Throughout this study "biomass" and "nutrient stock" refer to those of the above ground standing crop.

X-1. Methods

Biomass

A total of 51 individuals, ranging from small seedlings to canopy trees, were harvested for estimation of biomass. Leaves, twigs (green shoots), branches, and boles or stems were separated. Wet weight was measured immediately after harvest. Samples of each organ were oven-dried to a constant weight at 105°C and dry weight was

measured in the lab at the El Verde field station. Biomass of different organs of trees was calculated by multiplying the wet weight by the ratio of dry matter to wet matter. Gross biomass was summed for each sample plant.

Regression analysis was used to determine correlations of biomass with DBH and height. The purpose is to develop regression equations to estimate biomass for individuals in sample transects, and in turn, to estimate population biomass per unit area by measurements of tree size. As the population consists of individuals shorter than 1.3 m, their biomass has to be estimated by height. Therefore, regression equations were developed to relate biomass to height for individuals which had a height less than 5 m and to relate biomass to DBH for individuals which had a height greater than 5 m.

Nutrient measurements

Nutrient content (mg/g dry matter) of different organs (leaf, twig, branch and stem) was analyzed using standard methods by the laboratory of Institute of Tropical Forestry, U.S. Forest Service, in Puerto Rico. A total of 54 samples were obtained from 7 trees. Amounts of P, K, Ca and Mg for leaves, twigs, branches and stems were multiplied by the dry matter biomass for each organ of each of 51 Manilkara individuals. The total stock of P, K, Ca and Mg was also summed for each individual. Correlations of P, K, Ca and Mg

stock with height or DBH were determined by regression analysis for the two size categories as same as described for biomass estimation.

IX-2. Results

Biomass

According to biomass distribution in different size individuals and in each organ (Table 20), biomass of the total plant and each organ is highly correlated to plant size (Figure 14). These relationships ensure use of regression equations to estimate biomass for Manilkara populations based on size measurements. There was also a high logarithmic correlation of height with biomass for individuals less than 5 m in height (Figure 15, (A)). The regression equation

$$\log \text{Biomass} = -1.0204 + 2.2730 (\log \text{Ht}), \quad (R^2 = 0.987),$$

where Ht = tree height (in m) and biomass is in kg, is intended for estimation of biomass for individuals less than 5 m height in permanent transects. Correlations of biomass with DBH for individuals 5 m or more in height (n = 12) was also high (Figure 15 (B)). The regression equation

$$\log \text{Biomass} = -0.7607 + 2.4474 (\log \text{DBH}), \quad (R^2 = 0.994),$$

where biomass is in kg and DBH is in cm, is used for estimation of biomass of individuals 5 m or more in height. For the readers' convenience, regression equations are presented in Table 16.

According to biomass distributions in different organs (Table 20), the ratio of photosynthetic tissues (leaves and green twigs) decreases with increasing size (height or DBH) of plants (Table 21 and Figure 16).

Nutrient contents

Among 26 stem samples taken from different sections of different trees, nutrient contents were statistically similar (Table 22). All P values were greater than 0.10, ranging from 0.106 to 0.831. Among 15 samples of branches taken from different size categories on different trees, their nutrient contents were also statistically similar. All P values were greater than 0.05, ranging from 0.059 to 0.618. These similarities justify use of the average values of nutrient content of stems and branches to estimate nutrient stocks in stems and branches of other individuals. Nutrient contents of twigs, branches and stems were significantly different from one another. All P values were less than 0.002, ranging from 0.0027-0.0000. However, nutrient contents of leaves and twigs were statistically similar. All P values were greater than 0.13, ranging from 0.139 to 0.904.

According to nutrient stock distributions in 51 individuals of Manilkara (Table 23), correlations of P, K, Ca and Mg stock with tree height (Figure 17) and DBH (Figure 18) were very significant. Regression equations displayed in Figures 17 and 18 are converged into Table 16 and are intended for estimation of nutrient stocks for individuals in permanent transects.

IX-3. Discussion

High ratios (33 - 59%) of photosynthetic tissue to total biomass in seedling populations indicates a large portion of seedling tissue was photosynthetically active. In forest shade, photosynthetic rates of seedlings were low and the balance of photosynthesis to respiration was close to zero based on measurements of gas exchanges (Petty, personal communication). These measurements indicate that net photosynthetic products of seedlings were small. Low metabolism might be the basis for seedling ability to persist in forest shade for several decades without exceeding 50 cm in height.

Effective energy conversion and nutrient fixation and accumulation are among the most important functions of plants. Compared to other tree species of previous studies, biomass of an individual Manilkara tree is much greater than that of the same size tree of other species. For trees 30

cm in DBH, for example, Manilkara has 2.7 times the biomass of Cecropia peltata. For trees 5 cm in DBH, Manilkara has 5.3 times the biomass of Cecropia peltata. Because nutrient stocks are quantitatively correlated to biomass, nutrient stocks of individual Manilkara trees are expected to be greater than those of same size trees of other species.

Based upon correlations of biomass and nutrient stocks with tree DBH or height, biomass and nutrient stocks of each individual in permanent transects can be estimated by measurements of DBH and height. The next task was to estimate biomass and nutrient distribution in Manilkara populations throughout the forest by determination of population densities.

CHAPTER XI

POPULATION DENSITY, BIOMASS AND NUTRIENT STOCKS

Because of the difficulty of identifying ages in many tree populations, an arbitrary life-stage or size- class category is often used to study long-lived tree species and age-unknown tropical tree populations (Hartshorn, 1972; Harper and White, 1974; Sarukhan, 1978; Vandermeer, 1978; Harcombe, 1987). Size-class density and frequency distribution were studied for Inga vera (Muniz-Melendez, 1978) and Buchenavia capitata (Sastre-DeJesus, 1979) in the Tabonuco Forest at El Verde. In this study, both size-class and age-class density distribution were studied. Size-class density distribution of this species can be compared with that of other species. However age-class distribution may provide a more informative quantitative description of population dynamics.

XI-1. Methods

Sample transects and population densities

In February 1987, 13 permanent transects were established. Each transect was 100 m x 2 m. Total sample area of 13 transects was 0.26 hectare. These transects were randomly selected and included all topographic positions:

slopes, ridges, and valleys. All young seedlings (height < 15 cm) of Manilkara were counted for each transect. Height was measured for all Manilkara individuals 15 cm or more in height. DBH, crown-size and canopy position were measured for all Manilkara trees which were taller than 1.3 m. Density of the entire population of Manilkara was estimated by dividing the total number of individuals by 0.26 (ha.) and expressed as ind./ha (individuals/ha). Spatial variations of population density distribution were determined by comparisons between transects.

Size-class categories

Size class categories used in this study are based on two considerations: 1) biological and ecological characteristics; and 2) compatibility with data from other studies. Criteria for size-class classification are summarized in Table 24.

Size-classes I and II were young and old seedlings which were defined in chapter VII AGE ESTIMATION (page 38). Size-class I seedlings had a high population density and a higher risk of death due to such factors as unsuccessful establishment, destruction by litter burial, and variable microenvironmental factors. Size class II seedlings had access to a high light environment and experienced less risk of burial by litter than young seedlings.

Most tropical tree population data in previous studies

have a minimum size class of 4 cm DBH (e.g. Briscoe and Wadsworth, 1970; Crow, 1980) or 10 cm DBH (Okali and Ola-Adams, 1987; Manokaran and Kochummen, 1987; Swaine et al., 1987; Lieberman and Lieberman, 1987). A 10 cm DBH is approximately equivalent to 4 inches DBH which is the maximum DBH of saplings (Gove, 1971). In permanent transects, Manilkara trees with 4 cm DBH had an average of approximately 5 m in height (estimated by the equation Log Ht = 0.2192 + 0.7808 (Log DBH), refer to Table 16). Manilkara trees with 10 cm DBH were usually 12 m in height (Table 25). Therefore, individuals which had a height 0.5 m to 5 m were defined as size class III and individuals which had a height 5 m to 12 m as size class IV. Trees which had a crown height of 12 m or more but had not yet been in the canopy were defined as size class V or the subcanopy tree class. Most Manilkara canopy trees or mature trees have a DBH greater than 20 cm and a height greater than 20 m at El Verde. Canopy trees which had a DBH of 20 cm to 30 cm were defined as size class VI, and those which had a DBH greater than 30 cm as size class VII.

Size-class density distributions

All individuals of Manilkara in 13 transects were classified into size-classes. Densities in size-class were calculated in ind./ha. Density distribution was expressed as percent of each size-class in the entire population.

Age-class density distributions

Age was converted by size for all individuals 15 cm or more in height in permanent transects. The regression equation **As = -4.389 + 0.836 Hs** (page 42: As = age of seedlings and Hs = height of seedlings) was used to estimate age of seedlings. The regression equation **Asap = -57.465 + 54.298 (log Hsap)** (page 43: Asap = age of saplings and Hsap = height of saplings) was used to estimate age of saplings. The regression equation **At = 8.487 + 2.912 Dt** (page 42: At = age of trees and Dt = DBH of trees) was used to estimate the tree life period for each tree. Age of trees was estimated by the methods developed in chapter VII, AGE ESTIMATION (page 39). Age-classes were grouped into 10 year age classes except the first 20-year seedling class. Densities in age-class were estimated and expressed as ind./ha.

Population biomass and nutrient stocks

Biomass and nutrient (P, K, Ca, Mg) stocks were estimated by the height-correlated regression equations in Table 16 for individuals of size-classes I, II and III and estimated by the DBH-correlated regression equations (also in Table 16) for individuals of size-classes IV, V, VI and VII. Standing crop biomass and nutrient stocks were summed for each size-class and for each age-class, and were

calculated as amount per square meter of forest floor. Biomass and nutrient distribution patterns in age-classified populations were compared with those in size-classified populations.

XI-2. Results

Density distributions

All Manilkara individuals in permanent transects were grouped into size-classes (Table 26) and age-classes (Table 27). Density of the Manilkara population was 6846/ha in February 1987. Variations in densities among transects were high, ranging from 50 ind./ha to 24800 ind./ha. Figure 19 illustrates size-classified and age-classified density distributions, respectively.

Population biomass and nutrient stocks

There was an average of 5 kg/m^2 of biomass, 0.38 g/m^2 of P, 6.5 g/m^2 of K, 7.36 g/m^2 of Ca, and 2.01 g/m^2 of Mg maintained in the Manilkara population at El Verde in 1987 (Table 28). According to biomass and nutrient stock distributions in size-classified and age-classified populations (Table 28), biomass and nutrient distribution patterns are illustrated in Figure 20 and 21. There are very different patterns between size-classified and age-classified populations. Density, biomass, and nutrient

stock distributions in age-classified populations exhibit fluctuations.

XI-3. Discussion

High variations in population densities were found among transects. High variations may be caused by two major factors. First, Manilkara seed dispersal depends largely on bats. Therefore, spatial distribution pattern of Manilkara populations should be related to behaviors and habitats of bats. For example, as discussed in chapter V, bats prefer to stay on trees with sparse crowns (page 29). Several high density patches of old seedlings and saplings of Manilkara were found under trees with big but sparse crowns. Second, high variations in population density among transects may be caused by topographic factors. For example, transects #22, #23 and #24 crossed or ran along stream valleys where Manilkara seedlings could be washed out by flood.

Density fluctuations in age-classified populations (Figure 19) may reflect the influence of hurricanes that were reported to occur at approximately 60 year cycles (Scatena, 1989). Timing in density fluctuations is similar to timing of hurricane cycles. This pattern suggests that hurricanes released Manilkara populations from suppression of pre-hurricane microenvironments. Seedlings and saplings should grow rapidly in canopy openings created by

hurricanes. Mortality in released populations should be lower than in suppressed populations. Accordingly, released populations have high densities.

Crow (1980) recorded an increase in Manilkara density after the severe hurricane disturbance in 1932. Density of trees with DBH greater than 10 cm increased significantly over time after the 1932 hurricane (Table 29). This trend indicates significant recovery of Manilkara populations after the severe hurricane.

On the other hand, hurricane damage to tree crowns could disrupt seed production. This might lead to a very low density of young seedlings immediately following the hurricane. Therefore, post-hurricane populations have low densities. As one would expect, biomass and nutrient (P, K, Ca and Mg) distributions in Manilkara populations exhibit similar patterns (Figure 20 and 21).

Age-class intervals in this study (10 years) are short enough to detect density fluctuations caused by severe hurricane disturbances (which occur in cycles of approximately 60 years). However, the density distribution pattern in size-classified populations does not show fluctuations because size-class intervals are long enough to include both pre-hurricane and post-hurricane populations. Therefore, density fluctuations in size-classes due to hurricane influence are masked.

However, size-classified populations provide a better

understanding for biomass and nutrient distributions. Biomass and nutrients started to accumulate most rapidly in size-class IV. Size-class VII had only 0.1% of the population density but approximately 55% of the biomass (Figure 20 (a)) and more than 47% of the nutrient stocks (Figure 21 (a)) among the entire population. The general pattern of biomass and nutrient distributions in the population is that less than 1% of the late size-class population (DBH > 10 cm) accounts for greater than 95% of the biomass and nutrients.

CHAPTER XII

MORTALITY AND SURVIVAL THROUGHOUT THE LIFE CYCLE

For a specific cohort of a sexually obligated reproducing tree population, its density declines throughout life cycle because of mortality. In unmanaged forests, tree populations are usually composed of uneven-aged individuals. It is seldom practicable to trace a cohort of a long-lived tree species. One alternative quantitative method of studying population dynamics is the analysis of life tables (Harcombe 1987).

XII-1. Methods

Field investigations of short term mortality

Field investigations were conducted to determine young seedling (size-class I) mortality. 1) A total of 54 young seedlings under three parent trees were tagged when they germinated in September 1986. Seedling mortality was inventoried in February and October of 1987, March of 1988, and May of 1989. Duration of the observation was 2.667 years (32 months). 2) Another 45 young seedlings in three permanent plots in forest shade were tagged when they germinated in February 1987. Seedling mortality was inventoried in October of 1987, March of 1988, and May of

1989. The duration of observation was 2.25 years (27 months). 3) Young seedling populations in 13 permanent transects were inventoried in February of 1987 and May of 1989. The duration of observation was also 2.25 years (27 months). Continuous mortality rates were calculated by the equation:

$$N_t = N_0 e^{qt},$$

where N_t = average number of individuals at any moment of time during the investigation period; N_0 = initial number of individuals at the beginning of investigation period; e = base number of the natural logarithm; q = mortality rate (percent per year), and t = time (years).

A total of 116 larger individuals in 13 permanent transects were marked in February of 1987. Samples included 49 individuals of size-class II, 26 individuals of size-class III, 20 individuals of size-class IV, 10 individuals of size-class V, and 9 individuals of size-class VI. Mortality was inventoried in October of 1987, March of 1988, and May of 1989. The duration of observation was 27 months.

Life tables, survivorship curves, and mortality curves

Both size-classified and age-classified life tables were constructed based on 1987 estimate of population density distributions in 13 permanent transects.

Survivorship and mortality curves were derived from life tables. Methods of constructing life tables, survivorship curve, and mortality curves are similar to those developed by Deevey (1947) for animals and by Sharitz and McCormick (1973) for plants.

XII-2. Results

Short term mortality

Under parent trees, 14, 24, 28, and 40 tagged seedlings died within 5, 13, 18, and 32 months respectively. Corresponding mortality was 25.9%, 44.4%, 51.9%, and 74.1% (Figure 22). In forest shade, 6, 11, and 18 tagged seedlings died within 8, 13, and 27 months respectively. Corresponding mortality was 13.3%, 24.4%, and 40.0% (Figure 22). The continuous mortality rate was 22.70% per year (N_t = 27, N_0 = 45, t = 2.25) in forest shade during 2.25 years and was 50.62% per year (N_t = 14, N_0 = 54, t = 2.667) under parent trees during 2.667 years. The mortality rate of young seedlings under parent trees is higher than that under forest shade.

In permanent transects, 2731 young seedlings died and 3773 young seedlings survived during 2.25 years (Figure 23). The continuous mortality rate of young seedlings in transects was 24.20% per year (N_t = 3773, N_0 = 6504, t =

2.25). During this study period, there was no mortality of old seedlings or larger size-classes.

Life tables, survivorship curves, and mortality curves

In size-classified populations, 93.5% of seedlings died in transition from size-class I to size-class II (Table 30). In age-classified populations, only 69 out of 6504 young seedlings per hectare survived after 20 years (Table 31). The 20-year mortality was 95%. The even and continuous mortality rate was 22.73% per year.

The survivorship curve of size-classified populations (Figure 24) exhibits high and constant survival rates from size-classes II-VI. Higher mortality (rapid drop-down pattern) occurred in the first and the last size-classes than in the middle classes (sapling and subcanopy classes). This pattern corresponds to a U-shaped mortality curve (Figure 25). The pattern of the survivorship curve of age-classified populations indicates very variable survival rates of age-classes (Figure 26). Fluctuations on corresponding mortality curve of age-classified populations (Figure 27) have time intervals similar to hurricane cycles.

XII-3. Discussion

Mortality of young seedlings

High mortality rates of young seedlings under parent

trees (50.62% per year) indicate heavy predation, high risk from burial and/or killing by litter, or allelopathy with parent trees. Lower mortality rates of young seedlings under non-parent tree forest microenvironments (22.70% per year in plots and 24.20% per year in transects) confirm the importance of seed dispersal by bats.

The long term (20 years) seedling mortality rate which was derived from age-classified life table is remarkably similar to the short term (2.25 years) seedling mortality rate which was measured in permanent plots (22.73% vs 22.70% per yr). This similarity suggests that mortality of young seedlings was relatively constant in pre-hurricane forest environments. This result supports use of a constant mortality rate in population simulation model (page 88) for seedling populations under pre-hurricane forest environments.

Survivorship and mortality curves

Both age- and size-classified survivorship curves of Manilkara (Figures 26 and 24) exhibit a general pattern similar to the type II (declining line) of the classical survivorship curves (Harcombe, 1987). Compared to other tree species studied in the Tabonuco Forest, this pattern indicates that seedling survival of Manilkara is much higher than that of Cecropia (Silander, 1979), Inga (Muniz-Melendez, 1978), or Buchenavia (Sastre-De Jesus, 1979).

Manilkara's U-shaped mortality curve of size-classified populations is similar to those observed by many forest ecologists involved in long-term studies (Silvertown, 1982; Harcombe, 1987). The U-shaped mortality curve indicates that mortality of seedlings and old trees is high and mortality of saplings and subcanopy trees declines with increasing size or age (Harcombe, 1987).

Comparisons of mortality of age- or size-classes throughout the life cycle of Manilkara indicates that seedling populations had highest mortality (Tables 30 and 31). However, Manilkara seedling populations are sufficient to support recruitment of the consequent age- (Figure 19 [B]-1) or size-classes (Figures 19 [A]-1 and 24). This evidence supports the hypothesis that the most critical stage in the life cycle of Manilkara is transition from seedling to sapling stage.

Mortality curves of age-classified populations (Figure 27) have unique patterns. For example, in addition to coincidence of time intervals of fluctuations with hurricane cycles (low mortality occurred approximately 60 years ago and 120 years ago), high mortality 70 - 80 years ago and 130 - 140 years ago suggests suppression of seedlings under pre-hurricane shade forest environments.

CHAPTER XIII

POPULATION SIMULATION MODEL

XIII-1. Development of the simulation model

The purpose of using a simulation model as an analytical tool is to detect the possible influence of past hurricane disturbance upon the population dynamics of Manilkara in the LEF. Population matrix models have been an important approach to projecting processes of population dynamics throughout species life cycles (Caswell, 1989) and to determining the stability of populations (Hartshorn, 1975). Harcombe (1987) recently reviewed the application of population matrix models and life tables to studying tree population dynamics. Two models are often used to project (1) age-classified populations and (2) size- or stage-classified populations of tree species (Figure 28). The corresponding age-classified flow diagram of population dynamics of Manilkara is presented in Figure 29. Figure 30 is the conceptual matrix A for the equation $n(t+1) = An(t)$, where $n(t)$ is the population size at time t and $n(t+1)$ is the population size at time t+1.

A simplified simulation model is derived from the age-classified population matrix model. Three criteria used to select the simulation model are 1) it must be an age-

classified model, 2) it must be sensitive to changes in seedling mortality rates, and 3) it should be simple. As discussed in chapter XI, Manilkara population structure described by age-classes reflects impacts of hurricane disturbances better than if described by size-classes. Based on available field data, simulations focus on the movement of a cohort of young seedlings during the approximately 60 year period (1932-1989) since the last hurricane disturbance. This may be the maximum time a tree population has to approach equilibrium in the LEF. The major objective of the model is to examine changes in seedling mortality rates during the 60 year recovery period. Simulations do not include seed production and its contributions to subsequent seedling populations.

In the simulation model, Manilkara age-classified populations are treated as a linear donor-controlled multicompartment system (similar to Figure 29 without flows of seed production and the seed compartment). Transition occurs from one compartment to the adjacent compartment (the older age-class) and is assumed to be linear. A group of ordinary differential equations (ODE) was derived from the population model. Shampine and Gordon (1975) developed a PC FORTRAN program to quickly solve ODE problems. Emanuel (personal communication) developed a PC program (DSET) to manipulate other data files and a program (SOLVE) to access data files into the ODE program and to run combined

programs. The subroutine of the computer program is presented in Figure 31.

The simplified model is controlled by two variables: the initial population density value (the beginning density of a young seedling cohort) and transition parameters (mortality rates in each age-classes). Manipulation of either variable can lead to different results. However, mortality rates are more sensitive than initial density values. Initial density values are based upon field data. According to field studies, young seedling populations declined from 6504 ind./ha to 3773 ind./ha during 2.25 years and the annual mortality rate (24.20%) was similar to the average annual rate (22.73%) during 20 years (pages 79 - 81).

XIII-2. A scenario of hurricane impacts

This scenario of hurricane impacts is supported by results of the present field study. The most significant influence of hurricane disturbance is release from suppression of seedling growth. Following hurricane disturbance, seedlings grow faster under increased light conditions than under the non-hurricane shade conditions or in small tree fall gaps (supported by the experiment described in chapter VIII, SEEDLING GROWTH). Seedling mortality can be expected to decline significantly

(supported by the positive relationship between survival and growth for slowly growing species, refer to Harcombe, 1987). Increased (compared to non-hurricane disturbance situations) seedling survival should lead to a relatively high density of the subsequent age-class (saplings). During long term recovery of the forest, mortality rates of newly recruited seedlings should gradually return to those under non-hurricane disturbance conditions because of canopy re-closing.

Severe damage to crowns of mature trees causes disruption of seed production for at least a few years (You and Petty, in press). During long term recovery, gradually increasing mortality rates of newly recruited seedlings and initial disruption of seed production may lead to lower post-hurricane seedling population densities than immediately following hurricane disturbance. Therefore, age-classified population density distributions can be expected to exhibit a highly fluctuating pattern. For sapling and tree populations, hurricane disturbance mainly influences growth rates. During long term forest recovery, mortality rates of sapling and tree populations should not differ significantly from non-hurricane conditions. Loss of sapling and tree populations due to the direct force of the hurricane disturbance was also very low in the El Verde forest (4%, You and Petty, in press). The major effect of these age-class responses to hurricane disturbance is that

the relative density and abundance of the sapling age-class should increase. While direct field studies document increased seedling growth rates following hurricane scale disturbance, it is much more difficult to document changes in seedling mortality rates during the long period between hurricane disturbances. The time period is very long (approximately 60 years) and a variety of events may mask or alter mortality rates. Accordingly the matrix model is employed as an analytical tool to simulate the survival and mortality of a seedling cohort throughout this period.

XIII-3. Derivation of values used in the model

Simulations of seedling cohort mortality are conducted under two scenarios: scenario I in the absence of hurricane disturbance and scenario II following hurricane disturbance. The following descriptions and assumptions are made in selecting 1) initial values and 2) mortality rates for scenarios I and II.

1) The initial value (3773 ind./ha, see Figure 23) of the young seedling population in scenario I is the actual field value approximately 60 years following the 1932 hurricane disturbance. This value was measured in the field from 1987-89 and represents the longest time for recovery since the previous hurricane disturbance (1932). For scenario II, impacts on young seedling populations by

Hurricane Hugo (You and Petty, in press) are assumed to be representative of those experienced in 1932. Because 61% of young seedling populations were destroyed due to the direct force of Hurricane Hugo (You and Petty, in press), the initial seedling cohort value following a hurricane should be approximately 1471 ind./ha (3773 ind./ha x 61%).

2) For scenario I, mortality rates of age-classes 0-50 are based upon the field observations of population densities in May of 1989. An even and constant mortality rate is calculated for age-classes 50 to 230 (under the situation of no hurricane disturbance). Microenvironmental conditions in the El Verde forest 60 years following a hurricane are accepted as being representative of the non-hurricane scenario (supported by descriptions in chapter III, microenvironment of Manilkara populations). It is also assumed that age-classified density distributions in May of 1989 reflect the influence of these microenvironmental conditions.

For selection of mortality rates in scenario II, it is assumed that mortality rates 20 years after a hurricane are similar to those under non-hurricane conditions. This assumption is supported by the observation that pioneer trees (such as Cecropia peltata) and shrubs grow rapidly following disturbance (Silander, 1979; You and Petty, in press). They may shade the understory of the forest and create microenvironments with light conditions similar to

those under non-hurricane conditions for Manilkara old seedlings and saplings 20 years after hurricane disturbance. The mortality rate during the first 20 years following hurricane disturbance is adjusted by running the simulation model until the population density at age-class 60 corresponds to the observed value (46 ind./ha). In this way, the mortality rate which could lead to observed results was derived. Determination of mortality rates was the purpose of employing the model.

XIII-4. Results

According to simulated mortality rates and corresponding population densities (Table 32), scenario I produced a smooth curve of population density distribution (Figure 32, line curve). There would be 14 ind./ha and 13 ind./ha surviving in age-classes 60 and 70 respectively. However, actual field values are 46 ind./ha and 58 ind./ha at age-classes 60 and 70 respectively. The significance of these results is that in the absence of hurricane disturbance, mortality rates are too high to account for observed population densities.

Simulations under scenario II (Table 32) produced a population density distribution pattern similar to field observations (Figure 32, bar charts). The adjusted mortality rate required to achieve this result is 9.3% per

year which is significantly lower (9.3% vs 20%) than that under scenario I.

XIII-V. Discussion

The study area has been well protected and managed by the U.S. Forest Service since early this century (Brown et al., 1983; Odum, 1970a). Hurricanes are the most significant disturbance to the forest and the timing of occurrence of hurricanes (Wadsworth, 1951; Scatena, 1989) matches fluctuations in Manilkara populations. According to the simulation, the mortality rate of seedlings during the first 20 years following hurricane disturbance is much lower than that which occurs in the absence of hurricane disturbance. This indicates that a consequence of hurricane disturbance is a reduction of seedling mortality rates. This reduction of seedling mortality rates is probably a consequence of the release of seedling growth from suppression.

CHAPTER XV

CONCLUSIONS

The following conclusions are drawn from the present study:

1. Manilkara is a primary tree species. Seedlings are very shade-tolerant and can persist in forest shade for approximately 40 years without exceeding 50 cm in height. This trait ensures accumulation of well established seedling populations in the understory of the closed canopy forest. Consequently, seedling population densities are relatively high in spite of the relatively low production of viable seeds.

2. Survivorship and mortality curves of Manilkara are similar to those of many primary tree species. The U-shaped mortality curves indicate that mortality of seedlings and very old trees is high and mortality rates of saplings and subcanopy trees declines with increasing size or age.

3. Consistent with conclusions 1 and 2, the most critical stage in the life cycle of Manilkara is survival of seedlings into the sapling stage.

4. Manilkara flowers sporadically and seed production is light and continuous throughout the year. Low production of viable seed is offset by long range seed dispersal to favorable habitats by bats.

5. Manilkara is a "rapid germination" species. Seeds do not exhibit dormancy. Large epigeal seedlings with photosynthetic cotyledons and rapid development of a seedling root system enhance success of seedling establishment.

6. Seed dispersal by bats is one of the most important factors influencing Manilkara's distribution and abundance in the Tabonuco Forest. The majority of viable seeds which are moved away from parent trees are dispersed by bats. Seed dispersal by bats increases the probability that seeds are moved away from parent trees (possibly avoiding high predation) and increases success of seedling establishment under microenvironmental conditions which vary temporally and spatially throughout the forest. Benefits of seed dispersal by bats also (see conclusion #1) compensate for low production of viable seed and contribute to successful regeneration of Manilkara in the LEF.

7. If forest management or other human activities reduce bat populations, the distribution and abundance of Manilkara can be expected to suffer corresponding reductions.

8. Manilkara seedlings have an intrinsic ability to acclimatize to increasing light conditions. Strong solar radiation under large gap conditions is not harmful to seedlings which are accustomed to forest shade. In fact, seedlings grew considerably faster in large gap conditions

than in small gap or forest shade conditions (6x and 24x increases in height growth rates respectively). This characteristic enables Manilkara to adjust to large scale disturbances such as hurricanes.

9. Hurricanes appear to be one of the most important exogenous factors influencing Manilkara population dynamics. Fluctuations of age-classified density, biomass, and nutrient distributions within Manilkara populations reflect the influence of disturbances at approximately 60 year intervals. The time interval of population fluctuations is similar to the hurricane cycle. Results of a population simulation model support the interpretation that hurricane disturbance results in the release of seedling growth suppression. This contributes to a corresponding reduction of seedling mortality.

10. Because of faster seedling height growth in post-hurricane conditions (24x vs 4x in height growth rate in large and small gaps respectively) and a longer duration of open canopy, hurricane disturbances should have a more beneficial impact upon Manilkara populations than treefall gaps and other minor disturbances.

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APPENDIX

Table 1. Important research reports related to Manilkara bidentata produced by the Rain Forest Project of the U.S. Atomic Energy Commission 1964-1967 (published in 1970).

Author(s)	Subject
Cintron (1970)	Stomata.
Cowley (1970a) Cowley (1970b)	Litter microfungal population. Leaf microfungi.
Duke (1970)	Description of seedlings.
Estrata-Pinto (1970)	Phenology.
McCormick (1970)	Seedling density, radiation effects.
Murphy (1970)	Species description; geographic distribution; flower and fruit drop; tree (DBH>9 cm) growth measurements--DBH, basal area, radiation effects.
Odum (1970a)	Leaf damage by insects.
Odum and Cintron (1970)	Chlorophyll A content.
Odum, Murphy, et al.(1970)	Buds, crown, tree cores.
Odum, Abbott, et al.(1970)	Chlorophyll A content.
Odum, Lugo, et al. (1970)	Transpiration and metabolism records.
Ovington and Olson (1970)	Biomass and chemical content (only 4 subcanopy trees).
Smith (1970)	Altitude distribution, life form. successional status, density (DBH>10 cm), radiation effects.
Sollins and Drewry (1970)	Throughfall, stemflow, rainfall interception, etc.
Watson (1970)	Branch elongation.
Wiegert and Murphy (1970)	Leaf litter decomposition.

Table 2. Occurrence of Manilkara bidentata in tropical forests of several countries in the American tropics.

Country	Forest types (classification system)	Rain (mm/yr)	Source
Puerto Rico	Subtropical Moist Forest *	1000-2000	(1)
	Subtropical Wet Forest *	2000-4000	(1)
Dominica	Lower Mountain Rain Forest**	-3000	(2)
	Secondary Rain Forest **	-2000	(2)
St. Lucia	Lowland Rain Forest **	2000-2500	(2)
	Lower Mountain Rain Forest**	-3000	(2)
	Secondary Woodlands **	2000-2500	(2)
Grenada	Lowland Rain Forest **	2000-2500	(2)
	Lower Mountain Rain Forest**	-3000	(2)
	Dry Scrub Woodland **	-1500	(2)
	Secondary Rain Forest **	2000-2500	(2)
Barbados	Dry Scrub Woodland **	-1500	(2)
British Virgin Islands	Xerophytic Rain Forest **	-1500	(2)
Trinidad	Lower Mountain Rain Forest**	2000-2500	(3)
British Guiana	Evergreen Seasonal Forest**	1700-1900	(4)
Venezuela	Lower Mountain Rain Forest**	2000-3000	(3)
Surinam	Rain Forest ***	2000-2500	(5)
	Upland Rain Forest ***	2000-2500	(6)

* Sensu Holdridge, L.R. 1970.
** Sensu Beard, J.S. 1944.
*** Sensu Schulz, J.P. 1960.

Source: (1) Ewel, J.J. and J.L. Whitmore. 1973.
(2) Beard, J.S. 1949.
(3) Beard, J.S. 1946a and 1946b.
(4) Fanshawe, D.B. 1954.
(5) Lindeman, J.C. 1953.
(6) Schulz, J.P. 1960.

Table 3. Physical properties of soil in the Tabonuco Forest at El Verde of Puerto Rico (adapted from Odum, 1970b).

Measurement	Stations		
	1	2	3
Altitude (m)	343	406	469
Mean daily precipitation during the period (inches)	0.52	0.34	0.40
Root depth (inches)	16	14	13
Mechanical analysis:			
Sand (%, 2.0-0.05 mm)	28.4	18.4	32.4
Silt (%, 0.05-0.005 mm)	24.0	16.0	24.0
Clay (%, <0.005 mm)	47.6	65.6	43.6
Bulk density (g/ml)	0.87	0.74	0.83
Soil moisture (water/dry matter)	68	67	72
Organic matter (%)	5.8	9.8	11.2

Table 4. Chemical properties of upper soil layers in the Tabonuco Forest at El Verde of Puerto Rico.

Measurement	Horizon (cm)	
	0 - 12.7	12.7 - 25.4
Organic matter (%) *	17-20	13-15
pH (50% soil; 50% water) *	5.7	5.4
Cation-exchange capacity (meq/100g)*	29.1	17.1
P (acid-extr. ppm) *	13	6
K (exchangeable portion, ppm) *	186	30
Ca (exchangeable portion, ppm) *	3840	1110
Mg (exchangeable portion, ppm) *	1515	873
Zn (exchangeable portion, ppm) *	0.5	0.5
Cu (exchangeable portion, ppm) *	0.5	0.5
Mn (exchangeable portion, ppm) *	170	40
N (%) **		2.12
P (%) **		0.022
K (ppm) **		44

* Data were from soil samples taken at the North Cut Center in September 1964 (before the radiation experiments), adapted from Edmisten (1970).

** Data are taken from Gruenwoldt (1962), cited in Odum (1970b).

Table 5. Phenological records of 30 marked Manilkara trees at El Verde of Puerto Rico from 1986 to 1989. x = trees with flowers or/and fruits. There seemed to be a high seed production in 1986. Newly established seedlings were found under 73% of parent trees and the population was large in September 1986. After 1986 flowering was sporadic and seed production was light although approximately 50% of marked trees had some reproductive activity for three years.

Tree#	DBH (cm)	Season 6-7/1986	1-3/1987	10/1987	3/1988	6-1989
1	35.8	x	x	x	x	x
2	33.3	x	.	.	x	.
3	50.0	x	x	x	x	x
4	46.3	x	x	x	x	.
5	31.1	x	x	x	x	x
6	31.0	x	x	.	.	.
7	26.3	x	x	x	x	x
8	55.0	.	.	.	.	.
9	28.1	x	x	x	x	.
10	18.8	x	x	x	x	x
11	26.0	.	.	x	x	.
12	26.5	.	.	.	.	.
13	34.4	x	x	x	x	x
14	49.0	x	x	x	x	x
15	61.2	x	x	x	x	x
16	33.5	.	x	x	x	.
17	32.3	x	x	x	x	x
18	28.3	.	.	.	.	.
19	28.4	.	.	x	x	.
20	43.2	.	.	.	.	x
21	46.0	x	.	.	.	.
22	55.2	x	.	.	.	.
23	35.2	x	.	.	.	x
24	66.3	x	x	x	x	x
25	33.2	x	x	.	x	x
26	29.7	x	.	.	.	.
27	26.7	x	.	.	.	x
28	26.9	x	.	.	.	.
29	27.0	.	.	.	.	.
30	31.5	x	.	.	.	x

Table 6. Solar orientation of reproductive branches of Manilkara trees at El Verde of Puerto Rico in 1987. Observation periods are in parentheses. There is no relationship between orientation of reproductive branches and direction of sunlight.

Tree#	Orientations of breeding branches
1	Center top (1987).
3	Scattered on the whole top (1986, 1987).
4	NW 310° (1986,1987).
5	SE 120° & SW 260° (1986).
6	SE 160° (1986).
7	SW 200°-260° (1986). Center top (1987).
17	NE 20° - 70° (1986).
32	SE 145° (1986).
M24	Scattered on the whole top (1986).
M25	NW 340° (1986).

Table 7. Reproductive-twigs (R-Ts) (twigs supporting reproductive organs) on sample trees counted in February 1987. The number of B-Ts per m^2 crown-area (crown projection area of canopy trees) (column 4) is calculated by the total R-Ts on a tree (column 2) divided by the crown-area (column 3). Ratio of R-Ts is the percent of R-Ts/m^2 (column 4) taken from the total twigs per square meter of crown-area (53/m^2). A high variation in R-Ts among trees (CV=1.14) must lead to a high variation in seed production among trees.

Tree#	Number of R-Ts	Crown-area (m^2)	Number of R-Ts per m^2 crown-area	Ratio of R-Ts (%)
4	7	30.0	0.23	0.43
5	64	20.0	3.20	6.04
6	8	13.5	0.59	1.11
7	7	4.6	1.53	2.89
17	9	12.0	0.75	1.42
M23	2	9.0	0.22	0.42
M24	20	20.0	1.00	1.89
M25	19	19.4	0.98	1.85
M26	1	19.8	0.05	0.09
M32	39	64.0	0.61	1.15
M33	80	56.0	1.43	2.70
Average:	23.3	24.4	1.0	1.8
(CV):	(1.14)	(0.77)	(0.90)	(0.92)

Table 8. Annual reproductive potential and actual reproductive performance in 1987 for Manilkara trees at El Verde of Puerto Rico. Crown-area = crown projection area (m^2) of canopy trees.

Measurement	Estimation
Annual reproductive potential:	
Crown-area per m^2 forest-area	0.1244 [m^2]
No. of twigs per m^2 crown-area	53
No. of twigs per m^2 forest-area	6.6
No. of reproductive-twigs per m^2 forest-area	0.12 *
No. of inflorescences per reproductive-twig	10.5 (6.3)**
No. of flower-buds per inflorescence	6.3 (3.2)
No. of flower-buds per reproductive-twig	66.2
No. of flower-buds per m^2 forest-area	7.9
Actual reproductive performance in 1987:	
No. of inflorescences with flowers per twig	4.4 (3.2)
No. of flowers per inflorescence	3.8 (3.2)
No. of flowers per reproductive-twig	16.7
% of flowers to flower-buds	25%
No. of inflorescences with ripe fruits per twig	1.9 (1.2)
No. of ripe fruits (seeds) per inflorescence	1.3 (0.7)
No. of ripe fruits (seeds) per twig	2.5
% of seeds per flower-buds	4%
No. of seeds per m^2 forest floor (2.5 x 0.12)	0.3
No. of fruits deposited on the forest-floor 1963-1967	0.8/m^2/yr***

* Number of reproductive-twigs per square meter forest area is estimated by multiplying twigs per m^2 forest area (including non-reproductive twigs) by 1.8%, where 1.8% is the ratio of reproductive-twigs to total twigs in February 1987, refer to Table 7.

** Standard deviations in parentheses.

*** From Estrada-Pinto (1970).

Table 9. Percent germination of *Manilkara*.

Condition	Sample size	Percent germination
Under parent trees in the forest	1177	47%
Terrarium at UTK lab		
Sept.- Oct. 1986	75	9%
March - May 1987	53	42%

Table 10. Height and age of young Manilkara seedlings (height < 15 cm).

Distribution	Height (cm)	Age (years)
Individual	10.3	2.5
	8.3	2.5
	11.1	2.5
	8.5	2.5
	9.4	2.5
	11.3	2.5
	9.3	2.5
	8.4	2.5
	9.3	2.5
	10.0	2.5
	8.2	2.5
	11.1	2.5
	13.8	2.5
	8.6	2.5
	14.6	2.5
	13.0	2.5
	9.9	2.5
	6.4	2.5
	9.6	2.5
	7.6	2.5
	8.8	2.5
	10.0	2.5
	9.7	2.5
	12.4	2.5
	11.8	2.5
	8.5	2.5
	10.0	2.5
Average	10.0 (SD = 1.9)	2.5

Table 11. Measurements of height, number of leaf scars, annual increments of leaf numbers (AIL), and estimated ages of old Manilkara seedlings (height = 15 - 49.9 cm).

Height (cm)	Leaf scar (No.)	AIL (No./yr)	Age (years)
20.0	32	2.21	14.48
19.5	22	1.89	11.64
26.0	31	1.89	16.40
15.0	14	1.89	7.41
22.3	21	1.89	11.11
18.5	25	1.89	13.23
17.8	21	2.53	8.30
24.0	26	1.89	13.76
16.5	24	1.89	12.70
15.3	19	2.84	6.69
31.5	47	1.89	24.87
22.8	33	2.21	14.93
23.5	36	2.21	16.29
16.5	28	2.53	11.07
15.0	22	2.21	9.95
45.5	58	1.89	30.69
31.5	50	1.89	26.46
22.5	44	2.21	19.91
35.5	51	1.59	32.08
36.0	62	2.21	28.05
21.1	33	1.89	17.46
52.3	56	1.89	29.63
35.5	45	2.21	20.36
27.0	39	1.89	20.63
26.8	40	2.53	15.81
29.5	41	1.89	21.69
23.0	40	2.21	18.10
19.6	28	2.21	12.67
21.4	30	2.21	13.57
25.0	43	2.21	19.46
27.0	43	2.21	19.46
17.5	27	2.21	12.22
28.2	47	2.53	18.58
34.2	50	1.89	26.46

Table 12. Estimation of the time of sapling life period.

Tree#	Height (m)	Ring numbers on cross sections		Time of life period (years)
		At 50 cm	At 130 cm	
M-01	2.50	21	12	9
M-09	2.68	18	13	5
M-18	3.28	33	14	19
M-19	3.47	31	16	15
M-02	3.64	34	17	17
				Average: 13 SD = 5.8

Table 13. Estimation of age of 17 Manilkara trees by summing three life periods.

Tree#	Height (m)	DBH (cm)	Duration of life periods 0-50 cm	50-130 cm	>130 cm	Age (years)
M-01	2.50	2.00	37 *	9	12	58
M-09	2.68	2.25	37	5	13	55
M-19	3.28	2.80	37	15	16	68
M-18	3.47	2.45	37	19	14	70
M-02	3.64	2.80	37	17	17	71
M-22	5.47	4.20	37	13 **	20	70
M-21	5.80	5.00	37	13	24	74
M-20	7.85	6.30	37	13	28	78
M-27	12.90	9.58	37	13	35	85
M-28	15.10	12.50	37	13	48	98
M-31	16.10	15.00	37	13	58	108
M-29	16.40	16.30	37	13	50	100
M-23	18.50	18.60	37	13	66	116
M-25	21.13	21.05	37	13	72	122
M-30	19.20	25.20	37	13	89	139
M-24	22.00	30.01	37	13	94	144
M-26	21.80	32.00	37	13	94	144

* The average duration required for a seedling to reach 50 cm height, estimated by the regression equation $As = -4.389 + 0.836\ Hs$ (where As=age and Hs=height), see Figure 5.

** The average duration of this life period is derived from the average of the first 5 trees (M-01, M-09, M-19, M-18 and M-02).

Table 14. Mean monthly increments (MMI) in height of Manilkara seedlings in different microenvironments.

Size class	Condition	MMI in height (cm/month)	Sample size
Young seedlings	Closed canopy with competition	0.048 (0.029)*	27
	Closed canopy without competition	0.064 (0.023)	14
	Under parent trees	0.023 (0.025)	26
	Small gap	0.154 (0.055)	10
	Large gap	1.142 (0.442)	95
Old seedlings	Closed canopy forest	0.115 (0.055)	40
	Large gap	1.971 (0.591)	12
	Forest to large gap	1.252 (0.590)	27
	Forest to forest	0.118 (0.038)	20

* Standard deviations in parentheses.

Table 15. DBH, height, and crown-area of 103 Manilkara trees.

DBH (cm)	Height (m)	Crown-area (m^2)	DBH (cm)	Height (m)	Crown-area (m^2)
27.3	20.3	4.59	3.7	3.4	1.56
54.0	22.6	85.50	15.2	9.8	6.00
27.9	23.0	14.00	13.8	12.5	8.40
61.2	24.5	132.00	3.7	5.5	1.50
18.8	21.0	14.00	7.9	10.8	1.50
21.8	19.5	15.00	4.1	5.4	0.80
24.1	22.0	6.25	6.8	6.9	3.00
17.4	19.0	11.40	9.1	8.4	7.50
20.6	21.0	3.00	2.8	3.9	0.75
24.3	23.0	16.00	2.9	2.2	1.80
26.7	23.0	4.00	4.5	5.2	1.50
23.2	18.9	14.80	1.6	2.1	0.40
22.3	21.5	12.00	2.5	3.3	1.82
19.4	21.0	3.60	7.1	7.9	7.55
31.6	24.0	25.00	7.8	9.3	4.50
31.5	24.5	14.00	4.0	5.2	1.95
27.0	22.0	4.84	5.4	4.9	1.65
26.9	22.5	14.00	10.9	14.8	7.00
26.7	22.0	16.00	3.1	3.5	2.10
29.7	24.0	33.00	6.4	8.3	2.70
33.2	24.0	33.00	11.0	11.0	8.75
19.8	20.0	14.00	4.5	5.0	1.50
19.1	18.0	20.00	6.1	7.5	5.60
18.6	18.5	9.00	1.9	2.1	1.80
30.0	22.0	20.00	18.3	11.0	20.00
21.1	21.1	19.36	16.2	11.0	25.00
32.0	21.8	19.75	10.4	10.0	6.25
39.8	22.0	64.00	8.5	11.0	6.00
25.2	19.2	19.36	11.3	12.0	12.00
29.9	20.0	20.25	1.7	2.1	0.39
29.7	22.0	20.00	9.0	10.5	10.50
20.6	20.0	12.00	10.1	12.5	7.50
50.0	24.0	25.00	5.2	5.9	3.75
1.8	3.1	1.69	6.8	9.3	2.25
11.9	9.5	3.00	2.0	2.5	2.10

(continued)

Table 15. (continued)

DBH (cm)	Height (m)	Crown-area (m^2)	DBH (cm)	Height (m)	Crown-area (m^2)
4.5	3.7	1.50	2.8	3.6	3.60
6.6	8.5	4.00	2.3	2.7	3.06
8.2	9.5	7.50	6.3	7.9	7.50
2.3	3.2	2.00	9.6	12.9	8.40
4.1	4.9	5.29	12.5	15.1	10.25
13.6	15.8	6.25	16.3	16.4	6.76
17.5	18.0	10.50	2.8	3.3	4.05
2.8	3.6	2.25	2.5	3.5	2.25
16.9	15.5	12.25	5.0	5.8	6.25
12.5	13.0	6.00	4.2	5.5	5.00
4.7	6.0	6.00	15.0	16.1	12.00
27.0	16.5	14.00	3.8	3.5	2.25
14.6	16.5	10.00	6.6	8.0	5.00
10.0	12.0	6.25	10.3	11.0	9.00
4.1	5.0	1.50	4.6	5.0	3.00
6.5	7.5	4.50	7.7	8.2	6.00
8.7	10.0	12.50			

Table 16. List of important regression equations.

Correlation	Regression equation	R^2	N
Ht vs DBH	Log Ht = 0.2192+0.7808(Log DBH)	0.938	103
Ht vs BA	Log BA = -0.5070+2.4014(Log Ht)	0.938	103
Vol vs Ht	Log HD^2= -4.5070+3.4014(Log Ht)	0.968	103
LA vs Ht	Log LA = -0.5321+1.8115(Log Ht)	0.984	31
Tb vs Ht	Log Tb = -1.0204+2.2730(Log Ht)	0.987	19
Tb vs DBH	Log Tb = -0.7607+2.4474(Log DBH)	0.994	12
Sb vs DBH	Log Sb = -1.0453+2.5871(Log DBH)	0.996	17
Bb vs DBH	Log Bb = -1.8202+2.6632(Log DBH)	0.984	17
Lb vs DBH	Log Lb = -1.3644+1.8174(Log DBH)	0.978	17
LA vs DBH	Log LA = -0.28598+1.6100(Log DBH)	0.968	17
Vol vs DBH	Log HD^2= -3.8857+2.7808(Log DBH)	0.995	103
P vs DBH	Log P = -1.5327+2.2191(Log DBH)	0.989	12
K vs DBH	Log K = -0.3892+2.2805(Log DBH)	0.993	12
Ca vs DBH	Log Ca = -0.3325+2.2788(Log DBH)	0.993	12
Mg vs DBH	Log Mg = -0.7267+2.1677(Log DBH)	0.989	12
P vs Ht	Log P = - 1.5011+1.9003(Log Ht)	0.975	19
K vs Ht	Log K = - 0.4522+1.9156(Log Ht)	0.975	19
Ca vs Ht	Log Ca = - 0.3474+1.8491(Log Ht)	0.973	19
Mg vs Ht	Log Mg = - 0.7680+1.8650(Log Ht)	0.972	19

DBH (cm) = diameter at breast height (130 cm); Ht (m) = height of size-class I-III; BA (cm^2) = basal-area; Vol = volume, expressed as a function of HD^2 (height multiplied by square DBH); LA (m^2) = leaf-area; Tb (kg) = total above ground biomass; Sb (kg) = stem biomass; Bb (kg) = branch biomass; Lb (kg) = leaf biomass; P (g) = phosphorus; K (g) = potassium; Ca (g) = Calcium; Mg (g) = Magnesium.

Table 17. DBH, height, growth ring number, and annual growth rates of trees harvested from Manilkara populations at El Verde of Puerto Rico in 1987.

Tree#	DBH (cm)	Height (m)	Ring (#)	Growth rates		
				DBH (cm/year)	Height (m/year)	BA (cm^2)
M-01	2.00	2.50	12	0.17	0.10	0.26
M-09	2.25	2.68	13	0.18	0.11	0.31
M-19	2.45	3.47	16	0.16	0.14	0.38
M-18	2.80	3.28	14	0.20	0.14	0.34
M-02	2.80	3.46	17	0.16	0.13	0.36
M-22	4.20	5.47	20	0.21	0.21	0.69
M-21	5.00	5.80	24	0.21	0.19	0.82
M-20	6.30	7.85	28	0.23	0.23	1.11
M-27	9.58	12.90	35	0.27	0.33	2.06
M-28	12.50	15.10	48	0.26	0.29	2.56
M-31	15.00	16.10	58	0.26	0.26	3.05
M-29	16.30	16.40	50	0.33	0.30	4.17
M-23	18.60	18.50	66	0.28	0.26	4.12
M-25	21.05	21.13	72	0.29	0.28	6.93
M-30	25.20	19.20	89	0.28	0.20	3.91
M-24	30.01	22.00	94	0.32	0.22	7.52
M-26	32.00	21.80	94	0.34	0.22	8.56
Average	-	-	-	0.24	0.21	2.77
S.D.	-	-	-	0.06	0.07	2.74

Table 18. Leaf area and leaf index of individuals harvested from Manilkara populations at El Verde of Puerto Rico in 1987.

DBH (cm)	Height (m)	Crown* (m^2)	Leaf-area (m^2)	Leaf-index
-	0.08**	-	0.0014**	-
-	0.27	-	0.017	-
-	0.28	-	0.032	-
-	0.31	-	0.064	-
-	0.38	-	0.036	-
-	0.29	-	0.044	-
-	0.30	-	0.041	-
-	0.27	-	0.029	-
-	0.31	-	0.030	-
-	0.17	-	0.022	-
-	0.20	-	0.016	-
-	0.22	-	0.011	-
-	0.64	0.12	0.102	0.850
-	0.74	0.42	0.385	0.917
-	1.20	0.20	0.169	0.845
2.00	2.50	2.20	1.033	0.470
2.25	2.68	3.06	2.134	0.697
2.45	3.47	2.25	2.232	0.992
2.80	3.28	4.05	2.070	0.511
2.80	3.64	3.60	3.103	0.862
4.20	5.47	5.00	5.060	1.012
5.00	5.80	6.25	9.131	1.461
6.30	7.85	7.50	15.044	2.006
9.58	12.90	8.40	21.500	2.560
12.50	15.10	10.25	45.740	4.462
15.00	16.10	12.00	33.550	2.796
16.30	16.40	6.76	36.080	5.337
18.60	18.50	9.00	37.810	4.201
21.05	21.13	19.36	68.300	3.528
25.20	19.20	19.36	142.780	7.375
30.01	22.00	20.00	137.810	6.891
32.00	21.80	20.00	93.950	4.698

* Crown projection area.
** Average values from 20 samples.

Table 19. Comparison of several estimated radial growth rates of Manilkara trees.

Author	MAI (cm/yr)	CV* (%)	Stems (No.)	Growth interval (years)	Initial DBH rang (cm)	Forest stand condition
This study	0.24	25	17	tree ring analysis	2-32 mean=12	undisturbed, slope. (El Verde)
Weaver (1983)	0.16	111	6	30	4-30	undisturbed, slope.
,,	0.10	54	9	30	5-9	undisturbed, ridge.
,,	0.45	50	9	28	4-14	cutover.
Crow & Weaver (1977)	0.51	60	22	18	mean>17	thinned, secondary. (Rio Grande)
,,	0.58	46	27	18	mean>17	thinned, secondary. (Sabana 8)
Murphy (1970)	0.32	-	25	3	> 9.0	undisturbed, slope. (El Verde)
,,	0.24 **	-	135	10	mean=11.6	,,

* CV = coefficient of variation.

** Derived from the mean annual basal-area increase (4.17%) and the initial mean DBH (11.6 cm).

Table 20. Biomass (kg.dry-weight) distribution in fifty-one individuals of Manilkara.

DBH (cm)	Height (m)	Leaf (kg)	Twig (kg)	Branch (kg)	Stem (kg)	Total (kg)
-	0.08	-	-	-	-	0.0002
-	0.27	0.001	-	-	0.003	0.004
-	0.28	0.003	-	-	0.002	0.005
-	0.31	0.005	-	-	0.004	0.009
-	0.38	0.003	-	-	0.006	0.009
-	0.29	0.004	-	-	0.004	0.008
-	0.30	0.003	-	-	0.003	0.006
-	0.27	0.002	-	-	0.002	0.005
-	0.31	0.002	-	-	0.002	0.005
-	0.17	0.002	-	-	0.001	0.003
-	0.20	0.001	-	-	0.001	0.002
-	0.22	0.001	-	-	0.001	0.002
-	0.64	0.087	-	0.0014	0.022	0.032
-	0.74	0.034	-	0.0074	0.033	0.075
-	1.20	0.015	-	0.0042	0.076	0.095
2.00	2.50	0.105	0.042	0.115	0.545	0.807
2.25	2.68	0.200	0.057	0.133	0.631	1.020
2.45	3.47	0.213	0.050	0.086	0.876	1.225
2.80	3.28	0.245	0.055	0.241	1.373	1.914
2.80	3.64	0.322	0.064	0.267	1.103	1.756
4.20	5.47	0.582	0.121	0.876	4.613	6.192
5.00	5.80	1.051	0.193	1.198	5.281	7.722
6.30	7.85	1.731	0.335	2.567	10.15	14.79
9.58	12.90	2.574	0.388	5.786	37.35	46.10
12.50	15.10	7.158	0.982	21.04	74.41	103.6
15.00	16.10	4.432	0.570	9.02	115.1	129.1
16.30	16.40	5.468	0.725	22.80	114.0	143.0
18.60	18.50	5.368	2.253	37.64	183.6	228.9
21.05	21.13	12.40	2.451	62.91	304.2	382.0
25.20	19.20	17.60	3.598	59.63	299.8	380.7
30.01	22.00	26.45	4.862	130.09	506.0	667.4
32.00	21.80	18.40	3.735	208.42	616.8	847.4

* The average of twenty germinated seedlings.

Table 21. Distribution of biomass (in kg) of photosynthetic tissue in thirty-one individuals of Manilkara.

DBH (cm)	Height (m)	Biomass of Ps*	Total biomass	Ratio of Ps* (%)
-	0.27	0.0013	0.0039	33.33
-	0.28	0.0026	0.0049	53.06
-	0.31	0.0054	0.0094	57.45
-	0.38	0.0031	0.0091	34.07
-	0.29	0.0035	0.0077	45.45
-	0.30	0.0033	0.0059	55.93
-	0.27	0.0023	0.0046	50.00
-	0.31	0.0023	0.0047	48.94
-	0.17	0.0017	0.0029	58.62
-	0.20	0.0012	0.0023	52.17
-	0.22	0.0007	0.0017	41.18
-	0.64	0.0101	0.0321	31.46
-	0.74	0.0415	0.0745	55.70
-	1.20	0.0189	0.0948	19.94
2.00	2.50	0.1466	0.8066	18.18
2.25	2.68	0.2563	1.0203	25.12
2.45	3.47	0.2630	1.2250	21.47
2.80	3.28	0.2998	1.9138	15.67
2.80	3.64	0.3860	1.7560	21.98
4.20	5.47	0.7033	6.1923	11.36
5.00	5.80	1.2442	7.7232	16.11
6.30	7.85	2.0659	14.7869	13.97
9.58	12.90	2.9619	46.0979	6.43
12.50	15.10	8.1404	103.590	7.86
15.00	16.10	5.0020	129.088	3.87
16.30	16.40	6.1926	142.993	4.33
18.60	18.50	7.6210	228.871	3.33
21.05	21.13	14.851	381.961	3.89
25.20	19.20	21.198	380.658	5.57
30.01	22.00	31.312	667.392	4.69
32.00	21.80	22.135	847.365	2.61

* Ps = photosynthetic tissue.

Table 22. P, K, Ca and Mg content (mg/g) in different organs of Manilkara trees.

material	P	K	Ca	Mg
Leaves	0.4769	6.0430	6.2506	3.3165
------	(0.1130)*	(1.9729)	(1.4514)	(0.6992)
n=8				
Twigs	0.6748	6.5618	11.411	3.222
-----	(0.4826)	(2.2338)	(9.3227)	(2.013)
n=4				
Branches:				

<3 cm	0.2388	2.221	2.8045	1.0453
n=4	(0.0487)	(0.1943)	(0.7774)	(0.3041)
3-6 cm	0.1218	1.5117	1.5410	0.4792
n=6	(0.0567)	(0.5788)	(0.3259)	(0.1529)
>6 cm	0.0840	0.8640	1.6965	0.3170
n=2	(0.0028)	(0.1485)	(0.2213)	(0.0141)
average	0.1542	1.6711	2.0210	0.6422
n=15	(0.0787)	(0.6745)	(0.8166)	(0.3302)
Boles:				
------				
at 1.3**	0.0323	0.9400	1.3701	0.2776
n=7	(0.0147)	(0.1535)	(0.5749)	(0.5696)
at 5.6**	0.0423	1.2343	1.1506	0.2453
n=7	(0.0202)	(0.8095)	(0.4504)	(0.0512)
at 11.6**	0.0496	1.0519	1.1371	0.2511
n=9	(0.0229)	(0.3784)	(0.4680)	(0.0403)
average	0.0450	1.0900	1.2010	0.2611
n=27	(0.0222)	(0.4821)	(0.4692)	(0.0512)

* Standard deviation in parenthesis.

** Samples taken at 1.3 m, 5.6 m and 11.6 m height on tree boles.

Table 23. P, K, Ca and Mg stocks and biomass of fifty-one individuals of Manilkara.

DBH (cm)	Height (m)	Biomass (kg)	P (g)	K (g)	Ca (g)	Mg (g)
-	0.08*	0.0002*	0.0001*	0.001*	0.002*	0.0007*
-	0.27	0.004	0.002	0.025	0.038	0.013
-	0.28	0.005	0.003	0.031	0.042	0.016
-	0.31	0.009	0.005	0.059	0.079	0.031
-	0.38	0.009	0.006	0.058	0.088	0.030
-	0.29	0.008	0.005	0.049	0.070	0.025
-	0.30	0.006	0.003	0.037	0.050	0.019
-	0.27	0.005	0.003	0.029	0.041	0.015
-	0.31	0.005	0.003	0.030	0.042	0.015
-	0.17	0.003	0.002	0.018	0.024	0.010
-	0.20	0.002	0.001	0.014	0.020	0.008
-	0.22	0.002	0.001	0.011	0.016	0.006
-	0.64	0.032	0.008	0.099	0.115	0.047
-	0.74	0.075	0.026	0.310	0.364	0.158
-	1.20	0.095	0.022	0.243	0.293	0.111
2.00	2.50	0.807	0.180	2.010	2.465	0.906
2.25	2.68	1.02	0.251	2.855	3.438	1.335
2.45	3.47	1.225	0.284	3.223	3.845	1.485
2.80	3.28	1.914	0.403	4.537	5.419	2.026
2.80	3.64	1.756	0.408	4.655	5.513	2.154
4.20	5.47	6.192	0.702	10.81	12.33	4.088
5.00	5.80	7.722	1.054	15.38	17.54	6.256
6.30	7.85	14.79	1.904	28.02	32.02	11.12
9.58	12.90	46.10	4.062	68.48	77.07	23.25
12.50	15.10	103.6	10.67	166.0	187.8	59.85
15.00	16.10	129.1	9.07	171.0	190.6	52.37
16.30	16.40	143.0	11.74	200.2	225.4	64.88
18.60	18.50	228.9	18.15	310.3	355.8	97.18
21.05	21.13	382.0	30.96	527.7	598.0	168.8
25.20	19.20	380.7	33.51	556.4	631.7	186.5
30.01	22.00	667.4	58.72	960.7	1091.4	319.0
32.00	21.80	847.4	71.19	1156.3	1319.6	368.0

* The average of twenty germinated seedlings.

Table 24. Classification of size-classes of Manilkara populations in the Luquillo Experimental Forest, Puerto Rico.

Size class	Age (years)	Criteria
Size-class I (Young seedlings)	< 8	Height < 15 cm
Size-class II (Old seedlings)	8 - 36.9	Height 15 - 49.9 cm
Size-class III	37 - 70.9	Height 0.5 - 4.9 m (DBH < 4 cm)
Size-class IV	71 - 94.9	Height 5 - 11.9 m (DBH 4 - 9.9 cm)
Size-class V	95 - 116.9	Height 12 - 19.9 m (DBH 10 - 19.9 cm)
Size-class VI (Canopy trees)	117 - 145.9	DBH 20 - 29.9 cm
Size-class VII (Canopy trees)	≥ 146	DBH ≥ 30 cm

Table 25. Height, DBH, estimated age and size-class for all Manilkara individuals 15 cm or more in height which are located in permanent transects.

Height (m)	DBH (cm)	Size-class*	Age (years)
0.19	-	II	11.5
0.19	-	II	11.5
0.20	-	II	12.3
0.20	-	II	12.3
0.20	-	II	12.3
0.21	-	II	13.2
0.21	-	II	13.2
0.21	-	II	13.2
0.21	-	II	13.2
0.23	-	II	14.8
0.24	-	II	15.7
0.24	-	II	15.7
0.25	-	II	16.5
0.25	-	II	16.5
0.25	-	II	16.5
0.25	-	II	16.5
0.26	-	II	17.3
0.26	-	II	17.3
0.26	-	II	17.3
0.26	-	II	17.3
0.27	-	II	18.2
0.27	-	II	18.2
0.28	-	II	19.0
0.28	-	II	19.0
0.28	-	II	19.0
0.28	-	II	19.0
0.29	-	II	19.9
0.30	-	II	20.7
0.30	-	II	20.7
0.30	-	II	20.7
0.30	-	II	20.7
0.30	-	II	20.7
0.30	-	II	20.7
0.32	-	II	22.4
0.32	-	II	22.4
0.33	-	II	23.2
0.33	-	II	23.2
0.33	-	II	23.2
0.34	-	II	24.0

(continued)

Table 25. (continued)

Height (m)	DBH (cm)	Size-class*	Age (years)
0.36	-	II	25.7
0.36	-	II	25.7
0.36	-	II	25.7
0.38	-	II	27.4
0.38	-	II	27.4
0.39	-	II	28.2
0.44	-	II	32.4
0.47	-	II	34.9
0.47	-	II	34.9
0.49	-	II	36.6
0.51	-	III	35.3
0.53	-	III	36.2
0.55	-	III	37.0
0.56	-	III	37.5
0.66	-	III	41.3
0.70	-	III	42.7
0.70	-	III	42.7
0.79	-	III	45.6
1.00	-	III	51.1
1.13	-	III	54.0
1.18	-	III	55.0
1.40	-	III	59.1
2.10	1.4	III	62.6
2.13	1.6	III	63.1
3.10	1.8	III	63.7
2.13	1.9	III	64.0
3.17	2.3	III	65.2
3.30	2.5	III	65.8
3.60	2.8	III	66.6
3.90	2.8	III	66.6
2.16	2.9	III	66.9
3.50	3.1	III	67.5
3.40	3.7	III	69.3
5.50	3.7	IV	69.3
5.20	4.0	IV	70.1
5.40	4.1	IV	70.3
4.90	4.1	III	70.4
5.00	4.1	IV	70.4
3.70	4.5	III	71.6
5.00	4.5	IV	71.6
5.20	4.5	IV	71.6

(continued)

Table 25. (continued)

Height (m)	DBH (cm)	Size-class*	Age (years)
6.00	4.7	IV	72.2
4.90	5.4	III	74.2
7.50	6.1	IV	76.3
8.30	6.4	IV	77.1
7.50	6.5	IV	77.4
8.50	6.6	IV	77.7
6.90	6.8	IV	78.3
7.90	7.1	IV	79.2
9.30	7.8	IV	81.2
10.80	7.9	IV	81.5
9.50	8.2	IV	82.4
10.00	8.7	IV	83.8
8.40	9.1	IV	85.0
12.00	10.0	V	87.6
14.80	10.9	V	90.2
11.00	11.0	IV	90.5
9.50	11.9	IV	93.1
13.00	12.5	V	94.9
15.80	13.6	V	98.1
12.50	13.8	V	98.7
16.50	14.6	V	101.0
15.50	16.9	V	107.7
19.00	17.4	V	109.2
18.00	17.5	V	109.4
21.00	18.8	VI	113.2
21.00	20.6	VI	118.5
19.50	21.9	VI	122.3
18.90	23.2	VI	126.0
22.00	24.1	VI	128.7
23.00	24.3	VI	129.2
23.00	26.7	VI	136.2
16.50	27.0	V	137.1
20.30	27.3	VI	138.0
23.00	27.9	VI	139.7
22.60	54.0	VII	215.7
24.50	61.3	VII	237.0

* Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12-19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

Table 26. Manilkara size-class densities in 13 transects at El Verde of Puerto Rico in February 1987.

Distribution	Populations of size-classes**							In transect	
	I	II	III	IV	V	VI	VII	Total (No.)	Density (No./ha)
T-1*	147	1	0	0	0	1	1	150	7500
T-2	5	0	0	0	0	0	0	5	250
T-3	0	2	2	0	0	0	0	4	200
T-4	0	1	0	0	0	0	0	1	50
T-5	10	1	2	3	0	0	0	16	800
T-6	80	1	3	1	4	1	0	90	4500
T-7	446	1	0	0	0	0	1	448	22400
T-8	115	4	1	0	2	0	0	122	6100
T-9	477	1	5	8	2	3	0	496	24800
T-10	94	24	3	1	1	0	0	123	6150
T-11	96	6	1	1	0	0	0	104	5200
T-12	178	6	6	2	1	2	0	195	9750
T-13	16	1	3	4	0	2	0	26	1300
Total in S-C**	1664	49	26	20	10	9	2	1780	-
Density in S-C (#/ha)	6400	188	100	77	38	35	8	6846	-

* T-1 = transect number 1, and so on. Each trasect is 100 m x 2 m.

** S-C = size-class. Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size- class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

Table 27. Manilkara age-class densities in 13 transects at El Verde of Puerto Rico in February 1987.

	Populations in 13 transects (each=100m x 2m)														
A-C*	1	2	3	4	5	6	7	8	9	10	11	12	13	T**	D***
0	148	5	0	1	10	80	447	118	478	114	96	178	16	1691	6504
20	0	0	1	0	1	1	0	1	0	3	4	6	1	18	69
30	0	0	1	0	0	0	0	0	0	1	3	3	0	8	31
40	0	0	1	0	0	0	0	1	1	0	0	1	0	4	15
50	0	0	0	0	0	1	0	0	1	0	0	1	1	4	15
60	0	0	1	0	1	1	0	0	4	3	0	0	2	12	46
70	0	0	0	0	2	2	0	0	4	1	1	2	3	15	58
80	0	0	0	0	1	0	0	0	4	0	0	1	0	6	23
90	0	0	0	0	1	2	0	0	1	0	0	1	1	6	23
100	0	0	0	0	0	2	0	1	0	1	0	0	0	4	15
110	0	0	0	0	0	0	0	0	1	0	0	1	0	2	8
120	0	0	0	0	0	0	0	0	2	0	0	1	1	4	15
130	1	0	0	0	0	1	0	1	0	0	0	0	1	4	15
140	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
160	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
180	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
190	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
210	1	0	0	0	0	0	0	0	0	0	0	0	0	1	4
220	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
230	0	0	0	0	0	0	1	0	0	0	0	0	0	1	4
240	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T**	150	5	4	1	16	90	448	122	496	123	104	195	26	1780	6846

* A-C = age-class. The number represents the beginning of the age-class.

** T = Total.

*** D = density (No./ha).

Table 28. Above ground biomass and nutrient (P, K, Ca and Mg) stocks of size-classes and age-classes in 13 transects at El Verde of Puerto Rico in February 1987.

Distribution	Biomass (kg)	P (g)	K (g)	Ca (g)	Mg (g)
Size-class*					
I	0.33	0.16	1.99	2.06	1.09
II	0.32	0.16	1.75	2.40	0.89
III	37.14	5.85	77.28	89.64	32.37
IV	439.5	46.1	728.7	827.5	264.9
V	1633.2	142.5	2367.7	2685.0	786.0
VI	3774.7	307.4	5205.5	5900.1	1668.5
VII	7124.6	476.5	8508.2	9629.4	2474.0
Age-class					
0-19.9	0.444	0.220	2.691	3.013	1.458
20-29.9	0.143	0.071	0.780	1.068	0.398
30-39.9	0.161	0.069	0.760	1.012	0.380
40-49.9	0.178	0.067	0.741	0.964	0.364
50-59.9	0.565	0.174	1.957	2.460	0.937
60-69.9	18.66	3.50	42.45	49.62	18.71
70-79.9	164.56	18.68	289.26	328.67	109.3
80-89.9	218.19	22.31	355.38	403.48	127.5
90-99.9	477.01	45.39	737.12	836.45	255.2
100-109.9	678.01	60.23	996.41	1130.1	333.4
110-119.9	780.44	63.73	1078.3	1222.3	346.2
120-129.9	1415.7	117.5	1979.1	2243.5	640.1
130-139.9	2131.2	170.2	2897.9	3284.1	919.9
140-149.9	0	0	0	0	0
150-159.9	0	0	0	0	0
160-169.9	0	0	0	0	0
170-179.9	0	0	0	0	0
180-189.9	0	0	0	0	0
190-199.9	0	0	0	0	0
200-209.9	0	0	0	0	0
210-219.9	3014.0	205.0	3643.3	4123.9	1068.0
220-229.9	0	0	0	0	0
230-239.9	4110.7	271.6	4864.9	5505.5	1405.9
240-249.9	0	0	0	0	0
Total in 13 transects	13009.8	978.65	16891.0	19136.1	5227.6
Amount/m^2	5.00	0.38	6.50	7.36	2.01

* Refer to Table 24.

Table 29. Comparison of Manilkara population densities in this study to those in previous studies*.

Investigation	Site	Time	Absolute density (#/ha) DBH≥4cm	Absolute density (#/ha) DBH≥10cm
This study	El Verde 13 transects 0.26 ha.	1987	157.7	80.8
Crow (1980)	El Verde one plot 0.72 ha.	1976	202.8	76.4
		1951	200.0	56.9
		1943	155.6	30.6
Smith (1970)	El Verde 1.57 ba.	1970	-	35.5
Briscoe and Wadsworth (1970)	6 plots combined 2.09 ha.	1946	62.2	25.4

* The absolute densities are derived from data of previous studies.

Table 30. Size-classified life table of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico.*

Size-class	Age (years)	Density (#/ha)	N(x)	L(x)	D(x)	Q(x)
I	0	6400	6846	1000	935	0.935
II	8	188	446	65	27	0.415
III	37	100	258	38	15	0.395
IV	71	77	158	23	11	0.478
V	95	38	81	12	6	0.500
VI	117	35	42	6	5	0.833
VII	146	8	8	1		

* N(x) = number of survivors per hectare at the beginning of size-class

L(x) = number of survivors per thousand at the beginning of size-class, L(x) = N(x)/6846*1000

D(x) = number of deaths per thousand between size-classes, D(x) = L(x)-L(x+1)

Q(x) = mortality rate, Q(x) = D(x)/L(x)

Size-class I: height < 15 cm
Size-class II: height 15 - 49.9 cm
Size-class III: height 0.5 - 4.99 m
Size-class IV: height 5 - 11.99 m
Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm
Size-class VI: DBH 20 - 29.9 cm
Size-class VII: DBH ≥ 30 cm

Table 31. Age-classified life table of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico.*

Age-class	Density (#/ha)	n(x)	l(x)	d(x)	q(x)
0	6504	6846	1000	950	0.950
20	69	342	50	10	0.200
30	31	273	40	5	0.125
40	15	242	35	2	0.057
50	15	227	33	2	0.061
60	46	212	31	7	0.226
70	58	165	24	8	0.333
80	23	108	16	4	0.250
90	23	85	12	3	0.250
100	15	62	9	2	0.222
110	8	46	7	1	0.143
120	15	38	6	3	0.500
130	15	23	3	2	0.667
140	0	8	1	0	0.000
150	0	8	1	0	0.000
160	0	8	1	0	0.000
170	0	8	1	0	0.000
180	0	8	1	0	0.000
190	0	8	1	0	0.000
200	0	8	1	0	0.000
210	4	8	1	1	0.500
220	0	4	1	0	0.000
230	4	4	1	1	1.000
240	0	0	0		

* n(x) = number of survivors per hectare at the beginning of age-class

l(x) = number of survivors per thousand at the beginning of age-class, $l(x) = n(x)/6846*1000$

d(x) = number of deaths per thousand between age-classes, $d(x) = l(x)-l(x+1)$

q(x) = mortality rate, $q(x) = d(x)/l(x)$

Age-class: the number represents the beginning of the age-class.

Table 32. Hypothetical mortality rates and corresponding population densities in model simulations***.

	Scenario I		Scenario II	
Age-class	PD* (#/ha)	q** (%/yr)	PD (#/ha)	q (%/yr)
0-9.9	3773	20.00	1471	9.30
10-19.9	511	20.00	580	9.30
20-29.9	69	8.00	229	8.00
30-39.9	31	3.63	103	3.63
40-49.9	22	3.63	72	3.63
50-59.9	15	0.83	50	0.83
60-69.9	14	0.83	46	0.83
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.

* PD = population density.
** q = annual mortality rates.
*** Scenario I is the movement of young seedling populations (with an initial cohort of 3773 young seedlings) under the assumption of absence of hurricane. Scenario II is the movement of young seedling populations which is influenced by a hurricane. It is assumed that 61% of the initial cohort of 3773 young seedlings are directly destroyed by the hurricane [an analogy of damage by Hurricane Hugo (You and Petty, in press)] and 1471 young seedlings survive. Mortality rates 20 years after the hurricane are assumed to be similar to those under absence of hurricane conditions.

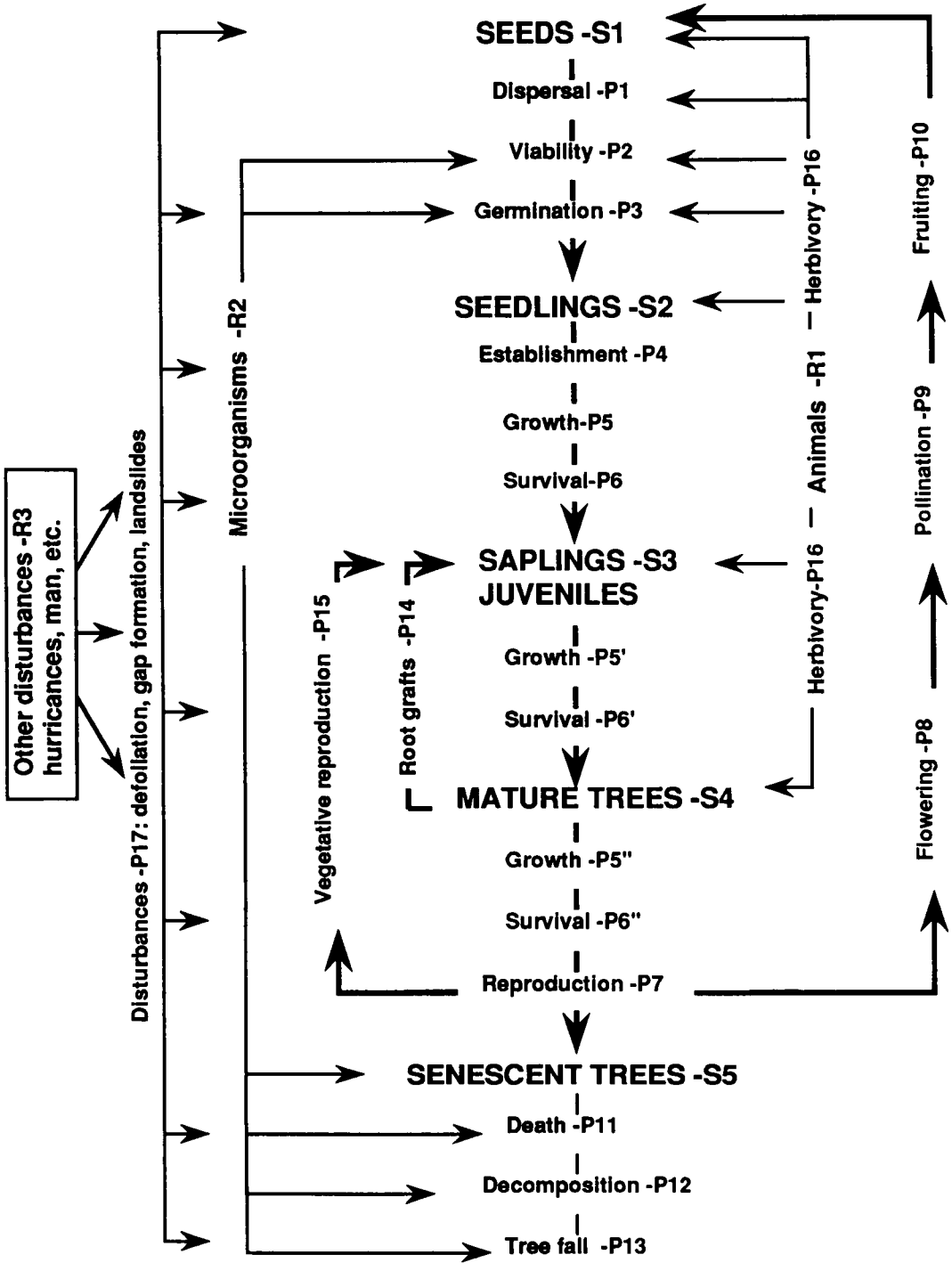


Figure 1. A conceptual model of the population dynamics of tropical trees. (From McCormick, in press)

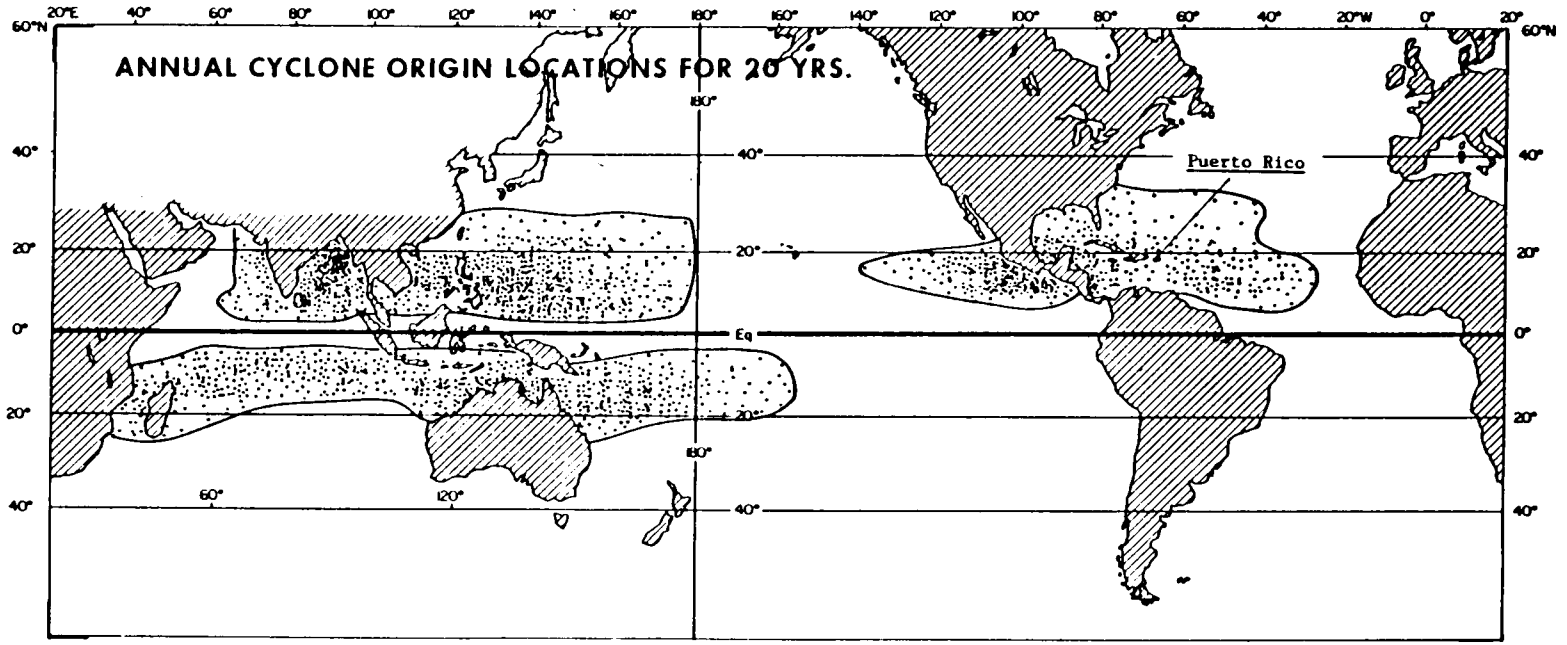
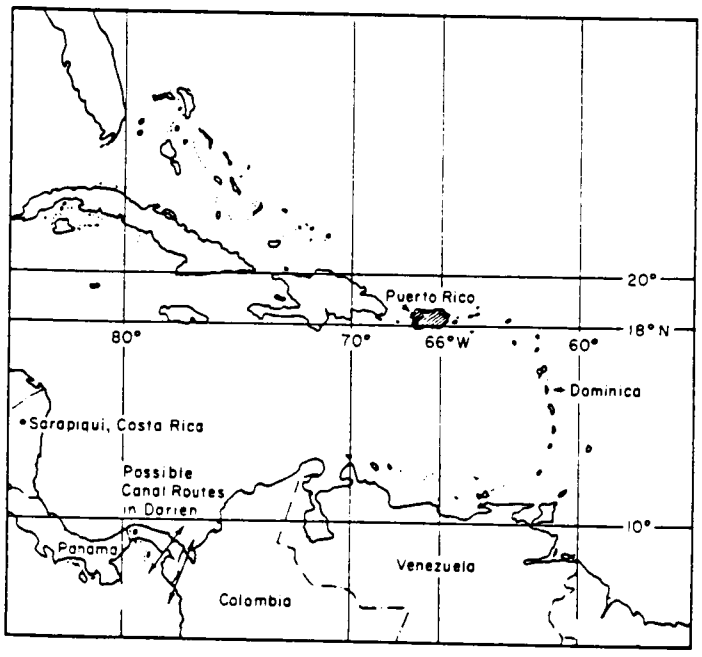


Figure 2. Location of the island of Puerto Rico within the "hurricane belt." Dots represent the locations of initial genesis points of tropical cyclones for a 20-year period (map adapted from Gray 1979, cited in Anthes, 1982).

(A)



(B)

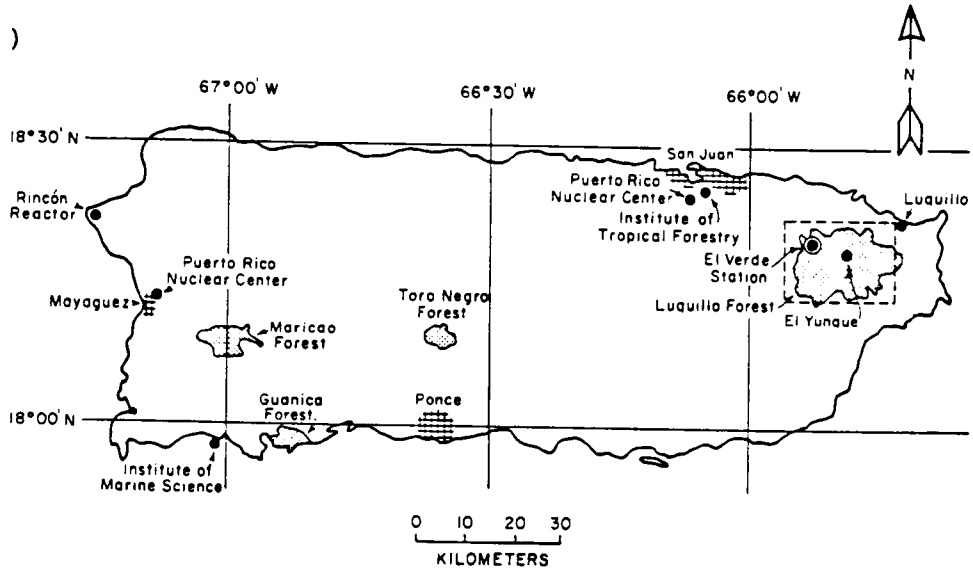


Figure 3. (A) Geographic location of the island of Puerto Rico. (B) The study area at the El Verde field station on the northwestern slope of the Luquillo Experimental Forest. El Yunque is the highest peak in the Luquillo Mountains. (Maps adapted from Odum, 1970a).

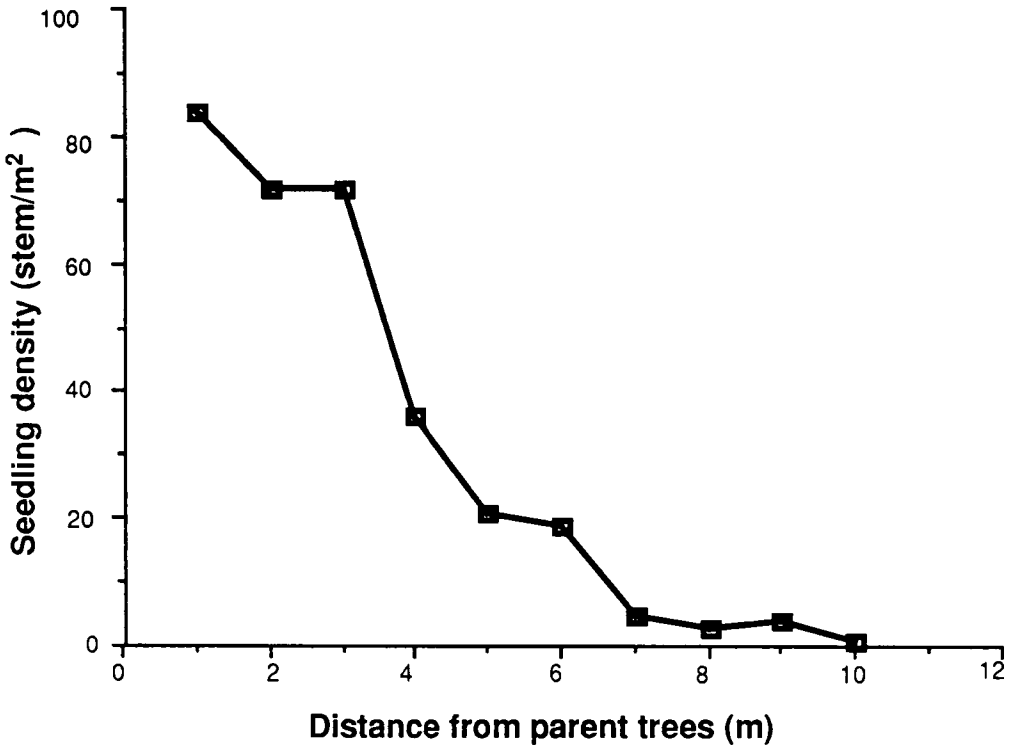


Figure 4. Seedling distribution pattern under parent trees. Most seedlings were dispersed within a radius of 10 m from the tree base by gravity and wind.

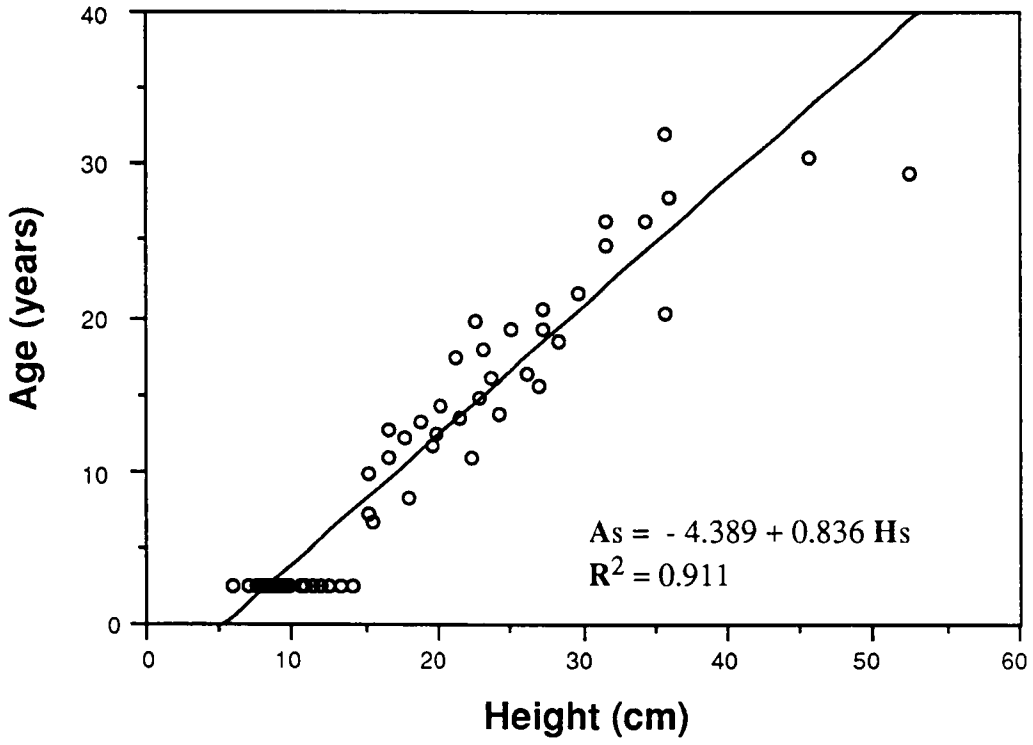


Figure 5. Regression of age on height for Manilkara seedlings (including 10 recently germinated seedlings, 27 young seedlings and 34 old seedlings).

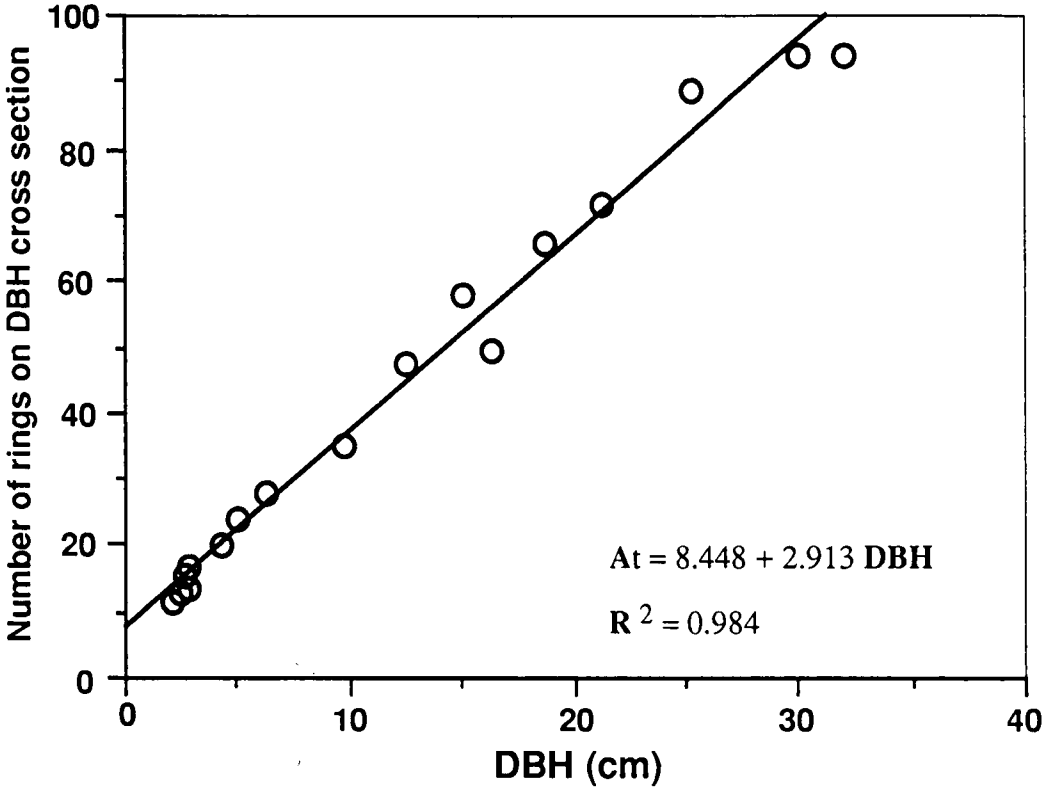


Figure 6. Regression of growth ring number against DBH for 17 Manilkara trees. This regression equation was used to estimate durations of the tree life period (after growth reached 130 cm in height) for all Manilkara trees which were measured in the permanent transects in 1987.

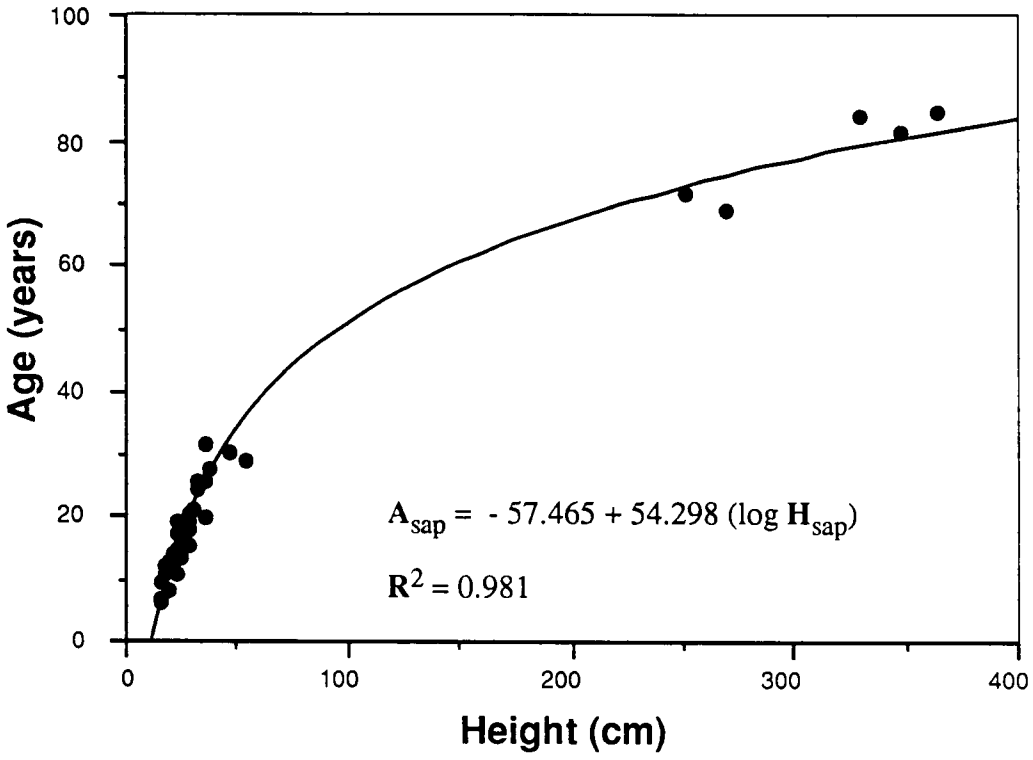


Figure 7. Regression of age on height for 34 old Manilkara seedlings and 5 small trees. The regression equation is used to estimate the age of Manilkara saplings in the permanent transects which have a height between 0.5 m to 1.3 m.

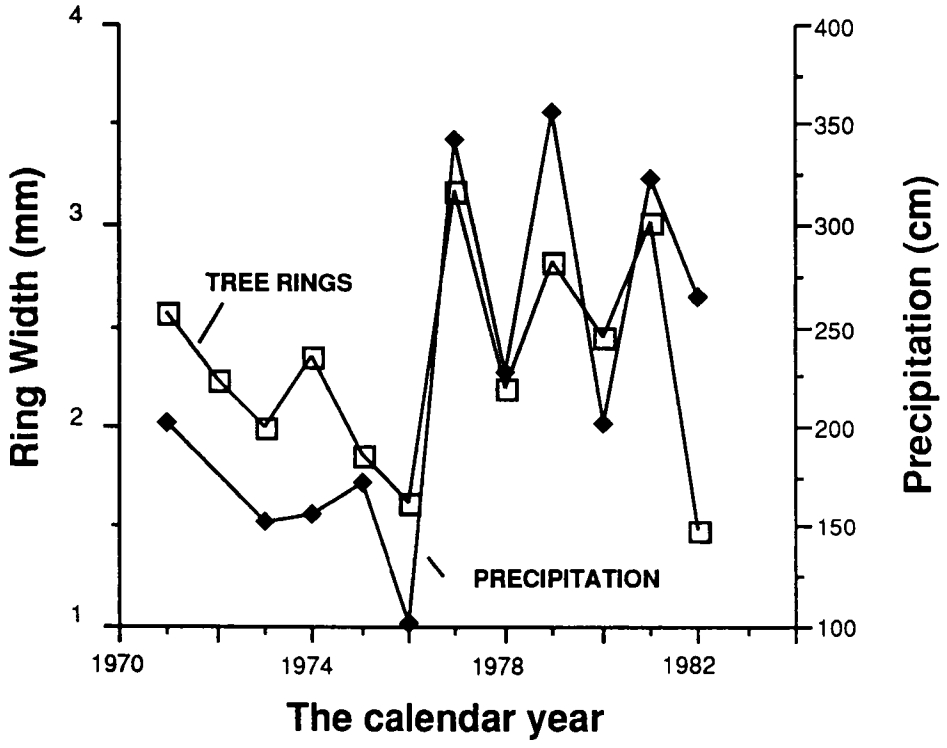


Figure 8. Patterns of rainfall and patterns of tree ring width from cross sections of selected Manilkara trees. [From Xia and McCormick, in preparation]

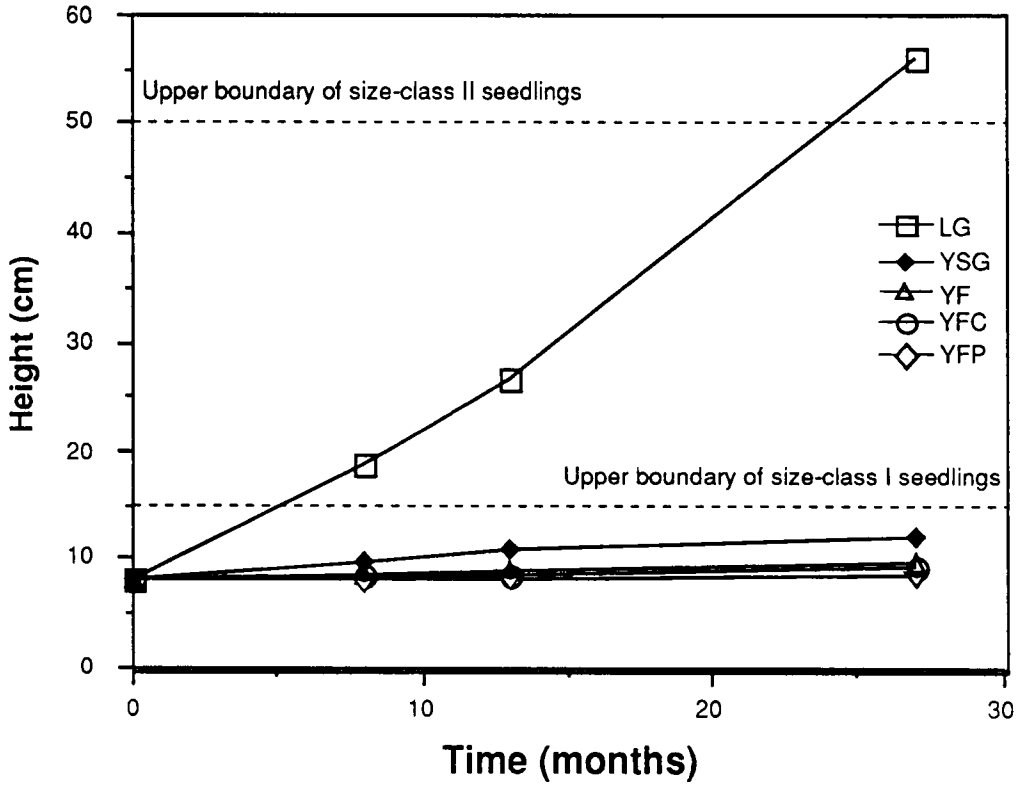


Figure 9. Height growth of young and old seedlings during the period of investigation. LG = under large gap conditions; YSG = in a small gap; YF = in the understory and without competition to herbaceous vegetation; YFC = in the understory and with competition to herbaceous vegetation; and YFP = under parent trees in forest shade.

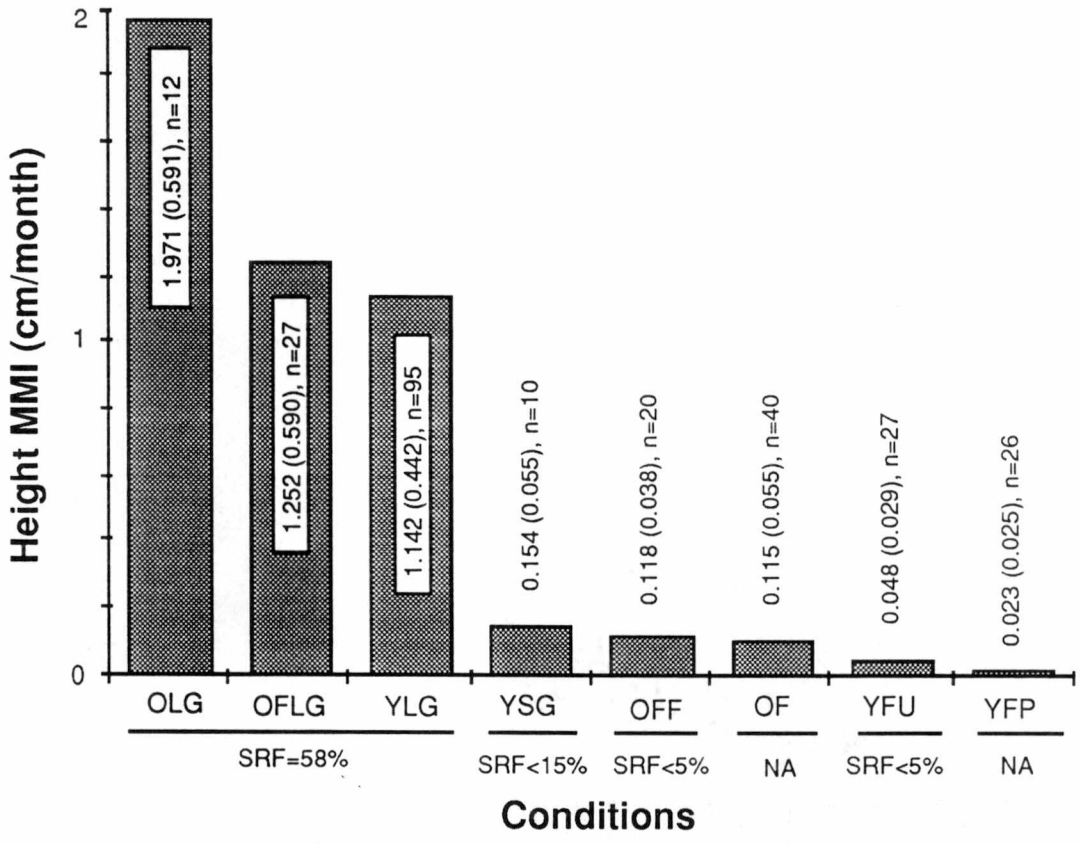


Figure 10. Seedling acclimatization to various light conditions. OLG = old seedlings growing up from young seedlings in large gap conditions; OFLG = old seedlings transplanted from forest shade to the large gap; YLG = young seedlings in the large gap; YSG = young seedlings in the small gap; OFF = old seedlings transplanted from forest shade to pots and returned to forest shade; OF = old seedlings in forest shade; YFU = young seedlings in forest shade; YFP = young seedlings under parent trees in forest shade; SRF = solar radiation factor (percent of the full solar radiation above the canopy); NA = data not available; and Height MMI = mean monthly increment of height.

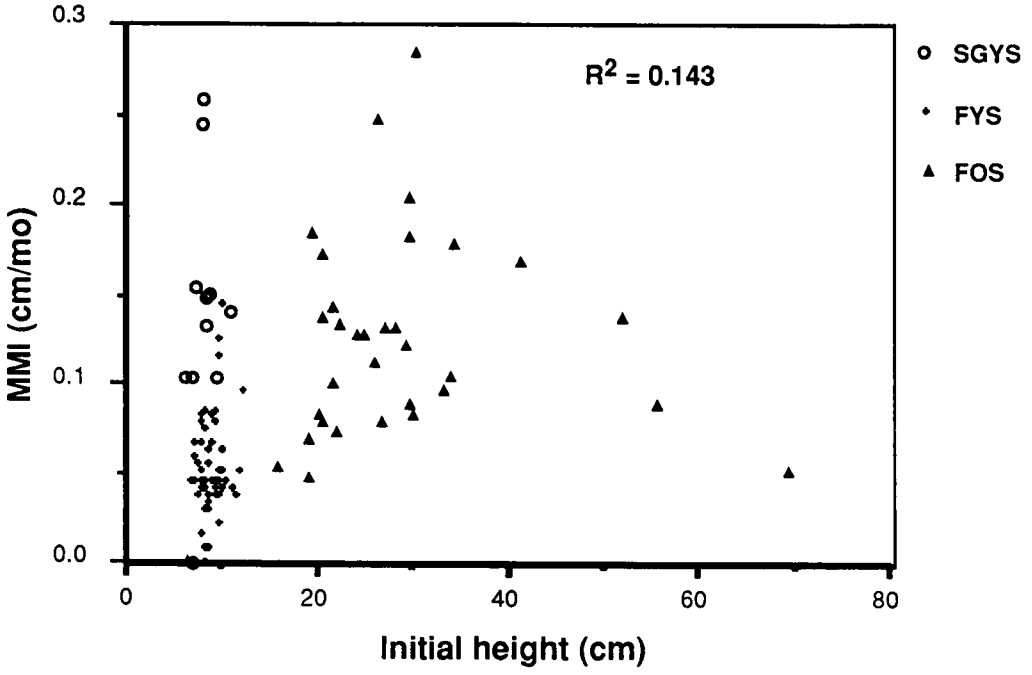


Figure 11. Relationship of Manilkara seedling height growth rate to initial height (the height in 1987). There is no significant correlation between mean monthly increments (MMI) and initial heights for all seedlings studied in the forest. Many small seedlings were able to grow faster under good light conditions (e.g. a small gap) than some taller old seedlings under forest shade. SGYS = young seedlings growing in a small gap; FYS = young seedlings growing in forest shade; FOS = large old seedlings growing in forest shade.

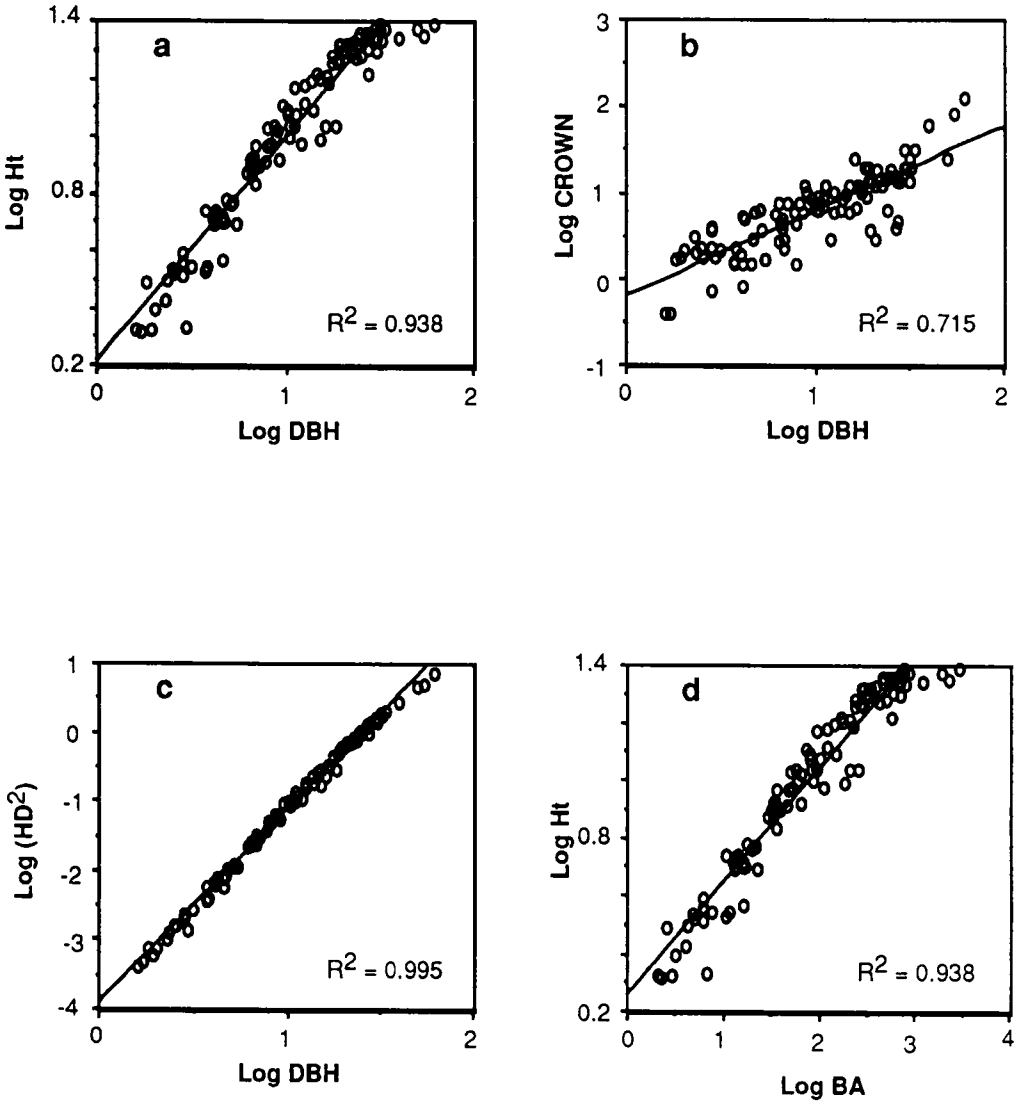
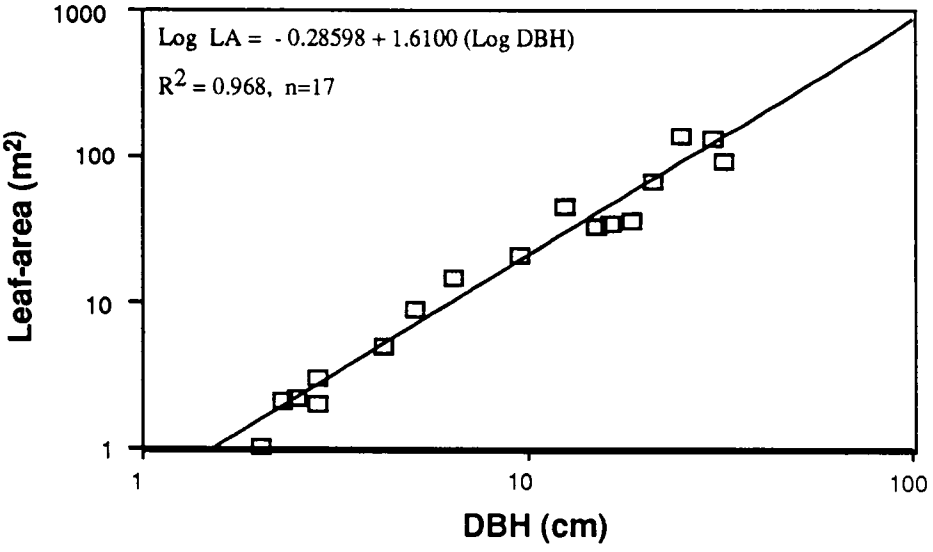


Figure 12. Correlations between tree growth parameters (DBH, height, basal-area and trunk volume).



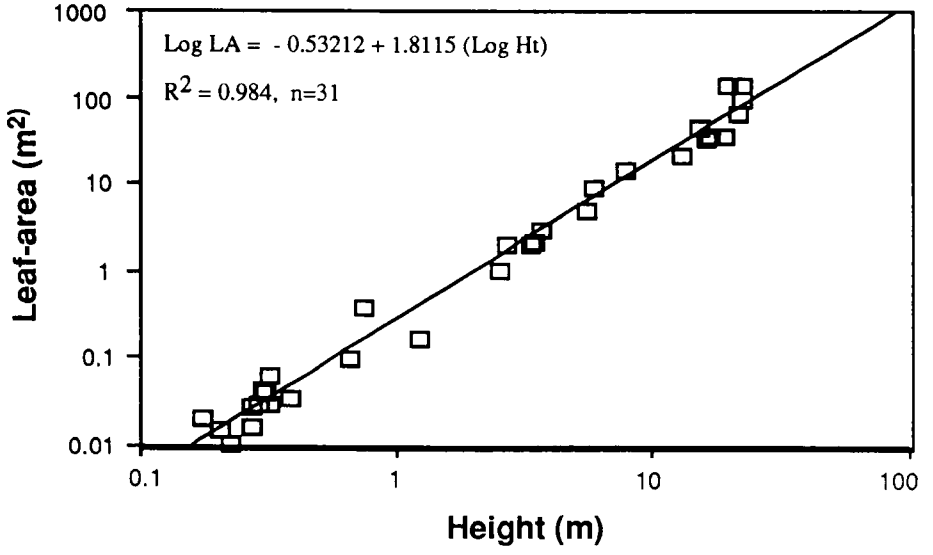


Figure 13. Regressions of leaf area on DBH and height (Ht) for 31 individuals of Manilkara.

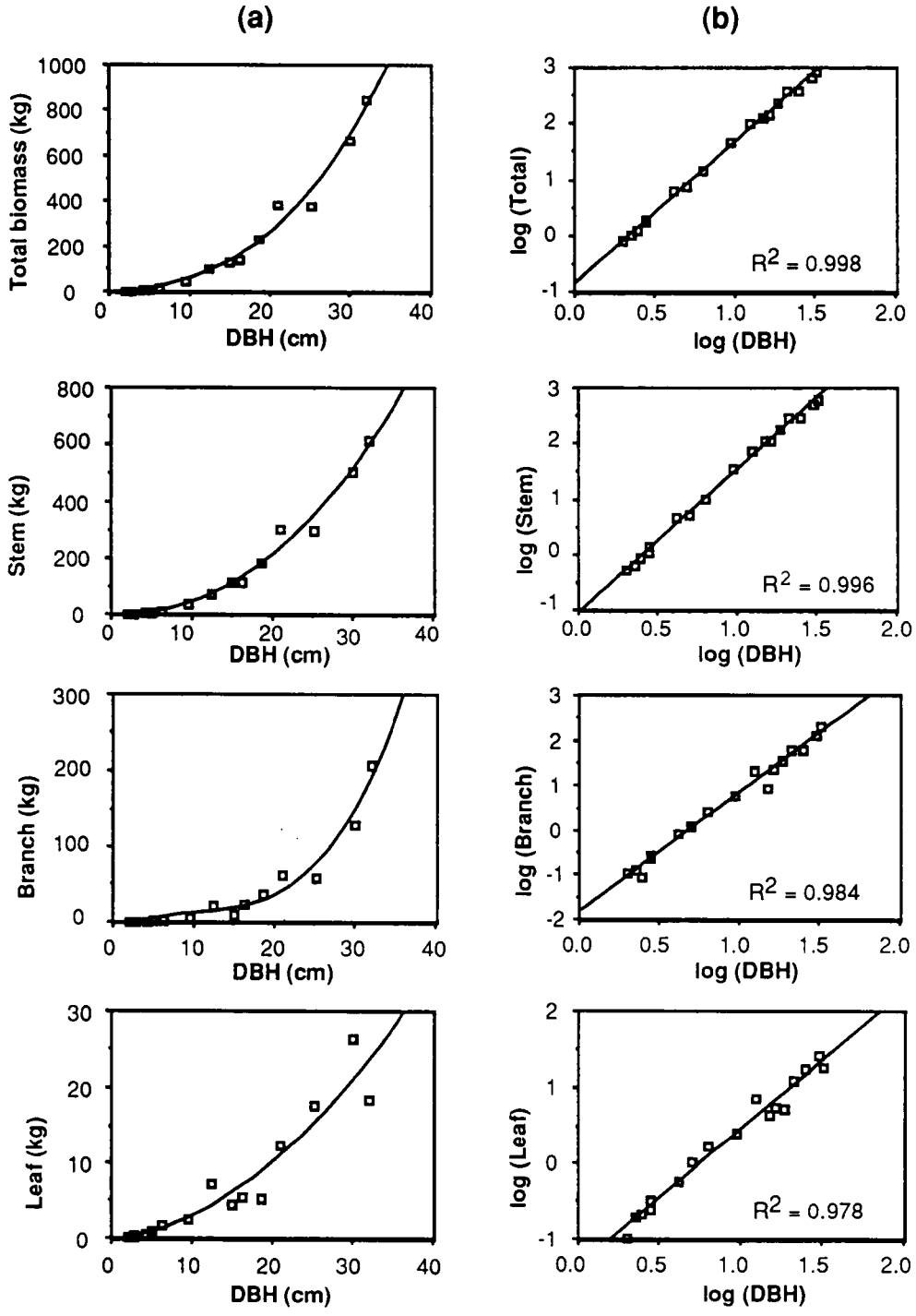


Figure 14. Correlations of biomass of different organs with tree DBH. Arithmetic relationships of biomass and DBH are displayed in (a), and logarithmic regressions are displayed in (b).

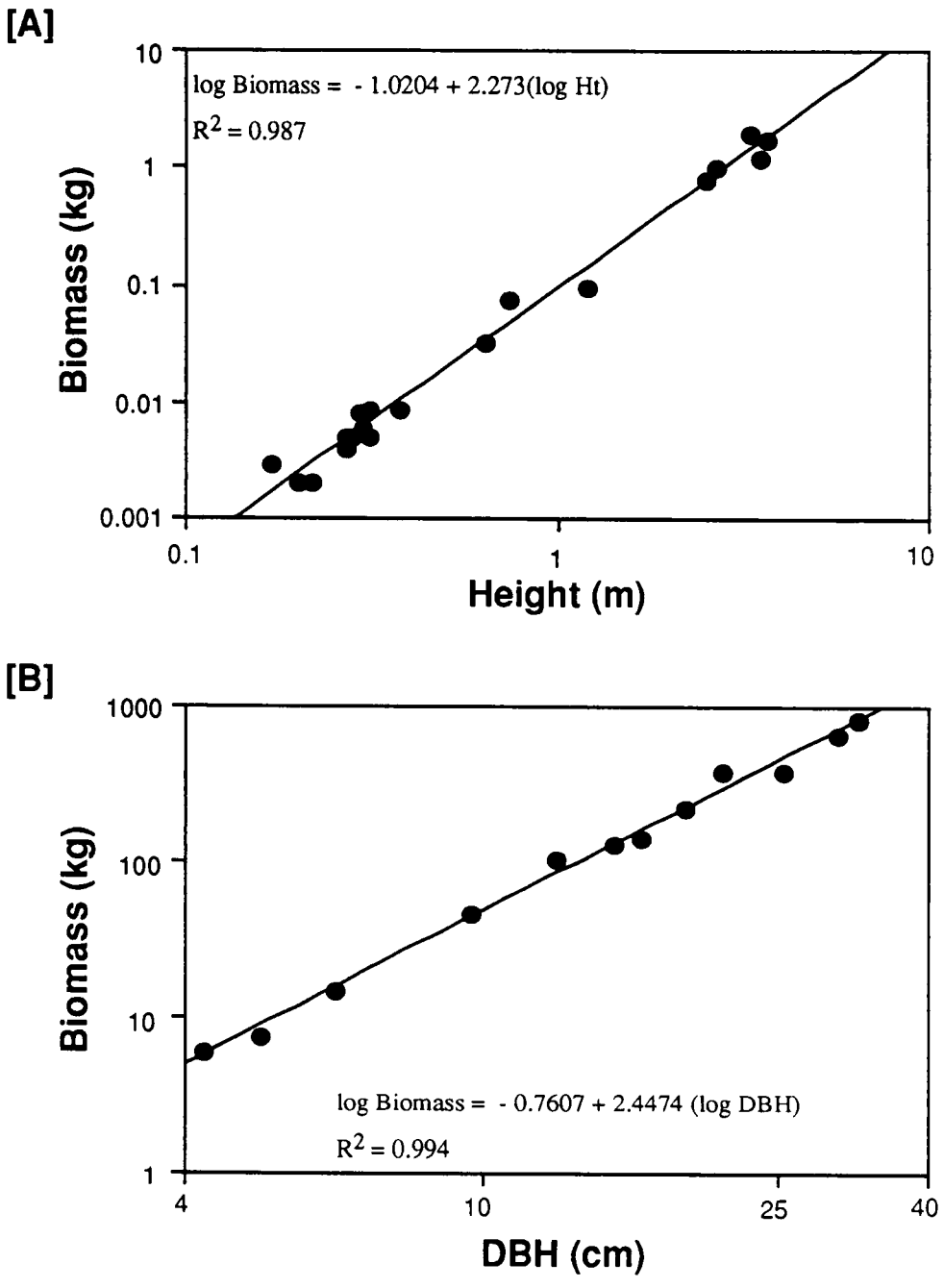


Figure 15. Regressions of biomass on height, presented in [A] (for individuals which had a height less than 5 m) and DBH, presented in [B] (for individuals 5 m or more in height) for Manilkara populations.

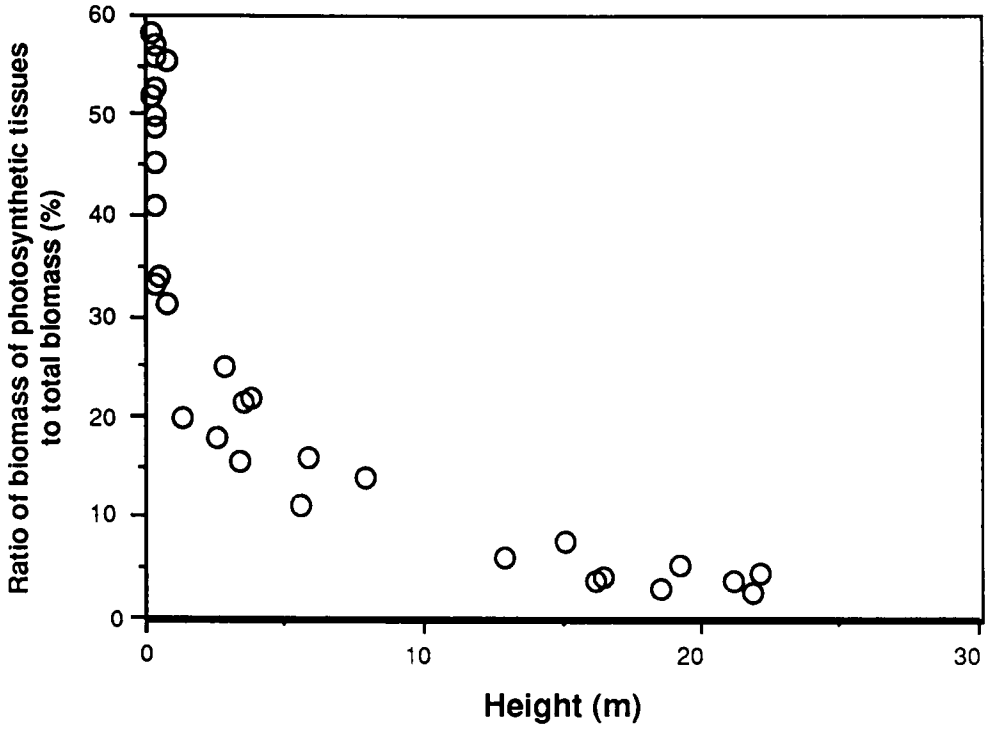


Figure 16. Changes in the ratio of biomass of photosynthetic tissues to total biomass with increasing plant size.

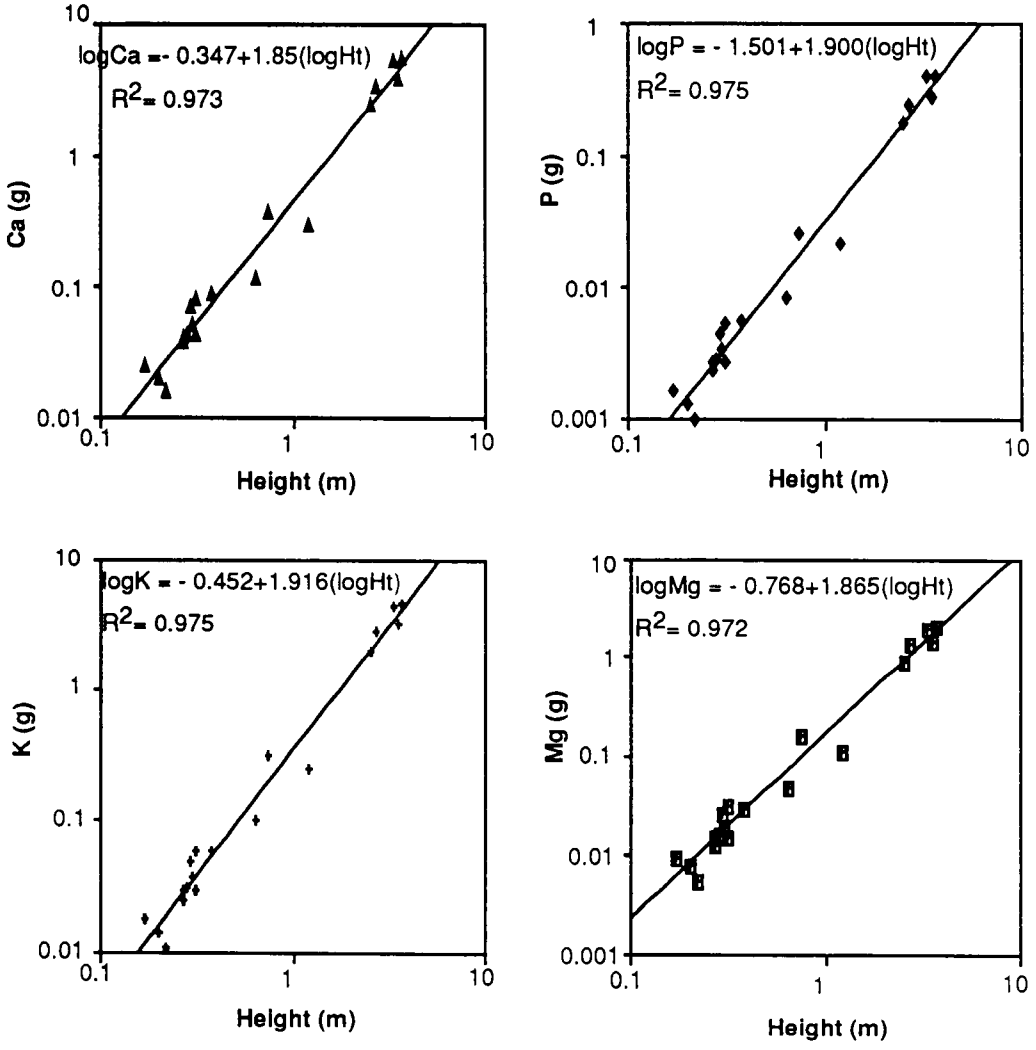


Figure 17. Regressions of P, K, Ca and Mg stocks (per tree) on height for Manilkara individuals which had a height less than 5 m.

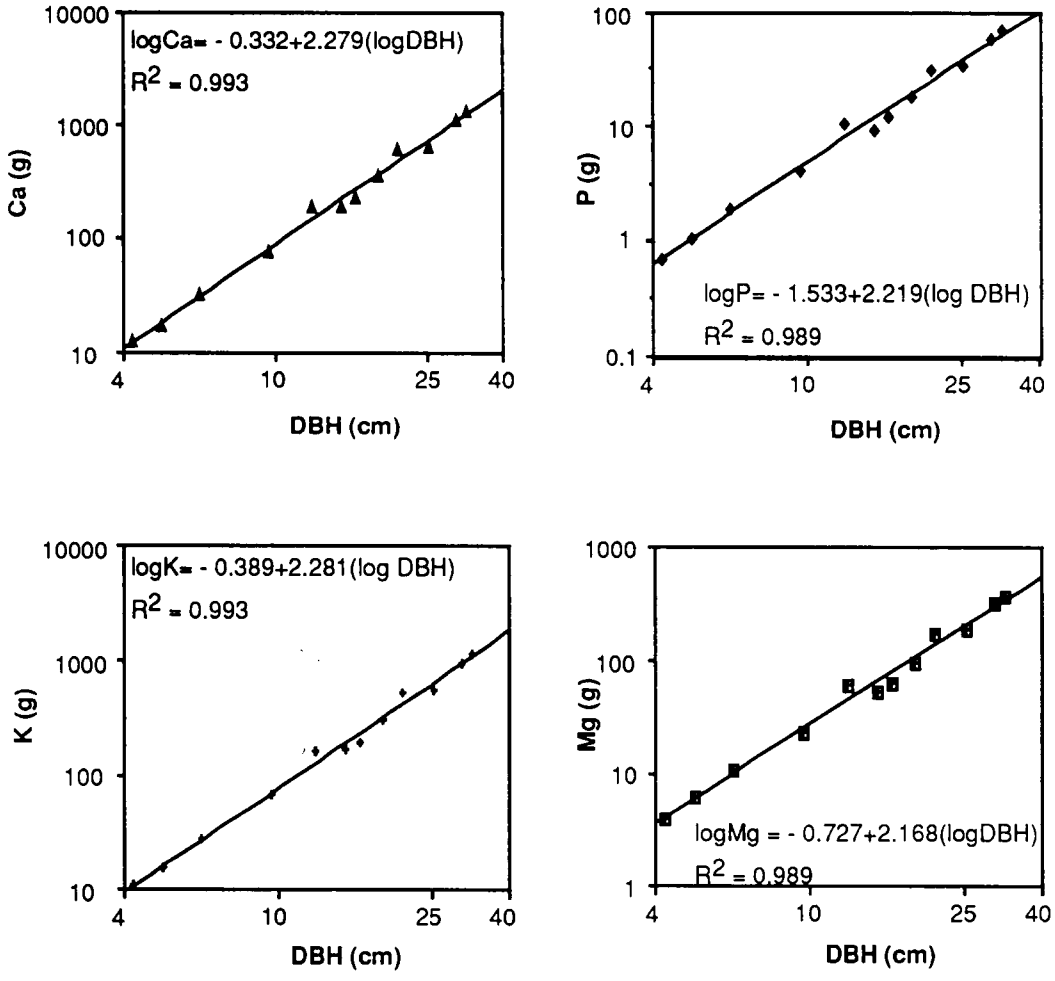


Figure 18. Regressions of P, K, Ca and Mg stocks (per tree) on DBH for Manilkara individuals 5 m or more in height.

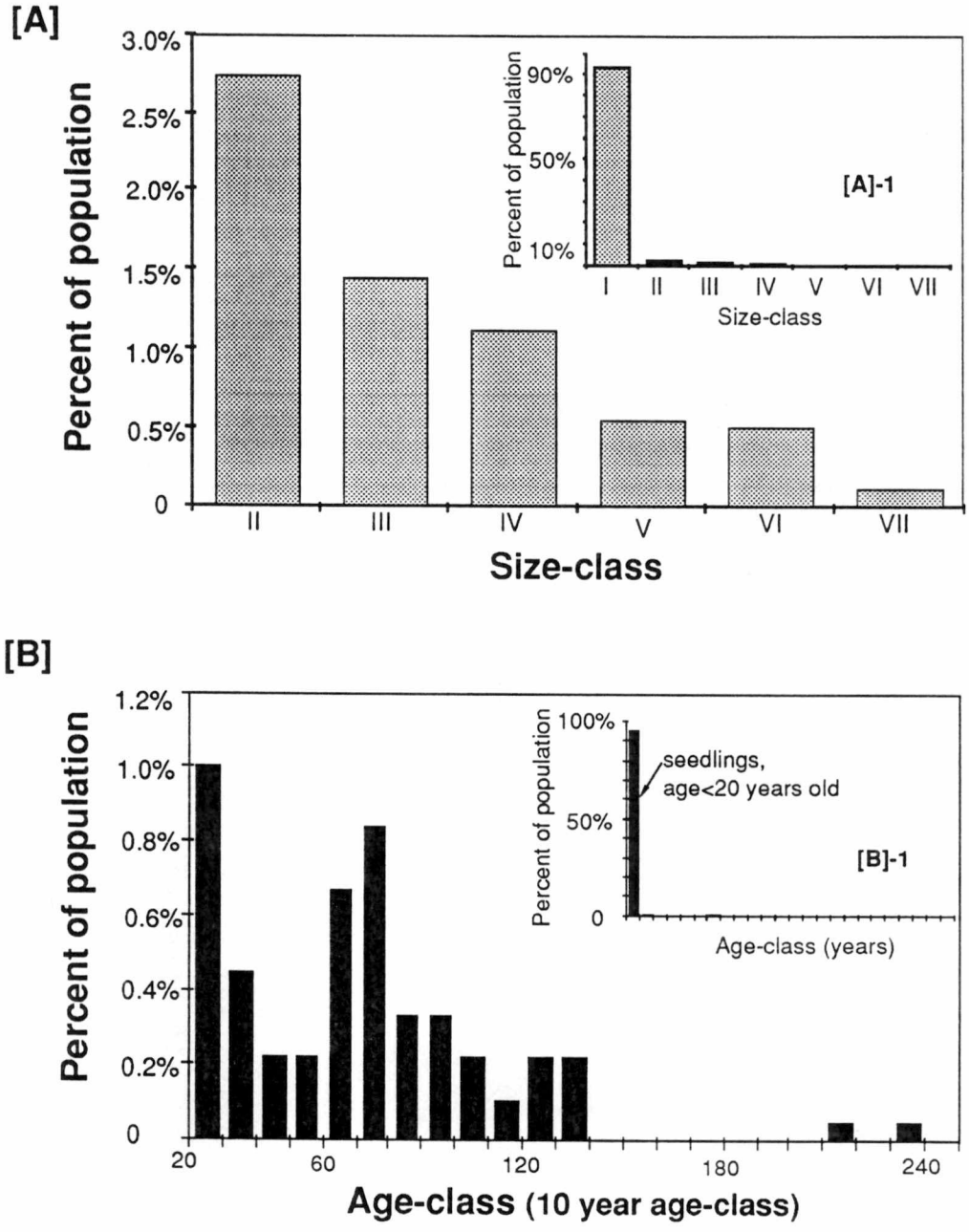


Figure 19. Frequency distributions of size-classes [A] and age-classes [B] of Manilkara populations in the Tabonuco Forest at El Verde of Puerto Rico in 1987. Inserted graphs include young seedling populations (size-class I in [A]-1 or age-class 0 - 19.9 years in [B]-1). Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

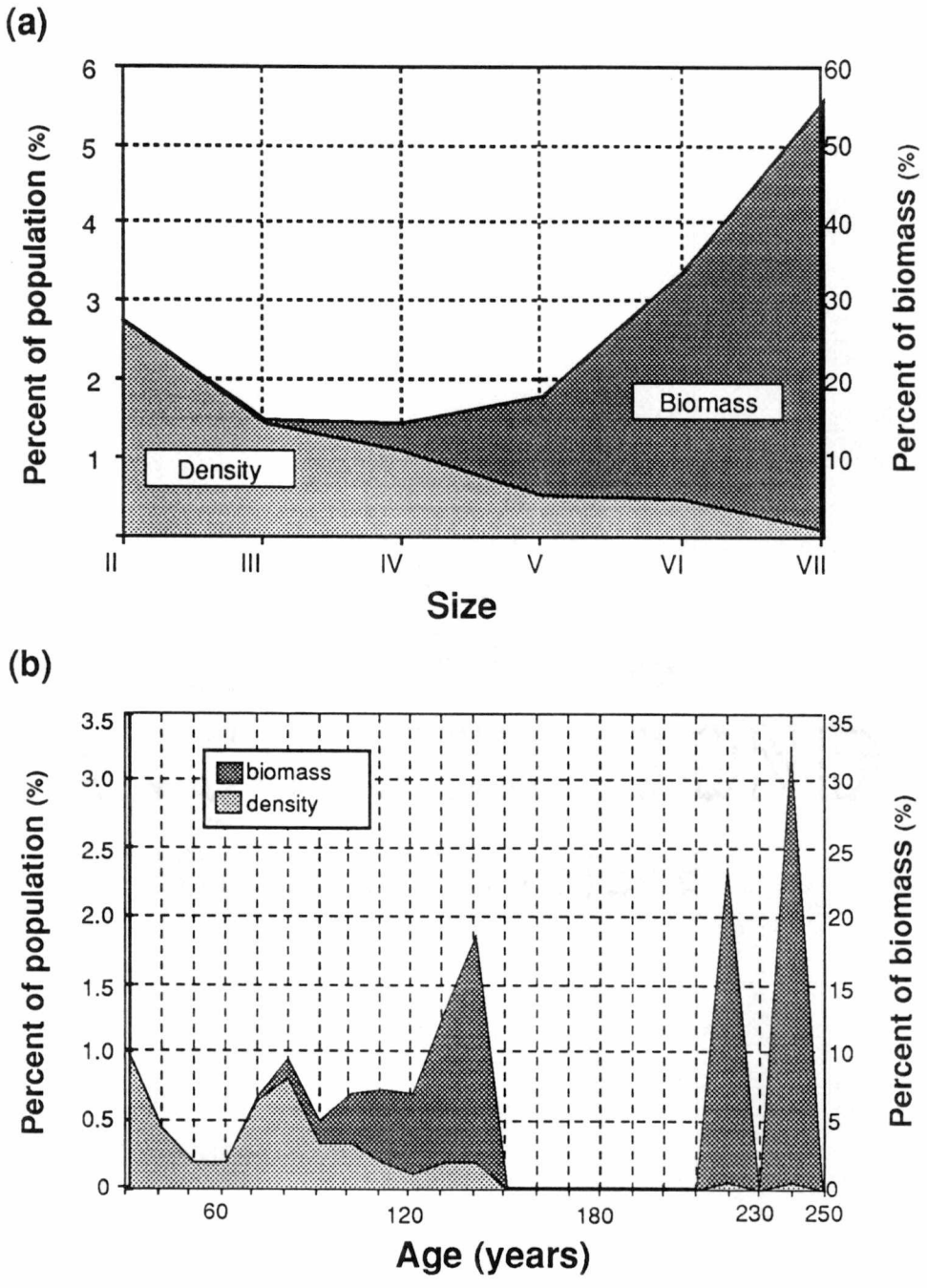


Figure 20. Comparison of Manilkara biomass frequency distributions with density frequency distributions of size-classes (a) and age-classes (b) in the Tabonuco Forest at El Verde of Puerto Rico in 1987. Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

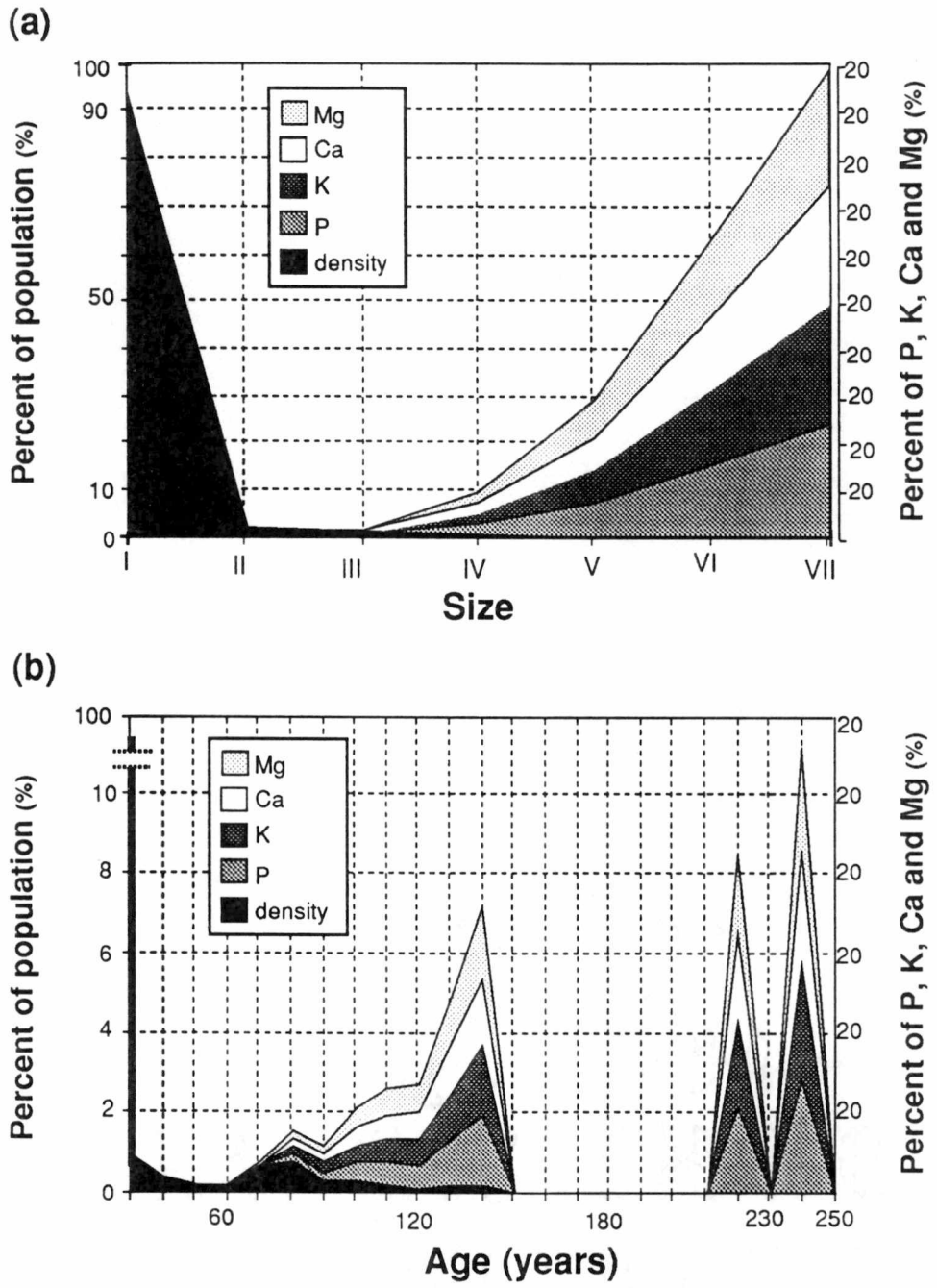


Figure 21. Comparison of Manilkara nutrient frequency distributions with density frequency distributions in size-classes (a) and in age-classes (b) in the Tabonuco Forest at El Verde of Puerto Rico in 1987. Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

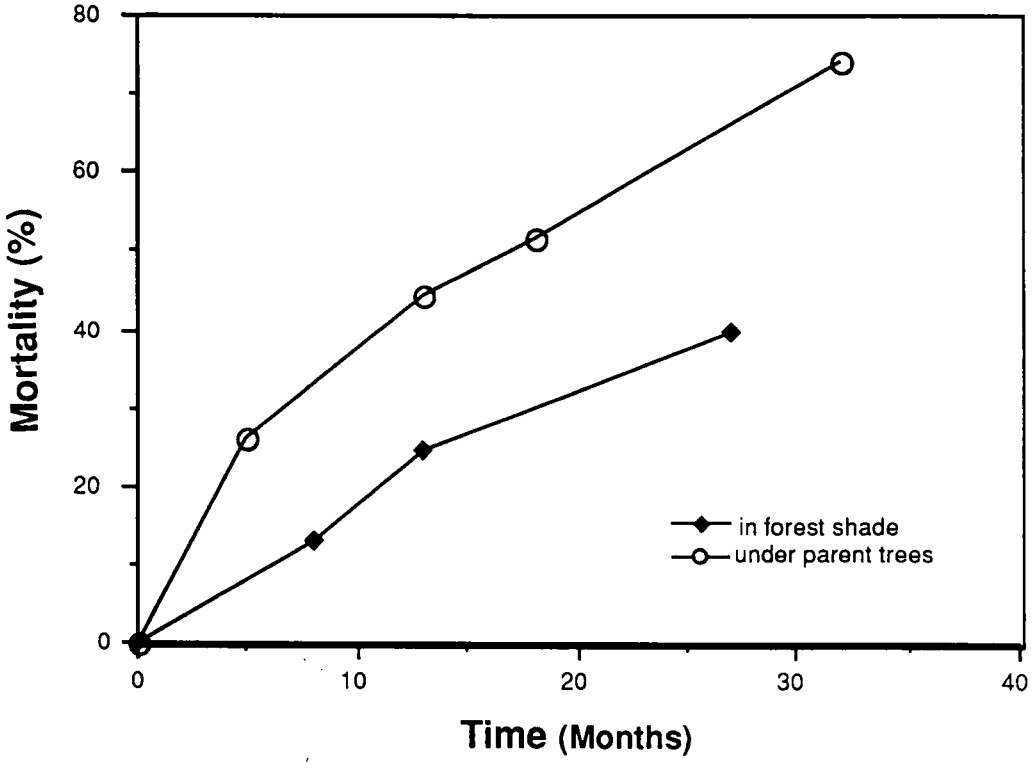


Figure 22. Mortality of young Manilkara seedlings in forest shade and under parent trees.

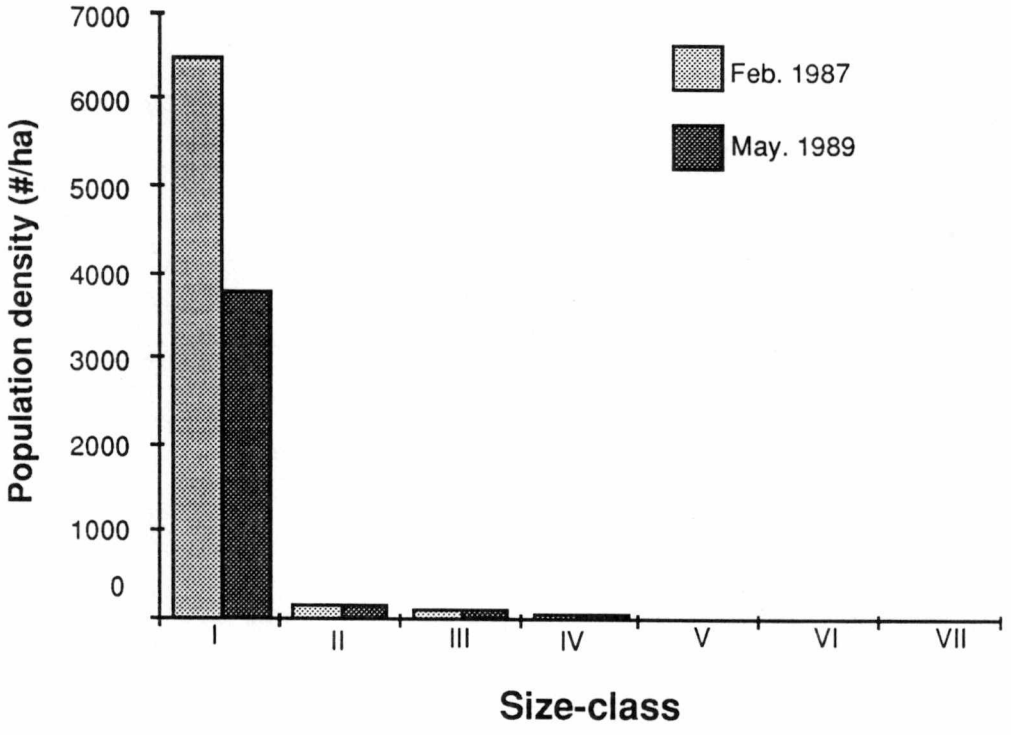


Figure 23. Changes in densities of size-classified populations of Manilkara from February of 1987 to May of 1989. Only size-class I (young seedlings) declined. Other size-classes remained unchanged. Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

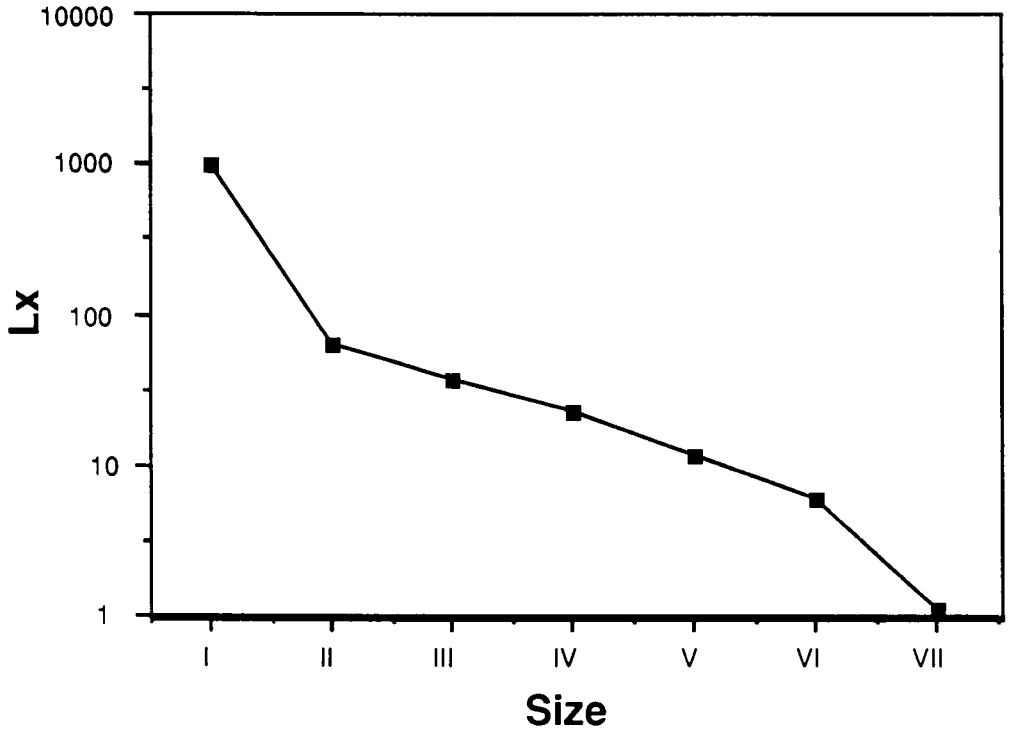


Figure 24. Survivorship curve of size-classified populations of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico. Lx = the number of survivors per thousand at the beginning of the size-class; Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 -29.9 cm; and Size-class VII: DBH ≥ 30 cm.

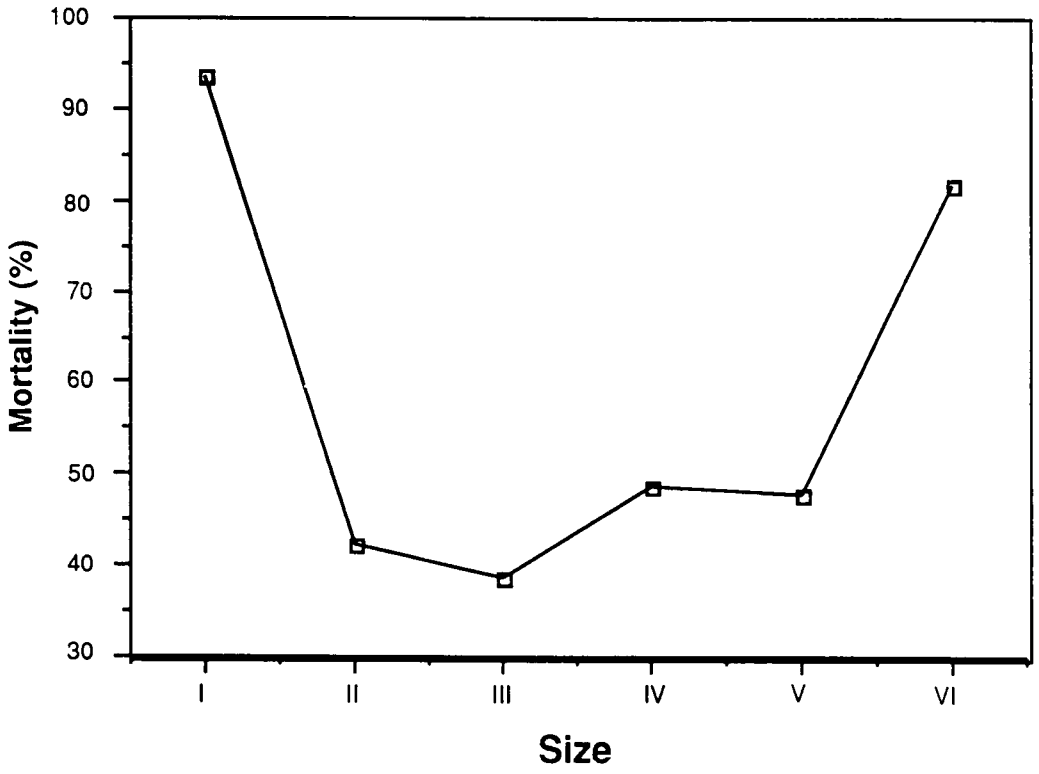


Figure 25. Mortality curve of size-classified populations of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico. Size-class I: height < 15 cm; Size-class II: height 15 - 49.9 cm; Size-class III: height 0.5 - 4.99 m; Size-class IV: height 5 - 11.99 m; Size-class V: height 12 - 19.99 m or DBH 10 - 19.9 cm; Size-class VI: DBH 20 - 29.9 cm; and Size-class VII: DBH ≥ 30 cm.

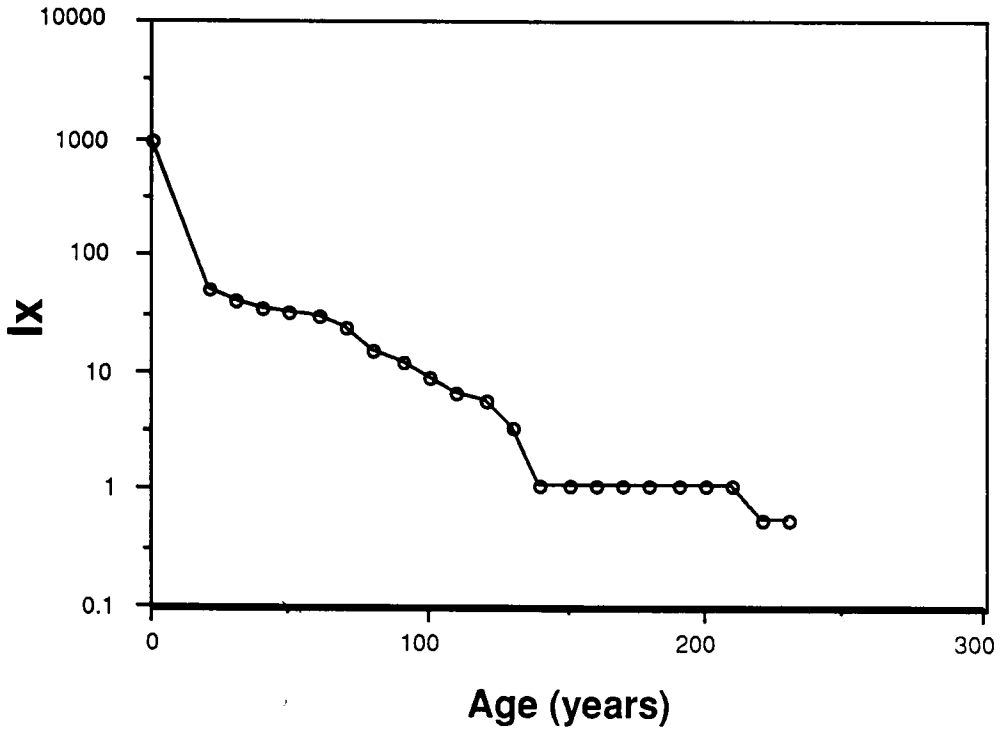


Figure 26. Survivorship curve of age-classified populations of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico. lx = the number of survivors per thousand at the beginning of the age-class.

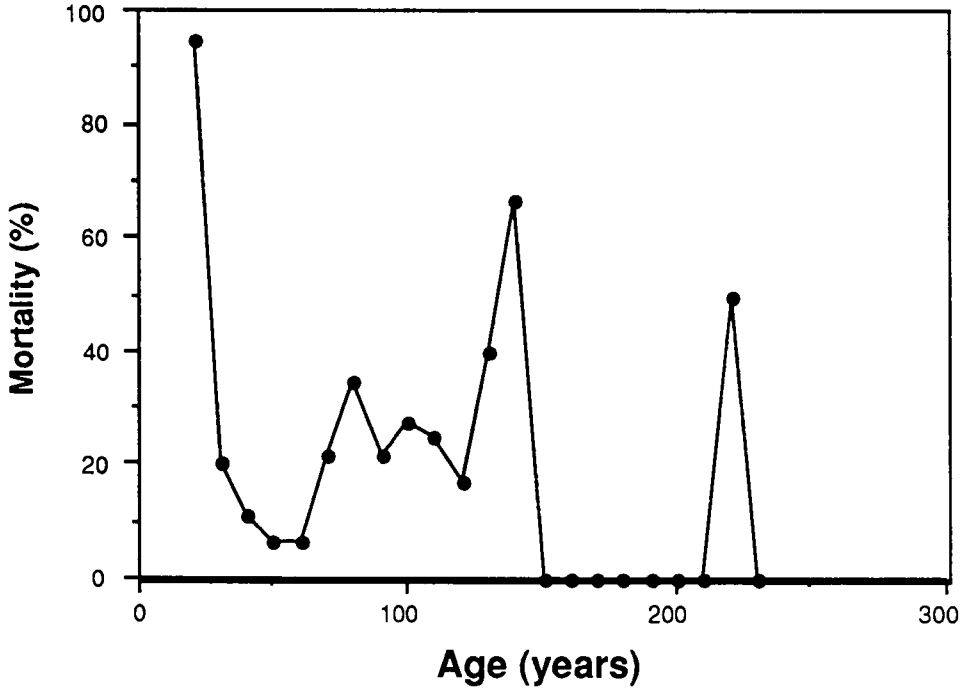


Figure 27. Mortality curve of age-classified populations of Manilkara in the Tabonuco Forest at El Verde of Puerto Rico.

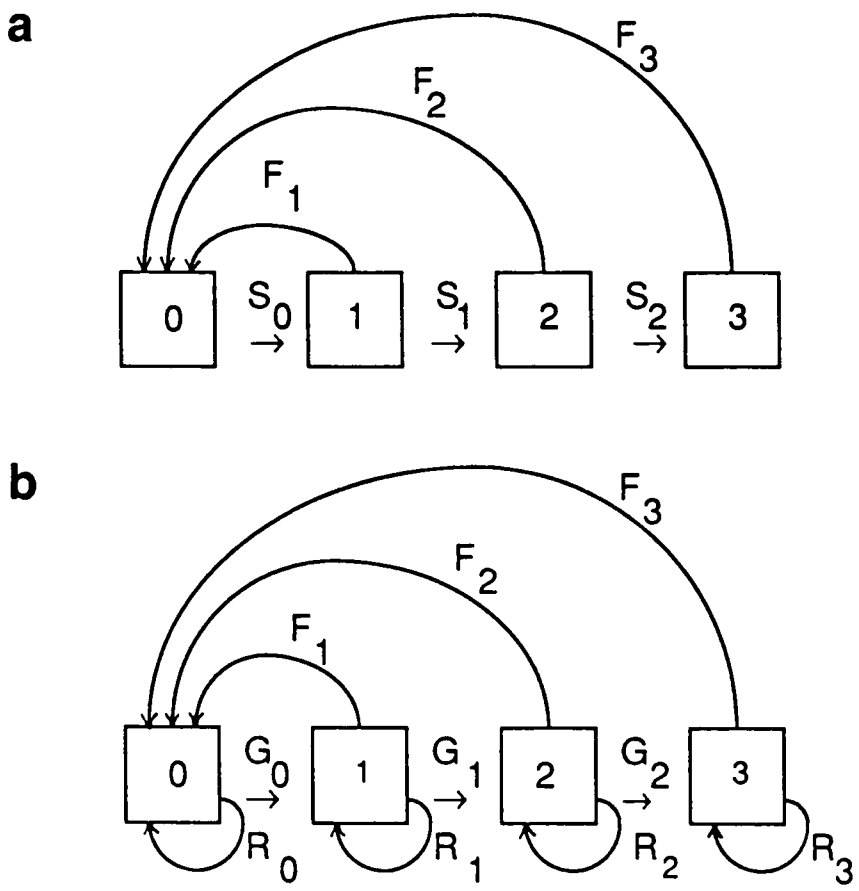


Figure 28. Two conceptual models used in tree population studies. Boxes represent life cycle stages; arrows are transitions. (a) an age-classified population; (b) a size-classified population. F = number of offspring per individual; S = probability of survival (1 - mortality); G = probability of growth into next size class; R = probability of remaining in size-class (mortality = 1 - G - R). [From Harcombe, 1987]

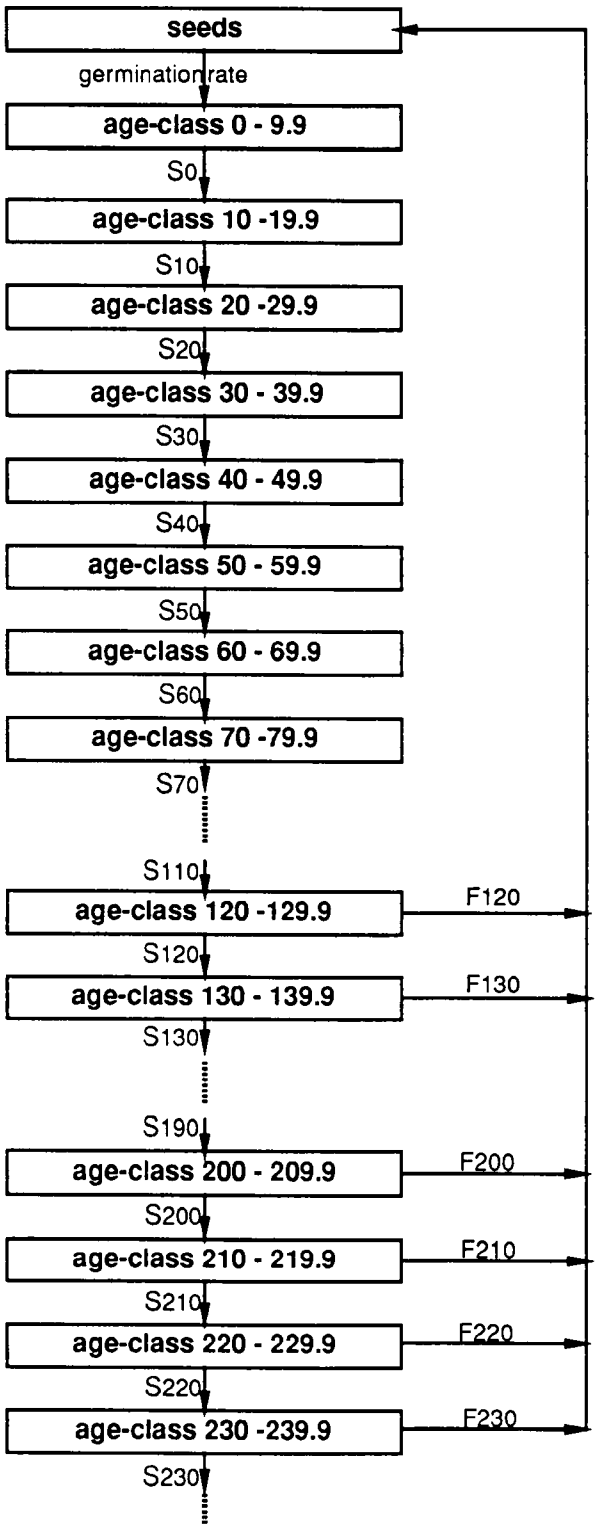


Figure 29. Flow diagram of an age-classified population model of Manilkara. Arrows are transitions. S = probability of survival (1 - mortality); F = number of seeds per individual. the number following S or F indicates the biginning age of the age-class.

0	0	0	0	0	0	0	...	F120	F130	...	F210	F220	F230
S0	0	0	0	0	0	0	...	0	0	...	0	0	0
0	S10	0	0	0	0	0	...	0	0	...	0	0	0
0	0	S20	0	0	0	0	...	0	0	...	0	0	0
0	0	0	S30	0	0	0	...	0	0	...	0	0	0
0	0	0	0	S40	0	0	...	0	0	...	0	0	0
0	0	0	0	0	S50	0	...	0	0	...	0	0	0
0	0	0	0	0	0	S60	...	0	0	...	0	0	0
0	0	0	0	0	0	0	...	0	0	...	0	0	0
0	0	0	0	0	0	0	...	S120	0	...	0	0	0
0	0	0	0	0	0	0	...	0	S130	...	0	0	0
0	0	0	0	0	0	0	...	0	0	...	0	0	0
0	0	0	0	0	0	0	...	0	0	...	S210	0	0
0	0	0	0	0	0	0	...	0	0	...	0	S220	0
0	0	0	0	0	0	0	...	0	0	...	0	0	S230

Figure 30. Conceptual matrix for an age-classified population of Manilkara. S = probability of survival (1 - Mortality); F = number of seeds per individual; the number following S or F indicates the biginning age of the age-class, corresponding to Figure 29.

```
c   A computer program to simulate Manilkara population
c   dynamics.

c dxdt: DERIVATIVE EVALUATION
c=====================================================

c state variables
c----------------
c     c(1)   Age-class   0-9.9   years
c     c(2)   Age-class  10-19.9  years
c     c(3)   Age-class  20-29.9  years
c     c(4)   Age-class  30-39.9  years
c     c(5)   Age-class  40-49.9  years
c     c(6)   Age-class  50-59.9  years
c     c(7)   Age-class  60-69.9  years
c     c(8)   Age-class  70-79.9  years
c     c(9)   Age-class  80-89.9  years
c     c(10)  Age-class  90-99.9  years
c     c(11)  Age-class 100-109.9 years
c     c(12)  Age-class 110-119.9 years
c     c(13)  Age-class 120-129.9 years
c     c(14)  Age-class 130-139.9 years
c     c(15)  Age-class 140-149.9 years
c     c(16)  Age-class 150-159.9 years
c     c(17)  Age-class 160-169.9 years
c     c(18)  Age-class 170-179.9 years
c     c(19)  Age-class 180-189.9 years
c     c(20)  Age-class 190-199.9 years
c     c(21)  Age-class 200-209.9 years
c     c(22)  Age-class 210-219.9 years
c     c(23)  Age-class 220-229.9 years
c     c(24)  Age-class 230-239.9 years

c parameters
c-----------
c      b(1) = mortality of age-class  0-9.9
c      b(2) = mortality of age-class 10-19.9
c      b(3) = mortality of age-class 20-29.9
c      b(4) = mortality of age-class 30-39.9
c      b(5) = mortality of age-class 40-49.9
c      b(6) = mortality of age-class 50-59.9
c      b(7) = mortality of age-class 60-69.9
c      b(8) = mortality of age-class 70-79.9
c      b(9) = mortality of age-class 80-89.9
c     b(10) = mortality of age-class 90-99.9
c     b(11) = mortality of age-class 100-109.9
c     b(12) = mortality of age-class 110-119.9
c     b(13) = mortality of age-class 120-129.9
c     b(14) = mortality of age-class 130-139.9
```

(continued next page)

(continued Figure 31)

```
c     b(15) = mortality of age-class 140-149.9
c     b(16) = mortality of age-class 150-159.9
c     b(17) = mortality of age-class 160-169.9
c     b(18) = mortality of age-class 170-179.9
c     b(19) = mortality of age-class 180-189.9
c     b(20) = mortality of age-class 190-199.9
c     b(21) = mortality of age-class 200-209.9
c     b(22) = mortality of age-class 210-219.9
c     b(23) = mortality of age-class 220-229.9
c     b(24) = mortality of age-class 230-239.9


c f(): Derivative Functions for nth Order System of
O.D.E.'s
c-----------------------------------------
      subroutine f(t, c, dcdt, b)
        double precision t, c(*), dcdt(*), b(*)

        dcdt(1)=-b(1)*c(1)
        dcdt(2)=-b(2)*c(2)
        dcdt(3)=-b(3)*c(3)
        dcdt(4)=-b(4)*c(4)
        dcdt(5)=-b(5)*c(5)
        dcdt(6)=-b(6)*c(6)
        dcdt(7)=-b(7)*c(7)
        dcdt(8)=-b(8)*c(8)
        dcdt(9)=-b(9)*c(9)
        dcdt(10)=-b(10)*c(10)
        dcdt(11)=-b(11)*c(11)
        dcdt(12)=-b(12)*c(12)
        dcdt(13)=-b(13)*c(13)
        dcdt(14)=-b(14)*c(14)
        dcdt(15)=-b(15)*c(15)
        dcdt(16)=-b(16)*c(16)
        dcdt(17)=-b(17)*c(17)
        dcdt(18)=-b(18)*c(18)
        dcdt(19)=-b(19)*c(19)
        dcdt(20)=-b(20)*c(20)
        dcdt(21)=-b(21)*c(21)
        dcdt(22)=-b(22)*c(22)
        dcdt(23)=-b(23)*c(23)
        dcdt(24)=-b(24)*c(24)

        return
      end
-------------------------------------------------------
```

Figure 31. Computer program to simulate Manilkara population dynamics.

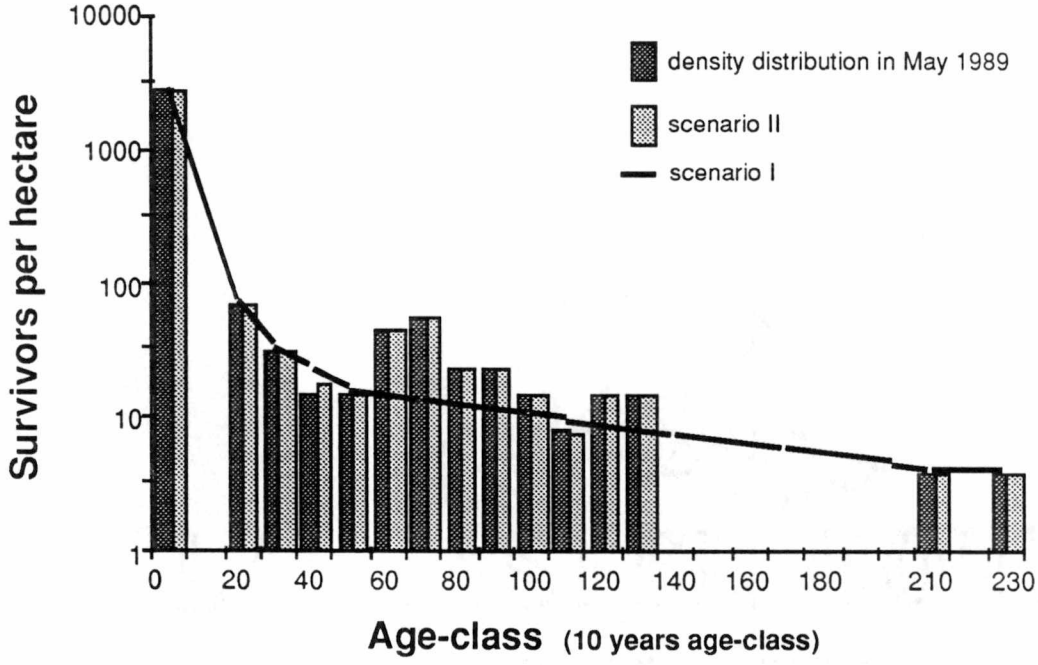


Figure 32. Computer simulation patterns of population density distributions.

VITA

Chengxia You was born in Chongqing (Chungking), China on November 5, 1948. He attended elementary schools in The Experimental Elementary School of Teachers College of Southwest China in Chongquing and in The Experimental Elementary School of Teachers School of Kunming, China. He graduated from The Twentieth Middle School of Kunming in July, 1964 and from The Fourteenth High School of Kunming in July, 1967. He entered Yunnan University, Kunming, China in September, 1973 and graduated from Biology Department of Yunnan University in September, 1976. At that time, there was no any degree system in China. After working as a botanist in Kunming Institute of Botany, Academia Sinica for three years, he reentered Yunnan University in September, 1979 and in September, 1982 received a Master of Science degree in Geobotany. After working as a botanist/ecologist in Kunming Institute of Ecology, Academia Sinica for four years, he came to the United States as a visiting scholar in August, 1986. He entered the Graduate School at University of Tennessee in January, 1988 and in December, 1991 received a Doctor of Philosophy in Ecology. He was a Research Assistant at the University of Tennessee, Knoxville during his study period.