To the Graduate Council:

I am submitting herewith a thesis written by Emma Muñiz-Meléndez entitled "Demographic Analysis of the Life History of Inga vera Subspecies vera." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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# DEMOGRAPHIC ANALYSIS OF THE LIFE HISTORY OF INGA VERA SUBSPECIES VERA

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Emma Muñiz-Meléndez

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## ABSTRACT

The life cycle of Inga vera (Willd.) subspecies vera was studied to determine critical stages of development, factors affecting survival, growth and mortality. The El Verde Field Station in the Luquillo Experimental Forest of Puerto Rico was chosen as the study area because it contains forest types in which Inga occurs and because the area has previously been studied extensively. Inga vera subspecies vera was selected for the experimental study because it is a very abundant secondary succession species in the rainforests of Puerto Rico, and because of interest in this species by the Institute of Tropical Forestry, U. S. Forestry Service.

The study consisted of (1) division of the Inga population into size classes (seeds, seedlings, young trees and mature trees), (2) determination of relative abundance of each class, (3) germination studies under natural conditions, and (4) observations of phenology and seed dispersal. From the size class census and germination studies, the species' survival rates were calculated.

Seed germination, subsequent seedling growth and seedling survival were high. A significant reduction in numbers between seedlings and young trees indicated that the end of the seedling phase is the critical stage of development for the survival of the species in the forest. Transplant experiments suggest that light is the most limiting factor in the development of seedlings into young trees.

There are no discernible specific adaptations for seed dispersal. Flowering and fruiting occur throughout the year with a peak in May. The large number of flowers and relatively low number of fruits result in a low reproductive potential of the population studied.

Relative density of I. vera subspecies vera trees in the study area was 1.8%. Absolute density was 33 trees per hectare. The density of the species in the forest is apparently limited by the availability of light which is necessary for the development of seedlings into juvenile trees. Inga exhibits rapid growth in the presence of sufficient light. Mature individuals are well adapted for survival in the forest, while seedlings and young trees require the higher light intensities that occur in disturbed environments.

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# CHAPTER I

## INTRODUCTION

For a better understanding of the structure and dynamics of tropical forest communities the ecology of its components should be thoroughly understood. One way of obtaining this information is suggested by Pelton (1951), who recommends one follow the entire course of the life cycle of individuals of each species in the community using quantitative methods wherever practicable. At present the knowledge of ecological life histories of tropical trees is exceedingly scarce. The present work integrates available ecological information concerning Inga vera (Willd.) subspecies vera with data acquired which fills in some of the wider gaps in our knowledge of the species.

The objective of this study was to investigate the life history of Inga vera (Willd.) subspecies vera in order to determine its critical stage of development from the standpoint of survival, and its growth and mortality rates. The entire course of the life cycle of this species was followed, describing and evaluating the environmental requirements, adaptations and relative mortality of each stage of development.

Work consisted of (1) division of the population into size classes, (2) determination of each class' abundance, (3) germination studies in natural conditions, and (4) phenological and seed dispersal observations. The most direct indication of success of a species in regeneration is the comparison of the relative numbers of individuals in each size class (Smith, 1970). From the size class census and germination studies,

survival and growth rates were calculated. A survivorship curve and a life table for this species were developed according to techniques previously employed by Sharitz and McCormick (1973).

## The Study Area

Field work was carried out at the El Verde Station of the Center for Energy and Environmental Research of the University of Puerto Rico, which is in the Luquillo Experimental Forest in northeast Puerto Rico at an elevation of 355 meters. Field studies were carried out from January to June 1978. Phenological observations were continued until September of the same year.

The type of vegetation at this altitude is the lower montane rain forest (Beard, 1942), locally called tabonuco forest (Wadsworth, 1951) which is dominated by Dacryodes excelsa (tabonuco) and Sloanea berteriana (motillo).

The El Verde Station was a coffee plantation until 1932. The area is dominated by secondary forest species due to selective cutting that took place in 1937, 1948, 1956 and 1957. Since then the area has been used exclusively for scientific research. Inga vera subspecies vera was the principal canopy tree used for coffee shade, and it dominates the station surroundings (Odum, 1970).

Soil in the study area is typical of descriptions associated with the Los Guineos clays and clay loams (Roberts, 1942). Surface horizons are usually saturated, the amount of soil water ranging between 75 and 180% (water/dry matter x 100) (Edmisten, 1970a). The soil has a

6 to 8 inch-deep layer of grayish-brown, slightly granular, medium plastic, strongly acid surface soil. Soil pH ranges from 3.8 to 6.1. Parent material is basalt; the litter layer is mull (Smith, 1970).

High rainfall has had a destructive leaching effect on the soils and most of them are deficient in calcium, magnesium and phosphorus (Roberts, 1942). Lower montane forest soils are well drained and aerated. This is due partly to quantity of rain and steepness of slope (Wadsworth and Bonnet, 1951).

The climate at the forest is very uniform with a mean temperature of 22.6°C and a relative humidity of 90.8%.

Forest throughfall has been estimated by the Nuclear Center (Annual Report, 1971) and varies from 67% at 0.1 inch of rain to 92% at one inch of rainfall.

Light intensity is 20g-cal/$cm^2$/day at the forest floor (3 to 8% of that above the canopy) (Odum, Drewry and Kline, 1970).

Table 1 shows mean values for temperature, relative humidity and light intensity in the forest and in the open areas. Table 2 presents monthly precipitation at El Verde during the time of study. These are fairly uniform throughout the year and reflect the stability of the mountain climate at El Verde.

## The Study Taxon

Inga vera is the type species of this large and complex genus which has been cultivated extensively throughout the New World tropics. On the whole the genus is well defined by its once-pinnate leaves. Inga

TABLE 1

ENVIRONMENTAL CONDITIONS AT EL VERDE

| | Mean Temperature (°C) | Mean Relative Humidity (%) | Light intensity* (g-cal/cm$^2$/day) |
|---|---|---|---|
| Forest | 22.6 | 90.8 | 20.0 |
| Open Areas | 24.3 | 86.2 | 363.6 |

*From: Odum, Drewry and Kline, 1970.

TABLE 2

PRECIPITATION AT EL VERDE FROM JANUARY TO JUNE 1978

| Month | Precipitation (ml/month) |
|---|---|
| January | 108 |
| February | 84 |
| March | 173 |
| April | 286 |
| May | 256 |
| June | 155 |

contains over 400 species and is distributed throughout the American tropics with some penetration into temperate areas both north and south (Baretta-Kuipers, 1973).

Inga vera occurs in the Greater Antilles, Central America, and northern South America. Inga vera subspecies vera occurs only in the Greater Antilles (Jamaica, Cuba, Hispaniola and Puerto Rico). Two other subspecies of I. vera have been identified. Inga vera subspecies eriocarpa occurs in western Mexico and Inga vera subspecies spuria occurs from Mexico to Panamá (León, 1966). Differentiation between subspecies is based on differences in the size and shape of the calyx and the leaflets.

Inga vera subspecies vera is either native or naturalized in the wet forests of Puerto Rico where it shares the forest canopy with many other species. No variability of this species has been reported in Puerto Rico. Inga belongs to the legume family and mimosa subfamily. Inga vera, along with I. fagifolia are the most abundant legumes in the tabonuco forest after Ormosia krugii (palo mato). Inga vera is commonly called guaba. The taxonomic description of the species is given by Little and Wadsworth (1964) and is summarized below.

Inga vera subspecies vera is an evergreen tree reaching from 12 to 20 meters high and 30 to 50 centimeters in trunk diameter, with a very widely spreading crown of long branches and thin foliage. It is characterized by (1) alternate, pinnate and hairy leaves with three to five pairs of stalkless, slightly dropping leaflets on a winged axis with a minute round yellow-green gland between each pair, (2) lateral clusters

of several large white flowers with long threadlike stamens 6.0 to 7.5 centimeters long, and (3) pubescent round pods 10 to 15 centimeters long, with four ribs and two longitudinal grooves, and containing white sweetish edible pulp. The bark is gray-brown, smoothish but becoming finely fissured.

The wood is moderately hard, moderately heavy (specific gravity 0.59), strong and tough. It is very susceptible to attack by drywood termites and other insects and to decay in contact with the ground. The wood is used almost solely for posts, fuel and charcoal, but is suitable for utility furniture, boxes, light construction, and general carpentry.

# CHAPTER II

## METHODS

### Size Class Census

Each life cycle stage was studied: seed production, germination, germinated seedlings, established seedlings, juveniles and mature trees. Size classes were divided into the following: (1) seedlings up to 0.3 meter tall), (2) juveniles (0.3 to 9 meters tall), and (3) mature trees (over 9 meters tall). Abundance of each class was measured to determine demographic characteristics, degree of success, establishment and adaptability.

The area has been studied previously. Transects were extended to verify that the particular study site was similar to previous descriptions of the forest. Eight transects 10 meters by 100 meters long were extended within the forest. This 8,000 square meter area (0.8 hectare) is hereinafter referred to as the study area. All *I. vera* trees were marked with red flagging tape. Height and diameter were measured on every individual with a Haga altimeter and a DBH (diameter at breast height) tape, respectively.

Data for the distribution of seeds and seedlings in the forest were obtained by making two transects one meter by 30 meters long, and counting all seeds and seedlings in each consecutive square meter. To obtain the density of *Inga* seeds and seedlings under parent trees five

one meter square plots were marked under 12 marked trees. Seeds were marked with red paint and counted monthly. Seed dispersion was observed in the marked seeds.

Germination and Seedlings' Growth

Germination studies were conducted to determine Inga's success in natural regeneration and factors affecting its germination and establishment.

Ten wooden boxes 35 x 25 x 10 centimeters each were filled with soil and the soil was planted with 100 freshly gathered seeds. Plastic screens were placed over the boxes before germination to prevent damage of seeds by rodents. The soil was obtained from the same area where the boxes were finally placed. To determine growth inhibition by shade, four boxes were placed in an open area and the rest were placed in the forest. Growth was recorded every week after germination. Factors affecting growth were noted. These were biotic factors (such as insects and rodents) and abiotic factors, especially light.

Growth of older seedlings was obtained by tagging 150 established seedlings in the forest floor and measuring their height monthly.

Based upon field observations it was suggested that light limits the development of old seedlings in the forest. To observe the effect of sunlight on growth of established seedlings, 100 of the largest seedlings found in the forest (12 to 30 centimeters in height) were transplanted to an open area. A control group of 100 seedlings was transplanted within the forest. Height was recorded monthly.

## Seed Viability

Seed viability during the time of study was determined by placing 144 seeds in plastic screen cages in the forest floor. This prevented damage from rodents and allowed natural moisture and light conditions to exist.

Twenty-eight of these seeds were gathered every two weeks and planted in wooden boxes in the forest. Percentage germination and growth were recorded weekly.

To observe the effect of moisture on seed viability, 50 seeds were kept in dry conditions in the laboratory for one week and subsequently planted in soil in wooden boxes on the forest floor.

## Phenology and Reproductive Potential

The number of trees with flowers and fruits in the study area was recorded monthly. Forty-three trees were observed.

The quantity of flowers per tree was calculated with cut branches from 11 trees by counting all inflorescences in every square meter of continuous foliage. The number of flowers in each inflorescence was recorded. The total number of square meters of foliage of every tree was obtained by using the crown-diameter method (Mueller-Dombois and Ellenberg, 1974).

## Environmental Observations

Rainfall and temperature at El Verde were obtained daily from the El Verde Station. Relative humidity and temperature at the forest floor were determined with a Weather Measure Corp. hygrothermograph Model H311 placed near the forest floor.

Forest light intensity data were obtained from Odum, Deevey and Kline (1970). Forest throughfall data were taken from the Puerto Rico Nuclear Center Annual Report (1971).

## Life Table

Survival at each size class was calculated from data obtained from field studies. A life table was constructed using the survivorship data. The life table stated for every interval of age the number of deaths, the survivors remaining, the rate of mortality, and the expectation of further life of a population (Deevey, 1947).

# CHAPTER III

# RESULTS

## Size Class Distribution and Density

In an area of 0.8 hectare, 27 mature and 18 young trees of I. vera were found. This is a density of 0.005 trees for every square meter in the forest. Relative density of I. vera trees in the study area was 1.8% (only those trees greater than 4 centimeters in DBH were used to calculate relative density). Absolute density of mature trees was 33 trees per hectare. Density results were in accordance with those of Smith (1970), who reported 1% relative density for I. vera trees greater than 10 centimeters in DBH, and to calculations made from data presented by Briscoe and Wadsworth (1970).

Distribution according to DBH showed that most mature trees occur in the 10 to 30 centimeters range (Figure 1). These correspond to trees 10 to 20 meters in height, which is the lower height limit of canopy trees (Figure 2). For comparison purposes, a density distribution graph was developed using the data of Briscoe and Wadsworth (1970) (Figure 3).

Average area covered by each tree was 38.3 square meters. This was obtained using the crown-diameter method. If 38.3 square meters was the area covered by a tree, then 27 mature Inga trees covered 1,035 square meters within the total study area.

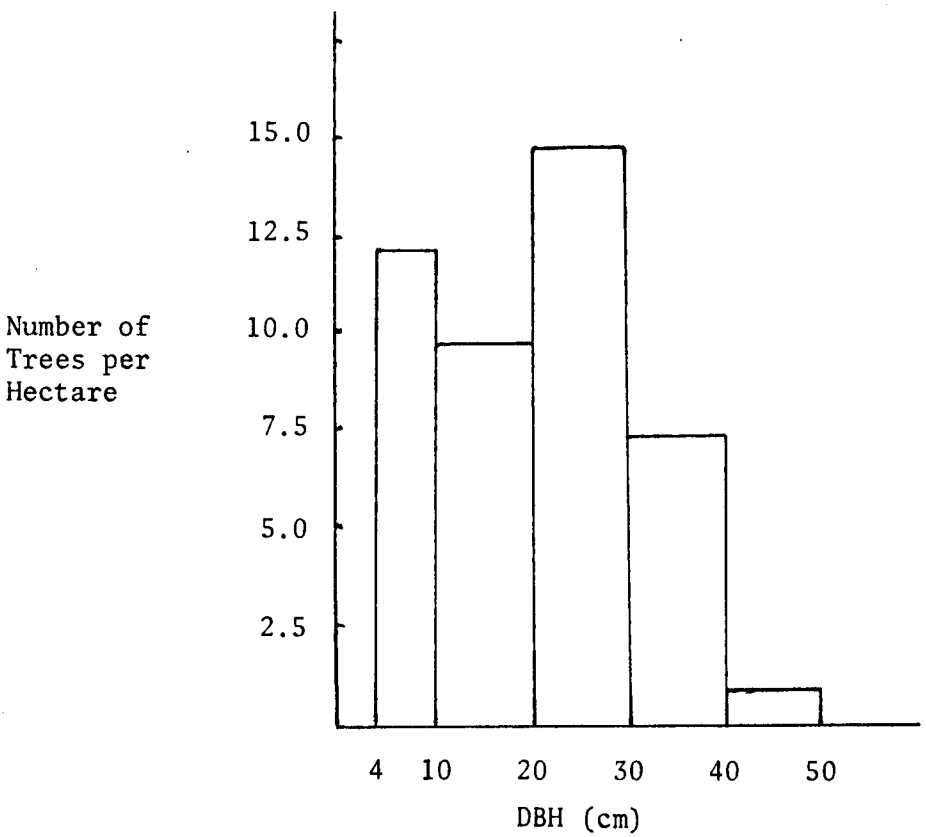


Figure 1. Density distribution of size classes of Inga vera at El Verde forest.

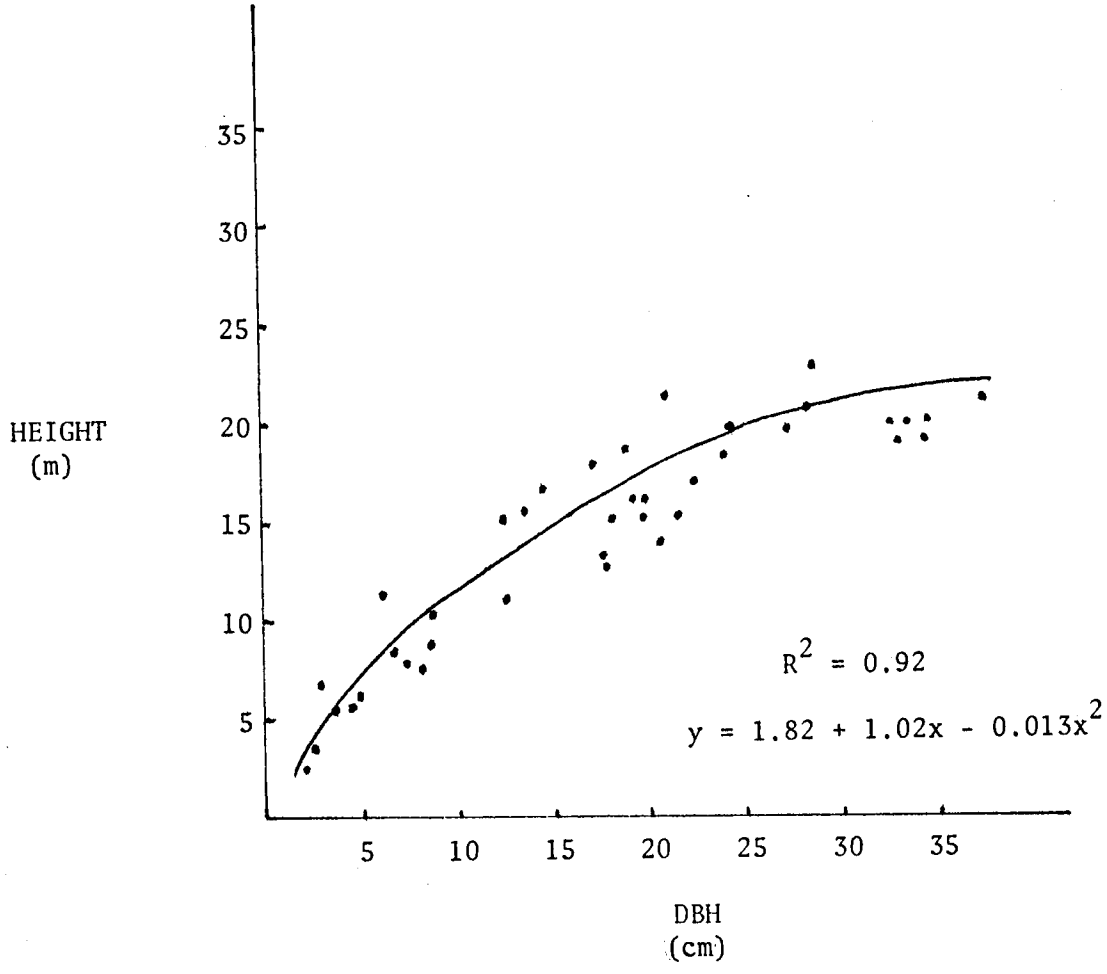


Figure 2. Height as a function of diameter of Inga vera trees at El Verde forest

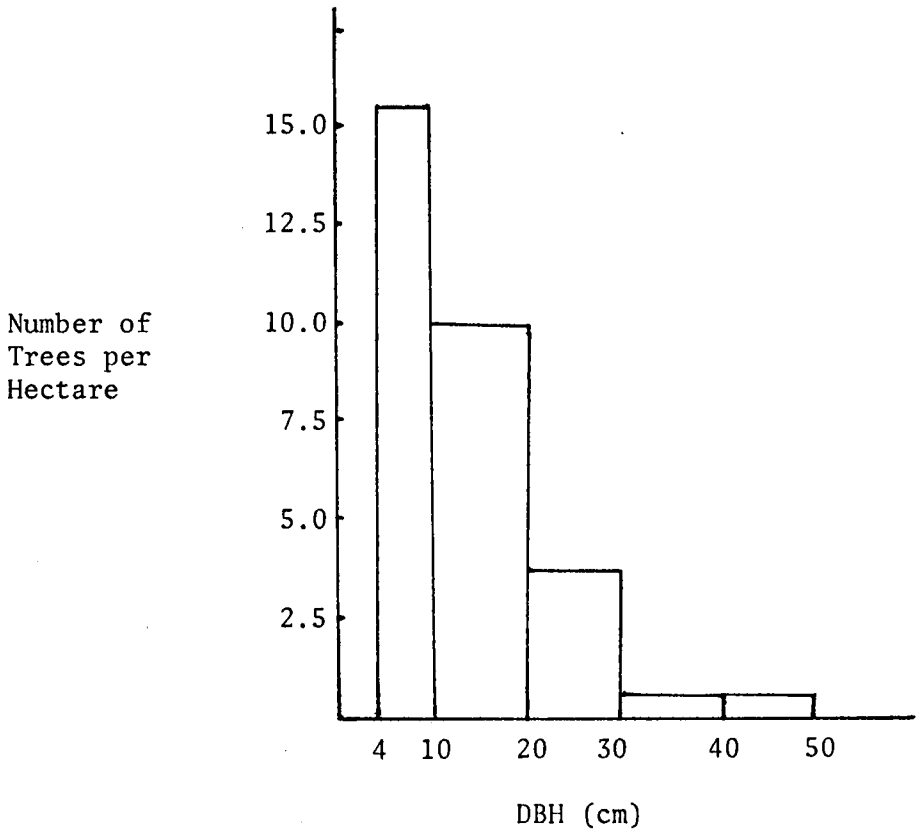


Figure 3. Density and size class distribution of Inga vera at El Verde. Data obtained from Briscoe and Wadsworth, 1970.

An average of 87.9 seedlings was found below parent trees or 2.3 seedlings per square meter. This totals to 2,380 seedlings in the area covered by Inga trees.

No I. vera plants were found in the forest in the diameter class of 0.5 to 2.0 centimeters (or 0.3 to 3.0 meters high). The 0.5 centimeter in diameter plants (or 0.3 meters high) were taken as those beginning the juvenile stage; this suggested that the end of the seedling stage is critical for individuals of this species living in the forest. The only plants 0.3 to 3.0 meters tall were observed outside the forest and along roads, where light intensity was higher.

There were 227.3 seeds below each parent tree, or 4.4 seeds per square meter (Table 3). There were 4,595 seeds below 27 parent trees in the area covered by Inga trees. An average of 40% of all fallen seeds were immature, therefore, 2,757 sees were available for germination in the study area.

Total number of Inga individuals in each size class is presented in Table 4.

## Germination and Growth

Germination of I. vera seeds in the forest boxes ranged from 82 to 100% two weeks after planting. Out of those that germinated, 9% failed to continue their growth. Germination in the high light boxes was 100%. No dormancy was evident.

Observations of natural germination in the forest revealed the following:

TABLE 3

SEED DENSITY BELOW *INGA VERA* TREES

| Month | Number/$m^2$ ± S.D. |
|---|---|
| January | 0.0 |
| February | 0.0 |
| March | 2.9 ± 1.0 |
| April | 6.2 ± 6.9 |
| May | 9.0 ± 10.9 |
| June | 8.3 ± 9.8 |
| July | 3.1 ± 3.5 |
| August | 1.1 ± 2.2 |
| September | 0.5 ± 1.4 |

TABLE 4

TOTAL NUMBER OF *INGA VERA* INDIVIDUALS
IN EACH LIFE CYCLE STAGE

| Flowers and Life Cycle Stage | Number/Hectare |
|---|---|
| Flowers | 1,955,846.0 |
| Seeds | 3,446.2 |
| Seedlings | 2,975.0 |
| Juveniles | 22.5 |
| Trees | 33.7 |

1. When the seed reaches maturity the radicle starts growing before the fruit falls from the tree and before opening of the fruit.

2. After the fruit reaches the forest floor the pod rots and opens, and the already advanced germination continues with rapid elongation of both plumule and radicle.

3. Seedlings then take root in the soil.

Seedlings grew from 5 to 8 centimeters before the first two opposite leaflets appeared. All subsequent leaves were alternate. The cotyledons, which remained above ground, fell after 2 months, especially after heavy rains.

Forest seedlings grew at an average of 2.3 centimeters per month during the first four months following germination. Growth of older seedlings under the forest canopy was 0.1 centimeters per month.

Growth in the open area was much faster than in the forest. Seedlings growing in exposed sunlight grew at an average of 3.8 centimeters during the first four months after germination. Figure 4 shows the difference in height and growth rate of seedlings in the forest and in the open area. Using a covariance analysis, it was found that the growth of seedlings in the shade and in the sunlight were significantly different at the 0.01% level of confidence.

Light intensity under the forest canopy is usually so low that it is expected to decrease the rate of growth of seedlings. Richards (1952) suggests that seedlings of some species grow at a minimum rate in the forest shade until a gap is opened in the canopy. He calls it the "suppression period" of seedlings.

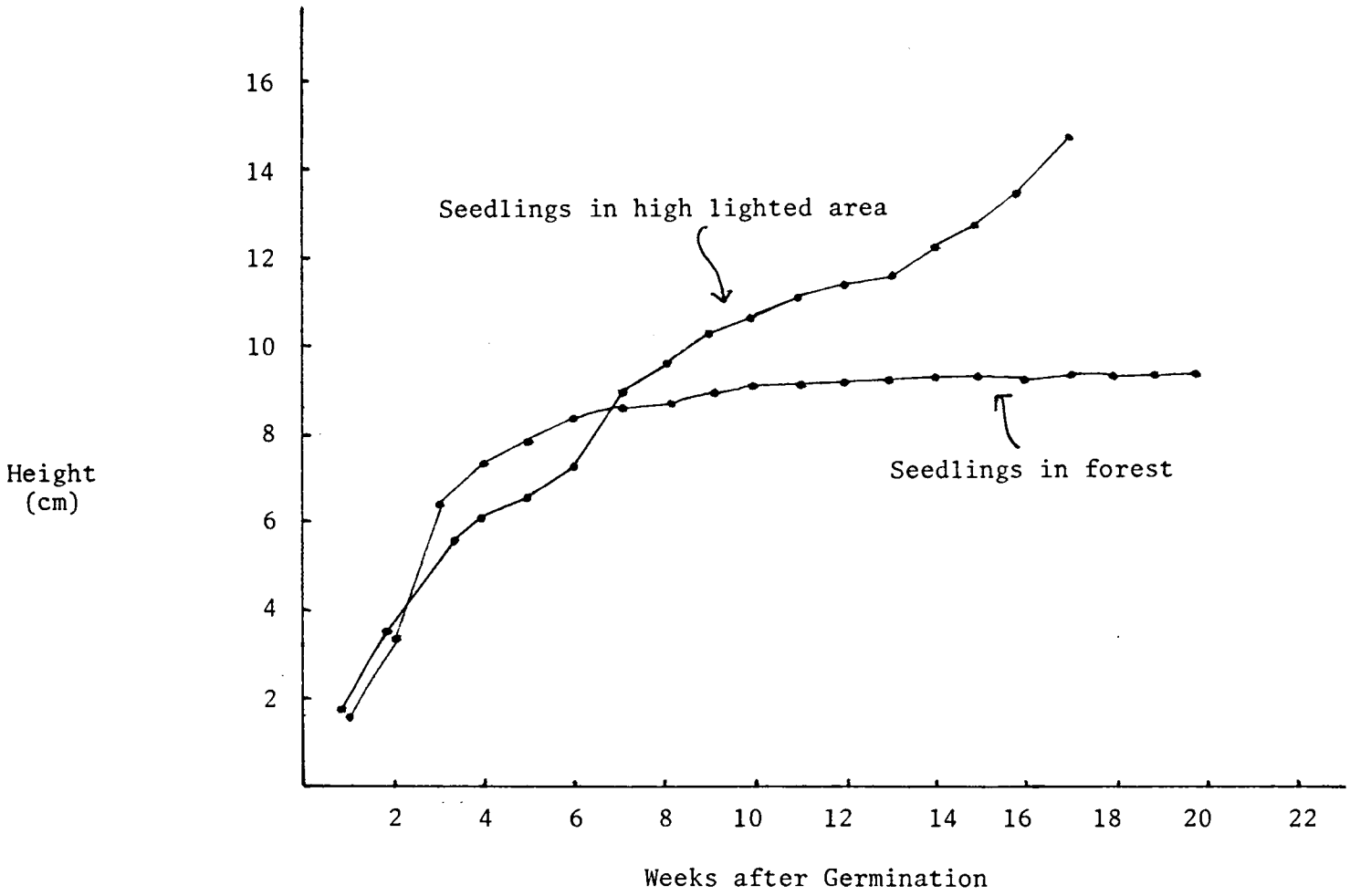


Figure 4. Height of Inga vera seedlings

To find out if this applied to I. vera, large seedlings were transplanted from the forest to the open area. After transplanting the seedlings to the lighted area they increased their growth from 0.1 centimeter per month to an average of 0.6 centimeter per month (Table 5).

TABLE 5

GROWTH RATES OF INGA VERA SEEDLINGS TRANSPLANTED WITHIN THE FOREST AND SEEDLINGS TRANSPLANTED TO OPEN AREAS

| Month | Forest | High Light |
|---|---|---|
| | (cm/month) | |
| February | 0.13 | |
| March | 0.06 | |
| April | 0.12 | |
| May | 0.09 | 0.30 |
| June | 0.05 | 0.37 |
| July | 0.03 | 0.73 |
| August | 0.08 | 1.03 |

## Seed Viability and Dispersal

Inga seeds were kept in plastic screen cages, which prevented germination, and were placed on the forest floor. After one month they were removed from the cages and planted in the forest soil. Germination was 82%. After three months of being kept on the forest floor, germination dropped to 20%. Seeds were affected by insect larvae and fungi. Only those not harmed remained viable. In nature most seeds germinate while on the tree and grow immediately after falling to the ground and opening of the fruit. Seeds kept in dry

conditions in the laboratory lost viability within one week. The inability of these seeds to germinate when planted in the forest is evidence of the importance of humidity in the seed environment.

This species does not seem to have evolved any adaptations for long-term viability. The highly stable environmental conditions of the areas where this species occurs have made no need for development of long-term viability of the species.

Due to their size and weight the pods of Inga fall to the ground and remain below the tree. Seed transects indicated that no seeds of I. vera occur in the forest except near parent trees. Other observations in the forest also confirmed this, although local dispersal could have been accomplished by birds and rodents. Damage of seeds by rodents was observed; they eat the pod coat and the seed, these being either mature or immature. Janzen (1967) reported that rodents are the major agents of dispersal of I. vera in Central America. The puertorican spindalis (Spindalis portoricensis) bird was observed in I. vera trees during the time of study. Whole I. vera seeds were also found in the crop of a ruddy quail dove (Geotrygon montana) found dead at the El Verde forest. The puertorican parrot (Amazona vitata) has been reported to eat I. vera seeds (Rodríguez-Vidal, 1959).

Seed removal can occur before or after fruit fall. León (1966) reports that birds open the pod, remove the fleshy seed coats and allow the rest of the seed to fall to the ground.

## Phenology and Reproductive Potential

Flower counts were conducted in May, when flowering was heaviest during the time of study (Figure 5). There was an average of 114 inflorescences per square meter of continuous foliage. Taking average foliage area per tree as 38.3 square meters, there were 4,390 inflorescences in each tree. Average number of flowers for each inflorescence was 13.2. This gives 1,512 flowers for each square meter or 57,951 flowers per tree. If there were 27 mature trees in 0.8 hectare, then there were 1,564,670 flowers in the study area. The reproductive potential of *I. vera* is presented in Table 6.

## Survivorship Curves and Life Table

The average age of a canopy tree is assumed to be 25 years. This assumption is based on the fact that logging took place in the study area during the 1950's and that many *Inga* trees were cut at that time (Estrada, personal communication). Most canopy trees present in the area are the result of self replacement of the *Inga* population. Richards (1952) mentions that the longer lived secondary succession trees can replace themselves from 3 to 5 times in 200 years, that is, they live from 40 to 65 years. Taking average age of a mature *Inga* tree as 25 years, and senescence beginning when it is 45 years old (the curve in Figure 2, page 13, would level off), it would be expected to live 20 years more.

Figure 6 is a survival curve presented in years. The shaded area represents the range between the beginning and the end of each life cycle stage. High mortality is visible during the first ten years of

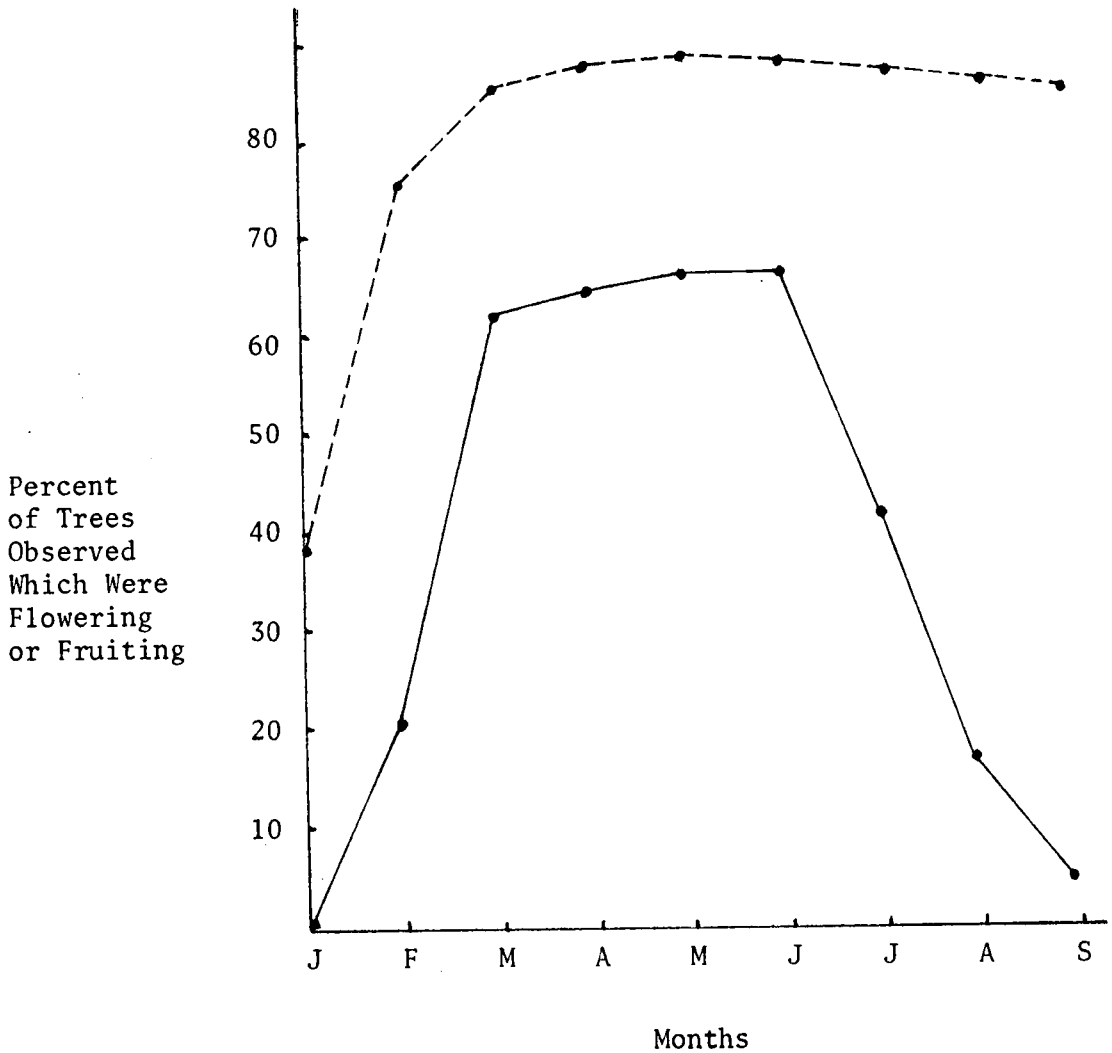


Figure 5. Flowering and fruiting of Inga vera at El Verde from January to September 1978. Dashed lines represent flowering and solid lines represent fruiting.

TABLE 6

REPRODUCTIVE POTENTIAL OF *INGA VERA*

| Flowers per Tree | Seeds per Tree | Trees per Hectare | Flowers per Hectare | Seeds per Hectare |
|---|---|---|---|---|
| 57,951.0 | 227.3 | 33.7 | 1,955,846.0 | 3,835.5 |

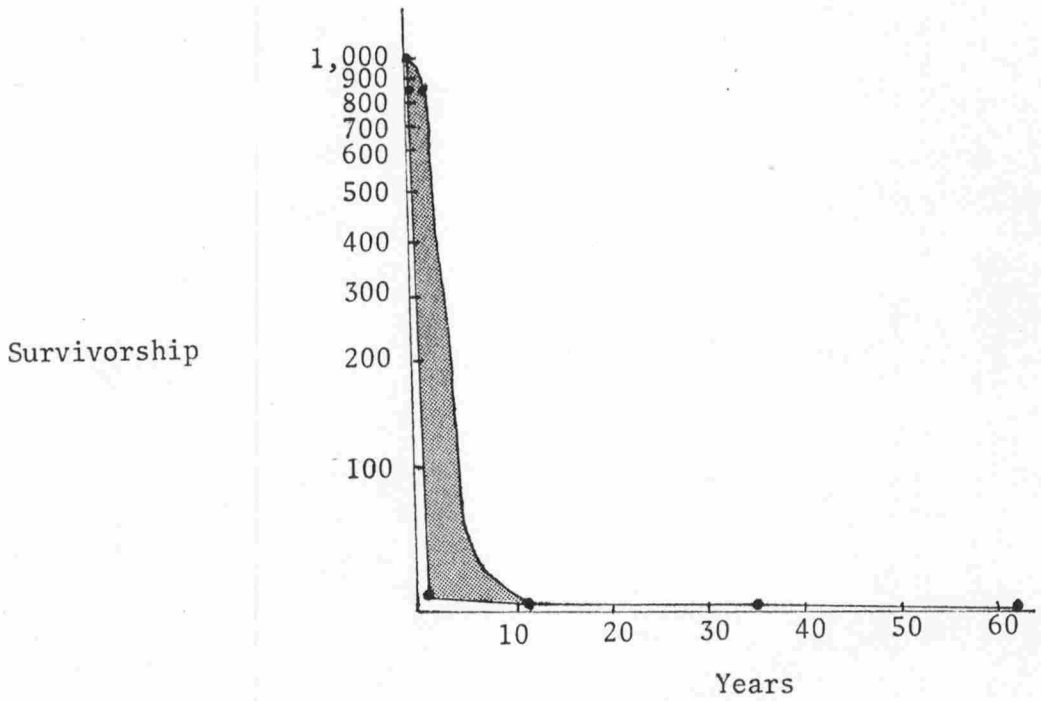


Figure 6. Survivorship of Inga vera in time. Shaded area is the range between beginning and end of each life cycle stage.

life. Figure 7 presents the survival of Inga based on size classes, which are the ecologically important divisions in the life cycle of a tree. Extremely high mortality is visible between seedling and juvenile stages.

The survivorship curves (Figures 6 and 7) and life table of I. vera (Table 7) indicate little loss of seeds, high germination and high seedling mortality. Once the plant reaches the juvenile stage the probability of death is low and the expected years of life are high.

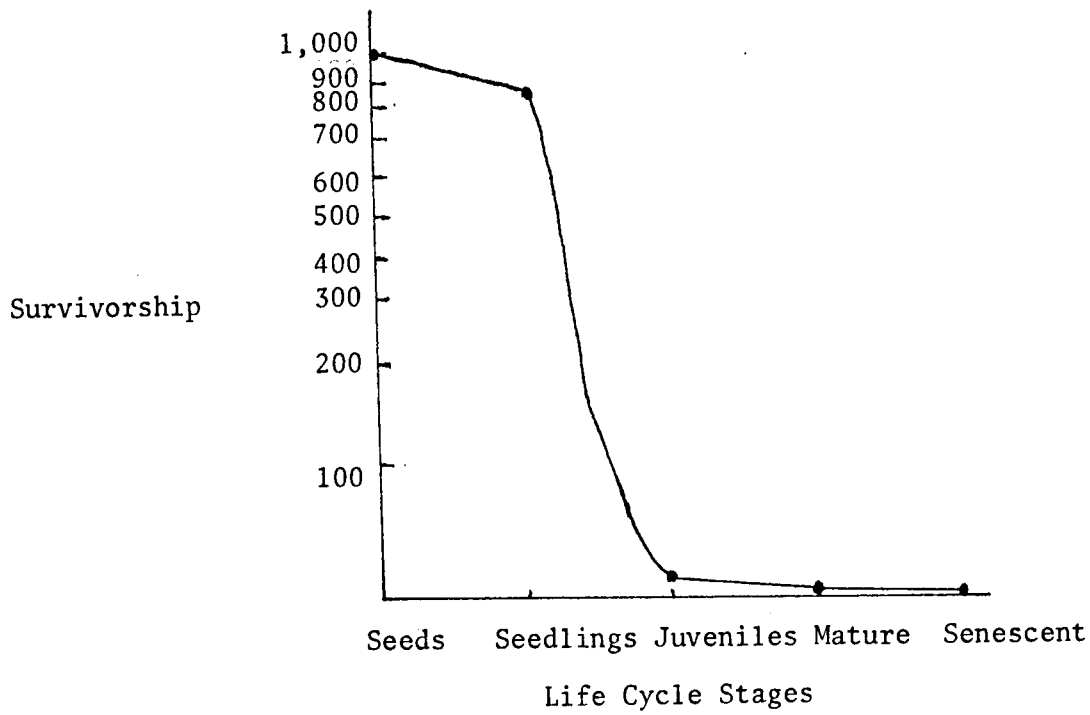


Figure 7. Survivorship of Inga vera during each life cycle stage.

TABLE 7

LIFE TABLE OF INGA VERA

| Life Cycle Stage | $D_x$ | $A_x$ | $l_x$ | $d_x$ | $q_x$ | $L_x$ | $T_x$ | $e_x$ |
|---|---|---|---|---|---|---|---|---|
| Seed | 0.2 | 0.0- 0.2 | 1,000 | 226 | 226 | 932 | 672 | 0.7 |
| Seedling | 0.8 | 0.2- 1.0 | 863 | 856 | 991 | 435 | 486 | 0.6 |
| Juvenile | 10.0 | 1.0-11.0 | 7 | 5 | 714 | 5 | 138 | 19.7 |
| Mature | 34.0 | 11.0-45.0 | 2 | 1 | 500 | 2 | 88 | 44.0 |
| Senescent | 20.0 | 45.0-65.0 | 1 | 1 | 1,000 | 1 | 20 | 20.0 |

$D_x$ - Life cycle stage duration in years

$A_x$ - Age of life cycle stage in years

$l_x$ - Number of individuals surviving at age interval per 1,000 alive

$d_x$ - Number dying at age interval per 1,000 alive, $d_x = l_x - l_{x+1}$

$q_x$ - Mortality rate out of 1,000 alive, $q_x = d_x / l_x$

$L_x$ - Stationary population life span, $T_x = D_x L_x + T_{x+1}$

$e_x$ - Life expectancy at beginning of life cycle expressed in years, $e_x = T_x / l_x$

# CHAPTER IV

# DISCUSSION AND CONCLUSIONS

## Germination and Growth

The high percent of germination obtained both in the forest shade and in the open area indicates that germination is not significantly affected by the light, humidity nor temperature ranges that occurred in the forest and open areas at El Verde during the study period.

The fact that Inga possesses viviparous seeds, in which germination starts inside the legume, is an advantage to the species. When the mature seed falls to the ground germination has already begun and the seed can become established immediately. Any environmental or biotic factor that would normally be injurious to seeds during the first days of germination would not affect the already germinated seed, resulting in relatively successful establishment of Inga seedlings.

Seedling growth is greatly inhibited in the low light of the forest. The results of the transplantation experiment and the growth rates of forest seedlings demonstrated that seedlings of I. vera grow at a slow rate until a gap in the canopy is opened.

Little and Wadsworth (1964) mention that individuals of I. vera can grow 2.5 centimeters in diameter per year. This extremely high growth rate is evidence of the fast growth that I. vera can attain when conditions are favorable for growth.

Growth rates of saplings and trees could not be determined directly during the time of study. Data on growth rates were obtained from the

U. S. Forest Service (unpublished) (Tables 8 and 9). Growth rates of saplings and trees varies from 0.0 to 1.35 centimeters per year in DBH. Average growth is 0.37 centimeters per year. These values are similar to the growth rates of a related species, Inga fagifolia (0.0 to 1.17 centimeters per year) (Crow and Weaver, 1977). Growth is variable between individuals. No relation between growth rate and diameter of trees could be found, but the data do not show growth rates of the largest trees of I. vera. Wadsworth (1953) noted that rapid growing trees such as I. vera grow faster in the concave lower slopes and valley bottoms. Soil drainage requirements of the species seem to be a partial reason for the variability of growth in individuals of I. vera.

## Pollination and Reproductive Potential

Salas (1974) discusses in great detail the pollination of I. vera subspecies spuria in Costa Rica. Although being a different subspecies occurring in a different geographical region some aspects of its reproduction can be applied to the species as a whole. Salas demonstrated that the pollinators of I. vera subspecies spuria include bats of the Phyllostomatidae. Nectarivorous bats of this family are found at El Verde (Tamsitt and Valdivieso, 1970), which suggests that pollination of I. vera subspecies vera could be carried out by these bats. Bats have been seen near Inga trees during the time of study. Many species of insects, especially butterflies were seen in I. vera crowns. These are minor pollinators of Inga (Salas, 1974).

Janzen (1967) reports that bees were the main visitors to flowers of I. vera in Costa Rica. Salas (1974) mentions that most bees,

TABLE 8

GROWTH OF INGA VERA DURING 30 YEARS
IN PALM FOREST

| | Tree Number | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Year | Diameter (cm) of Seven Trees | | | | | | |
| 1946 | 11.25 | 15.50 | 17.75 | 20.00 | 15.00 | 13.50 | 20.25 |
| 1951 | 11.75 | 16.00 | 24.50 | 23.25 | 19.25 | 17.50 | 12.50 |
| 1956 | 11.75 | 16.00 | 26.25 | 25.25 | 24.75 | 20.75 | 24.50 |
| 1976 | death | death | death | 32.00 | 24.75 | 27.25 | 27.75 |

Source: U. S. Forest Service

TABLE 9

GROWTH OF INGA VERA DURING 28 YEARS
IN TABONUCO FOREST

| | Tree Number | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Year | Diameter (cm) of Seven Trees | | | | | | |
| 1947 | 6.25 | 4.50 | 6.25 | 12.00 | 9.75 | — | — |
| 1949 | 6.75 | 4.75 | — | — | — | — | — |
| 1952 | 6.75 | death | 6.75 | 17.00 | 14.25 | 7.00 | — |
| 1957 | 6.75 | — | 6.75 | 18.00 | death | 9.75 | 4.25 |
| 1975 | death | — | death | death | — | 12.00 | death |

Source: U. S. Forest Service

butterflies and small flies are nectar consumers, but do not carry out pollination.

Although flowering capacity was extremely high, few flowers developed into fruits (Table 6, page 23). The ratio of flowers to seeds was 1,000:1. León (1966) points out that this high floral sterility, or low reproductive potential, is characteristic of some species of the genus Inga. Marrero (1954) states that low reproductive potential of Inga is due to the attack of seeds by insects. Salas (1974) also discusses the reasons for the low reproductive potential: parasites of ovaries and nectar consumers cause great damage to flowers. Furthermore, he states that the abundance of parasites and predators is important from an evolutionary point of view because they have affected the species to the extent that its high flowering capacity not only satisfies the needs of its pollinators, but also counteracts the negative effects of consumers and parasites. The species has survived by producing numerous flowers.

Phenology

Reports of the phenology of I. vera are variable. Salas (1974) observed that although most trees were in flower most of the year, flowering was heaviest from January to May; he observed a second but lower peak in August and September. Little and Wadsworth (1964) report flowering and fruiting throughout the year with a peak in the fall.

Fournier (1976) observed that flowering of I. vera subspecies spuria in Costa Rica occurred from January to October; fruiting occurred from February to October; leaf fall was variable and leaf flushing

occurred throughout the year. Estrada (1970), who made phenological observations at El Verde, reported variable flowering and fruiting of I. vera. During the time of the present study, flowering and fruiting were heaviest from March to June (Figure 5, page 22).

From the above mentioned phenological studies, it can be concluded that I. vera exhibits flowering and fruiting during most of the year, usually having a high peak in April and May.

The reproductive phenology of I. vera is variable from year to year (Salas, 1974 and Estrada, 1970).

During the time of study fruiting decreased markedly in August and September, while flowering remained high. This suggests a marked decrease in the activity of pollinators of I. vera. The rainy season starts in July and extends through November. At this time bats and insects are in little need of water, therefore, their visit to flowers is greatly reduced (Janzen, 1967). Evolution of this species to synchronize the time of flowering with pollinators has been suggested (Salas, 1974 and Janzen, 1967), but this may apply more to places with a more marked season of rainfall than at El Verde.

## Dispersal and Distribution

The natural dispersal of Inga seeds is limited to the action of birds, rodents and moving water. León (1966) points out that rivers could be the major contributors for long distance dispersal of Inga. Pigeons may be good agents of dispersal of seeds between islands (Smith, 1970).

Dispersal by man has been of significant ecological and economic importance. Because of Inga's importance for fuel and shade for coffee and cacao, this species has been planted extensively in the tropics. It has been introduced to Cuba (H. León, 1946) and to several of the Lesser Antilles (Little and Wadsworth, 1964).

The distribution of species is usually limited by some weak point in the adaptation of a particular stage of the life cycle (Pelton, 1953). Inga seeds have proved to lose viability in dry conditions. This might explain its occurrence only in wet areas. Furthermore, seedlings require a wet ground on which to grow (León, 1966), which might explain why Inga is found on flooded areas, mesophytic forests and in the margins of rivers.

León (1966) discussed the geographic distribution of I. vera.

> The geological history of the area may help to explain the present geographic distribution. Fossils attributed to Inga have been found in the Cretaceous, both in Europe and North America, in Panamá [Oligocene], in Costa Rica [Miocene] and in Bolivia [Pliocene]. All consist of leaf impressions, and it is very difficult to assign them with certainty to Inga rather than to some other related genus. According to the present views on the biogeography of the area [Scuchert, Historical Geology of the Antillean-Caribbean Region, 106-110, 1935], it is quite possible that a migration of species from South America could have reached the Central American mainland in the upper Cretaceous. One of the most widely distributed species, I. vera seems to have taken two routes of migration in Central America; one to northwestern Mexico, and the other towards the Greater Antilles; the latter were connected to the continent until the middle Miocene, which may explain the present distribution of that species in Jamaica, the eastern tip of Cuba [introduced?], Hispaniola, and Puerto Rico.

Although Little and Wadsworth (1964) doubt if this species is native to Puerto Rico, Pittier (1916), Marrero (1954), and other authors who have studied the species regard it as native to Puerto Rico.

Ecological Significance

Being a legume, I. vera apports nitrate to the soil. Edmisten (1970b) found large nodules in the roots of the main legumes at El Verde: Ormosia krugii, Inga vera, I. fagifolia and Andira inermis. All these legumes fix nitrogen in the forest soil and concentrate nitrate in the soil around them (Edmisten, 1970c). Two to three times as much available nitrate was found in the soil around these legumes compared to nearby soil. Since these species are very common in the El Verde forest they may contribute significant amounts of usable nitrogen in the soil.

The importance of the ability of I. vera to harbor bacteria that fix nitrogen is reflected in its use in coffee and cacao plantations. It is not only suitable for shade but also prevents erosion and serves as a good fertilizer or nitrogen source. South American Indians used to plant Inga trees near coffee because it gave a better crop. Centuries of experience have made Inga the most widely used species in coffee agriculture.

Edmisten (1970b) reports ectotrophic mycorrhiza in roots of I. vera. Mycorrhizas serve as very efficient nutrient traps in areas of heavy rainfall such as the forest at El Verde where rainfall leaches nutrients from the soil.

It is well established that the glands found between each pair of leaflets of I. vera are a type of extrafloral nectary. Elías (1970) found that trees of Inga with actively functioning nectaries had a varying number of stinging or biting ants feeding upon the nectar. Nectaries on the younger leaves are more active than the older ones. Virtually inactive nectaries had more leaf damage. Elías suggested a facultative relationship between various species of ants and Inga for the mutual benefit of both.

Leaves of I. vera observed at El Verde had a great number of insects on them. The nectary glands may be an adaptation of the species to defend itself against the great number of insects that attack its leaves. Salas (1974) points out that its glands benefit insects because they are a trophic source for many insects, especially in deforested sites, where this species is very abundant.

Martorell (1945), in his survey of the forest insects of Puerto Rico, listed the species of insects he found in different parts of plants of I. vera (Appendix). Plagues or insect outbreaks have frequently invaded Inga (Marrero, 1954). Insects associated with these plagues are listed in the Appendix.

## Successional Status

It is well established in the literature that I. vera is a secondary succession species. Richards (1952) characterized secondary forest species by the following: (1) seeds, usually small, with a good dispersal mechanism, (2) production of many seeds, (3) rapid growth, (4) wood of low density, (5) wood and leaves that decay rapidly, (6) a

short life span, (7) low ability to survive in the forest shade, and (8) the ability to live in disturbed environments. Inga vera exhibits rapid growth, intermediate wood density (0.6 $g/cm^3$), wood and leaves that decay rapidly and the ability to live in disturbed environments with wide ranging environmental factors. In contrast, the seeds are large and with limited dispersal mechanisms. Seedlings can survive in the forest shade for several years. Production of seeds and life span are intermediate in comparison with other species. Inga can be classified as a late secondary succession species.

Kenoyer (1929) has reconstructed the course of succession on old clearings in Barro Colorado Island, Panamá. He found that Inga species grew in the area after 15 to 20 years of succession. At the time Inga came in, the soil and microclimatic factors favorable for its development had already developed. The establishment of Inga and other late secondary species made conditions favorable for primary species, which had started to establish after 20 years of succession.

Survival

The high number of canopy trees observed in the study area (Figure 1, page 12) as compared to the rest of the forest (Figure 3, page 14), is probably due to three factors: (1) planting of Inga trees while the area was a coffee plantation, (2) enhancement of survival when the tree reaches the canopy, where light availability is high, and (3) less likely, small sampling area.

Inga possesses large seeds. Richards (1952) mentions the advantages of species with large seeds. He states that large, heavy seeds provided

with abundant food reserves, a common feature among tall growing species, may have an advantage in enabling the seedling to grow to a large size and live a long life. It would thus have a better chance of surviving until the canopy is opened in the forest shade.

The fact that Inga possesses viviparous seeds, in which germination starts inside the legume fruit, results in advantage of the species for survival.

The life table of I. vera (Table 7, page 27) presents low mortality from seed to seedling stages and high mortality in the transition from seedlings to juveniles. The drastic reduction in numbers from seedlings to juveniles suggests that the inability of individuals to develop into young trees is due to low light intensities. Transplant experiments confirmed this hypothesis. In Inga, light is an important factor needed for growth and development. Since light at the forest floor is limited, most individuals will die; only those growing most rapidly under a gap in the forest canopy are the most likely to survive. The density of I. vera in the forest is limited by the availability of light which controls the development of seedlings into the juvenile stage. Richards (1952) points out that large numbers of young trees, having survived successfully the dangerous period of seedling mortality, probably die after a suppression period lasting for several years or even decades. Inga vera seems to have the ability to live suppressed for several years, but many individuals die after the suppression period. Based on these facts, it could be said that Inga is a "gap opportunist," that is, a species that can maintain itself under

undisturbed forest conditions but which will benefit greatly from forest disturbances (Baur, 1964 and Lebrón, 1977). The death of a parent tree would be the most favorable disturbance of the canopy for Inga's regeneration because of its poor dispersal mechanisms.

The survivorship curve of I. vera based on years is concave (Figure 6, page 24), which indicates that this species experiences heavy mortality early in life (Pearl and Miner, 1935 and Deevey, 1947).

Comparable studies on survival of tropical plant species are very few. These are mentioned below.

The first survivorship curve developed for a tropical tree was that of the palm Euterpe globosa by Van Valen (1975), who constructed it from data obtained by Bannister (1970). The overall shape of the curve is concave, but the young tree presents a constant probability of death. There is high mortality of seeds, which is expected of most tree species.

The survivorship cuve of Buchenavia capitata is strongly concave, due to a very low capacity of seedlings to establish on the forest floor (Sastre, personal communication).

Cecropia peltata exhibits a concave survivorship curve. Mortality is high in the early stages of development, but it is more gradual than in Buchenavia and Inga (Silander, personal communication).

Data used in the present study represent observations obtained within one year of study. These observations are not conclusive of the behavior of I. vera, but are exemplary of the population dynamics of the species at the El Verde forest during the study period.

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# APPENDIX

TABLE A-1

LIST OF INSECTS AFFECTING *INGA VERA*

| Part of Tree: | Order: | Family: | Species: |
|---|---|---|---|
| Pods | Lepidoptera | Stenomidae | *Stenoma* spp. |
| | Homoptera | Chermidae | *Psylla minuticona* |
| | | | *P. martorelli* |
| | | | *Icerya montserratensis* |
| | | | *Pseudococcus virgatus* |
| | | | *Inglisia vitrae* |
| | | | *Lepidosaphes crotonis* |
| | Coleoptera | Chrysomelidae | *Cryptocephalus tristiculus* |
| | | | *C. perspicax* |
| | | | *Diachus nothus* |
| | | | *Metachroma* spp. |
| | | Curculionidae | *Exophtalmodes roseipes* |
| | | | *Diaprepes abbreviatus* |
| | | | *Lachnopus curvipies* |
| | | | *Apodrosus volcotii* |
| | Lepidoptera | | *Phoebis argante* |
| | | | *Eulepidotis addens* |
| | | | *Phostria humeralis* |
| | | | *Tetralopha scabridella* |
| | | | *Brenthia pavonacella* |
| | | | *Trichotaphe* spp. |
| | | | *Acrocercops dives* |
| | | | *Megalopyge krugii* |
| | Hymenoptera | Braconidae | *Microbracon* spp. |
| | | | *Yelicones* spp. |
| | | | *Leptomastidea antillicola* |
| Twigs | Homoptera | Membracidae | *Nessorhinus gibberulus* |
| | | Cercopidae | *Philaenus frisco-varius* |
| | | Fulgoridae | *Bothriocera venosa* |
| | | | *Neurotmeta angustata* |
| | | | *Ormenis marginata* |
| | | | *Flatoides brunneus* |
| | | Coccidae | *Asterolecanium ingae* |
| | | | *A. pustulans* |
| | | | *Cryptostigma inquilina* |
| | Hymenoptera | Formicidae | *Myrmelachista ramulorum* |
| | | | *Camponotus ustus* |
| Trunk | Isoptera | Termitidae | *Nasutitermes costalis* |
| | Homoptera | Coccidae | *Lecaniodiaspis* spp. |
| | Coleoptera | Bostrychidae | *Apate monachus* |

TABLE A-1 (continued)

| Part of Tree: | Order: | Family: | Species: |
|---|---|---|---|
| | | Cerambycidae | Neoclytus araneiformis |
| | | Platypoidae | Platypus excisus |
| | | | P. ratzenburgi |
| | | Scolytidae | Xyleborus affinis |
| | | | X. sacchari |
| | Lepidoptera | Pyraustidae | Agathodes designalis |
| | | Tineidae | Mea spp. |
| | Hymenoptera | Chalcididae | Trigonura spp. |
| Dead Wood | Isoptera | Termitidae | Nasutitermes discolor |
| | Coleoptera | Briprestidae | Chrysobothris tranquebarica |

Source: Martorell, 1945

TABLE A-2

INSECT OUTBREAKS AFFECTING *INGA VERA*

| Insect: |
|---|
| *Myrmelachista ambigua ramulorum* (hormiguilla) |
| *Pseudococcus citri* (chinches harinosas) |
| *Cryptostigma inquilinax* (querezas carnosas) |
| *Psylla minuticona* |
| *P. martorelli* |
| *Drapepes* spp. |
| *Lachnopus* spp. |
| *Tetralopha acabridella* (butterfly larvae) |
| *Eulopidotis addens* (butterfly larvae) |
| *Megalopyge krugii* (plumilla) |
| *Nasutitermes costalis* (comején) |

Source: Marrero, 1954

# VITA

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