To the Graduate Council:

I am submitting herewith a thesis written by Inés Sastre-De Jesús entitled "Ecological Life Cycle of Buchenavia capitata (VAHL.) Eichl., A Late Secondary Successional Species in the Rain Forest of Puerto Rico." 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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ECOLOGICAL LIFE CYCLE OF BUCHENAVIA CAPITATA (VAHL.) EICHL., A LATE SECONDARY SUCCESSIONAL SPECIES IN THE RAIN FOREST OF PUERTO RICO

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Inés Sastre-De Jesús

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This manuscript was reviewed critically by my graduate committee Dr. J. F. McCormick, Dr. H. R. De Selm and Dr. C. C. Amundsen to whom I express my appreciation.

ABSTRACT

Different life stages of Buchenavia capitata (Vahl.) Eichl., were studied to determine the most critical stage in terms of survival. The investigation was conducted at El Verde Field Station in the Luquillo Experimental Forest of Puerto Rico. Buchenavia capitata was selected for the study because of interest in this species by the Institute of Tropical Forestry, U.S. Forestry Service.

The study was composed of the following divisions: (1) B. capitata population was divided into size classes (seeds, seedlings, young trees and mature trees), (2) density of each size class was determined, (3) phenological observations, (4) germination studies were carried in the forest and in a forest clearing, (5) seed dispersal and rate of mesocarp decomposition. Obtained data was summarized in a life table.

B. capitata showed a strong seasonal periodicity. Leaf fall and flowering were related to relatively dry and wet periods in the rain forest. Large number of flowers were produced, but few developed into fruits. Seed germination and seedling mortality were high. Seedlings that were growing in the forest clearing showed an extensive grwoth indicating that light was a main factor responsible for seedlings establishment and development. Senescence was identified as beginning at approximately 40 years. B. capitata presented typical characteristics of a late secondary

successional species, exhibiting a behavior of a gap opportunistic species.

B. capitata could be an alternative for a reforestation program because it presented a fast growth, good wood quality and as a native species will not require intensive management, fertilizers or pesticides for assuring a high quality crop.

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CHAPTER I

INTRODUCTION

Human activity in tropical rain forests has been increasing over the last twenty-five years. More knowledge is needed to acquire a better understanding of the ecological effects of these activities upon fauna and flora, and how to better manage tropical rain forests. One of the methods of studying tropical forests is by employing an autecological approach. One of the central objectives of autecological studies is to find clues or ideas for understanding the structure and dynamics of species populations (Pelton, 1951).

Main objectives of this research were to investigate reproduction, seed dispersal, germination, growth, and size distribution of *Buchenavia capitata* (Vahl.) Eichl., one of the components of the tropical rain forest. Different life stages of this species were studied to determine the most critical stage in terms of survival. Another aspect determined was the influence of environmental factors (precipitation, light, etc.) on the life cycle. Data obtained is presented in a life table (Deevey, 1947) summarizing vital statistics of the population. A life table allows one to make inferences of survivorship, and chances of mortality of individuals of any particular age. A final objective of this study was to clarify the role of *B. capitata* in in succession. Evidence is presented to clarify the successional status of this species.

This study is the fifth in a series of ecological life cycle studies conducted in the El Verde forest by graduate students under the direction of Dr. J. F. McCormick. This study of _B. capitata_ contributes to a greater understanding of ecological succession in tropical forests thru an analysis of the specific roles of successional species.

The Taxon

The genus _Buchenavia_ belongs to the subtribe Terminalieeae of the Combretaceae family. The Combretaceae is a family of trees, shrubs, and lianes in a wide variety of habitats throughout the tropics (Exell, 1972). However, _Buchenavia_ is confined to tropical America. It has been suggested by Exell and Stace (1963), that the genus _Buchenavia_ of the South American rain forests is derived from the genus _Terminalia_, which is mainly an African genus.

Buchenavia species are shrubs and trees occupying two different habitats. Small trees and shrubs of the genus are common in lowland forests often inundated by water, while tall trees occupy the upland rain forest. _Buchenavia capitata_ is one of the prominent trees of the limestone and lower montane regions of Puerto Rico. These forests occur at approximately 150 meters above sea level. _B. capitata_ is mainly Caribbean, its northern limit is Cuba, and its southern limit is in Brazil (Fig. 1).

In the lower montane forests of Puerto Rico Buchenavia is a canopy tree growing from 20 meters to 25 meters tall and 60 to 130 centimeters in trunk diameter (Little and Wadsworth, 1964). The flat, multi-layered crown of this tree can be identified from any high observation point in the forest.

Another characteristic of B. capitata is erect clusters of small alternate leaves at the end of the branches. Leaves are rounded at the apex and long pointed at the base. The upper surface is yellow-green and the lower surface is more pale.

The small greenish flowers are arranged in spikes. One important taxonomic feature in this genus is that the calyx is almost as broad as it is long (cup-shaped) and bears five scarcely developed calyx lobes. There are 10 stamens, and the pistil has an inferior, hairy, one-celled ovary.

In size and shape, the fruits resemble an olive. The mesocarp, or fleshy part, is bitter. The embryo is protected by a very hard endocarp that is difficult to open.

The wood of B. capitata is very attractive and of good quality. It is heavy, strong, moderately hard, and though not widely used, is recommended for furniture and cabinet-work. It is also good for construction, framing, ply wood, and turnery.

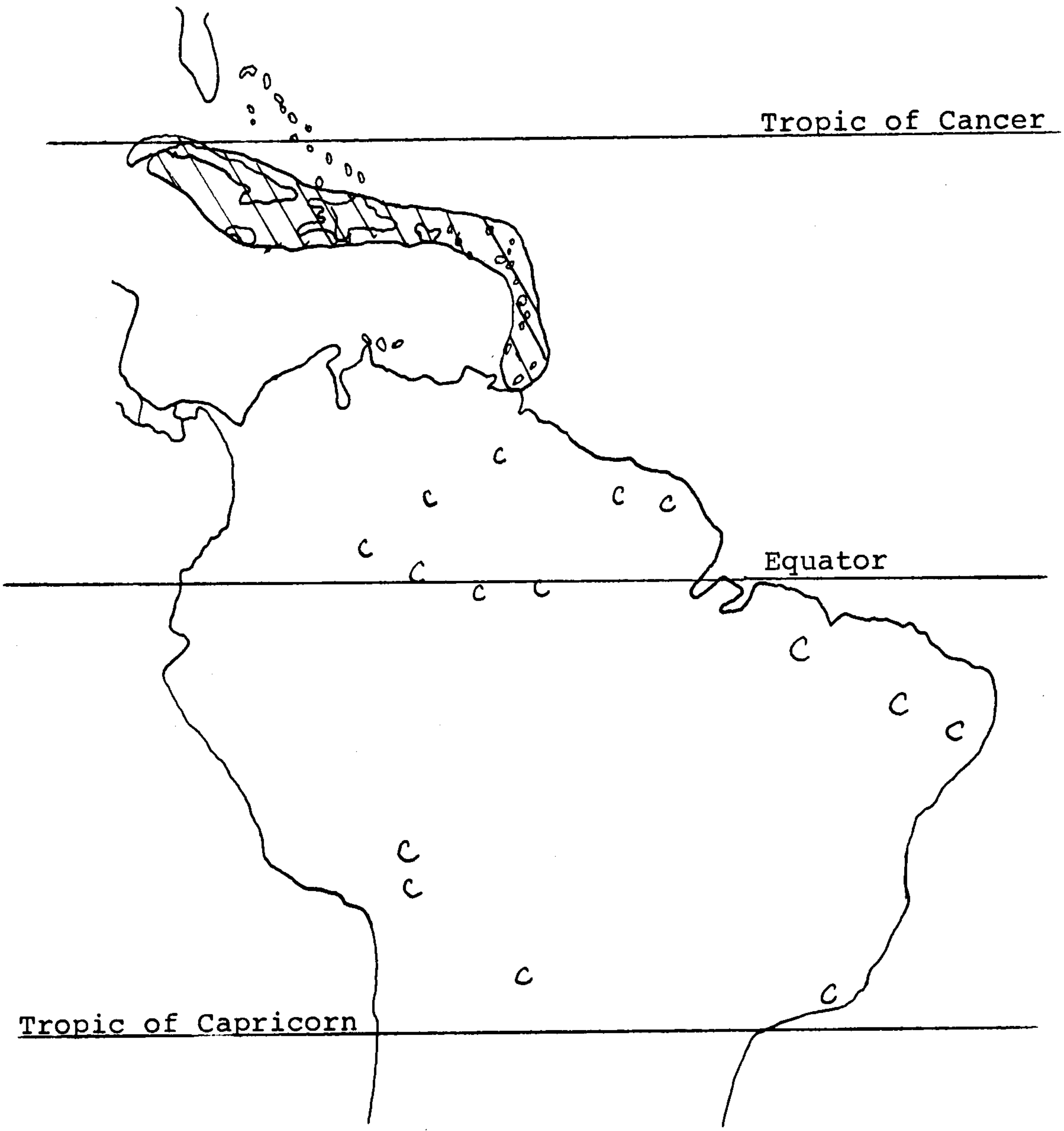


Fig. 1. Geographic distribution of Buchanavia capitata according to Exell and Stace (1963). "C" indicates the distribution of the species in South America.

General Description of the Area

Puerto Rico is the smallest island of the Greater Antilles, its center is near latitude 18° oo'N and longitude 65° 45'W. The island is divided into two vegetation regions by a chain of mountains which extend east to west along the central section of the island. The eastern part (Sierra de Luquillo) of this chain is in the path of the Trade Winds and receives regular orographic rain. The El Verde study area is in the northwestern side of the Luquillo mountains. According to Richards (1952), Odum et al. (1970), the El Verde site can be classified as a tropical rain forest.

The vegetation of El Verde is classified as a lower montane forest (Beard, 1942), dominated by *Dacryodes excelsa* (tabonuco) and *Sloanea berteriana* (motillo).

Highest temperatures are registered from May to August. Mean annual temperature at the base of the mountains is 26°C and at the summits is 19°C (Odum et al., 1970). Average monthly precipitation is 102 mm.

According to Boul (1973), El Verde is characterized by weakly developed soils. These soils are of volcanic origin and composed of andesite and basaltic materials. Soils in this area have been classified as Los Guineos clay and clay loams. Soil pH's range from 3.8 to 6.1.

Climate during Period of Study

Temperatures recorded at El Verde are presented in Table 1. Temperature in the forest clearing was one to two degrees higher than in the forest. Figure 2 is an adaptation from Lebrón (1977), which presents rainfall data and number of dry days at El Verde. Highest precipitation was recorded in October-December and a dry season in April-June. Light intensity is 20g-cal/cm^2/day at the forest floor and 363.6g-cal/cm^2/day at the open area (Odum, Drewy and Kline, 1970).

TABLE 1

TEMPERATURE RECORDED IN THE FOREST AND IN A FOREST CLEARING AT EL VERDE, 1978

Month	Mean temperature (°C) Forest Clearing	Mean temperature (°C) Forest
JANUARY	21.0	21.7
FEBRUARY	22.0	21.2
MARCH	22.7	22.0
APRIL	23.1	22.5
MAY	24.6	22.8
JUNE	24.4	23.1

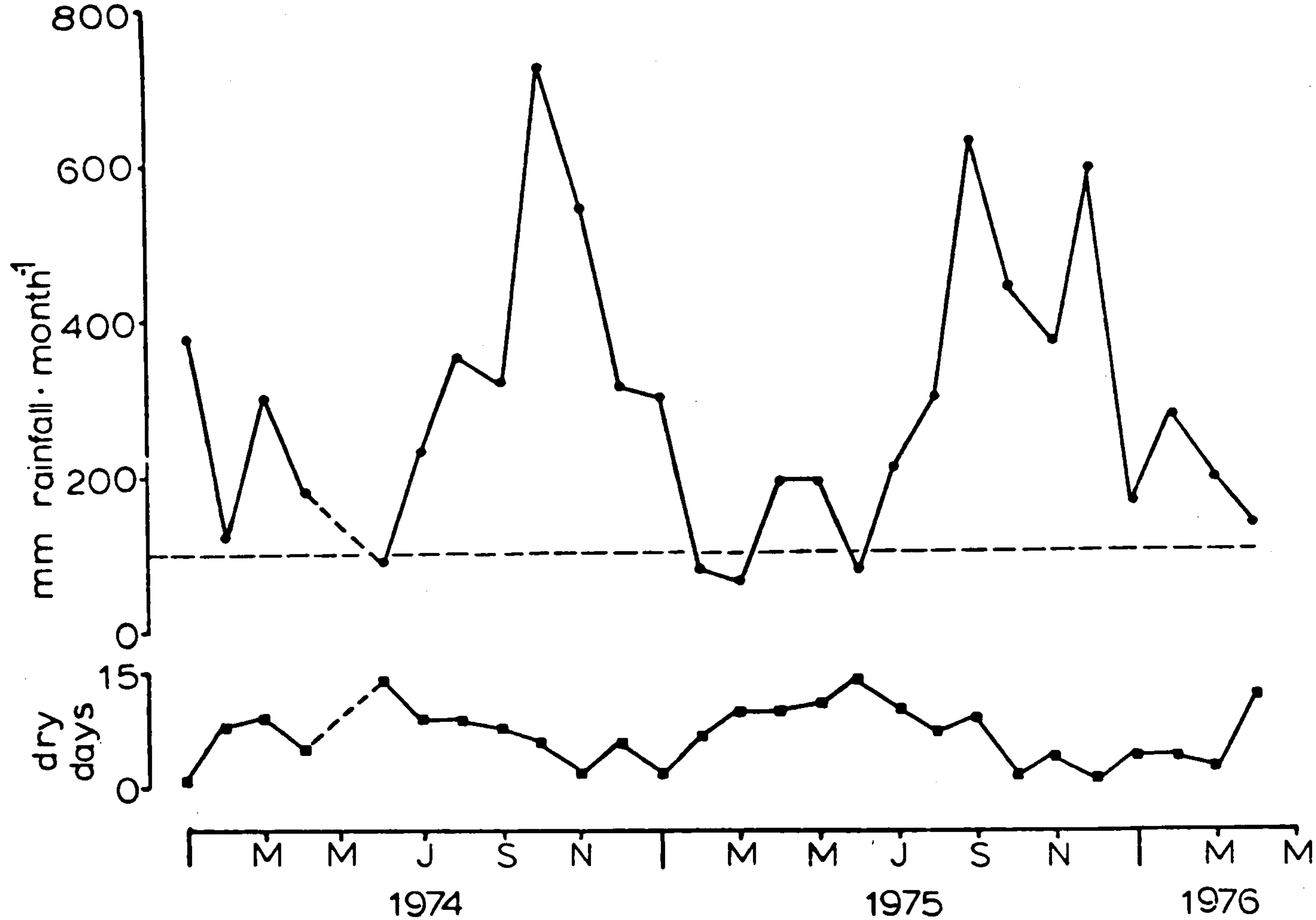


Fig. 2. A two and one-half year record of monthly precipitation and number of dry days in the forest at El Verde. A dry day was one without rainfall. Adaptation from Lebrón (1977).

CHAPTER II

METHODS

Phenological studies were conducted following the method described by Fournier (1974). A group of 15 trees near the research station was selected for quantitative phenological observations. Development stage of different phenological characteristics (leaf fall, flowering, and fruiting) were ranked in terms of a scale. The scale used was the following:

0 ..... Absence of the characteristics

1 ..... Presence of the characteristic with a range from 1-25%

2 ..... Presence of the characteristic with a range from 26-50%

3 ..... Presence of the characteristic with a range from 51-75%

4 ..... Presence of the characteristic with a range from 76-100%.

These observations were taken every two weeks during the months of April through August, 1978. A value from 0-4 was assigned to each tree that was observed. Observations were made with the aid of a pair of binoculars (7 × 50). Data obtained were used for constructing a graph of seasonality of _B. capitata_.

Another sample of 75 trees was selected in the Palo Hueco area. These trees were observed every two weeks. During each trip made to Palo Hueco the number of trees without leaves, with buds, in flower, and with new leaves was recorded. Results were expressed in percentages.

After counting the number of branches on each tree, a branch was cut from each tree. Each branch was labeled and removed to the laboratory where the following data was recorded: length of branch, and number of buds, spikes, and flowers. Flowers were removed from a sample of 100 spikes. In order to determine number of flowers, the spikes were microscopically observed and the scars per spike were counted. Numbers of spikes and flowers were averaged. Reproductive capacity of each tree was obtained by multiplying the average number of flowers per spike, by the product of the average spikes per branch and number of branches per tree.

A sample of 75 trees was used for analysis of size class distribution. Dbh and height (measured with an Abney level) of each was measured and recorded. The following size classes of _B. capitata_ were arbitrarily established: seeds, seedlings (plants to 0.29m tall), saplings or young trees (plants to 8m tall), older trees (over 8m tall). Density in each size class was determined using 12 (10m × 50m) transects in El Verde.

In April, 1978, permanent transects were established at El Verde under the canopy of trees which had previously shed their fruits. Transects were as long as the branches of the trees. Most of the transects were from 6 to 11 meters long. Number of fruits and seedlings in each successive square meter along the transects were recorded every month, and used for calculating the percentage of ungerminated seeds, germination and seedling mortality.

In the first week of April, 1978, 100 fruits were marked under the canopy of _B. capitata_. Each week fruits were examined to determine dispersal, and predation. A scale was used to determine decay or duration of the mesocarp. Fruits were examined assigning values from zero to four.

0 ..... The mesocarp is complete

1 ..... 1-25% of the endocarp exposed

2 ..... 26-50% of the endocarp exposed

3 ..... 51-75% of the endocarp exposed

4 ..... 76-100% of the endocarp exposed.

Another group of 200 fruits was selected for studying germination in an open area in the forest near the laboratory at El Verde. Mesocarp and endocarp of each fruit were removed and the embryos were planted in square meter wood boxes. Wood boxes were filled with soil from the same area of parent trees (_B. capitata_), and then were placed in an open area near the research station.

Growth rate of seedlings was determined by tagging and measuring 300 seedlings under the canopy. All measurements were taken from the base of the stem, to the terminal bud.

CHAPTER III

RESULTS

Phenology

Both mature trees and saplings of *B. capitata* exhibited leaf-fall in April through June (Fig. 3). Most trees remained without leaves from seven to fourteen days. The greatest number of trees without leaves occurred in the first two weeks of May at both El Verde and Palo Hueco.

Following leaf-fall the trees flowered, reaching their flowering peak between May 15 and May 24. This peak at El Verde and Palo Hueco was on May 15 (Fig. 4) and May 24 (Fig. 3), respectively. By the last week of June, 92% of the trees had new leaf clusters containing nine to ten leaves.

Maturation of fruits took from seven to nine months. According to Estrada (1970) fruiting reaches a peak between January and March. Fruit drop occurred from March through May, and maximum rate occurred in April (Table 2).

Reproductive Capacity

Buchenavia capitata produces four to five inflorescences per bud. Each spike has an average of 32 flowers, which are polygamous. Honeybees were the most frequent pollinators observed by the investigator. One fruit with a single large seed is produced per flower.

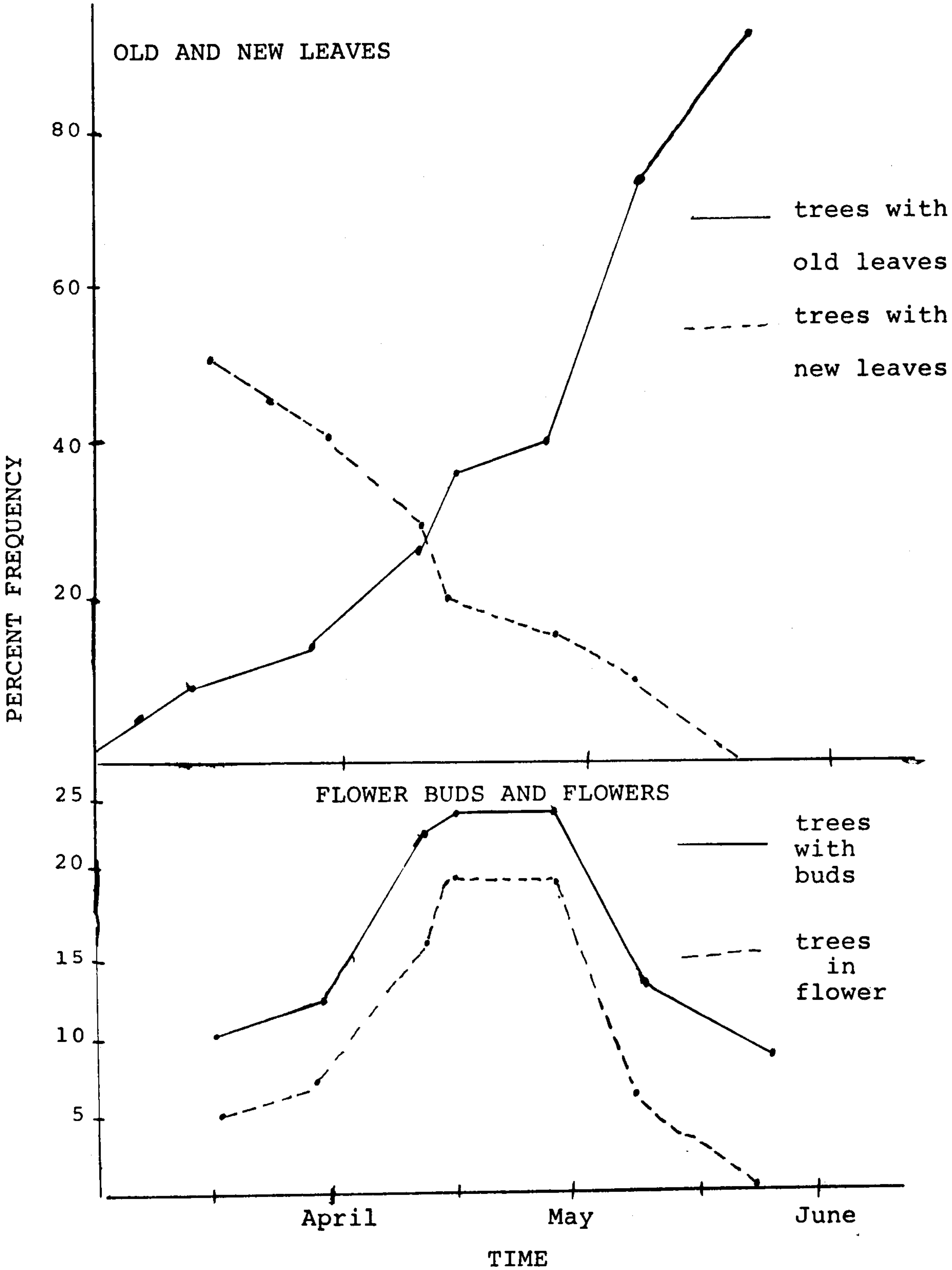


Fig. 3. Percent frequency of trees with old or new leaves and with buds or flowers at Palo Hueco.

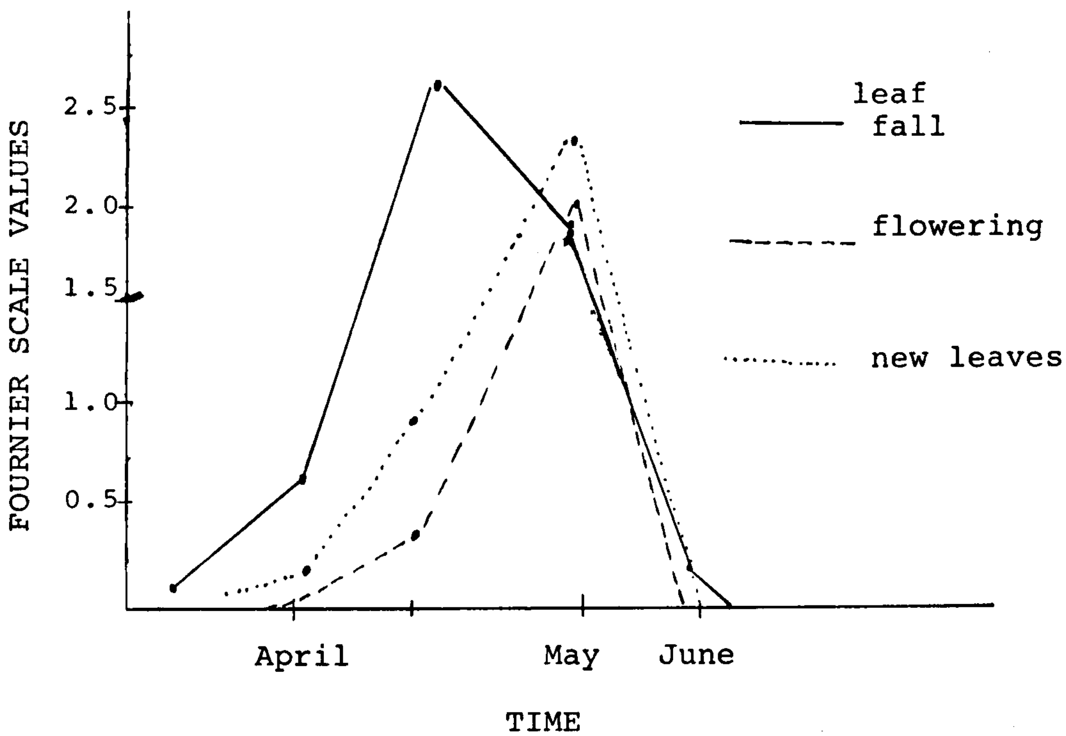


Fig. 4. Time of leaf fall and flowering based upon sample of 15 trees at El Verde, 1978. Data are expressed according to the methods of Fournier (1974).

TABLE 2

SEED AND SEEDLING DENSITY BELOW *B. CAPITATA* TREES IN AN AREA OF 14,300m2 AT EL VERDE

MONTH	SEEDS/m^2	SEEDLINGS/m^2
APRIL	5.20	2.12
MAY	3.11	3.00
JUNE	.68	4.96
JULY	0.00	5.11
AUGUST	0.00	3.86
SEPTEMBER	0.00	1.83
OCTOBER	0.00	1.73
NOVEMBER	0.00	——
DECEMBER	0.00	1.35

Mature trees have the potential of producing an estimated average of 25,000 inflorescences (Table 3). Approximately 11,000 additional inflorescences per tree were found on the ground below flowering trees. This suggests that each tree could conceivably produce 448,000 fruits and seeds in a year.

Seed Density and Seed Dispersal

Average number of seeds under trees was observed in April when it reached a density of 5.2 seeds per square meter (Table 2). Seeds were found only under the canopy of *B. capitata*, and the chance of finding seeds in other areas was very low. Density of seeds obtained from transects in different areas of the forest was .6 seeds per square meter in April. In the following months the number of seeds started to decrease because of predation and germination.

Transects established below trees showed how seeds were distributed. Density of seeds was greatest within a distance of four meters from the base of the tree, and decreased sharply beyond this distance (Fig. 5).

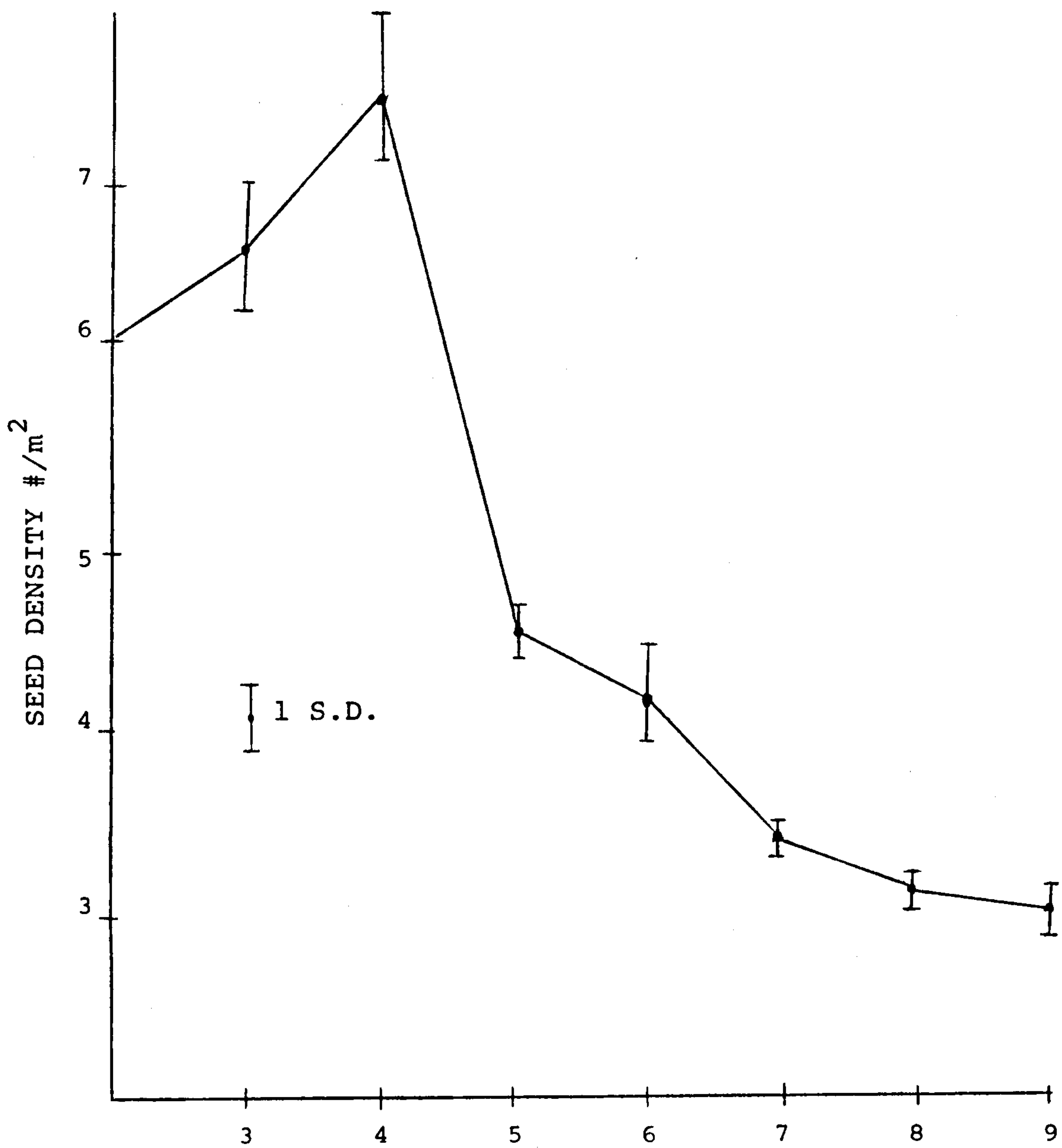
The mesocarp of the fruit is decomposed by microorganisms and eaten by insects. These insects are, (1) black beetles of the family Nitidulidae and, (2) larvae of Lepidoptera. They penetrate the fruits two weeks after the fruits have fallen from the tree. The mesocarp was removed in an average of 45 days leaving the bony endocarp exposed. Half

TABLE 3

REPRODUCTIVE CAPACITY BASED UPON 15 TREES IN A 14,300m^2 AREA AT EL VERDE

Buds per Tree		Inflorescences per tree*		Flowers per tree**		Seeds per tree	
$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
5500 ±	1800	25000 ±	8300	448000 ±	317000	448000	317000

*there are 4-5 inflorescences per bud.
**there are 32 flowers per inflorescences.



Distance in meters from tree trunk to periphery of canopy.

Fig. 5. Seed density along a distance gradient from the tree trunk to the periphery of the area covered by the canopy. Average area covered by the canopy of B. capitata trees is 1,000m^2 each, based upon the sample of 15 trees.

of the tagged fruits had the endocarp exposed in the last week of April and by the last week of May, 86%, were without the mesocarp (Fig. 6).

After the mesocarp was eaten or decomposed, rats separate or split the endocarp and eat the embryos. Seeds were not observed being carried away from the trees. They were collected by rodents, accumulated in small caches, and then opened. Number of endocarp sections were counted. An estimated 20% were eaten or damaged by rats. *B. capitata* fruits are listed as a food source of the Puerto Rican parrot, *Amazona vittata* (Rodriguez-Vidal, 1959). Besides predation by rats, there were no observations during this study of other organisms damaging embryos of seeds.

Germination and Seedling Development

Emergence of radicles occurred soon after the mesocarp was removed. Germination was classified as epigeal since cotyledons were maintained above ground. It was estimated that 70% of the undamaged seeds in the forest germinated.

Number of seedlings observed was highest in July where the greatest density was 5 per square meter. An estimated 14% of the new seedlings were still alive in December and presumably were alive the next growing season (Fig. 7).

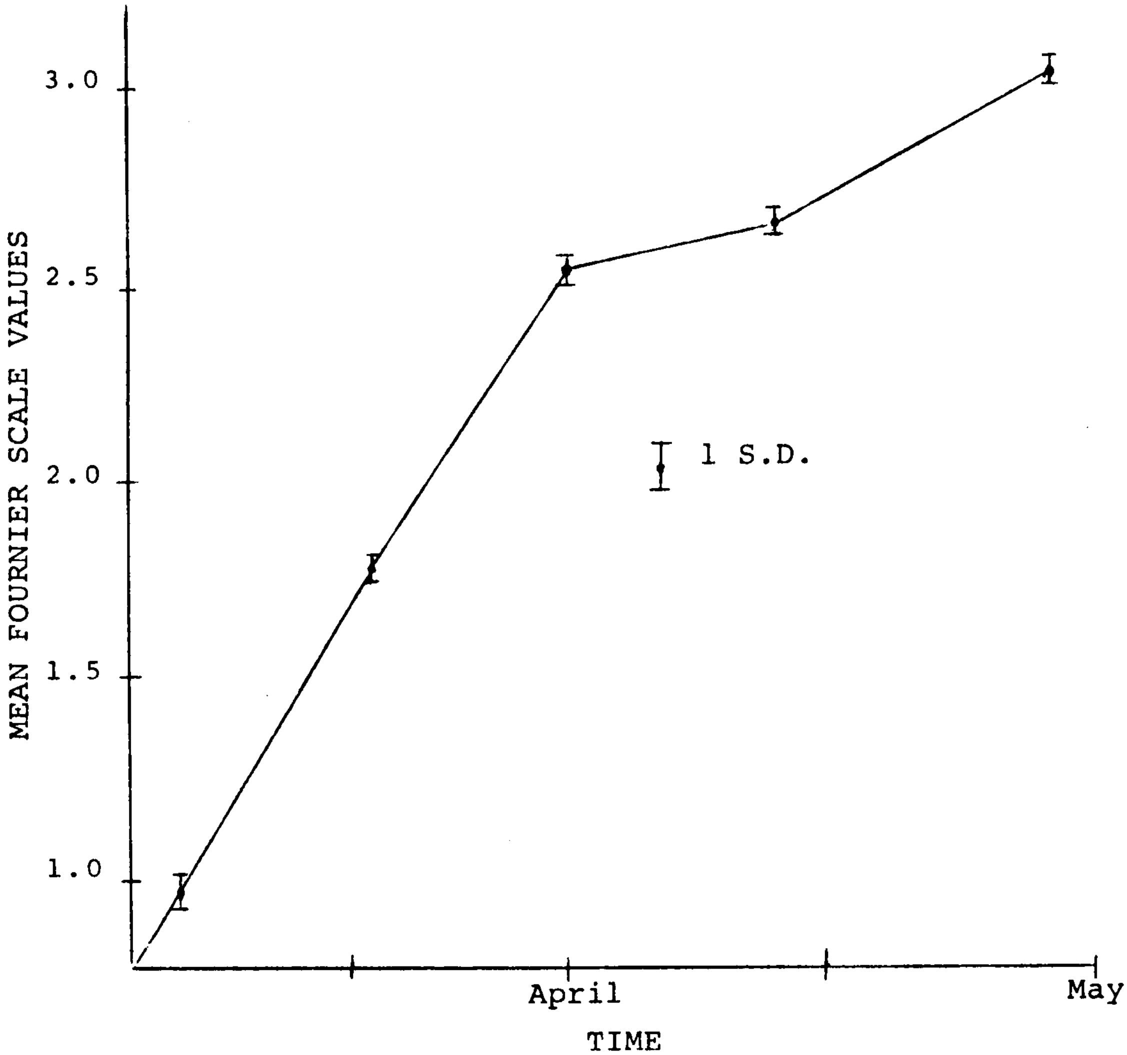


Fig. 6. Time required for decomposition of the mesocarp, expressed in Fournier scale values.

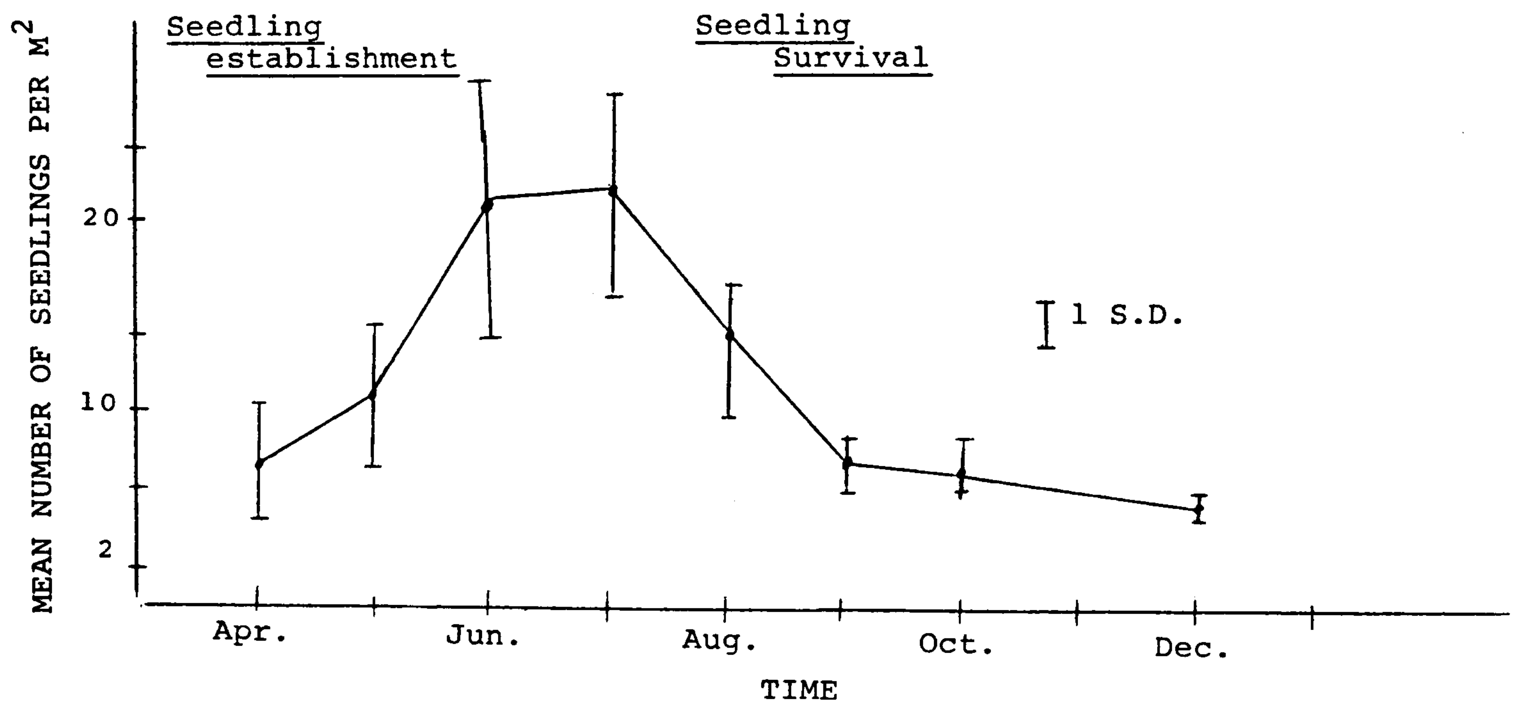


Fig. 7. Success of seedling establishment (April-June) and Survival (July-December) under *B. capitata* canopy at El Verde.

Seedling Growth

Seedling growth was estimated by measuring stem length of seedlings in the forest and in a forest clearing for 153 and 245 days, respectively during April-December. During May, seedlings in the forest did not have an increase in stem length, but progressive length was always expressed by seedlings growing in the forest clearing (Fig. 8). Average growth of seedlings in the forest was .71 cm per month. In the forest clearing monthly average growth was 3.7 cm (Table 4). According to Crow and Weaver (1977), mature *B. capitata* grow 0.80-1.83 cm in diameter per year.

By July, 70% of the seedlings had developed a pair of eophylls. Most seedlings developed eophylls in the fourth month of growth.

Size Classes

Figure 9 illustrates height distribution of young and old trees. Average height in the measured trees was 14.9m. Average height of the saplings was 2.2m. There were two peaks in the distribution, the first peak from one to two meters corresponding to saplings, and the second from 10 to 12 meters which corresponds to young reproductive trees. Density of trees and saplings on a 5,400m^2 area was .005 trees/m^2 and .003 saplings/m^2. Figures 10 and 11 present dbh and frequency distributions of saplings and trees,

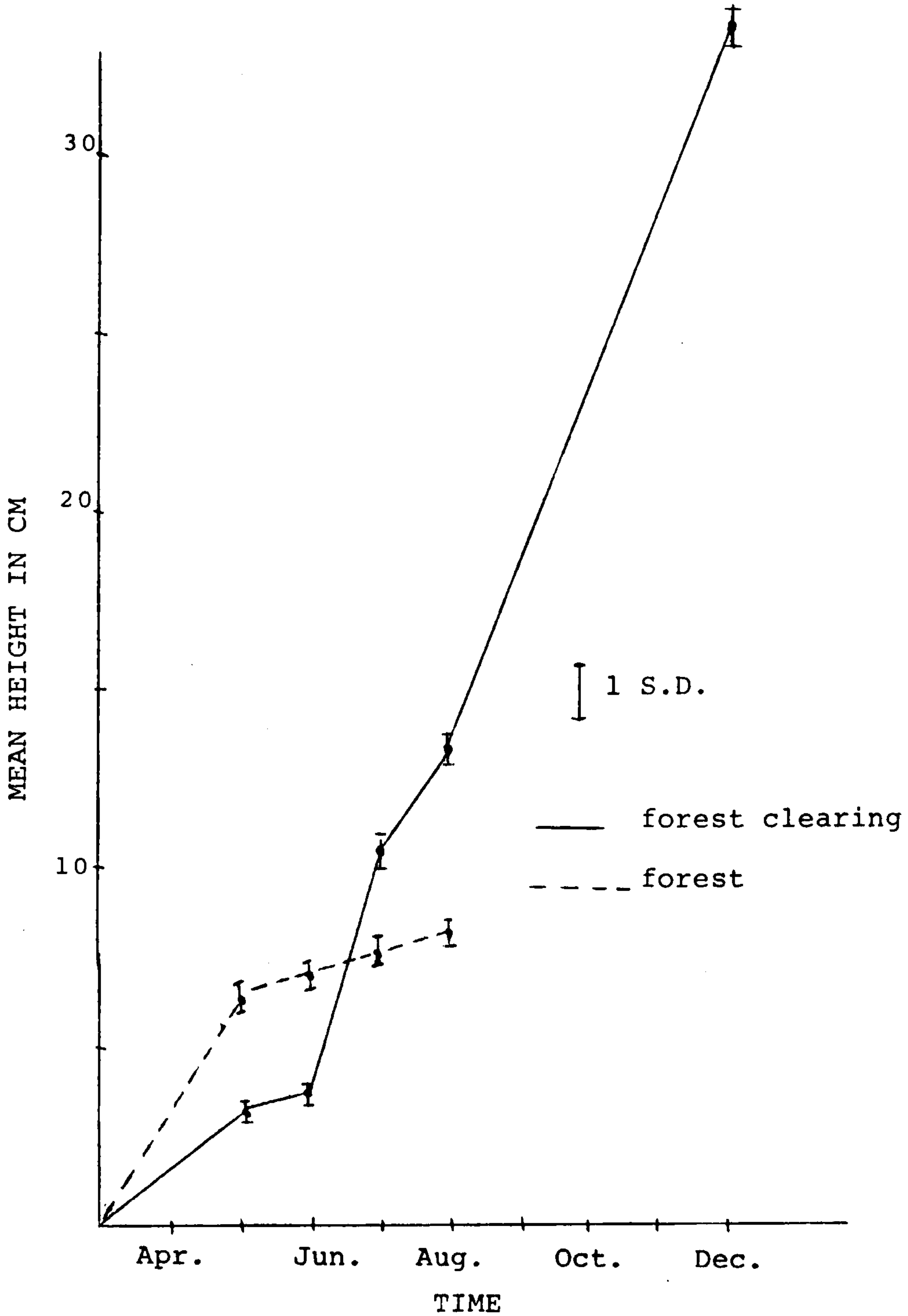


Fig. 8. Growth in height of B. capitata seedlings in the forest and in a forest clearing at El Verde from April to December.

TABLE 4

MONTHLY GROWTH RATES (CM/MONTH) OF SEEDLINGS IN THE FOREST AND IN A FOREST CLEARING

		June	July	Aug.
forest	$\bar{x}$	0.70	0.48	0.97
	s.d.	±1.10	0.73	1.00
forest clearing	$\bar{x}$	4.50	3.75	3.27
	s.d.	±1.86	1.26	1.79

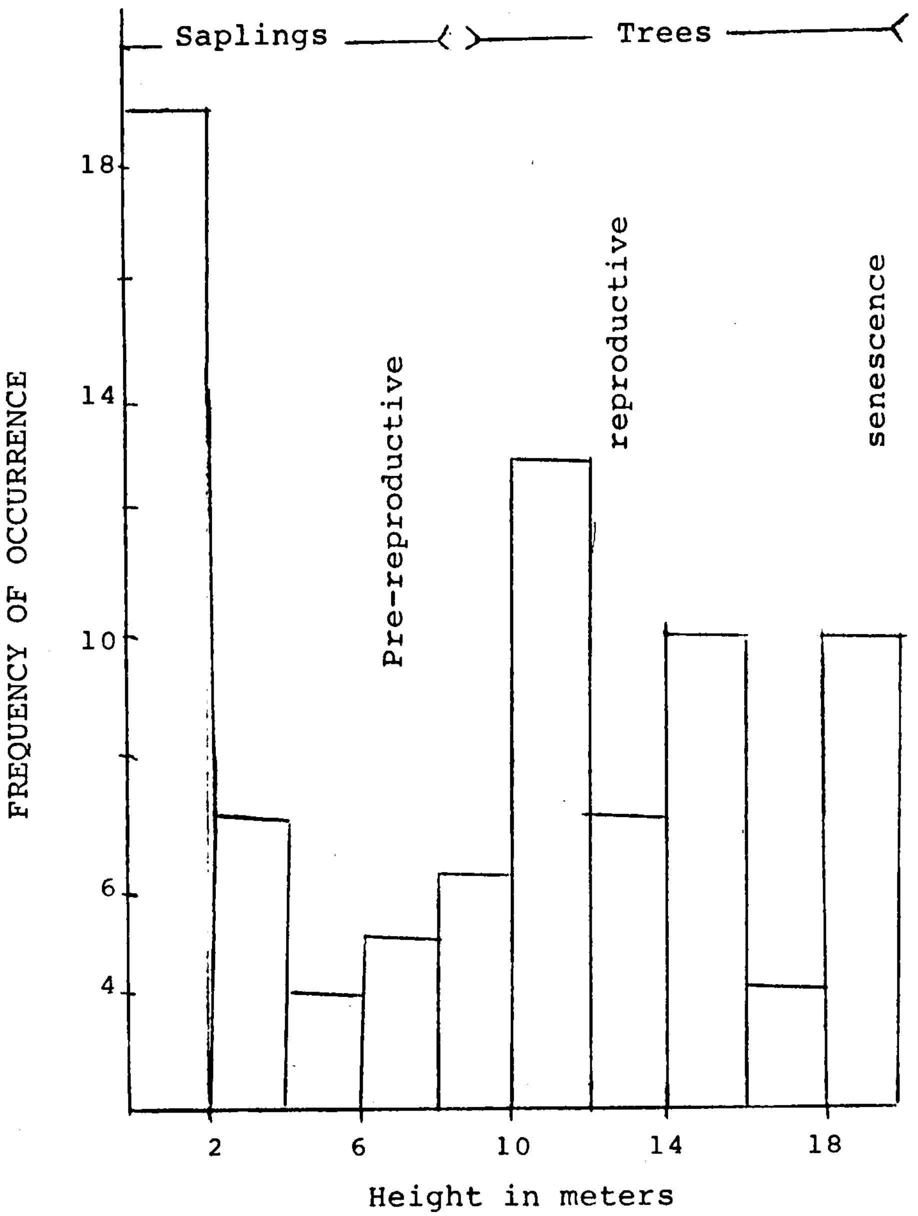


Fig. 9. Height class distribution among saplings and trees of B. *capitata* at El Verde.

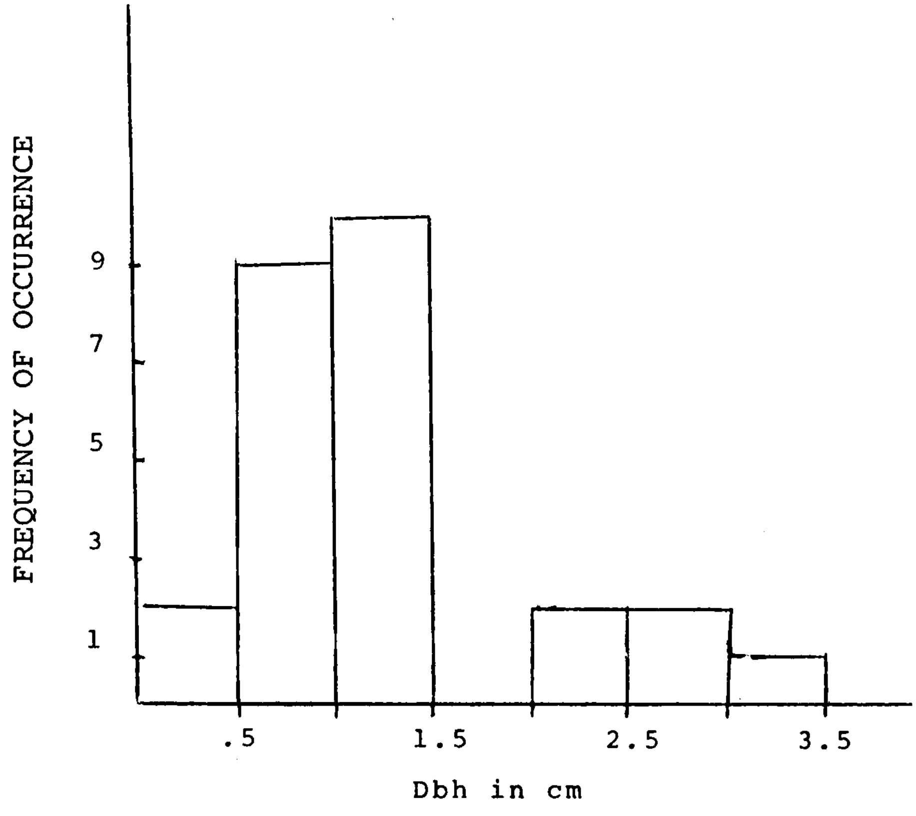


Fig. 10. Dbh class distribution among saplings at El Verde.

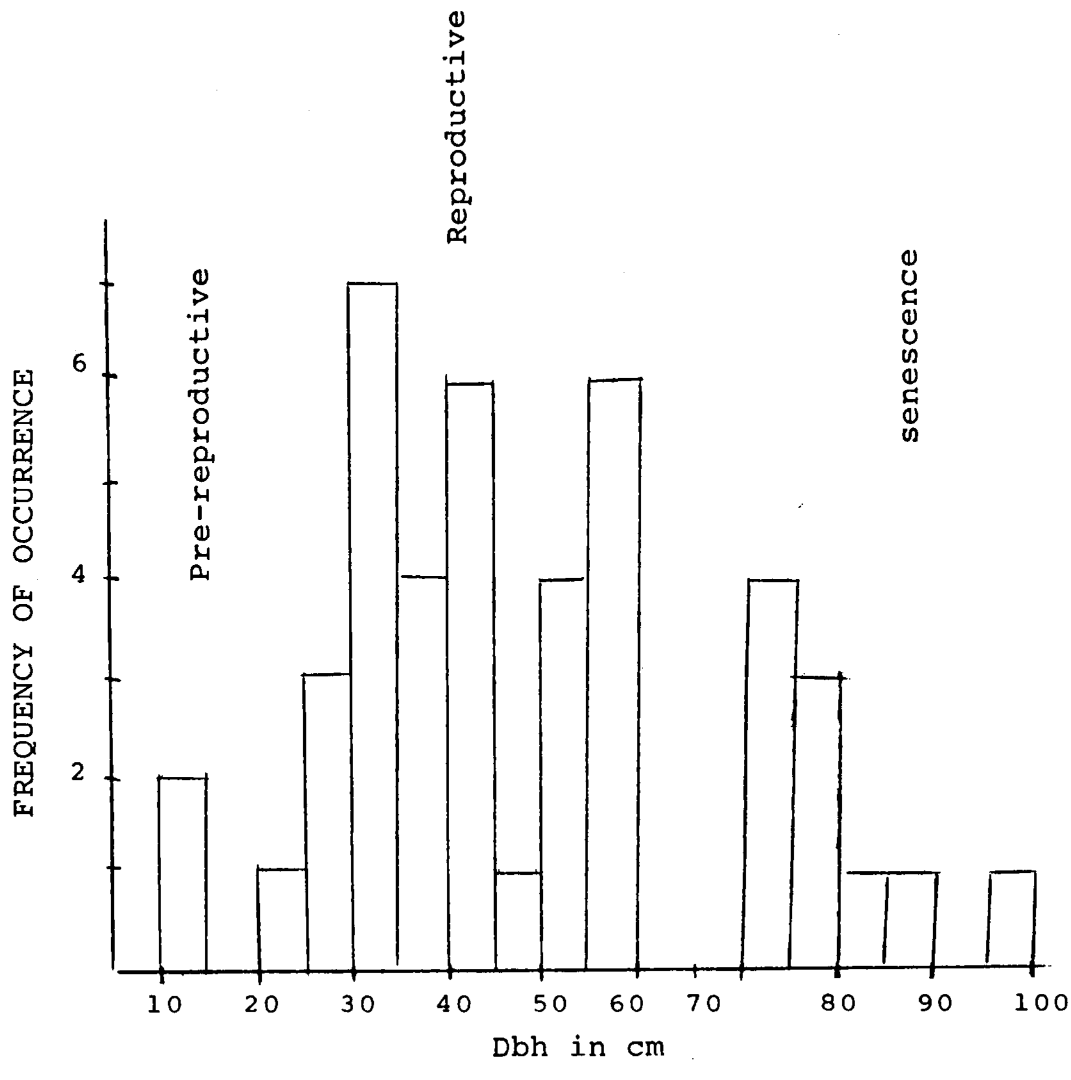


Fig. 11. Dbh class distribution among trees at El Verde.

respectively. Sapling distribution is skewed toward the left indicating that there were more individuals in the small size classes. Reproductive trees exhibit a more normal distribution.

Survivorship Curve and Life Table

A survivorship curve and a life table (Fig. 12 and Table 5) were constructed using field data obtained by the investigator (phenology, reproductive capacity, seed and seedling transects), and data (dbh increment measurements) provided by Mr. Carlos Rivera. These dbh increments were from 1946 to 1966. An estimated growth rate of 1.83 cm in dbh per year (Crow and Weaver, 1977) was used for calculating the minimum age of trees in Mr. Rivera's study. Dbh increments of trees in the present study were compared to estimates of the Forest Service and minimum possible age of each size class was calculated.

There is high mortality in the early stages of the life cycle. Although there is a high percentage of germination most of the seedlings die. After this point, mortality declines until mature trees attain an age of approximately 40 years. At this time, survival again decreases significantly. This point can be identified as the onset of senescence.

The life table was constructed following the method described by Sharitz and McCormick (1973).

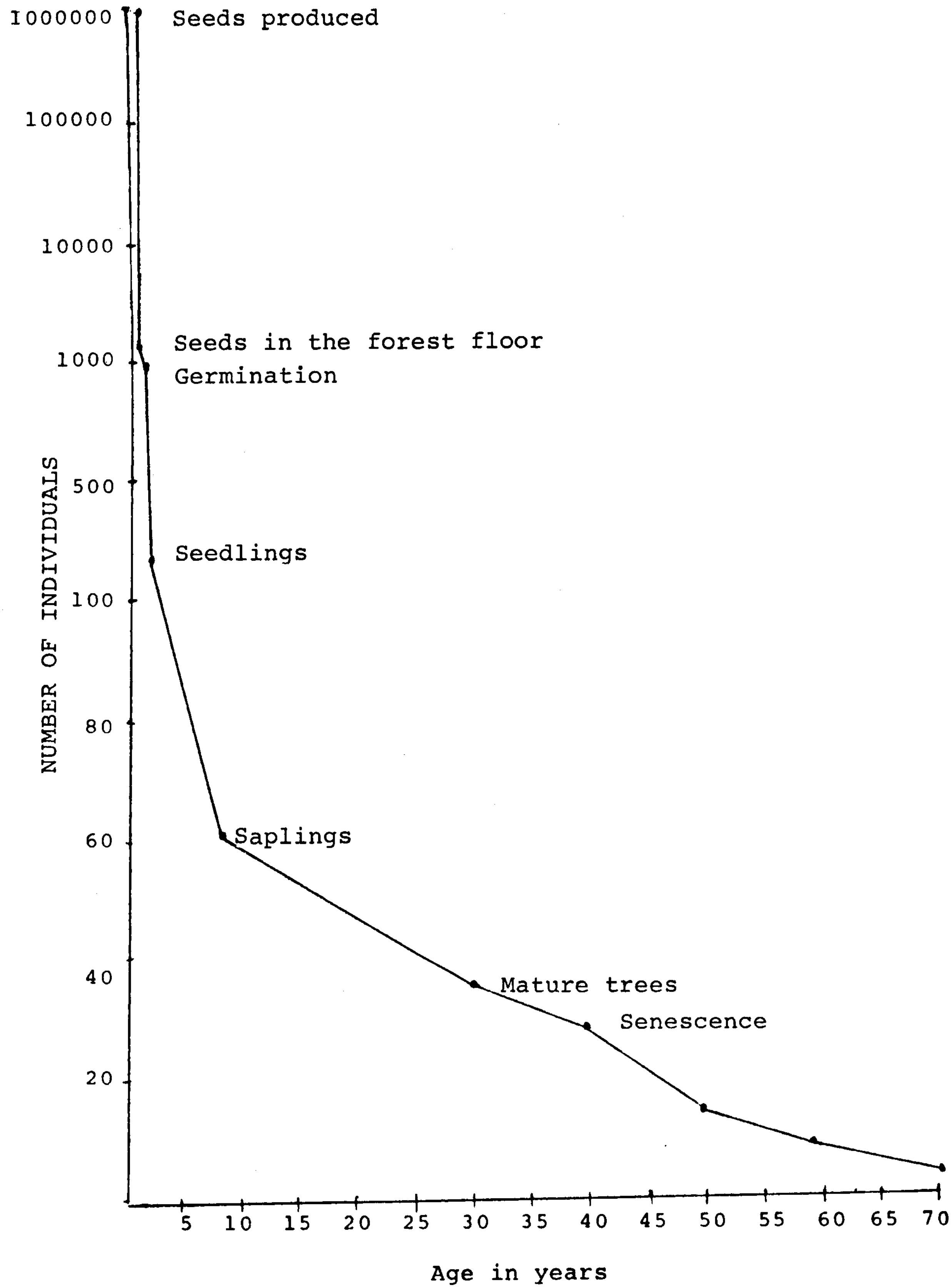


Fig. 12. Survivorship of *B. capitata*.

TABLE 5

ECOLOGICAL LIFE TABLE OF BUCHENAVIA CAPITATA

Life Cycle Stage	D_x	A_x	l_x	d_x	q_x	L_x	T_x	e_x
Seed (formation)	0.75	0-.75	1,000,000.0	998834.83	.998	500582.58	502497.72	.502
Seeds (in the forest floor)	0.08	0.75-.83	1,165.17	133.92	.114	1098.21	1915.14	1.643
Germination	0.08	0.83-.91	1,031.25	883.93	.857	589.28	816.93	.992
Seedlings (established)	0.59	0.91=1.50	147.32	87.06	.590	103.79	227.65	1.545
Saplings	7.50	1.50-9.00	60.26	24.55	.407	47.98	123.86	2.055
Mature	21.00	9.00-30.00	35.71	4.46	.124	33.48	75.88	2.124
	10.00	30.00-40.00	31.25	15.63	.500	23.43	42.40	1.356
senescence	10.00	40.00-50.00	15.62	4.46	.285	13.39	18.97	1.214
↓	10.00	50.00-60.00	11.16	.88	.078	5.58	5.58	.050
↓	10.00	60.00-70.00	10.28	—	—	—	—	—

D_x Life cycle stage duration in years.

A_x Age of the population of each life cycle stage in years.

l_x Number of individuals surviving.

d_x Number of individuals dying at each stage $d_x=l_x-l_{x+1}$.

q_x Mortality rate $q = {}^{d}x/l_x$.

L_x Number of individuals alive at each stage $L_x = (l_x + l_{x+1})/2$.

T_x Total number of individuals times age units.

$T_x \equiv \sum_{i=x} L_i$

e_x Life expectancy $e_x + {}^{T}x/l_x$ in years.

CHAPTER IV

DISCUSSION

Phenology

Phenological data (leaf fall, flowering, and fruiting) obtained in this study and from Estrada (1970) shows that *B. capitata* has a marked seasonal periodicity. Increased leaf fall during the dry season (April-August), can be considered a water-stress response. Trees observed in Palo Hueco shed leaves ealier and faster than trees at the El Verde research station. This could be due to the fact that Palo Hueco is on the drier leeward side of the island.

Flowering also occurred during the dry season, but only after three or more consecutive days in which scattered showers occurred. Previous studies have demonstrated that rainfall is an important factor in the timing and spacing of flowering in some tropical plants (Holdsworth, 1961; Frankie et al., 1974). After the trees have shed their leaves and entered dormancy, flowering occurs during the dry season (Opler et al., 1976). A dry period followed by scattered showers may be considered the stimulus triggering the flowering period of *B. capitata*. Janzen (1967) has proposed the hypothesis that many trees of lower montane regions have developed the capacity to flower during the dry season to better compete or to have a better distribution of energy during vegetative growth. In order to avoid pollen damage by rainfall some plants may have evolved to flower during the dry season.

Fruit drop occurred in March-April (part of the dry season), before leaf fall. During the dry season organic decomposition in the forest is very slow, but when rains begin, decomposition of the accumulated litter occurs very rapidly. Fruit drop before leaf fall assures that nutrients newly released by mineralization are available during growth (Smythe, 1970).

Different phenological events of *B. capitata* are synchronized with particular climatic conditions. Seasonal changes in tropical populations are keyed either directly or indirectly to variations in rainfall (Emmel, 1976). *B. capitata* is an example of a tropical tree which may have adapted to a periodicity of rainfall.

Reproductive Capacity

The number of flowers that trees are able to produce is very high, but few ovaries develop into fruits. One factor that can explain the small number of fruits produced is wind velocities which increase during spring and summer (Odum et al., 1970). During this period, the trees are without leaves, inflorescences are exposed and may easily be blown from trees.

Seed Density and Dispersal

Most of the seeds on the ground are concentrated between three and four meters from the trunk of the tree. Because *B. capitata* foliage occurs at the ends of branches, seeds are distributed thereunder forming a seed shadow. According to Janzen (1971) seed in the litter should be most numerous near the parent tree from which fruits or seeds drop. Seed density decreases with distance (from four meters outward) from the parent tree. There is a higher survival of seeds with increasing distance from the parent tree, apparently because predators concentrate at the points of higher seed density. Rats were not observed carrying seeds away from trees. This fact can partially explain why there is a low density of seeds in the forest (seeds have a very low probability of dispersal). Seeds carried by run-off water from an intense shower could be a possible mechanism of dispersal.

Elsewhere in Central America a high density of seeds or seedlings is not observed below the parent tree because of very efficient seed dispersal mechanisms and high predation. The structure of tree populations on tropical islands differs strikingly from those on adjacent mainlands (Janzen, 1971). In the Puerto Rican forest there is a high density of seeds and seedlings below the parent trees because of the absence of large rodents (other than rats) and large terrestrial birds in these forests dispersal is slight.

Germination and Seedling Development

One might expect that germination would occur at a time which would favour survival of the seedlings (Mayer, 1966). Germination was observed during the dry season. At this time *B. capitata* is without leaves and the light that reaches the forest floor reaches its annual maximum. The new seedling then receive the most light available during the year. In the rain forest light, not water, is most commonly a limiting factor in seedling establishment and survival (McCormick, 1970). Germination and seedling survival is enhanced by the increased sunlight reaching the forest floor beneath the parent tree.

There was high seedling mortality in the first few months, and only a small fraction of the germinated seeds became established seedlings. Hartshorn (1972) in his population dynamics study of *Pentaclethra macroloba* gave reasons for the high seedling mortality of this Costa Rican species. His conclusions explain the high mortality in *B. capitata*. He found that high seedling mortality was due to the falling of palm leaves, branches of other trees, heavy fruits on the seedlings, flooding and biological interactions (e.g. competition). Silander (1979) also conducted experiments in which she found that one reason for mortality in Cecropia seedlings was due to falling palm leaves (*Euterpe globosa*). *B. capitata* seedlings are very fragile, and are easily destroyed by falling litter. Some tropical species in the Far East also show a huge population of seedlings progressively dying off until boosted again by the next gregarious fruiting (Whitmore, 1975).

Seedling Growth

Results obtained from studies of seedlings growing in a forest clearing indicated that light is a limiting factor in seedling growth and development of B. capitata. Seedlings and saplings are believed to grow to maturity if a gap in the forest canopy is formed by death of a large or overstory tree, or by loss of branches from the canopy trees.

Size Classes

There are two distinctive peaks in Figure 10 that illustrate how B. capitata populations are structured in the forest. The graph shows that there are not many individuals in the 6-10 meter size range. Bannister (1970) in a similar study found that Euterpe globosa exhibited two peaks in the size distribution, which corresponds to trees that are below the canopy and trees that are at least partially emergent. Survival of individuals 6-10 meters in height is difficult because of competition for sunlight. Dbh distribution of mature trees also shows a low number of individuals in some dbh ranges (10-25 cm and 85-100 cm). The height and dbh histograms are similar, each showing that few individuals can grow to 6-10 meter size classes and the ones that can grow to this size class are in an area where light is available (a gap).

Successional Status

There are different opinions of the successional status (climax or secondary succession) of *B. capitata*. Information compiled in this study clarifies the status of *B. capitata* in the lower montane forest. According to Budowski (1965) and Gomex-Pompa (1971) there are a group of features that distinguish the late secondary successional species. *B. capitata* has some of these characteristics: fruits dispersed by gravity, wide crown, deciduousness (even in areas of heavy rainfall), great mortality in early stages, and a rapid growth rate. *B. capitata* can attain a great size and remain in the area for a long period (Estrada, personal communication). Therefore, it is concluded that *B. capitata* is a late secondary successional species.

Survival

The survivorship curve of *B. capitata* can generally be classified as a concave curve typical of plant species. Mortality rates are high during early life cycle stages. The most critical or drastic stages are seedlings and juveniles. Juveniles are very rare in the forest. The life table also shows a high mortality occuring during the transition from seedlings to juveniles. Most of the seedlings failed to become established because of low light intensities in the closed forest. Also they are easily damaged by falling forest litter. Seedlings growing in the forest clearing grew faster and to a greater height than seedlings in the closed forest, strengthening the indication that light is an important factor in the development of seedlings.

Senescence was identified as beginning at approximately 40 years of age. Mortality probability of mature trees seems to increase at 40 years. Many similar late secondary successional tree species attain old age between 20 and 50 years (Budowski, 1965).

Previous ecological life cycle studies of lower montane species at El Verde (Van Valen, 1975; Muniz, 1978; and Silander, 1979) also showed concave survivorship curves. *B. capitata* presented a more strongly concave curve than the other species. A high mortality was observed in early stages of the life cycle of *Euterpe* (Van Valen, 1975), *Inga* (Muniz, 1978), *Cecropia* (Silander, 1979) and *Buchenavia*. Light proved to be a very important factor in the establishment of seedlings and in controlling the course of the life cycle.

According to the Baur (1964) and Lebrón (1977) concept of a gap opportunistic species, *B. capitata* falls in that classification. Saplings of *B. capitata* can survive in unfavorable environments but growth will increase when disturbance occurs. The population is maintained by replacement of parent trees by juveniles surviving near the parent tree.

B. capitata has great potential for being a good alternative for a reforestation program because it grows rapidly, has good wood quality and reaches maximum volume within 40 years. As a native species it does not require intensive management, chemical fertilizers, or pesticides for assuring a high quality crop. Even without intensive cultivation it grows at rates similar to pines in plantations throughout the Southern United States and it reaches maturity within the same period of time.

CHAPTER V

CONCLUSIONS

1. *B. capitata* exhibits strong seasonal periodicity. Phenological responses are related most strongly to relatively dry and wet periods in the rain forest at El Verde.

2. *B. capitata* is deciduous. It flowers during the relatively dry season following leaf fall.

3. Dispersal mechanisms are very poorly developed in *B. capitata*.

4. Light is the main factor responsible for seedling establishment in early stages of the life cycle.

5. If light becomes available, growth is rapid and extensive.

6. Senescence was identified as beginning at approximately 40 years.

7. *B. capitata* is a late secondary successional species, exhibiting behavior characteristic of gap opportunistic species.

8. *B. capitata* appears to be a potential source of valuable wood products. In terms of growth rate, wood quality, and early maximum volume it may be equivalent to pine species grown extensively in the Southeastern United States.

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