

STUDIES OF THE POPULATION ECOLOGY OF THE MISTLETOE *Phoradendron
anceps* (VISCACEAE) AND ITS HOST *Pisonia albida* (NYCTAGINACEAE) IN
THE GUÁNICA FOREST RESERVE, PUERTO RICO

by

Marcela Mora Pinto

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER IN SCIENCE
in
BIOLOGY

UNIVERSITY OF PUERTO RICO
MAYAGÜEZ CAMPUS
2005

Approved by:

Gary J. Breckon, Ph.D.
Member, Graduate Committee

Date

Jesús D. China, Ph.D.
Member, Graduate Committee

Date

Allen R. Lewis, Ph.D.
Member, Graduate Committee

Date

Duane A. Kolterman, Ph.D.
President, Graduate Committee

Date

Raúl Macchiavelli, Ph.D.
Representative of Graduate Studies

Date

Lucy B. Williams, Ph.D.
Chairperson of the Department

Date

ABSTRACT

I studied the spatial distribution and the demographic structure of the mistletoe *Phoradendron anceps* in relation to the distribution of its host (*Pisonia albida*), in a 5.29 ha plot in the Guánica forest. Both parasite and host species had an aggregated spatial pattern. The mistletoe spatial pattern was mainly explained by the host size and by dispersal. Larger *Pisonia* trees were generally more frequently and intensively parasitized than smaller trees. Parasitized trees were more prevalent in low-density stands than in high-density stands. Foraging and feeding behavior of *Euphonia musica* suggested that it could be the main disperser of the mistletoe seeds. Seed dispersal appeared to be distance-limited. The demographic structure of the mistletoe was analyzed by considering the mistletoe population in the study plot as a metapopulation of mistletoe subpopulations on individual trees. Subpopulation structures were not correlated with the spatial distance between them. Six subpopulation structure patterns were identified. Apparently, larger subpopulations with a high number of reproductive individuals may be the sources of seeds not only for these subpopulations themselves but also for nearby subpopulations. The overall mistletoe metapopulation structure suggests that recruitment of young mistletoes has been relatively continuous over the past few years. The *Phoradendron anceps-Pisonia albida* system in Guánica best fits the habitat-tracking metapopulation model in which the habitat patches are dynamic.

RESUMEN

Estudí la distribución espacial y la estructura demográfica del muérdago *Phoradendron anceps* en relación con la distribución de su hospedero (*Pisonia albida*), en una parcela de 5.29 ha. en el bosque de Guánica. Ambos, parásita y hospedero presentaron un patrón de distribución agregado. El patrón espacial del muérdago se explicó principalmente por el tamaño del hospedero y la dispersión. Los árboles de *Pisonia* de mayor tamaño generalmente estuvieron parasitados más frecuente e intensivamente que los de menor tamaño. Los árboles parasitados predominaron más en donde había menor densidad de árboles que en donde había mayor densidad. El comportamiento de forrajeo y alimentación de *Euphonia musica* sugirió que éste podría ser el dispersor principal de las semillas del muérdago. La dispersión de las semillas estuvo limitada a cortas distancias. La estructura demográfica del muérdago fue analizada considerando la población del muérdago en la parcela de estudio como una metapoblación de subpoblaciones del muérdago sobre árboles individuales. Las estructuras de las subpoblaciones no estuvieron correlacionadas con la distancia espacial entre ellas. Se identificaron seis patrones de la estructura demográfica de las subpoblaciones. Aparentemente, las subpoblaciones más grandes con un gran número de individuos reproductivos, podrían ser fuentes de semillas no sólo para sus propias subpoblaciones sino también, para las subpoblaciones cercanas. La estructura general de la metapoblación sugiere que el reclutamiento de muérdagos jóvenes ha sido relativamente continuo durante los últimos años. El sistema *Phoradendron anceps-Pisonia albida* en Guánica se ajusta mejor al modelo de metapoblaciones de rastreo de hábitat (“habitat-tracking metapopulation model”) en el cual los parches son dinámicos.

©Marcela Mora Pinto 2005

To the memory of my father, to my mother and to my siblings

ACKNOWLEDGMENTS

I wish to thank to Drs. Duane Kolterman, Gary Breckon, Danilo Chinaa and Allen Lewis for their advice, comments and review of this manuscript. I am very grateful to Dr. Chinaa for providing me with the digital maps of Guánica Forest and for helping me to handle the program Arc View. Thanks to Dr. Yoshioka, Dr. Macchiavelli, and Juan Carlos Benavides for their statistical advice. I am grateful to the Department of biology at the University of Puerto Rico, Mayagüez Campus for support as a Teaching Assistant. I acknowledge the collaboration of the Puerto Rico Department of Natural and Environmental Resources for providing a permit to conduct research in the Guánica Commonwealth Forest; and the assistance of Mr. Miguel Canals, DNER Management Official for the Guánica forest. I sincerely thank to Dr. Kolterman, Paola, Manuel, Vladimir, Miguel Gina and Alejandro for their help in the field data collection. Special thanks to Paola Bracho for her unconditional friendship and unlimited support during all the phases of this work. My warm thanks to Mr. Luis Rodriguez for being so friendly and caring. Finally, I am especially grateful to my family and friends for encouraging me and giving me the support I needed.

TABLE OF CONTENTS

| | |
|---------------------------------------|-----|
| ABSTRACT..... | ii |
| RESUMEN | iii |
| ACKNOWLEDGMENTS | vii |
| TABLE OF CONTENTS..... | vii |
| LIST OF TABLES | x |
| LIST OF FIGURES | x |
| INTRODUCTION | 1 |
| LITERATURE REVIEW | 3 |
| Parasitism..... | 3 |
| Distribution of mistletoes..... | 4 |
| Pollination and fruit dispersal | 5 |
| Aging mistletoes | 5 |
| spatial pattern..... | 7 |
| OBJECTIVES..... | 9 |
| General objective | 9 |
| Specific objectives | 9 |
| METHODS | 10 |
| Study area..... | 10 |
| Study species..... | 11 |
| Sampling methods..... | 12 |
| Data analysis | 14 |

| | |
|--|----|
| RESULTS | 18 |
| Mistletoe–host infection patterns | 18 |
| Mistletoe mortality | 20 |
| Effect on host | 21 |
| Distribution of mistletoes within a tree | 21 |
| Mistletoe size distribution | 23 |
| Sizes of infected host branches | 23 |
| Demographic structures of mistletoes | 24 |
| DISCUSSION | 31 |
| CONCLUSIONS | 45 |
| RECOMMENDATIONS | 46 |
| LITERATURE CITED | 48 |
| TABLES | 54 |
| FIGURES | 60 |
| APPENDICES | 87 |

LIST OF TABLES

| | |
|--|----|
| Table 1. Morisita's indices of dispersion for host and mistletoes..... | 55 |
| Table 2. Wilcoxon (U Mann-Whitney) test for tree traits of infected and non-infected trees..... | 56 |
| Table 3. Spearman rank correlation of infected trees of a size class against the different tree trait class..... | 57 |
| Table 4. Spearman rank correlation coefficients of tree traits against number of mistletoes per tree..... | 58 |
| Table 5. Spearman rank correlation coefficients of mistletoe size/age variables..... | 59 |

LIST OF FIGURES

| | |
|---|----|
| Figure 1. Map showing the location of the Guánica Forest Reserve in southwestern Puerto Rico..... | 61 |
| Figure 2. Location of the study plot in the Guánica forest. | 62 |
| Figure 3. Individual of <i>Pisonia albida</i> infected by <i>Phoradendron anceps</i> | 63 |
| Figure 4. Frequency distribution of parasitic attack among infected hosts.. | 64 |
| Figure 5. Simple regression testing for effects of host (<i>Pisonia albida</i>) density per quadrat. | 65 |
| Figure 6. Frequency distribution of the tree traits of <i>Pisonia albida</i> in the plot, and the percentage of trees in each size class infected by <i>Phoradendron anceps</i> | 66 |
| Figure 7. Dead individual of <i>Phoradendron anceps</i> | 67 |
| Figure 8. Dead branches of <i>Pisonia albida</i> with dead mistletoes..... | 68 |
| Figure 9. Distribution of living and dead mistletoes on the infected host. | 69 |
| Figure 10. Frequency distribution of size classes of <i>P. anceps</i> | 70 |
| Figure 11. Frequency distribution of proximal host branch diameter for <i>P. anceps</i> | 71 |
| Figure 12. Logarithmic regression for the number of mistletoes per tree against the number of canopy diameter classes in which mistletoes are distributed. | 72 |
| Figure 13. Distribution of the infected trees in the study plot. | 73 |
| Figure 14. Demographic structure of mistletoe subpopulations in group A..... | 74 |
| Figure 15. Demographic structure of mistletoe subpopulations in group B. | 75 |
| Figure 16. Demographic structure of mistletoe subpopulations in group C. | 76 |
| Figure 17. Demographic structure of mistletoe subpopulations in group D..... | 77 |

| | |
|--|----|
| Figure 18. Demographic structure of mistletoe subpopulations in group E. | 78 |
| Figure 19. Demographic structure of mistletoe subpopulations in group F. | 79 |
| Figure 20. Demographic structure of mistletoe subpopulations in group G. | 80 |
| Figure 21. Demographic structure of mistletoe subpopulations in group H. | 81 |
| Figure 22. Demographic structure of mistletoe subpopulations in groups I-K. | 82 |
| Figure 23. Reproductive plant of <i>Phoradendron anceps</i> | 83 |
| Figure 24. Seeds of <i>Phoradendron anceps</i> excreted by <i>Euphonia musica</i> | 84 |
| Figure 25. Termite nest on <i>Pisonia albida</i> | 85 |
| Figure 26. Juvenile individuals of <i>Phoradendron anceps</i> | 86 |

INTRODUCTION

Most people associate mistletoes with Christmas. Some families of Europe, Canada and United States used to put a mistletoe twig above the door frame or hang it up on the ceiling, so that any person who stood under the mistletoe could be kissed inoffensively by another. The supernatural and mystical powers of mistletoes date back to nearly two thousands years ago (Kuijt 1969). These powers have been attributed to mistletoes because they grow from branches of other plants and because many species fruit in winter when other temperate zone plants are dormant (Aukema 2003). Beyond the magic and the folklore that surrounds mistletoes, they are today a source of scientific interest for taxonomists, biochemists and ecologists, among others.

Although the literature on mistletoes is large (over 5,700 articles on North American mistletoes), it is widely scattered for some topics and rare for other topics (Geils et al. 2002) such as population ecology. Most of the studies about mistletoe ecology are from Australia and New Zealand (e.g. Ladley and Kelly 1996; Norton and de Lange 1999; Reid and Stafford-Smith 2000; Watson 2002). Watson (2001) argues that tropical regions are underrepresented in the mistletoe literature. For instance, there is not yet any publication about ecological studies of mistletoes in Puerto Rico.

Most parasites are viewed as pests because of their impacts upon human health or animals and plants exploited by humans. Both the study and management of parasites have historically focused on the control and even the elimination of parasite populations

(Marvier and Smith 1997). Recently, mistletoes have been considered as a keystone resource for fauna in forests and woodlands worldwide (Reid et al. 1995; Watson 2001, 2002). They provide abundant nutritional and nesting resources for a diverse range of birds, mammals and insects, which may be especially important during droughts and other periods of scarcity (Watson 2002).

In some regions mistletoes are pests due to the parasitic habit, particularly under disturbed conditions, while in other regions they are declining towards extinction due to loss of habitat, pollinators and dispersers or excessive predation (Norton et al. 1995; Norton and Reid 1997; Reid and Stafford-Smith 2000). If pest mistletoes are to be managed and threatened species conserved, their population biology must be sufficiently well understood to formulate management strategies (Reid and Stafford-Smith 2000).

In the Guánica forest in southwestern Puerto Rico, *Phoradendron anceps* (Spreng.) M. Gómez is the most abundant mistletoe, and it seems to be exclusively parasitizing *Pisonia albida* (Heimerl) Britton ex Standl. (Nyctaginaceae). Its relative abundance makes individuals of *P. anceps* ideal organisms for studying the ecological interactions between this species and its hosts, which partly determine the temporal and spatial patterns in mistletoe populations. The aim of this study is to provide insight into the population ecology of *P. anceps* to help in the understanding of its role and/or impact in the ecosystem. It is also intended to serve as a model for studies of other host–parasite interactions.

LITERATURE REVIEW

Parasitism

Parasitism is a common way of life in nature and includes organisms such as viruses, bacteria, nematodes, fungi, ecto- and endoparasites of animals, some phytophagous insects and parasitic plants, among others. All are distinguished by completing a whole stage of their life associated with a single host individual in a relationship that is beneficial to the parasite but not to the host (Thomson 1994, cited in Norton and de Lange 1999). Parasitic plants account for about 1% of flowering plants, with more than 3,000 species distributed in 16 families (Kuijt 1969). Among these species, mistletoes are widely recognized as an ecologically important functional group (Watson 2001). The group is polyphyletic and includes members of five families of the order Santalales: Loranthaceae, Viscaceae, Misodendraceae, Eremolepidaceae and Santalaceae. Nearly all of them are obligate stem hemiparasites, with a few species being endophytes within their host, such as *Tristerix aphyllus* (Loranthaceae), an unusual holoparasitic mistletoe endemic to arid regions in northern Chile (Botto-Mahan et al. 2000; Medel 2000; Medel et al. 2002). Mistletoes are considered hemiparasites because, although they are able to photosynthesize, they are dependent on their host for water and other xylem-borne nutrients (Overton 1994). The hemiparasites draw these compounds unidirectionally through a physical connection, the haustorium, by maintaining transpiration rates up to an order of magnitude higher than those of their host (Ehleringer et al. 1985).

Distribution of mistletoes

Mistletoes are distributed worldwide in forests, woodlands and shrublands on every continent except Antarctica, with most species in the tropics. The majority of mistletoe species (> 98 %) belong to the families Loranthaceae and Viscaceae, which together contain approximately 1300 species (Reid et al. 1995) These families are not sister taxa and their aerial parasitic-growth form is thought to have evolved independently (Kuijt 1969; Watson 2001). Loranthaceae is considered a Gondwanan lineage that subsequently dispersed to Africa, Europe and North America, whereas Viscaceae is thought to have originated in eastern Asia, radiating through Laurasia in the early Tertiary period, and then secondarily dispersing to the southern continents (Barlow 1983, cited in Watson, 2001). There are several anatomical, embryological, and chromosomal differences between the two families (Kuijt 1969), but a practical difference is that the flowers in the Viscaceae are small and inconspicuous, whereas those in the Loranthaceae are large, colorful, and possess a calyculus, an irregular rim of tissue below the petals that crowns the gynoecium (Kuijt 1969). The Viscaceae occur in tropical and temperate zones of the Northern Hemisphere; the Loranthaceae are generally tropical (Barlow 1983, cited in Geils et al. 2002). The two families overlap in Mexico (Cházaro and Oliva 1987, cited in Geils et al. 2002) and the Antilles.

Pollination and fruit dispersal

Whereas most species of Loranthaceae are pollinated by birds, members of the Viscaceae are pollinated primarily by wind and insects (Kuijt 1969). Whether anemophily or entomophily is the main means of pollination remains controversial, with many species displaying pollination syndromes that favor the two agents, and most species-specific studies have implicated both (Hawksworth and Wiens 1996).

Birds that eat mainly mistletoe fruit are responsible for most of the mistletoe dispersal in many parts of the world (Reid et al. 1995). The relationship between some species of mistletoe and avian frugivores has been described as a mutualism; while birds obtain nutritional value from the berries, mistletoes benefit by having their seeds dispersed (Reid et al. 1995; Ladley and Kelly 1996). The mesocarp of the berries contains nutrients attractive to the birds and the seed is covered by a sticky viscin that allows the seed to adhere to host branches once deposited there by defecation, regurgitation or bill wiping (Kuijt 1969; Reid et al. 1995; Aukema 2003).

Aging mistletoes

Ecological studies at a population level are one of the most accurate ways to understand the causes and mechanisms of selection and evolution of organisms (Piñero et al. 1977). Demography is the key to understanding spatial and temporal variation in the

abundance of plants and has been considered to be the main goal of plant population studies. The classic theory of demography is based on the premise that the life history of an individual is determined by its age (Sarukhán et al. 1985).

In host species with identifiable growth rings, the age of a mistletoe can be determined destructively by counting the maximum number of annual host rings that bury the mistletoe haustorium in the host wood (Dawson et al. 1990b). However, many host species do not exhibit annual growth rings. Plant size is therefore sometimes used as a substitute for age in plant population studies (Reid et al. 1995). Frequently it has been found that the ecological effects of size have a stronger impact on birth and mortality rates than age does. The variability in growth rate is large enough that age poorly predicts the size of an individual, as well as its fecundity and life expectancy (Kirkpatrick 1984). Considerations in this respect have led many plant ecologists to reject the “age” criterion in favor of “age stages” as a useful criterion to describe individuals (Uranov 1975, cited in Begon and Mortimer 1986). Kirkpatrick (1984), for instance, argues that demographic studies based on size are preferable to those based on age, since the first can provide additional information and a better interpretation of the ecological processes. Thus individuals can be classified into categories of development that could include: seeds, seedlings, juveniles, immature, reproductive and subsenile and senile states. This classification recognizes that there are morphological changes that occur during the growth and development of a species, but the length of each state differs considerably (Begon and Mortimer 1986).

It has been suggested that many aspects of mistletoe biology are age-dependent (Dawson et al. 1990b; Powell and Norton 1994). Since counting the number of annual rings in host species as an estimation of age is not always possible or desirable for conservation reasons, new aging techniques have been developed. Work by Dawson et al. (1990b) with the mistletoe *Phoradendron juniperum* in western North America has shown that the number of bifurcating branching events on the longest stem of the mistletoe was strongly correlated with mistletoe age based on anatomical work. Working with Australian loranthaceous mistletoes, Reid and Lange (1988) argued that the maximum diameter of the host branch proximal to the haustorium was proportional to mistletoe age because seedlings of most mistletoes established on young host branches. Norton et al. (1997) investigated a variety of non-destructive measures as potential predictors of mistletoe age as determined anatomically for three mistletoe species. They found that the diameter of the host stem immediately below the haustorial attachment was consistently the best predictor of mistletoe age. They also suggested that host branch diameter can be used in future studies of mistletoe population dynamics and other age-dependent aspects, although they advise caution when applying them at other sites or to other mistletoe species and hosts.

Spatial patterns

Spatial patterns reflect the net effect of various physical and biological factors affecting the birth, death of individuals in single species populations (Hutchinson 1953).

Because spatial patterns reflect underlying causal processes, ecologists often infer process from pattern (Grieg-Smith 1983). In studying spatial patterns, plant ecologists have generally recognized three distinct spatial distributions: random, aggregated (also called contagious, clumped, clustered or patchy) and uniform (regular).

A population is said to be distributed at random if the relative location of an individual is independent of the location of any other individual in the population. An aggregated population is one in which the individuals occur in clumps of varying densities and sizes. Cole (1946) defines a contagious distribution as one in which the presence of one or more organisms within a sample unit increases the probability of other organisms occurring in the same sample. On the other hand, a regular or uniform, spatial distribution is one in which the individuals are evenly distributed over a given area.

Kareiva (1994) argued that it is important to recognize spatial patterns and processes to understand the factors that shape distribution, dynamics, and interaction of organisms. Models of disease dynamics suggest that patterns of disease spread depend on many factors including vector preference, prevalence of disease, and spatial structure of host and disease (McElhany et al. 1995). Although host population size can directly influence parasite population size, the spatial distribution of the host as well as the age or size structure of the host population could be even more important to the parasite than the total host population size (Donohue 1995).

OBJECTIVES

General objective

- To analyze the spatial distribution and the demographic structure of the mistletoe population in relation to host tree distribution in the Guánica Forest Reserve

Specific objectives

- To generate a map of the locations of host trees and hemiparasites
- To determine whether there is a correlation between the size of the host and the density of mistletoes they carry
- To estimate population structure based on size classes of the mistletoes
- To identify the main species involved in fruit dispersal of *Phoradendron anceps*

METHODS

Study area

I studied aspects of the population biology of *Phoradendron anceps* (Spreng.) M. Gómez during June-December 2004 and January 2005 in the Guánica Forest Reserve (Fig. 1), located on the southwestern coast of Puerto Rico (ca. 66°51'W, 17°57'N). The forest became a Commonwealth Forest in 1917 and has been protected since the 1930's; its extent (ca. 4000 ha) encompasses a variety of edaphically correlated associations, resulting in part from the complex disturbance history (Murphy and Lugo 1990).

Ewel and Whitmore (1973) classified the Guánica forest in the Subtropical Dry Forest Life Zone, exhibiting an annual rainfall of 860 mm with a major period of drought from December to April and a minor one between June and August. Annual mean temperature is about 25.1°C (Murphy and Lugo 1990), with a mean monthly maximum of 28°C between August and October and a mean monthly minimum of 24°C between January and February (Medina and Cuevas 1990).

The Guánica forest overlies limestone. Soils are shallow, alkaline and high in organic content with a low water holding capacity (Murphy and Lugo 1986), which would compound the effect of low, seasonal rainfall. The topography is undulating; elevation ranges from sea level to about 185 m (Cintrón and Lugo 1990). The vegetation

is composed of various floristically and structurally distinguishable plant associations: scrub forest, deciduous forest, transition between deciduous and semi-evergreen forest and mahogany plantations. This variety of vegetation can be attributed to the variation in the soil depth, slope angle and orientation, as well as effects of these factors on soil moisture availability (Lugo et al. 1978).

The present study was conducted in the Municipality of Guánica, Barrio Carenero, at an elevation ranging from about 25 to just over 55 m, in the cactus scrub association, which is characterized by having few scattered large-diameter trees with a mean tree height of about 6.5 m, generally belonging to deciduous species [e.g. *Bursera simaruba* (L.) Sarg, *Bucida buceras* L.], interspersed with low spiny shrubs, grasses, abundant cacti and leguminous herbs and open areas with exposed limestone (Lugo et al. 1978; Cintrón and Lugo 1990).

Study species

The genus *Phoradendron* is considered by Kuijt (2003) as the largest genus of mistletoes in the world. The genus includes 234 species and is restricted to the New World, occurring in the West Indies, the U.S.A., and all countries in South America except Chile (Kuijt 2003). Hosts include several genera of conifers, many broadleaf trees and shrubs, and other mistletoes. Their large, fleshy berries that are attractive to birds clearly identify them as *Phoradendron*, “the tree thief” (Geils et al. 2002). *Phoradendron anceps* (Spreng.) M. Gómez has three inconspicuous yellow tepals and yellowish fruits. It

is native to lowlands of Puerto Rico, the Virgin Islands and the Lesser Antilles (Kuijt 2003). The representative specimens of *P. anceps* cited by Kuijt (2003) were found on *Cissus verticillata* (L.) D.H. Nicolson & C. Jarvis, *Cordia alliodora* (Ruíz & Pav.) Cham., *Cordia nitida* Willd., *Bourreria succulenta* Stahl, *Bursera simaruba* (L.) Sarg, *Ficus* sp., *Gouania lupuloides* Urb., *Guarea* sp., *Tabebuia heterophylla* Britton, and *Sideroxylon* sp., but most of the specimens were found on *Pisonia albida* (Heimerl) Britton *ex* Standl. throughout its range of distribution.

Pisonia albida (Nyctaginaceae) is a tree 6-12 m tall with a light grey bark, dioecious flowers and coriaceous fruits. It often has multiple “basal branches” emerging from ground level. *Pisonia albida* grows on limestone hills and in coastal thickets at lower elevations in dry districts of Hispaniola and Puerto Rico and adjacent islands (Liogier 1985). The species flowers and fruits from the end of January to May. In the Guánica forest some individuals have been seen parasitized by *Phoradendron anceps*.

Sampling methods

For the host species, the basal diameter, maximum canopy diameter, canopy height and tree height were measured, and the number of live and dead mistletoes was counted for infected individuals. To examine the spatial distribution of mistletoes and their hosts, their location was mapped within a 5.29-hectare plot. The plot was located in an area that was judged to be representative of the cactus scrub association community as well as for

its accessibility. Individual host trees were tagged with a unique number and the location of each tree was also determined by using a Garmin 76 GPS (Global Positioning System) receiver. Coordinate accuracy was improved by differential GPS with WAAS (Wide Area Augmentation System) capability (cf. <http://gps.aa.gov>); RMS (root mean square) values obtained this way are usually accurate within 3 m. For those trees whose canopies overlapped or were less than 6 m apart, distance and position (azimuth) were measured using a metric tape and a compass.

The following variables were recorded for each mistletoe: (1) height on the tree above the ground; (2) the compass aspect of each mistletoe on the host, assigned to one of four sectors NE to SE (45-135°), SE to SW (136-225°), (3) SW to NW (226-315°), and NW to NE (316-45°), these compass aspects being referred to as east, south, west and north respectively (Dawson 1990a); (3) length of the mistletoe; (4) maximum mistletoe canopy width; (5) diameter of the host branch proximal to the haustorium; (6) diameter of the mistletoe stem immediately above the haustorium; (7) whether the branch distal to the mistletoe was alive; (8) exposure of the mistletoe to light (in sun or shade) and (9) its reproductive status (vegetative, buds, flowers, fruits). While looking for mistletoes, I also noted any seeds that I observed on the branches of infected trees.

In conjunction with the other studies, binoculars were used to identify the birds handling the mistletoes' fruits and seeds. I observed birds twice a week between the hours of 0630-0900, in July 2004.

Data analysis

A digital map of mistletoe and host distributions was produced in ArcView 8 based on the GPS data. I investigated the spatial distribution of parasitism among the hosts and in the plot. A chi-squared goodness of fit test was performed to test the null hypothesis of a negative binomial distribution of individuals of *P. anceps* among the host trees. Host trees with at least one mistletoe (alive or dead) were categorized as infected. To describe the spatial pattern of *P. albida* and *P. anceps* in the study site, the plot was divided into 529, 10 × 10 m quadrats. The degree of patchiness for infected and non-infected *P. albida* individuals as well as the patchiness of mistletoes within the plot were measured by means of the Morisita index of dispersion:

$$I_{\delta} = n \left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \right]$$

Where

I_{δ} = Morisita's index of dispersion

n = Sample size

x = Counts of non-infected trees, infected trees or mistletoes in each quadrat

$\sum x$ = Sum of the quadrat counts

$\sum x^2$ = Sum of the quadrat counts squared

This coefficient is essentially equivalent to the Lloyd (1967) Index of Patchiness and to the one employed by Hill (1973) and Yoshioka (1997), and represents the inverse of the exponent k in the negative binomial distribution. Among all the indices for pattern detection currently available, the Morisita Index (1959) is the most often used and preferred because it is less affected by the sampling unit size (Malhado and Petrere 2004). All the formulas, calculations and statistical tests of goodness of fit were based on Krebs (1999).

I also investigated how the density of *Pisonia albida* influences the distribution of *P. anceps* individuals among hosts. Density was calculated as the number of *P. albida* trees within each 10×10 m quadrat of the plot. The effect of *P. albida* density on the proportion of trees infected within each quadrat was estimated using simple regression. The effect of the host tree density on the number of mistletoes within each quadrat was also tested with simple regression.

To determine whether host tree size (basal area, canopy diameter, canopy height and tree height) influenced the probability of infection, each tree size variable was compared between all infected and non-infected trees using the nonparametric Wilcoxon (U Mann-Whitney) test for independent samples. Nonparametric statistics were used since none of the tree size variables except height was normally distributed (Appendix I). To determine whether each tree size variable influenced the number of mistletoes per tree on infected trees only, nonparametric Spearman rank correlation was performed.

The ages (diameter of the host branch) and sizes (canopy width, length and diameter above haustorium) of the mistletoes on each host were grouped into classes to estimate the demographic or population structure of *P. anceps*. Chi-square analyses of contingency tables (Zar 1999) were used to test if there is a correspondence between the age and/or size of the mistletoe and its reproductive condition. The same analyses were also used to test the significance of differences between the distribution of living and dead mistletoes on the tree with respect to compass aspect, exposure to light and vertical position of mistletoes on host canopies. Vertical position or height of the mistletoe in the canopy was categorized in three classes corresponding to the lower, middle and upper thirds of the host canopy.

To analyze the population structure of *P. anceps*, I first define some concepts in the context of this study. A **subpopulation** is defined as the population of mistletoes living on a single host tree, the **metapopulation** as the group of subpopulations in the entire study plot, and a **patch** as a synonym of host tree.

I used Mantel's test, which determines the relationship between two distance matrices (Fortin et al. 2002), to test the hypothesis that frequency distributions of canopy size classes (demographic structure) of *P. anceps* between adjacent host trees were more similar than between distant trees. The Mantel statistic, Z , sums the products between corresponding elements of the distance matrices:

$$Z = \sum_{i=1}^n \sum_{j=1}^n x_{ij}y_{ij}$$

where x is the variable distance matrix and y comprises the actual Euclidean (spatial) distances among the n sampling units (host trees). The Mantel statistic, Z , can be normalized into a product–moment correlation coefficient, r , which varies from -1 to 1 (Fortin et al. 2002).

For the mistletoe subpopulations, the first matrix contained the Euclidean distances between each pair of host trees, and the second matrix contained the Euclidean distances of the demographic structure between the same pairs of mistletoe subpopulations. The analysis described above was performed for both absolute and relative frequencies of the canopy size classes using standardized and non-standardized Euclidean distances, respectively.

High values of the Mantel test statistic indicate that the two distance measures are positively correlated. Statistical significance of the correlation is tested by a permutation of the elements in one of the two distance matrices (Fortin et al. 2002). To estimate the significance of the correlation coefficients, I used the NTSYSpc package (Rohlf 1998) with 10,000 random permutations using the Mantel test. Other statistical analyses were done in InfoStat (2004).

RESULTS

Mistletoe–host infection patterns

One hundred and thirty-three individuals of *Pisonia albida* occurred across the study plot as scattered individuals or denser stands (Fig. 2). Forty-three (32%) of the host trees were parasitized by *Phoradendron anceps* (Fig. 3). The distribution of parasitic infection among hosts approximated a negative binomial, with a few hosts having a very large number of infections and most hosts having very few infections (Fig. 4), indicating an aggregated distribution. Single infections occurred on six trees, while the greatest number of mistletoes on any single tree was 270. Morisita's indices of dispersion for mistletoes and infected and non-infected hosts indicated an aggregated spatial pattern for all cases (Table 1). Confidence intervals indicate that there is not a significant difference between the Morisita Index of the infected and non-infected hosts. The Morisita Index for mistletoes is much higher, indicating that they have a patchier pattern compared with that of *P. albida*.

Out of the total of 529 quadrats, 71 were occupied by *Pisonia albida*, 31 of them with 1–4 infected individual(s). A lower proportion of infected trees was positively correlated with a higher *P. albida* density per quadrat (Fig. 5). This result is highlighted by the fact that a large number (42%) of the infected trees were found alone in a quadrat.

On the other hand, density of host individuals was not linearly correlated with the number of parasites per quadrat (Appendix II).

Infected trees did not show significantly higher basal area, canopy height or tree height in comparison with uninfected trees; however, they proved to be significantly different with respect to canopy diameter (Table 2).

The frequency distributions of *Pisonia albida* size are given in Fig. 6. The host population was skewed toward smaller basal area classes (Fig. 6a). The distributions of canopy diameter, canopy height and tree height were hump-shaped but skewed towards smaller trees (Fig. 6b, c, d). Although more trees had a canopy diameter ranging from 1.61 to 3.20 m (Fig. 6b) compared with other size classes, many of the infected trees (30%) had a canopy diameter that ranged from 4.95 to 6.0 m. Only one tree was less than 1 m high; it was not infected. The smallest and the largest infected tree measured ca. 1.3 and 6.1 m high respectively. The majority of trees presented intermediate canopy height classes (Fig. 6c). Fifty-seven percent of all sampled trees were 3 to 3.9 m high and most of the infected trees (51%) belonged to the same height size class (Fig. 6d). When host individuals were grouped into canopy diameter, canopy height and tree height classes, the percentage of the size class infected with one or more mistletoes was positively and significantly correlated with all three size class variables (Fig. 6b, c, d). The Spearman rank correlation coefficients for Fig. 6 are given in Table 3. The r_s values for all size variables were high except for basal area (Table 3). In general, the proportion of infected

trees and the percentage of trees infected by mistletoes tended to increase with tree size; therefore, measures of canopy diameter, canopy height and height of a host are good predictors of the probability that the host will be infected.

Among infected trees, the number of mistletoes per tree was significantly correlated with both canopy height and tree height (Table 4) such that small trees bore few mistletoes, and taller trees bore more. Neither canopy diameter nor basal area was significantly correlated with the number of mistletoes on the host. Of the four tree traits only basal area was not significantly related to presence or intensity of parasitism.

Mistletoe mortality

Of the 1370 mistletoes found, 743 (54%) were dead (Fig. 7). Overton (1994) suggested a cross-sectional index of mistletoe mortality rate. If the rate at which dead mistletoes disappear from trees is constant, then the mistletoe death rate can be estimated by the ratio $d_m = D / (D+A)$, where D = number of dead mistletoes per tree and A = number of live mistletoes per tree. The index d_m is calculated for all infected trees in the plot, and then averaged to obtain a mean d_m for the plot (Overton 1994).

The mean (\pm SE) d_m at the plot was 0.40 ± 0.05 for the infected trees. Eleven (25%) of infected trees bore only live mistletoes, three (7%) bore only dead mistletoes and 29

(68%) trees bore both live and dead mistletoes. The number of dead mistletoes surpassed the number of living mistletoes on eight of the infected trees.

Effect on host

All individuals of *Pisonia albida* were alive. However, on some trees I observed many dead branches (Fig. 8) and/or scars of these branches. At least two of the host trees with very few branches alive were observed. For 492 (35 %) of the mistletoes, the host branch distal to the haustorium was dead; of these mistletoes, 449 (91%) were dead.

Distribution of mistletoes within a tree

A comparison of the frequency distribution of the number of live and dead mistletoes classified by their compass orientation within a tree, their exposure to light and their height on the tree is given in Fig. 9. There is a significant association between the live or dead condition of the mistletoe with respect to its compass orientation ($\chi^2 = 9.20$, $df = 3$, $P < 0.05$), exposition to light ($\chi^2 = 48.88$, $df = 1$, $P < 0.05$), and its vertical position ($\chi^2 = 35.97$, $df = 2$, $P < 0.05$).

The most marked difference in the number of mistletoes among cardinal positions was between east and south (Fig. 9a). Seventy-six mistletoes more than expected were oriented toward the east with respect to the main trunk of the host tree, while 100 fewer

than expected were oriented toward the south. In all positions except the south, the number of dead mistletoes surpassed the number of live mistletoes. On the other hand, distribution of living and dead mistletoes facing north does not appear to be different from those individuals facing either west or east (Fig. 9a).

Phoradendron anceps typically occurs on branches exposed to sun and is less common in shade (Fig. 9b). Sixty-eight percent of living plants and 84% of the dead plants were exposed to the sun. Of the mistletoes in shade, the majority (Fig. 9b) were alive. On the other hand, although *P. anceps* is present throughout the canopy, it is more abundant in the lower and middle thirds of the canopy (Fig 9c). This is true for seeds too: 61%, 31% and 9% of a total of 304 were distributed in the lower, middle and upper canopy respectively. Living mistletoes tended to occur more in the middle canopy while dead mistletoes predominated in the lower and upper thirds.

Mistletoe variables such length, canopy width, above-haustorium diameter (AHD) and proximal host branch diameter (HBD) were all positively and significantly intercorrelated (Table 5). However, the r_s values of HBD vs. any other variable were low, ranging from 0.2 to 0.29. Thus, the proximal host branch diameter of *P. albida* is a significant but poor predictor of the mistletoe size.

Mistletoe size distribution

The overall size class distributions for pooled *Phoradendron anceps* subpopulations are given in Fig. 10. The maximum canopy width of a mistletoe was ca. 165 cm. A high number of the individuals belonged to the first class (<10 cm) of canopy width and to a lesser extent to the third and fourth classes (Fig. 10a). Although in the first class individuals of all reproductive status were found, the vegetative ones were predominant. In other classes individuals in fruit were predominant, except in the sixth class with individuals 51-60 cm in canopy width, in which the flowering status prevailed. The distribution of the number of mistletoes in length classes had a pattern similar to that of the maximum canopy width, but individuals more than 10 cm long followed a hump-shaped distribution, with more mistletoes in intermediate classes (Fig. 10b). In all length classes except the first and second ones, fruiting mistletoes prevailed. In the second class (11-20 cm length) individuals of all reproductive status were almost equally distributed. Considering the diameter above the haustorium, the distribution of mistletoes was consistently skewed towards the smallest diameters, again with vegetative individuals dominating in the first class (Fig. 10c).

Size of infected host branches

Most live mistletoes sampled on the infected individuals of *P. albida* grew on host branches 11-20 mm diameter (Fig. 11a). The largest infected branch was 300 mm in diameter and bore one vegetative mistletoe. All branch classes were infected with both

vegetative and reproductive mistletoes. Fruiting mistletoes were preponderant in all branch size classes except class 10 (91-100 mm diameter) where the vegetative state predominated. On the other hand, the majority of the vegetative individuals (61%) were found growing on branches < 20 mm in diameter. The results suggest that an association does exist between both variables ($\chi^2 = 103.95$, $df = 30$, $P < 0.05$).

The largest infected branch on which a dead mistletoe was found measured 220 mm in diameter. The frequency distribution of proximal host diameter for dead mistletoes was very similar to that for live mistletoes, with most individuals belonging to the second class (Fig. 11b). On the contrary, most seeds were found on either the smallest branch size class (<11 mm) or the largest one (> 101), showing a bimodal size distribution, with a particular scarcity of seeds in the 11-20 mm diameter class (Fig. 11c).

Demographic structure of mistletoes

For the analysis that follows, I will analyze the demographic structure of each subpopulation of the mistletoe, assuming the metapopulation approach of Overton (1994). He assumed that the mistletoes inhabiting a host plant constituted a subpopulation by habitable patches (host trees), and uninhabitable patches (non-host trees). Here I only consider canopy width as a size measure of the mistletoe, since it was correlated with the other size variables (Table 5). Therefore, the population structure of each subpopulation supported by a host tree was represented by means of the canopy size class distributions

(Fig. 10a). Because this variable was unavailable for dead mistletoes, only living mistletoes were included in this analysis. The number of canopy size classes of each subpopulation (mistletoes in a tree) was logarithmically related to the number of living mistletoes per host tree (Fig. 12).

To describe and compare the structure of the subpopulations of mistletoes in the study plot, the subpopulations (i.e. infected trees) were grouped in 11 groups (A-K, Fig. 13). The subjective criterion for choosing these groups was that any host tree of the group had to be within a distance of 20 m or less from any other member of that group. Therefore, host trees isolated by more than 20 m from any other individual in the plot were alone in a group (i.e. groups I-K). Although all infected trees (43) appear in Fig. 13, three host trees were excluded from the population structure analysis since they bore only dead mistletoes. Each host tree appears in Fig. 13 labeled with a number that was used for tagging the individuals in the field; the same number will also be used hereafter to name the subpopulation of mistletoes harbored by the corresponding host tree. The explanation of the mistletoe subpopulation structures within each group is as follows:

Group A (Fig. 14). Two subpopulations of mistletoes (850 and 835) exhibited a slightly bimodal (U-shaped) structure with more individuals belonging to the smallest and the largest size classes than in other intermediate stages. The other two subpopulations (836 and 838) were similar to one another in being small, with 1 and 2 individuals respectively.

Group B (Fig. 15). Only the subpopulation belonging to the host tree labeled as 802 had a relatively high number of individuals respect to the other populations within the group. Moreover, it had a wider range of canopy size classes than the rest of subpopulations.

Group C (Fig. 16). In this group composed of two subpopulations, one (871) had a slightly bimodal structure whereas the other (874) had only one individual belonging to an intermediate size stage.

Group D (Fig 17). The subpopulation labeled as 805 was located furthest from the rest of the individuals in the group and corresponded to the largest subpopulation (highest number of mistletoes) not only within its group but in the whole study plot. This subpopulation had a skewed size distribution with a higher number of individuals in the first class than in the other stages (reverse J-shape). Subpopulation 810 was located far from subpopulation 805 (Fig. 13), and was the second largest one. This subpopulation exhibited a hump-shaped structure, slightly skewed to smaller size classes but with a higher proportion of individuals in intermediate size classes. A similar structure but with fewer individuals was exhibited by subpopulation 806. The remaining four subpopulations of this group had only one individual, except 809, which contained two individuals.

Group E (Fig. 18). All three subpopulations in this group were characterized by having few individuals distributed in four or five size classes, with a maximum of two individuals per size class.

Group F (Fig. 19). The individuals in the subpopulation belonging to the host tree labeled as 912 were distributed almost evenly (1-3 individuals per class) in nine of the eleven size classes. The other subpopulation (914) only had one individual belonging to an intermediate class.

Group G (Fig. 20). Subpopulation 862 showed a positively skewed population structure with seedlings and small plants dominating while larger sized individuals were few (reverse J-shape). Subpopulation 870 had a more or less hump-shaped pattern with individuals belonging to small and intermediate size classes. Subpopulation 866 had few individuals with more individuals in the first class than the rest of stages. The remaining four subpopulations in this group had few individuals (3-7) distributed in either one or three size classes.

Group H (Fig. 21). Subpopulation 833 had the highest number of individuals in class 1 (mostly seedlings and juveniles) with respect to other subpopulations in the study plot. The structure of this subpopulation was bimodal with more individuals in class 1 and 4 than in other classes. A less evident bimodal distribution was exhibited by subpopulation 824. On the other hand, subpopulation 821 had more individuals belonging to an intermediate size class than in other size stages. Subpopulation 822 exhibited a rather uniform structure, with similar numbers of individuals in most size classes. The other four subpopulations within this group had few individuals (five or fewer) distributed in a maximum of three classes.

Groups I- K (Fig. 22). These groups had in common the fact that they are relatively isolated and are each constituted by only one subpopulation. The subpopulations in

groups I and J both had few individuals distributed in only two size classes. On the other hand, the subpopulation in group K had many individuals, with a higher number of individuals in intermediate classes than in other size stages.

The demographic structure of each mistletoe subpopulation was not correlated with the spatial distance between them, as shown by the results of Mantel's test ($r = -0.05$, $P > 0.3$ and $r = 0.13$, $P > 0.9$, for absolute and relative frequencies, respectively).

Mistletoe phenology

Phenological observations were conducted during the peak of the mistletoe's fruiting, and during peak hours of bird activity. I observed that *Phoradendron anceps* has a long span of the fruiting season, and that its peak was between July and August, although I found fruiting individuals even at the end of January. Although the numbers of fruits were not quantified, I did observe that in June most of the reproductive plants had flowers and few fruits while from July to November fruits prevailed. In January most of the fruits had been consumed and the remaining had been lost (dried out and still attached to the plant or dropped to the ground) and most of the plants were in a vegetative state or with buds or flowers. From the herbarium specimens of MAPR, I found no reproductive individual collected in the interval from February to April.

Bird disperser and seeds

I observed different birds such as *Coereba flaveola* (bananaquit), *Icterus icterus* (troupiat), *Loxigilla portoricensis*, *Spindalis zena*, and other unidentified birds perching on *Pisonia albida*. However, only *Euphonia musica* (Antillean euphonia) was observed feeding on the fruits of *Phoradendron anceps*. I just observed once, about 0730 hours, a female *Euphonia* perching on the naked branches of a deciduous tree, higher than the closest *Pisonia* tree. The bird flew to the upper branches of the *Pisonia* tree, descended to the lower branches, consumed some fruits of *Phoradendron* (Fig. 23) and then rubbed the seed off on the branch of the host. It went back to the deciduous tree and again went to the host tree and ate more fruits. After that, the bird defecated the seeds on a low branch located on the east-facing side of the *Pisonia* tree and subsequently left the tree. The foraging and feeding behavior described above took a maximum of five minutes. The seeds defecated by *Euphonia* formed a long chain of ca. 25 seeds (Fig. 24) united by means of a viscid thread. The *Pisonia* tree that was seen visited harbored the second largest number of mistletoes in the study area. On another occasion I heard and observed three euphonias in the tree with the most mistletoes but I could not observe their behavior since they flew away quickly.

While it was not an objective of this study to quantify the number of seeds deposited by birds on host branches, they were counted while looking for mistletoe plants. It is clear that the number of seeds found represent only a fraction of the total number of seeds

deposited by birds during the fruiting season 2004, since seeds on each host tree were counted just once and host trees were not examined in different seasons throughout the duration of the study. A total of 304 seeds distributed on nine hosts were counted; seed deposition ranged up to 164 seeds per tree and was aggregated within trees (variance: mean ratio = 104.9). Overton (1994) considers that a way to estimate between-tree dispersal is to calculate the proportion of seeds dispersed to uninfected hosts and nonhosts; in this study, nonhosts were not checked for seeds. No seeds were found on uninfected trees, so the between-tree dispersal efficiency is null. On the other hand, of the 304 seeds found on infected hosts, 150 were found in safe locations *sensu* Overton (1994), i.e. live host branches less than 3 cm in diameter, for a within-tree dispersal efficiency of 0.493. In *P. albida*, the number of seeds deposited on a tree was significantly correlated with the number of live mistletoes found on the tree ($r_s = 0.61$, $n = 40$, $P < 0.001$).

During this study I made several casual observations that are relevant to the research objectives. I noticed vegetative reproduction by means of root suckers (cf. tree # 823 in Fig. 13). I observed, on different occasions, ants with eggs inhabiting the largest stems of dead mistletoes. I also observed small bromeliads (*Tillandsia* sp.) growing on robust dead mistletoes.

DISCUSSION

Pisonia albida was the only host of *Phoradendron anceps* in the study plot. Although I observed a vine (*Cissus* sp.), growing on *P. albida*, with live and dead mistletoe seeds, no seedlings were observed. The lack of seedlings, coupled with the fact that most of the germinated seeds were dead, indicates that the haustorium of the mistletoe never penetrated the vine tissue. Norton and Carpenter (1998) pointed out that mistletoes may exhibit local adaptation to their host and specialize on a subset of potential host species. Mistletoe host specialization has been attributed to the behavior of birds, regional host abundance, and the influence of host compatibility on seedling establishment (Norton and Reid 1997; Norton and de Lange 1999). Interestingly, Kuijt (2003) cited specimens of *P. anceps* from Haiti, Dominican Republic and Guadeloupe found on *Bursera simaruba*, a species abundant in the Guánica forest. The fact that *B. simaruba* is not a host of *P. anceps* in the Guánica forest cannot be explained by bird behavior. Although I never observed the disperser of *P. anceps* perching on *B. simaruba*, I did find a few infected trees of *Pisonia* growing very close to *Bursera* individuals, even with overlapping branches of the two species. This indicates that it is very likely that seeds of *P. anceps* fall upon branches of *B. simaruba* but that those seeds may be unable to penetrate the bark because of host resistance and/or parasite infectivity, assuming that *B. simaruba* and *P. albida* from Guánica are different genetic races with respect to the others from the West Indies. Previous studies have found distinct genetic races of a species of dwarf mistletoe (*Arceuthobium americanum*) for different species of hosts, as

well as biochemical differences in the vascular tissues within the same host species infected by *A. vaginatum* (Aukema 2003). Future genetic and/or biochemical studies and experiments on germination and compatibility would be necessary to elucidate the nature and mechanism of *P. anceps* specificity.

Both species of mistletoe and host had an aggregated pattern at the study site. According to many ecologists (e.g. Pielou 1960; Krebs 1999), the aggregated type is the most commonly observed dispersion pattern in nature. I observed that many *P. albida* individuals were the result of vegetative reproduction, explaining in part its aggregated pattern in the plot. The aggregated pattern of both infected and non-infected host trees suggest that an infected tree is more likely to have an infected neighbor than an uninfected one and vice versa. It could be possible that the probability of uninfected potential hosts becoming infected could be affected by the proportion of infected individuals. Nevertheless, evidence for this hypothesis only can be collected by studying other populations with different mistletoe prevalence (the percentage of infected hosts in a given population) in the Guánica forest.

Clumped or aggregated distribution for mistletoes has also been reported in other species (Donohue 1995; Bannister and Strong 2001; Aukema and Martínez del Río 2002). The fact that individuals of *P. anceps* were spatially patchier than those of *P. albida* according to the Morisita index (Table 1) was expected since the number of mistletoes per host followed a negative binomial distribution. Thus, its *per se* aggregate pattern is

added to the aggregate spatial pattern of its hosts. In any case, the high degree of patchiness of *Phoradendron anceps* is an indication that the processes that are responsible for its aggregation are more intense than the ones that shape the distribution of the host. The characterization of those dynamic processes is very complex not only because several processes may be involved, but also because different factors may lead to the same contagious pattern (Pacala and Dobson 1988). Some mechanisms have been proposed to explain this aggregation. Dobson (1985) suggested that aggregated distributions reduce the level of interspecific competition among parasites (competitive host exclusion), and this appears to be true for *P. anceps* in the study site, since no other mistletoe species were found. Other mistletoe species reported for the whole Guánica forest are *Dendropemon caribaeus* Krug & Urb., *D. purpureus* (L.) Krug & Urb. and *Phoradendron trinervium* (Lam.) Griseb. (Quevedo et al. 1990).

If the basal area of *Pisonia albida* is indeed proven to be related to age, then the hypothesis that older individuals continually accumulate more individuals through time could be discarded. Nevertheless, on some occasions I observed old scars on the main stem of the tree. Hence, it is possible that older *P. albida* individuals that have supported many infections have lost basal branches through time, and for that reason their basal area could have been underestimated.

In general, larger trees showed greater predisposition to being infected than smaller ones. Canopy diameter, canopy height and height of a size class of trees were good

predictors of the occupancy (proportion of infected trees) of that size class, explaining 70-80% of the variance in the proportions of the size class infected (Table 3). On the other hand, the number of mistletoes seems to depend only upon canopy height and height (Table 4). A common explanation is that larger trees could be more attractive to frugivorous birds for perching, which would therefore deposit more mistletoe seeds onto perches (Reid and Lange 1988; Overton 1994; Donohue 1995). However, Reid and Stafford-Smith (2000) suggest that a high number of mistletoes per tree results more from the attraction of dispersers to the presence of established mistletoes on trees than to host size *per se*.

Low host tree density was correlated with the presence of parasitism on a tree (Fig. 3) but it was not associated with the number of parasites on a tree. This might be explained in two ways: (1) dispersers may be more attracted to sparsely located trees or, alternatively, (2) smaller or younger trees tend to be more clustered than larger ones on average, and it is because of their size and not due to their aggregation that birds are not attracted to those trees. In any case, behavior of the birds could be contributing to a slow spread of mistletoes.

As mentioned before, other causal mechanisms of the mistletoe aggregation could be attributed to the feeding and foraging behavior of its avian disperser agents. Based on the observations made on the foraging and feeding behavior of *Euphonia musica*, it seems to be an effective disperser of the mistletoe seeds within a tree. Carlo et al. (2002)

documented a mean of 2.06 ± 0.16 minutes per visit for *Euphonia* in other ecosystems in Puerto Rico. They argue that such short times confirm that indeed ingested fruits were removed from the parent plants. Moreover, they found the highest seed-removal index scores for *Phoradendron* in all site-periods where the species coincided, when compared with other bird and plant species. *Euphonia musica* has been considered a mistletoe specialist, although Pérez-Rivera (1991) observed changes in *E. musica* and its foraging behavior after Hurricane Hugo, in 1989, when its usual food (*Phoradendron* spp.) was depleted. Carlo et al. (2003) reported a strong preference of *Euphonia musica* for *Phoradendron* spp., which only switched to consume the epiphytic *Anthurium scandens* at the exhaustion of the former. From all this might be inferred a strong mutualistic relationship between *Euphonia musica* and *Phoradendron anceps*. This mutualistic interaction highlights the importance of *E. musica* as a disperser of the mistletoe. The preference of disease vectors for infected hosts is often associated with a mutualistic parasite-vector interaction (Aukema 2003). From the host perspective, *E. musica* individuals act as disease vectors that transmit the infection. Therefore they are both seed dispersers and disease vectors (Martínez del Río et al. 1996).

Coereba flaveola and *Loxigilla portoricensis* have been reported to consume mistletoe fruits in other areas (Watson 2001; Carlo et al. 2003), and it is probable that they do the same in the Guánica forest. It is likely that other birds consume the fruits of the mistletoe species in the study site. Many of them could be seed predators but others, although not specialized dispersers, still could disperse the seed by bill wiping. Several

authors (e.g. Terborgh 1986, cited in Carlo et al. 2003) have documented the importance of a small group of neotropical plant species in sustaining the frugivore community in times of scarcity due to having an extended (or asynchronous) fruiting season. From this point of view, *P. anceps* might be considered as a keystone species in the Guánica forest. Mistletoes not only play an important role in providing food for bird populations but also can provide habitat for ants and bromeliads. On the other hand, mistletoes also play a double role in an ecosystem, since they are mutualists of their bird dispersers and parasites of their hosts (Reid et al. 1995; Aukema 2003).

Kuijt (2003) argued that the behavior of the birds handling fruits and excreting their seeds has a biological significance for the mistletoe. He points out that the only detailed field study in this respect is the one performed by Restrepo (1997), who describes three different manners in which mistletoe fruits may be manipulated. One strategy results in seeds attached individually to host branches, the second is when seeds are attached in masses after regurgitation or defecation, and the third is the one in which seeds are deposited in long linear series that Restrepo called “rosarios” (Kuijt 2003). The last strategy described above is the one that *Euphonia musica* uses to defecate the seeds of *Phoradendron anceps* (Fig. 24). Interestingly, Restrepo (1997) reported that dispersers of *Phoradendron dipterum* and *P. inaequidentatum* move along the branches until all seeds have been eliminated. Kuijt (2003) consider that “rosaries” have two evolutionary advantages. First, the fact that seeds are not defecated in masses avoids intraspecific competition. Second, portions of a long rosary can gyrate and attach to other twigs below.

It is likely that the number of seeds in the upper canopy was underestimated because of difficulties in detecting seeds high in the host tree canopies of the tallest trees. However, the fact that most of the seeds were distributed in the lower and middle canopy can be explained by the manner (long linear series) that seeds are defecated by its probable main disperser bird (*Euphonia musica*). Even if the birds perch on upper branches, there is going to be more probability for the droppings to land on lower branches because of gravity.

There is no evidence to explain the lower number of mistletoe individuals toward the south of the main trunk of the tree. Perhaps it could be only an artifact of a lower number of host branches located in that position and not a consequence of bird preferences for perching.

There was no evidence of new infections, since seed deposition was not found on any of the uninfected trees. It is probable that colonization of new patches does exist, but at such a low rate that it was overlooked. The fact that only infected trees had seeds, coupled with the fact that the number of seeds was correlated with the number of living mistletoes, suggests a very limited dispersal distance of mistletoe seeds in relation to dispersal sources, as reported by Overton (1996) for other mistletoe species. A high within-dispersal efficiency and such limited between-dispersal is producing a high rate of autoinfection. Overton (1994) attributes the aggregated distribution of the mistletoes as a consequence of these reiterative infections.

Calder (1983 cited in López-de Buen and Ornelas 1999) suggested that among-tree movement of the seed dispersers will not be influenced by the abundance of mistletoe fruit because recognition of infections will not be possible from a distance. However, he studied cryptic mistletoes. This study and previous ones (Martínez del Río et. al 1996; López-de Buen and Ornelas 1999; Aukema 2003) suggest the contrary for larger mistletoe species. Not only can birds be attracted by the fruits of *P. anceps* but also they could recognize the mistletoes from a distance because, at least for the human eye, they can be easily distinguished from afar, since many of those are exposed directly to light have yellowish foliage and dark stems that contrast with the foliage and whitish stems of *P. albida* (Fig. 3).

Phoradendron anceps did not lead to host mortality at least in the study plot, although it is possible that hosts with many shed branches may die within a few years. This might suggest that the mistletoe does not draw too heavily on the host's resources, as found for two species of loranthaceous mistletoes from Australia (Reid & Lange 1988), or that *Pisonia albida* is highly resistant to their presence.

Most of the mistletoes were dead, suggesting a relatively high rate of mortality and a slow mistletoe turnover. In general, most of the mistletoes were exposed to the sun (Fig. 9b). The results indicate a higher likelihood of encountering dead mistletoes in the upper and lower canopy (Fig. 9c). I observed that the individuals more exposed to sun were located in the upper canopy and on the outermost lower canopy branches. Therefore, it is

possible that mistletoes more exposed to sun have higher transpiration rates, being more detrimental to the host branches that finally die together with the mistletoes.

Mistletoe mortality seems not to be dependent upon the host branch size, since the frequency distribution of living and dead mistletoes were very similar (Fig. 11a, b). Many remaining stems of dead mistletoes were robust or thick, indicating that they belonged to old mistletoes, which may have died after killing the branch. Some mistletoes were herbivorized and herbivory could also be a cause of their death. The presence of mistletoes in a tree may also contribute to individual-tree susceptibility to harmful insects or plant pathogens. Termite nests were observed on infected and non-infected trees (Fig. 25). Termites could also cause host branch mortality and hence, indirectly, could cause mistletoe death. In any case, it is not uncommon to see dead branches of *P. albida* even in the absence of mistletoes.

Many dead mistletoes were found aggregated, so they may also die due to density-dependence since they are competing for the same resource. Thus, all together, demographic, stochastic, and exogenous processes could be causing mistletoe mortality.

The results showed that *P. anceps* establishment mainly occurred on branches smaller than 30 mm in diameter (Fig. 11) although it occurred on branches up to 300 mm in diameter. Most of the dead and live mistletoes were found in the second smaller host branch diameter class (Fig. 11a, b). The distribution of proximal host branch diameter for

seeds was U-shaped: strongly skewed towards the smallest stems (modal class, 0-4 mm) and to the largest stems (modal class > 100 mm). The fact that seeds were scarce specifically in the second class could be due to the fact that those branches were already occupied by older live and dead mistletoes. It could be inferred that those seeds that landed or were deposited on the branches in the largest class are not going to succeed since seedling mistletoes generally only establish on branches that are small relative to the diameter range occupied by older mistletoes (Reid and Stafford-Smith 2000). I used proximal host branch diameter classes as a surrogate for age distribution (Fig. 11; Norton et al. 1997). However, mistletoe canopy width, length and diameter above the haustorium classes (Fig. 10) showed a stronger relationship with the life stage since most of the smaller individuals (first size class) coincided with the ones that were in vegetative condition. Most of the sterile individuals corresponded to seedlings and juvenile individuals (Fig. 26). Those vegetative individuals in the second class were almost all juveniles and those in higher classes were mature but sterile when they were counted. Although individuals with buds, flowers and/or fruits were found in the first class, they corresponded to mature individuals that had been herbivorized and were resprouting. Data from this study (Fig. 10) suggest that recruitment of young mistletoe plants has been relatively continuous, at least over the past few years.

When analyzing mistletoe subpopulations it can be observed that the higher the number of individuals, the more complex is the population structure (Fig. 12). Complex structures indicate a periodic recruitment of seedlings resulting in subpopulations

constituted of plants from different cohorts. Hence, it might be inferred that, on average, larger trees (which support more mistletoes), host the full range or at least a wider range of mistletoe canopy widths than smaller trees do.

From the subpopulation structures given in Figs. 14-22, at least six different patterns of size structures were distinguished. The first pattern showed a positively skewed population structure with seedlings and small plants dominating while larger-sized individuals were few (reverse J-shape). The second pattern had higher proportions of individuals in intermediate size classes and smaller numbers in the first and last classes (hump-shape). In the third pattern, the relative frequencies were highest for the first and the last class (U-shape). The fourth pattern had a bimodal structure, similar to the U-shaped pattern but with other classes different from the first and the last being the modes. The fifth pattern was somewhat flattened with individuals distributed almost evenly among the range of size classes. The last pattern, common in all the groups, had very few individuals distributed in few size classes. As a trend, all groups with two or more subpopulations had at least one that presented a wide range of size classes and a relatively high number of individuals while the remaining usually had few individuals (almost always two or one). These differences in population structures among subpopulations within a group were corroborated with the results of Mantel's test. The results in this respect might suggest that larger subpopulations with a high number of reproductive individuals may be the sources of seeds not only for their own patch (host trees) but for nearby patches, but since the between-dispersal is not as efficient and birds

may bias their foraging and feeding behavior towards infected trees, neighboring patches have few or no individuals.

Subpopulations with most individuals in the first size classes, and no dead individuals, may reflect recent colonizations. Subpopulations with a high number of individuals, most of them seedlings and juveniles, indicate a dynamic population with a high turnover rate. Conversely, an absence or a scarcity of the first classes, and most individuals belonging to the last classes (with many senescent individuals) could indicate declining subpopulations. On the other hand, subpopulations with a wide range of stages might be catalogued as stable. Although subpopulations in the plot exhibit different patterns, on average the mistletoe metapopulation in the study plot could be considered as dynamic.

Snäll et al. (2003) summarized four conceptual metapopulation models proposed from different authors that have been formulated to generalize species dynamics in a landscape: (1) The **classical metapopulation model** assumes species colonizations of patches and extinctions from patches. In this model colonizations are connectivity-dependent and the population risk increases with decreasing population size, mainly because of demographic or environmental stochasticity. (2) The **source-sink model** focuses on local population demography and suggests that source patches are required for long-term species persistence. (3) The **remnant species model** stresses that some plant species disperse over time rather than space through periods of poor patch quality. (4)

The **habitat-tracking metapopulation model** is one in which the habitat patches are dynamic. Additional to short-term stochasticity, a local extinction can be a consequence of a gradual long-term patch quality deterioration, which deterministically decreases the population size to extinction. Snäll et al. (2003) also proposed their own model that they called the **patch-tracking metapopulation model** based on the study of epiphytic bryophytes. This model is similar to the classical habitat-tracking metapopulation model but in this case, local extinction rate is caused mainly by patch destruction rather than by stochastic population processes.

Among the above models, the **habitat-tracking metapopulation model** best explains what is happening with the *Phoradendron anceps*-*Pisonia albida* system in the study plot. The empirical studies with other parasite-host species systems have also supported this model (i.e. Overton 1996). Inferring from these results and the literature I present the following qualitative explanation for this parasite-host system: First, *Pisonia albida* trees establish in the landscape. Birds (mainly *Euphonia musica*) initially deposit the seeds of *Phoradendron anceps* on *Pisonia* trees by means of long-distance dispersal that is rare in this system, and the trees become colonized by the mistletoe. *Phoradendron anceps* becomes fertile, flowers and fruits. Birds are attracted to the fruits, and deposit the seeds on the same tree or on the nearest neighbor trees that are large enough to be attractive to birds for perching. Since the trees that became more intensively infected offer more fruits, they are more prone to be revisited by birds and to be more infected and so on. Those mistletoe subpopulations that are small might be susceptible to be

extinguished. Local population extinction risk increases with decreasing population size (Gotelli 2001). On the other hand, large mistletoe subpopulations may also become extinguished because of host tree death that could be influenced by mistletoe density. Hence, mistletoe extinction from a host tree not only might be due to environmental and demographic stochasticity, but also to patch destruction that seems to be a relatively slow process in this system. Because of dispersal limitation, it could take some years for the mistletoe to colonize new patches.

CONCLUSIONS

Based on the present work, the following conclusions can be drawn from the study plot in the Guánica Forest Reserve:

- *Phoradendron anceps* is virtually host-specific to *Pisonia albida*.
- Both parasite and host species have an aggregated spatial pattern.
- Larger *Pisonia* trees have a higher frequency of parasite attack and more intense infection than smaller trees.
- Infected *Pisonia* trees are more prevalent in low-density stands than in high density stands.
- *P. anceps* is more abundant on host branches 11-20 mm in diameter.
- *P. anceps* is a relatively benign parasite insofar as it did not provoke host mortality in this system, at least at a short-temporal scale.
- *P. anceps* has a extended fruiting season.
- *Euphonia musica* is probably the main disperser of *P. albida*.
- Mistletoe seed dispersal is limited: the seed shadow of individual mistletoes may often be restricted to the canopy of the host tree.

- The mistletoe subpopulations exhibit different size structures: some stable, others increasing and other declining that in sum produce a net dynamic metapopulation structure with a high turnover rate.
- The **habitat-tracking metapopulation model** best explains the *Phoradendron anceps-Pisonia albida* system in the study plot.

RECOMMENDATIONS

To understand better the role that *Euphonia musica* and other birds play in the *Phoradendron anceps*-*Pisonia albida* system in the Guánica forest, a more detailed study of their foraging and feeding behavior would be necessary.

To study accurately the dynamics of the subpopulations and the overall metapopulation in the study plot, a study of more years would be necessary to estimate different parameters, such as the rate of births and deaths, fecundity, survival, growth, etc., that are needed to construct matrices and simulation models to model the dynamics of plant species.

It would be interesting to study this system at a larger scale, to see if the patterns persist and to investigate what happens when other mistletoe species are present.

It is hoped that future studies will be performed to compare mistletoe population structures and distributions among mistletoe species and sites as a basis for a better understanding of the ecology of these interesting plants.

LITERATURE CITED

- Aukema J.E. 2003. Vectors, viscin and Viscaceae: mistletoes as parasites, mutualists and resources. *Front. Ecol. Environ.* 1: 212-219.
- Aukema J.E. and C. Martínez del Río. 2002. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* 83: 489-496.
- Bannister P. and G.L. Strong. 2001. The distribution and population structure of the temperate mistletoe *Ileostylus micranthus* in the Northern Cemetery, Dunedin, New Zealand. *New Zeal. J. Bot.* 39: 225-233.
- Begon M. and M. Mortimer. 1986. *Population ecology: A unified study of animals and plants*. Blackwell Scientific Publ., Boston. 220 pp.
- Bliss C.I. and R.A. Fisher. 1953. Fitting the negative binomial distribution to biological data and a note on the efficient fitting of the negative binomial. *Biometrics* 9: 176-200.
- Botto-Mahan C., R. Medel, R. Ginocchio and G. Montenegro. 2000. Factors affecting the circular distribution of the leafless mistletoe *Trixteris aphyllus* (Loranthaceae) on the cactus *Echinopsis chilensis*. *Rev. Chil. Hist. Nat.* 73: 525-531.
- Carlo T.A., J.A. Collazo and M. Groom. 2003. Avian fruit preferences across a Puerto Rican forested landscape pattern: consistency and implications for seed removal. *Oecologia* 134: 119-131.
- Cintrón B. and A.E. Lugo, 1990. Litter fall in a subtropical dry forest: Guánica, Puerto Rico. *Acta Ci.* 4: 37-49.
- Cole L.C. 1946. A theory for analyzing contagiously distributed populations. *Ecology* 27: 329-341.
- Dawson T., J.R. Ehlinger and J.D. Marshall. 1990a. Sex-ratio and reproductive variation in the mistletoe *Phoradendron juniperum* (Viscaceae). *Am. J. Bot.* 77: 584-589.
- Dawson T.E., E.J. King and J.R. Ehlinger. 1990b. Age structure of *Phoradendron juniperum* (Viscaceae), a xylem-tapping mistletoe: inferences from a non-destructive morphological index of age. *Am. J. Bot.* 77: 573-583.
- Dobson A.P. 1985. The population dynamics of competition between parasites. *Parasitology* 9: 317-347

- Donohue, K. 1995. The spatial demography of mistletoe parasitism on a Yemeni *Acacia*. *Int. J. Plant Sci.* 156: 816-823.
- Ehleringer J.R., E.D. Schulze, H. Ziegler, O.L. Lange, G.D. Farquhar and I.R. Cowar. 1985. Xylem-tapping mistletoes: water or nutrient parasites? *Science* 227: 1479-1481.
- Ewel J.J., and J.L. Whitmore. 1973. The ecological zones of Puerto Rico and the U.S. Virgin Islands. U.S Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico. 72 pp.
- Fortin M.-J., M.R.T. Dale and J. ver Hoef. 2002. Spatial analysis in ecology. In: El-Shaarawi, A. and W.W. Piegorsch, eds., *Encyclopedia of Environmetrics*, pp. 2051-2058. Wiley, Chichester.
- Geils B.W., J. Cibrián-Tovar, B. Moody and tech. coords. 2002. Mistletoes of North American conifers. Gen. Tech. Rep. RMRS-GTR-98. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 123 pp.
- Gotelli N.J. 2001. *A primer of ecology*. 3rd edition. Sinauer Associates, Inc., Sunderland, MA.
- Grieg-Smith, P. 1983. *Quantitative plant ecology*. University of California Press, Berkeley.
- Hawksworth F.G. and D. Wiens. 1996. Dwarf mistletoes: biology, pathology, and systematics. *Agric. Handb.* 709. Washington, DC: U.S. Department of Agriculture, Forest Service. 410 pp. [Online 2004]. Available: <http://www.rms.nau.edu/>
- Hill, M.O. 1973. The intensity of spatial pattern in plant communities. *J. Ecol.* 61: 225-235.
- Hutchinson G.E. 1953. The concept of pattern in ecology. *Proc. Natn. Acad. Sci. U.S.A.* 105: 1-12.
- InfoStat. 2004. InfoStat versión 2004. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Kareiva P. 1994. Space: the final frontier for ecological theory. *Ecology* 75:1
- Kirkpatrick M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. *Ecology* 65: 1874-1884.

- Krebs C.J. 1999. Ecological methodology. 2nd ed., A. Wesley Longman, New York.
- Kuijt J. 1969. The biology of parasitic flowering plants. Univ. California Press, Berkeley. 246 pp.
- Kuijt J. 2003. Monograph of *Phoradendron* (Viscaceae). Syst. Bot. Monogr. 66: 1-414.
- Ladley J.J. and D. Kelly. 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds: New Zeal. J. Ecol. 20: 69-79.
- Liogier H.A. 1985. Descriptive flora of Puerto Rico and adjacent islands. Spermatophyta. Vol. 1. Editorial de la Universidad de Puerto Rico, Río Piedras, Puerto Rico. 352 pp.
- Lloyd M. 1967. Mean crowding. J. Anim. Ecol. 36: 1-30.
- López-de Buen L. and J.F. Ornelas. 1999. Frugivorous birds, host selection and the mistletoe *Psittacanthus schiedeanus*, in central Veracruz, Mexico. J. Trop. Ecol. 15: 329-340.
- Lugo A.E., J.A. González-Liboy, B. Cintrón and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10: 278-291.
- Malhado A.C. and M. Petreire Jr. 2004. Behaviour of dispersion indices in pattern detection of a population of angico, *Anadenthera peregrine* (Leguminosae). Braz. J. Biol., 64: 243-249.
- Martínez del Río C.A., A. Silva, R. Medel and M. Hourdequin. 1996. Seed dispersers as disease vectors: bird transmission of mistletoe seeds to plant host. Ecology 77: 912-921.
- Marvier M.A. and D.L. Smith. 1997. Conservation implications of host use for rare parasitic plants. Conserv. Biol. 11: 839-848.
- McElhany P., L. Real, and A.G. Power. 1995. Vector preference and disease dynamics: a study of barley yellow dwarf virus. Ecology 76: 444-457.
- Medel R. 2000. Assessment of parasite-mediated selection in a host-parasite system in plants. Ecology 81: 1554-1564.
- Medel R., C. Botto-Mahan, C. Smith-Ramírez, M.A. Méndez, C.G. Ossa, L. Caputo and W. Gonzáles. 2002. Historia natural cuantitativa de una relación parásito-

- hospedero: el sistema *Tristerix*-cactáceas en Chile semiárido. *Rev. Chil. Hist. Nat.* 75: 127-140.
- Medina E. and E. Cuevas. 1990. Propiedades fotosintéticas y eficiencia del uso de agua en plantas leñosas del bosque decíduo de Guánica: consideraciones generales y resultados preliminares. *Acta Ci.* 4: 25-36.
- Morisita M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci., Kyushu Univ. Ser. E (Biol.)*. 2: 215-235.
- Murphy P.G. and A.E. Lugo 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* 18: 89-96.
- Murphy P.G. and A.E. Lugo. 1990. Dry forest of the tropics and subtropics: Guánica Forest in context. *Acta Ci.* 4: 15-24.
- Norton D.A and M.A Carpenter. 1998. Mistletoes as parasites: host specificity and speciation. *Trends Ecol. Evol.* 101-105.
- Norton D.A and P.J. de Lange. 1999. Host specificity in parasitic mistletoes (*Loranthaceae*) in New Zealand. *Funct. Ecol.* 13: 552-559.
- Norton D.A., R.J. Hobbs and L. Atkins. 1995. Fragmentation, disturbance and plant distribution: distribution in woodland remnants in Western Australia wheatbelt. *Conserv. Biol.* 9: 426-438.
- Norton D.A., J.J Ladley and H.J. Owen. 1997. Distribution and population structure of the loranthaceous mistletoes *Alepis flavida*, *Peraxilla colensoi* and *Peraxilla tetrapetala* within two New Zealand *Nothofagus* forest. *New Zeal. J. Bot.* 35: 323-336.
- Norton D.A. and N. Reid. 1997. Lessons in ecosystem management from management of threatened and pest loranthaceous mistletoes in New Zealand and Australia. *Conserv. Biol.* 11: 759-69
- Overton J.M. 1994. Dispersal and infection in mistletoe metapopulation. *J. Ecol.* 82: 711-723.
- Overton J.M. 1996. Dispersal spatial autocorrelation and dispersal in mistletoes: field and simulation results. *Vegetatio* 125: 83-98.
- Pacala S.W. and A.P. Dobson. 1988. The relation between the number of parasites/host and host age: population dynamics causes and maximum likelihood estimation. *Parasitology* 96:197-210.

- Pérez-Rivera R.A. 1991. Change in diet and foraging behavior of the Antillean euphonia in Puerto Rico after Hurricane Hugo. *Field Ornithol.* 62:474-478.
- Pielou E.C. 1960. A single mechanism to account for regular, random and aggregated populations. *J. Ecol.* 48:574-584.
- Piñero D., J. Sarukhán, and E. González, 1977. Estudios demográficos en plantas: *Astrocarium mexicanum* Liebm. Estructura de las poblaciones. *Bol. Soc. Bot. Mex.* 37: 69-118.
- Powell G.R. and D.A. Norton. 1994. Contrast in crown development of the mistletoe *Alepis flavida* (Hook.f.) Tiegh. and *Peraxilla tetrapetala* (L.f.) Tiegh. (Loranthaceae) parasitic on *Nothophagus solandri* (Hook.f.) Oerst., Craigieburn Ecological District, New Zealand. *New Zeal. J. Bot.* 32. 497-508.
- Quevedo V., S.R. Silander, and Woodbury R.O. 1990. Plantas críticas y en peligro de extinción en el bosque de Guánica. *Acta Ci.* 4: 25-36.
- Reid N., and R.T. Lange 1988. Host specificity, dispersion and persistence through drought of two arid zone mistletoes. *Aust. J. Bot.* 36: 299-313.
- Reid N. and M. Stafford-Smith. 2000. Population dynamics of an arid zone mistletoe (*Amyema preissii*, Loranthaceae) and its host *Acacia victoriae* (Mimosaceae) *Aust. J. Bot.* 48:45-58.
- Reid N., M. Stafford-Smith, and Z. Yan. 1995. Ecology and population biology of mistletoes. In: M.D. Lowman and N.M. Nadkarni, eds., *Forest canopies*, pp. 285-310. Academic Press, San Diego, CA.
- Restrepo C. 1997. Aspectos ecológicos de la diseminación de cinco especies de muérdagos para aves. *Humboldtia* 1: 65-116.
- Rohlf F.J. 1998. NTSYSpc Numerical taxonomy and multivariate analysis system. Version 2.02. Applied Biostatistics, Inc., New York.
- Sarukhán J., D. Piñero and., M. Martínez-Ramos. 1985. Plant demography: a community-level interpretation. In: J. White, ed. *Plant population ecology*, pp. 17-31. Blackwell, Oxford, England.
- Snäll T., J. Ribeiro Jr. and H. Rydin. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos* 103: 566-578.
- Watson D.M. 2001. Mistletoe - a keystone resource in forest and woodlands worldwide. *Annu. Rev. Ecol. Syst.* 32: 219-249.

- Watson D.M. 2002. Effects of mistletoe on diversity: a case-study from southern New South Wales. *Emu* 102: 275-281.
- Yoshioka P. 1997. A community-level analysis of spatial mortality patterns. *J. Exp. Mar. Biol. Ecol.* 214: 167-178.
- Zar J.H. 1999. *Biostatistical analysis*. Prentice-Hall Inc. New Jersey, Englewood Cliffs, NJ. 663 pp.

TABLES

Table 1. Morisita's indices of dispersion for host and mistletoes in the study plot.

| Individuals | I_{δ} | 95% CL intervals | n | χ^2 |
|--------------------|--------------|-------------------------|------|--------------|
| Non-infected trees | 8.982 | 8.057 – 9.906 | 90 | 5181.376*** |
| Infected trees | 9.373 | 7.996 – 10.750 | 43 | 5435.050*** |
| Mistletoes | 47.872 | 44.862 – 50.883 | 1370 | 24435.624*** |

gl = 528, *** = $P \leq 0.001$

Table 2. Wilcoxon (U Mann-Whitney) test for tree traits of infected and non-infected trees.

| Tree trait | Infected <i>n</i> = 43 | | Non-infected <i>n</i> = 90 | | W | <i>P</i> (2 -tailed) | |
|-----------------|---------------------------|--------|-------------------------------|--------|--------|----------------------|----|
| | Mean | SD | Mean | SD | | | |
| Basal area | 608.77 | 612.32 | 612.32 | 441.28 | 3162.0 | 0.1765 | |
| Canopy diameter | 5.25 | 2.21 | 4.12 | 2.01 | 3492.0 | 0.0033 | ** |
| Canopy height | 2.64 | 1.04 | 2.34 | 0.85 | 3186.0 | 0.1421 | |
| Tree height | 3.41 | 1.06 | 3.20 | 0.94 | 3094.5 | 0.3043 | |

** = $P \leq 0.01$

Table 3. Spearman rank correlation of infected trees of a size class against the different tree trait class.

| Tree trait | Coefficient r_s |
|-------------------------------|-------------------------------------|
| Basal area (cm ²) | 0.68 |
| Canopy diameter (m) | 0.86* |
| Canopy height (m) | 0.89* |
| Tree height (m) | 0.90* |

* = $P \leq 0.05$

Table 4. Spearman rank correlation coefficients of tree traits against number of mistletoes per tree.

| Tree Trait | Coefficient r_s |
|-------------------------------|-------------------------------------|
| Basal area (cm ²) | 0.03 |
| Canopy diameter (m) | 0.17 |
| Canopy height (m) | 0.35* |
| Tree height (m) | 0.31* |

$(r_s)_{0.05(2), 43} = 0.301$, * = $P \leq 0.05$

Table 5. Spearman rank correlation coefficients of mistletoe size/age variables.

| Compared mistletoe size variables | r_s |
|--|---------|
| Canopy diam. vs. length | 0.90*** |
| Canopy diam. vs. above-haustorium diameter (AHD) | 0.82*** |
| Canopy diam. vs. host branch diameter (HBD) | 0.29*** |
| Length vs. AHD | 0.82*** |
| Length vs. HBD | 0.28*** |
| AHD vs. HBD | 0.20*** |

*** = $P < 0.001$

FIGURES

Figure 1. Map showing the location of the Guánica Forest Reserve in southwestern Puerto Rico. The black rectangle on the lower map indicates the location of study plot (Fig. 2).

Figure 2. Location of the study plot in the Guánica forest. Infected and non-infected individuals are represented by solid and open stars, respectively. Coordinates given along the bottom and left hand edges of the map are in the UTM Puerto Rico datum reference system.

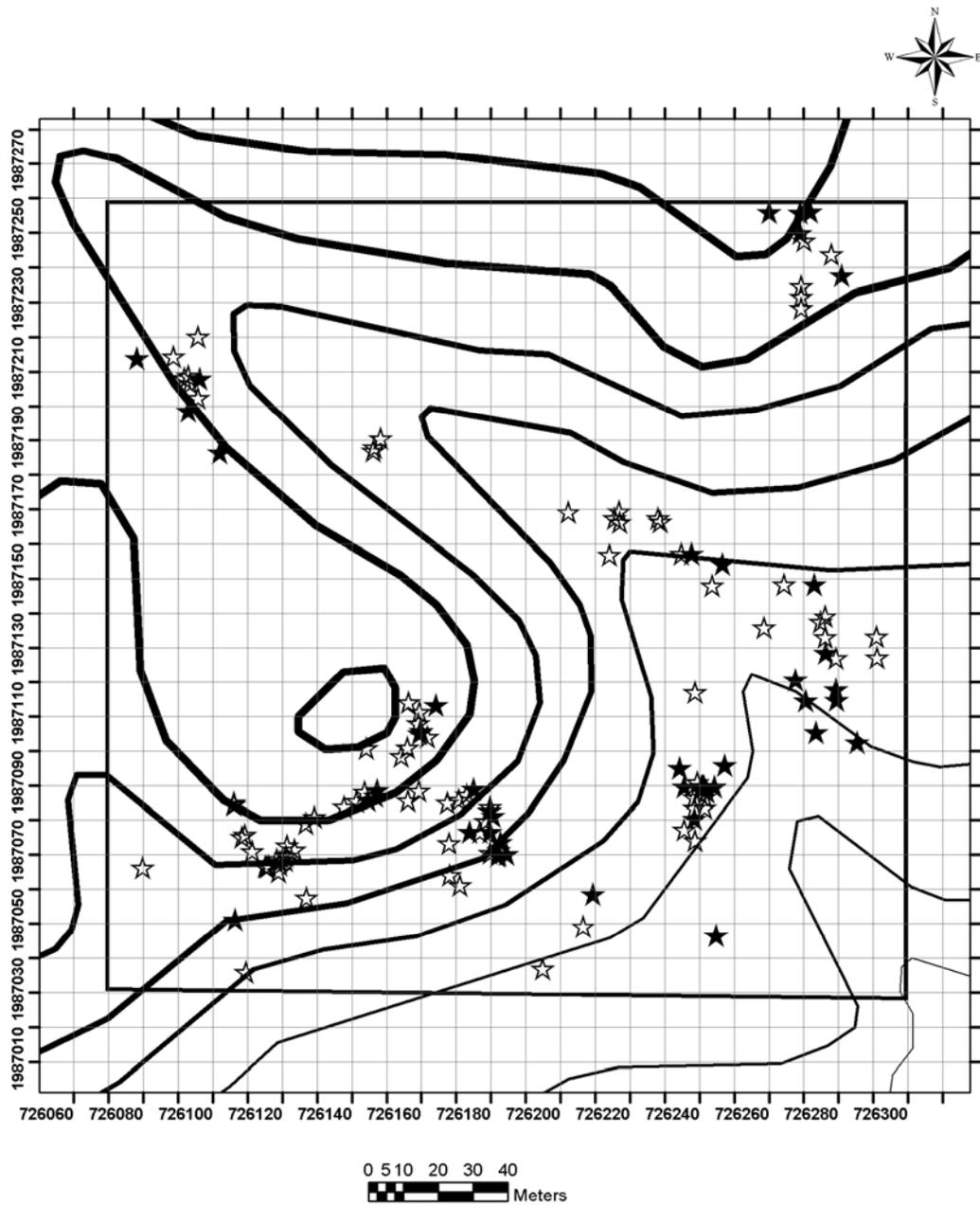




Figure 3. Individual of *Pisonia albida* infected by *Phoradendron anceps* (center).

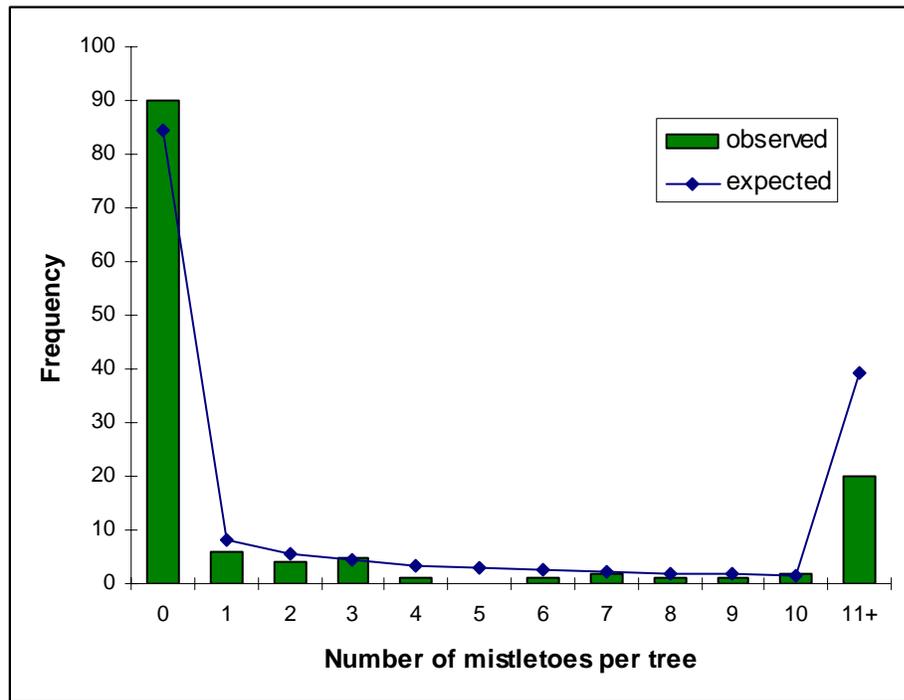


Figure 4. Frequency distribution of parasitic attack among infected hosts. Thirty-two percent of the trees within the plot had at least one mistletoe infection. The frequency distribution is negative binomial, with $\bar{x} = 10.301$ (SD = 2.940) and $k = 0.093$ (SD = 0.039); χ^2 for goodness of fit = 17.56, df = 9, $P = 0.04$. Parameter estimates and expected values were calculated after Bliss and Fisher (1953).

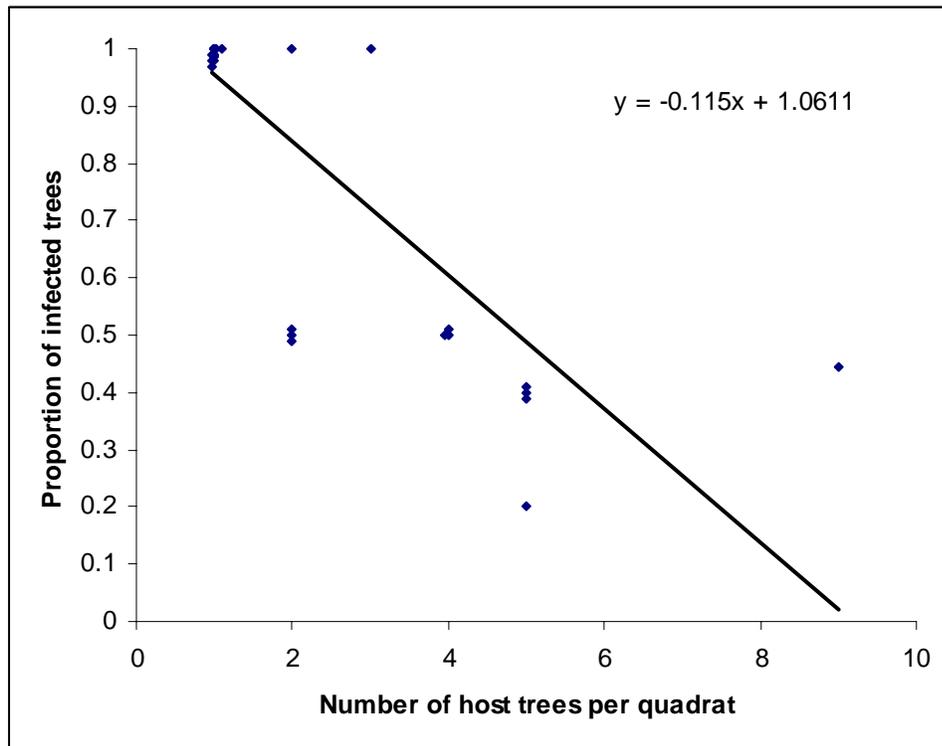


Figure 5. Simple regression testing for effects of host (*Pisonia albida*) density per quadrat (100 m²) on proportion of trees infected ($r^2 = 0.641$ F = 54.5, $P < 0.001$, $n = 31$, for number of quadrats with infected trees).

Figure 6. Frequency distribution of the tree traits of *Pisonia albida* in the plot, and the percentage of trees in each size class infected by *Phoradendron anceps*; (a) basal area, (b) canopy diameter, (c) canopy height, and (d) tree height.

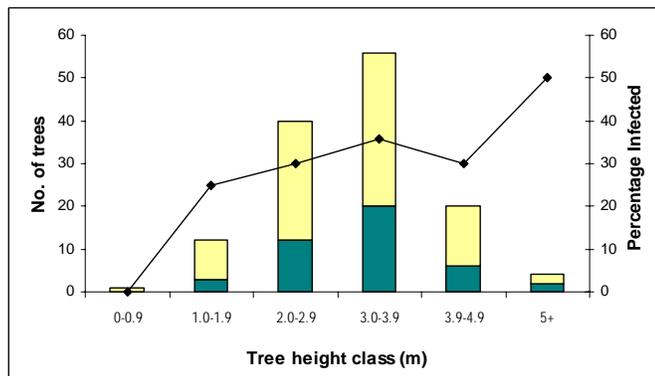
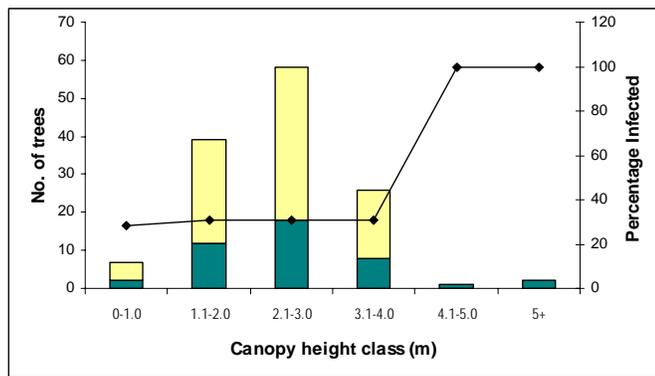
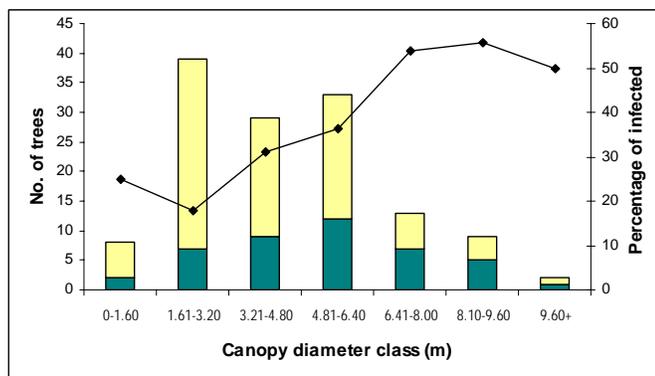
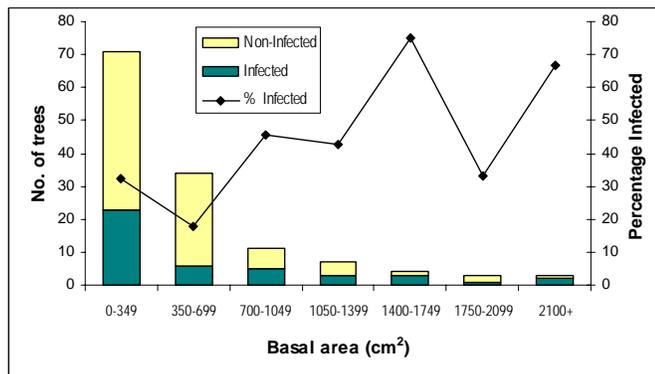




Figure 7. Dead individual of *Phoradendron anceps* (center) surrounded by living mistletoes.



Figure 8. Dead branches of *Pisonia albida* with dead mistletoes (arrows).

Figure 9. Distribution of living and dead mistletoes on the infected host with respect to (a) compass orientation, (b) exposure to light and (c) height on the host tree.

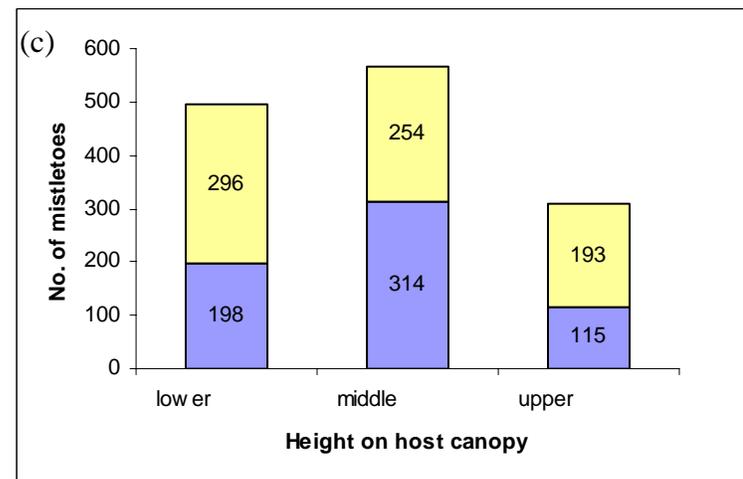
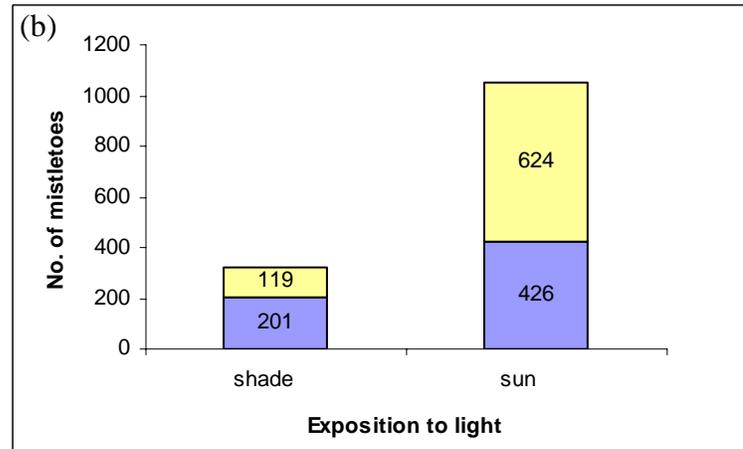
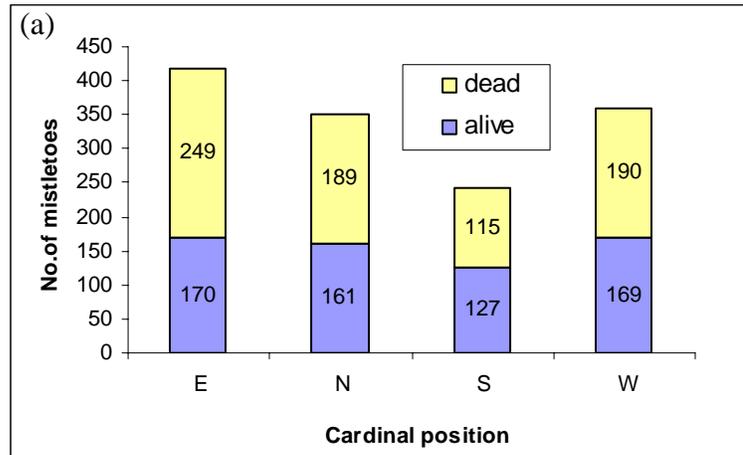


Figure 10. Frequency distribution of size classes of *P. anceps* by: (a) maximum canopy width; (b) length, and (c) diameter above haustorium.

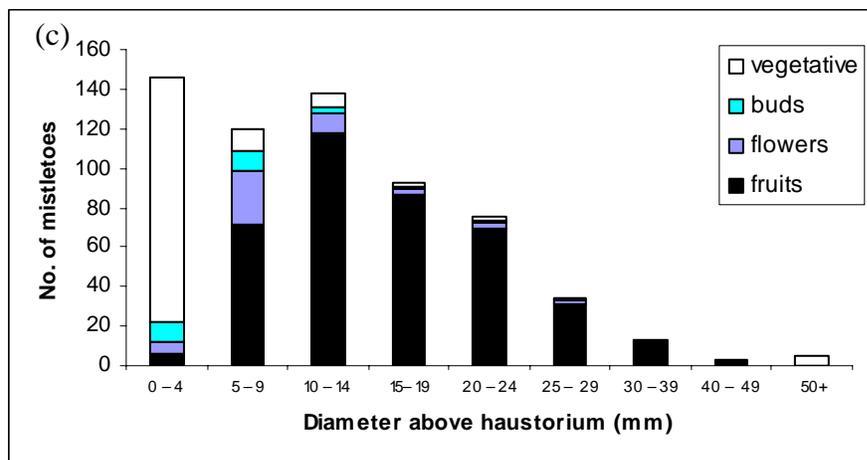
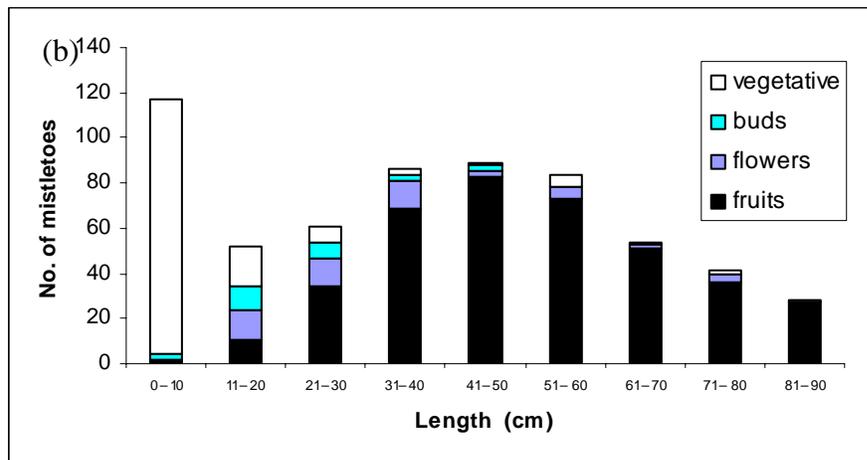
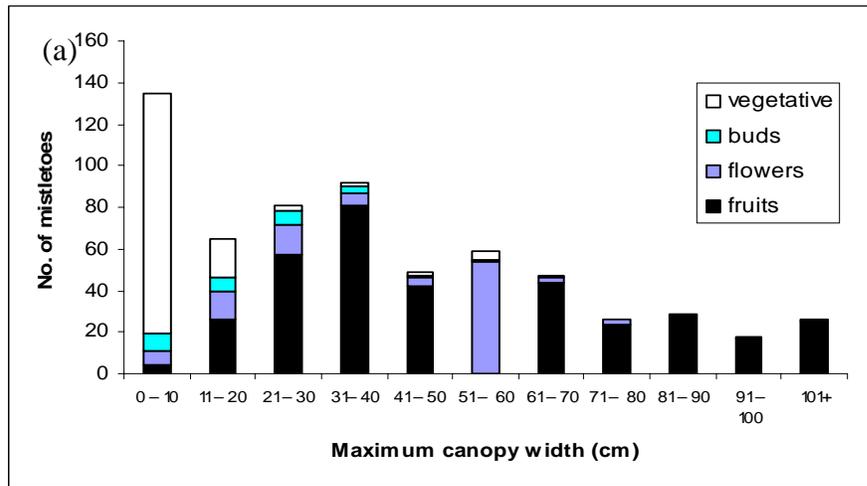
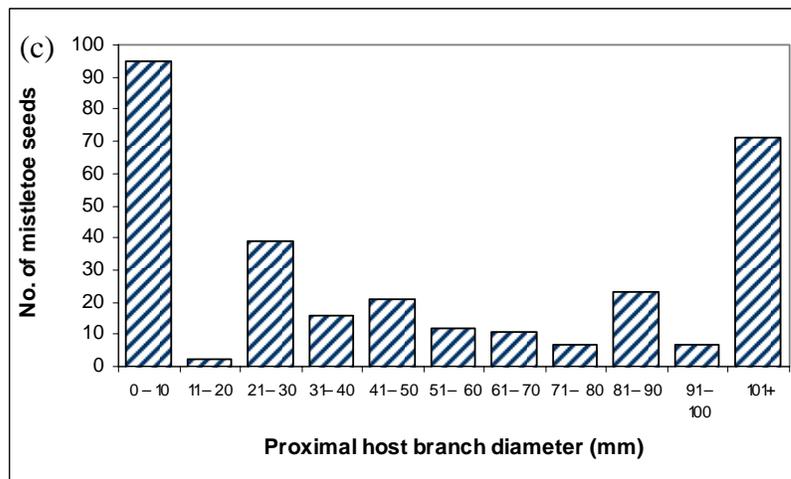
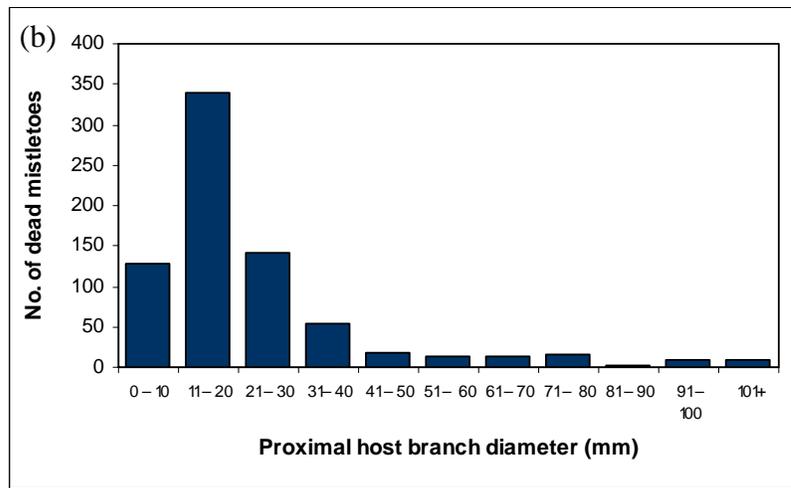
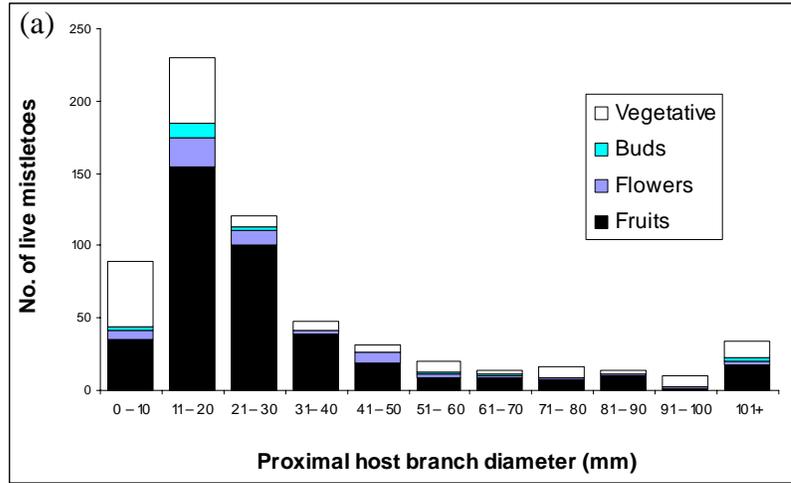


Figure 11. Frequency distribution of proximal host branch diameter for *P. anceps* of (a) live mistletoes classified by their reproductive state ($n = 627$); (b) dead mistletoes ($n = 743$), and (c) mistletoe seeds ($n = 304$).



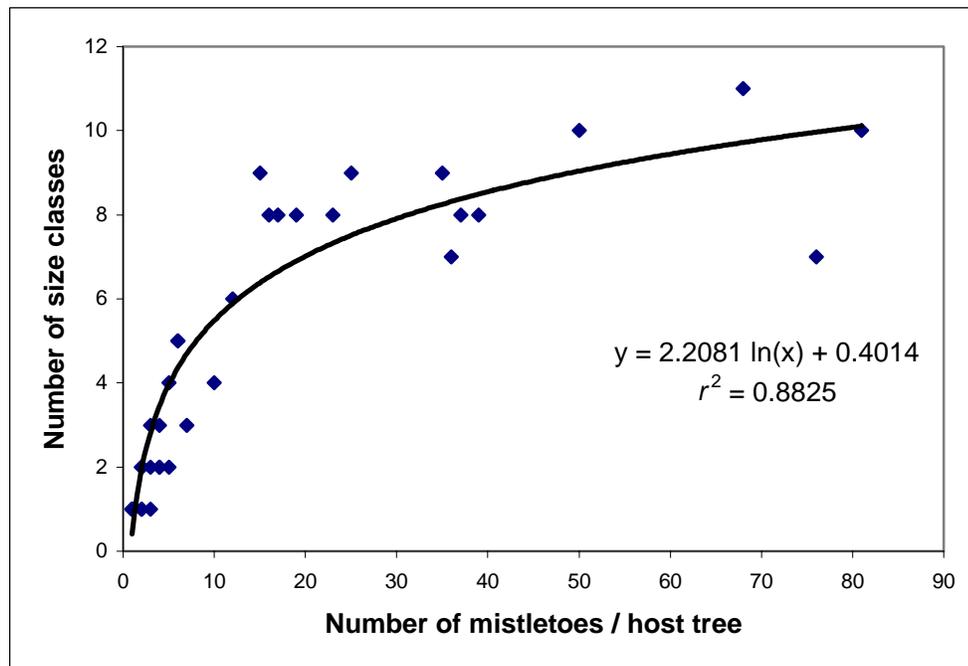


Figure 12. Logarithmic regression for the number of mistletoes per tree against the number of canopy diameter classes in which mistletoes are distributed.

Figure 13. Distribution of the infected trees in the study plot. The asterisk next to # 823 signifies the presence of two additional trees (# 823b and # 823c) immediately adjacent to tree # 823. Parentheses indicate three infected trees that bore only dead mistletoes.

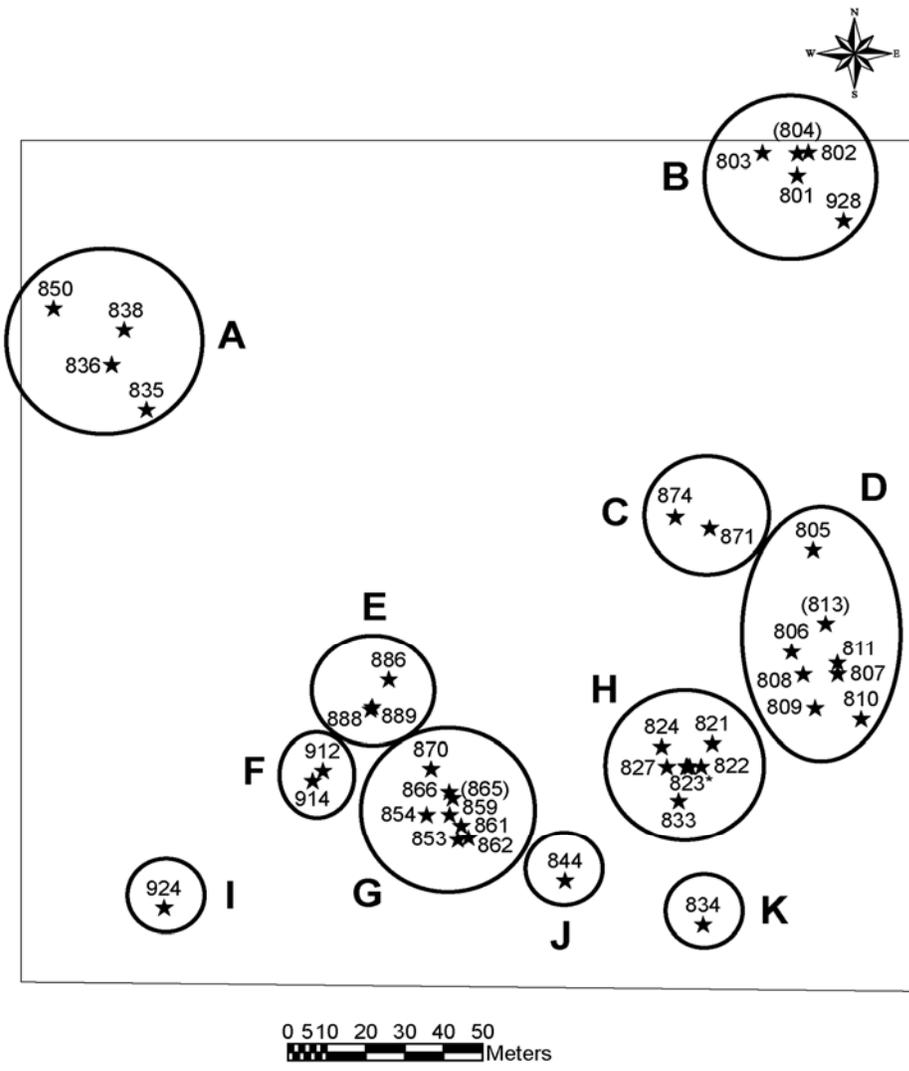


Figure 14. Demographic structure of mistletoes in group A based on mistletoe size class (maximum canopy width).

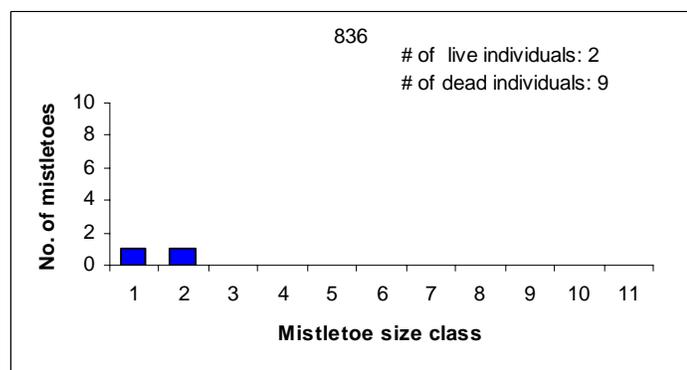
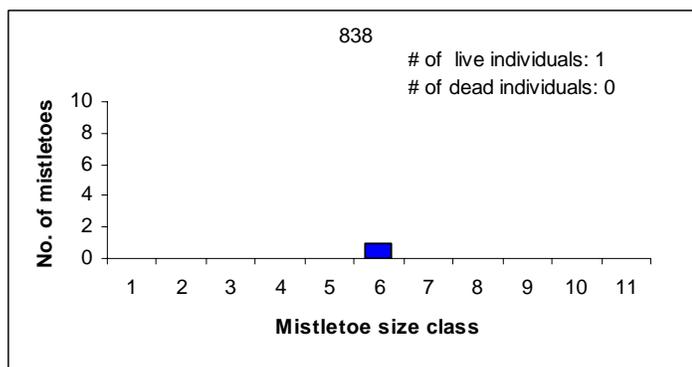
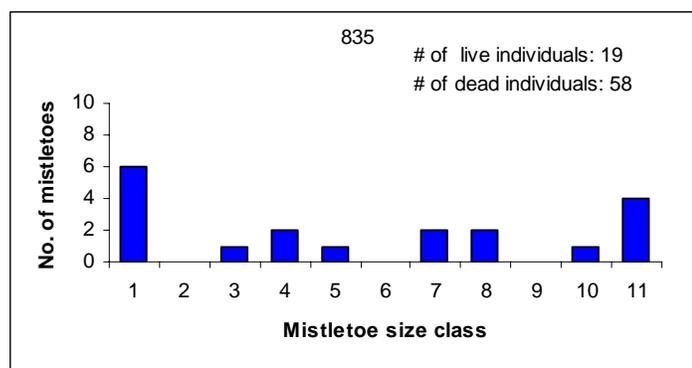
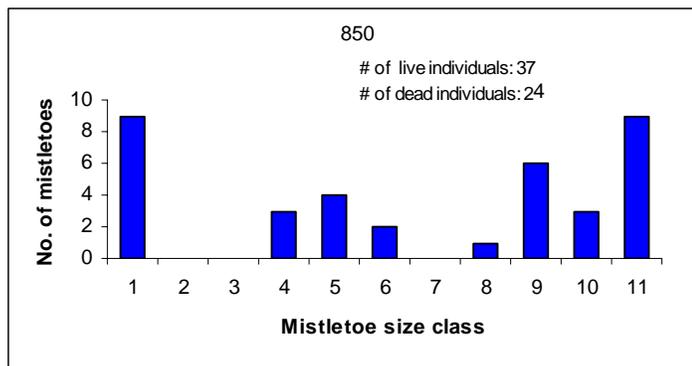


Figure 15. Demographic structure of mistletoes in group B based on mistletoe size class (maximum canopy width).

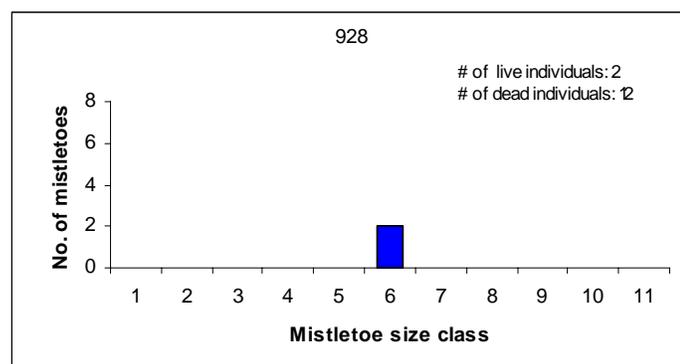
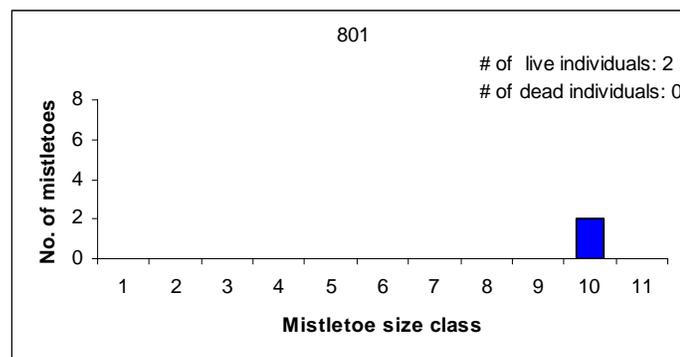
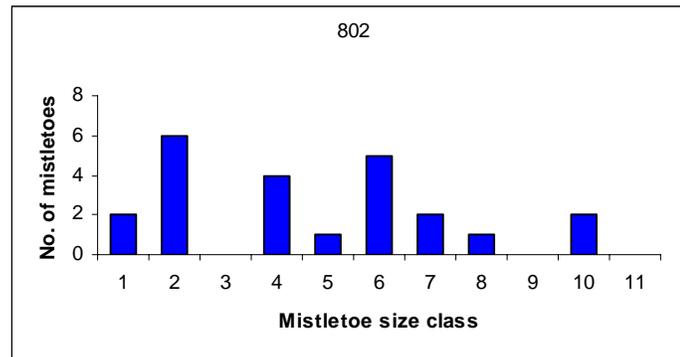


Figure 16. Demographic structure of mistletoes in group C based on mistletoe size class (maximum canopy width).

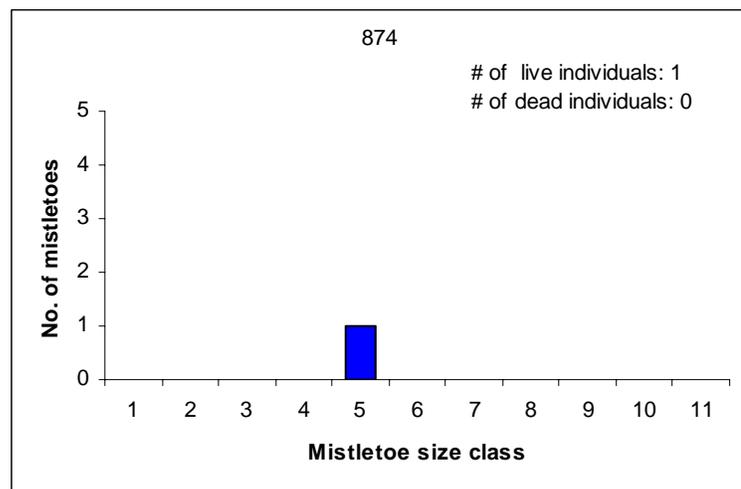
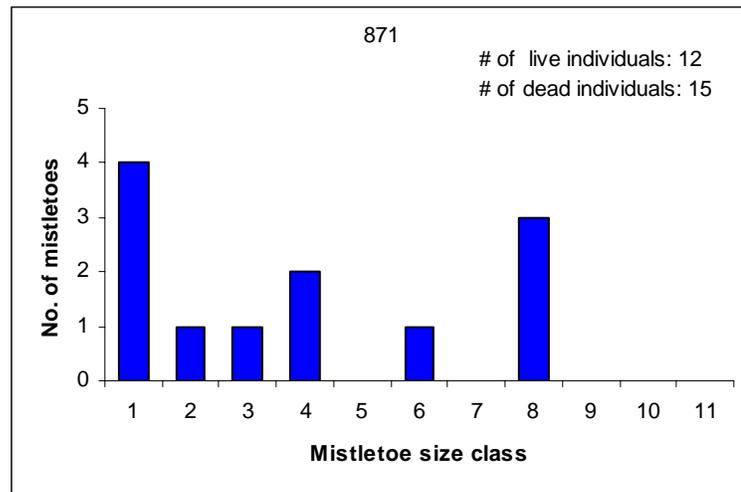


Figure 17. Demographic structure of mistletoes in group D based on mistletoe size class (maximum canopy width).

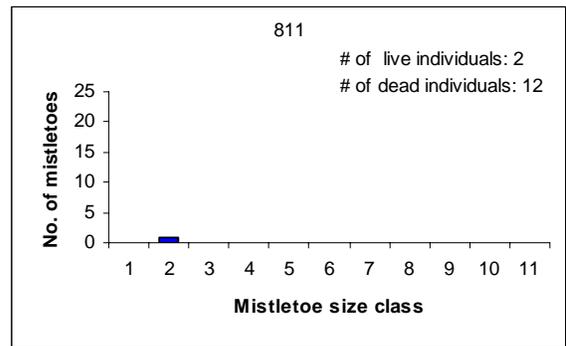
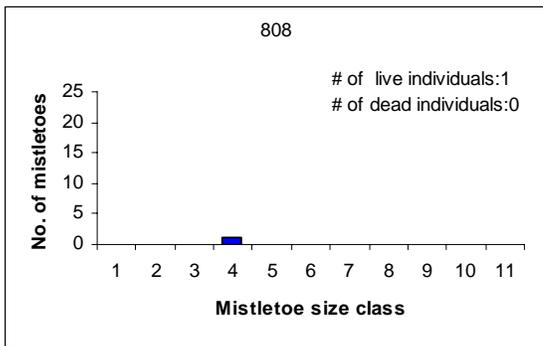
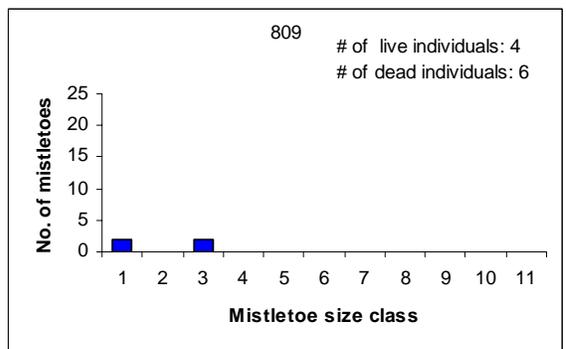
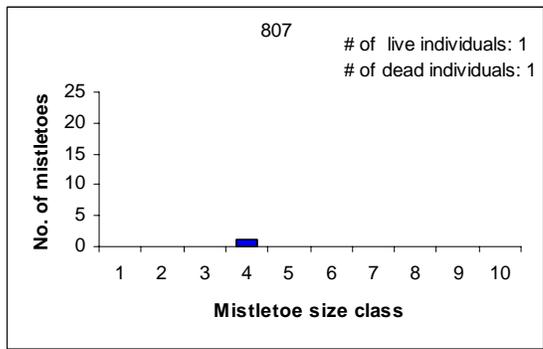
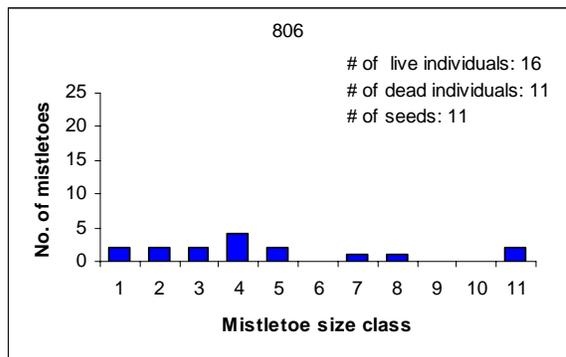
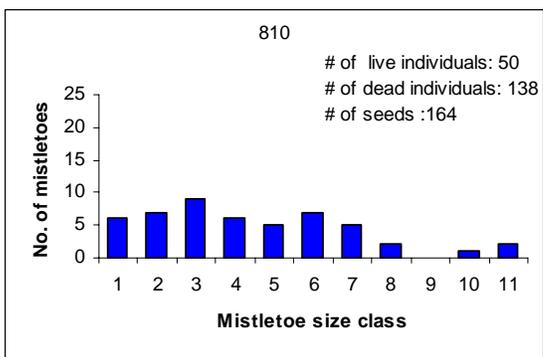
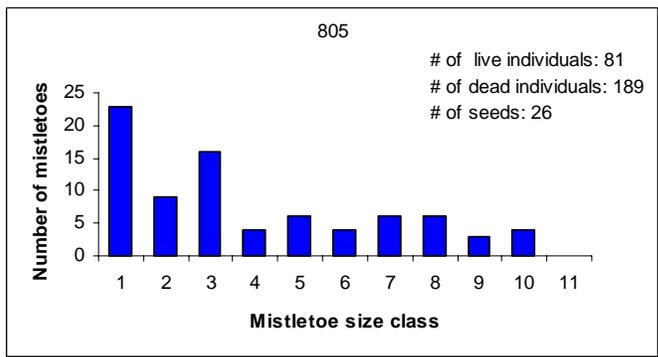


Figure 18. Demographic structure of mistletoes in group E based on mistletoe size class (maximum canopy width).

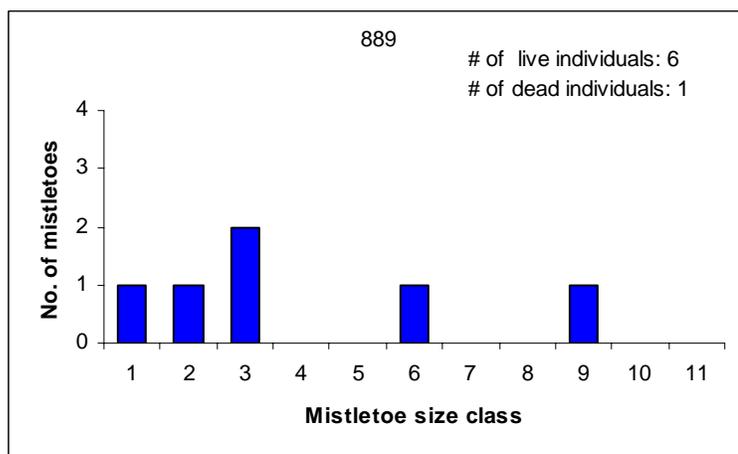
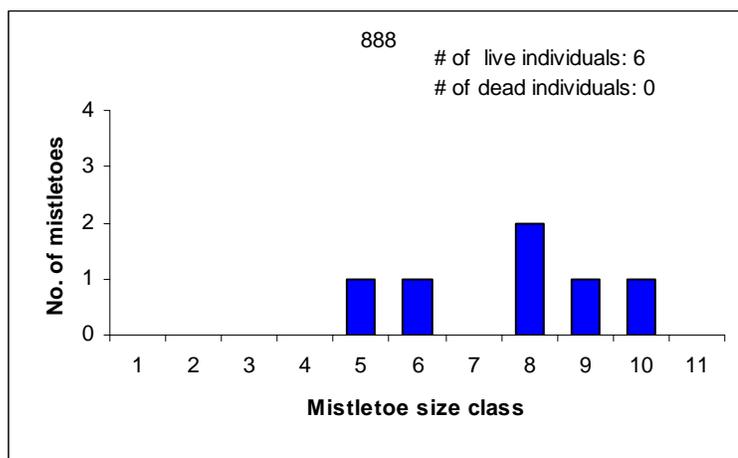
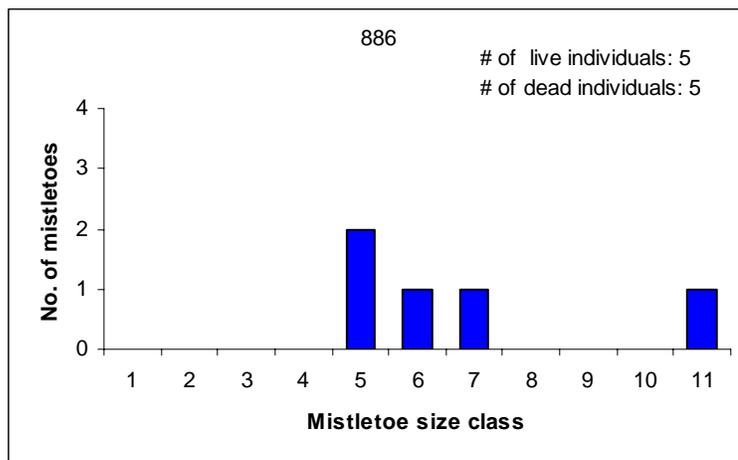


Figure 19. Demographic structure of mistletoes in group F based on mistletoe size class (maximum canopy width).

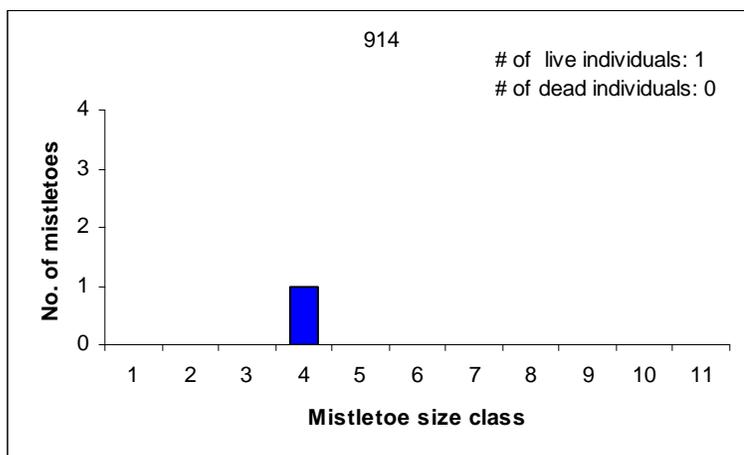
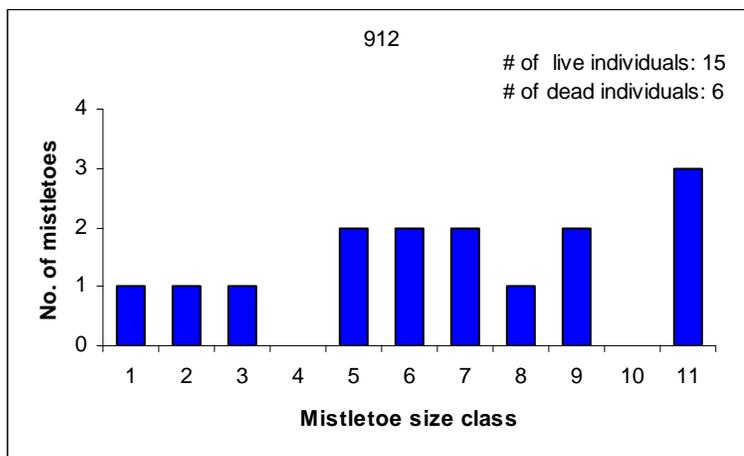


Figure 20. Demographic structure of mistletoes in group G based on mistletoe size class (maximum canopy width).

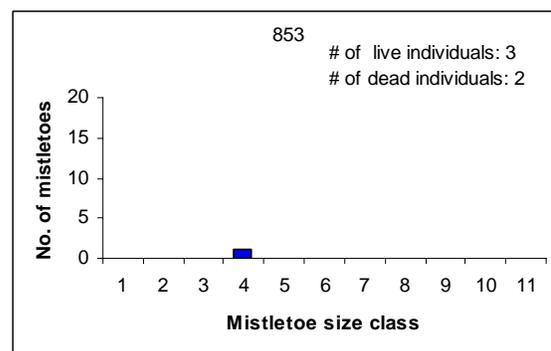
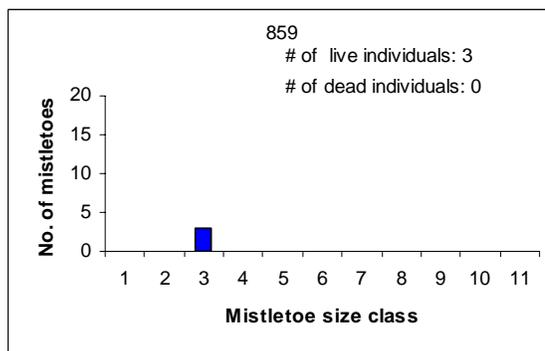
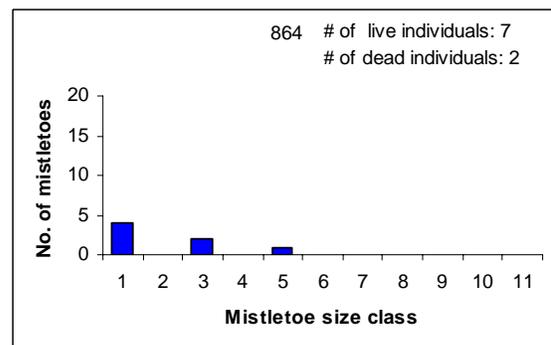
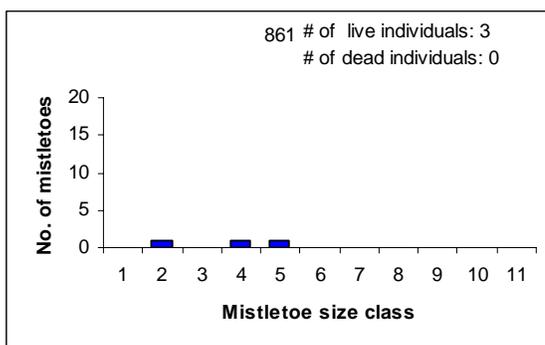
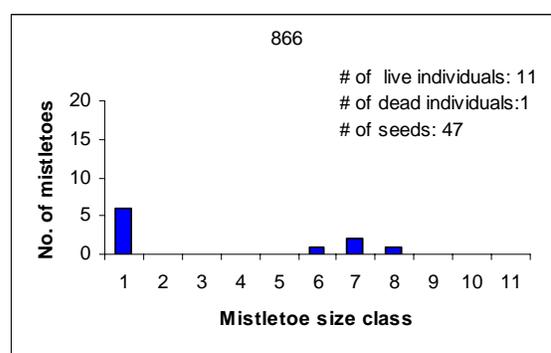
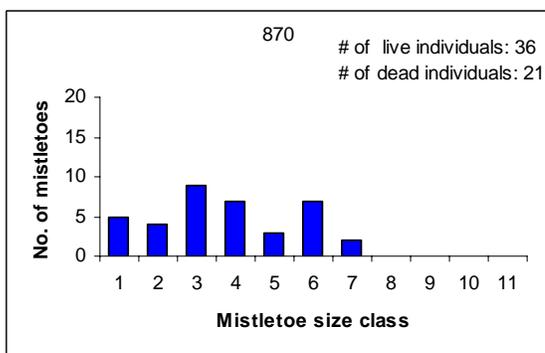
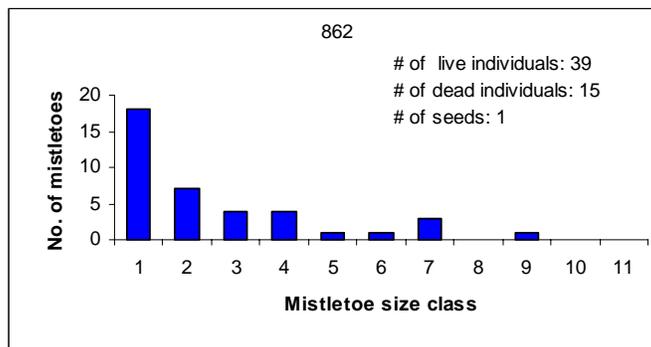


Figure 21. Demographic structure of mistletoes in group H based on mistletoe size class (maximum canopy width).

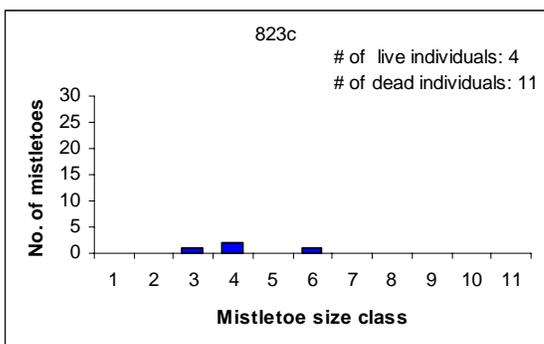
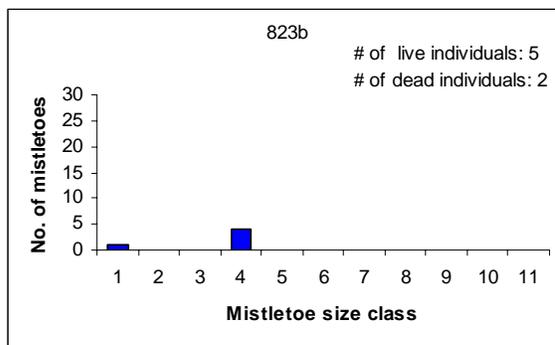
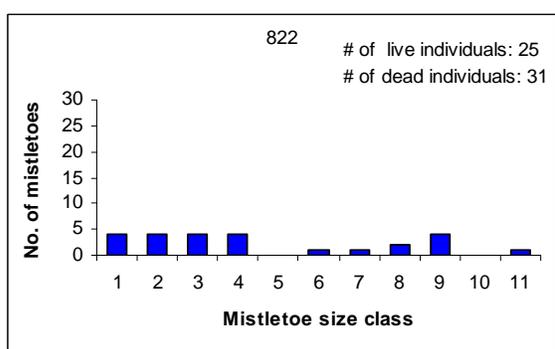
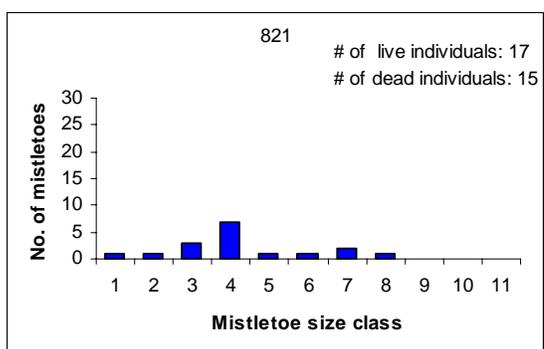
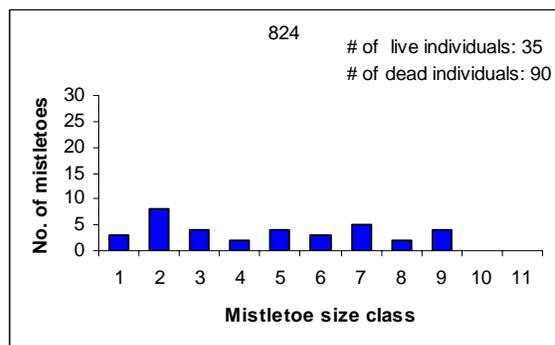
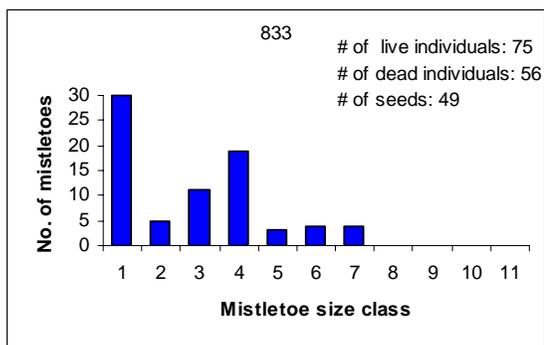


Figure 22. Demographic structure of mistletoes in groups I-K (isolated trees based on mistletoe size class (maximum canopy width). a) Group I (subpopulation 924), b) group J (subpopulation 844), c) group K (subpopulation 834).

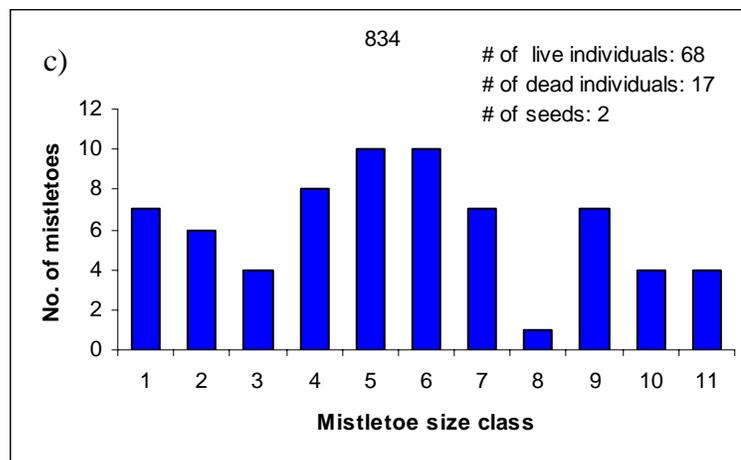
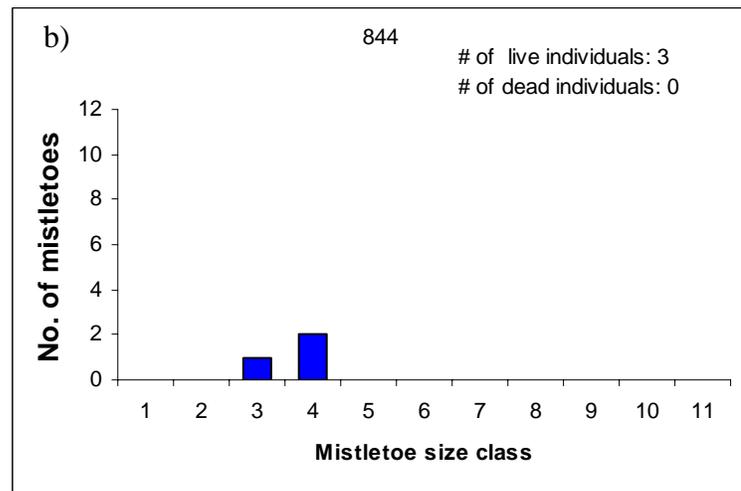
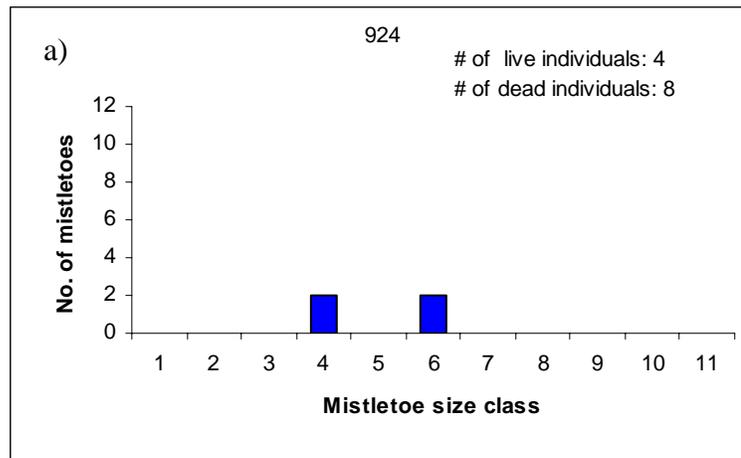




Figure 23. Reproductive plant of *Phoradendron anceps* (above). Detail of the fruits (below).



Figure 24. Seeds of *Phoradendron anceps* defecated by *Euphonia musica*.



Figure 25. Termite nest on *Pisonia albida* . Notice that some dead mistletoes are covered by the nest.



Figure 26. Juvenile individuals of *Phoradendron anceps*.

APPENDIX I

Appendix. Shapiro-Wilks test for normality of the *Pisonia albida* tree traits.

| <i>n</i> = 133 | | | | | |
|-----------------|--------|--------|--------|----------------------|-----|
| Tree trait | Mean | SD | W* | <i>P</i> (2 -tailed) | |
| Basal area | 488.94 | 507.45 | 3162.0 | <0.0001 | *** |
| Canopy diameter | 4.49 | 2.13 | 3492.0 | <0.0001 | *** |
| Canopy height | 2.44 | 0.92 | 3186.0 | 0.0048 | ** |
| Height | 3.27 | 0.98 | 3094.5 | 0.4449 | |

** = $P \leq 0.01$, *** = $P < 0.001$

APPENDIX II

Appendix. Simple regression testing for effects of host (*Pisonia albida*) density per quadrat (100 m²) on number of mistletoe ($r^2 = 0.0014$, $F = 0.04$, $P > 0.05$, $n=31$, for number of quadrats with infected trees).

