

HOW THE SAPLING SPECIALIST SHOOT-BORER, *CROMARCHA*  
*STROUDAGNESIA* (LEPIDOPTERA, PYRALIDAE, CHRYSAUGINAE), ALTERS  
THE POPULATION DYNAMICS OF THE COSTA RICAN DRY FOREST TREE  
*TABEBUIA OCHRACEA* (BIGNONIACEAE)

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I dedicate this work to my parents, Peter and Diane Sullivan. Their encouragement of my curiosity, together with their unwavering conviction that I should be whatever I wanted to be, make this dissertation as much their work as mine.

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so we could position *and activate* it up to 7 m above the forest floor while it sat perfectly horizontal, facing due north. The solution that Alex and I developed was built with the head of an old broom, a piece of wood, a plastic level bought from the local hardware store, two strips of bungee, a piece of insect-mounting rubber, two bicycle spokes, two bicycle patches, the spring from a ballpoint pen, the cap of a syringe, and a ten meter long piece of nylon string. This invention worked flawlessly throughout the study.

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## ABSTRACT

HOW THE SAPLING SPECIALIST SHOOT-BORER, *CROMARCHA*  
*STROUDAGNESIA* (LEPIDOPTERA, PYRALIDAE, CHRYSAUGINAE), ALTERS  
THE POPULATION DYNAMICS OF THE COSTA RICAN TROPICAL DRY  
FOREST TREE *TABEBUIA OCHRACEA* (BIGNONIACEAE)

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Daniel H. Janzen

This dissertation details how herbivory by the shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae), alters the growth and population dynamics of its host tree *Tabebuia ochracea* (Bignoniaceae) in the tropical dry forests of the Area de Conservación Guanacaste, Costa Rica. Insect herbivory of tree saplings can affect tree population dynamics by increasing sapling prereproductive mortality and increasing the age of first reproduction (by decreasing the rate of sapling height increment). Herbivory of *T. ochracea* saplings by the larvae of *C. stroudagnesia* has large direct and indirect effects on both these variables. Just a single *C. stroudagnesia* larva attacking the top shoot of a canopy gap sapling reduces sapling annual height increment on average by 77.9% - equivalent to the difference in annual height increment between saplings in canopy gaps and understory shade. Each year, an average 40.1% of canopy

gap saplings had their top shoot attacked by a *C. stroudagnesia* larva. Assuming a sapling remains at the top of canopy gap vegetation, this will result in a 45.1% increase in the duration of the pre-reproductive sapling lifestage (0.5 m to 10 m high) relative to undamaged plants. *C. stroudagnesia* herbivory increases the probability that canopy gap saplings are overtopped and shaded by surrounding vegetation, and so will further, indirectly increase the age of first reproduction. Sapling mortality was directly increased by *C. stroudagnesia* herbivory — 10% of heavily damaged young saplings (initially 0.7 - 1.5 m high) died in four years while no protected saplings died. *C. stroudagnesia* herbivory will also indirectly increase sapling mortality by increasing the likelihood that a sapling is killed by falling debris before it reaches reproductive age. *Cromarcha stroudagnesia* shoot herbivory is greatest in areas of high sapling density, and so is predicted to cause a Janzen-Connell effect. Together, these results suggest that sapling herbivory, especially herbivory of the highest apical meristems of saplings, plays an important, but largely unexplored, role in the population dynamics of tropical tree species.

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## PREFACE

This dissertation is built in four chapters. The first two chapters focus respectively on the ecology of the tree, *Tabebuia ochracea* (Bignoniaceae), and of one of its specialist herbivores, *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae). The last two chapters then explore the interaction between these two species, and its implications for the population dynamics of *T. ochracea* and the coexistence of other tree species with *T. ochracea*.

**Chapter One** details the patterns of growth and survival of juvenile *T. ochracea* trees in the dry forests of Sector Santa Rosa, of the Area de Conservación Guanacaste. Such detailed demographic studies of tropical tree species, especially tropical dry forest tree species, are rare. This chapter sets the ecological scene for an exploration of how the herbivore *C. stroudagnesia* may alter the dynamics of *T. ochracea* saplings. **Chapter Two** details the natural history of *C. stroudagnesia*, with an emphasis on larval ecology. This is the most detailed study to date of a tropical tree shoot-borer species in a wild forest, and reveals numerous parallels with well-studied shoot-borers of tropical timber plantations.

**Chapter three** brings these two species together to focus on how *C. stroudagnesia* shoot herbivory reduces the rate of height increment and increases mortality of *T. ochracea* saplings. The effects are surprisingly large, showing that *C.*

*stroudagnesia* herbivory is at least as important as the variation in the amount of light for determining the rates of height increment and survival of *T. ochracea* saplings. **Chapter Four** looks at how *C. stroudagnesia* shoot herbivory varies with *T. ochracea* sapling density. *Cromarcha stroudagnesia* shoot herbivory is found to be much more common in areas of high than low *T. ochracea* sapling density. Because of this, it is possible that *C. stroudagnesia* shoot herbivory will cause the density-dependent regulation of *T. ochracea* population densities in the Santa Rosa dry forests. By implication, sapling herbivory may play a much more important role in tropical tree species coexistence than has been previously suspected.

Together, these chapters constitute one of the most detailed explorations yet published of how insect herbivory of tropical forest tree saplings may alter tree population dynamics. The large effects of *C. stroudagnesia* on *T. ochracea* growth and survival that are described, together with the fact that *C. stroudagnesia* is only one of at least 36 insect species that feed on the aboveground parts of *T. ochracea* saplings, suggests that insect herbivory is a major factor shaping the dynamics of tropical tree populations.

This dissertation uses of the name *Cromarcha stroudagnesia* throughout to refer to the tabebuia shoot-borer. While this dissertation will most likely constitute the first printed use of this name, in no circumstance should this work be interpreted as "published" within the meaning of the International Code of Zoological Nomenclature.



Readers should instead consult the full description of the species *Cromarcha stroudagnesia* currently in preparation by Alma Solis, myself, and Daniel H. Janzen.

**CHAPTER ONE: Seedling and sapling dynamics of the tree *Tabebuia ochracea*  
(Bignoniaceae) in the understory of a Costa Rican dry forest**

*Abstract*

The rates and patterns of growth and survival are described for seedlings and saplings of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae) in tropical dry forests of the Area de Conservación Guanacaste, northwestern Costa Rica. This is one of the first detailed descriptions of the juvenile dynamics of a tropical dry forest tree species. Sapling height increments were highly variable, and much greater in single treefall canopy gaps than understory shade. It is estimated that most, if not all, juvenile *T. ochracea* will require a period of growth in one or more canopy gaps to reach reproductive maturity. Seedlings and saplings of *T. ochracea* were more abundant on mesa habitats than in adjacent valley habitats, and most abundant at intermediate distances (15 - 40 m) from adult *T. ochracea* trees. Almost no saplings > 2 m high occurred within a 10 m radius of conspecific trees. Seedling survival and sapling height increments also significantly increased with distance away from adult *T. ochracea* trees. Both the habitat specialization and increased juvenile mortality near parent trees may promote the local coexistence of other tree species with *T. ochracea*. Using the annual growth rings of *T. ochracea*, one 10.5 m high sapling was found to be 60 years old, with past annual height increments unrelated to height. Unlike tropical wet forest tree species,

annual growth rings are present in many tropical dry forest tree species, and further studies of tropical dry forest trees can greatly improve understanding of juvenile tropical tree dynamics and tropical tree demography.

## **Introduction**

The bulk of our current understanding of the structure and dynamics of the juvenile portion of tropical tree populations comes from studies in tropical wet forests (e.g., Augspurger 1984, Clark and Clark 1985, Lieberman et al. 1985, Schupp 1990, Clark and Clark 1991, Welden et al. 1991, Clark and Clark 1994, Condit et al. 1995, Lieberman 1996, Hubbell et al. 1999, Pitman et al. 1999). Much less attention has been paid to the population dynamics of juvenile trees of tropical dry forests, a once widespread tropical forest habitat now largely destroyed or heavily disturbed (Janzen 1988, Gillespie et al. 2000).

Unlike wet forest trees (Clark 1994), many dry forest trees can be reliably aged with standard dendrochronological techniques because the long and defined dry seasons cause trees of many species to form annual growth rings (e.g., Belingard et al. 1996, Bullock 1997, Worbes 1999, Enquist and Leffler 2000). Tropical dry forests therefore have the potential to provide an understanding of juvenile tropical tree dynamics at a much greater resolution than tropical wet forests.

Knowledge of the seedling and sapling dynamics of tropical trees is necessary not

just to understand the population dynamics of tropical trees, but also to understand tree species coexistence in tropical forests. There is currently an unresolved debate over the relative importance of niche-assembly processes (e.g., Janzen-Connell effects, regeneration niche differences) and dispersal-assembly processes (i.e., seedling recruitment limitation in non-equilibrium states) for explaining the coexistence of hundreds of tropical tree species (e.g., Terborgh et al. 1996, Hubbell 1998, Clark et al. 1999, Hubbell et al. 1999, Tilman 1999). To assess the strength and extent of niche-assembly processes in tropical tree communities, a thorough understanding of the processes influencing the rates and spatial distribution of seedling and sapling growth and mortality is needed for many tropical tree species.

This paper documents the juvenile dynamics of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae), in old growth and secondary successional tropical dry forests of the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica. The ACG is the largest remaining conserved area of tropical dry forest in Central America, a habitat that once covered the Pacific coastal lowlands and parts of the Atlantic coastal lowlands throughout Central America (Janzen 1988, Gillespie et al. 2000). *Tabebuia ochracea* (Bignoniaceae) is a well known species that is locally common at many tropical dry forest sites throughout Central and South America (Gentry 1983, Gentry 1992).

Several spatial and temporal scales were combined in this study, from tree ring counts and two population censuses of a 16.3 ha forest plot made 20 years apart, to

repeated observations over several years of seedling and sapling growth and survival. Few studies of tropical trees have spanned all of these scales for any one species (De Steven 1994). Rates of seedling and sapling survival and height increment were observed in different light, soil moisture, and topographical microhabitats and at different distances from adult *T. ochracea* trees. These data were used to assess the potential for habitat specialization and Janzen-Connell effects to increase the ability of other tree species to coexist with *T. ochracea* in the ACG dry forests.

## **Methods**

### *Study site.*

Sector Santa Rosa (formerly Parque Nacional Santa Rosa) is the historical core of the Area de Conservación Guanacaste (ACG), a 110,000 ha conserved wildland in northwestern Costa Rica (<http://www.acguanacaste.ac.cr>). Santa Rosa includes a few small fragments of old growth dry forest and large expanses of secondary successional tropical dry forest between 0 - 400 years old, regenerating on abandoned cattle pastures, agricultural fields, and logged areas (see Janzen 1986a, 1988, 1992). Within the ACG, sector Santa Rosa is bordered by conserved marine habitats in the Pacific Ocean to the west and sectors of progressively wetter conserved forests to the east, including cloud forest and Atlantic rain forest.

Annual rainfall at the Santa Rosa Biological Station during the four years of the

study (1995 - 1999) was 2081 mm (s.d. = 612), which included the wettest and fifth driest years since 1980. The local climate is highly seasonal, dominated by a pronounced 6-month dry season from December to mid May when essentially no rain falls. During much of the dry season, most individual trees of most species in all but the oldest fragments of forest are nearly leafless (including *T. ochracea*). This contrasts with the completely foliated forests throughout the 6-month wet season (see Janzen 1993).

All observations were made in the forests immediately surrounding the Santa Rosa Biological Station (300 m, 10° 50' 27.26'' N latitude , 85° 37' 14.26'' W longitude, Fig. 1). Study plants were located within the Bosque San Emilio forest plot, a 16.3 ha plot in 80 - 100 year old secondary successional forest (Stevens 1987, Enquist et al. 1999), and within the Bosque Humedo forest plot, a 4.8 ha plot within a fragment of old growth forest (Janzen 1986b). Plants were also studied in Cerco de Piedra, an area of approximately 20-40 year old secondary successional forest, and in areas neighboring the Bosque San Emilio plot.

### *Study species*

*Tabebuia ochracea* (Chamisso) Standley (Bignoniaceae) is a neotropical dry forest tree up to 30 m high and > 0.5 m dbh with palmate five-foliate tomentose leaves (see Gentry 1983, Gentry 1992, Sullivan et al. 1998 for full description). The Central American subspecies of *T. ochracea*, *T. o. neochrysantha* (A. Gentry) A. Gentry, was

previously known as *T. neochrysantha* A. Gentry. *Tabebuia ochracea* ranges from El Salvador to southern Brazil and northern Argentina, occurring in tropical dry forests from 0 - 1000 m elevation (Gentry 1992).

*Tabebuia ochracea* has been the subject of several previous ecological, physiological, and chemical studies (Daubenmire 1972, Reich and Borchert 1982, Gibbs and Bianchi 1993, Borchert 1994, Ribeiro et al. 1994, Perez et al. 1997). *Tabebuia ochracea* has also been the subject of occasional forestry research (e.g., César Moya et al. 1992, Vasquez 1994, Molina Artavia et al. 1996), as it has one of the hardest, heaviest, most durable woods of the neotropical tree flora (Gentry 1980). However, despite *T. ochracea* being described as having “una de las maderas más finas de Costa Rica” (Nichols and González 1991, p. 21), its slow growth and poor form in plantation situations have prevented the species from becoming an important plantation timber crop (Nichols and González 1991).

*T. ochracea* is famous throughout tropical America for its brief, spectacular, population-wide synchronized displays of large yellow flowers in the dry season. This highly synchronous dry season flowering in *T. ochracea* can be triggered by brief unseasonal rains or unseasonably cool air temperatures (Reich and Borchert 1982, Sullivan et al. 1998). In the early wet season, fruit pods up to 40 cm long each release hundreds of winged, up to 25 mm wide, wind-dispersed seeds. *Tabebuia ochracea* has no seed bank; at least in Santa Rosa, all viable seeds germinate in the first months of the wet

season (J. J. Sullivan, unpublished data). Flowering intensity and seed output vary dramatically between years in Santa Rosa, with *T. ochracea* seedlings carpeting the forest floor in the early wet season of some years and scarce in other years (personal observation).

For the purposes of this study, saplings were defined as any *T. ochracea* juveniles 50 cm high (*sensu* De Steven 1994). This division marked the point where aboveground height increments substantially increased for some juveniles, and where aboveground height became greater than root depth (see Results).

#### *Study saplings and environmental measurements*

This study reports on the growth and survival of 131 wild *T. ochracea* seedlings, initially more than one-year old, and 342 wild *T. ochracea* saplings, initially between 0.5 m and 7 m high. Various plant growth variables were recorded for each plant between 1995/1996 and 1999, and soil moisture and canopy light were recorded for each plant in 1999. Shoot herbivory by the shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae)(Sullivan 2000a) was also recorded for these plants throughout the study. The distribution and impact of this herbivory on *T. ochracea* sapling growth and mortality is presented in Sullivan (2000b) and Sullivan (2000c).

For 116 of the study plants, height, stem diameter, and the length of each shoot were recorded twice annually throughout the study. Each shoot of each study plant was



labeled with a unique combination of four colored beads, which were attached to the shoot with a large loop of thin copper wire. New shoots from natural branching or regrowth following meristem destruction received new unique labels. Each census, the shoot length, number of mature leaf nodes, and status (natural branching, herbivory, damage from falling debris, unexplained death) were recorded per shoot. Sapling height was recorded with a weighted measuring tape attached to a 7 m long telescoping pole, and stem diameter was recorded at 30 cm above the soil surface across the thickest horizontal axis with vernier calipers.

These 116 plants included the 15 *T. ochracea* seedlings >1-year old and 66 *T. ochracea* saplings that were found in two searches of the 4.8 ha Bosque Humedo forest plot in 1995 and early 1996. A third, more thorough mapping of the locations of juvenile *T. ochracea* in the Bosque Humedo plot was made in 1999, and showed that the study plants represent 57% of the >1-year old seedlings and 48.1% of the saplings 7 m high in Bosque Humedo. The Bosque Humedo forest plot includes a series of mesas and eroded valleys, and the site of each study seedling and sapling was classified as “valley”, “slope”, or “mesa”. “Slope” included only substantial inclines (greater than about 15 degrees) connecting mesas and valleys.

The remainder of the 116 study plants were located in the Bosque San Emilio forest plot. Selected were all 13 saplings located inside and within an approximately 80 m radius of a 1995 canopy gap caused by a single large tree fall. A haphazard selection of 9

saplings was made within a 50 m radius of an adult *T. ochracea* tree that snapped in half in a wind storm in the 1996 dry season (this site allowed for a comparison of shoot herbivory by the shoot-borer *C. stroudagnesia* in a tree canopy and the understory — see Sullivan 2000a). A further 12 saplings were selected near the entrance to the Bosque San Emilio plot (these plants were revisited every 1-5 days throughout the first four months of the 1997 wet season to document the annual phenology of sapling shoot growth — see Sullivan 2000a).

For an additional 94 study saplings, only the height and stem diameter were recorded twice annually throughout the study. Half of these saplings were located inside tree fall canopy gaps within the Bosque San Emilio forest plot. All canopy gap saplings were purposefully selected as initially of equal or greater height than the surrounding gap vegetation. Each gap sapling was paired with a similarly sized sapling ( $\pm 1.5$  m high) in understory shade more than about 15 m from the edge of the gap. Initial sapling heights ranged from 0.52 m to 6.63 m. Measurements were begun on these saplings in November 1996 or July 1997, and continued until July 1999.

For a further 147 saplings and 41 seedlings initially >1 year old, the height and stem diameter were measured only at the beginning (1995) and the end (1999) of the study. These included all surviving juvenile *T. ochracea* along 60 m long and 10 m wide transects away from two adult *T. ochracea* trees in Cerco de Piedra ( $n = 111$ ) and five adult *T. ochracea* trees in Bosque San Emilio ( $n = 57$ ). Also included were all saplings

inside and near to a single recent tree fall canopy gap in Bosque San Emilio ( $n = 16$ ).

Canopy light was estimated for each study plant in 1998 and 1999. A digital canopy photo was taken from the top of each study sapling using a Sony Mavica digital camera with a wide-angle lens attachment, attached to a telescoping pole. Photographs were taken in mid-wet season in 1998 and 1999. The percentage of the canopy area that was sky was calculated from these images using the Histogram feature of Adobe Photoshop 4.01. Setting the color selection to pure white and the fuzziness to 200 was sufficient to encompass the variation between white cloud and blue sky without selecting foliage.

Soil moisture was estimated for each plant in the middle of the veranillo of the 1999 wet season, with a Rapidtest Mini Moisture Tester (Luster Leaf Products, Inc., Woodstock, IL, USA). All readings were taken at 10 cm depth, approximately 1 m from the base of each plant. Readings were made on 7 August after four days without any rain. Any differences in recorded soil moisture among the study saplings should therefore represent true variation in soil water retention rather than any recent local spatial variation in rainfall. All readings were calibrated to percentage soil moisture using Rapidtest measurements and wet and dry weights from soil sampled from each site and dehydrated at 68 degrees Celsius in a drying oven until stable weight.

In August 1999, 37 *T. ochracea* seedlings and small saplings were excavated to calculate how the ratios of belowground:aboveground biomass and depth:height change

with plant size. Between five and eight plants were carefully excavated in each of six height categories: 1999 new seedlings (<1 year old), old seedlings <10 cm high, seedlings 10 - <30 cm high, seedlings 30 - <50 cm high, saplings 50 - <70 cm high, and saplings 70 - <90 cm high. All plants occurred within a 30 m radius of a single old adult *T. ochracea* tree growing in an area of approximately 25 year old secondary successional forest near the Santa Rosa Biological Station. Height and root depth were recorded for each plant. Wet weights were recorded for above and belowground tissues separately using a Denver Instrument TR-603D scale. All plants were then dried in a drying oven (68 degrees Celsius) for 3.5 days, before being reweighed.

To assess the minimum height of first reproduction of *T. ochracea* forest saplings, all flowering *T. ochracea* trees in the Bosque San Emilio forest plot were visited during the local *T. ochracea* flowering event of 1 May 1997. Tree heights were estimated, and the exact heights of the smallest five flowering saplings were later recorded with a weighted measuring tape attached to a telescoping measuring pole. A large sapling in the Bosque Humedo forest plot was observed flowering during the same flowering event, and its exact height was also later recorded.

### *Dendrochronology*

One 10.5 m high *T. ochracea* sapling was found recently dead in 1999 under the trunk of a large tree fall. This sapling was sectioned at 50 cm high, 1 m high, and

subsequent 1 m height intervals for growth ring analysis. All sections were polished with two grades of sandpaper and the rings counted under a dissecting microscope while the wood was wet. Smaller sections were set in BioPlastic, sectioned with a microtome, and mounted on slides (see LePage and Basinger 1995 for methodology). Rings were counted under a compound microscope. In all cases, two perpendicular transects were ran out from the center of each section at a random angle, and the width of each ring was measured using a graduated ocular lens (method follows Lieffers et al. 1996).

#### *Bosque San Emilio long-term vegetation plot data*

Also presented is information on the density, distribution, and mortality of *T. ochracea* in the Bosque San Emilio long-term forest plot (Enquist et al. 1999). In 1976 and 1995-1996, the locations of all saplings and trees of *T. ochracea*  $\geq 3$  cm dbh were mapped throughout the 16.3 ha forest plot, which is laid out on a grid of 20 m by 20 m squares. The dbh of each *T. ochracea* was also recorded. These results were not collected by the author, but rather are previously unpublished data from B. J. Enquist, C. A. Enquist, and G. C. Stevens. They are presented here, with gracious permission of the authors, to add a larger spatial and temporal scale to the understory population dynamics of *T. ochracea* in Bosque San Emilio.

## *Analysis*

All analyses were performed using SPSS for Macintosh version 6.1.1 (<http://www.spss.com>). Growth variables used in multiple regression analyses were log transformed when an exponential curve better fitted the data than a line.

## **Results**

### *Densities and spatial distribution of seedlings and saplings*

Adult and juvenile densities of *Tabebuia ochracea* were lower in the old growth forest (Bosque Humedo) than in younger, secondary successional forests (Bosque San Emilio and Cerco de Piedra)(Fig. 2). *Tabebuia ochracea* saplings and trees of reproductive height (  $> 10$  m height and  $> 16$  cm dbh, see below) occurred at an average density of 0.96 per hectare in Bosque Humedo, and 3.2 per hectare in Bosque San Emilio (B. J. Enquist, C. A. Enquist and G. C. Stevens, unpublished data). Similarly, non-reproductive saplings  $< 3$  m high occurred at an average density of 3.2 per hectare in Bosque Humedo, while such saplings  $< 3$  cm dbh (equivalent to saplings approximately  $> 3$  m high) occurred at 27.2 per hectare through Bosque San Emilio (B. J. Enquist, C. A. Enquist and G. C. Stevens, unpublished data). The highest densities of *T. ochracea* saplings occurred in Cerco de Piedra (Fig. 2).

Between 1976 and 1996, the density of all *T. ochracea*  $< 3$  cm dbh in the Bosque San Emilio plot rose from 18.7 per hectare in 1976 to 30.4 per hectare in 1996 (B. J.

Enquist, C. A. Enquist and G. C. Stevens, unpublished data).

Densities of *T. ochracea* seedlings, saplings, and adults in Bosque Humedo were disproportionately high on elevated mesas and slopes relative to valley bottoms (but still lower than the average densities of seedlings and saplings in Bosque San Emilio)(Table 1). This pattern persisted in the seedling and sapling shadows around two *T. ochracea* trees growing within 10 m of a mesa border (personal observation). Densities of adults and saplings  $\geq 3$  cm dbh in the Bosque San Emilio forest plot were also disproportionately high on mesas and slopes relative to valleys (B. J. Enquist, C. A. Enquist and G. C. Stevens, unpublished data).

Bosque Humedo soils were significantly drier around seedlings and saplings on mesas than in valleys (one-way ANOVA,  $P < 0.01$ , treatment SS = 14.50, error SS = 118.41,  $F = 5.44$ , total df = 80, planned comparisons: mesa versus slope and valley  $P < 0.01$ , slope versus valley n.s.). There were no significant differences among the three habitat types in the percentage of the canopy above Bosque Humedo seedlings and saplings that was sky.

Across the forest plots, seedling and sapling distributions were strongly clumped around adult trees (Fig. 2), as is expected for a wind-dispersed tree. However, very few saplings  $> 2$  m high occurred within 10 m of an adult *T. ochracea* tree (Fig. 2, Fig. 3). In all three forest sites, the densities of saplings  $> 2$  m high were highest between more than 10 m and less than 40 m away from adult trees (Fig. 2). This is despite strongly leptokurtic

seed shadows around *T. ochracea* trees (Fig. 4), and the highest seedling densities generally occurring within 10 m of adult trees (Fig. 2).

In only one of the 17 transects used to produced the above results was a sapling >3 m high found within 10 m of a neighboring tree (the outlier point of Fig. 3). This was a 9.8 m high, 10.6 cm dbh sapling growing 4.8 m from one of the Bosque San Emilio trees. Several other *T. ochracea* plants growing close to *T. ochracea* adults in this area of Bosque San Emilio were found to be root suckers growing from large surface roots of the adult trees. While a cursory evacuation did not reveal a belowground connection between the 9.8 m high sapling and the neighboring tree, the possibility of such a connection (past or present) cannot be discounted.

All of the trees used to produce the transect data that is summarized in Fig. 2 and Fig. 3 were > 20 cm dbh and all were observed to flower and seed during the four years of the study. All those transect trees within the Bosque San Emilio forest plot were also present in 1976 (B. J. Enquist, C. A. Enquist and G. C. Stevens, unpublished data), and 75% of these were already of reproductive size (>16 cm dbh, see below) in that year.

#### *Seedling and sapling height increments*

Average annual height increments over the four year study ranged between -5.7 cm and 18 cm for seedlings more than one year old ( $2.1 \pm 0.5$  cm, average  $\pm$  s.e.,  $n = 56$ ), and between -22.7 cm and 51.7 cm for saplings initially < 7 m high ( $7.8 \pm 0.6$  cm,  $n =$



336)(Fig. 5). Seedlings and saplings with greater initial heights had significantly greater height increments, although initial height explained only 2.7% of the variation in height increment (Table 2). For saplings greater than 1.5 m high, there was no longer a significant relationship between initial height and height increment, even when the saplings with negative height increments were removed (linear regression,  $P=0.082$ ,  $R^2 = 0.016$ ).

Substantial variation existed in the average height increment of seedlings and saplings irrespective of initial plant height (Fig. 5). Significant amounts of this variation are explained by the variation in canopy light, soil moisture, and distance to the nearest conspecific adult tree (Table 2). Seedling and sapling growth significantly increased with increasing canopy light, soil moisture, and distance away from adult conspecifics (Fig. 6). Despite these significant effects, 87.2% of the variation in *T. ochracea* seedling and sapling growth could not be explained (Table 2).

Canopy gap soils were not significantly drier than understory shade soils in the veranillo, and sites beneath conspecific trees were no more or less moist or insulated than more distant sites (all partial correlation coefficients,  $P>0.05$ ,  $N=394$ , controlling for initial height).

Saplings grew substantially more in canopy gaps than in understory shade. For the saplings that were paired in single treefall canopy gaps and neighboring understory shade, gap saplings had an average annual height increment of 18.1 cm (s.e. = 2.0 cm) while shade saplings had an average annual height increment of only 4.2 cm (s.e. = 0.9 cm)

(paired t-test,  $t = -6.86$ ,  $P < 0.001$ ,  $n = 92$ , note that one shaded sapling died (see below) so this pair was removed from the analysis). There was no significant difference in initial height between the gap and shade plants (paired t-test,  $P = 0.53$ ). The canopy gap saplings had an average 21.0% of their canopy as sky (s.e. = 1.5%), while the understory shade saplings had an average 13.2% of their canopy as sky (s.e. = 0.9%)(c.f., Fig. 6). As was found in the analysis of all saplings, soils in canopy gaps were not significantly drier than understory soils (at least at the 10 cm depth measured) (paired t-test,  $P = 0.70$ ).

#### *Root:shoot ratios during seedling establishment and growth*

The growth over the four years of the study of small seedlings initially more than one year old was consistently low. The average annual height increment of seedlings greater than one year old and initially less than 30 cm high was only 1.8 cm, with little variation among plants (s.e. = 0.36 cm,  $n = 45$ , max = 7.8 cm). In contrast, the average annual height increment of saplings initially 70 - 90 cm high was both higher and substantially more variable (average = 4.9 cm, s.e. = 9.0 cm,  $n = 35$ , max = 28.8 cm).

These consistently small height increments aboveground for small seedlings more than one year old correspond to relatively large root depth increments belowground. Small seedlings more than one year old had much larger root:shoot ratios than small saplings by both depth:height (Fig. 7a) and biomass (Fig. 7b). Small seedlings were much deeper than they were tall, while saplings between 0.7 m and 0.9 m high were taller than they were

deep (Fig. 7a).

#### *Falling debris and seedling and sapling mortality*

Sixty nine seedlings initially more than one year old (52.7%) and six saplings (1.75%) died over the four years of the study. In most cases, the cause of death was unknown, especially among the seedlings. Three of the six saplings were killed by falling debris, and one died following a year of heavy attack by larvae of the shoot-borer *Cromarcha stroudagnesia* (Sullivan 2000b). All saplings that died were less than 2.5 m high. Small non-study saplings were also observed to die after repeated defoliation by the *Pseudomyrmex* ants of neighboring *Acacia collinsii* trees (Janzen 1967).

The three study saplings killed by falling debris equates to 0.22% of saplings per year. This is likely to be an underestimate, as saplings badly damaged by falling debris often took several years to die. The estimate is consistent with the results of Clark and Clark (1991) in the eastern Costa Rican rain forests of La Selva Biological Station, who estimated the total annual mortality due to falling debris for saplings >1 - 30 cm dbh to be 0.36%.

Survival of seedlings initially more than one year old significantly increased with distance from adult *T. ochracea* trees (Fig. 8)(one-way ANOVA,  $P < 0.01$ , treatment SS = 864.91, error SS = 92.66,  $F = 9.33$ , total df = 130, with initial height included as a (non-significant) covariate). Seedlings more than 25 m from the nearest adult *T. ochracea* tree

were more than twice as likely to survive through the four years of the study than seedlings less than 5 m from adult *T. ochracea* trees (Fig. 8). Too few saplings died to attempt a similar analysis with saplings.

Twenty saplings (5.8%) and four seedlings (4.0%) suffered impacts by falling debris that reduced their height by more than 10%. The average height reduction of the surviving saplings immediately following impact was 41.9%. Most saplings responded with regrowth from dormant lateral buds, with only three of the saplings dying during the study.

#### *The minimum height of first reproduction*

The minimum height of first reproduction for saplings in forest was about 10 m. The seven shortest flowering saplings found in Bosque San Emilio and Bosque Humedo ranged from 9.0 m to 12.9 m high (average 10.6 m) and from 15.8 cm to 25.9 cm dbh (average 18.3 cm). None of the study saplings initially > 7 m high ever produced flower buds over the four years of this study.

A very different situation occurs with *T. ochracea* saplings in Santa Rosa growing in old pastures. These saplings are of a much less erect stature than forest saplings, and can flower when much shorter than forest saplings (as low as 3 m, personal observation).

### *Sapling ages and growth trajectories*

One 10.5 m high sapling was found dead in Bosque San Emilio, very recently killed by a fallen tree. It was likely to have flowered in the following year, as flower buds terminated many of its higher shoots. It was sectioned every meter of its height to count tree rings, and the basal section had 60 growth rings. This is likely to correspond to 60 years of age, as the average annual height increment calculated for each meter of this sapling's height falls well within the range of annual height increments observed (Fig. 9).

The annual height increment of this one large sapling did not increase with age (Fig. 9), and through most of its life was consistent with the height increments observed in canopy gaps.

### *Rainfall and annual variation in sapling growth*

A common method used to confirm that tree growth rings are annual is to correlate ring widths with rainfall in a given or previous year (e.g., Worbes 1999, Enquist and Leffler 2000). No significant relationships were found between the ring widths of the 10.5 m sapling from Bosque San Emilio and any combination of rainfall variables using stepwise multiple regressions (all  $P > 0.05$ ). The rainfall variables used were total rainfall in the current and previous year, rainfall in the wet season and dry season of both the current and previous year, and rainfall in each month of the current and previous year.

While a strong relationship between growth rings and rainfall is good evidence that

the rings are annual, the lack of a relationship does not imply that the growth rings are not annual. For example, soil moisture plays a minor role in the variation in rates of height increment of understory *T. ochracea* saplings (Table 2). No significant correlations were found between any of the above rainfall variables and the variation in annual height increments or total annual shoot growth of the study seedlings and saplings over the four years of this study. Stepwise multiple regressions were performed with each of the above sets of rainfall variables, as well as initial sapling height, canopy light, soil moisture, and distance to the nearest conspecific (all  $P > 0.05$ ).

## Discussion

Both habitat specialization and distance-dependent Janzen-Connell effects were found for *T. ochracea* in the tropical dry forests of the ACG, both of which could help explain coexistence of other tree species with *T. ochracea* in the Santa Rosa forests. Saplings of *Tabebuia ochracea* were found to be disproportionately abundant on mesa and slope habitats than adjacent valley habitats, and most abundant at intermediate distances (15 - 40 m) from adult *T. ochracea* trees. Seedling survival and sapling growth were found to increase with distance away from adult *T. ochracea* trees.

One mechanism suggested to play an important role in increasing tropical tree coexistence is habitat specialization causing resource partitioning (e.g., Ricklefs 1977, Pacala 1997), where the rates of survival and height increment of juveniles of different tree

species are greatest at different points along environmental gradients. Most past studies testing this idea have attempted, largely unsuccessfully, to identify such habitat specialization by juvenile tropical trees species along gradients of understory light (Hubbell and Foster 1986, Welden et al. 1991, Denslow and Hartshorn 1994, Hubbell et al. 1999, Brokaw and Busing 2000). Studies looking within wet forests for specialization along edaphic and topographic gradients have been fewer, but more successful (e.g., Newbery and Proctor 1984, Basnet 1992, Tuomisto and Ruokolainen 1994). For example, Clark et al (1998, 1999) recently showed that at least 30% of the tree species in wet forests of the La Selva Biological Station, Costa Rica, have disproportionately high abundances on one of five identified local soil types.

The results with *T. ochracea* in Santa Rosa shows that this type of habitat specialization is not restricted to tropical wet forest trees. The true generality of differential survival of juvenile tropical trees along soil and topography gradients, and the mechanisms underlying such patterns, remain largely unknown (Clark et al. 1999). They have the potential to greatly influence the ability of forests (and especially isolated forest fragments) to maintain high tree species richness.

Why *T. ochracea* densities are higher on mesas than in valleys within the Bosque Humedo and Bosque San Emilio forest plots is unclear. The difference is more than a result of differential dispersal, as the pattern persisted around adult trees growing on mesa borders. Mesa habitats were significantly drier than valley habitats, and yet *T. ochracea*

seedling and sapling height increments were significantly greater in moister areas. The difference in relative abundances of juvenile *T. ochracea* between mesas and valleys becomes more pronounced in larger height classes (Table 1), suggesting that not only do more seedlings establish on mesa sites but also that mortality of saplings is greater in valleys than on mesas. While the canopies above valley saplings were not found to be significantly darker than above mesa saplings, the valley understory in general (i.e., not just where the few *T. ochracea* study saplings were found) is noticeably darker than mesa areas, having substantially less lateral light and remaining leafed out for longer into the dry season (personal observation). It may be that *T. ochracea* seedlings and saplings are less able to tolerate the generally darker valley understory than the more insulated mesa understory.

Another striking pattern in the distribution of *T. ochracea* seedlings and saplings is the near absence of large *T. ochracea* saplings (> 2 m) within 10 m of adult *T. ochracea* trees, despite the heaviest seed rain and highest seedling densities occurring within this distance (Fig. 2-3). Increased mortality of juvenile trees near conspecific adults has long been recognized as an important density-dependent factor potentially limiting tree populations and enhancing tree species coexistence (e.g., Janzen 1970, Connell 1971, Clark and Clark 1984, Barone 1996, Pacala and Crawley 1992, Packer and Clay 2000). The near absence of large *T. ochracea* saplings within a 10 m radius of adults should dramatically increase the likelihood that a tree of a species other than *T. ochracea* sapling



will replace a fallen *T. ochracea* adult tree in the canopy.

The mechanism driving the increased seedling mortality and decreased sapling growth observed within 10 m of adult conspecific trees is unknown. Aboveground herbivory of *T. ochracea* seedlings (largely by generalist insects) was infrequent and only weakly correlated with distance from parent trees (J. J. Sullivan, unpublished data). It is more likely that one or more *T. ochracea* specialist fungal or microbial pathogens or parasites associated with the rhizospheres of adult trees are weakening nearby seedlings and increasing seedling mortality. Such an effect has been previously found for both tropical (Augspurger 1983) and temperate tree species (Packer and Clay 2000), and is conspicuous near adults of the dry forest tree *Enterolobium cyclocarpum* (Fabaceae, Mimosoideae) in sector Santa Rosa (D. H. Janzen, personal communication).

Annual height increments of *T. ochracea* seedlings and saplings were enormously variable, even after accounting for the significant effects of soil moisture, canopy light, and distance from parent trees on height increments (Fig. 2, Table 2). While it is likely that much of this variation could be accounted for by more accurate and sapling-relevant measurements of soil moisture and canopy light, it is also clear that other factors must be involved.

One such factor is shoot herbivory by the shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae) (Solis et al. 2000, Sullivan 2000a). Herbivory of just the top shoot of *T. ochracea* saplings reduces annual height increments on average by 31 cm, a

greater magnitude than the average difference in height increments between canopy gap and understory shade saplings (Sullivan 2000b). Top shoot herbivory by *C. stroudagnesia* occurs frequently (once every 2.5 years for canopy gap saplings in Bosque San Emilio), and increases with local sapling density (Sullivan 2000b,c). This herbivore is predicted to produce a density-dependent Janzen-Connell effect in the Santa Rosa population of *T. ochracea*, and further enhance the ability of other tree species to coexist with *T. ochracea* in Santa Rosa forests (Sullivan 2000c).

A less spatially predictable variable that strongly influences *T. ochracea* understory population dynamics is canopy gaps. The sapling height increment and tree ring data show that canopy gaps will be necessary for most, if not all, *T. ochracea* saplings to reach reproductive maturity (Fig. 6b, Fig. 9). For example, the observed height increments of canopy gap and understory shade *T. ochracea* saplings can be linearly extrapolated across the understory lifetime of saplings, since no relationship was found between initial height and height increment for saplings initially >1.5 m high. Doing so estimates that an average 1.5 m high sapling in a canopy gap, with an annual height increment of 18.1 cm, will take 47.0 years to become 10 m high (the minimum height of first reproduction). This estimate is consistent with the 60 year age of the one 10.5 m high sapling that was aged with ring counts. In comparison, an average 1.5 m high sapling consistently in understory shade, with an annual height increment of 4.2 cm, would require 202 years to become 10 m high.

These are likely to be overestimates for most saplings, as they ignore the observations that about 1.5% of *T. ochracea* saplings each year are hit by large falling debris. These collisions killed at least 15% of the impacted saplings, and reduced the height of survivors by an average 42%. It is therefore highly unlikely that a sapling requiring at least 202 years to reach reproductive status could ever do so. *Tabebuia ochracea* saplings will require one or more canopy gaps above them if they are to reach reproductive maturity.

If *T. ochracea* is not exceptional among tropical dry forest trees for its degree of habitat specialization and Janzen-Connell effects, and there is no reason to suggest that it is, then niche-assembly processes have the potential to play a large role in structuring tropical dry forest tree communities. It has been suggested that such niche-assembly processes are relatively unimportant in tropical wet forests (Hubbell 1998, but see Terborgh et al. 1996). For example, Hubbell et al. (1999) presented evidence suggesting that most of the tree sapling dynamics in the wet forest of Barro Colorado Island, Panama, are driven by chance processes operating on species distributions structured by limited seed dispersal. The proportion of wind-dispersed tree species is much higher in neotropical dry forests than neotropical wet forests, and it is possible that these dispersal-assembly processes will be relatively less important in these dry forests. The juvenile dynamics of more tropical dry forest tree species will need to be studied before such predictions can be assessed.

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TABLE 1. The abundance of *Tabebuia ochracea* plants in different size classes in different habitat types (mesa, slope, and valley) in the old growth forest plot Bosque Humedo. Areas of each of the habitat types are approximate. They were created from a subjective mapping of the topography within each of the 10 m by 10 m grids through the forest plot, made when the *T. ochracea* saplings were mapped. “Slope” only includes substantial inclines (greater than about 15 degrees) connecting mesas and valleys. Seedlings < 0.5 m high only include plants more than 1 year old. A chi-square test is applied to each height class separately, with expected abundances proportional to the relative areas of each habitat type. “\*” refers to a P<0.05. “\*\*\*” refers to a P<0.001.

Habitat type	Number of plants per height class				Area (ha)
	< 0.5 m	0.5 - <3 m	3 m - <10 m	>10 m	
Mesa	18	43	13	6	3.04
Slope	6	78	6	0	1.55
Valley	4	18	1	0	2.42
Chi-square	6.12*	96.25***	7.74*	7.82*	

TABLE 2. The results of a stepwise multiple regression with the average annual height increment of *Tabebuia ochracea* saplings as the dependent variable. The independent variables that contributed to the model at the P=0.05 level are shown below. “Forest” was coded by approximate relative age (Cerro de Piedra = 1, Bosque San Emilio = 2, Bosque Humedo = 5) and analyzed as an independent variable, but did not contribute to the model (P = 0.59). N = 394.

Independent variable	Partial coefficient	P	R <sup>2</sup>
Canopy light	0.365	0.0000	0.075
Initial height	0.011	0.0008	0.027
Soil moisture	2.677	0.0002	0.020
Distance to nearest adult	1.1051	0.0440	0.005
Constant	-6.453		
Total		0.0000	0.128

Figure 1. A map of the area surrounding the Area Administrativa of the Santa Rosa Biological Station, showing the forests used in this study. Also shown is the experimental forest used in Sullivan (2000c). The solid line is the last portion of the approximately 7 km long entrance road, which joins the Panamerican highway approximately 35 km north of the town of Liberia. Shown also are a selection of the maintained dirt roads (dashed lines). La Casona is the historic homestead that was the core of the original Parque Nacional Santa Rosa. (The GPS coordinates on which this map is based are courtesy of Martin Dohrn and Lisa Rose.)

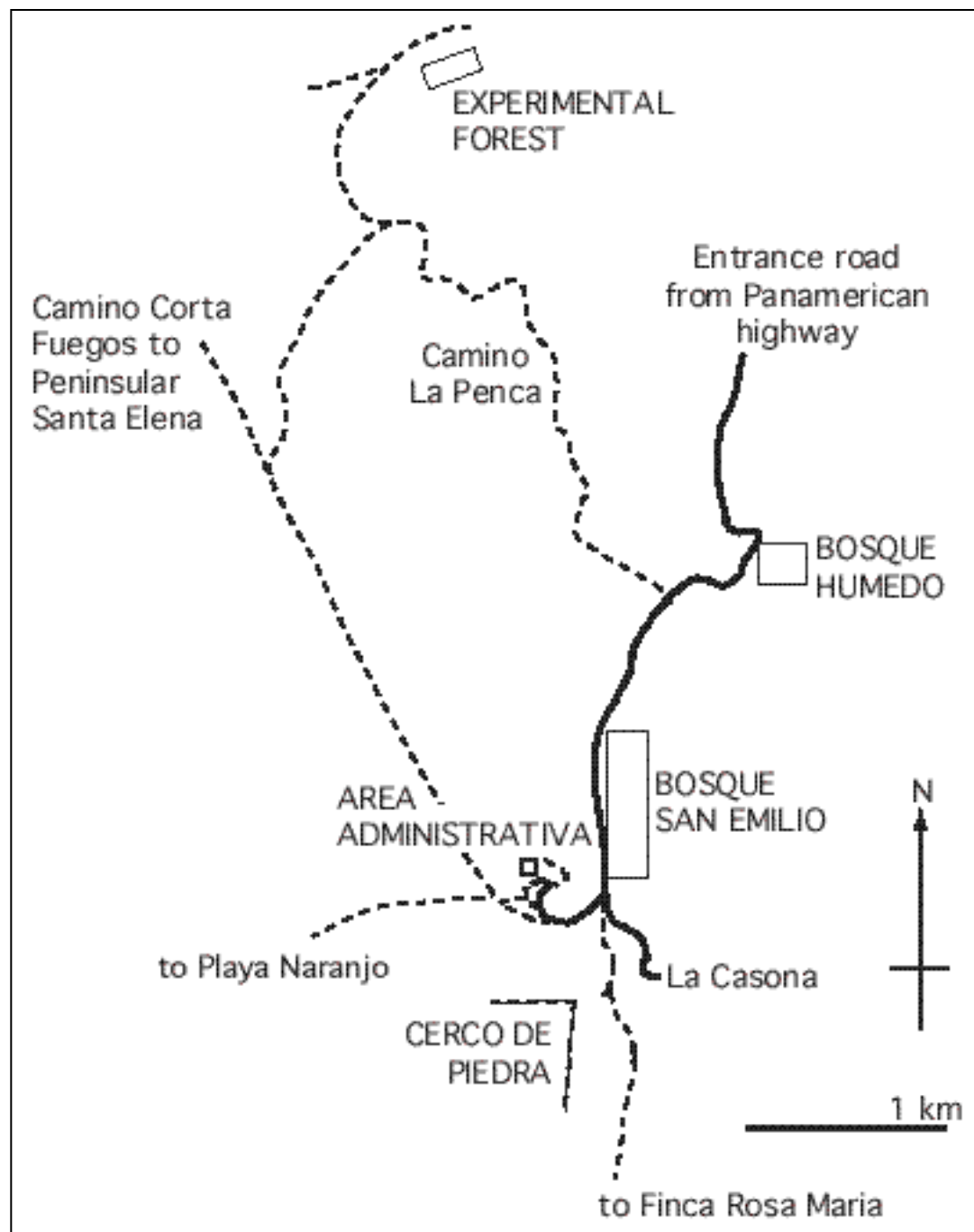


Figure 2. Average densities of *Tabebuia ochracea* seedlings and saplings of five height classes at distances away from adult trees were generated from seventeen 10 m wide transects. The distributions are shown for three forests, in order of increasing age: Cerco de Piedra, Bosque San Emilio, and Bosque Humedo. The Cerco de Piedra forest results summarize one transect from each of two trees. The Bosque San Emilio results summarize transects from five trees; one transect from one tree, two transects from each of three trees, and four transects away from one tree. The Bosque Humedo results summarize two transects from each of two trees. In all cases, the density measures shown for each forest are averaged across tree, not transect. The height class  $<0.5$  m includes only seedlings more than one year old. Two plants sprouting from the roots of two adult Bosque San Emilio trees are not included — these were a 0.3 m high sucker 7 m away from one tree, and a 3.5 m high sucker 4 m away from another tree. The single sapling  $> 3$  m high within 5 m of an adult San Emilio tree, labeled with an asterisk (\*), is the outlier in Fig. 3. It may also be a root sprout.

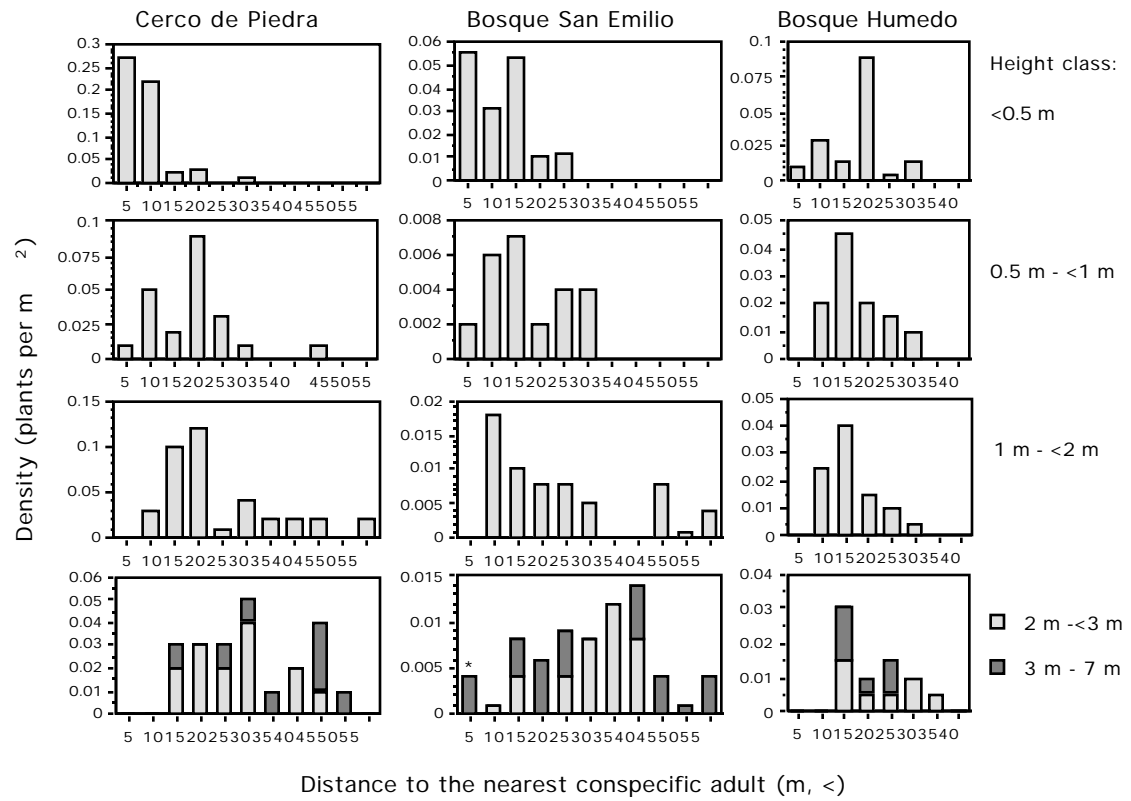




Figure 3. All *Tabebuia ochracea* seedlings and saplings from the seventeen transects (see Fig. 2) are plotted by height and distance away from the nearest adult *T. ochracea* trees. This relationship is significantly different from horizontal using linear regression:

$$\ln(\text{height}) = -3.162 + 1.010 \cdot \ln(\text{distance}), P < 0.0001, R^2 = 0.389, n = 357.$$

Note that this is a conservative test, as the distribution of juveniles would be expected to follow the shape of the seed shadow (Fig. 4) if distance had no effect on juvenile survival and growth.

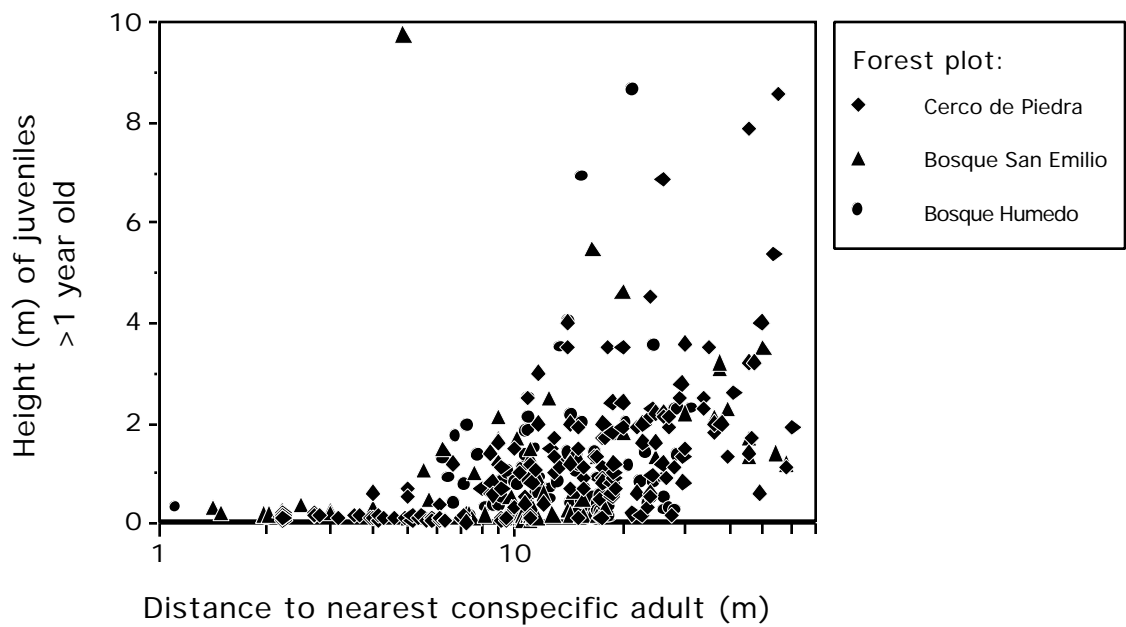


Figure 4. Shown are the average densities ( $\pm 1$  s.e.) of seeds measured at distances away from two *Tabebuia ochracea* trees, one in Cerco de Piedra forest and one in Bosque San Emilio, in June 1995. The results are from counts of seeds and germinating seedlings in 1 m by 1 m quadrats positioned at random points 5 m, 10 m, 15 m, and 25 m away from each tree (n = 45). The inverse curve,  $\text{density} = -2.1317 + 125.845 / (\text{distance})$ , is fitted to the data ( $P < 0.001$ ,  $R^2 = 0.819$ ).

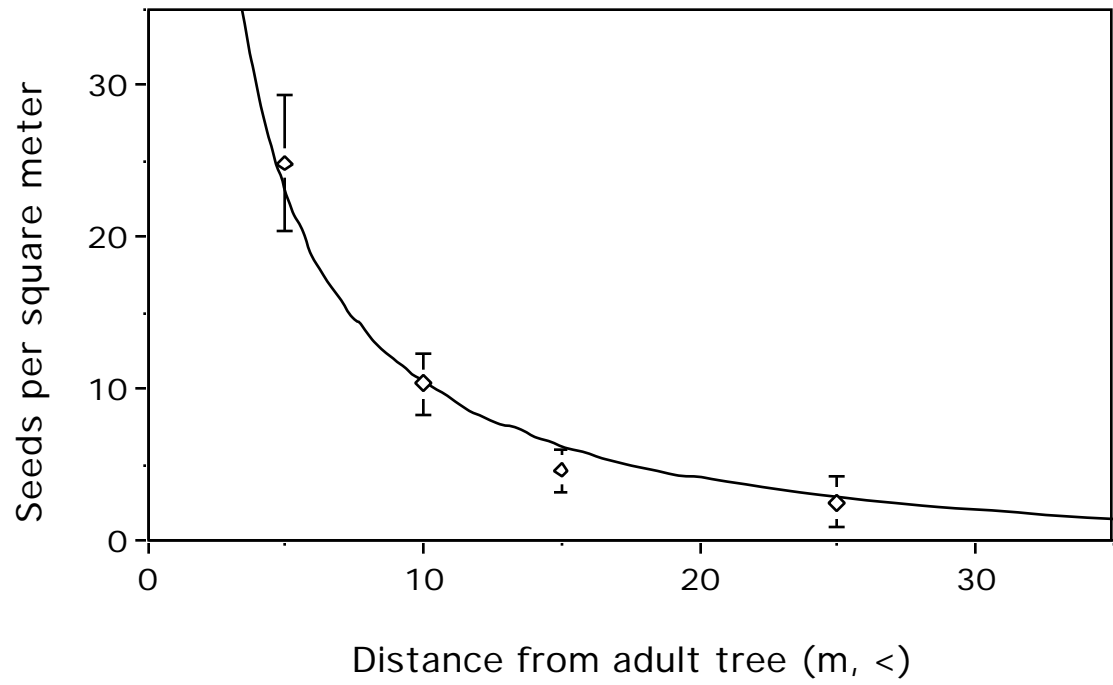


Figure 5. Average annual height increments of *Tabebuia ochracea* seedlings and saplings over the four year study are plotted as a function of initial height. No error bars are presented because most of the data points represent the results of height measurements made only at the beginning and end of the study. Two plants have been removed that had been crushed by falling debris at the beginning of the study (one was 0.30 m high and had an average annual height increment of 0.27 m; the other was 0.45 m high and had an average annual height increment of 0.45 m). N = 392.

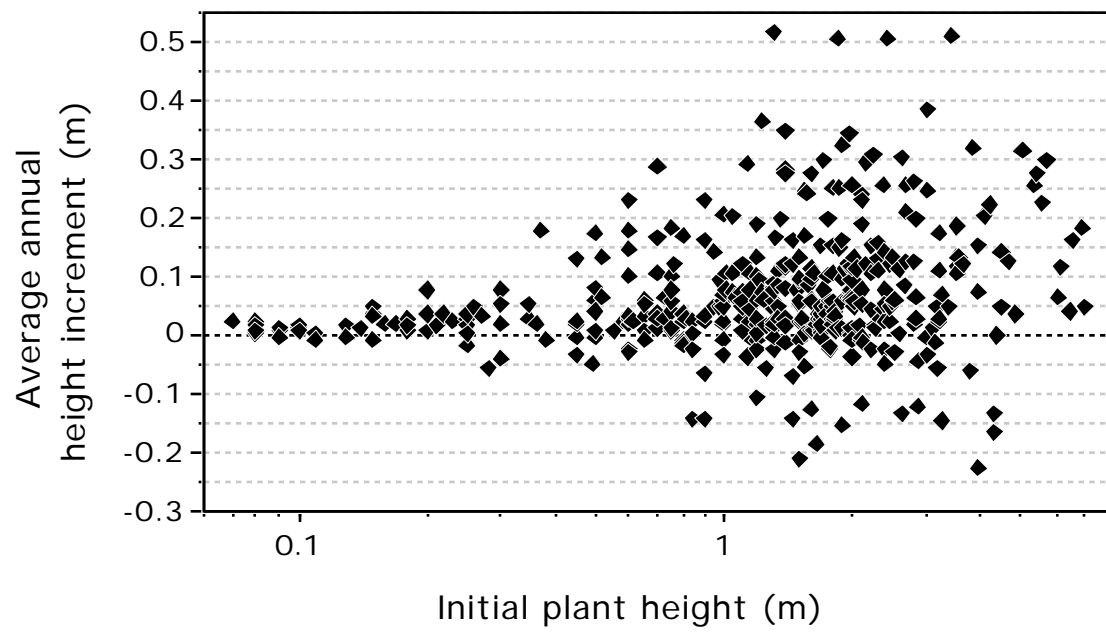


Figure 6. Effects of distance to conspecific adult trees (A), canopy light (B), soil moisture (C) on the average annual height increments of *Tabebuia ochracea* seedlings and saplings. Plotted are averages  $\pm$  1. s.e. “% sky in canopy” is the percentage of the canopy cover that is sky. “% soil moisture” is by dry weight. All effects are significant when included in a multiple regression with initial height (Table 2).

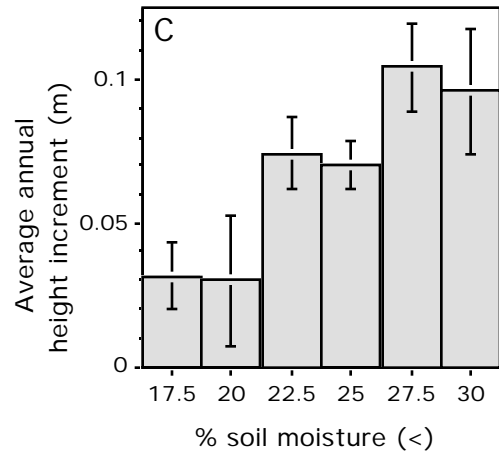
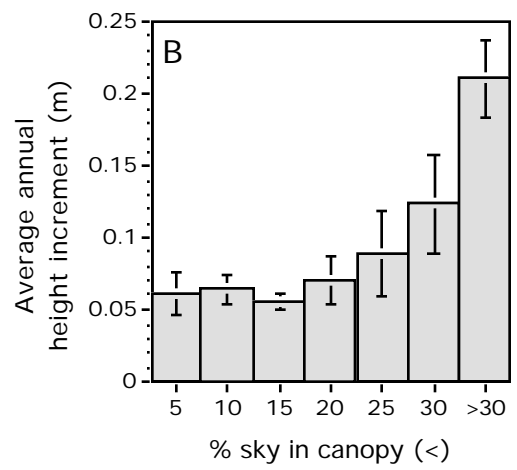
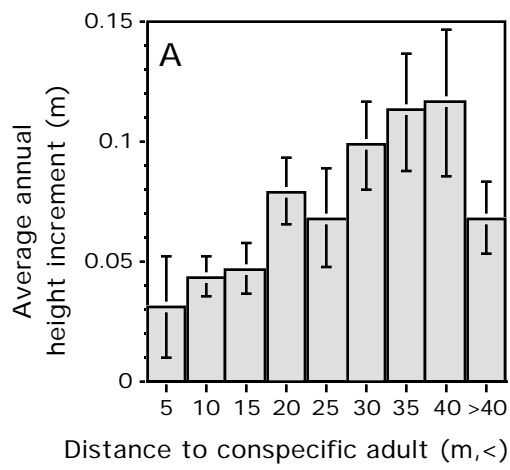




Figure 7. The relationships between height and depth, and dry weights aboveground and belowground, are shown for 37 *Tabebuia ochracea* seedlings and small saplings of various sizes. **A.** Depth is plotted against height and compared to the 1:1 line (dashed). All of the points in the lower left of the graph are newly germinated seedlings (n = 8). A line fitted through the older seedlings and small saplings (N=29) significantly differs in slope from the 1:1 line (linear regression,  $P < 0.001$ ,  $R^2 = 0.83$ , the equation of this line as shown for x,y coordinates is  $\text{depth} = 0.322(\text{height}) + 0.316$ ). **B.** The ratio of belowground:aboveground biomass (“root:shoot”) by dry weight, plotted only for seedlings more than 1 year old and small saplings (n = 29).

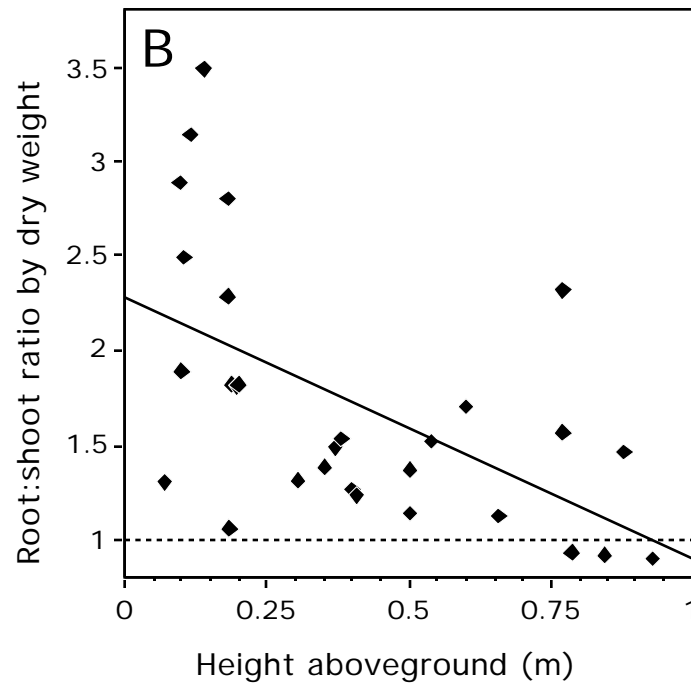
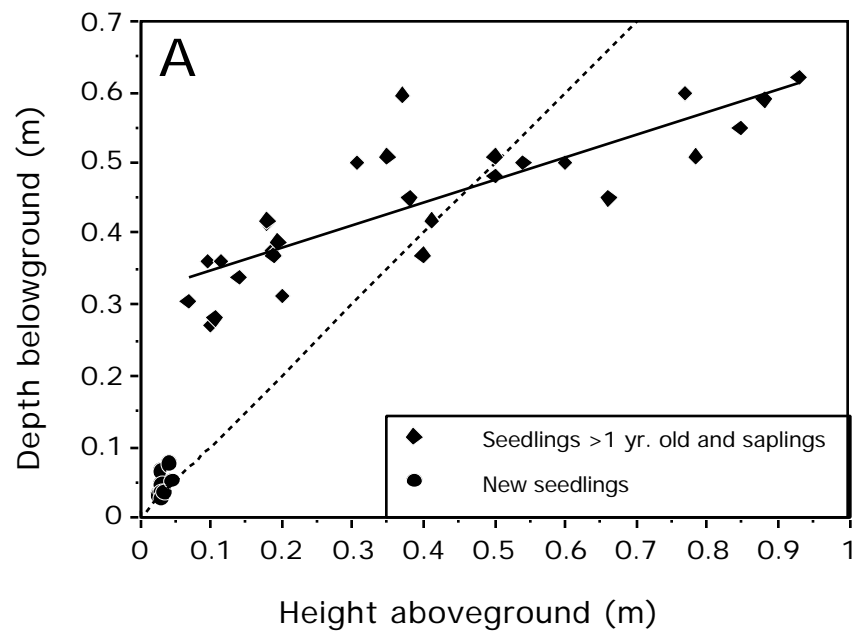


Figure 8. Survival rates over the four year study for *Tabebuia ochracea* seedlings initially more than one year old, shown as a function of distance from the nearest conspecific tree. The number of seedlings in each distance category is shown above each bar. All study seedlings from all three forests are included together.

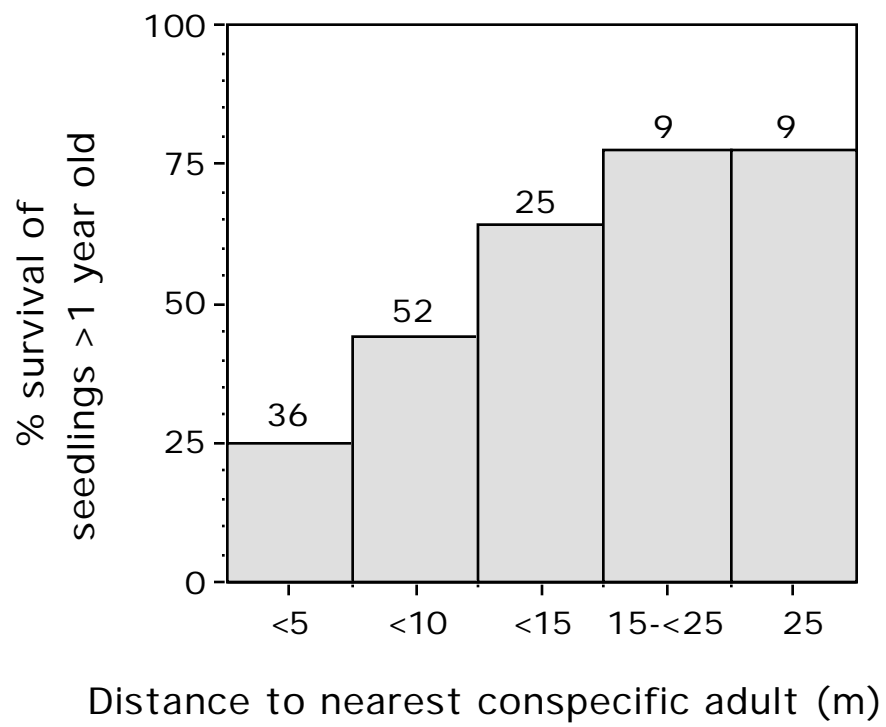
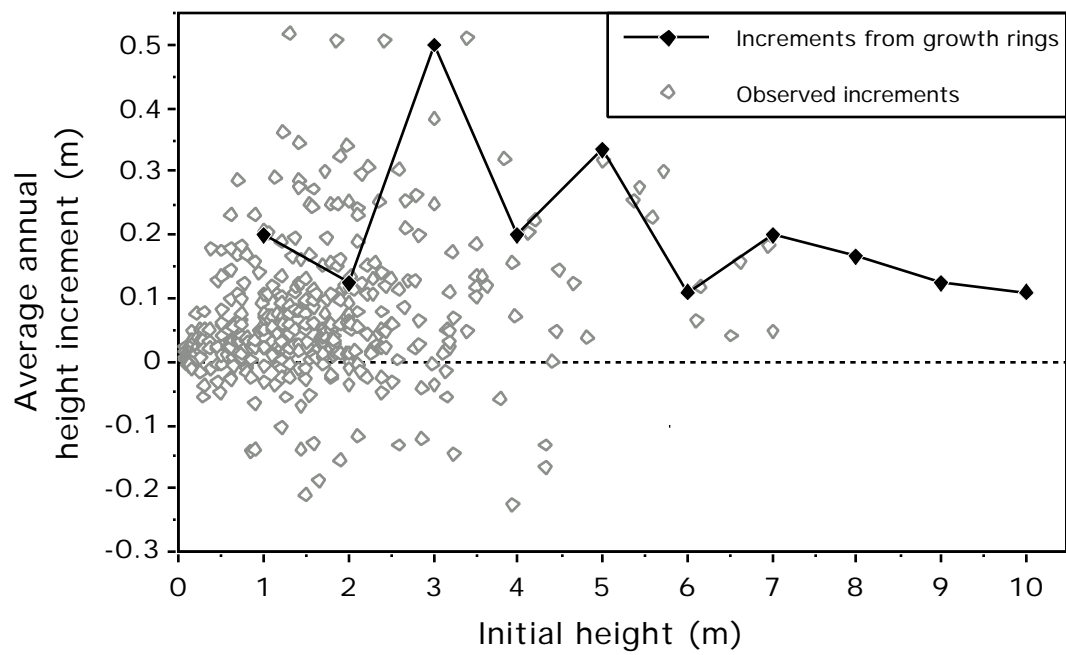


Figure 9. The height increments calculated from growth rings in sections made at 1 m height intervals up a single 10.5 m high sapling are compared with average annual height increments observed for the study saplings over the four year study. The close match between the annual height increments calculated from the growth rings and the range of observed annual height increments is evidence that the rings are annual. There is no significant linear relationship between the average annual height increments and height intervals for this sapling (linear regression,  $P=0.25$ ).



**CHAPTER TWO: Natural history of the tabebuia shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae) in a Costa Rican dry forest**

*Abstract.*

The tabebuia shoot-borer, *Cromarcha stroudagnesia* (Lepidoptera: Pyralidae: Chrysauginae) is a common, multivoltine herbivore of saplings of the neotropical dry forest trees *Tabebuia ochracea* and *Tabebuia impetiginosa* (Bignoniaceae) in northwestern Costa Rica. Various species of shoot-borers are destructive pests in tropical timber tree plantations, and much is known about them in plantation habitats. This is the first detailed examination of the ecology of a species of shoot-borer in a natural tropical forest. The feeding of each *C. stroudagnesia* larva kills an apical meristem and several lateral meristems. The loss of apical dominance usually releases lower lateral buds from dormancy, and the resulting regrowth alters sapling architecture and slows height growth rate. *Cromarcha stroudagnesia* herbivory is strongly biased towards the longest shoots, which usually occur in the upper crowns of saplings. An average of 9.8% of all shoots and 23.8% of the single tallest shoots of study saplings were attacked by *C. stroudagnesia* larvae each year, for 203 study saplings of various heights and microhabitats between 1996 and 1999. Larvae were most abundant on saplings between 2 m and 5 m high, especially saplings growing in canopy gaps and moist sites. Tropical forestry plantation studies suggest that all of these life history characteristics also apply

to other tropical tree shoot-borers. Because they destroy apical meristems and their damage occurs in the tops of the fastest growing saplings of tree populations, shoot-boring insects will have a strong impact on the population dynamics of their host trees.

## **Introduction**

Shoot-boring insects mine through the pith and vascular tissues of recently grown (< 1 year old) plant shoots (unlike stem-boring insects which mine in the wood and vascular tissues of stems and branches). Certain species of shoot-borers are important pests in plantations of many timber tree species, both tropical and temperate, and several of these shoot-borer species have been the focus of much applied forestry research (Gray 1972, Speight and Speechly 1982, Newton et al. 1993, Hall 1996, Speight 1997). Shoot-borer herbivory in timber plantations is typically concentrated on the most rapidly growing, largest shoots, which typically occur at the tops of intermediate-aged saplings (e.g., Gray 1972, Price 1991, Yamazaki et al. 1992, Qi et al. 1994, Mo et al. 1997a,b, de Groot and Schnckenburger 1999). A single shoot-borer larva typically destroys at least one apical meristem during feeding, and elicits regrowth from lateral meristems below the damaged tissue (e.g., Roberts 1968, Grijpma 1976, Singh et al. 1981, Qi et al. 1994). These traits cause pest shoot-borer species in tree plantations to alter sapling and tree architecture, substantially reduce sapling height growth rates, and create deformities in commercial timber, even when shoot-borers occur at relatively low densities (Speight



1997).

These traits also suggest that shoot-borers may play an important ecological role in the fitness and population dynamics of their host trees in natural tropical forests. Janzen (1983, p. 168) stated that “a half gram of shoot tip eaten from the terminal axis may lower the competitive performance of a tree sapling more than the consumption of 10 kg of leaves”. Shoot-borer herbivory in wild tropical forests may not only alter tree architecture, as it does in timber plantations, but also influence the rate and proportion of host saplings recruited to the canopy. Shoot-borers may thus play a important role in structuring tropical tree communities. Despite this, the ecology of shoot-borers in wild tropical forests remains largely unknown (Newton et al. 1993), and their effect on the population ecology of their wild hosts is unexplored.

This study documents the natural history and local patterns of distribution and abundance of one species of tropical tree shoot-borer, the tabebuia shoot-borer, *Cromarcha stroudagnesia* (Lepidoptera: Pyralidae: Chrysauginae), in the natural tropical dry forests of Sector Santa Rosa of the Area de Conservación Guanacaste (ACG), northwestern Costa Rica. The natural history of this newly described species (Solis et al. in prep.), reported here for the first time, underlies a five year study of the role that this shoot-borer plays in the fitness and population dynamics of its primary host plant, *Tabebuia ochracea* (Bignoniaceae) (Sullivan 2000a,b,c). The large variation in densities, growth rates, and microhabitats of wild *T. ochracea* saplings also allowed examination of

an area of confusion in the shoot-borer forestry literature (Newton et al. 1993, Speight 1997). How does the incidence of shoot-borer herbivory change with sapling growth rates, canopy light intensity, soil moisture, and plant density?

By finding close parallels between the life histories of the tabebuia shoot-borer and other tropical timber shoot-borer species, this study forms a bridge for a two-way transfer of knowledge between the disciplines of ecology and forestry. The results from this study in wild forests offer a fuller ecological perspective of the biology of tropical timber shoot-borers, and can offer insights into management and control. In return, the large literature on tropical timber shoot-borers allows increased confidence in the potential ecological generality of the results of this study.

## **Methods**

### *Study Site*

Sector Santa Rosa (formerly Parque Nacional Santa Rosa) is the historical core of the Area de Conservación Guanacaste (ACG), a 110,000 hectare conserved wildland in northwestern Costa Rica (<http://www.acguanacaste.ac.cr>). Santa Rosa includes a few small fragments of old growth dry forest and large expanses of secondary successional tropical dry forest between 0 - 400 year old, regenerating on abandoned cattle pastures, agricultural fields, and logged areas (see Janzen 1986, 1988b, 1992). The dry forests of sector Santa Rosa and neighboring sectors are the largest area of conserved dry forest in

Central America, a habitat that once covered the Pacific coastal lowlands and parts of the Atlantic coastal lowlands of Central America (Janzen 1988b, Gillespie et al. 2000).

Within the ACG, Santa Rosa is bordered by conserved marine habitats in the Pacific Ocean to the west and sectors of progressively wetter conserved forests to the east, including cloud forest and Atlantic rain forest.

Annual rainfall at the Santa Rosa Biological Station during the four years of the study (1996 - 1999) was 2076 mm (s.d. = 706), which included the wettest and fifth driest years since 1980. The local climate is highly seasonal, dominated by a pronounced 6-month dry season from December to mid May when essentially no rain falls. During much of the dry season, most individual trees in all but the oldest fragments of forest are leafless or nearly leafless, contrasting with the completely foliated forests throughout the 6-month wet season (see Janzen 1993). Rainfall is typically heaviest in May - June and September - October, and there is a lull in rainfall for 2 - 6 weeks in July - August called the “veranillo” (little dry season).

#### *Study saplings and environmental measurements*

The bulk of the observations and experiments were made in the forests within 3 km of the Santa Rosa Biological Station (about 300 m, 10° 50' 27.26'' N latitude , 85° 37' 14.26'' W longitude), including within the Bosque San Emilio forest plot, a 16.3 ha plot in 80 - 100 year old secondary successional forest (Stevens 1987, Enquist et al. 1999), and

the Bosque Humedo forest plot, a 4.8 ha plot in a fragment of old growth forest (Janzen 1986b). Sullivan (2000a) presents a map with the locations of the study forests. In these forests, I monitored the growth and shoot-borer herbivory of 131 marked study seedlings and 342 saplings (up to 7.0 m high) of *Tabebuia ochracea* between 1995 or 1996 and 1999 (see Sullivan 2000a). Saplings were defined as juvenile *T. ochracea* 50 cm high (*sensu* De Steven 1994), which corresponds with well established plants usually much greater than 5 years old (Sullivan 2000a). I individually tagged all shoots on 13 of these seedlings and 98 of these saplings (in total comprising 3943 shoots in 1999) and annually monitored their growth and shoot-borer status. Plant height was measured for all plants with a weighted measuring tape attached to a 7 m long telescoping pole. Stem diameters were recorded 30 cm above the soil surface across the thickest horizontal axis with vernier calipers. The shoot-borer distribution and abundance data reported are from the 298 study saplings, unless otherwise stated.

I measured canopy light and soil moisture for each study plant in 1998 and 1999. Digital canopy photos were taken from the top of each study sapling using a Sony Mavica digital camera with a wide-angle lens attachment, attached to a telescoping pole. Photographs were taken in mid-wet season in 1998 and 1999. The percentage canopy cover was calculated from these images using the Histogram feature of Adobe Photoshop 4.01, with the color selection set to pure white with a fuzziness of 200, which was sufficient to encompass the variation between white cloud and blue sky without selecting

foliage. I took soil moisture readings at the base of each plant in mid-wet season 1999 with a Rapidtest Mini Moisture Tester (Luster Leaf Products, Inc., Woodstock, IL, USA). All readings were taken at 10 cm depth, approximately 1 m from the base of each plant. These readings were calibrated using percentage soil moisture measurements from local soil dehydrated at 68 degrees Celsius in a drying oven until stable weight.

Collections of larvae and pupae were made outside of Bosque San Emilio and Bosque Humedo so as to minimize disturbance to the portion of the local population of shoot-borers living around the study saplings. Each year, wild pupae and last instar larvae were collected and reared to adults to assess rates of parasitism.

Very few shoots in tree canopies were found to contain *C. stroudagnesia* larvae (see Results). To investigate whether adult shoots were unsuitable for *C. stroudagnesia* larval development, in mid-June 1996, 41 intermediate instar larvae of *C. stroudagnesia* were collected and transplanted into 23 shoots in the canopies of two *T. ochracea* trees (accessed with ascenders and climbing rope), and into 18 shoots of saplings. All saplings were < 3 m high and within a 30 m radius of the base of each of the two trees. The longest shoots of both canopy trees and saplings were selected for transplanting, and there were no significant differences in shoot length between the sapling and tree canopy shoots (independent samples t-test,  $t = 0.13$ ,  $df = 29$ ). Individual larvae were placed in 2.5 cm long sections of clear PVC tubing, of a selection of diameters to match the variation in sapling and tree shoot diameters. Each tube was blocked at one end with old *T. ochracea*

stem wood, and the open end was firmly pushed onto the end of the focal shoot after the tip of each focal shoot was removed to aid larval entry. Shoots were later dissected open at on July 31 (when most wild *C. stroudagnesia* had pupated) and the status of each transplanted larva was recorded.

## Results

### *Hosts, Habitat, and Geographical Range of Cromarcha stroudagnesia*

The tabebuia shoot-borer, *Cromarcha stroudagnesia*, is a specialist on at least two species of the neotropical tree genus *Tabebuia* (Bignoniaceae). Within Santa Rosa, larvae of *C. stroudagnesia* commonly infest the vigorous shoots of saplings and basal trunk sprouts of the locally very common tree *Tabebuia ochracea* (Chamisso) Standley (see Gentry 1983, Gentry 1992, Sullivan et al. 1998, Sullivan 2000a, for a taxonomic and ecological description of *T. ochracea*). The Central American "subspecies" of *T. ochracea*, *T. o. neochrysantha*, was previously known as *T. neochrysantha* A. Gentry. Larvae also occasionally occur in saplings and trunk sprouts of the locally much less abundant and more habitat-restricted *Tabebuia impetiginosa* (Mauritius ex A. P. de Candolle) Standley. Larvae are noticeably absent from the similarly less abundant *T. rosea* (Bertoloni) A. P. de Candolle, and from all other local bignoniaceous species of tree and vine (e.g., *Arrabidaea patellifera*, *Crescentia alata*, *Cydista diversifolia*, *Godmania aesculifolia*, *Pithecoctenium crucigerum* — all names follow Janzen and Liesner 1980).

Curiously, intermediate instar *C. stroudagnesia* larvae transplanted into cut *T. rosea* shoots can develop to adults (3 of 9 transplanted larvae). Larvae transplanted into shoots of *Godmania aesculifolia*, the other local bignoniaceous tree of the tribe Tecomeae, fed for about a week before dying (n = 8).

A local search for shoot-borers of tree saplings in the 1999 wet season found 22 tree species (of a total resident tree flora of approximately 190 species) that are frequently infested with other species of shoot-borer larvae (J. J. Sullivan and A. Pérez, unpublished data) (Janzen and Liesner 1980). None of these other tree species contained *C. stroudagnesia*.

Larvae of *C. stroudagnesia* have been observed in sapling and trunk sprout shoots of *T. ochracea* throughout the lowlands of Guanacaste province, Costa Rica, including the habitats of old secondary successional wild forest, timber plantations, “living fence” trees along the boundaries of farms, and ornamental trees in urban areas. Characteristic shoot-borer damage to saplings of *T. chrysantha*, a species very closely related to *T. ochracea*, have been observed in the rain forests of the Atlantic slopes of the ACG, but no larvae have yet been collected and reared.

The extent of the geographic range of this species of moth is unknown. Adults have also been collected in the Puntarenas province of Costa Rica (M. A. Solis, in prep.). The genus *Tabebuia*, which includes all known host species of *C. stroudagnesia*, occurs throughout the neotropics, and *Tabebuia ochracea* occurs from El Salvador to southern

Brazil and northern Argentina (Gentry 1992). A thorough study of the herbivore fauna of *Tabebuia ochracea* in the paramo of Brazil revealed no shoot-boring lepidopteran species (Ribeiro and Pimenta 1991, Ribeiro et al. 1994, S. P. Ribeiro, personal communication).

### *Eggs*

Eggs of *C. stroudagnesia* are longitudinally striated, white ovoids and about 1 mm long. A moth glues a single egg onto the wall of a growing shoot of a *T. ochracea* sapling. Unhatched eggs are encountered very rarely, despite careful searching at times and in forests where first instar larvae and associated egg remains are abundant. I infer from this that the egg hatches very soon after oviposition. First instar larvae apparently enter the shoot very soon after hatching. First instar larvae dissected from shoots and placed on the surface of other young shoots begin to eat inwards within minutes.

### *Larvae*

First instar *C. stroudagnesia* larvae are nondescript pale cream colored caterpillars about 2 mm in length with a dark brown head capsule. There are at least four, and probably five, instars, and larval development to pupation takes about 11 weeks (Fig. 1b). Healthy last instar larvae are dark chocolate brown, 19 - 21 mm long with a dark, about 2 mm wide head capsule (Fig. 2b).

Larvae that hatch onto newly grown shoot tissue typically enter the shoot by



boring directly through the shoot wall, while larvae that hatch onto older shoot tissue typically enter the shoot by boring into a leaf bud (Table 1). A minority of larvae also enter the shoot through a leaf rachis, and then mine down the rachis and into the shoot (Table 1). Larvae cover their entry holes with a loose web of silk and frass.

Once inside the shoot, first instar larvae eat out a partial or complete transverse ring around the outside of the shoot pith, before eating into the center of the pith. Initial pith feeding is usually above this transverse ring. The portion of the shoot above this bored ring wilts within days of a larva's entry, suggesting damage to the vascular tissues. The apical meristem quickly dies. This wilting makes newly infested shoots and young larvae easy to find.

Later instar larvae feed downward and completely hollow out the full length of most shoots, causing the death of all leaves and lateral meristems along the bored length of shoot. Leaves start to wilt and blacken soon after a *C. stroudagnesia* larva has bored below their node, suggesting that the larva feeds on or damages the vascular tissues of the shoot as well as the pith. Late instar larvae will sometimes eat several centimeters into the lignified core of last year's stem if they eat out all of the core from this year's green shoot tissue. As the larva bores down the shoot, the tunnel behind it usually becomes filled with frass. Every few centimeters along the tunnel, the larva scrapes a small (about 1 mm diameter) window almost through the side of the shoot, leaving only the shoot epidermal layer intact. Also at intervals along the bore, the larva builds a silk-frass barrier

completely blocking off the bore. This barrier may obstruct the entry of predaceous insects (see below).

Only one larva occurs per shoot (rarely two can occur in exceptionally long shoots), and one larva almost always completes its life cycle within a single shoot. The average length of shoots containing *C. stroudagnesia* tunnels was 14.8 cm (s.e. = 0.44 cm, n = 539). A sample of 105 *C. stroudagnesia* attacked shoots from late-July and early-August 1998 included 47 tunnels containing pupae or pupal skins. The average tunnel length in the shoots that successfully reared pupae was 15.4 cm (s.e. = 1.21, n = 47) (the average tunnel length of empty shoots was 10.1 cm (s.e. = 0.99, n = 47)). No tunnel less than 5 cm long was found containing a pupa or pupal remains, and 84.5% of tunnels containing pupae or pupal remains were  $\geq$  9 cm long.

Larvae that enter shoots that are too short to support their full development usually die rather than successfully move into a neighboring shoot to continue feeding. In an experiment where wild shoot-borers were excluded from saplings over the egg laying period and a single young instar larvae was then transplanted into a shoot of each sapling (see Sullivan 2000b), no more than 10.8% (N= 93) of transplanted larvae fed on more than one shoot. This was even though the majority of larvae were transplanted onto shoots that were of insufficient length for complete development (58.2% of shoots <9 cm long). There was only low success with experimental field transplants of larvae (46.7% of larvae failed to enter their new shoots), largely due to ant predation and larvae dropping

from the plant during ant encounters. This behavior of dropping when attacked may also explain the lack of success of larvae naturally moving between shoots.

### *Pupae*

New pupae of *C. stroudagnesia* are 8 - 10 mm long, 2 - 2.5 mm wide, and bright red. Within 2-3 days, they change to a black-brown color. Pupae occur naked in the base of the tunnel, with the head upward, just below a large hole cut in the shoot wall leaving only the outer epidermis intact, and below a silk and frass barrier blocking the tunnel above the pupa. Male pupae complete metamorphosis sooner than female pupae; male pupae eclose after an average 16.7 days (s.e. = 1.3, n = 11) while female pupae eclose after an average 20.1 days (s.e. = 0.41, n = 16)(independent samples t-test,  $P < 0.05$ ,  $t = 2.52$ , corrected for significantly unequal variances; Levene's test for equality of variances,  $P < 0.05$ ,  $F = 6.517$ ). Moth sex was estimated from body size (see below); five moths of intermediate body size and uncertain sex are not included in the analysis.

Eclosion occurs during the day, usually in the morning. The adult moth pushes its way out of the anterior end of the pupal skin and then breaks the epidermal skin of the exit hole to expand its wings and leave the shoot.

### *Adult moths*

The small adult moths of *C. stroudagnesia* are characterized by a distinctive orange and red color pattern on their forewings (Fig. 2a, M. A. Solis, in prep.). The body is covered with prominent tufts of scales, which disrupt the outline of the moth when at rest. Moths pass the day hanging from the undersides of foliage and on bark. It is not known if they visit flowers, nor how long an adult may live.

Male moths are typically smaller than females, although there is overlap in body sizes. Relatively large moths (wing span about 14 mm, body length about 6.5 mm) are females (e.g., Fig. 2a) and relatively small moths (wing span about 10 mm, body length about 4.9 mm) are males (D. H. Janzen, personal communication, M. A. Solis, in prep.?).

*Cromarcha stroudagnesia* moths rarely appear at black lights in the forest. For example, only a single moth arrived at a fluorescent white light and a blacklight maintained for 8 nights between 5 August and 13 September 1997. This was a time when almost all wild-collected pupae eclosed (see below) and was in an area with high densities of *T. ochracea* saplings and high shoot attack frequencies.

### *Seasonal Cycle*

There are two generations of *C. stroudagnesia* per year. Each coincides with a peak of new shoot growth of *T. ochracea* saplings, which in turn coincides with the bimodal pattern of annual rainfall (Fig. 1a,b,c). This life cycle is typical of many dry

forest lepidopteran larvae (Janzen 1993). Moths of the first generation lay their eggs on the new growth that appears in the first 1-2 weeks of the wet season (mid-May)(Fig. 1a). Shoot-borer larvae spend the next 2.5 months feeding, through which time virtually all vertical elongation of sapling shoots has ceased (Fig. 1a). Pupation occurs in late July - early August, coinciding with the veranillo (little dry season)(Fig. 1b,c). All eclosion occurs around late August to early September (80.8%, 85.5%, 84.8%, and 84.0% of wild-collected pupae eclosed in the last three weeks of August in 1996, 1997, 1998, and 1999 respectively,  $n = 26, 55, 33,$  and  $25$ ). Development from egg to eclosion takes 61-96 days (Fig. 1b).

The second annual bout of egg laying coincides with a second, smaller flush of sapling growth in late-August-early September, following the end of the veranillo (Fig. 1a,b,c). This second generation pupates and ecloses throughout December, at the end of the wet season. In some years, a much diminished third generation of shoot-borers can persist through the dry season (January - May) on those rare saplings that produce new shoots in the early dry season (e.g., along stream margins). These occasional third generation larvae are insufficiently abundant to explain the large and synchronized oviposition event at the beginning of each wet season in May. Because of this, I conclude that most adults from the second generation are reproductively dormant during the dry season and lay their eggs at the onset of the May rains, as is commonplace with other ACG dry forest moths (Janzen 1993).

*Parasitism, Predation, and General Mortality of larvae and pupae*

In the dry forests around the Santa Rosa Biological station, larvae and pupae of *C. stroudagnesia* are attacked by two species of parasitoid wasp and a species of predaceous beetle. Mounted individual specimens of the adults of these species are referenced in the online caterpillar rearing voucher database of Daniel H. Janzen and Winnie Hallwachs (<http://www.janzen.sas.edu>), and example voucher numbers are supplied below.

A single cream colored larva of a braconid wasp emerges from a last instar *C. stroudagnesia* larva to spin a white, 5 mm long cocoon inside the shoot-borer tunnel. The adult wasp is black with a body length of approximately 3 mm (e.g., voucher number 95-SRNP-8478). This species was identified as an *Apanteles* species (Braconidae: Microgastrinae) by J. B. Whitfield. During 1996 - 1999, natural parasitism frequencies during the first borer generation of the year ranged from 0% (n = 74) to 16.5% (n = 97) of late instar borer larvae.

A single 9 mm long yellow and brown chalcidid wasp ecloses from within a borer pupa (e.g., voucher number 95-SRNP-7179, family level identification by Daniel H. Janzen). During 1996 - 1999, natural parasitism frequencies during the first borer generation ranged from 2% (n = 53) to 17% (n = 86) of borer pupae.

*Cromarcha stroudagnesia* larvae are killed by unidentified predaceous beetle larvae of the family Cleridae (e.g., voucher number 95-SRNP-7184, family level

identification by Daniel H. Janzen). Four of these larvae have been collected, three associated with shoot-borer pupae and one with a late instar larva. These larvae fed on both shoot-borer larvae and pupae in captivity. While only four beetle larvae have been collected from many hundreds of tunnels opened in the field, these larvae are highly mobile, and predation rates are likely to be far higher than indicated by this rare encounter rate.

Of 247 wild pupae collected and retained during the study, 15 (6.1%) died without eclosing either a moth or chalcidid wasp. Seven of these dead pupae became covered with distinctive pale yellow fungal spore bodies (although this fungus was not necessarily the cause of death).

Total mortality between shoot entry and eclosion may be substantially higher than 50%, despite shoot-borer larvae being largely protected from most generalist lepidopteran larval predators (such as predatory wasps, salticid spiders, ants, and insectivorous birds). A sample of bored shoots between 3 - 10 August 1998 found that 44.8% ( $n = 105$ ) of tunnels were either empty or contained caterpillar remains but no pupal remains. Most of the remaining shoots at this time contained pupae (19% contained larvae and prepupae, 65.5% contained pupae, and 15.5% contained pupal skins). A sample of bored shoots between 18-21 August 1999 found the same pattern, with 35% ( $n = 80$ ) of bores empty or containing caterpillar remains but no pupal remains.

Most, if not all, of these empty shoots represent larval/pupal mortality through

starvation and predation. Empty bored shoots were significantly shorter than shoots containing late instar larvae, pupae, or pupal skins (average shoot lengths are 13.4 cm (n = 58) and 18.6 cm (n = 47) respectively, one-tailed independent samples t-test,  $P < 0.01$ ,  $t = -2.38$ ). This difference suggests that many of the larvae may have starved in shoots with insufficient tissue for complete development. Predation by clerid beetle larvae is also likely to have caused some fraction of these empty bores.

#### *Frequency and distribution of shoot-borer attacks*

During the four years of this study, 57.1% of saplings (n = 203) were attacked at least once by a *C. stroudagnesia* larva. There were disproportionately far more *C. stroudagnesia* larvae in the longest *T. ochracea* shoots than in the shortest shoots (Fig. 3). The average length of shoots containing *C. stroudagnesia* tunnels was 14.8 cm (s.e. = 0.44 cm, n = 539), while the average length of all sapling shoots was only 5.1 cm (s.e. = 0.14 cm, n = 1909) (one-tailed independent samples t-test,  $P < 0.001$ ,  $t = 21.15$ ). 83.1% of shoots containing *C. stroudagnesia* were  $\geq 5.5$  cm long, and 67.9% of shoots containing *C. stroudagnesia* were  $\geq 9$  cm (recall that 84.5% of *C. stroudagnesia* tunnels rearing pupae were  $\geq 9$  cm long)(n = 539).

Sapling height increments are significantly increased in areas of relatively high light and soil moisture (Sullivan 2000a), and the shoots of saplings in these conditions were also significantly more likely to contain *C. stroudagnesia* larvae than shaded saplings



and/or saplings on drier soils. The percentage of shoots containing *C. stroudagnesia* larvae was significantly positively correlated with both sapling canopy light and soil moisture (partial correlations, canopy light : $P < 0.05$ , coefficient = 0.117; soil moisture:  $P < 0.001$ , coefficient = 0.168; d.f. = 379, controlling for initial height).

The top shoot of saplings is usually among the longest shoots on a sapling, and is also much more likely to be attacked by a *C. stroudagnesia* larva than a random shoot. Of the 203 study saplings that had the status of their top shoot recorded twice annually, 116 were attacked at least once by a *C. stroudagnesia* larva during the four year study. Each of these saplings had on average 16.7% of its shoots attacked by *C. stroudagnesia* larvae per year (s.e. = 1.4%). In contrast, on average 38.1% of these saplings had their top shoot attacked by a *C. stroudagnesia* larva per year (s.e. = 3.4%).

Can shoot length alone explain the disproportionately high likelihood of *C. stroudagnesia* herbivory among the highest shoots of saplings? In 1997, all shoots were individually ranked by height for each of a selection of the study saplings that were having the growth and herbivory of all of their shoots annually censused. Twenty-four of these saplings had 10 shoots and were attacked by at least one shoot-borer larva during the two *C. stroudagnesia* generations of 1997. For these saplings, 31.1% ( $n = 77$ ) of the highest 10% of shoots were attacked by *C. stroudagnesia* larvae, versus only 15.4% ( $n = 434$ ) of the lowest 70% of shoots. When shoot rank was combined with shoot length in a logistic regression of *C. stroudagnesia* larva presence/absence, only shoot length

significantly increased the likelihood of *C. stroudagnesia* attack. Therefore, it is likely that the disproportionately high likelihood of an apical shoot being attacked by a *C. stroudagnesia* larva can be wholly explained by the increased length of shoots near the apex of saplings.

After a shoot has been attacked by a *C. stroudagnesia* larva, a sapling commonly produces regrowth shoots from lateral buds below the damage. These regrowth shoots are on average no different in length than the shoots they replace (independent samples t-test,  $t = 0.75$ ,  $df = 1099$ ). Regrowth shoots were also no more or less likely to be attacked by an *C. stroudagnesia* larva than non-regrowth shoots of equivalent length (regrowth status was not significant when added to a logistic regression of shoot length and *C. stroudagnesia* larva presence/absence,  $n = 5432$ ).

*Cromarcha stroudagnesia* larvae very rarely attack *T. ochracea* seedlings (< 50 cm high), and occur in very low frequencies in adult tree crowns (Fig. 4). Unlike older and taller plants, seedlings tend to invest most of their resources in growth belowground (Sullivan 2000a), and it is not until plants are taller aboveground that they begin to produce shoots of lengths that typically contain shoot-borers. For example, in 1997 the average shoot length of plants more than one year old and < 50 cm high was 3.1 cm (s.e. = 0.67) with only 5.9 % of shoots  $\geq 9$  cm long ( $n = 51$  shoots from 42 plants). In comparison, the average shoot length of saplings between 2 m and 5 m high was 6.2 cm (s.e. = 0.27) with 24.3% of shoots  $\geq 9$  cm long ( $n = 891$  shoots from 36 plants). None of

these 42 seedlings were attacked by *C. stroudagnesia* larvae, while all of the 36 saplings contained larvae, with an average 15.1% (s.e. = 2.7%) of their shoots attacked.

Shoot-borer herbivory is substantially lower in adult tree crowns than would be expected from the distribution of shoot lengths alone; while 16.2% of shoots were > 9 cm long, only 0.37% of shoots (s.e. = 0.11%) contained *C. stroudagnesia* larvae or tunnels (n = 2734 shoots from two trees in 1996, both in areas and at times of high sapling shoot herbivory). Both microclimate and shoot morphology differ dramatically between the understory/canopy gaps and the canopy. Canopy shoots are tougher, thicker, and hairier than understory shoots and terminate in reproductive buds for most of the year.

No significant differences were found among the fates of intermediate instar larvae transplanted into sapling versus canopy tree shoots of equivalent length (chi-square = 0.309, df = 2). Of the larvae transplanted into sapling shoots, 5 were alive after 1.5 months, 8 had fed but were either dead or absent, and 5 never fed. Of the larvae transplanted into canopy tree shoots, 5 were alive after 1.5 months, 10 had fed but were either dead or absent, and 8 never fed. Moths were reared successfully from the pupae of both sapling and canopy tree shoots. I conclude that *C. stroudagnesia* moths must therefore infrequently oviposit eggs in the canopy, and/or canopy tree shoots are unsuitable for first instar larvae.

### *Effects of shoot-borer attack on host plant growth, architecture, and mortality*

Repeated attack of *T. ochracea* saplings by *C. stroudagnesia* can dramatically alter sapling architecture; repeated attack of the highest shoots can result in multiple terminal branches (i.e., multiple leaders) that compete for apical dominance (Fig. 5). Both the repeated destruction of the top shoot and the creation of multiple leaders greatly reduce sapling height increments (Sullivan 2000b,c). The magnitude of these effects and their implications for plant fitness and population dynamics are examined in detail in other papers (Sullivan 2000b,c). Adult trees of *T. ochracea* in Guanacaste, Costa Rica typically have contorted trunks, although it is unknown to what degree this growth form is caused by *C. stroudagnesia* herbivory of saplings.

## **Discussion**

The natural history of *Cromarcha stroudagnesia* closely parallels the natural history of well-known lepidopteran timber shoot-boring pests, such as *Hypsipyla* species (Pyralidae) on tropical meliaceous trees (e.g., Gray 1972, Yamazaki et al. 1992, Howard and Meerow 1993, Newton et al. 1993, Mo et al. 1997a,b), *Eucosma* spp. (Tortricidae), *Dioryctria* spp. (Pyralidae), and *Petrova* spp. (Tortricidae) on tropical and temperate *Pinus* species (Pinaceae)(e.g., Speight and Speechly 1982a,b, de Groot and Schnekenburger 1999), *Orygmophora mediofoveata* (Noctuidae) on *Nauclea diderrichii* (Rubiaceae)(Eidt 1965), and *Sinomphisa plagialis* (Pyralidae) on Chinese *Catalpa* species

(Bignoniaceae)(Qi et al. 1994). Shared traits among these species include the ability of a single shoot-borer larva to destroy at least one apical meristem, and the preferential utilization of rapidly growing large shoots at the tops of plants. Like *C. stroudagnesia*, the highest attack rates are also typically on intermediate-aged saplings. These traits can result in substantial commercial damage to timber plantations, and are likely to be similarly important in wild forest systems.

The best known and most economically notorious of the tropical timber shoot-borer pests are the species of mahogany shoot-borers, *Hypsipyla robusta* and *H. grandella* (e.g., Gray 1972, Yamazaki et al. 1992, Howard and Meerow 1993, Rodan et al. 1992, Newton et al. 1993, Speight 1997). *Hypsipyla* have made plantation production of many meliaceous timbers (the mahoganies and tropical cedars) impossible in most parts of the world (Rodan et al. 1992, Newton et al. 1993, Speight 1997). This is widely believed to have exacerbated the high rates of removal of mahogany trees (*Sweitenia* species) from wild neotropical forests (e.g., Rodan et al. 1992). *Hypsipyla* slows sapling growth and stunts tree architecture, but only infrequently kills saplings (e.g., Gray 1972, Rodan et al. 1992). These combined effects have caused the loss of thousands of hectares of mahogany and cedar plantations (Rodan et al. 1993). In an experimental mixed plantation of *Cedrela odorata* (Meliaceae) and two other tropical timber species, *Hypsipyla grandella* attacks were shown to further slow *Cedrela* growth through damaged saplings being overshadowed by the other species (Menalled et al. 1998).

*Cromarcha stroudagnesia* and *Hypsipyla* have very similar life histories and have comparable effects on the architecture and rates of height increment of their host trees (Fig. 5, Sullivan 2000b,c). Like *C. stroudagnesia*, *Hypsipyla* is normally only a pest of young trees, with saplings between 1 m and 6 m high attacked most heavily (Yamazaki et al. 1992, Mo et al. 1997b, Newton et al. 1998). Also like *C. stroudagnesia*, larvae of *Hypsipyla* are concentrated on the longest, highest shoots of saplings (Mo et al. 1997a). The life cycle of *Hypsipyla* can be as short as 40 days (Yamazaki et al. 1992), while the *C. stroudagnesia* life cycle can be as short as 61 days (Fig. 1b). Both *Hypsipyla* and *C. stroudagnesia* are multivoltine. *Hypsipyla* female moths are attracted by volatiles emanating from fresh leaves, and place eggs on the longest shoots (Grijpma and Gara 1970). Like larvae of *C. stroudagnesia*, *Hypsipyla* larvae enter the shoot immediately after hatching (Grijpma 1974, cited in Newton et al. 1998). Also like *C. stroudagnesia*, *Hypsipyla* larvae can occur in the dry season at low densities, and reach peak densities just after the onset of the rainy season (Yamazaki et al. 1992, Howard 1991). However, unlike *C. stroudagnesia*, individual *Hypsipyla* larvae frequently feed on several shoots to complete development (Mo et al. 1997a), and can feed on other plant parts such as flowers, fruits, bark, and sometimes leaves (Mo et al. 1997a).

The same traits that make shoot-borers like *Hypsipyla* such economically destructive forestry pests cause *C. stroudagnesia* to have large detrimental effects on the fitness and potentially the population dynamics of *T. ochracea* (Sullivan 2000b,c). For

example, *C. stroudagnesia* herbivory of just the top shoot was estimated to reduce the height increments of canopy gap saplings of *T. ochracea* by on average 77.9% cm per year, a difference of equivalent magnitude to the difference in height increments between undamaged saplings in canopy gaps and understory shade (Sullivan 2000b). Top shoot herbivory occurred on average once every 2.5 years for canopy gap saplings of *T. ochracea* in Bosque San Emilio. When extrapolated over the prereproductive understory lifetime of canopy gap saplings, this frequency was estimated to increase the age of first reproduction by at least 10 years (45%) (Sullivan 2000b). Top shoot herbivory was also found to increase the probability that canopy gap saplings of *T. ochracea* were overshadowed by surrounding vegetation (Sullivan 2000b), a result which parallels the plantation results of Menalled et al. (1998) with *Hypsipyla grandella* and *Cedrela odorata*.

Some *Hypsipyla* researchers have suggested that mahogany and cedar saplings growing in suboptimal sites are attacked more frequently (Entwhistle 1967, Speight 1997), although the evidence for this is admittedly weak (Newton et al. 1993, Speight 1997). This study suggests the opposite is true for *C. stroudagnesia*. The frequency of attack is highest instead on those fastest growing saplings growing at high light and high moisture sites. This pattern well matches the observed preference for vigorous shoots in both species, and there is some evidence from the *Hypsipyla* - Meliaceae forestry literature suggesting that this is the case (Speight 1997). It is likely that the highest

*Hypsipyla* attack frequencies in wild forests will also be found on the fastest growing saplings. All saplings in high light, high density forestry plantation settings are likely to be infested to some degree by shoot-borers, with those plants in suboptimal sites being the most likely to die following repeated damage. It has been observed that faster growing trees (Newton et al. 1993) and trees on more fertile soils (Cintron 1990, cited in Menalled et al. 1998) are better able to survive repeated *Hypsipyla* herbivory by producing lateral growth.

Given the many similarities in the natural histories of *C. stroudagnesia* and the several studied tropical forestry shoot-borers, it is likely that many tropical tree shoot borers will have effects on the fitness and population dynamics of their hosts in wild forests as large as *C. stroudagnesia* has on *T. ochracea*. By destroying the most vigorous, highest shoots of saplings, shoot-borers are likely to have proportionately far larger effects on the fitness of their hosts than insect herbivores that feed on plant parts such as mature leaves and wood (Janzen 1983). Only the most vigorous saplings in a population recruit to the forest canopy, and by concentrating herbivory on the tops of these few individuals, shoot-borers also have the potential to alter the population dynamics of their host trees far beyond the influence predicted from their small biomass. Understanding the biologies of shoot-borers and other insect herbivores that attack the apical tissues of tree saplings (see Price 1991, Price 1994) will be necessary to understand the dynamics of many tropical tree populations.



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TABLE 1. The shoot entry points of first instar *Cromarcha stroudagnesia* larvae in the first generation, two weeks into the 1997 wet season (7-10 June, n = 37), and in the second generation, in the middle of the wet season (7 October, n = 35). All observations are made on saplings of *Tabebuia ochracea* in secondary successional dry forest. There were no old shoot walls or old shoot tips in June, and new shoot walls and growing shoot tips are very rare in October. “Old shoot wall” refers to a length of shoot tissue that grew at the beginning of the wet season and has since begun to lignify. “Old shoot tips” are those apical meristems that have not produced a second spurt of growth after the veranillo.

# caterpillars entering shoot		
Entry point on shoot	Generation One (June)	Generation Two (October)
Leaf rachis	7 (18.9%)	7 (20%)
New shoot wall	22 (59.5%)	1 (2.9%)
Leaf bud	4 (10.8%)	24 (68.6%)
Growing shoot tip	4 (10.8%)	1 (2.9%)
Old shoot wall	NA	0 (0%)
Old shoot tip	NA	2 (5.7%)

Figure 1. The *Cromarcha stroudagnesia* life cycle closely parallels the phenology of *T. ochracea* sapling shoot growth. **A.** The lengths and shoot-borer status of all shoots was recorded throughout 1997 for eleven understory saplings (between 38-352 cm high and growing in secondary successional dry forest). Plotted is the cumulative shoot length grown per plant, as a percentage of the total shoot length at the end of the year, averaged across all plants (error bars are  $\pm$  one standard error). The appearance of first instar shoot-borer larvae in these shoots can be seen to closely match the two periods of annual shoot growth in *T. ochracea* saplings. The eleven saplings had 119 shoots at the beginning of 1997, which together grew 1380 cm in shoot length and received 73 shoot-borer larvae. By the end of the year, there were 185 shoots, largely due to regrowth from shoot-borer killed shoots. **B.** The life cycle of the two annual generations of tabebuia shoot-borer closely match the growth phenology of *T. ochracea*. The outermost dates of each life stage are the earliest and latest dates that each life stage was observed through collection or rearing. The bulk of individuals occurred in the middle portions of each bar, except for at the onset of the wet season. The life cycle is built from field observations of hundreds of larvae and pupae and the rearing of 116 collected larvae and pupae in 1997. Five larvae and pupae that were collected in the 1997 dry season after substantial searching are

excluded from the graph as they represent a minuscule proportion of the total population.

**C.** Both sapling shoot growth and shoot-borer phenology well match the bimodal pattern of local rainfall. Plotted is the total amount of rainfall per ten days at the Santa Rosa Biological Station < 1 km from the study site through 1997. The initial months without rain are the dry season. The decline in rainfall around day 240 is the “veranillo”.

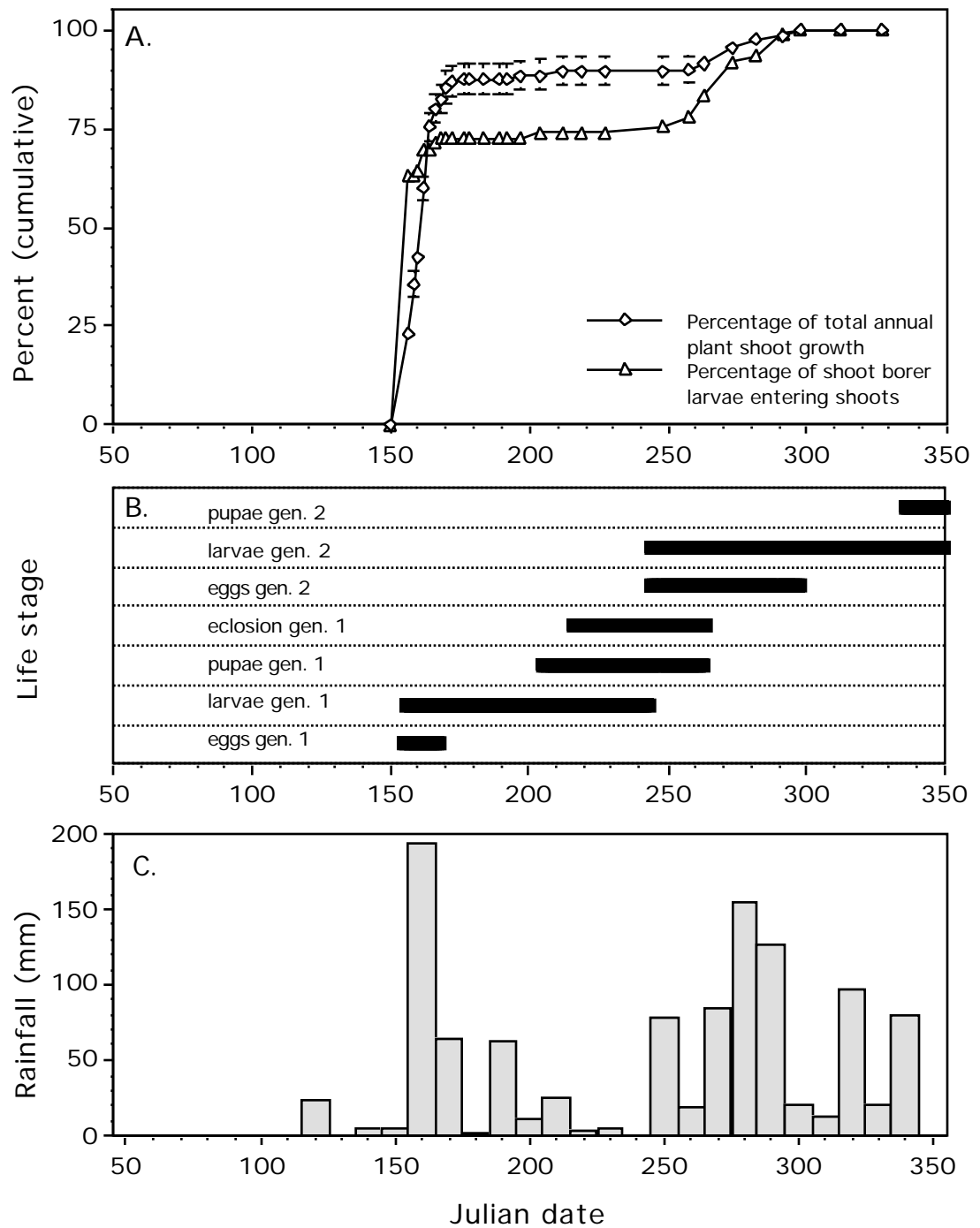




Figure 2. An adult moth (**A**) and last instar larva (**B**) of the tabebuia shoot-borer. The rule in B is centimeters with millimeter gradations. The larva is shown inside a dissected shoot bore of *Tabebuia ochracea*.

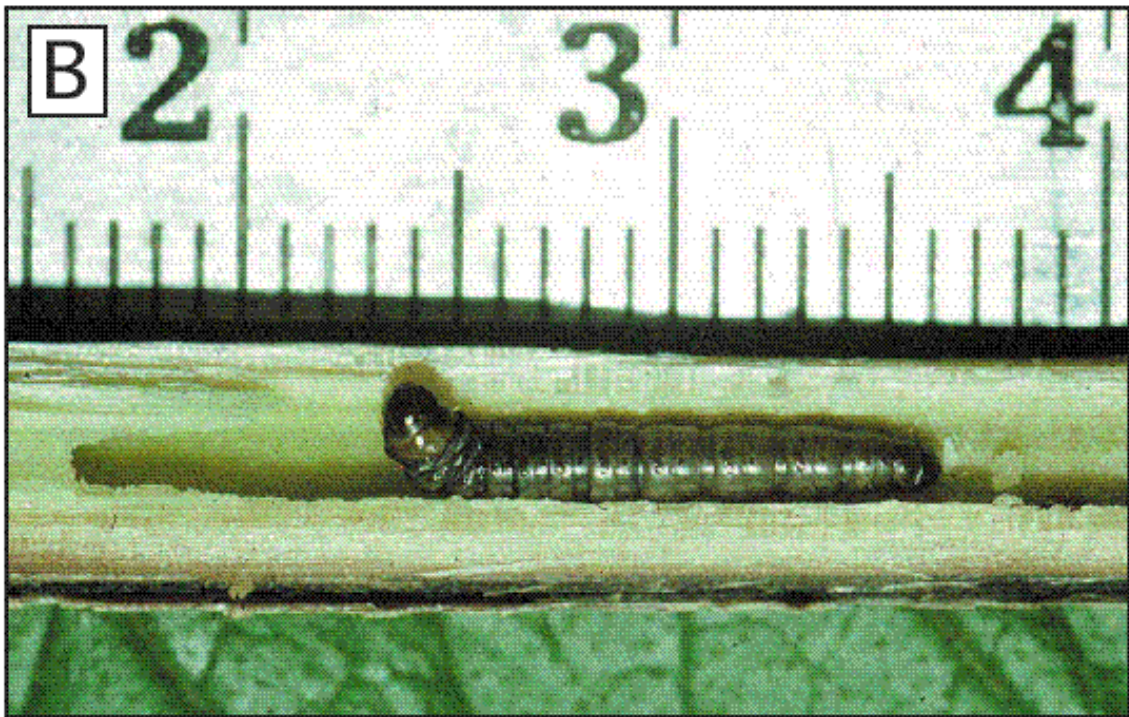
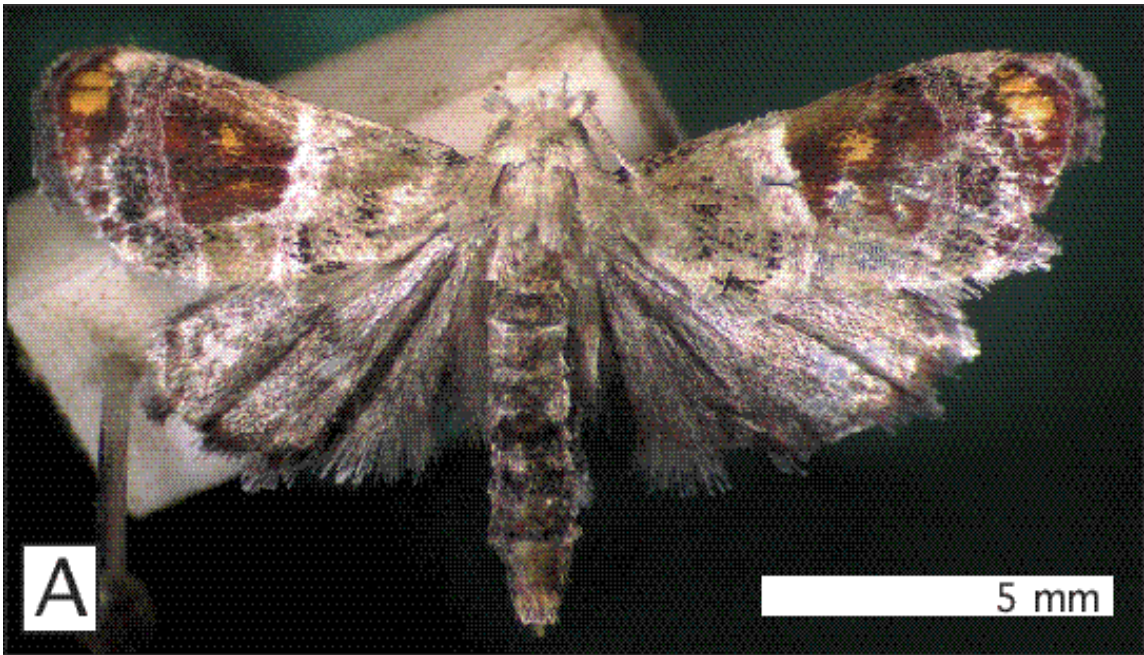


Figure 3. Long shoots are disproportionately infested with *C. stroudagnesia* larvae.

Plotted is the shoot length frequency distribution and percentage of shoots in each length category containing a shoot-borer larvae. These data are from all 889 shoots from 105 study saplings of *Tabebuia ochracea* (between 52 and 449 cm high) through the first half of the 1997 wet season. A total of 18.3% of these shoots were destroyed by first generation shoot-borer larvae.

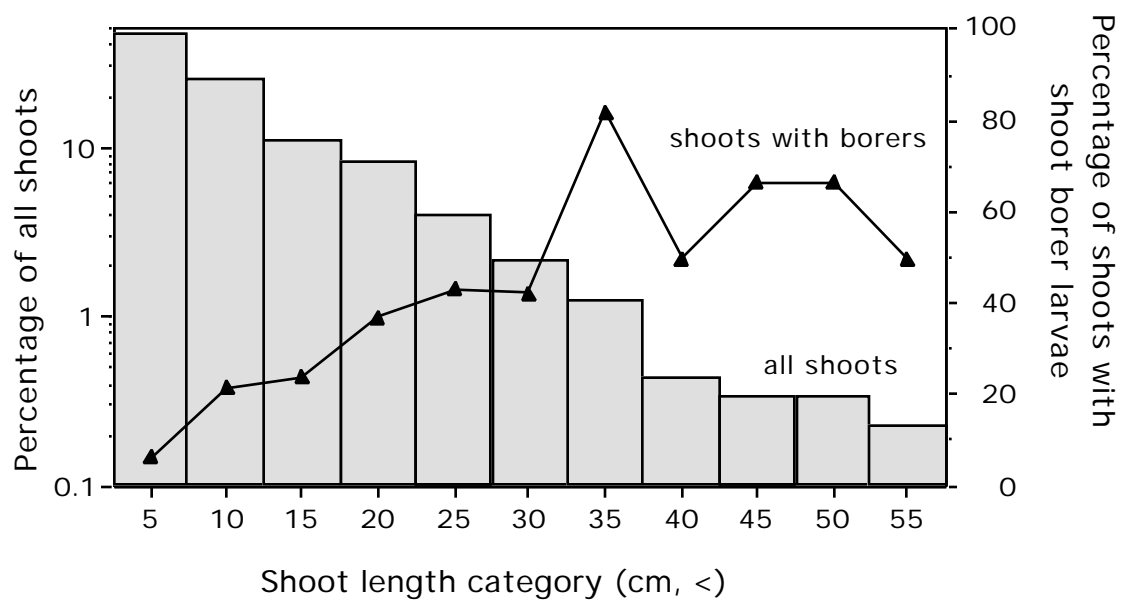


Figure 4. Shoot-borer larvae are most abundant in the shoots of *Tabebuia ochracea* saplings of intermediate height. **A.** The 4 - 5 year long term average percentage shoots attacked by *Cromarcha stroudagnesia* per year is averaged across all 298 study saplings and plotted against 1999 sapling height. Exceptions to this are the two approximately 20 m high trees that were censused in 1996 only (one was a new tree fall, the other was accessed with climbing equipment). 1996 was a year of higher than average shoot-borer herbivory among saplings. **B.** The 4 - 5 year long term average annual probability of the apical shoot of a sapling containing a shoot-borer is shown for the 111 of the above study saplings where shoot status was recorded annually. Saplings are again categorized by final 1999 height. All error bars are  $\pm 1$  standard error, and the number of plants per height category is noted above each bar.

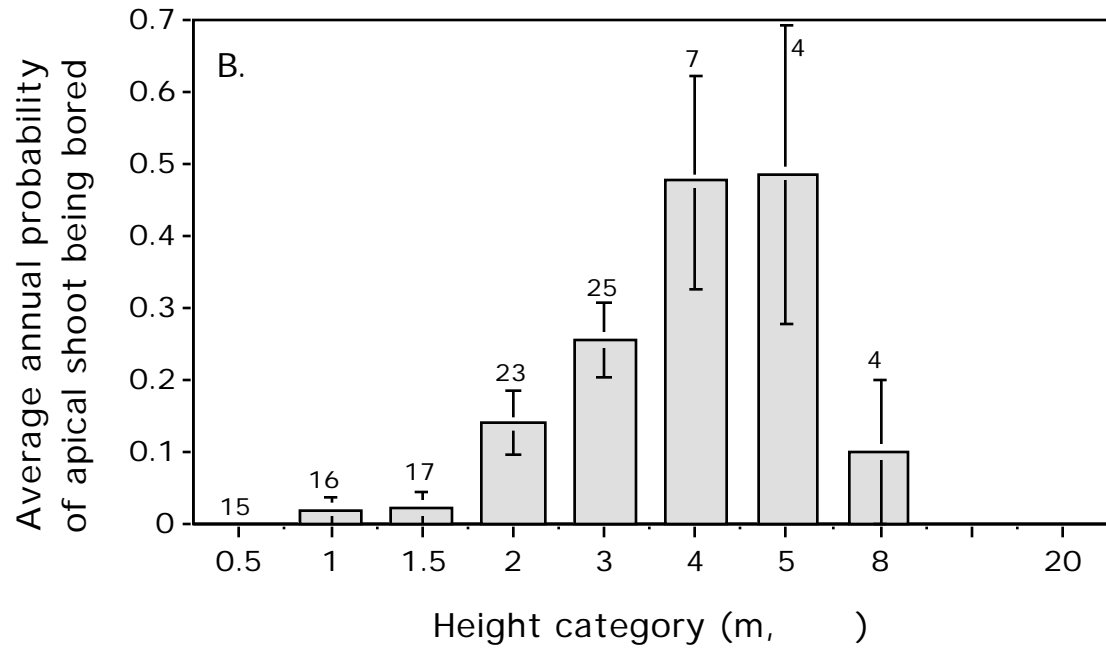
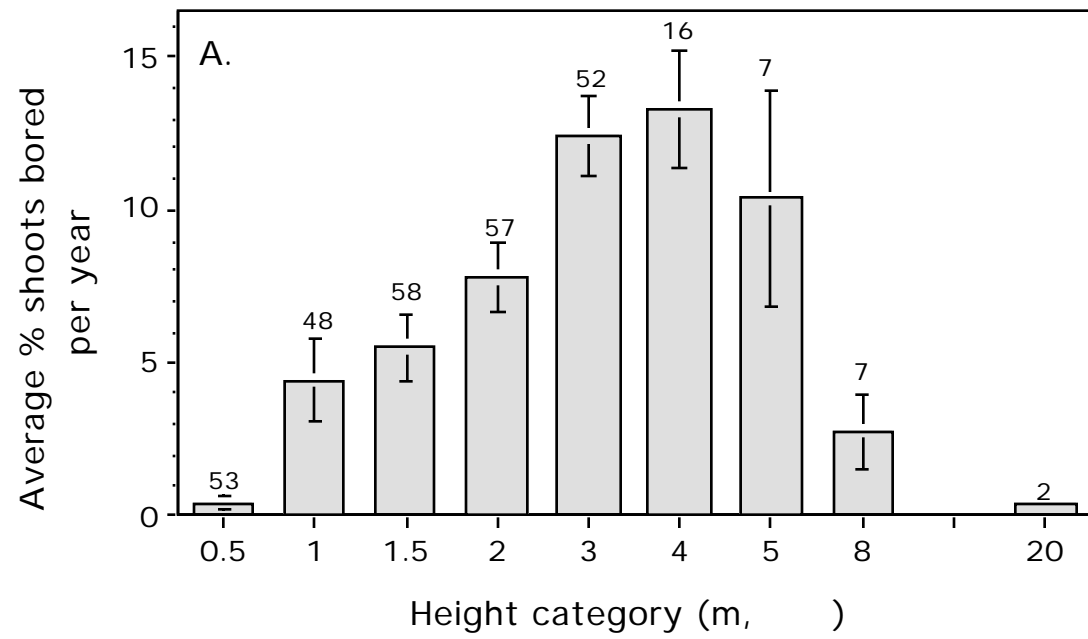
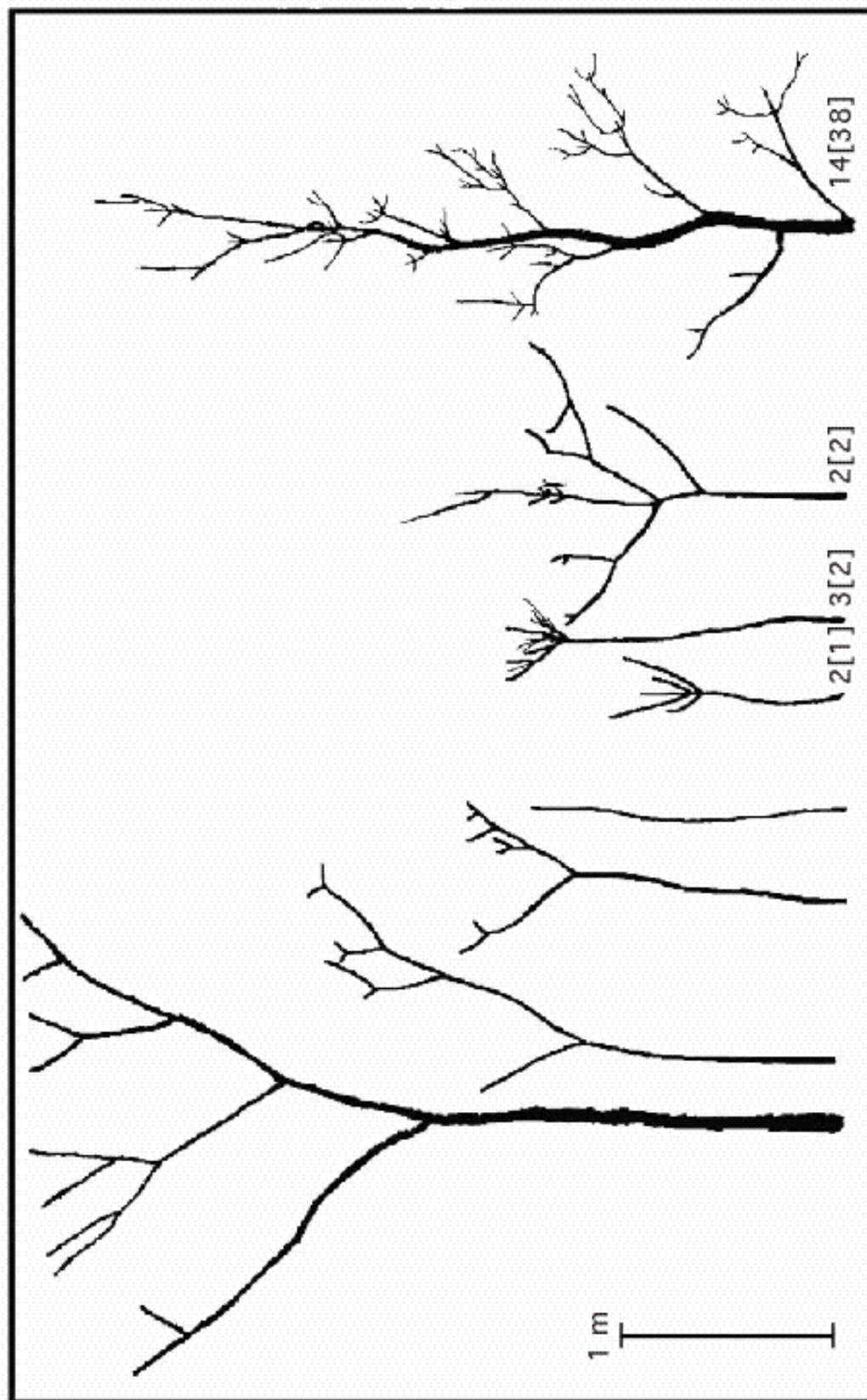


Figure 5. Silhouettes of eight saplings of *Tabebuia ochracea* selected to illustrate the effects of shoot-borer herbivory on plant architecture. The leafless silhouettes were constructed from digital photos of actual saplings growing in secondary successional dry forest around the Santa Rosa Biological Station. The four saplings on the left contained no shoot-borers, and had not been damaged in the recent past. The four saplings on the right had live shoots containing shoot-borer larvae and the remains of old shoots destroyed by borer larvae in past years (characterized by hollow branch ends with a distinctive moth exit hole). The first number at the base of each damaged plant is the number of current shoot-borer larvae, and the bracketed number is the number of dead shoots caused by shoot-borer herbivory.





**CHAPTER THREE: Effects of shoot-borer herbivory of saplings on survival and age of first reproduction of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae)**

*Abstract.*

Shoot herbivory by the sapling specialist shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae) is shown to have large direct and indirect effects on the height increments and mortality of saplings of its host tree, *Tabebuia ochracea* (Bignoniaceae), in the secondary successional tropical dry forests of the Area de Conservación Guanacaste, Costa Rica. The longterm effects of insect herbivory on tropical sapling growth in wild forests are essentially unstudied — these effects were estimated by focusing on the effects of *C. stroudagnesia* herbivory on *T. ochracea* sapling height increment and mortality over four years. An increase in mortality and/or a longterm reduction in the average rate of sapling height increment will alter tree population dynamics and potentially change tree fitness. Experiments and field observations showed that *C. stroudagnesia* herbivory directly reduces the rate of sapling height increment. Top shoot herbivory alone reduces annual sapling height increment by 77.9% in canopy gaps and 83.1% in understory shade, a reduction equivalent to the difference in the height increments of undamaged saplings in canopy gaps and understory shade. Each year, an average 40.1% of canopy gap saplings had their top shoot attacked

by *C. stroudagnesia*. When extrapolated over the prereproductive lifetime of saplings, this frequency results in at least a 45.1% increase in the duration of pre-reproductive sapling lifestage relative to undamaged plants (23.7 years to 34.4 years). Top shoot herbivory by *C. stroudagnesia* was also found to increase the probability of canopy gap saplings being overtopped and therefore shaded by surrounding vegetation, which will indirectly increase the age of first reproduction even further. Sapling mortality was directly increased by *C. stroudagnesia* herbivory — 10% of the heavily damaged young saplings died in four years while no undamaged saplings died. By reducing the rates of height increment, *C. stroudagnesia* herbivory is also predicted to indirectly increase sapling mortality by increasing the likelihood that a sapling is killed by falling debris before it reaches reproductive age. These results suggest that sapling herbivory, especially herbivory of terminal meristems, may play an important but largely unexplored role in the population dynamics of tropical tree species.

## **Introduction**

The cumulative fitness effects of insect herbivory on tree saplings in tropical forests is difficult to assess and poorly understood (Marquis 1992, Barone 1996, Coley and Barone 1996, Hulme 1996). Tropical tree saplings typically lose between 7% and 20% of their aboveground green tissue per year to herbivores (Janzen 1988a, Marquis and Braker 1994, Coley and Barone 1996). Yet assessing the effects of sapling herbivory on

the fitness of individual trees through effects on individual mortality and reproduction is inherently difficult to document, as saplings are typically long-lived, non-reproductive, and die slowly and infrequently (Marquis 1992). Quantifying these effects is important for understanding tropical tree population dynamics and tree species coexistence, as they have the potential to alter recruitment patterns dramatically and the tree species composition of tropical forests (Janzen 1970, Connell 1971, Armstrong 1989, Pacala and Crawley 1992, Tilman and Pacala 1993, Packer and Clay 2000). This study documents the effects of sapling herbivory by a species of shoot-boring lepidopteran on the fitness of one neotropical tree species, by focusing on the effects of herbivory on sapling height increment and mortality in canopy gaps and understory shade.

The fitness of an individual tree is the contribution that tree makes to the next generation, relative to other members of its generation (e.g., Endler 1986). Fitness is especially difficult to measure for long-lived organisms such as trees, but is assumed to be normally correlated with such variables as long-term average seed production and seed quality (e.g., Marquis 1989). Both genetic factors and environmental factors, such as herbivory, interact to determine the fitness of an individual tree. Selective pressure will result if effects of herbivory on individual fitness are correlated with the genetic variation in the population (and evolution will only result if this correlation is consistent over sufficiently large temporal and spatial scales). This study only documents the effects of sapling herbivory on individual tree fitness — the implications of these effects for

selection are not addressed.

Sapling herbivory can potentially reduce tree fitness in several ways. First, herbivory may increase the age of first reproduction, which, all else being equal, will directly relate to fitness (e.g., Charlesworth 1980, Emlen 1984). In forest trees species, saplings typically do not begin to reproduce until they are within close proximity of the forest canopy (Kimmins 1997). Therefore, if herbivory reduces the average height increment over the understory lifetime of a sapling, it will increase the age of first reproduction. Second, herbivory may increase the probability of prereproductive sapling death (fitness = 0). Third, it is plausible, although far less tractable experimentally, that the understory lifetime exposure of saplings to herbivory could decrease reproductive life length and/or decrease the annual reproductive output of adult trees (for example, reduced annual seed set could result from herbivore-induced changes in adult tree architecture, Browne 1968).

Documenting the fitness effects of herbivory on tropical saplings via any of these three mechanisms is complicated by the interactions of herbivory with other variables in a sapling's environment. The interaction of herbivory with a sapling's light environment is likely to be especially important, as most tropical tree species are light-limited in the understory and show gap-phase regeneration (e.g., Swaine 1996). It has been suggested that a reduction in the height increment of canopy gap saplings by herbivory may substantially increase the probability of saplings being over-topped and shaded by

competing saplings, which will in turn further decrease sapling height increment (Janzen 1967, Janzen 1983, Edwards and Gillman 1987, Marquis 1992, Crawley 1997). In this way, any direct effects of herbivory on sapling height increment have the potential to cause further indirect, competition-mediated reductions in height increment (Janzen 1967).

The probability of sapling death may increase not only as a direct result of cumulative losses of resources from herbivory, but also indirectly through a decreased capacity to tolerate shading (Kulman 1971) or pathogen attacks (Marquis and Alexander 1992). If herbivory decreases sapling height increments and therefore increases the time a sapling spends in the understory, the probability of death by falling debris also increases (Clark and Clark 1991, Coley and Barone 1996).

Herbivores that damage sapling apical meristems are especially likely to reduce sapling height increments, and therefore fitness (Janzen 1983, Clark and Clark 1985). Janzen (1983) observed that herbivores that commonly damage the terminal apex of tree saplings will lower the competitive performance of these saplings far more than folivores feeding on leaves. Shoot-borers are one group of herbivores that typically destroy apical meristems and target the terminal apices of the most vigorously growing tree saplings (Price 1991, 1994, Sullivan 2000b). Shoot boring insects can have large effects on tree saplings in tropical timber plantations (e.g., Newton et al. 1993, Speight 1997), and may have similarly large effects on tree fitness in tropical forests (Sullivan 2000b).

This study investigated how herbivory by a sapling specialist shoot-borer, *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae) alters the height increment and mortality of saplings of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae) in northwestern Costa Rica. Specifically, experiments and field observations addressed the following questions; (1) by how much does shoot-borer herbivory reduce sapling height increment and increase sapling mortality?, (2) how does the reduction in height increment vary between canopy gap and understory shade microhabitats?, (3) how does the reduction in height increment due to shoot herbivory compare with the height increment of nonspecific vegetation in natural canopy gaps?

## Methods

### *Study Site*

Sector Santa Rosa (formerly Parque Nacional Santa Rosa) is the historical core of the Area de Conservación Guanacaste (ACG), a 110,000 hectare conserved wildland in northwestern Costa Rica (<http://www.acguanacaste.ac.cr>). Santa Rosa includes a few small fragments of old growth dry forest and large expanses of secondary successional tropical dry forest between 0 - 400 year old, regenerating on abandoned cattle pastures, agricultural fields, and logged areas (see Janzen 1986, 1988b, 1992). It was subject to extensive anthropogenic fires for three centuries prior to 1985. The dry forests of sector Santa Rosa and neighboring sectors are the largest area of conserved dry forest in Central

America, a habitat that once covered the Pacific coastal lowlands and parts of the Atlantic coastal lowlands of Central America (Janzen 1988b, Gillespie et al. 2000). Within the ACG, Santa Rosa is bordered by conserved marine habitats in the Pacific Ocean to the west and sectors of progressively wetter conserved forests to the east, including cloud forest and Atlantic rain forest.

Average annual rainfall at the Santa Rosa Biological Station during the four years of the study (1996-1999) was 2076 mm (s.d. = 706), which included the wettest and fifth driest years since 1980. The local climate is highly seasonal, dominated by a pronounced 6-month dry season from December to mid May when essentially no rain falls. During much of the dry season, most individual trees in all but the oldest fragments of forest are nearly leafless, contrasting with the completely foliated forests throughout the 6-month wet season (see Janzen 1993). Rainfall is typically heaviest in May - June and September - October, and there is a lull in rainfall for 2 - 6 weeks in July - August called the “veranillo” (little dry season).

All experiments and field observations in this study were made in forests on the Santa Rosa upland plateau (*c.* 300 m elevation). All longterm study saplings are located in forests surrounding the Santa Rosa Biological Station (10° 50' 27.26'' N latitude , 85° 37' 14.26'' W longitude), including within the Bosque San Emilio forest plot, a 16.3 ha plot in 80 - 100 year old secondary successional forest (Stevens 1987, Enquist et al. 1999). All experiments were located in an approximately 1.5 hectare area of a secondary successional

forest 3.6 km to the north-northwest of the biological station, near the border between sector Santa Rosa and the Santa Elena peninsular. This forest was chosen for its combination of ease of access (along an old farm road), relatively large distance from the biological station and its surrounding research plots, low canopy (mostly 5 m - 15 m), and high density of *T. ochracea* saplings. Sullivan (2000a) presents a map with the locations of these study forests.

### *Study species*

*Tabebuia ochracea* (Chamisso) Standley (Bignoniaceae) is a neotropical dry forest tree up to 30 m tall and  $> 0.5$  m dbh with palmate five-foliate tomentose leaves (see Gentry 1983, Gentry 1992, Sullivan et al. 1998, Sullivan 2000a for full description). The species is famous throughout Central America for its brief, spectacular, population-wide synchronized displays of large yellow flowers in the dry season, at which time a great many trees (and therefore areas with saplings) could be easily located. *Tabebuia ochracea* has shade-tolerant saplings that require canopy gaps for most understory height increment (Swaine and Whitmore 1988, Sullivan 2000a). Undamaged *Tabebuia* saplings are characterized by an apical branch and successive pairs of lateral branches, with the longest shoots being found on the apical branch (c.f., Borchert and Tomlinson 1984, Borchert and Honda 1984, Sullivan 2000a). I defined saplings as any *T. ochracea* juvenile 50 cm high (*sensu* De Steven 1994), which corresponds with well established plants



usually much greater than 5 years old (Sullivan 2000a).

The tabebuia shoot-borer, *Cromarcha stroudagnesia*, (Lepidoptera, Pyralidae, Chrysauginae)(Solis ref, Sullivan 2000b) commonly bores into the shoots of saplings of *Tabebuia ochracea* and the much less abundant *T. impetiginosa*. Each larva typically destroys a single shoot, killing the apical meristem and as many nodes as are bored through. *Cromarcha stroudagnesia* is a sapling specialist. Larvae typically destroy between 5-15% of the shoots of understory saplings per year, but are largely absent from juvenile *T. ochracea* <50 cm high, and occur at very low frequencies (about 0.4% of shoots per year) in adult crowns (Sullivan 2000b). There are two generations of larvae per wet season, the first from beginning at the onset of the wet season in mid-May to late-August, and the other beginning after the veranillo, in September to December. See Sullivan 2000b for a detailed account of the natural history of *C. stroudagnesia*.

*Cromarcha stroudagnesia* is one of at least 36 insect species that feed on aboveground parts of *T. ochracea* saplings in the Santa Rosa forests (Janzen and Hallwachs 2000, J. J. Sullivan, unpublished data). No evidence of vertebrate browsing of *T. ochracea* sapling leaves in Santa Rosa has been found (*personal observation*), and a Baird's tapir (*Tapirus bairdii*) rejected *T. ochracea* leaves in feeding trials (Janzen 1982)).

### *Experimental designs*

In the dry season of 1997, 582 wild naturally established saplings between 70 cm

and 150 cm high were found in the experiment forest. Canopy gaps were cleared above each of these saplings through the first months of the 1997 wet season. This was done by decapitating understory vegetation and climbing trees and sawing off branches. These gaps were maintained throughout the experiment. All saplings were randomly assigned to either light or shade treatments. Shade saplings were shaded with a double layer of opaque nylon sacking that was suspended above each sapling with nylon twine (Fig. 1). This shading material reduced light levels to 3 - 4 % of full sunlight, which is within the range of light intensity of understory shade in local successional forests in the wet season. To better mimic canopy gaps and prevent side-lighting from causing uncontrolled variation in sapling growth rates (Whitmore 1996), both shade and light treatment saplings were also laterally shaded to the east and west with nylon sacking (Fig. 1).

These 582 saplings were randomly segregated into three experimental designs, each of which was run for three years, terminating in December 1999.

### I. Herbivory experiment

The herbivory experiment tested for the effects of shoot herbivory on sapling growth in the light and shade treatments. 360 saplings were randomly allocated to each of three artificial shoot herbivory treatments: two shoots damaged per shoot-borer generation (four per year, hereafter denoted “2x2”), two shoots damaged per year (see below), and no damage (denoted “0x0”). These damage levels span the range of naturally

observed average annual shoot herbivory for saplings of this height range (Sullivan 2000b). Three further treatments were nested within the intermediate damage category to assess the importance of the timing of herbivory. These treatments were two shoots damaged in the first generation and none in the second (hereafter denoted “2x0”), two shoots damaged in the second generation and none in the first (denoted “0x2”), and one shoot damaged each generation (denoted “1x1”).

Wild shoot-borers were excluded from experimental saplings by lightly wrapping 2 cm wide strips of nylon sacking material around shoots and coating the strips with TangleTrap adhesive (<http://www.tanglefoot.com>). These strips were only applied during the two egg laying periods of each year, being the first three weeks of the wet season and the month from mid-August through mid-September (Sullivan 2000b). This method prevented wild shoot-borer herbivory, as the vast majority of larvae enter shoots by eating through the shoot wall or a lateral bud (Sullivan 2000b). Very rarely larvae will enter shoots through leaf petioles (Sullivan 2000b) - such attacked leaves were manually removed before each larva had entered the shoot. At the end of the experiment, the few *C. stroudagnesia* attacked saplings were excluded from the design, and the experiment was randomly balanced at a reduced sample size (see below).

Artificial shoot-borer damage was performed with a rechargeable drill with a 2.0 mm diameter drill bit. The average shoot bore length for wild caterpillars is 14.8 cm long and is created over *c.* 6 weeks (Sullivan 2000b). This damage was mimicked by drilling out

5 cm from the pith of each selected shoot every two weeks for six weeks. For each treatment, the longest shoot(s) of each sapling were selected for damage, as wild shoot-borer herbivory is strongly biased towards the longest shoots (Sullivan 2000b). When shoots were shorter than 15 cm, the pith was drilled out from all of a given year's shoot but none from the previous year's stem growth, again matching the behavior of wild shoot-borer larvae. Between each plant, the drill bit was cleaned and sterilized by flaming with 90% ethanol.

## II. Larval transplant experiment

A larval transplant experiment tested whether drill damage and shoot-borer larva damage had significantly different effects on sapling growth. Sixty saplings were randomly allocated to drill and larval transplant treatments. Each treatment damaged one shoot per sapling per generation (two per year, "1x1"). Young larvae were collected from shoots from surrounding areas of forest. Each larva was left inside a portion of its shoot and tied with twine to an experimental shoot. Each sapling was inspected every 1 - 2 days, and the frequent failed transplants were replaced with fresh larvae until a larva successfully entered each experimental shoot. This method proved far too time consuming and unreliable to apply to the main herbivory experiment.

### III. Tangletrap experiment / Supplemental herbivory experiment

The third experiment tested whether the TangleTrap shoot-borer exclusion method itself affected sapling growth. The Tangletrap method was applied to 61 saplings, and another 74 saplings were left unprotected for the duration of this experiment. All *C. stroudagnesia* attacked saplings were removed.

#### Experiment data collection

In all experiments, each shoot of each sapling was labeled with a unique coding of four colored beads loosely attached to the sapling with thin copper wire. New shoots from natural branching or regrowth events received new, unique labels. Twice a year, the shoot length, number of mature leaf nodes, and status (natural branching, regrowth from drill damage, regrowth from shoot-borer larva damage) were recorded per shoot. Sapling height was recorded with a measuring tape (kept vertical with a small fishing lure weight), and stem diameter was recorded at 30 cm above the soil surface across the thickest horizontal axis with vernier calipers.

Leaf areas of all mature leaves were estimated for a random eight saplings per insolation x damage level treatment from the herbivory experiment. Leaf areas were estimated from measures of the length and width of the longest leaflet ( $L_l$  and  $L_w$  respectively) and shortest leaflet ( $S_l$  and  $S_w$  respectively) per leaf, using the following allometry equation.

$$\text{Leaf area (cm}^2\text{)} = 44.88 + 1.14*(1.1*(L_l*L_w) + 0.5*\pi*(S_l*S_w))$$

This equation was generated from the allometry of 80 haphazardly collected wild sapling leaves, for which actual leaf area was calculated using digital photos and the histogram function of Adobe Photoshop 4.0 (linear regression  $P < 0.001$ ,  $R^2 = 0.885$ ). The latter technique was too time consuming to apply to the experimental saplings.

Over the course of the experiments, a scattering of saplings died, were attacked by wild larvae, or were inadvertently damaged. For all analyses, these saplings were removed and all experiments were randomly rebalanced. The herbivory experiment was reduced to 51 saplings per insolation x main damage level treatment combination ( $n = 306$ ). The larval transplant experiment was reduced to 15 saplings per insolation x damage type treatment combination ( $n = 60$ ). The TangleTrap experiment was reduced to 30 saplings per insolation x exclusion method treatment combination ( $n = 120$ ).

Soil moisture readings were made at the base of each study sapling in 1999 with a Rapidtest Mini Moisture Tester (Luster Leaf Products, Inc., Woodstock, IL, USA). All readings were taken at 10 cm depth, approximately 1 m from the base of each sapling. These readings were calibrated using percentage soil moisture measurements from local soil dehydrated at 68 degrees Celsius in a drying oven until stable weight. Readings were made on August 7, in the middle of the 1999 veranillo and after four days without any rain. Any differences in recorded soil moisture among the experimental saplings and wild study saplings (see below) should therefore represent true variation in soil water retention

rather than any recent local spatial variation in rainfall.

#### *Observations in canopy gaps and understory shade*

Between November 1996 or July 1997 and July 1999, the growth of *T. ochracea* saplings and surrounding vegetation were recorded for 24 treefall canopy gaps in the Bosque San Emilio longterm forest plot. Each gap contained at least one *T. ochracea* sapling that was initially of equal or greater height than the surrounding gap vegetation. The height, diameter, and top shoot herbivory status were recorded each July and November for the 48 *T. ochracea* sapling(s) in each of these canopy gaps. Sapling height was measured with a weighted measuring tape attached to an up to 7 m long telescoping pole. Sapling stem diameters were recorded 30 cm above the soil surface across the thickest horizontal axis with vernier calipers. Each canopy gap sapling was paired with a similarly sized sapling ( $\pm 1.5$  m height) in understory shade  $> c. 15$  m from the edge of the gap, and identical measurements were taken for these shaded saplings. Initial sapling heights ranged from 52 cm to 663 cm.

Each November (July in 1999), a graduated telescoping pole was used to record the height of the highest vegetation at the four points 3 m in each compass direction from the base each canopy gap *T. ochracea* sapling. The highest vegetation at each point was identified, and a digital photo was taken. At the end of the study, the height increment at each point was classified as either “gap growth” or “canopy closure”. Canopy closure

was defined as any new lateral growth into the gap by a large individual sapling or tree on the gap edge that increased the vegetation height at a sampling point by more than 2 m.

In the first week of August, soil moisture measurements were made at the base of each sapling with the same method described above.

### *Analysis*

All analyses were performed using SPSS for Macintosh version 6.1.1 (<http://www.spss.com>). Experimental data were analyzed with fixed-effects two-way ANCOVAs, with initial height, initial diameter, and 1999 soil moisture used as covariates. Where necessary, experimental variables were square-root transformed to produce nonsignificant heterogeneity of variances with Cochran's test (Underwood 1997). Observational data were analyzed with fixed effects two-way ANOVAs and independent samples t-tests. To avoid pseudoreplication when analyzing the observational data for differences in annual height increments with and without top shoot herbivory, a single year's height increment was randomly selected from each sapling to represent one of either of the two states. A G-test for independence using the William's correction was used to analyze for effects of shoot herbivory on sapling mortality (Sokal and Rohlf 1995).



## Results

### *Shoot herbivory effects on sapling growth and mortality: experimental results*

Artificial shoot herbivory had large detrimental effects on sapling growth (Table 3, 4, Fig. 2, 3). For most growth variables measured, the effects of shoot herbivory were greater over the three year study than the effects of the insolation treatment (Fig. 2, 3). Both the intermediate (two shoots damaged per year) and high (four shoots damaged per year) levels of shoot damage significantly reduced sapling height increment, diameter increment, shoot length, number of leaves, and average leaf area (Table 3, 4, Fig. 2, 3). While shoot damage significantly increased the number of shoots (Table 3), total leaf area was significantly reduced by shoot damage at the damage frequency of four shoots per year (Table 4). The reduction in height increment and total shoot length in damaged saplings relative to undamaged saplings was significantly greater for insulated saplings than shaded saplings (Fig. 2, Table 3).

The timing of shoot damage within a year also significantly affected sapling growth (Fig. 4). At the end of the study, saplings damaged once each shoot-borer generation (“1x1”) had a significantly lower average height increment than saplings receiving either two shoots damaged in the first or second shoot-borer generations (“2x0” and “0x2”) (two-way fixed effects ANCOVA,  $SS = 67.65$ ,  $F = 5.04$ ,  $P < 0.01$ ,  $n = 102$ ). There were no significant effects of the timing of shoot damage on diameter increment, shoot length, number of shoots, number of leaves, or average leaf area (saplings damaged

once each shoot-borer generation tended to have fewer, and shorter shoots).

Sapling mortality was unrelated to insolation but substantially increased by shoot damage (G-test for independence of shoot damage and mortality,  $G = 24.09$ ,  $P < 0.01$ ,  $n = 345$ ). Thirteen saplings died over the course of the herbivory experiment (3.6%). Twelve of these were in the highest damage frequency treatment, with six saplings dying in each of the insolation treatments. An additional, shaded sapling died in the intermediate damage treatment. No undamaged saplings died.

#### *Larva Transplant Experiment*

No significant differences were found between transplanted *C. stroudagnesia* larvae and three-stage shoot drilling for any of the recorded sapling growth variables: height increment, diameter increment, final total shoot length, shoot number, or leaf number (Table 1). As expected, shading significantly reduced sapling growth for all growth variables (Table 1). The power for the larva-drill treatment was low for most growth variables (Table 1), making it impossible to conclude with confidence that there were no real differences in sapling growth between larval transplants and drilling. However, there were also no consistent trends in the data between drill and larva damaged saplings. Also, more often than not the effects of drilling on sapling growth were slightly less than the effects of transplanted larvae (Table 1). The effects of drill damage are therefore conservative estimates of the effects of *C. stroudagnesia* larvae on the measured

sapling growth variables.

#### *TangleTrap exclusion experiment*

There were no significant differences found between the growth of naturally undamaged saplings and saplings protected from shoot-borers by the TangleTrap exclusion technique (Table 2). As in the larva-drill experiment, shading significantly reduced sapling growth for all growth variables (Table 2). Also as in the larva-drill experiment, there was insufficient power to conclude with confidence that there were no real main effects of TangleTrap application on sapling growth, although there were no consistent effects across growth variables (Table 2).

Significant interactions were found between the insolation and TangleTrap treatments for total shoot length and total number of leaves per sapling (Table 2). Both shoot length and number of leaves were greatest for TangleTrap protected saplings in the light treatment and greatest for control saplings in the shade treatment. Planned comparisons found no significant differences between TangleTrap versus control plants in either light or shade, and the magnitude of these significant interactions was minor in comparison to the magnitude of the insolation treatment effects (Table 2). This interaction could have resulted from the biased exclusion from the control treatment of the fastest growing saplings, as these are most likely to have been attacked by wild *C. stroudagnesia* larvae (Sullivan 2000b).

*Shoot herbivory effects on sapling height increment, mortality, and age of first reproduction: observational data*

Despite the strong effects of shoot herbivory on sapling growth revealed by the herbivory experiment, there were no significant relationships between wild sapling height increment and the total percentage of shoots bored, for both shaded saplings and canopy gap saplings (Fig. 5). However, unlike in the experiments, wild shoot-borer herbivory is not distributed randomly with respect to sapling condition. Instead, shoot-borer abundance is strongly biased towards the longest shoots of the fastest growing wild saplings (Sullivan 2000b).

Strong negative effects of shoot herbivory on height increment were found when only herbivory on the top shoot was considered, and one 12-month interval was selected per sapling representing either no top shoot herbivory or a single attack by *C. stroudagnesia* (Fig. 6). Both top shoot herbivory and understory shade significantly reduced sapling height increment (Table 5). Attack of the top shoot by a single *C. stroudagnesia* larva decreased the height increment in that 12 month interval by 77.9% in canopy saplings, and by 83.1% in understory shade saplings (Fig. 6). These 12 month intervals include the height increment of saplings in the six months following a shoot-borer attack, and so include any compensatory shoot growth that follows shoot herbivory. The top shoot is typically among the longest and most frequently attacked shoots on a sapling, and the top shoot of even a heavily shaded sapling can be sufficiently

long to support the development of a *C. stroudagnesia* larva (Sullivan 2000b).

Canopy gap saplings had their top shoot attacked by *C. stroudagnesia* larvae significantly more frequently than shaded saplings ( $t = -3.39$ ,  $P < 0.01$ ,  $n = 96$ ). Between 1996 and 1999, 71.4 % of saplings in canopy gaps and 52.9 % of saplings in understory shade had their top shoot attacked at least once by a *C. stroudagnesia* larva. The average probability of a canopy gap sapling having its top shoot bored in a year was 0.401 (s.d. = 0.321,  $n = 48$  saplings), equivalent to one top shoot bored every 2.5 years. The frequencies of top shoot herbivory for canopy gap saplings over the four year study ranged from 13 saplings (27%) that were never attacked to four saplings (8.3%) that attacked every year. The average probability of an understory shade sapling having its top shoot bored in a year was 0.219 (s.d. = 0.258,  $n = 48$  saplings).

Only one of the 96 wild saplings died during the study. This sapling was initially 196 cm high, and grew in understory shade. In the year before its death, eight of its nine shoots were attacked by *C. stroudagnesia* larvae. This was the highest percentage shoot herbivory recorded for any study sapling in any year.

*Canopy gap growth rates relative to T. ochracea sapling height increment with and without shoot herbivory*

To compare the height increments of *T. ochracea* saplings with the height increments of the surrounding gap vegetation, two 12-month height increments were

randomly selected from each canopy gap sapling, one interval without top shoot herbivory and the other with a single top shoot attacked. If the top shoot of a sapling was never attacked, a random 12 month interval was selected. These increments were then compared with the annual height increments of canopy gap vegetation at four points surrounding each sapling (excluding canopy closure) (Fig. 7).

These data show that it is unlikely that canopy gap saplings that have their top shoots repeated attacked by *C. stroudagnesia* will remain at the top of canopy gap vegetation (Fig. 7). The height increments of *T. ochracea* saplings in years with no top shoot herbivory were on average slightly greater than the average height increment of the surrounding vegetation, but less than the maximum height increment of the surrounding vegetation (Fig. 7). The height increments of the *T. ochracea* saplings in years *with* top shoot herbivory were on average less than both the average and maximum height increments of the surrounding vegetation (Fig. 7). In years with no top shoot herbivory, saplings had significantly greater height increments relative to gap vegetation than in years with top shoot herbivory (one-way paired t-test,  $t = 2.05$ ,  $P = 0.027$ ,  $df = 20$ ). For three of the 48 *T. ochracea* study saplings over the four years of this study, the reduction in height increment due to top shoot herbivory made the difference between a positive and negative height increment relative to the maximum height increment of the surrounding vegetation.

## Discussion

Shoot herbivory by larvae of *C. stroudagnesia* on saplings of *Tabebuia ochracea* are decreasing the height increments and increasing mortality rates of *T. ochracea* in the successional forests of Sector Santa Rosa of the Area de Conservación Guanacaste. Top shoot herbivory alone reduced annual sapling height increment by 77.9% in canopy gaps and 83.1% in understory shade (Fig. 6). This effect was equivalent to the effects of understory shade on sapling height increments: average understory shade sapling height increments were 17% of canopy gap sapling height increments (Fig. 6). Artificial shoot herbivory mimicking *C. stroudagnesia* herbivory reduced height increments of small saplings by 89.0% in the light and 91.5% in the shade in the intermediate damage frequency of two shoots per year. These effects were greater than the reduction in height increment caused by shading saplings (Fig. 2). The highest frequency of artificial shoot herbivory increased mortality from 0% to 10% of saplings over the three year experiment, and the only wild study sapling that died during the study was heavily attacked by *C. stroudagnesia* larvae in the previous year.

These large effects of *Cromarcha stroudagnesia* herbivory on sapling growth and survival are likely to translate into large detrimental effects on the fitness of *T. ochracea*, by increasing mortality rates and increasing the age of first reproduction. An estimate of the effects of *C. stroudagnesia* on the age of first reproduction of *T. ochracea* can be made by linearly extrapolating the height increments from Fig. 6 to the prereproductive

life length of saplings. This is because the average annual height increment of saplings is unrelated to initial height (Sullivan 2000a), and the minimum height of first reproduction for *T. ochracea* in closed canopy forest is around 10 m (Sullivan 2000a).

If it is assumed that a canopy gap sapling remains at the top of gap vegetation throughout its life regardless of height increment, extrapolating the sapling height increment data predicts that a 50 cm high canopy gap sapling that never has its top shoot bored by a *C. stroudagnesia* larva will on average reach 10 m high and begin reproducing after 23.7 years (Fig. 8). Since canopy gap saplings have their top shoot attacked by a *C. stroudagnesia* on average every 2.5 years, the average 50 cm high canopy gap sapling would not first reproduce until after 34.4 years (again, if it remained at the top of the canopy gap vegetation and was not therefore slowed further by shading)(Fig. 8). This corresponds to a 45.5% increase in the age of first reproduction solely due to *Cromarcha stroudagnesia* larvae attacking top shoots at the average observed frequencies. An average 50 cm high canopy gap sapling with its top shoot attacked by a *C. stroudagnesia* larva every year would not first reproduce until after 107.3 years (Fig. 8). The frequencies of top shoot herbivory for canopy gap saplings over this four year study completely spanned this range.

This extrapolation to the understory lifetime of saplings is likely to substantially underestimate the effects of *C. stroudagnesia* on the age of first reproduction, as it applies only to canopy gap saplings that remain at the top of the gap vegetation



throughout their understory lives. The canopy gap vegetation data show that it is common for *T. ochracea* to be overtopped by neighboring vegetation, and that the probability of being overtopped is increased by *C. stroudagnesia* larvae attacking the top shoots. The magnitude of this indirect effect of top shoot herbivory on sapling height increment is difficult to estimate but is potentially large.

*Cromarcha stroudagnesia* larvae also reduce *T. ochracea* fitness by increasing sapling mortality. However, very few saplings experience *C. stroudagnesia* herbivory at the high frequencies that resulted in the 10% mortality in the experiment, and any general increase in mortality from lower attack frequencies of *C. stroudagnesia* on *T. ochracea* saplings is likely to be more subtle and indirect than could be revealed by this study.

For example, by decreasing sapling height increments, *C. stroudagnesia* herbivory is likely to indirectly increase sapling mortality by increasing the likelihood of a sapling being crushed during its life span by falling debris. Clark and Clark (1991) assessed the frequency of falling debris and its consequences for seedlings and saplings in the rain forest of the La Selva biological station, Costa Rica. While mortality due to falling debris was much higher for seedlings (< 1 cm dbh), this physical damage was a proportionately more important agent of mortality for saplings (Clark and Clark 1991). Total annual mortality due to falling debris for saplings >1 - 30 cm dbh was 0.36% (Clark and Clark 1991). A similar rate (minimum = 0.22%) was estimated for *T. ochracea* in Santa Rosa based on a much smaller sample size (Sullivan 2000a). If Clark and Clark's (1991) rate is

applied to the prereproductive lifetime extrapolation of *T. ochracea* sapling height increments (Fig. 8), average frequencies of top shoot herbivory will increase prereproductive mortality due to physical damage from 8.2% to 11.7% in canopy gaps, and from 39.4% to 52.9% in understory shade. While these number are unlikely to be accurate, they illustrate how *C. stroudagnesia* herbivory is likely to indirectly increase *T. ochracea* prereproductive mortality by increasing the period of time that saplings are exposed to the risk of lethal collisions with falling debris.

The large fitness effects of *C. stroudagnesia* on *T. ochracea* may be an historically recent phenomenon. The probability of a *T. ochracea* shoot being attacked by *C. stroudagnesia* is increases with sapling density (Sullivan 2000c), and the understory densities of *T. ochracea* in the secondary successional forests of this study are much higher than in the darker understory of Bosque Humedo, a local old growth forest fragment (Sullivan 2000a). It is likely that *T. ochracea* sapling densities would also have been similarly low in the extensive old growth tropical dry forests that existed before European settlement of Costa Rica.

Most of the neotropical dry forests are now successional forest of some sort, and the increased understory densities of saplings combined with the lower densities of mammalian herbivores due to overhunting and fragmentation (Dirzo and Miranda 1991), may mean that insect herbivory on saplings has a greater influence on tree fitness now than it once did. Before human hunter settlement of the neotropics >10,000 years ago,

when gomphotheres and ground sloths walked Santa Rosa's forests, tree saplings would have encountered a very different set of impediments to canopy recruitment. *Tabebuia ochracea*'s lack of effective defenses against *C. stroudagnesia* may be as much a neotropical anachronism as are the many giant megafauna dispersed fruits found in Santa Rosa's tree flora (Janzen and Martin 1982).

The interactions between *C. stroudagnesia* and *T. ochracea* demonstrated here indicate that sapling herbivory can have large effects on tree fitness in modern tropical forests. *Cromarcha stroudagnesia* is only one of more than 36 insect herbivores that feed on the aboveground tissues of *T. ochracea* saplings, and the total cumulative effect of all these species on *T. ochracea* prereproductive mortality and age of first reproduction is likely to exceed the effects of *C. stroudagnesia* alone. *Tabebuia ochracea* is not exceptional among the tree species of Santa Rosa's forests in either the size of its herbivore fauna or the presence of apical meristem feeding insects (Janzen and Hallwachs 2000, Sullivan 2000b). It is likely that sapling herbivory by insects in Santa Rosa's successional forests reduce the fitness most, perhaps all, of the local tree flora to some degree.

How the large fitness effects of *C. stroudagnesia* on *T. ochracea* translate into selection pressures and altered population dynamics remains to be discovered. It is unknown how well the variation in *C. stroudagnesia* herbivory among saplings maps onto genetic variation in the local *T. ochracea* population. Until this is known, the magnitude

of the selective pressure that *C. stroudagnesia* represents for *T. ochracea* in Santa Rosa cannot be estimated.

It is likely that *C. stroudagnesia* is altering the population dynamics of the Santa Rosa *T. ochracea* population, by decreasing the rates of canopy recruitment and the potential rate of population increase. Since *C. stroudagnesia* herbivory increases with sapling density (Sullivan 2000c), it is also possible that *C. stroudagnesia* sapling herbivory will play an important role in limiting the local abundance of *T. ochracea* and enhancing species coexistence in Santa Rosa's tropical dry forests (*sensu* Janzen 1970, Connell 1971, Armstrong 1989, Pacala and Crawley 1992).

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TABLE 1. The effects of larva transplants versus rechargeable drill shoot damage (“Larva-drill”) and shade versus direct sunlight (“insolation”) on the growth of 60 small saplings of *Tabebuia ochracea*. Shown are the results of two-way fixed effects ANCOVAs, with relative soil moisture and each respective initial growth variable as covariates. For each growth variable, the non-adjusted averages and standard errors for each treatment combination are shown to the right of the table.

Dependent variable	Treatment	df	SS	F	P (Power)*	Average (standard error)		
						Light	Shade	
Total shoot length (cm)	Larva-drill	1	0.48	0.31	0.582(0.049)	Drill	20.6(3.8)	14.3(2.8)
	Insolation	1	7.25	4.61	<b>0.036</b>			
	Interaction	1	0.65	0.41	0.523(0.075)	Larva	18.9(3.1)	15.3(2.9)
	Error	54	84.92					
Number of shoots	Larva-drill	1	0.25	1.92	0.172(0.274)	Drill	3.93(0.4)	3.40(0.3)
	Insolation	1	0.75	5.68	<b>0.021</b>			
	Interaction	1	0.05	0.41	0.523(0.075)	Larva	3.80(0.4)	2.87(0.3)
	Error	54	7.09					
Number of nodes	Larva-drill	1	1.05	3.42	0.070(0.442)	Drill	6.13(0.7)	4.73(0.6)
	Insolation	1	1.44	4.67	<b>0.035</b>			
	Interaction	1	0.65	2.11	0.152(0.296)	Larva	4.93(0.9)	4.73(0.8)
	Error	54	16.32					
Height increment (cm)	Larva-drill	1	3.04	0.55	0.460(0.139)	Drill	16.1(3.2)	6.33(2.1)
	Insolation	1	34.88	6.35	<b>0.015</b>			
	Interaction	1	1.68	0.31	0.583(0.049)	Larva	13.1(3.7)	5.33(2.4)
	Error	54	296.56					
Diameter increment (mm)	Larva-drill	1	0.02	0.04	0.850(0.041)	Drill	2.53(0.6)	1.81(0.7)
	Insolation	1	4.24	6.86	<b>0.011</b>			
	Interaction	1	0.67	1.09	0.301(0.179)	Larva	2.59(0.4)	1.13(0.3)
	Error	54	33.40					

\* Significant P values ( $P < 0.05$ ) are shown in bold. The power of a treatment is only supplied in cases with a non-significant P-value.

TABLE 2. The effects of TangleTrap larva exclusion versus control saplings

(“TangleTrap”) and shade versus direct sunlight (“insolation”) on the growth of 120 small saplings of *Tabebuia ochracea*. Shown are the results of two-way fixed effects ANCOVAs, with relative soil moisture and each respective initial growth variable used as covariates. The non-adjusted averages and standard errors are shown for each treatment combination (Control = no TangleTrap, T-trap = TangleTrap application).

Dependent variable	Treatment	df	SS	F	P (Power)*	Average (standard error)	
						Light	Shade
Total shoot length (cm)	TangleTrap	1	0.05	0.01	0.926 (0.034)	Control	40.5(6.4)
	Insolation	1	135.82	40.09	<b>0.000</b>		24.8(3.8)
	Interaction	1	20.76	6.13	<b>0.015</b>	T-trap	49.1(5.9)
	Error	114	386.19				18.4(2.4)
Number of shoots	TangleTrap	1	0.37	1.55	0.216 (0.232)	Control	4.43(0.7)
	Insolation	1	4.56	19.06	<b>0.000</b>		2.43(0.3)
	Interaction	1	0.06	0.24	0.627 (0.045)	T-trap	3.77(0.7)
	Error	114	27.26				2.43(0.3)
Number of nodes	TangleTrap	1	0.00	0.00	0.984 (0.033)	Control	11.8(1.4)
	Insolation	1	26.17	49.93	<b>0.000</b>		6.33(0.7)
	Interaction	1	2.10	4.00	<b>0.048</b>	T-trap	12.8(1.5)
	Error	114	59.76				5.87(0.6)
Height increment (cm)	TangleTrap	1	5.73	2.81	0.096 (0.383)	Control	21.3(2.6)
	Insolation	1	104.74	51.43	<b>0.000</b>		9.70(1.3)
	Interaction	1	4.16	2.04	0.156 (0.293)	T-trap	29.5(3.3)
	Error	114	232.19				11.0(1.7)
Diameter increment (mm)	TangleTrap	1	0.03	0.09	0.769 (0.046)	Control	3.60(0.3)
	Insolation	1	17.05	53.57	<b>0.000</b>		1.50(0.2)
	Interaction	1	0.03	0.10	0.754 (0.047)	T-trap	3.58(0.3)
	Error	114	36.29				1.47(0.2)

\* Significant P values ( $P < 0.05$ ) are shown in bold. The power of a treatment is only supplied in cases with a non-significant P-value.

TABLE 3. The effects of artificial shoot herbivory (“herbivory”) and shade versus direct sunlight (“insolation”) on the growth of 306 small saplings of *Tabebuia ochracea*. The shoot herbivory treatments are no shoots damaged per year (“0”), two shoots damaged per year (“2”), and four shoots damaged per year (“4”). The insolation treatments are direct sunlight (“L”) and shade (“S”). Shown are the results of two-way fixed effects ANCOVAs, with relative soil moisture and each respective initial growth variable as covariate (increasing soil moisture was found to significantly increase only the number of shoots; initial growth variables were significant covariates for shoot length, number of shoots, and number of leaves, but not height or diameter increment).

Dependent variable	Treatment	df	SS	F	P (Power)*	Direction of effects^
Total shoot length	Herbivory	2	345.09	82.33	<b>0.000</b>	0>2>4
	Insolation	1	125.74	60.00	<b>0.000</b>	L>S
	Interaction	2	28.02	6.68	<b>0.001</b>	
	Error	298	624.51			
Number of shoots	Herbivory	2	2.78	4.77	<b>0.009</b>	0<2=4
	Insolation	1	5.26	18.06	<b>0.000</b>	L>S
	Interaction	2	0.50	0.85	0.427 (0.196)	
	Error	298	86.85			
Number of leaves	Herbivory	2	115.33	75.34	<b>0.000</b>	0>2>4
	Insolation	1	18.64	24.35	<b>0.000</b>	L>S
	Interaction	2	0.06	0.04	0.963 (0.057)	
	Error	298	228.10			
Height increment	Herbivory	2	1545.65	133.33	<b>0.000</b>	0>2>4
	Insolation	1	204.58	35.29	<b>0.000</b>	L>S
	Interaction	2	51.67	4.46	<b>0.012</b>	
	Error	298	1727.36			
Diameter increment	Herbivory	2	67.09	42.10	<b>0.000</b>	0>2>4
	Insolation	1	33.59	42.16	<b>0.000</b>	L>S
	Interaction	2	4.28	2.68	0.070 (0.529)	
	Error	298	237.45			

TABLE 3 (continued).

\* Significant P values ( $P < 0.05$ ) are shown in bold. The power of a treatment is only supplied in cases with a non-significant P-value. In all other cases, the power was  $> 0.75$ .

^ The direction of effects shows the qualitative nature of the differences between treatment levels, revealed by planned comparisons. Only differences significant at the  $P < 0.05$  level are shown (denoted by a “<” or “>”).

TABLE 4. The effects of artificial shoot herbivory (“herbivory”) and shade versus direct sunlight (“insolation”) on the total and average leaf area per sapling of 80 small saplings of *Tabebuia ochracea*. Included are saplings that differ both in the quantity and timing of shoot herbivory (see Methods). The insolation treatments are direct sunlight (“L”) and shade (“S”). Shown are the results of two-way fixed effects ANCOVAs, with relative soil moisture and the initial number of mature nodes as covariates.

Dependent variable	Treatment	df	SS	F	P (Power)*	Direction of effects^
Total leaf area	Herbivory	4	689.89	3.67	<b>0.009</b>	0=[2]>4 L>S
	Insolation	1	468.59	9.98	<b>0.002</b>	
	Interaction	4	348.40	1.85	0.129 (0.534)	
	Error	68	3193.85			
Average leaf area	Herbivory	4	178091	16.71	<b>0.000</b>	0>[2]=4
	Insolation	1	6.88	0.00	0.960 (0.35)	
	Interaction	4	12590.1	1.18	0.327 (0.351)	
	Error	68	181195			

\* Significant P values ( $P < 0.05$ ) are shown in bold. The power of a treatment is only supplied in cases with a non-significant P-value.

^ The direction of effects shows the qualitative nature of the differences between treatment levels, revealed by planned comparisons. Only differences significant at the  $P < 0.05$  level are shown (denoted by a “<” or “>”). For both dependent variables, there were no differences in the timing of damage among the two shoots damaged per years treatments. These three treatments are combined as “[2]” above.

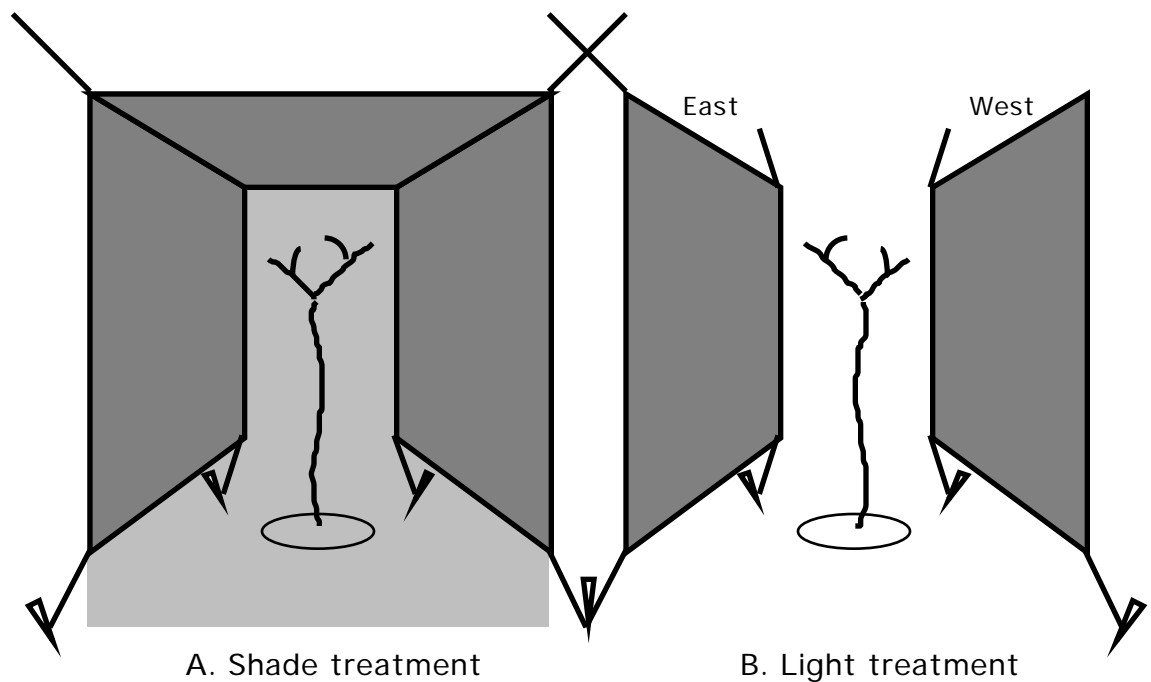
TABLE 5. The effects of shoot herbivory of the top shoot (“Top bore”) on 12-month height increments of *T. ochracea* saplings in canopy gaps and understory shade (“Insolation”). Saplings that had their apices bored over the study (November 1996 to July 1999) were randomly assigned to either the “apex not bored” or “apex bored once” categories. For the “apex not bored” saplings, one 12 month interval when the top shoot was undamaged was randomly selected. For the “apex bored once” saplings, one 12 month interval bracketing a single shoot-borer infestation of the top shoot was randomly selected. The “apex never bored” saplings were never bored over the study — one random 12 month height increment was selected from each. Shown are the results of a two-way fixed effects ANOVA, with initial height and percentage of all shoots bored per sapling used as covariates (neither covariate was significant, and the results are not shown on the ANCOVA table). N = 80. See Fig. 6 for the direction of the effects.

Dependent variable	Treatment	df	SS	F	P (Power)*
Height increment	Top bore	2	64.27	5.15	<b>0.008</b>
	Insolation	1	181.39	29.08	<b>0.000</b>
	Interaction	2	18.88	1.51	0.227 (0.311)
	Error	72	449.14		

\* Significant P values ( $P < 0.05$ ) are shown in bold. The power of a treatment is only supplied in cases with a non-significant P-value.

Figure 1. Experimental shade (A) and light (B) treatments. In each treatment, the top of the sapling was set at approximately 50 cm below the top of the suspended nylon sacking at the beginning of each year. All sacking was held taut with nylon twine staked to the ground and tied to nearby tree trunks.





A. Shade treatment

B. Light treatment

Figure 2. The effects of different frequencies of artificial shoot herbivory (with a rechargeable drill, mimicking *Cromarcha stroudagnesia* shoot-borer herbivory) on four growth parameters for small *Tabebuia ochracea* saplings. Light and shade saplings refer to the experimental treatments illustrated in Fig. 1. The “total shoot length” and “total mature nodes” are per sapling values from the end of experiment. Plotted are the averages  $\pm$  one standard error (n = 306). See Table 3 for the ANOVA tables for each graph.

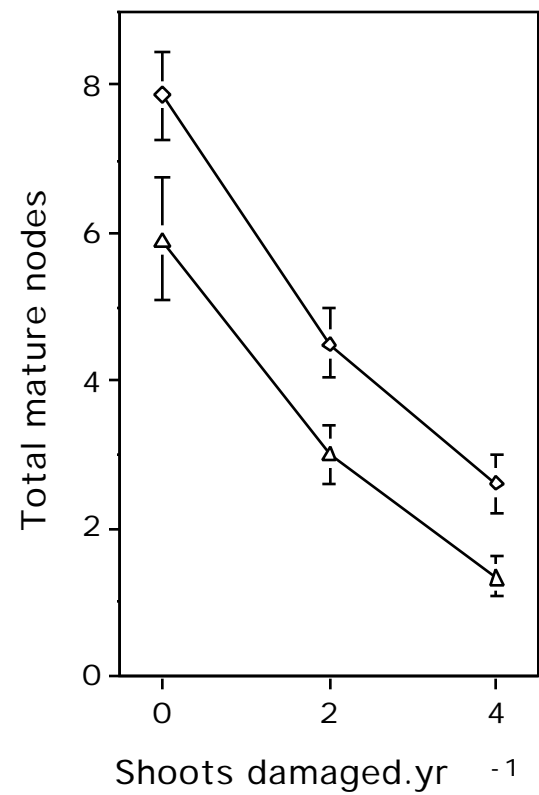
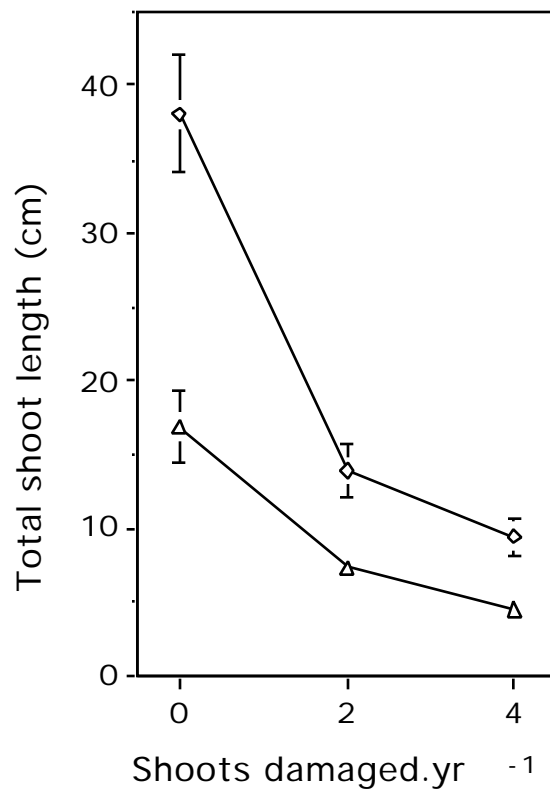
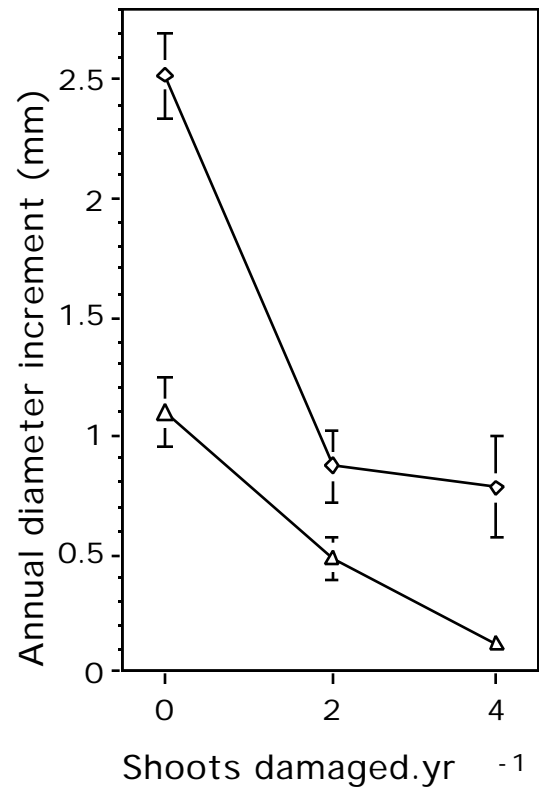
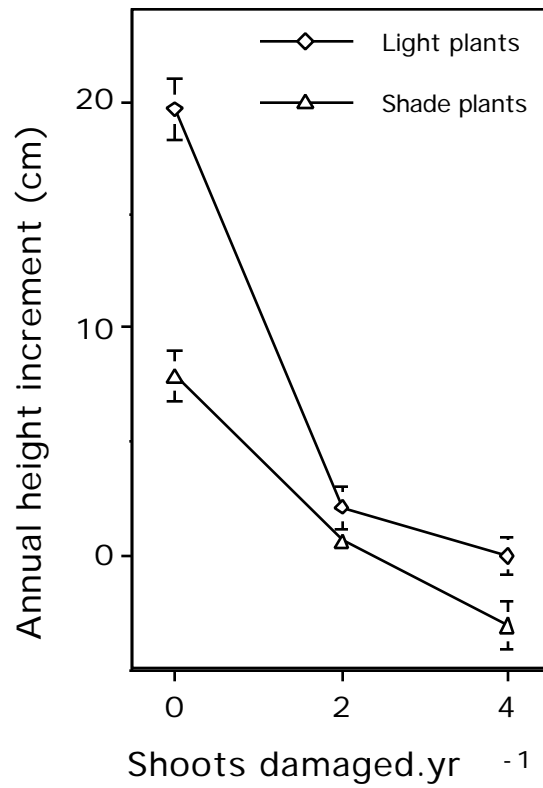


Figure 3. The effects of different frequencies of artificial shoot herbivory (with a rechargeable drill, mimicking *Cromarcha stroudagnesia* shoot-borer herbivory) on the leaf area of small *Tabebuia ochracea* saplings. Light and shade saplings refer to the experimental treatments illustrated in Fig. 1. All leaf areas are per sapling values from the end of experiment. Plotted are the averages  $\pm$  one standard error (n = 80). See Table 4 for the ANOVA tables for each graph.

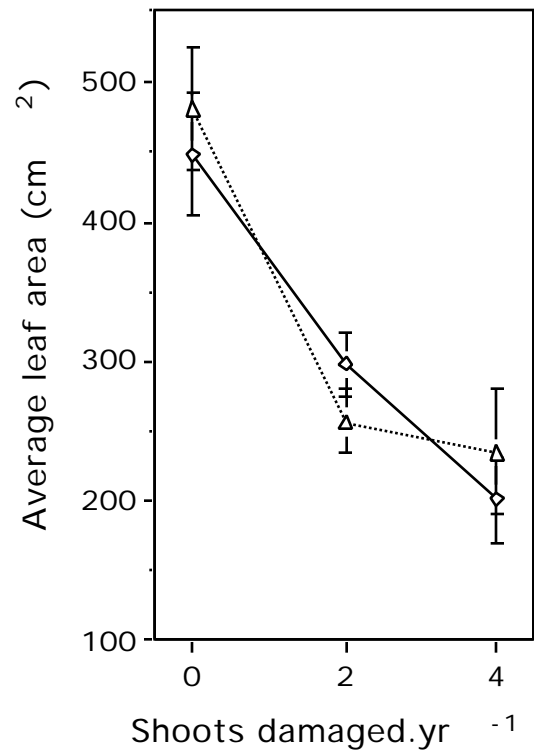
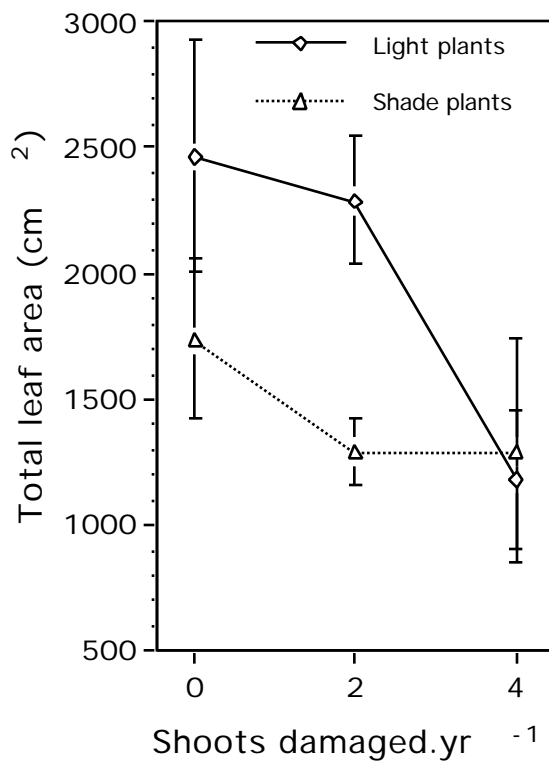


Figure 4. The effects of the timing of artificial shoot herbivory (“herbivory”) and insolation on the average annual height increment of small saplings of *Tabebuia ochracea*. All saplings had one shoot damaged per shoot-borer generation (two per year), but differed in the timing of this damage. The shoot herbivory treatments are one shoot damaged per generation year (“1x1”), two shoots damaged only in the first generation per year (“2x0”), and two shoots damaged only in the last generation per year (“0x2”). Plotted are the averages  $\pm$  one standard error ( $n = 102$ ). Bars with shared letters represent groups that did not differ at a  $P < 0.05$  level in planned comparisons of canopy gap and understory shade saplings (an asterisk is used for the shade saplings to separate like letters).

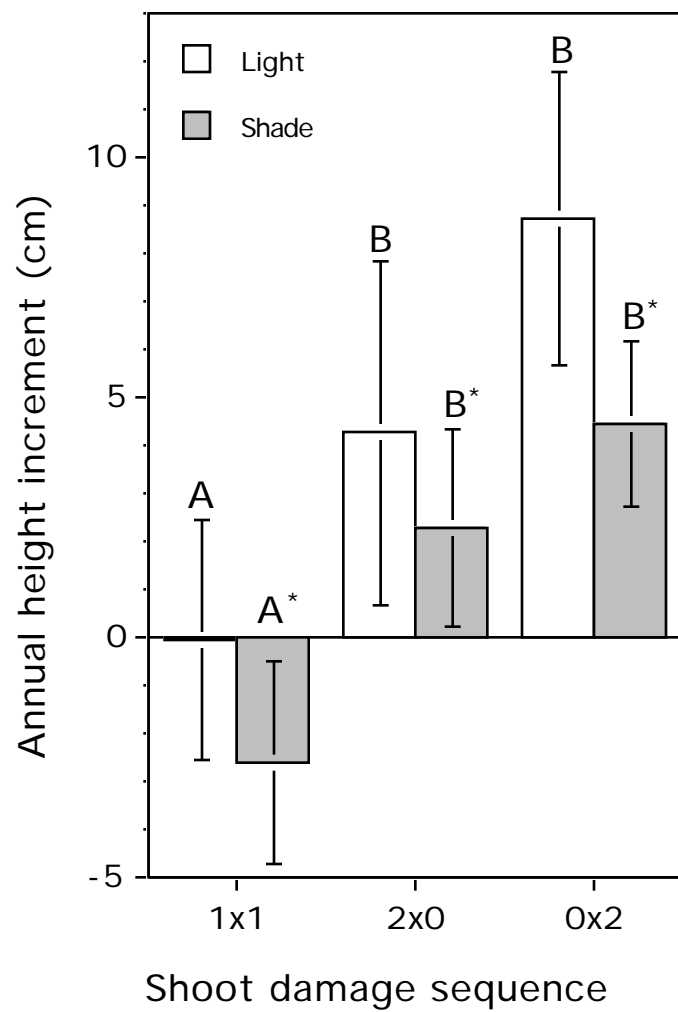


Figure 5. During the first half of the 1998 wet season (May - July 1998), the total percentage of shoots bored by *Cromarcha stroudagnesia* larvae was recorded for each of the 96 *Tabebuia ochracea* saplings paired in canopy gaps and nearby understory shade. Shown here is the lack of significant relationship between this infestation frequency and height increment over the same interval, for either group of saplings. This distribution is likely due to the greater percentage of shoots bored on faster growing saplings.



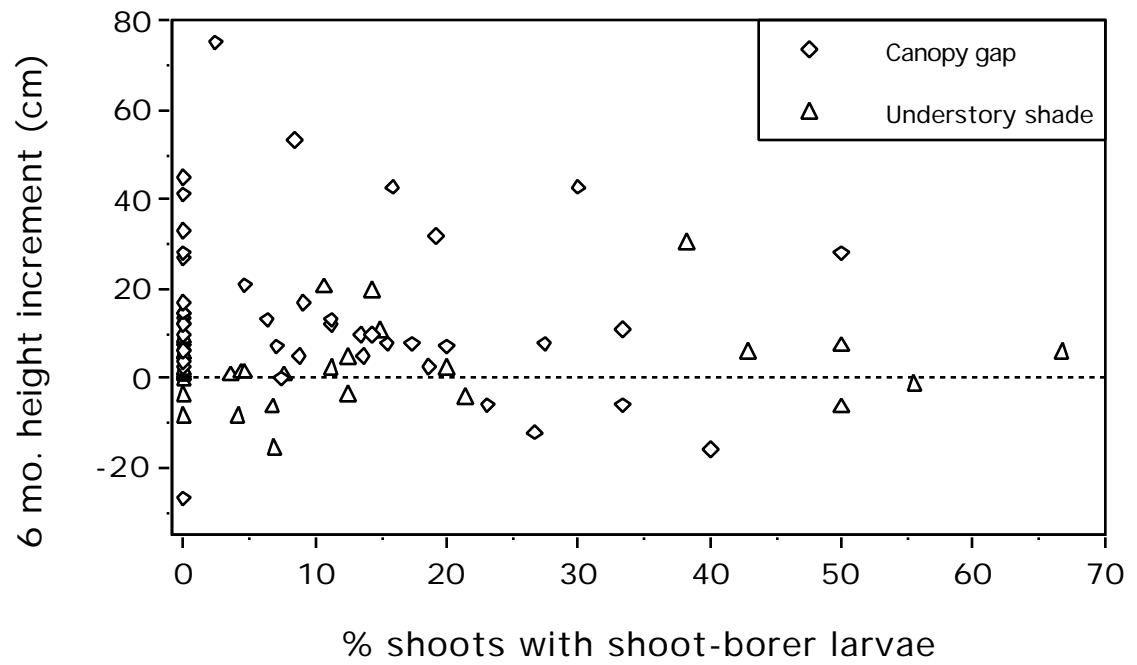


Figure 6. Top shoot herbivory by *Cromarcha stroudagnesia* causes a large reduction in the height increment of *Tabebuia ochracea* saplings, both in canopy gaps and understory shade. Saplings that had their top shoot bored one or more times over the study (November 1996 to July 1999) were randomly assigned to either the “apex not bored” or “apex bored once” categories. For the “apex not bored” saplings, one 12 month interval when the top shoot was undamaged was randomly selected. For the “apex bored once” saplings, one 12 month interval bracketing a single shoot-borer infestation of the top shoot was randomly selected. The “apex never bored” saplings were never bored over the study — one random 12 month height increment was selected from each sapling. Plotted are averages  $\pm$  one standard error. Bars with shared letters represent groups that did not differ at a  $P < 0.05$  level in planned comparisons of canopy gap and understory shade saplings (an asterisk is used for the shade saplings to separate like letters). Sample sizes were randomly balanced to  $n = 42$  for the canopy gap saplings and  $n = 39$  for the understory shade saplings. See Table 5 for the ANOVA table of these results.

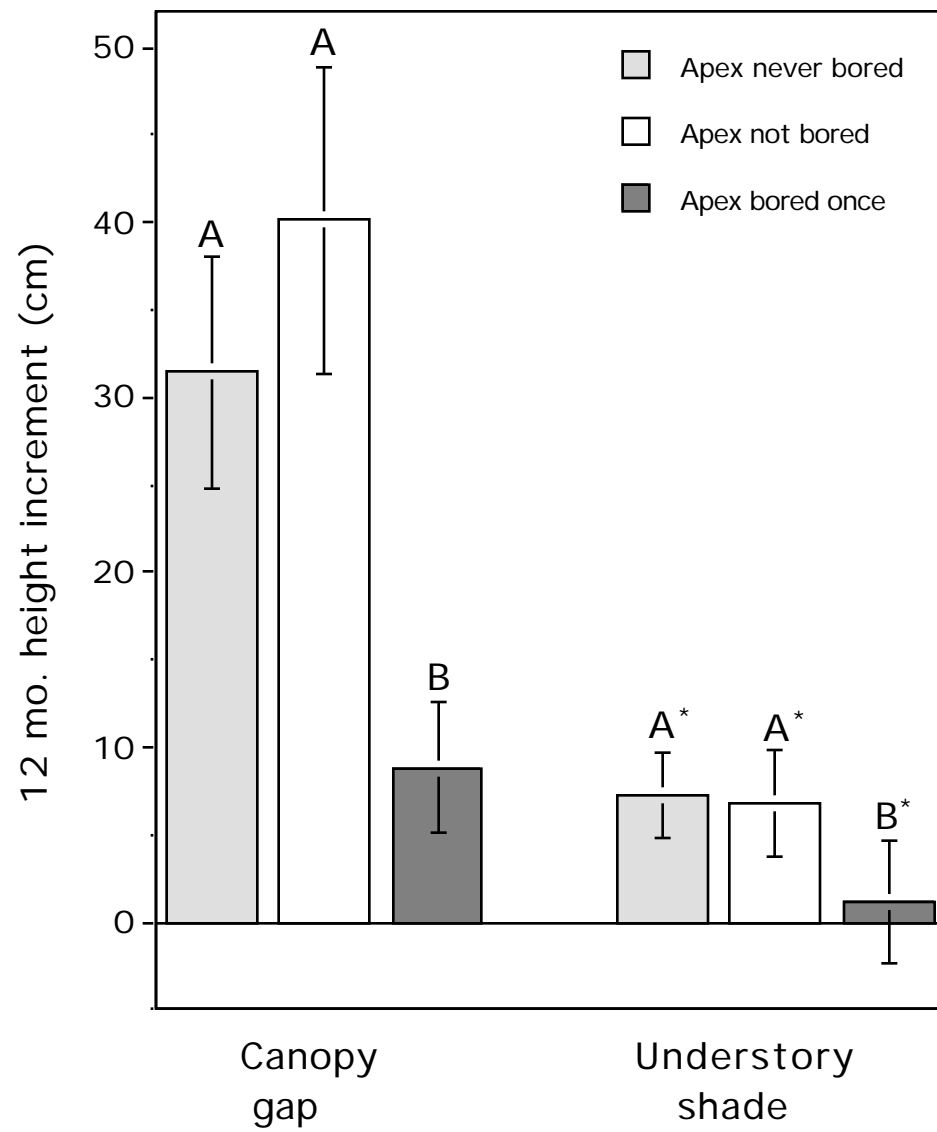


Figure 7. The height increments of *Tabebuia ochracea* saplings compared with the average and maximum height increments of the surrounding gap vegetation. Two 12-month height increments were randomly selected from each canopy gap sapling, one interval without top shoot herbivory (“Apex not bored”) and the other with a single top shoot attacked (“Apex bored once”). If the top shoot of a sapling was never attacked, a random 12 month interval was selected (“Apex never bored”). These increments are compared with the height increments of canopy gap vegetation at four points surrounding each sapling (excluding canopy closure). The maximum gap growth is the maximum height increment from a single one of these four points. Plotted are the average differences in height increment  $\pm$  one standard error (gray bars) and  $\pm$  95% confidence intervals (lines).

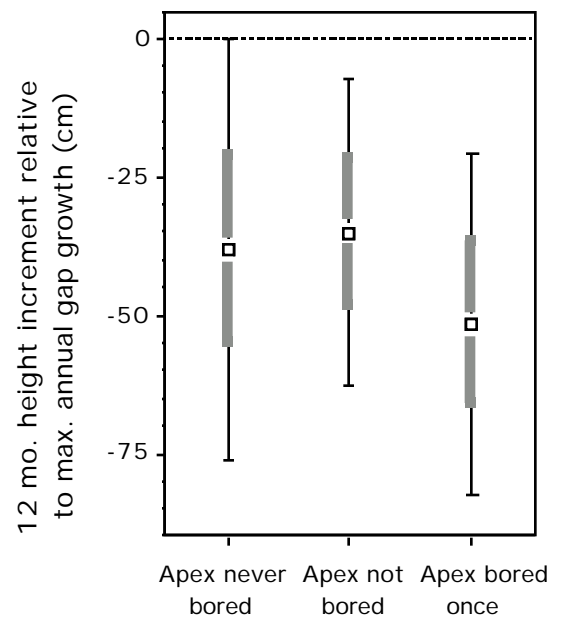
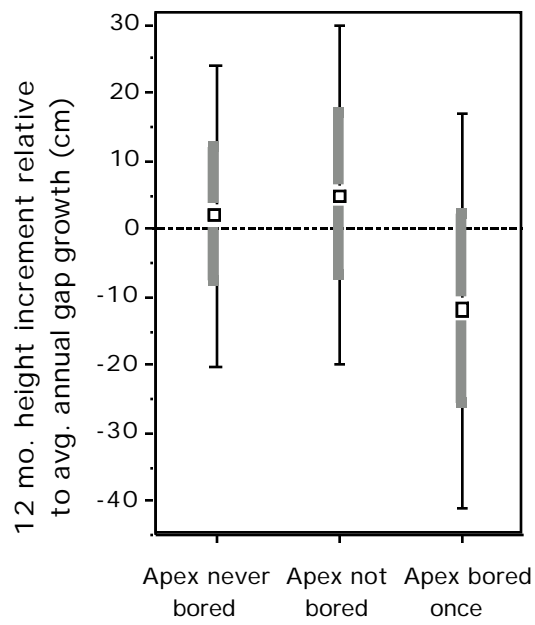
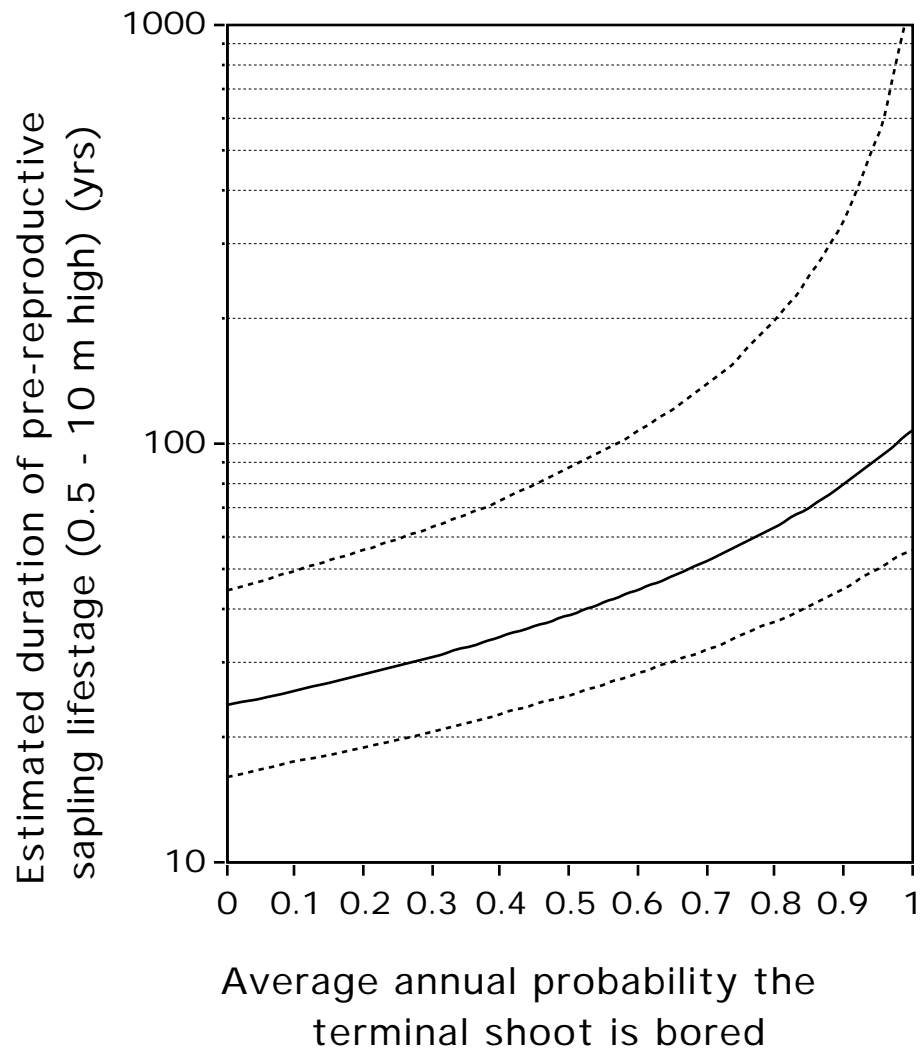


Figure 8. The differences in 12 month sapling height increments with and without top shoot herbivory (Fig. 6) extrapolated to the entire prereproductive understory lifetime of saplings in canopy gaps (between 50 cm and 10 m high). The assumption is made that canopy gap saplings will remain at the top of the canopy gap vegetation throughout their prereproductive understory lives (because of this, these estimates should be regarded as minimum limits rather than accurate field averages of sapling age at first reproduction). Plotted are the average and 95% confidence intervals across all lifetime average annual probabilities of top shoot herbivory. The average annual probability of annual top shoot herbivory across the four years of this study was 0.401, and individual saplings spanned the full range from 0 to 1.0.



**CHAPTER FOUR: Shoot-borer herbivory of saplings increases with sapling density  
for the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae)**

*Abstract*

Shoot herbivory of saplings of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae) by larvae of the shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae) was found to increase with the number of conspecific individuals (between 3 cm and 20 cm dbh) and the number of shoots within 50 m of study saplings. For example, the average annual percentage of shoots per sapling attacked by *C. stroudagnesia* larvae was 1.99% for saplings with <300 *T. ochracea* shoots within a 50 m radius, and 10.7% for saplings with >2000 *T. ochracea* shoots within a 50 m radius. This density-dependent herbivory was independent of all recorded environmental and growth variables that correlated with density. No relationship was found between *C. stroudagnesia* shoot herbivory and the distance to the nearest conspecific adult tree, as was expected because *C. stroudagnesia* occurs infrequently in adult canopies. Previous studies at the same study site have shown that *C. stroudagnesia* herbivory increases the age of first reproduction of *T. ochracea* saplings by at least 45%, increases the probability that canopy gap saplings are over-shaded by neighboring vegetation, and directly and indirectly increases pre-reproductive mortality by at least 10%. *Cromarcha stroudagnesia* herbivory is also highest on the fastest growing individuals. *Cromarcha*



*stroudagnesia* is therefore likely to disproportionately decrease the number and rate of recruitment of saplings to reproductive age in areas of high conspecific sapling density, and so increase the ability of other tree species to coexist with *T. ochracea*. This study demonstrates that sapling herbivory has the potential to play an important role in influencing tree species coexistence in tropical forests.

## **Introduction**

It has long been recognized that predation and parasitism of juvenile plants by animals, fungi, and microbes can alter the dynamics of tree populations and increase tree species coexistence (Janzen 1970, Connell 1971, Hubbell 1980, Armstrong 1989, Pacala and Crawley 1992). Tree species coexistence will be increased when damage by herbivores, seed predators, or pathogens disproportionately decreases juvenile tree survival or competitiveness in areas of high conspecific juvenile density and/or close proximity to conspecific adults. As statistical methods have become more refined, these “Janzen-Connell effects” are being detected in progressively greater proportions of the tropical tree species in long-term forest plots (Wills et al. 1997, Harms et al. 2000, Muller-Landau et al. in press), and are likely to play an important role in maintaining tree species coexistence in tropical forests (Hubbell 1998).

The biological mechanisms behind most of these statistically described density-dependent patterns are unknown. Many studies have demonstrated Janzen-Connell

effects for herbivores and fungal pathogens attacking tropical tree seeds and seedlings (see reviews by Clark and Clark 1984, Barone 1996, Coley and Barone 1996, see also Packer and Clay 2000). However, these effects have often been weak (Coley and Barone 1996) and typically occur at too fine a spatial scale to explain many of the large scale density-dependent patterns of recruitment and survival observed in tree populations (Wills et al. 1997, Hubbell 1998). The distances of these observed Janzen-Connell effects, typically 10 - 20 m from conspecific adults, are also too short to explain the coexistence of more than a small fraction of the hundreds of tropical tree species that typically occur in a tropical forest (Hubbell 1980).

There is much mortality and population structuring that occurs between seedlings and the next generation of adult trees (e.g., Clark et al. 1999), and sapling herbivory by insects therefore also has the potential to create strong Janzen-Connell effects (Coley and Barone 1996). However, the effects of herbivory on tree saplings remains largely unstudied (Barone 1996). Here I report one such example, documenting how damage by a species of shoot-boring lepidopteran is most common in areas of high host sapling density.

For sapling herbivory by insects to create Janzen-Connell effects, it must not only be distributed in a density dependent manner but it also must reduce sapling survival or competitiveness. Unlike the large, immediately detrimental effects of insect herbivory on tree seeds and seedlings (e.g., Marquis 1992, Crawley 1997), the effects of herbivory on

tree saplings in tropical forests are more difficult to assess. However, they have the potential to accumulate over many years into similarly large detrimental effects (Marquis 1992, Coley and Barone 1996, Sullivan 2000c).

In a previous study (Sullivan 2000c), I demonstrated that insect herbivory by the shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae) has large effects on the rates of mortality and height increment of saplings of the neotropical dry forest tree *Tabebuia ochracea* (Bignoniaceae). In the secondary successional dry forests of the Area de Conservación Guanacaste, Costa Rica, *C. stroudagnesia* increases the age of first reproduction of *T. ochracea* saplings by at least 45%, increases the probability that canopy gap saplings are over-shaded by neighboring vegetation, and directly and indirectly increases pre-reproductive mortality by at least 10% (Sullivan 2000c).

In this study, the population consequences of these detrimental effects of *C. stroudagnesia* on *T. ochracea* are assessed. Specifically I asked (i) does *C. stroudagnesia* shoot herbivory increase with *T. ochracea* sapling densities, measured within both 10 m and 50 m radii of saplings?, (ii) do increases in *C. stroudagnesia* shoot herbivory with density cause *T. ochracea* sapling height increments to decrease with density? and (iii) what are the likely consequences of reduced sapling height increments for the population dynamics of *T. ochracea* and for the ability of other tree species to coexist with *T. ochracea*?

## Methods

### *Study site*

Sector Santa Rosa (formerly Parque Nacional Santa Rosa) is the historical core of the Area de Conservación Guanacaste (ACG), a 110,000 hectare conserved wildland in northwestern Costa Rica (<http://www.acguanacaste.ac.cr>). Santa Rosa includes a few small fragments of old growth dry forest and large expanses of secondary successional tropical dry forest between 0 - 400 year old, regenerating on abandoned cattle pastures, agricultural fields, and logged areas (see Janzen 1986a, 1988, 1992). It was subject to extensive anthropogenic fires for three centuries prior to 1985. The dry forests of sector Santa Rosa and neighboring sectors are the largest area of conserved dry forest in Central America, a habitat that once covered the Pacific coastal lowlands and parts of the Atlantic coastal lowlands of Central America (Janzen 1988, Gillespie et al. 2000). Within the ACG, Santa Rosa is bordered by conserved marine habitats in the Pacific Ocean to the west and sectors of progressively wetter conserved forests to the east, including cloud forest and Atlantic rain forest.

Average annual rainfall at the Santa Rosa Biological Station during the five years of the study (1995-1999) was 2082 mm (s.d. = 612), which included the wettest and fifth driest years since 1980. The local climate is highly seasonal, dominated by a pronounced 6-month dry season from December to mid-May when essentially no rain falls. During much of the dry season, most individual trees in all but the oldest fragments of forest are

leafless or nearly leafless, contrasting with the completely foliated forests throughout the 6-month wet season (see Janzen 1993). Rainfall is typically heaviest in May - June and September - October, and there is a lull in rainfall for 2 - 6 weeks in July - August called the “veranillo” (little dry season).

All observations were made in the forests within 3 km of the Santa Rosa Biological Station (300 m, 10° 50' 27.26'' N latitude , 85° 37' 14.26'' W longitude). Study plants were located within the Bosque San Emilio forest plot, a 16.3 ha plot in 80 - 100 year old secondary successional forest (Stevens 1987, Enquist et al. 1999), and within the Bosque Humedo forest plot, a 4.8 ha forest plot within an area of old growth forest (Janzen 1986b). The Bosque Humedo plot is about 950 m northeast of the Bosque San Emilio plot, and the plots are connected by a continuous cover forest of similar or greater age than Bosque San Emilio. Sullivan (2000a) presents a map shows the locations of these study forests within Santa Rosa.

### *Study species*

*Tabebuia ochracea* (Chamisso) Standley (Bignoniaceae) is a neotropical dry forest tree up to 30 m tall and > 0.5 m dbh with palmate five-foliate tomentose leaves (see Gentry 1983, Gentry 1992, Sullivan et al. 1998, Sullivan 2000a for full description). *Tabebuia ochracea* has shade-tolerant saplings that require canopy gaps for most understory height increment (Sullivan 2000a). I defined saplings as any *T. ochracea*

juvenile 50 cm high (*sensu* De Steven 1994), which corresponds with well established *T. ochracea* juveniles usually 5-15 years old (Sullivan 2000a). *Tabebuia ochracea* was chosen as the focal species for this and associated studies (Sullivan 2000a, 2000c) for three pragmatic reasons: it is locally abundant, its brief, population-wide synchronized displays of large yellow flowers in the dry season made it easy to locate a great many trees (and therefore areas with saplings), and it had a large seeding year in 1995 (when the pilot study that resulted in this work focused on seed predation and seedling herbivory).

The shoot-borer *Cromarcha stroudagnesia* (Lepidoptera, Pyralidae, Chrysauginae)(Sullivan 2000b, Solis et al. in prep.) commonly bores into the new shoots of saplings of *Tabebuia ochracea* and the much less abundant *T. impetiginosa*. Each larva typically destroys a single shoot, killing the apical meristem and as many nodes as are bored through. *Cromarcha stroudagnesia* is a sapling specialist. Larvae typically destroy 5 - 15% of the shoots of understory saplings per year, but are largely absent from juvenile *T. ochracea* <50 cm high, and occur at very low frequencies (about 0.4% of shoots per year, or 3-6 larvae) in adult crowns (Sullivan 2000b). There are two generations of larvae per wet season, the first beginning at the onset of the wet season in mid-May, and the second beginning after the veranillo, in August-September. (Sullivan 2000b gives a detailed account of the natural history of *C. stroudagnesia*).

*Cromarcha stroudagnesia* is one of at least 36 insect species that feed on aboveground parts of *T. ochracea* saplings in the Santa Rosa forests (Janzen and

Hallwachs 2000, J. J. Sullivan, unpublished data). *C. stroudagnesia* was chosen as the focal herbivore for this study as it was abundant, and commonly destroyed sapling apical meristems Janzen (1983) suggested that apical-feeding insect herbivores will have much more detrimental effects on tree saplings than will insects that feed on mature leaves.

#### *Longterm observations of study saplings*

This study reports on the shoot herbivory and height increments of 153 *T. ochracea* saplings, initially between 0.5 m and 7 m high, between 1995 and 1999. Sixty-six of these saplings occurred in the Bosque Humedo forest plot, and 87 occurred in the Bosque San Emilio forest plot. These saplings and many study saplings outside of the forest plots formed the basis for a understory demography study of *T. ochracea* (Sullivan 2000a), a natural history of *C. stroudagnesia* (Sullivan 2000b), and part of the examination of the effects of *C. stroudagnesia* on the fitness of *C. stroudagnesia* (Sullivan 2000c). The details of the locations and growth measurements made from these saplings, and the reasons for their selection, are given in Sullivan (2000a). Details of the herbivory measurements are given in Sullivan (2000b). Only a summary of the relevant components of those methods is given here.

Height, stem diameter, and shoot herbivory, were recorded each mid- and late-wet season from 1995 to 1999 for 66 saplings in the Bosque Humedo forest plot and 59 saplings in the Bosque San Emilio forest plot. Sapling height was recorded with a

weighted measuring tape attached to a 7 m long telescoping pole and stem diameter was recorded at 30 cm above the soil surface across the thickest horizontal axis with vernier calipers. For each sapling, I also recorded the number of all shoots, the number of shoots containing *C. stroudagnesia* larvae, and whether or not the tallest shoot contained a *C. stroudagnesia* larva. For each sapling I then calculated the average annual height increment, the average annual number of shoots attacked by *C. stroudagnesia*, and the average number of times per year that the tallest shoot of each sapling was attacked by *C. stroudagnesia*.

For a further 28 saplings in the Bosque San Emilio forest plot, the height and stem diameter were measured only at the beginning (1995) and the end (1999) of the study. In 1995, an architectural map was drawn for each sapling, including the *C. stroudagnesia* shoot herbivory status of all shoots. These maps were used in 1999 to record how many shoots had been attacked by *C. stroudagnesia* between 1995 and 1999 (all or part of old *C. stroudagnesia* killed shoots remain on saplings for many years and are usually easily identifiable as *C. stroudagnesia* damage — see Sullivan (2000b) for more details). The number of all live shoots and the number of these containing *C. stroudagnesia* larvae were also recorded in 1999. These data provide the average annual height increment and average annual percentage of shoots attacked by *C. stroudagnesia* for each sapling. It was impossible to determine for these plants how many times the tallest shoot of each sapling had been attacked by *C. stroudagnesia* over the study.



For all study saplings, the soil moisture and canopy light were recorded in 1999. Soil moisture was estimated at 10 cm depth for each sapling in mid-wet season with a Rapidtest Mini Moisture Tester (Luster Leaf Products, Inc., Woodstock, IL, USA), calibrated at each site for percentage soil moisture by dry weight. Canopy light was estimated by the percentage of canopy that was sky. This was calculated from wide-angle digital photos using Adobe Photoshop 4.0. See Sullivan (2000a) for details.

Both the Bosque Humedo and Bosque San Emilio forest plots include a series of mesas and eroded valleys, and the site of each study seedling and sapling was classified as “valley”, “slope”, or “mesa”. “Slope” included only substantial inclines (greater than about 15 degrees) connecting mesas and valleys.

#### *Density measurements*

Densities of conspecifics surrounding each sapling were calculated from comprehensive maps of *T. ochracea* in the Bosque Humedo forest plot (Sullivan 2000a) and Bosque San Emilio forest plot (B. J. Enquist, C. A. Enquist, and G. C. Stevens, unpublished data), made in 1999 and 1996 respectively. Also mapped were all areas outside of the Bosque Humedo plot but within 50 m of study saplings located near to the border of the plot. Only saplings  $\geq 3$  cm dbh were recorded in the Bosque San Emilio forest plot, and so only saplings of this size or greater were included in density calculations from the Bosque Humedo map. The number of *T. ochracea* individuals  $<20$

cm dbh within 10 m and 50 m of each study sapling was calculated using Microsoft Excel worksheets. Trees  $\geq 20$  cm dbh are canopy trees, and there is minimal *C. stroudagnesia* shoot herbivory in tree canopies (Sullivan 2000b).

The numbers of shoots within 10 m and 50 m of each sapling were estimated from the allometry equation: number of shoots =  $10.785 * \text{dbh}$ . This equation was generated from two allometry equations relating stem diameter at 30 cm height (d30cmh) to dbh, and dbh to shoot number, generated from a larger sample of study saplings (Sullivan 2000a). These equations are:  $\text{dbh} = 0.737966 * \text{d30cmh}$  (linear regression,  $P < 0.0001$ ,  $R^2 = 0.961$ ,  $n = 132$ ), and number of shoots =  $0.795898 * \text{d30cmh}$  (linear regression,  $P < 0.0001$ ,  $R^2 = 0.848$ ,  $n = 344$ ). Various curves were fitted through this data, and in each case the linear fit gave the highest  $R^2$  value.

### *Analysis*

All analyses were performed using SPSS for Macintosh version 6.1.1 (<http://www.spss.com>). Partial correlations were used to compare density and shoot herbivory variables while holding constant all recorded environmental and initial growth variables, many of which correlated with density and/or shoot herbivory. The variables controlled were canopy light, soil moisture, initial sapling height and stem diameter, and the distance to the nearest conspecific adult tree. Saplings with missing values were excluded listwise from the correlation analyses. Missing values existed for those 28 saplings measured only at the beginning and the end of the study (no average annual

frequency of tallest shoot herbivory), for one sapling that died in 1998 (no height increment), and for three large saplings from which the total percentage of shoots bored was not recorded.

Some variables used in partial correlation analyses were ln transformed to improve the normality and homoscedasticity of residuals. Transformed were soil moisture, initial height, distance to the nearest conspecific, and the two shoot herbivory variables (the annual average percentage of all shoots attacked by *C. stroudagnesia* and the average number of times the tallest shoot was attacked by *C. stroudagnesia* per year). All significance levels are based on two-tailed tests (except for one case, noted in the results, where a one-tailed test was used because independent data from Sullivan (2000c) predicted the direction of this correlation).

## Results

Both measures of *C. stroudagnesia* herbivory, the average annual percentage of shoots attacked by *C. stroudagnesia* per sapling and the average number of times the tallest shoot was attacked by *C. stroudagnesia* per year per sapling, significantly increased with local *T. ochracea* sapling densities at the 50 m radius (Fig. 1, 2, Table 1, 2). This relationship applied for both the number of *T. ochracea* individuals (between 3 cm and 20 cm dbh), and the estimated number of *T. ochracea* shoots within a 50 m radius of each sapling. For example, the average annual percentage of saplings that had their tallest

shoot attacked by a *C. stroudagnesia* larva was 2.62% for *T. ochracea* saplings with <300 *T. ochracea* shoots within 50 m, and 22.32% for saplings with >2000 *T. ochracea* shoots within 50 m (see Table 2). All density effects occurred independently of all other measured variables, including the distance to the nearest conspecific adult (Table 1). No significant relationships were found at the 10 m radius for either measure of *C. stroudagnesia* herbivory with either measure of density (Table 1).

Several significant correlations were found in the data set between the density measurements and many of the recorded environmental and growth variables (Table 3). Density measurements at both 10 m and 50 m radii decreased significantly with increasing distance from the nearest adult *T. ochracea* tree. Soil moisture was higher in areas of high sapling density at both scales. Canopy light levels were significantly higher in areas of low density at the 50 m radius. Sapling height increments increased significantly with increasing density at the 10 m radius. The partial correlation coefficients (Table 1) confirm that these linear relationships between density and other variables do not drive the observed positive relationship between sapling density and shoot herbivory.

Shoot herbivory was substantially less on saplings in the old-growth Bosque Humedo forest plot than saplings in the younger Bosque San Emilio forest plot saplings. For example, the average annual percentage of shoots attacked by *C. stroudagnesia* per sapling was 1.9% in Bosque Humedo (s.e. = 0.46, n = 65) and 11.0% in Bosque San Emilio (s.e. = 1.54, n = 81). This difference can be wholly explained by the differences in

*T. ochracea* density between the two forest plots, as a partial correlation between forest and the percentage of shoots bored shows no significant result when only the four density measures were controlled for (partial correlation coefficient = -0.078,  $P = 0.41$ , d.f. = 112).

Many of the trends previously reported in Sullivan (2000a,b) are also evident in the zero-order correlation matrix of all variables (Table 3). For example, there was a significant positive correlation between sapling height and distance from conspecific adult trees, but individual sapling densities were significantly higher nearer to conspecific trees (see Sullivan 2000a). Average annual sapling height increments were greatest in areas of high canopy light and high soil moisture (see Sullivan 2000a). Higher saplings were more likely to have their tallest shoot attacked by *C. stroudagnesia*, and shoots of saplings growing in moister areas were more frequently attacked by *C. stroudagnesia* than saplings growing at drier sites (see Sullivan 2000b). As expected from the low numbers of *C. stroudagnesia* observed in tree canopies (Sullivan 2000b), distance to the nearest conspecific was not correlated with either measure of *C. stroudagnesia* herbivory.

All else being equal, saplings that had their tallest shoot attacked more frequently by *C. stroudagnesia* had significantly reduced average annual height increments (partial correlation coefficient = -0.215, one-tailed  $P = 0.025$ , d.f. = 81, holding constant all environmental and growth variables as well as the four density measures and the average annual percentage of shoots bored). This agrees with the findings of Sullivan (2000c), and

is despite a significantly *positive* zero-order correlation between height increment and tallest shoot herbivory (Table 3). The latter result indicates that saplings in conditions that favor high rates of height increment (e.g., relatively high canopy light and soil moisture) are those saplings most likely to have their tallest shoot attacked by *C. stroudagnesia* (see Sullivan 2000a).

There was no significant relationship between the average annual percentage of all shoots bored and average annual height increments, when all other variables were controlled for including tallest shoot herbivory (partial correlation coefficient = 0.143, one-tailed  $P = 0.099$ , d.f. = 81). As with tallest shoot herbivory, there was a significantly positive zero-order correlation coefficient between height increment and shoot herbivory (Table 3).

No significant relationships were found between *T. ochracea* sapling annual height increments and *T. ochracea* density in a 50 m radius. Partial correlations of annual height increment versus the number of saplings and shoots within 50 m were compared, both when shoot herbivory was and was not controlled. In each analysis, all environmental and growth variables and the 10 m radius density variables were controlled for, and the 28 saplings for which tallest shoot herbivory was not recorded were excluded. The partial correlation coefficients of height increment versus density were expected to be significantly greater when tallest shoot herbivory was controlled than uncontrolled. This is because tallest shoot herbivory was found to be both significantly positively correlated

with density and significantly negatively correlated with annual height increments. No such significant differences were found. However, the pattern of partial correlation coefficients was as expected: controlling for tallest shoot herbivory increased the partial correlation coefficient from 0.112 to 0.137 for the number of saplings within 50 m ( $P = 0.21$  and  $P=0.31$  respectively), and from 0.042 to 0.074 for the number of shoots within 50 m ( $P = 0.51$  and  $P=0.70$  respectively,  $df = 82$ ).

## Discussion

The amount of shoot herbivory of *Tabebuia ochracea* saplings by *Cromarcha stroudagnesia* was found to increase significantly with increasing conspecific density at a 50 m radius, irrespective of the distance to the nearest conspecific adult tree (Table 1, Table 2). This pattern was found for both the percentage of all shoots attacked by *C. stroudagnesia* (Fig. 1) and the frequency at which the tallest shoot of saplings was attacked (Fig. 2). The pattern should produce Janzen-Connell effects in the local *T. ochracea* population, as *C. stroudagnesia* herbivory substantially increases sapling mortality (Sullivan 2000c)

In a previous study (Sullivan 2000c), I showed that *C. stroudagnesia* herbivory of the shoots of *T. ochracea* saplings increases sapling mortality and decreases rates of sapling height increment. Experimental damage of shoots of small saplings (initially between 0.7 m and 1.5 m high) at natural frequencies of herbivory over three years

increased mortality from 0% to up to 10% relative to protected saplings (Sullivan 2000c). Natural frequencies of shoot herbivory were also found to reduce the rates of sapling height increment by more than 75%, for both the experimental saplings and larger wild saplings. This reduction was equivalent to the difference in height increments between undamaged saplings growing in canopy gaps and understory shade, and was sufficient to increase the probability of canopy gap saplings being over-shaded by surrounding vegetation. Both the reduction in the rate of sapling height increment and the increased likelihood that saplings are shaded by other vegetation are likely to greatly increase pre-reproductive mortality of *T. ochracea* sapling by other causes, such as pathogen infection or the lethal impact of falling debris (Clark and Clark 1991, Coley and Barone 1996, Sullivan 2000c).

The combined results of density-dependent *C. stroudagnesia* herbivory and an impact of *C. stroudagnesia* herbivory on sapling mortality indicate that *C. stroudagnesia* herbivory will produce a density-dependent Janzen-Connell effect. All else being equal, *C. stroudagnesia* herbivory will cause the rate and proportion of *T. ochracea* saplings reaching reproductive size to be reduced in areas of high conspecific densities in the dry forest of the Area de Conservación Guanacaste (ACG). This conclusion is further strengthened by *C. stroudagnesia* herbivory being strongly biased towards the fastest growing saplings in the population (Sullivan 2000b, 2000c). It is these saplings that will have the greatest probability of reaching reproductive maturity.



Despite this prediction of a strong Janzen-Connell effect, no significant effect was found of *T. ochracea* density on average annual sapling height increments. Such an effect must exist, given that the frequency of tallest shoot herbivory increases substantially with density (Fig. 2, Table 2), and that tallest shoot herbivory causes large reductions in the rate of height increment (Sullivan 2000c). The discrepancy is likely due to the small sample size ( $n = 95$ , being those saplings at least 50 m from forest plot boundaries and for which tallest shoot herbivory was recorded). It is perhaps not unexpected that the effect of density on height increments was swamped by variability in this data set, given the large range of environmental conditions (canopy gaps, understory shade, mesas, valleys, dry and wet soils, etc.) and initial sapling heights (50 cm to 7 m) that were included in the study. The variables measured also captured on a small portion of this variation, explaining only 12.8% of the variation in sapling annual height increments in a multiple regression analysis (Sullivan 2000a).

The significant effects of density on sapling shoot herbivory were found at a 50 m radius but not a 10 m radius. This 50 m radius is larger than most distance-dependent seed and seedling predation Janzen-Connell effects that have been documented (e.g., Janzen 1971, Augspurger 1983, Clark and Clark 1984, 1985, Burkey 1994, Barone 1996, Blundell and Peart 1998, but see Wright 1983). This scale is also larger than the 10-15 m distance-dependent seedling mortality and growth pattern that I previously documented for *T. ochracea*, a pattern hypothesized to be due to belowground pathogens associated

with adult *T. ochracea* trees (Sullivan 2000a). The spatial scale over which Janzen-Connell effects occur is important, as, all else being equal, the larger the spatial scale of Janzen-Connell effects in a forest community, the stronger the density-dependent regulation of the population and the greater the number of tree species that will be able to coexist (Hubbell 1980, Hubbell 1998).

It is difficult to generalize these results to other tropical trees, as few other studies have looked for Janzen-Connell effects caused by sapling herbivory. Several studies have documented density- and distance-dependent patterns of folivory on tropical tree seedlings (e.g., Janzen 1971, Denslow 1980, Clark and Clark 1985, Blundell and Peart 1998), although in the majority of cases no effects of this variation in herbivory on seedling mortality (or growth) were shown (but see Janzen 1971, Clark and Clark 1985). Barone (1996) found significantly negative distance-dependent effects on leaf herbivory of seedlings and small saplings (20 cm to 2 m high) on three of six tree species in Barro Colorado Island (BCI), Panama. Again, no effects of this herbivory on juvenile mortality or growth were demonstrated. Gilbert et al. (1994) documented an analogous system where the infection of juveniles of the tree *Ocotea whitei* on BCI by a species of stem canker was increased with both density and proximity to conspecific adult trees. In this case, there was evidence that the stem canker increased juvenile mortality.

While density- and distance-dependent effects on sapling survival have been detected for only the minority of tree species surveyed in the BCI long-term forest plot

(Wills et al. 1997), statistically detecting these Janzen-Connell effects without knowing the biology of the mechanisms causing them is fraught with difficulty (Clark and Clark 1984). For example, natural patterns of sapling distribution, growth, and survival are unlikely to be independent of underlying environmental gradients (Clark and Clark 1985, Clark et al. 1998, 1999). Because of this, strong Janzen-Connell effects may be occurring even if overall sapling survival is found to increase with conspecific density, so long as this increase is substantially less than would occur without herbivory and pathogen attack (Fowler 1988, Condit et al. 1994).

Such a problem is expected if *T. ochracea* was included in a community-scale analysis of density-dependent survival, as both sapling survival and sapling densities tend to be much higher on mesas than in valleys (Sullivan 2000a). Therefore, at the scale of forest plots, *T. ochracea* sapling survival is expected to be positively correlated with observed density. This relationship (and any other correlations between density and environmental variables) would have to be controlled for when searching for a causal relationship between density and survival. There are likely to be many subtle relationships between juvenile densities and underlying environmental gradients in tropical forests (Clark et al. 1999), and these will greatly complicate the mechanism-free searching for patterns consistent with Janzen-Connell effect in tropical forest plots.

Processes that influence seed dispersal and seedling recruitment have been emphasized as particularly important for controlling population dynamics of tropical

trees (De Steven 1994, Hubbell et al. 1999, but see Clark et al. 1999) and it has been suggested that, at least in the short-term, Janzen-Connell effects will tend to be strongest for seeds and seedlings and decrease as seedlings and saplings mature (Muller-Landau et al., in press). While the importance of seed and seedling predation should not be understated, insect herbivory of saplings may have an even larger impact on tropical tree population dynamics than these well-documented cases of distance-dependent seed and seedling predation by insects and fungi associated with parent trees.

This is for two reasons. First, the effects of sapling herbivory on sapling survival are integrated over much larger spatial and temporal scales than the effects of seed or seedling predation (Coley and Barone 1996). Unlike saplings, a cohort of seeds can escape distance-dependent herbivory and recruit into older size classes in one or a series of exceptional years when the densities of specialist seed predators or pathogen populations are low. Any density-dependence in the effects of herbivory on sapling growth and survival, by being averaged over many decades, are likely to be far more consistent than effects on seeds and seedlings. Second, many tropical insect herbivores, like *C. stroudagnesia*, occur far more frequently on saplings than in adult canopies (Coley and Barone 1996, Sullivan 2000a), and so sapling herbivory by these species is likely to be density- rather than distance-dependent. Because of this, sapling herbivory is likely to act over larger spatial scales and affect groups of saplings establishing in suitable microhabitats hundreds of meters from adult trees.

In conclusion, density-dependent shoot herbivory of *T. ochracea* saplings by *C. stroudagnesia* is likely to disproportionately decrease the number and rate of recruitment of saplings to reproductive age in areas of high conspecific sapling density. This result suggests that insect herbivory of saplings in tropical forests may play a major and largely unexplored role in structuring tree populations and tropical tree communities. Research on the interactions of saplings with their natural enemies for many other tropical tree species is needed to assess the generality of this result.

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TABLE 1. The results of partial correlations of density and shoot herbivory variables, holding the following variables constant: canopy light, ln(soil moisture), topography, ln(initial sapling height), ln(number of shoots), ln(stem diameter), ln(distance to the nearest conspecific adult tree), and the average annual height increment. The zero-order correlation matrix for all variables is shown in Table 3. The degrees of freedom is greater or the 10 m radius than the 50 m radius density measurements, as saplings within 50 m of the Bosque San Emilio plot border had to be excluded to calculate densities within a 50 m radius. Both herbivory variables were ln transformed. Tallest shoot herbivory refers only to shoot herbivory of the single tallest shoot on each sapling (this was not recorded for 28 of the study saplings). Significance levels are abbreviated as follows: n.s. = not significant ( $P>0.05$ ), \* =  $P<0.05$ , \*\* =  $P<0.01$ .

Herbivory		10 m radius # saplings	# shoots	50 m radius # saplings	# shoots
No. of all shoots bored	coefficient	-.046 n.s.	-.016 n.s.	.220*	.198*
	d.f.	134	134	107	107
tallest shoot herbivory	coefficient	.030 n.s.	.019 n.s.	.278*	.299**
	d.f.	109	109	84	84

TABLE 2. *Cromarcha stroudagnesia* herbivory of *T. ochracea* saplings is presented at the high and low extremes of *T. ochracea* sapling density, for density measured both by the number of *T. ochracea* saplings and the number of *T. ochracea* shoots within 50 m of each focal sapling. “% all shoots bored.yr<sup>-1</sup>” is the percentage of shoots attacked by *C. stroudagnesia* per sapling per year. “% tallest shoot bored.yr<sup>-1</sup>” is the percentage of saplings in a given year that have their tallest shoot attacked by a *C. stroudagnesia* larva.

Density within 50 m		% all shoots bored.yr <sup>-1</sup> average (s.e., n)	% tallest shoot bored.yr <sup>-1</sup> average (s.e., n)
Number of saplings	<10	2.02 (0.50, 59)	2.40 (0.79, 59)
	>30	9.54 (1.73, 39)	12.50 (4.31, 17)
Number of shoots	<300	1.99 (0.54, 54)	2.62 (0.85, 54)
	>2000	10.68 (1.98, 37)	22.32 (0.14, 14)

TABLE 3. The matrix of zero-order correlation coefficients for all variables (correlations between the different density measures are excluded, as all were  $>0.50$ ,  $P<0.001$ ). The variables are abbreviated as nm10 (number of saplings within a 10 m radius), sh10 (number of shoots within a 10 m radius) nm50 (number of saplings within a 50 m radius), sh50 (number of shoots within a 50 m radius), nbor (average annual number of shoots bored), tbor (average number of times the tallest shoot is bored per year), psky (percentage of canopy that is sky), agua (soil moisture), high (initial sapling height), diam (initial sapling stem diameter), dist (distance to the nearest conspecific tree), and hinc (average annual height increment). Sample sizes and ln transformations follow Table 1. Significance levels are abbreviated as follows: \* is  $P<0.05$ , \*\* is  $P<0.01$ , and \*\*\* is  $P<0.001$ . All correlation coefficients without asterisks are not significant ( $P>0.05$ ).

Table 3 (continued)

	nm10	sh10	nm50	sh50	nbor	tbor	nsho	%sky	agua	high	diam	dist
nbor	.171*	.153	.401***	.379***								
tbor	.229*	.178	.413***	.440***	.619***							
nsho	.178*	.136	.171	.153	.563***	.375***						
%sky	.003	-.025	-.215*	-.187*	.141	.096	.254**					
agua	.232*	.174*	.558***	.538***	.348***	.421***	.264**	.099				
high	.084	.052	-.016	-.015	.441***	.284**	.862***	.295***	.184*			
diam	.203*	.145	.149	.147	.534***	.361***	.912***	.393***	.290***	.913***		
dist	-.170*	-.270**	-.272**	-.32***	.127	.089	.285***	.139	.061	.261**	.271**	
hinc	.292***	.207*	.091	.083	.288***	.259**	.315***	.293***	.218**	.307***	.394***	.041

Figure 1. The relationship between *Tabebuia ochracea* density within a 50 m radius and the average annual percentage of *T. ochracea* shoots attacked by *Cromarcha stroudagnesia* for each study sapling. Two measures of density are plotted: **A**, the number of *T. ochracea* individuals (between 3 cm and 20 cm dbh), and **B**, the estimated number of *T. ochracea* shoots within a 50 m radius of each study sapling. n = 118. Note that these graphs present the raw data and not the residuals that are compared in the partial correlations to assess the significance of these relationships (see Table 1). The linear regression lines plotted on these graphs are only provided to illustrate the trends in the data given the large the number of zero values at lower densities in both plots.

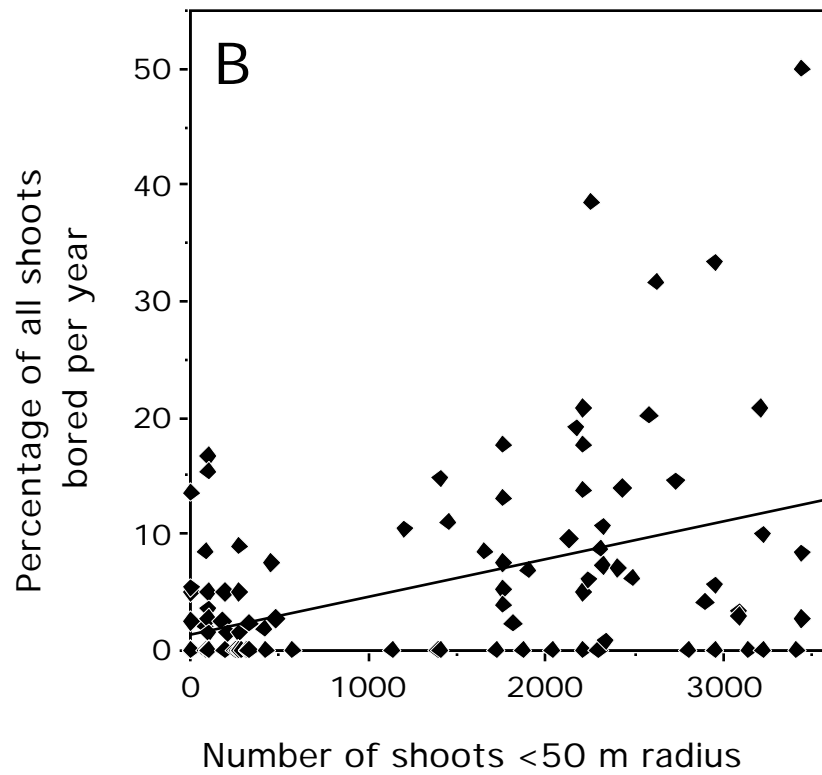
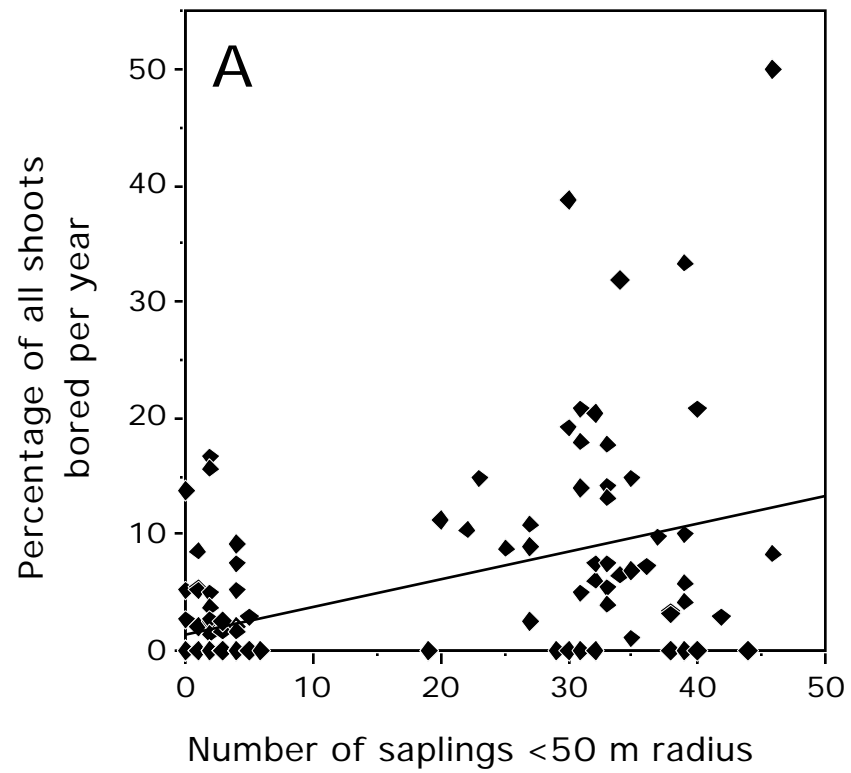




Figure 2. The relationship between *Tabebuia ochracea* density within a 50 m radius and the average number of times the tallest shoot is attacked by *Cromarcha stroudagnesia* per year per sapling. The maximum potential value is two shoots attacked a year, as there are two annual generations of *C. stroudagnesia*. Two measures of density are plotted: **A**, the number of *T. ochracea* individuals (between 3 cm and 20 cm dbh), and **B**, the estimated number of *T. ochracea* shoots within a 50 m radius of each study sapling. n = 95. The interpretation follows Fig. 1.

