PLANT ANIMAL INTERACTIONS

Jon J. Sullivan

Density-dependent shoot-borer herbivory increases the age of first reproduction and mortality of neotropical tree saplings

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 rates of height increment 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. Experiments and field observations over 3–4 years show a substantial reduction in sapling height increments due to *C. stroudagnesia* herbivory, of equivalent magnitude to the difference in height increments between undamaged saplings in canopy gaps and full understorey shade. Extrapolating this data at average amounts of *C. stroudagnesia* herbivory increases the duration of the pre-reproductive sapling life stage by about 40% relative to undamaged plants. This is an underestimate, as top shoot herbivory by *C. stroudagnesia* also increased the probability of canopy gap saplings being overtopped and shaded by surrounding vegetation. Sapling mortality was increased by *C. stroudagnesia* herbivory, with 11.8% of the most heavily damaged young saplings dying in 3 years while no undamaged saplings died. *Cromarcha stroudagnesia* herbivory strongly increases with the number of conspecific *T. ochracea* saplings and the number of conspecific shoots within 50 m of focal saplings. It is therefore likely to disproportionately decrease the number of saplings and rate of recruitment to reproductive age in areas of high conspecific sapling density. These results suggest that sapling herbivory, especially herbivory of terminal meristems, has an important but largely unexplored influence on the population dynamics of tropical tree species. They further demonstrate that sapling

herbivory by insects, in addition to the well-studied insect predation and herbivory of seedlings, is likely to influence tree species coexistence in tropical forests.

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Introduction

How does insect herbivory affect the growth and survival of tropical tree saplings? Can these effects accumulate over the usually substantial understorey life of saplings to alter the outcome of interspecific competition in canopy gaps, and the rates and patterns of recruitment in tree populations? These questions remain largely unexplored (Marquis 1992; Coley and Barone 1996), as saplings are typically long-lived, non-reproductive, and die slowly and infrequently. Yet tropical tree saplings typically lose between 7% and 20% of their aboveground green tissue each year to herbivores (Janzen 1988a; Marquis and Braker 1994; Coley and Barone 1996). Cumulative effects of this herbivory could be substantial (Coley and Barone 1996), which would affect tree population dynamics and could alter the composition and relative abundance of tree species in tropical forests (Janzen 1970; Connell 1971).

Sapling herbivory can potentially influence tree populations in several ways. First, herbivory may increase the age of first reproduction, which, all else being equal, will reduce individual trees' reproductive success (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 annual height increment over the understorey lifetime of a sapling, it will increase the age of first reproduction. Second, herbivory may increase the probability of preproductive sapling death. Third, it is plausible, although far less tractable experimentally, that the understorey 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 sapling herbivory-induced changes in adult crown architecture (Browne 1968)].

Documenting the effects of insect herbivory on tropical saplings via any of these processes 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 understorey and show gap-phase regeneration (Swaine 1996). It has been suggested that a reduction in the height increment of canopy gap saplings by insect herbivory may increase the probability of saplings being over-topped and shaded by competing saplings, which would in turn cause a further, potentially dramatic, reduction in sapling height increment (Janzen 1967, 1983; Edwards and Gillman 1987; Marquis 1992; Crawley 1997). To my knowledge, this has not been documented in a tropical forest habitat (cf. Janzen 1967).

The probability of sapling death may increase not only as a direct result of cumulative losses of resources due to 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 understorey, the probability of death by falling debris will also increase (Clark and Clark 1991; Coley and Barone 1996).

Tree species coexistence should be increased if insect herbivory has large detrimental cumulative effects on saplings, and if this herbivory is strongly positively dependent on conspecific sapling density (Janzen 1970; Connell 1971; Coley and Barone 1996). Tree species coexistence will be facilitated when sapling damage by herbivores (or other natural enemies) disproportionately decreases sapling survival or competitiveness in areas of high conspecific sapling density and/or close proximity to conspecific adults.

This study documents how herbivory by a sapling specialist shoot-borer, *Cromarcha stroudagnesia* Solis (Lepidoptera, Pyralidae, Chrysauginae) alters the height increment and mortality of saplings of the neotropical dry forest tree *Tabebuia ochracea* (Chamisso) Standley (Bignoniaceae) in north-western Costa Rica. Specifically, experiments and field observations addressed the following questions: (1) By how much does shoot-borer herbivory directly reduce sapling height increments and increase sapling mortality, in both canopy gap and understorey shade microhabitats? (2) How does the reduction in height increment of canopy gap saplings due to shoot herbivory compare with the height increments of competing gap vegetation? (3) By how much are these effects likely to increase the age of first reproduction of *T. ochracea* saplings? and (4) Does shoot-borer herbivory increase with *T. ochracea* sapling densities? No prior study has simultaneously quantified these impacts of sapling herbivory on tropical trees. This is also the first detailed exploration of the impacts of a shoot-borer insect on wild tropical tree saplings.

Materials and methods

Study site

Sector Santa Rosa (formerly Parque Nacional Santa Rosa) is the tropical dry forest core of the Area de Conservación Guanacaste (ACG), a 120,000 hectare conserved wildland in north-western Costa Rica containing the largest area of conserved dry forest in Central America. Santa Rosa includes a few small fragments of old growth dry forest and large expanses of 0- to 400-year-old secondary successional tropical dry forest (see Janzen 1988b). The local climate is highly seasonal, dominated by a pronounced 6-month dry season from December to mid May when essentially no rain falls. Average annual rainfall at the Santa Rosa Biological Station during the 4 years of this study (1996–1999) was 2,076 mm (SD=706).

All experiments and field observations in this study were made in forests on the Santa Rosa upland plateau (ca. 300 m elevation). All unmanipulated study saplings were found in forests surrounding the Santa Rosa Biological Station (10°50′27.26″ N latitude, 85°37′14.26″W longitude), including the Bosque San Emilio forest plot, a 16.3 ha plot in 80–100 year old secondary successional forest (Enquist et al. 1999), and the Bosque Humedo forest plot, a 4.8 ha forest plot within an area of old growth forest (Janzen 1986). All experimental saplings were found in an approximately 1.5 ha area of secondary successional forest 3.6 km north-northwest of the biological station, near the border between sector Santa Rosa and sector Santa Elena. This forest was chosen for its combination of ease of access (along an old farm road), remoteness from the biological station and its surrounding research plots, low, accessible canopy (mostly 5 m–15 m), and high density of *T. ochracea* saplings.

Study species

Tabebuia ochracea is a neotropical dry forest tree up to 30 m tall and >0.5 m diameter at breast height (DBH) with palmate five-foliate tomentose leaves (Gentry 1983, 1992). It was chosen as the focal species for this and associated studies (Sullivan 2000) because it is locally common and its brief, population-wide synchronized displays of large yellow flowers in the dry season made it easy to find.

Tabebuia ochracea has shade-tolerant saplings requiring canopy gaps for most understorey height increment (J.J. Sullivan, unpublished data). 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 (Borchert and Tomlinson 1984). I defined *T. ochracea* saplings as individuals ≥0.5 m high (sensu De Steven 1994), being well-established plants greater than 5 years old, and<10 m high, being the minimum flowering height in local forests (J.J. Sullivan, unpublished data).

A shoot-borer, *Cromarcha stroudagnesia,* was chosen as the focal herbivore for this study, because as an apical meristem feeder, it is especially likely to reduce sapling height increments (Janzen 1983; Clark and Clark 1985). It is a sapling specialist found only in *Tabebuia ochracea* and the locally much less abundant *T. impetiginosa.* Each larva typically destroys a single shoot, killing the apical meristem and as many nodes as are bored through. There are two generations per wet season. The complete natural history of *C. stroudagnesia* is outlined by Solis et al. (2003).

The use of the name *Cromarcha stroudagnesia* in this paper is not for purposes of zoological nomenclature, and is not published within the meaning of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). Solis et al. (2003) will be the first published description of *Cromarcha stroudagnesia* for purposes of the Code.

No evidence of vertebrate browsing of *T. ochracea* saplings in Santa Rosa has been found (J.J. Sullivan, personal observation), and a Baird's tapir (*Tapirus bairdii*) rejected *T. ochracea* leaves in feeding trials (Janzen 1982).

Sapling growth and herbivory in canopy gaps and understorey shade

The growth and *C. stroudagnesia* herbivory of wild *T. ochracea* saplings in canopy gaps and understorey shade were observed for 4 years to search for relationships between the frequency of *C. stroudagnesia* shoot herbivory and sapling height increments and mortality. The growth of neighbouring canopy gap vegetation was also recorded, to assess how the frequency of shoot herbivory of canopy gap saplings reduced saplings' height increments relative to that of the neighbouring vegetation.

Between November 1996 or July 1997 and July 1999, the growth of 48 *T. ochracea* saplings and their surrounding vegetation was recorded inside 29 treefall canopy gaps in the Bosque San Emilio long-term forest plot. Each study sapling was initially of equal or greater height than the surrounding gap vegetation. Each canopy gap sapling was paired with a similarly sized sapling (±1.5 m height) in understorey shade >ca. 15 m from the edge of the gap. Identical measurements were taken for these shaded saplings. Initial sapling height ranged from 52 cm to 6.63 m.

Sapling height, diameter, and top shoot herbivory status were recorded each July and November for each of the 96 *T. ochracea* saplings. Sapling height was measured with a weighted measuring tape attached to an up to 7 m long telescoping pole. In the first half of the 1998 wet season (May–July), the percentage of all shoots bored by *C. stroudagnesia* was also recorded.

Each year, a graduated telescoping pole was used to record the height of the highest vegetation at the four points 3 m in each cardinal direction from the base each canopy gap *T. ochracea* sapling. The height increment at each point was classified as either "gap growth" or "canopy closure." Gap growth was defined as vertical growth of the vegetation present inside the gap. Canopy closure was defined as any new lateral growth into the gap by a large individual sapling or tree on the gap edge.

Experimental manipulation of shoot herbivory in light and shade

A field experiment was performed to confirm the causal relationship between the amount of shoot herbivory and the rates of annual sapling height increment and mortality. The experiment was run for 3 years, ending in December 1999.

In the dry season of early 1997, 360 wild undamaged 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, by decapitating understorey vegetation and climbing neighbouring young trees and sawing off overhead 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. This locally available shading material reduced light levels to 3–4% of full sunlight, which is within the range of light intensity of understorey shade in local mid-successional forests in the wet season (and produced growth rates equivalent to those of understorey shade saplings—see Results). 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.

The 360 saplings were randomly divided between three artificial shoot herbivory treatments: four shoots damaged per year (two per shoot-borer generation), two shoots damaged per year, and no damage. These damage levels span the range of naturally observed average annual shoot herbivory for saplings of this height range (J.J. Sullivan, unpublished data).

Wild shoot-borers were excluded from experimental saplings by gently 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 *C. stroudagnesia* egg laying periods of each year, being the first 3 weeks of the wet season and the month from mid-August through mid-September (Solis et al. 2003). 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 (Solis et al. 2003). Very rarely larvae will enter shoots through leaf petioles—such attacked leaves were manually removed before the larva entered the shoot. At the end of the experiment, the few saplings still successfully attacked by *C. stroudagnesia* were excluded from the design, as were saplings that had died or been inadvertently damaged. The experiment was randomly rebalanced to 51 saplings per insolation×main damage level treatment combination (*n*=306).

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 *C. stroudagnesia* larvae is 14.8 cm long and is created over ca. 6 weeks (J.J. Sullivan, unpublished data). This damage was mimicked by drilling out 5 cm from the pith of each selected shoot every 2 weeks for 6 weeks, beginning at the apical meristem and drilling downwards. First instar larvae normally begin feeding at or near the shoot tip, entering either through the apical meristem, or feeding upwards from an entry point in recently grown shoot wall or a leaf bud (J.J. Sullivan, unpublished data). For each treatment, the longest shoot(s) of each sapling were selected for damage, since wild *C. stroudagnesia* herbivory is strongly biased towards the longest shoots (Solis et al. 2003). 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 behaviour of wild *C. stroudagnesia* larvae. Between each plant, the drill bit was cleaned and sterilized by flaming with 90% ethanol to prevent any transmission of pathogens.

Sapling height was recorded twice a year with a measuring tape (kept vertical with a small lead weight). Numerous other sapling variables were also recorded (J.J. Sullivan, unpublished data), but are not reported here as they are not directly relevant to the study questions. To account for any variation in sapling height increments caused by variation in soil moisture across the experiment, soil moisture measurements were made at the base of each sapling with a Rapidtest Mini Moisture Tester (Luster Leaf Products, Woodstock, Ill., 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°C in a drying oven until stable weight. All readings were made on 7 August 1999 after 4 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.

A further 222 saplings were used to ensure that differences between artificial shoot damage and damage by transplanted larvae were negligible and that the TangleTrap larval exclusion method did not affect sapling growth. No significant sapling differences were found between artificial damage and transplanted larva damage (more often than not, the effects of artificial damage were slightly less than the effects of larvae), and there were no significant direct effects of TangleTrap on sapling growth [for full details see Sullivan (2000)].

Field observations of density-dependent herbivory

The dependence of *C. stroudagnesia* herbivory on *T. ochracea* sapling density was assessed by correlating average annual shoot herbivory with the local density of conspecific saplings. Sapling density was not experimentally manipulated.

Total shoot herbivory and height increments of an additional 153 *T. ochracea* saplings, initially between 0.5 m and 7 m high, were recorded between 1995 and 1999. Sixty-six of these saplings were found in a brief survey of the Bosque Humedo forest plot. The remainder were haphazardly selected from within the Bosque San

Emilio forest plot. The Bosque Humedo and Bosque San Emilio plots are about 950 m apart and connected by a continuous cover forest of similar or greater age than Bosque San Emilio.

Height, stem diameter at 30 cm height, and shoot herbivory, were recorded each mid- and late-wet season from 1995 to 1999 for all Bosque Humedo saplings and 59 of the Bosque San Emilio saplings. For each sapling, I recorded the number of all shoots, the number of shoots containing *C. stroudagnesia* larvae, and if the top shoot contained a *C. stroudagnesia* larva. The remaining 28 Bosque San Emilio saplings were only visited in 1995 and 1999. Shoot architecture maps drawn in 1995, including sapling height and past and current shoot-borers, were used in 1999 to record how many shoots had been subsequently attacked (old *C. stroudagnesia* killed shoots remain on saplings for many years and are easily identifiable by the basal exit hole). These data provided the average annual height increment and average annual percentage of shoots attacked by *C. stroudagnesia* for each sapling, but not the frequency of top shoot herbivory.

For all study saplings, soil moisture and canopy light were recorded in 1999 for use as covariates in the analysis. Canopy light was estimated from the percentage of canopy that was sky in digital photos taken from the top of each sapling with a Sony Mavica digital camera with wide-angle lens attachment attached to a telescoping pole. Canopy light was calculated with the Histogram feature of Adobe Photoshop 4.01, setting the colour selection to pure white and the fuzziness to 200, sufficient to select white cloud and blue sky without selecting foliage.

Densities of conspecifics surrounding each *T. ochracea* sapling were calculated from comprehensive maps of *T. ochracea* in the Bosque Humedo forest plot (J.J. Sullivan, unpublished data) and the Bosque San Emilio forest plot (B.J. Enquist, C.A. Enquist, 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 ≥3 cm DBH had been 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 between 3 cm and <20 cm DBH within 10 m and 50 m of each study sapling were calculated. Trees ≥20 cm DBH were excluded from the density measurements as they are canopy trees and there is negligible *C. stroudagnesia* shoot herbivory in tree canopies (Solis et al. 2003). The distance to the nearest such adult tree was calculated separately for each sapling.

The numbers of conspecific shoots within 10 m and 50 m of each sapling were estimated from the allometry equation, number of shoots=10.785× DBH. This equation was generated from two allometry equations, the first relating stem diameter at 30 cm height (*D* 30 cm *H*, measured in this study) to DBH (included in the Bosque San Emilio forest plot map data), and the second relating *D* 30 cm *H* to shoot number, generated from a sample of 344 study saplings (J.J. Sullivan, unpublished data). These equations are: DBH=0.738× *D* 30 cm *H* (linear regression, $P<0.0001$, $R^2=0.96$, $n=132$), and number of shoots=0.796× *D* 30 cm *H* (linear regression, $P<0.0001$, $R^2=0.85$, $n=344$). 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). Canopy gap and understorey shade sapling data were analyzed with independent samples t-tests and fixed effects two-way ANCOVAs with initial height and the 1998 percentage of all shoots bored as covariates. Experimental data were analyzed with fixed-effects two-way ANCOVAS, with initial height 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). A *G*-test for independence with William's

correction was used to analyze for effects of experimental shoot herbivory on sapling mortality (Sokal and Rohlf 1995).

Correlating *C. stroudagnesia* herbivory with sapling height increments in the observational data was complicated by *C. stroudagnesia* herbivory being strongly biased towards the longest shoots of the fastest growing wild saplings (Solis et al. 2003). This bias for the fastest growing saplings was avoided in the top shoot herbivory data by randomly selecting equal numbers of saplings to represent a period of either top shoot herbivory or no top shoot herbivory. One appropriate 12-month height increment was then randomly sampled from each sapling. In this manner, the fastest growing saplings were as likely to occur in the "no top shoot herbivory" category as the "top shoot herbivory" category. If the top shoot of a sapling was never attacked during the study, a random 12 month interval was selected to represent this third category. Since about one-third or more of saplings never had their top shoot attacked by *C. stroudagnesia* during the study (see Results), the statistics were simplified by randomly excluding saplings to maintain a balanced statistical design across these three categories.

Partial correlations were used to compare conspecific sapling 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 list-wise 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 top shoot herbivory), for one sapling that died in 1998 (no height increment), and for three saplings so large that it was impractical to record the total percentage of shoots bored. 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 top shoot was attacked by *C. stroudagnesia* per year). All significance levels reported are based on two-tailed tests.

Results

Shoot herbivory reduces sapling height increment and increases mortality

From the field observations, there was no significant overall relationship between the height increments of *T. ochracea* saplings and the total percentage of shoots bored by *C. stroudagnesia* [linear regressions, $P>0.05$. $R^2<0.05$, for both paired gap-shade saplings ($n=96$, 1998 only) and density-dependence saplings ($n=153$, all years)]. This is because *C. stroudagnesia* herbivory is strongly biased towards the longest shoots of the fastest growing wild saplings (Solis et al. 2003).

In contrast, strong negative effects of *C. stroudagnesia* herbivory on height increment were found (Fig. 1) when the paired gap-shade data were randomly sampled to remove the bias in *C. stroudagnesia* herbivory towards the fastest growing saplings (see Analysis). Sapling height increment was significantly reduced by both top shoot herbivory and understorey shade (Fig. 1). Attack of the top shoot by a single *C. stroudagnesia* larva decreased the height increment in that 12 month interval by an average 77.9% for canopy saplings, and 83.1% for understorey
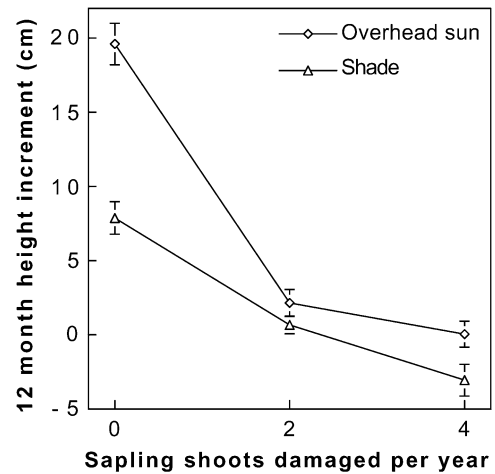
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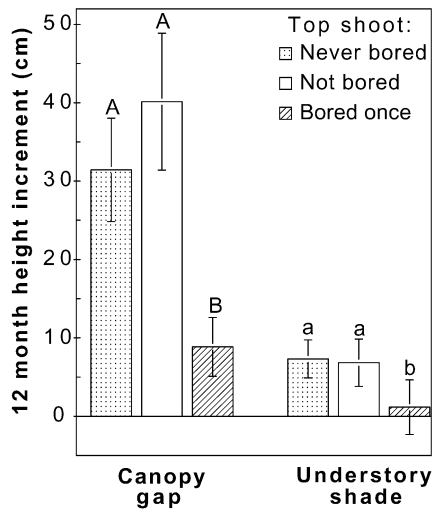
Fig. 1 Top shoot herbivory by *Cromarcha stroudagnesia* reduces the annual height increment of *Tabebuia ochracea* saplings, both in canopy gaps and understorey shade. Over the duration of the study, saplings either experienced or escaped top shoot herbivory by *C. stroudagnesia* larvae. From the former group, a 12-month increment was randomly selected from when the top shoot was bored (*Bored once*) and was not bored (*Not bored*) by *C. stroudagnesia*. From the latter group (*Never bored*), a random 12-month increment was selected for each sapling. Plotted are averages ±1 SE. Letters above bars label groups that did not differ at a *P*<0.05 level in planned comparisons within canopy gap saplings (*A-B*) and understorey shade saplings (*a-b*). Sample sizes were randomly balanced to *n*=42 for the canopy gap saplings and *n*=39 for the understorey shade saplings. Two-way ANCOVA: top shoot herbivory, *P*<0.01, *df*=2, SS=64.3, *F*=5.2; insolation *P*<0.001, *df*=1, SS=181.4, *F*=29.1; interaction n.s., *df*=2, SS=18.9, *F*=1.5; error SS=449.1; covariates n.s.

Fig. 2 The effects of different frequencies of artificial shoot herbivory (with a rechargeable drill, mimicking *C. stroudagnesia* shoot-borer herbivory) on the height increment of small *T. ochracea* saplings either shaded or with overhead sun. Plotted are averages ±1 SE (*n*=306). Both treatment effects and their interaction are significant (two-way ANCOVA: shoot herbivory, *P*<0.001, *df*=2, SS=1545, *F*=133; insolation *P*<0.001, *df*=1, SS=205, *F*=35.3; interaction *P*<0.05., *df*=2, SS=51.7, *F*=4.46; error SS=1727; all covariates n.s.)

shade saplings (Fig. 1). These 12 month intervals include any shoot regrowth in the 6 months following shoot-borer attack.

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 in Bosque San Emilio, 71.4% of the study saplings in canopy gaps had their top shoot attacked at least once by a *C. stroudagnesia* larva; four saplings (8.3%) were attacked every year and 13 saplings (27%) were never attacked (*n*=96). The average probability of a canopy gap sapling having its top shoot bored in a year was 0.401 (SD=0.321, *n*=48 saplings), equivalent to one top shoot bored every 2.5 years. In contrast, 52.9% of study saplings in understorey shade had their top shoot attacked at least once, and the average probability of an understorey shade sapling having its top shoot bored in a year was 0.219 (SD=0.258, *n*=48 saplings). The top shoot of even an understorey shade sapling is often sufficiently long to support the development of a *C. stroudagnesia* larva (Solis et al. 2003).

Only one of the 96 wild saplings died during the field study. This was an understorey shade sapling initially 196 cm high. In the year before its death, eight of its nine shoots were attacked by *C. stroudagnesia* larvae, the

highest percentage shoot herbivory recorded for any study sapling in any year.

In the field experiment, artificial shoot herbivory caused a significant reduction in sapling height increment, comparable to the field observations (Fig. 2). Artificial shoot herbivory reduced sapling height increments by 89.0% in the light and 91.5% in the shade in the intermediate damage frequency of two shoots per year (Fig. 2). Most shaded saplings experiencing the highest level of shoot damage shrunk in height during the experiment (average height increment, −3.1 cm, SE=0.07, *n*=51). This shrinkage was also observed in many of the unmanipulated shaded saplings (Fig. 1).

Sapling mortality was unrelated to insolation but was 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. Twelve of these were in the highest damage frequency treatment (11.8% of heavily damaged plants), with six saplings dying in each of the insolation treatments. An additional shaded sapling died in the intermediate damage treatment. No undamaged saplings died.

Shoot herbviory reduces sapling height increments to below average canopy gap growth rates

The height increments of *T. ochracea* saplings in canopy gaps, when measured relative to gap vegetation height increments, were significantly greater in years with no top shoot herbivory by *C. stroudagnesia* than in years with top shoot herbivory (Fig. 3). In years without top shoot
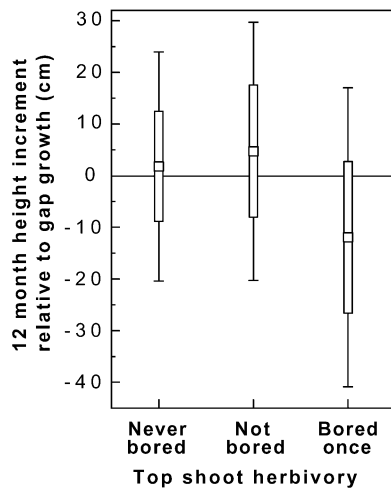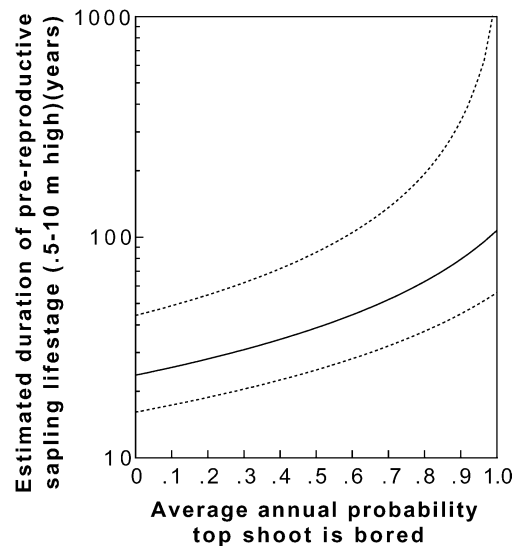
Fig. 3 The average height increments of *T. ochracea* saplings compared with the average height increments of the surrounding gap vegetation. Plotted are averages ±1 SE (*open bars*) and ±95% confidence intervals (*lines*). One-way paired *t*-test: $t=2.05$, $P<0.05$, $df=20$, excluding plants that never had a top shoot bored

Fig. 4 The differences in 12 month sapling height increments with and without top shoot herbivory (Fig. 1) extrapolated to the prereproductive understorey lifetime of saplings in canopy gaps (between 50 cm and 10 m high). These are minimum estimates, not predictions of actual ages at first reproduction, as they assume canopy gap saplings will remain at the top of the canopy gap vegetation throughout their lives. Plotted are averages and 95% confidence intervals across all lifetime average annual probabilities of top shoot herbivory. The 95% confidence intervals are estimated from the 95% confidence intervals around the average growth rates of Fig. 1. The average annual probability of annual top shoot herbivory across the 4 years of this study was 0.401, and individual saplings spanned the full range from 0 to 1.0

herbivory, the average height increment was greater for *T. ochracea* saplings than most of the surrounding gap vegetation (Fig. 3). In years with top shoot herbivory, the average height increment was less than most of the surrounding vegetation (Fig. 3). At the observed average rate of one top shoot attacked by *C. stroudagnesia* per 2.5 years, the average annual *T. ochracea* height increment is still at least 9.7 cm less than most of the surrounding vegetation.

Over the three years, most saplings did not follow these average statistics—9.3% of saplings had annual height increments greater than the surrounding gap vegetation in each year when their top shoot was not bored, but less in each year when the top shoot was attacked by *C. stroudagnesia*. Regardless of top shoot herbivory, 51.1% of saplings had average annual height increments less that the surrounding vegetation each year, and 18.6% of saplings had annual height increments greater than the surrounding vegetation each year.

Shoot herbivory increases age of first reproduction

The large experimental and observed effects of *C. stroudagnesia* herbivory on sapling growth and survival are likely to translate into large increases in the age of first reproduction of *T. ochracea*. A conservative 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. 1 to the prereproductive life length of saplings (the non-experimental growth and herbivory data are used because they span a greater range of initial sapling sizes and are supported by the experimental results). A linear extrapolation is possible because the average annual height increment of *T. ochracea* saplings is unrelated to initial

height, and the minimum height of first reproduction in closed canopy forest is 10 m or greater (J.J. Sullivan, unpublished data).

If it is assumed that a canopy gap sapling remains in overhead sun at the top of gap vegetation throughout its life regardless of its annual height increment, extrapolating the sapling height increment data predicts that an average 50 cm high canopy gap sapling (already at least 5 years old) would on average reach 10 m high and begin reproducing after 23.7 years if it never had its top shoot bored by a *C. stroudagnesia* larva (Fig. 4). 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 (Fig. 4). This corresponds to about a 40% increase in the age of first reproduction solely due to *C. 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, if it survived.

The above estimates are likely to substantially under-estimate the true impact of *C. stroudagnesia* on the age of first reproduction of *T. ochracea*. The assumption that a canopy gap sapling remains at the top of the gap vegetation until at reproductive height will be increas-ingly unrealistic as annual height increments are increas-

Table 1 *Cromarcha stroudagnesia* herbivory of *Tabebuia ochracea* saplings at the high and low extremes of *T. ochracea* sapling density, for density measured both by the number of *T. ochracea* saplings and the estimated number of *T. ochracea* shoots within 50 m of each focal sapling. *Average percent all shoots bored.year^{-1}* is the percentage of shoots attacked by *C. stroudagnesia* per sapling per year. *Average percent top shoot bored.year^{-1}* is the percentage of saplings in a given year that have their top shoot attacked by a *C. stroudagnesia* larva. All effects are statistically significant (see Results)

	Density within 50 m	Average percent all shoots bored.year^{-1} (SE, n)	Average percent top shoot bored.year^{-1} (SE, 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)
	>2,000	10.68 (1.98, 37)	22.32 (0.14, 14)

ingly reduced by shoot-borer herbivory (Fig. 3). Furthermore, canopy gap saplings overtopped by competing vegetation due to *C. stroudagnesia* herbivory may eventually starve in the thickening shade, and the longer a sapling remains pre-reproductive in the understorey, the proportionately greater its risk of a pre-reproductive lethal impact from falling debris (Clark and Clark 1991).

Shoot herbivory is positively host-density-dependent

Cromarcha stroudagnesia herbivory was significantly positively correlated with local *T. ochracea* sapling densities measured in a 50 m radius (Table 1). This applied for both measures of herbivory with both measures of conspecific density. For density measured as the number of *T. ochracea* saplings within 50 m, the partial correlations were 0.220 ($P<0.05$, $df=107$) for the average annual percentage of shoots attacked by *C. stroudagnesia* per sapling, and 0.278 ($P<0.05$, $df=84$) for the average number of times the top shoot was attacked by *C. stroudagnesia* per year per sapling. For density measured as the estimated number of *T. ochracea* shoots within 50 m, the respective partial correlations were 0.198 ($P<0.05$) and 0.299 ($P<0.01$). These density effects occurred independently of all other measured variables, including the distance to the nearest conspecific adult.

No significant relationships were found at the 10 m radius for either measure of *C. stroudagnesia* herbivory with either measure of density. For density measured as the number of *T. ochracea* saplings within 10 m, the partial correlations were −0.046 (n.s., $df=107$) for the average annual percentage of shoots attacked per sapling, and 0.030 (n.s., $df=84$) for the average number of times the top shoot was attacked per year per sapling. For density measured as the estimated number of *T. ochracea* shoots within 10 m, the respective partial correlations were −0.016 (n.s.) and 0.019 (n.s.).

Shoot herbivory was substantially less on saplings in the old-growth Bosque Humedo forest plot than the younger Bosque San Emilio forest plot. For example, the average annual percentage of shoots attacked by *C. stroudagnesia* per sapling was 1.9% in Bosque Humedo (SE=0.46, $n=65$) and 11.0% in Bosque San Emilio (SE=1.54, $n=81$). This difference can be wholly explained by the differences in *T. ochracea* density between the two forest plots. 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, $P=0.41$, $df=112$), despite a strong, significant uncontrolled correlation between forest and the percentage of shoots bored (Pearson's correlation coefficient=−0.507, $P<0.001$).

As expected from the rarity of *C. stroudagnesia* in tree canopies (Solis et al. 2003), the distance to the nearest conspecific adult was not correlated with either measure of *C. stroudagnesia* herbivory (top shoot herbivory: Pearson's correlation coefficient =0.127, n.s.; total percentage of shoots bored: Pearson's correlation coefficient =0.089, n.s.).

Discussion

Sapling herbivory affects tree population dynamics

The interactions between *C. stroudagnesia* and *T. ochracea* demonstrate that sapling herbivory by insects, especially apical meristem feeding insects such as shoot-borers, can have large effects on tree growth and age of first reproduction in tropical forests (Figs. 1, 2, 3, 4). The average direct effects of *C. stroudagnesia* on *T. ochracea* sapling height increments are as great as the difference between undamaged sapling growth in understorey shade and canopy gap light (Figs. 1, 2). The substantial body of literature on tropical gap phase regeneration (e.g., Whitmore 1996) has already documented how important effects of this magnitude can be for structuring tropical tree populations and communities. Added to this is the further decrease in canopy gap sapling height increments when *C. stroudagnesia* herbivory alters the outcome of interspecific sapling competition (Fig. 3) and the increased pre-reproductive mortality due to cumulative herbivory, increased shading, and an increased risk of pre-reproductive mortality from falling debris. *Cromarcha stroudagnesia* herbivory must therefore reduce the rate of canopy recruitment in the *T.ochracea* population and the potential rate of population increase.

The cumulative effect of all insect herbivores on *T. ochracea* prereproductive mortality and age of first

reproduction must well exceed the effects of *C. stroudagnesia* alone. There are more than 36 insect herbivores that feed on the aboveground tissues of *T. ochracea* saplings (Janzen and Hallwachs 2002; J.J. Sullivan, unpublished data), and insect herbivory is almost universally detrimental for host plants (Crawley 1997). *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 2002). This suggests that sapling herbivory by insects reduces the growth and reproductive performance of most, probably all, of the local tree flora.

Shoot-borer herbivory is particularly damaging

While this study of shoot-borer herbivory in a wild tropical forest is currently unique, it is supported by much research on shoot-borer pests in tropical timber plantations and temperate forestry (e.g., Gray 1972; Newton et al. 1993; Solomon 1995; Mo et al. 1997a, 1997b; Speight 1997; De Groot and Schnekenburger 1999). These studies suggest that the large effects of *C. stroudagnesia* on *T. ochracea* are not unusual. Forestry shoot-borers typically slow sapling growth and can dramatically stunt tree architecture (e.g., Solomon 1995). Menalled et al. (1998) also found that the neotropical shoot-borer, *Hypsipyla grandella,* caused its host tree, the tropical cedar *Cedrela odorata* (Meliaceae), to be overshaded by other species in an experimental mixed plantation, paralleling my result here with *Cromarcha stroudagnesia* and canopy gap *T. ochracea* saplings.

It is likely shoot-borers, per capita, have a greater influence on tropical saplings and tree population dynamics than most other insect herbivores (Janzen 1983). Shared traits among studied tropical and temperate shoot-borers 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, typically at the tops of plants (e.g., Solomon 1995; Mo et al.1997b; Solis et al. 2003). Relatively few shoot-borer larvae can therefore have large effects on the height increment, architecture, and competitive performance of their hosts. The highest attack rates of shoot-borers are typically on intermediate-aged saplings (e.g., Gray 1972; Newton et al. 1998), and typically on the most rapidly growing saplings (Price 1991; Newton et al. 1993; Solomon 1995; Mo et al. 1997a; Speight 1997). Shoot-borers will therefore preferentially attack and kill the top shoots of those saplings most likely to otherwise recruit to the forest canopy.

Shoot-borers species are also not uncommon (e.g., Solomon 1995). A brief survey during this study found shoot-borer larvae attacking saplings of 22 tree species (J.J. Sullivan, unpublished data). This represents 12% of the Santa Rosa tree flora, most of which was not adequately sampled.

Sapling herbivory and density-dependent regulation of tree populations

This study is important because it shows both reductions in sapling growth and survival due to herbivory and a strong relationship between sapling herbivory and host density. *Cromarcha stroudagnesia* herbivory increased markedly with sapling density (Table 1), regardless of the distance to the nearest conspecific adult tree. While only correlational, I anticipate this relationship is causal, as it is neither biologically unreasonable nor unprecedented (Bernays and Chapman 1994). The combination of detrimental effects and positive density-dependent herbivory indicate that *C. stroudagnesia* will produce a density-dependent Janzen-Connell effect (Janzen 1970; Connell 1971). A density-dependent Janzen-Connell effect occurs when recruitment within a tree population is relatively low in areas of high conspecific density (or near conspecific adults), due to the mortality effects of positive density-dependent (or negative distance-dependent) seed predation and herbivory. Hence, 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 ACG dry forests, potentially limiting the local abundance of *T. ochracea* and facilitating species coexistence. This conclusion is strengthened by *C. stroudagnesia* herbivory being strongly biased towards the fastest growing saplings in the population (Solis et al. 2003), those most likely to reach reproductive maturity.

Many studies have documented conspecific 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), but very few studies have done the same for saplings. 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. No effects of this herbivory on juvenile mortality or growth were assessed. 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.

As data sets have grown and statistical methods have improved, patterns of mortality and recruitment consistent with Janzen-Connell effects have been detected for progressively greater proportions of the tropical tree species in long-term forest plots (Hubbell et al. 1990, 2001; Condit et al. 1992; Wills et al. 1997; Harms et al. 2000; John et al. 2002; Muller-Landau et al. 2003; cf. Wright 2002). These patterns have strengthened the conclusion that Janzen-Connell effects play a dominant role in maintaining alpha tree diversity in tropical forests (Hubbell 1998; Harms et al. 2000; Wright 2002; cf. Hubbell 2001). However, the biological mechanisms

driving almost all of these statistically described density-dependent patterns are unknown.

Processes that influence seed dispersal and seedling recruitment have been emphasized as particularly important for controlling population dynamics of tropical trees (De Steven 1994; Whitmore 1996; Hubbell et al. 1999; but see Clark et al. 1999), and it has been suggested that Janzen-Connell effects will be strongest for seeds and seedlings and decrease as seedlings and saplings mature (Nakashizuka 2001; Muller-Landau et al. 2003). Numerous studies have demonstrated Janzen-Connell effects, usually associated with adult conspecific trees, for species-specialist insect 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 fine spatial scales that will have relatively weak effects on tropical tree alpha diversity (Hubbell 1980; Becker et al. 1985). While I do not wish to understate the importance of seed and seedling predation, insect herbivory of saplings, especially by apical feeding insects like shoot-borers, could be having at least as large an influence on tropical tree population and community dynamics.

This is for two reasons. First, the effects of sapling herbivory on sapling growth and 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 accumulating over many decades, are likely to be far more consistent than effects on seeds and seedlings.

Second, many tropical insect herbivores, including most shoot-borers, occur far more frequently on saplings than in adult canopies or on seedlings (Coley and Barone 1996; Solis et al. 2003; cf. Basset et al. 2001). This sapling herbivory is therefore likely to be density-dependent rather than dependent on distances to adult conspecific trees. Groups of saplings establishing in suitable microhabitats hundreds of meters from adult trees will still be affected. This specialist sapling herbivory is also likely to vary on a larger (coarser) spatial scale than incidental herbivory of juveniles by insects sourced from adult trees. For example, the significant effects of *T. ochracea* density on *C. stroudagnesia* herbivory were found at a 50 m radius (and not a 10 m radius), and were unrelated to the distance to conspecific adult trees. This scale is larger than typical distance-dependent seed and seedling predation Janzen-Connell effects (e.g., Janzen 1971; Augspurger 1983; Clark and Clark 1984, 1985; Burkey 1994; Barone 1996; Blundell and Peart 1998). All else being equal, the larger the scale of this density-dependence, the greater the number of competitively equivalent tree species can coexist (Hubbell 1980; Becker et al. 1985).

In conclusion, the results of this study suggest that insect herbivory of saplings, especially herbivory by shoot-borers and analogous apical meristem feeding insects, may play a major and largely unexplored role in structuring tropical tree populations and communities. Research on the interactions of saplings with their insect herbivores is needed for more tropical tree species to assess the generality of this result.

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