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# Effect of shrubs on tree seedling establishment in an abandoned tropical pasture

KAREN D. HOLL
*Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA*

**Summary**

**1** The objective of this study was to evaluate whether early successional shrubs facilitate, tolerate or inhibit different stages of tree establishment in abandoned tropical pasture.
**2** Seed rain, seed predation, seed germination and seedling survival of tropical forest trees in pasture grass, below small ($< 25\ m^2$) shrub patches and below large ($> 40\ m^2$) shrub patches, were compared in one abandoned pasture in Costa Rica over 2 years.
**3** Seed rain of animal-dispersed trees was higher below both large and small shrub patches than below grass. Seed rain of wind-dispersed trees did not differ in the three patch types.
**4** Predation of all animal-dispersed seeds combined and of three individual species was significantly higher below large and small shrub patches compared with below grass; predation of five species did not differ significantly in the three patch types.
**5** Germination did not differ significantly in the three patch types for any of the species.
**6** Seedling survival was highest below large shrub patches for three of four species.
**7** Computer simulations of probabilities of seeds arriving in the pasture and surviving to the seedling stage suggest that early successional shrubs have a net facilitative effect on the early stages of forest tree seedling establishment compared with areas without shrubs in the pasture studied, although variance was high. Shrubs may facilitate, inhibit and tolerate different stages of tree seedling establishment.

*Key-words*: Costa Rica, dispersal, germination, predation, seed, succession

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## Introduction

Research in the tropics suggests that many factors impede forest succession in abandoned pastures, primarily low seed dispersal, high seed and seedling predation, competition with grasses and lack of soil nutrients (e.g. Uhl *et al.* 1988; Aide & Cavelier 1994; Nepstad *et al.* 1996; Holl *et al.* 2000). Few studies in the tropics, however, have evaluated the effect of early colonizing shrubs on these factors and their consequences for woody seedling establishment. Understanding vegetation dynamics in tropical old fields is critical to broadening theories of succession, as well as to tropical forest restoration efforts.

The role of shrubs in temperate old field and grassland succession has been well-studied (McDonnell & Stiles 1983; Berkowitz *et al.* 1995; Callaway & Davis 1998), but has received little study in the tropics despite the growing area of abandoned agricultural lands. Past research indicates that it is usually not possible to categorize shrubs as clearly 'facilitating', 'tolerating' or 'inhibiting' establishment of woody species (*sensu* Connell & Slatyer 1977), because early successional shrubs may have variable effects on different stages of seedling regeneration (Pickett *et al.* 1987; Walker & Chapin 1987; Myster 1993; Callaway & Walker 1997).

The few tropical studies suggest differential effects of early successional shrubs on tree establishment. Some have documented higher establishment of woody seedlings below shrubs compared with areas of dense grass (Vieira *et al.* 1994; Aide *et al.* 1995; Holl *et al.* 2000), whereas others suggest that shrubs may 'arrest' succession (Zahawi & Augspurger 1999) and compete with larger seedlings both below- and above-ground (Holl 1998; Loik & Holl 2001). Many studies in the tropics have demonstrated higher animal dispersal of seeds below shrubs compared with grass (Vieira *et al.* 1994; Cardoso da Silva *et al.* 1996; Duncan & Chapman 1999), and at least one study concluded that shrubs provide more favourable nutrient and microclimatic conditions (Vieira *et al.* 1994). The objective of this study was to compare

Correspondence: Karen D. Holl, Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA (tel. +831-459-3668; fax +831-459-4015; e-mail kholl@cats.ucsc.edu).

the effects of pasture grasses and early successional shrubs on different stages of tree seedling establishment in abandoned tropical pasture, including seed dispersal, post-dispersal seed predation, germination and seedling survival.

## Materials and methods

### SITE DESCRIPTION

This study was conducted in a 5-ha pasture abandoned in 1995 that is adjacent to primary, seasonal montane wet forest in southern Costa Rica (8°57′ N, 82°50′ W, 1500 m elev.; see Holl 1999 for further description). Average annual rainfall is *c.* 3000 mm, > 95% of which normally falls between April and December.

At the start of the study, the vegetation consisted predominantly of the non-native grasses *Axonopus scoparius* and *Melinis minutiflora*. Shrubs covered 2.4% and 6.1% of the pasture 1 and 3 years after abandonment (Holl *et al.* 2000). Almost all shrub patches included multiple shrub and vine species, the most common of which were *Heterocondylus vitalbae*, *Piper arboreum*, *Pithecoctenium echinatum*, *Rubus urticaefolius*, *Solanum rudepannum* and *S. umbellatum*. Small trees of *Inga edulis*, *I. punctata* and *Saurauia montana* were occasionally present in shrub patches, but were not sufficiently mature to fruit during the study.

### EXPERIMENTAL DESIGN AND BACKGROUND INFORMATION

Seed rain, predation, germination and seedling survival of early successional tree species were measured over a 2-year period in eight large (> 40 m$^2$; range 40–100 m$^2$) shrub patches, eight small (< 25 m$^2$; range 8–25 m$^2$) shrub patches, and eight areas of pasture with no shrub cover (referred to as 'grass'). The two shrub patch sizes were categorized based on the distribution of shrub patches observed during pasture sampling. All patches were randomly selected from those located > 5 m from the canopy of remnant pasture trees and > 15 m from the forest/pasture edge. Grass patches were located > 5 m from shrubs. In February 1998, a small fire burned one small shrub patch. An additional patch was selected for seed rain and 1998 predation and germination studies, but the sample size for seedlings was reduced by one.

Herbaceous cover was estimated to the nearest percentage in three 1-m$^2$ quadrats in each patch in July 1997. Photon flux density (PFD) was recorded at 5 cm height below one of each of the patch types simultaneously for three 3-day periods between 14 and 22 February 1998. Measurements were taken every 5 s and averaged over 15 min using LI-1000 data loggers and LI-190SA quantum sensors (Li-Cor, Lincoln, Nebraska, USA). Maximum PFD and total daily PFD (06.00–18.00 hours) were calculated for each 3-day period and the range of values is reported.

### FOCAL SPECIES

The tree species studied were those most abundant in previous seed-dispersal studies (Holl 1999) and commonly recorded in mapping tree seedlings > 0.5 m tall in the pasture (Holl *et al.* 2000). Seed predation, germination and seedling survival were measured separately, as often low and variable survival in the preceding stage would have resulted in an insufficient sample size at subsequent stages. All life history parameters were measured for three species representing different life-history and dispersal strategies: *Cecropia polyphlebia*, *Heliocarpus appendiculates* and *Sorocea trophoides.* Data were collected on an additional six common colonizing species at as many life-history stages as possible (Table 1). Seed predation and germination were measured for species in 2 years when possible. A number of species either did not set seed in both years or seed germination was insufficient to provide sufficient seedlings for outplanting.

### SEED RAIN, PREDATION AND GERMINATION

Seed rain was measured twice monthly between 1 August 1997 and 15 July 1998 in three seed traps for each patch, with traps separated by ≥ 2 m. Seed traps consisted of

**Table 1** Seed fresh weight and habitat of focal tree species. Habitat indicates location where trees are most frequently found: C = forest canopy, E = forest edge, G = forest gap, RP = remnant pasture trees, S = forest subcanopy

| Species | Seed fresh weight mean (SE) mg | Habitat |
|---|---|---|
| *Ardisia standleyana* P. H. Allen | 73.0 (4.5) | S |
| *Cecropia polyphlebia* Donn. Smith. | 0.9 (0.1) | G, E |
| *Dendropanax arboreus* (L.) Decne & Planch | 2.8 (0.1) | S |
| *Hasseltia floribunda* Kunth. | 12.0 (0.8) | S |
| *Heliocarpus appendiculatus* Turcz.* | 4.9 (0.5) | G, E, RP |
| *Inga punctata* Willd. | 1309.7 (47.6) | RP†, S |
| *Ocotea whitei* Woodson | 744.4 (43.0) | C |
| *Saurauia montana* Seem. | 0.7 (0.1) | E |
| *Sorocea trophoides* Burger | 174.8 (16.5) | S |

*Wind-dispersed. †*Inga punctata* trees may have been planted for shade when the land was used for coffee.

plastic, close-mesh, grain bags suspended below 0.5 × 0.5 × 0.5 m frames. All apparently healthy seeds (except grasses) were identified, and categorized based on dispersal type (animal or wind) and the primary habitat of mature plants (pasture or forest).

For predation and germination studies, seeds from a minimum of five plants of each species were collected either directly from the plant or from recently fallen fruits. *Heliocarpus* seeds were collected in February and stored at ambient temperature. All other species were collected immediately prior to use and the fleshy mesocarp was removed.

To measure predation, seeds were placed in single-species groups (depots) with 5–20 seeds per depot, depending upon seed size and availability. Six depots were placed in a 3 × 2 grid with depots separated by 50 cm in each patch. To facilitate recovery, seeds were placed on 8 × 8 cm pieces of fine-meshed, grey netting that was secured at the corners using small nails. The netting was stapled at the corners to create a 1-cm side that prevented seeds from washing away but allowed for entry of seed predators. Seed predation studies were initiated on 22 July 1997 and 25 June 1998, the middle of the rainy season and when most species are naturally dispersed. Remaining, intact seeds were counted after 3, 6, 12 and 24 days. Preliminary repeated measures analyses indicated that seed predation trends were consistent over time, so results are reported from the final sampling date only.

To measure germination, 25 seeds of most species were placed on the soil surface in an 8 × 8 × 7 cm pot in each of the 24 patches. For the two largest seeded species (*Inga* and *Ocotea*) 10 seeds were placed in 10.5 × 10.5 × 9.5 cm pots. Pots were filled with soil collected from the appropriate patch type that had been heated at 200 °C for 4 h to kill existing seeds. Each pot was covered with a 1.3-cm metal mesh and coated with Tanglefoot$^{TM}$ to prevent seed predation. Seeds were set out on 21–22 July 1997 and 28–29 June 1998. Germination was monitored weekly for 3 months.

### SEEDLING SURVIVAL

In July 1997, seeds of *Cecropia* and *Heliocarpus* were placed on soil spread *c.* 4 cm deep in a 25 × 51 cm seed flat in a shade house. Seedlings were transplanted after 4 weeks when they had their first true leaves. Seedlings of *Hasseltia* and *Sorocea* were collected from the forest floor. Their exact age was unknown but their fruiting times suggest that they were 1–2 months old. Seedlings ranged from 1 cm to 4 cm in height when transplanted. *Cecropia*, *Hasseltia* and *Heliocarpus* were outplanted on 30–31 July 1997. *Sorocea* was outplanted on 2 October 1997. Sixteen seedlings of each species were transplanted in 4 plant × 4 plant grids with plants separated by 10 cm. Immediately following transplanting seedlings were watered but no additional treatments were given. Survival was monitored 1 week after planting and seedlings that had died were replaced. Seedling survival was monitored after approximately 1, 3, 6, 12 and 18 months.

### STATISTICAL ANALYSES

One-way ANOVA followed by Tukey's LSD multiple comparison procedure was used to compare percentage herbaceous cover, seed rain, predation and germination in the three patch types. Percentage values were arcsine transformed, and seed rain was log-transformed to meet assumptions of normality and homogeneity of variances. Percentage seedling survival was calculated for each patch. Since measurements were repeated on the same plants, data were analysed using MANOVA (von Ende 1993). Pillai's trace was used as the test statistic for the date and date × patch type interaction terms.

Computer simulations were used to estimate the likelihood of a seedling establishing in a 100-m$^2$ area covered by each of the three patch types. I randomly selected from the measured values for seed rain and probability of surviving to each of the subsequent stages in each patch type (bootstrapping, Dixon 1993), and multiplied these to determine the number of seedlings established in each run. Simulations were run 1000 times for each species by patch type combination. Measured seed rain (per m$^2$) was multiplied by 100. When seed rain was 0 in all eight plots, an arbitrarily low seed rain value of 1 seed m$^{-2}$ was assigned for one of the eight values; similarly, when seedling survival was 0 in a given patch type, a survival percentage of 1% was assigned in one of the replicates. When predation and germination were measured in 2 years, data from both years were averaged. For animal-dispersed species, transition values for all species used in each part of the study were averaged. The simulation results were highly skewed with a few high values and many zeros; therefore, means, as well as ranges and percentage, of simulations with at least one seedling establishing are reported.

## Results

### BACKGROUND INFORMATION

Total herbaceous cover was 99%, 78% and 49% in grass, small shrub and large shrub patches, respectively. Grass covered 99% of the soil surface in grass patches, compared with 72% in small shrub patches and 24% in large shrub patches. Herb and vine cover increased from grass (4%) to small shrub (10%) to large shrub patches (23%). Mean cover of shrub and tree seedlings in the herbaceous layer was low and highly variable in all sites (shrubs < 4%; trees < 0.5%).

Both total daily PFD and maximal instantaneous PFD were generally an order of magnitude higher under large shrub patches compared with grass, and were highly variable under small shrub patches (range of daily PFD in mol m$^{-2}$ day$^{-1}$: grass 0.1–0.3, small shrub 0.1–1.5, large shrub 1.1–2.6; range of maximal

**Table 2** Mean seed rain (1 SE) of focal species in grass, small shrub and large shrub patches between 1 August 1997 and 15 July 1998. Means with the same letter superscript are not significantly different ($P < 0.05$) across patch type based on Tukey's LSD. $n = 8$ for each patch type

| | Seed rain (seeds m$^{-2}$) | | |
|---|---|---|---|
| Species | Grass | Small shrub | Large shrub |
| *Ardisia* | 0.0 (0.0)$^{a}$ | 0.5 (0.2)$^{ab}$ | 1.3 (0.5)$^{b}$ |
| *Cecropia* | 0.7 (0.4)$^{a}$ | 45.7 (21.2)$^{b}$ | 44.8 (7.9)$^{b}$ |
| *Dendropanax* | 0.0 (0.0)$^{a}$ | 0.2 (0.2)$^{a}$ | 0.2 (0.2)$^{a}$ |
| *Hasseltia* | 0.0 (0.0)$^{a}$ | 1.0 (0.7)$^{ab}$ | 2.3 (1.1)$^{b}$ |
| *Heliocarpus* | 2.2 (0.7)$^{a}$ | 1.2 (0.4)$^{a}$ | 2.3 (0.7)$^{a}$ |
| *Inga* | 0.0 (0.0)$^{a}$ | 0.0 (0.0)$^{a}$ | 0.7 (0.7)$^{a}$ |
| *Ocotea* | 0.0 (0.0)$^{a}$ | 1.5 (0.6)$^{b}$ | 5.5 (2.4)$^{b}$ |
| *Saurauia* | 0.2 (0.2)$^{a}$ | 7.0 (4.5)$^{b}$ | 7.7 (3.2)$^{b}$ |
| *Sorocea* | 0.0 (0.0)$^{a}$ | 0.8 (0.7)$^{a}$ | 1.0 (0.7)$^{a}$ |
| Total animal-dispersed | 0.8 (0.4)$^{a}$ | 59.3 (22.4)$^{b}$ | 68.7 (10.6)$^{b}$ |
| Total wind-dispersed | 15.0 (6.0)$^{a}$ | 7.8 (3.8)$^{a}$ | 30.9 (12.7)$^{a}$ |

**Table 3** Mean percentage of seeds remaining after 24 days (1 SE) in grass, small shrub and large shrub patches in 1997 and 1998. Means with the same letter superscript are not significantly different ($P < 0.05$) across patch type based on Tukey's LSD. $n = 8$ for each patch type

| | | | Seeds remaining (%) | | |
|---|---|---|---|---|---|
| Species | Year | Initial no. seeds | Grass | Small shrub | Large shrub |
| *Ardisia* | 98 | 10 | 86 (7)$^{a}$ | 69 (13)$^{a}$ | 53 (9)$^{a}$ |
| *Cecropia* | 97 | 20 | 23 (9)$^{a}$ | 1 (1)$^{b}$ | 0 (0)$^{b}$ |
| | 98 | 20 | 35 (12)$^{a}$ | 0 (0)$^{b}$ | 1 (1)$^{b}$ |
| *Dendropanax* | 97 | 10 | 46 (13)$^{a}$ | 13 (7)$^{a}$ | 23 (11)$^{a}$ |
| *Heliocarpus* | 97 | 10 | 80 (10)$^{a}$ | 60 (11)$^{a}$ | 83 (5)$^{a}$ |
| | 98 | 10 | 91 (4)$^{a}$ | 49 (12)$^{b}$ | 70 (7)$^{ab}$ |
| *Inga* | 97 | 5 | 73 (12)$^{a}$ | 20 (11)$^{b}$ | 13 (8)$^{b}$ |
| | 98 | 5 | 63 (10)$^{a}$ | 18 (10)$^{b}$ | 28 (13)$^{ab}$ |
| *Ocotea* | 97 | 5 | 90 (8)$^{a}$ | 93 (5)$^{a}$ | 88 (5)$^{a}$ |
| *Saurauia* | 97 | 20 | 1 (1)$^{a}$ | 0 (0)$^{a}$ | 0 (0)$^{a}$ |
| *Sorocea* | 98 | 8 | 58 (9)$^{a}$ | 38 (15)$^{a}$ | 34 (10)$^{a}$ |
| Average animal dispersed | 97 | | 47 (6)$^{a}$ | 24 (2)$^{b}$ | 26 (4)$^{b}$ |
| | 98 | | 60 (6)$^{a}$ | 27 (6)$^{b}$ | 33 (5)$^{b}$ |

PFD in µmol m$^{-2}$ s$^{-1}$: grass 24–77, small shrub 17–503, large shrub 137–581). PFD in all patch types was only a small fraction of the total PFD typical of open pasture during the dry season (30–40 mol m$^{-2}$ day$^{-1}$), but PFD under large shrubs was much higher than below dense forest (0.2–0.3 mol/m$^{2}$/day; Holl, unpubished data).

### SEED RAIN, PREDATION AND GERMINATION

Over 90% of seeds collected in all patch types were from common pasture shrubs and vines including *Heterocondylus vitalbae*, *Piper* spp., *Rubus* spp., *Solanum* spp. and *Vernonia patens*. The number of animal-dispersed seeds of forest trees and shrubs was significantly higher below both small and large shrub patches compared with below grass (Table 2). *Cecropia* and *Saurauia* were the only animal-dispersed tree species recorded in grass patches, whereas seeds of 10 and 14 animal-dispersed tree species were found below small and large shrub patches, respectively. For three of the animal-dispersed species (*Cecropia*, *Ocotea*, *Saurauia*), higher numbers of seeds fell below both large and small shrub patches compared with grass; for *Ardisia* and *Hasseltia* seed rain was higher below large shrub patches compared with grass, and for the three remaining species (*Dendropanax*, *Inga*, *Sorocea*), seed rain was extremely low and showed no patch type differences (Table 2). The total number of wind-dispersed tree seeds and *Heliocarpus* seeds were not significantly different in the three patch types (Table 2).

Seed predation was high in both years, with only 32% and 41% of all seeds remaining after 24 days in 1997 and 1998, respectively. The percentage of seeds remaining ranged from < 1% for *Saurauia* to 90% for *Ocotea*. Average animal-dispersed seed predation and predation of three species – *Cecropia*, *Heliocarpus* (1 year) and *Inga* – were lower in grass than under small or large shrubs (Table 3). For the other five species, there was no significant effect of shrub cover on seed predation.

Seed germination was highly variable among species, ranging from 9% for *Dendropanax* and *Saurauia* to 77% for *Sorocea*. Germination rates did not differ

**Table 4** Mean percentage of seeds germinating (1 SE) in grass, small shrub and large shrub patches in 1997 and 1998. Means with the same letter superscript are not significantly different ($P < 0.05$) across patch type based on Tukey's LSD. $n = 8$ for each patch type

| Species | Year | No. seeds planted | Grass | Small shrub | Large shrub |
|---|---|---|---|---|---|
| *Ardisia* | 98 | 25 | 51 (6)$^{a}$ | 54 (6)$^{a}$ | 68 (6)$^{a}$ |
| *Cecropia* | 97 | 25 | 42 (10)$^{a}$ | 25 (8)$^{a}$ | 38 (8)$^{a}$ |
| | 98 | 25 | 36 (9)$^{a}$ | 25 (7)$^{a}$ | 19 (4)$^{a}$ |
| *Dendropanax* | 97 | 25 | 15 (4)$^{a}$ | 7 (2)$^{a}$ | 5 (1)$^{a}$ |
| *Heliocarpus* | 97 | 25 | 69 (4)$^{a}$ | 52 (7)$^{a}$ | 66 (6)$^{a}$ |
| | 98 | 25 | 14 (3)$^{a}$ | 13 (3)$^{a}$ | 9 (3)$^{a}$ |
| *Inga* | 98 | 10 | 34 (9)$^{a}$ | 29 (6)$^{a}$ | 26 (5)$^{a}$ |
| *Ocotea* | 97 | 10 | 64 (5)$^{a}$ | 58 (10)$^{a}$ | 58 (8)$^{a}$ |
| *Saurauia* | 97 | 25 | 11 (4)$^{a}$ | 11 (3)$^{a}$ | 7 (2)$^{a}$ |
| *Sorocea* | 98 | 8 | 72 (5)$^{a}$ | 76 (3)$^{a}$ | 86 (5)$^{a}$ |
| Average animal | 97 | | 33 (3)$^{a}$ | 27 (2)$^{a}$ | 25 (4)$^{a}$ |
| dispersed | 98 | | 48 (3)$^{a}$ | 50 (3)$^{a}$ | 46 (3)$^{a}$ |

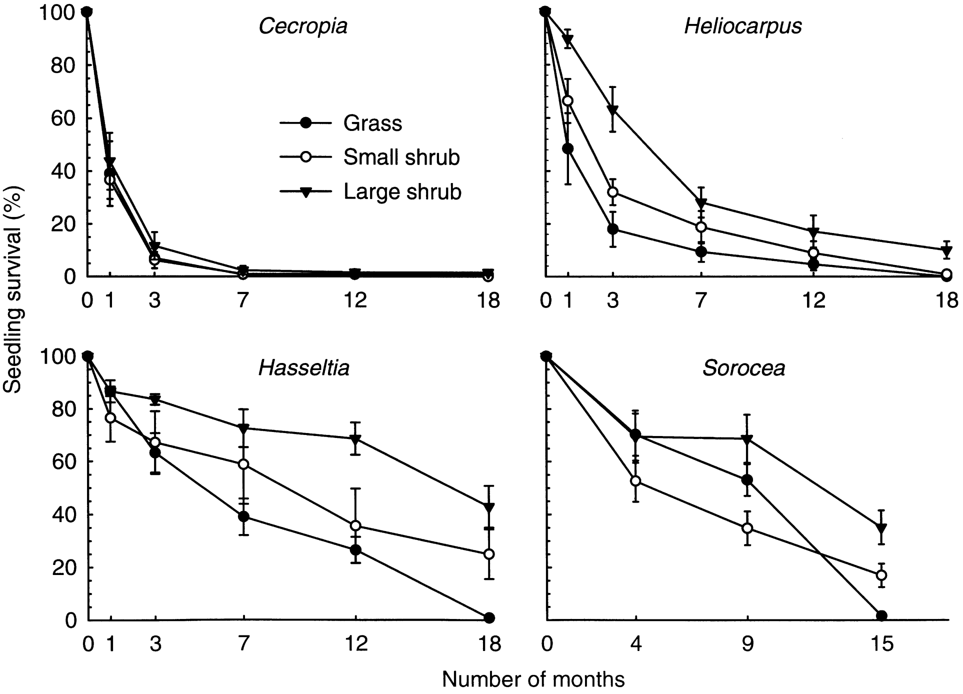

**Fig. 1** Percentage seedling survival for four tree species below grass, small shrub and large shrub patches. Values are means for experimental blocks ±1 SE; $n = 8$ for each patch type.

significantly in the three patch types for any of the eight species measured (Table 4). For the two species measured in 2 years, *Cecropia* showed similar germination rates in both years, whereas *Heliocarpus* germination was 62% in 1997 and was 11% in 1998 averaged over all patch types.

### SEEDLING SURVIVAL

Seedling survival of all species was low (Fig. 1). Three of the four species had the highest survival in large shrub patches and the lowest in grass (*Cecropia*: $F = 0.2$, $P > 0.05$; *Hasseltia*: $F = 5.2$, $P < 0.01$; *Heliocarpus*: $F = 10.2$, $P < 0.0001$; *Sorocea*: $F = 4.4$, $P < 0.01$). Less than 1% of seedlings of all species survived in grass. Two species had significant date × patch type interactions (*Hasseltia*: $F = 3.3$, $P < 0.001$; *Sorocea*: $F = 5.6$, $P < 0.001$). For both species, seedling survival was similar in grass and large shrub patches initially but survival decreased more in grass than in large shrub patches over time (Fig. 1). Seedling survival of *Cecropia* was particularly low; after 1.5 years only two seedlings in large shrub patches and one in grass survived.

### LIKELIHOOD OF SEEDLING ESTABLISHMENT

In computer simulations (Table 5), overall survival of animal-dispersed species was highest in large shrub patches and intermediate in small shrubs compared with grass, due to higher seed dispersal and seedling survival below shrubs; the range in values was extremely high in all patch types. *Sorocea* showed a similar trend, although there was a substantial overlap in the range of values observed in each patch type. *Cecropia* seed dispersal

**Table 5** Survival of three species and all animal-dispersed species measured at each life history stage under grass, small shrub and large shrub patches using 1000 computer simulations of bootstrapped data. Values are: (i) mean number of individuals surviving averaged over all 1000 simulations; (ii) range of number of individuals surviving in individual simulations (in parentheses); (iii) percentage simulations with at least one individual surviving (in italics)

| Species | Patch type | Dispersed | Survived predation | Germinated | Seedlings survived |
|---|---|---|---|---|---|
| All animal-dispersed | Grass | 85<br>(0–267)<br>*51* | 44<br>(0–220)<br>*51* | 18<br>(0–128)<br>*51* | 0.1<br>(0–4)<br>*9* |
| | Small shrub | 5976<br>(667–19200)<br>*100* | 1473<br>(0–9744)<br>*93* | 536<br>(0–5602)<br>*89* | 72.6<br>(0–869)<br>*89* |
| | Large shrub | 6685<br>(3203–11863)<br>*100* | 1995<br>(304–6821)<br>*100* | 771<br>(66–4297)<br>*100* | 201.5<br>(13–1305)<br>*100* |
| *Cecropia* | Grass | 66<br>(0–267)<br>*37* | 19<br>(0–213)<br>*28* | 8<br>(0–161)<br>*24* | 0.04<br>(0–7)<br>*2* |
| | Small shrub | 4995<br>(533–18533)<br>*100* | 13<br>(0–926)<br>*8* | 3<br>(0–222)<br>*6* | 0<br>(0–0)<br>*0* |
| | Large shrub | 4524<br>(2133–8800)<br>*100* | 29<br>(0–439)<br>*13* | 8<br>(0–280)<br>*12* | 0.1<br>(0–17)<br>*3* |
| *Heliocarpus* | Grass | 205<br>(0–530)<br>*73* | 176<br>(0–530)<br>*73* | 70<br>(0–445)<br>*73* | 0.04<br>(0–3)<br>*2* |
| | Small shrub | 117<br>(0–270)<br>*63* | 63<br>(0–270)<br>*57* | 19<br>(0–191)<br>*57* | 0.2<br>(0–11)<br>*6* |
| | Large shrub | 241<br>(0–533)<br>*77* | 181<br>(0–533)<br>*77* | 70<br>(0–445)<br>*69* | 6.6<br>(0–85)<br>*46* |
| *Sorocea* | Grass | 10<br>(0–80)<br>*12* | 5<br>(0–70)<br>*12* | 4<br>(0–63)<br>*12* | 0.1<br>(0–7)<br>*2* |
| | Small shrub | 80<br>(0–533)<br>*19* | 24<br>(0–533)<br>*9* | 18<br>(0–479)<br>*9* | 3<br>(0–149)<br>*7* |
| | Large shrub | 90<br>(0–533)<br>*34* | 30<br>(0–399)<br>*25* | 26<br>(0–399)<br>*25* | 9<br>(0–224)<br>*25* |

was higher below both small and large shrub patches compared with grass, but this difference was counteracted by higher seed predation below shrubs. *Cecropia* seedling survival was sufficiently low in all patch types to make it impossible to compare. For *Heliocarpus*, dispersal, predation and germination were similar in the three patch types. The average number of seedlings surviving, however, was > 10 times higher below large shrub patches, and at least one seedling established in 46% of large shrub patch simulations compared with 6% and 2% in small shrub patches and grass.

## Discussion

### EFFECT OF SHRUBS ON COLONIZATION OF TREE SPECIES

This research suggests that shrubs have a net facilitative effect on the early stages of tree seedling establishment compared with areas of grass without shrubs in the abandoned tropical pasture studied, consistent with observations of natural seedling establishment at this site (Holl *et al.* 2000). Given the mortality at different life-history stages, the likelihood of a seedling establishing is low in this pasture regardless of existing vegetation. For animal-dispersed seedlings, however, the average likelihood of establishment, based on simulations, was three orders of magnitude higher under large shrub patches, compared with areas of grass without shrubs.

The large differences in the model suggest that shrubs facilitate tree seedling establishment, but the actual numbers from the model should be considered as rough estimates for a few reasons. First, the transition probabilities assume that each stage is independent of one another, which may not be the case. Secondly, results are based on 1 or 2 years of data. Thirdly, the measured parameters, seed rain in particular, often included a few high values and some zeros; these are expected for seedling establishment, which is often clumped (Hutchings 1997). The number of zeros increased with life history stage; when the probability of survival is zero in any earlier stage then no seedlings will establish regardless of the subsequent transition probabilities. This skewed distribution, while representative of natural establishment, results in large variances and makes statistical comparisons problematic.

The work is consistent with results from a number of studies in temperate and boreal zones that have demonstrated that facilitation, tolerance and competition are not mutually exclusive (e.g. Pickett *et al.* 1987; Walker & Chapin 1987; Callaway & Walker 1997). The results show that existing vegetation has varying effects on processes affecting tree seedling establishment in a tropical ecosystem. Shrubs tended to increase seed dispersal of animal-dispersed seeds and enhance early stages of seedling survival. In contrast, seed losses to predation were often higher under shrubs compared with grass, and there was no effect of existing vegetation on germination. Related research at this site (Loik & Holl 2001) shows that tree seedlings increasingly compete with shrubs as they grow larger.

### BOTTLENECKS TO TREE SEEDLING ESTABLISHMENT

Many studies in both the temperate zone and the tropics suggest that the process comprising the greatest bottleneck to tree seedling establishment may vary among species (e.g. Myster 1993; Hammond 1995; Hardwick *et al.* 1997). Lack of dispersal limits the establishment of most animal-dispersed species studied, yet seedling survival is also important. Data for *Cecropia* demonstrate that high seed predation may also be a crucial factor.

The results concur with previous research showing that shrubs in tropical and temperate abandoned pastures attract birds, thereby enhancing seed dispersal (Werner & Harbeck 1982; McDonnell & Stiles 1983; Vieira *et al.* 1994; Cardoso da Silva *et al.* 1996). Wind-dispersed seed rain in this study was similar in open pasture and below shrubs, but wind-dispersed seeds comprise a small component of the flora in most neotropical moist forests. Seed rain is critical for succession as most tropical forest seeds rapidly lose viability and therefore are rarely present in the pasture seed bank (Garwood 1989; Vázquez-Yanes & Orozco-Segovia 1993).

I had hypothesized that larger shrub patches would attract more birds, and therefore would have the highest seed rain. The results, however, show that even small shrub patches may serve to enhance seed rain. It is important to note, however, that seed rain is patchy (Foster 1982; Holl 1999), making it difficult to detect anything but gross differences.

The results agree with previous studies demonstrating that post-dispersal predation of seeds is high and species-specific in abandoned tropical pastures (Aide & Cavelier 1994; Osunkoya 1994; Hammond 1995; González Montagut 1996). Although studies comparing seed predation below grass and shrubs in the tropics are lacking, research in temperate old fields, as in this study, has shown higher seed predation below shrubs and small trees compared with areas with dense herbaceous cover (Webb & Willson 1985; Myster & Pickett 1993). This difference in predation is likely to be related to the reduced grass cover below shrub patches, which increases the probability of animals encountering seeds.

This study, as well as others, demonstrates that seed germination can be highly variable among species (Aide & Cavelier 1994; Everham *et al.* 1996; González Montagut 1996; Holl 1999). It is somewhat surprising that germination was not higher below shrubs, given the lower PFD below grasses, as some studies indicate that higher light conditions favour germination of many early successional woody species (Metcalfe & Grubb 1995; Everham *et al.* 1996). Light levels below all patch types may have been sufficiently low that the differences were inconsequential for germination. Differences in vegetation may also have affected light quality and in turn seed germination (Vásquez-Yanez & Orozco-Segovia 1993; Everham *et al.* 1996).

Seedling survival was low for all species in this study, which is typical of small seedlings in the tropics (Ellison *et al.* 1993; De Steven 1994; Nepstad *et al.* 1996). Seedling survival may vary greatly between years (De Steven 1991) and I only have data for one seedling cohort. *Cecropia* seedling survival was particularly low. Studies on other species of *Cecropia* have demonstrated low survival and growth due to high herbivory (Kobe 1999), low light (Kobe 1999) and low nutrient levels (C. Gleeson, personal communicaton). *Cecropia* might also have been susceptible to outplanting stress, as the seedlings were the smallest (1–2 cm tall) outplanted.

Seedling survival for most species was highest under large shrub patches, intermediate under small patches, and lowest in grass. The only other similar study also reported higher seedling survival under shrubs (Vieira *et al.* 1994). Given similarities in temperature (Holl, unpublished data), the most likely explanation for this result is grass competition, which was much lower under large shrubs (24%) and somewhat reduced under small shrubs (72%). Several tropical studies have demonstrated that competition with grasses reduces seedling survival and growth (De Steven 1991; González Montagut 1996; Hardwick *et al.* 1997). At my study site, the dominant pasture grass, *Axonopus scoparius*, forms a dense cover, up to 1.5 m tall, with *c.* 10-cm thick litter layer (Holl, personal observation).

Grasses can affect tree seedling survival and growth in a number of ways including shading, below-ground competition for water and nutrients, through allelopathic chemicals, or by altering herbivore abundance and activity; separating the effects of these factors requires further manipulative experiments. Low light levels below grass were likely to be a primary cause, as instantaneous PFD below dense pasture grass was less than 5 μmol $m^{-2}$ $s^{-1}$ the majority of the time and never reached above 77 μmol $m^{-2}$ $s^{-1}$. Tinoco-Ojanguren &

Pearcy (1995) measured photosynthetic parameters for *Heliocarpus appendiculatus* and *Cecropia obtusifolia* (also a pioneer species of *Cecropia*). The light compensation point for both species ranged from 2.2 to 5.2 $\mu$mol m$^{-2}$ s$^{-1}$ depending on light quality. These results, as well as previous research at my study site on photosynthetic responses of seedlings to different light levels (Loik & Holl 2001), suggest that light levels below dense grass may not be sufficient for seedlings to maintain a net positive carbon balance, whereas PFD below large shrubs usually is. Total daily PFD below large shrub patches was an order of magnitude higher than below grass, partly due to sun flecks, which are important for many tropical forest species (Chazdon & Fetcher 1984; Tinoco-Ojanguren & Pearcy 1995).

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