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Abstract

Forest regeneration in abandoned pastures is often slower than in areas of natural disturbance. Lack of seed dispersers is often the major limiting factor. Shade trees left in pastures are potential perch sites and food sources for birds that act as seed dispersers. This study compared diversity and stem density of colonizing tree species under the crowns of *Ficus tuerckheimii* and *Sideroxylon portoricense* and compared change in diversity from a previous study measuring the same parameters at the same site. *Ficus tuerckheimii* had a significantly greater diversity of seedlings than *Sideroxylon portoricense*. For *Ficus* and *Sideroxylon*, significant negative correlation was found between stem-density and distance from the trunk of both species. Both species of trees are effective as nuclear species for seed dispersal and aid in accelerating forest regeneration.

Resumen

La regeneración de bosques en potreros abanonados es a menudo más lenta que en areas con perturbaciones naturales. La falta de dispersores de semillas es el factor restrictivo más importante. Los árboles para sombra en los potreros son lugares de percha potencial y de fuentes de comida para aves que son dispersores de semillas. Este estudio comparó la diversidad y densidad de tallos de especies de árboles colonizadoras debajo de las copas de *Ficus tuerckheimii* y *Sideroxylon portoricense*. Se comparó el cambio de la diversidad con un estudio anterior que midió las mismas características en el mismo sitio. *Ficus tuerckheimii* presentó una diversidad considerablemente mayor de plántulas que *Sideroxylon portoricense*. Las dos especies, *Ficus* y *Sideroxylon*, mostraron una correlación negativa significativa entre la densidad de tallos de plántulas y la distancia al tronco de ambos árboles. Ambas especies de árboles son efectivas como especies clave para la dispersión de semillas y ayudan a acelerar la regeneración del bosque.

Introduction

Abandoned pastures are poor sites for forest regeneration and are often slower in recovery as compared to disturbance types such as hurricane and treefall gaps (Cubina and Aide 2001). This can result from factors such as predation of seeds and seedlings, destruction of the seedbank due to trampling, shortage of mycorrhizae and competition with grasses (Nepstad et al. 1990, Cubina and Aide 2001). Attraction of seed dispersers is crucial to replenishing the seed bank and subsequently, regenerating abandoned pastures.

Seed recruitment is an important component of the regeneration of pastures and is dependent on dispersal by vertebrates, especially birds, or by wind. Many species of birds are less likely to disperse seeds into agricultural sites due to their avoidance of open areas, which may increase their risk of predation (Howe and Smallwood 1982, Groom 2000). This limits the types of plants that will be recruited into regenerating areas

(Groom 2000, Tabarelli and Peres 2002). The presence of shade trees in abandoned pastures can foster regeneration of forests by attracting birds and arboreal mammals, which have the potential to function as seed dispersers (Holl 1999).

Habitat loss, fragmentation, and selective hunting have led to the loss of large-gaped bird species and large mammals that are capable of dispersing large seeds in Malaysia (Corlett 1998). These pressures are present in Costa Rica as well. Studying tree species composition in regenerating pastures over time can indicate if management practices are effectively aiding in the replenishment of the tree species found in the areas pre-disturbance.

The density of recolonizing species around shade trees has been shown to be greater than the densities observed in edges or open areas (Groom 2000). Schuster (2000) evaluated regeneration effectiveness of two shade tree species, *Ficus tuerckheimii* (Moraceae) and *Sideroxylon portoricense* (Sapotaceae), in an abandoned pasture in Monteverde, Costa Rica. He used the diversity of seedlings under and near the shade trees as a measure of the shade tree's function in promoting regeneration. He found no significant difference in regenerating plant diversity between the areas under the canopies of *Sideroxylon portoricense* and *Ficus tuerckheimii*. The goal of this study was to repeat Schuster's (2000) research and evaluate the current regeneration success and diversity of seedlings as a function of shade tree type and distance from the trunk of the shade tree. It is predicted that this study will show no significant differences in the trends observed by Schuster.

Methods and Materials

Study Site

The study site was located in premontane-moist lifezone (Holdridge) with an average rainfall of 2519 mm/yr (Clark et al. 2000). The study was conducted on a (ca. 5 ha.) farm located near the main road in Monteverde, Costa Rica, across from the Monteverde Friend's School. The farm originally belonged to the late Miguel and Molly Figuerola, who willed the property to the Monteverde Conservation League (MCL). From 1976-1995, the farm was used for dairy production during which, the understory vegetation was cleared and planted with *Cynodon nlemfuensis* (Poaceae). Cows were removed from the land in 1995, at which point regeneration began.

The methods followed Schuster (2000) with the exception of the use of five individuals of each shade-tree species. Schuster's methods required sampling around shade trees that were at least 10 m apart so as to avoid crown overlap and seed rain overlap, but two of the *S. portoricense* (#23 and #41) (the numbering system was established by William Haber after the MCL took over the property) used by Schuster were found to be 7 m apart, so # 41 was excluded from this study. One less *F. tuerckheimii* was sampled to maintain an even representation of each species. A shade tree from the previous study was misidentified as *S. portoricense* (#9) and is actually *Pouteria exfoliata* (Sapotaceae), but was included with the *S. portoricense*.

Sampling took place from July 28, 2005 through August 2, 2005. Three transects measuring 10m x 1m, at compass points 0º, 120º and 240º, were established, beginning 0.5 m from the base of each shade tree trunk. The transects were divided into ten 1 m x 1 m plots. Woody plants taller than 50 cm were identified and counted. Percent herbaceous cover was visually estimated and recorded for plots containing herbaceous vegetation. Plant species were identified to species using help from Dr. Carlos Guindon and Haber et al. (2000). One plant was identified to genus (*Cestrum spp.*) and three were not identified (sp #5, sp 1a, sp 2a).

The Shannon-Weiner diversity index was used to determine diversity under the two selected species of shade tree. A modified t-test was used to determine if a significant difference exists between the diversity indices for the two species. Combined diversity of all plots located a given distance away from the shade tree species were calculated using the Shannon-Weiner diversity index. Each distance was compared between the two species using a modified t-test to determine if a significant difference between the ten sets of diversity indices existed. A paired t-test was used to determine if there was significant difference in stem densities between the two study species as a function of distance. A Spearman-rank correlation was used to determine with each *Ficus* and *Sideroxylon* if a relationship existed between the distance from shade tree and the diversity and stem density of the plants colonizing underneath. Spearman-rank correlations and simple regressions were performed using Statview v.5.0.1

Results

Ficus had significantly greater diversity of woody plants (H' = 1.0880) than *Sideroxylon* (H' = 0.9100) (modified t-test, $p < 0.001$) (Table 2). Diversity as a function of distance from the shade-tree trunk showed no significant difference between *Ficus* and *Sideroxylon* (paired t-test, $p = 0.1191$). Stem density as a function of distance from the trunk of *Ficus* and *Sideroxylon* also showed no significant difference (paired t-test, $t = 2.040$, $p = 0.07$). No significant correlation was found between diversity and distance from the trunk of *Ficus* ($R_s = -0.382$, $p = 0.252$) or *Sideroxylon* ($R_s = -0.309$, $p = 0.354$). A significant negative correlation was found between stem density and distance from the *Ficus* ($R_s = -.770$, $p = 0.021$) and *Sideroxylon* ($R_s = -.770$, $p = 0.021$) (Figures 1 and 2). *Ficus* had significantly greater diversity indices than *Sideroxylon* at the following distances: 3 m ($p < 0.01$), 4 m ($p < 0.001$) and 8 m ($p < 0.05$) (Table 2).

Ficus had a significantly greater diversity in the current study (H' = 1.0880) than in Schuster's (H' = 0.9154) (modified t-test, $p < 0.001$). *Sideroxylon* had a significantly lower diversity in the current study (H' = 0.9100) than Schuster's (H' = 1.020) (modified t-test, $p < 0.001$). A total of 45 species were found in the 868 stems sampled, under the eight shade trees combined. *Ficus* had 37 total species and *Sideroxylon* had 30 total species. Nine of the ten most abundant species were bird dispersed, while only one species in the study was wind dispersed (Table 1). Schuster (2000) sampled 10 trees and found 858 woody individuals in 50 different species with 36 bird and two wind-dispersed species. *Ficus* had 42 species under its crown, while *Sideroxylon* had 31 species. The data was standardized by dividing the number of shade trees sampled by the number of stems found under their crowns. The number of stems per shade tree was 86.8 for both species combined, 98.5 for *Ficus* and 118.5 for *Sideroxylon*. Schuster found 85.8 stems per shade tree, combined, 108.6 for *Ficus* and 63 for *Sideroxylon* (Figure 3).

Schuster found 24 species that were not found in the current study, with *Solanum umbellatum* (13) being the only species with 10 or more individuals. The current study found 14 species that were not found by Schuster, with *Eugenia acapulcensis* (12), *Bunchosia macrophylla* (10) and *Koanophyllon pittieri* (10) being the only species having 10 or more individuals. *Ocotea whiteii* represented 44% of all stems under *Sideroxylon* with 210 individuals. *Hampea appendiculata* represented 37% of all stems under *Ficus* with 148 individuals.

Discussion

The higher species diversity under the *Ficus* could be attributed to a higher abundance and greater richness of birds providing heavy and diverse seed rain (Wheelright et al. 1984). More birds are likely to visit *Ficus* for its fruits, which contain small seeds and occur irregularly year round. Birds are also likely to visit *Ficus* for the fruits of its host (if alive), and its large spreading crown (C. Guindon, pers. comm.). *Ocotea whiteii* dominated the number of stems (44%) at *Sideroxylon* plots, which drove down species evenness and thus diversity as compared to *Ficus*.

The strong trend of declining stem density as a function of distance from the shade tree base is attributable to physical features provided by the tree. Micro-climatic conditions near the base of the trees provide a stable moisture source as well as a relatively stable temperature, which would favor seed germination (Uhl et al. 1982). Dispersers may spend more time near the interior of the tree as it may provide more protection from predators. Density would be lower as you move away from the trunk and the amount of shade is reduced, thus allowing for increased competition for seedlings from herbaceous species, such as *Cynodon nlemfuensis*, which was prevalent throughout remaining pasture areas (Appendix 1). Significantly higher diversity at 3m, 4m, and 8m away from the *Ficus* as compared to *Sideroxylon* is not a trend that is supported by other literature. The difference in crown morphologies, between *Ficus* and *Sideroxylon* could contribute to this.

Comparing Schuster (2000) to the current study, an 11% decrease in species richness under *Ficus* was outpaced by the 27% loss in number of stems. These data indicate causation of overall increase in diversity for *Ficus* between the studies. Under the *Ficus*, competition for light increases under the developing canopy leading to domination of some species and individuals and suppression of others (Weiner 1990, Vandemeer et al. 2000).

Sideroxylon had a 3% loss in richness coupled with a 50% increase in stem density. Under *Sideroxylon*, O. *whittei* represented approximately 16% of stems in the first study and 44% in the current study, which reduced species evenness and thus diversity. The high ratio of bird-dispersed species to wind dispersed species is common in a more mature forest stand (Tabarelli and Peres 2002). These data combined with data from Schuster's study indicate that recruitment of bird dispersers into the pasture areas occurred at high levels soon after abandonment and has remained high.

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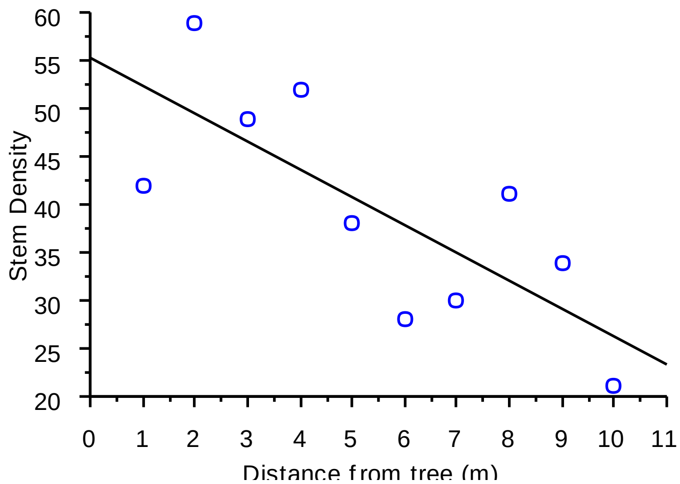

Figure 1. Relationship between stem density of woody plants under four *Ficus tuerckheimii* in an abandoned pasture as a function of distance from the tree-base (Spearman-Rank correlation, R_s = -.770, p = 0.021).

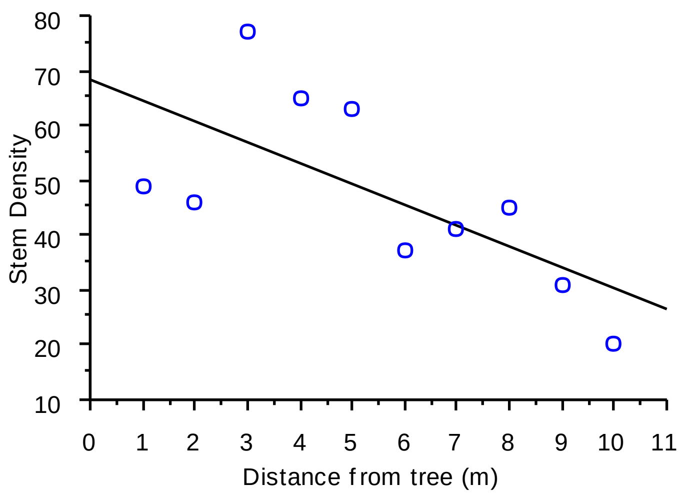

Figure 2. Relationship of stem density of woody plants under *Sideroxylon portoricense* in an abandoned pasture as a function of distance from the tree-base (Spearman-Rank correlation, R_s = -.770, p = 0.021).

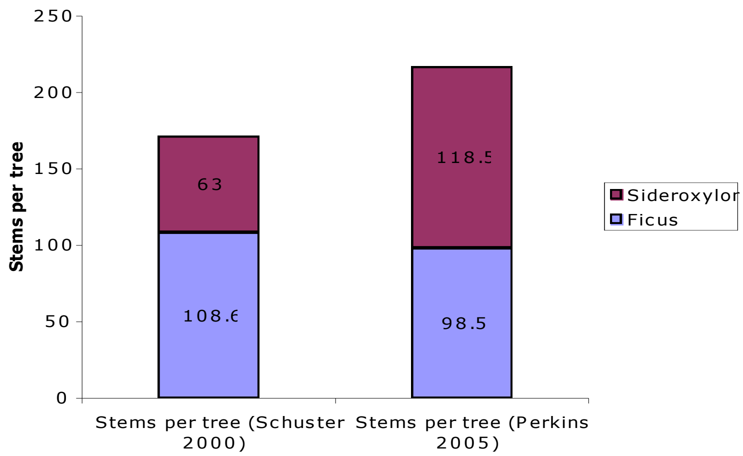

Figure 3. Comparison of stems per tree under *Ficus* and *Sideroxylon* from Schuster (2000) and the current study.

Table 1. Abundance of plants regenerating under four *Ficus tuerckheimii* and four *Sideroxylon portoricense* in an abandoned pasture. The right column shows seed dispersal types (AM = arboreal mammal, BD = bird, BT = bat, BL = ballistic, GR = gravity, TM = terrestrial mammal, WD = wind).

Species	Total Abundance	*Ficus tuerckheimii*	*Sideroxylon portoricense*	Seed Dispersal
Ocotea whiteii	212	2	210	BD
Hampea appendiculata	173	148	25	BD
Ocotea monteverdensis	105	35	70	BD
Viburnum costaricanum	70	22	48	BD
Styrax argentatus	48	31	17	BD
Cestrum megalophyllum	41	33	8	BD
Cinnamomum neurophyllum	34	20	14	BD
Nectandra membranaceae	19	8	11	BD
Myrsine coriaceae	17	2	15	BD
Daphnopsis americana	12	6	6	TM
Eugenia acapulcensis	12	6	6	BD, BT
Cestrum #2	12	6	6	BD
Koanophyllon pittieri	10	9	1	WD
Citharexylum costaricensis	9	9	0	BD
Solanum aphyodendron	9	5	4	BT
Coffea arabica	8	1	7	BD
Sp #5	6	0	6	?

Pouteria exfoliata	6	2	4	AM
Tapirira mexicana	5	4	1	BD
Cinnamomum cinnamomifolium	5	4	1	BD
Meliosma vernicosa	4	4	0	AM, BD
Oreopanax xalapensis	4	4	0	BD
Meliosma idiopoda	4	4	0	BD
Sapium glandulosum	3	3	0	BD
Cupania glabra	3	2	1	BD
Erythrina lanceolata	3	2	1	TM
Piper hispidum	2	2	0	BT
Piper auritum	2	2	0	BT
Bunchosia macrophylla	2	0	2	BD
Conostegia xalapensis	2	0	2	BD
Ocotea tenera	2	2	0	BD
Ardisia palmana	2	2	0	BD
Erythroxylum macrophyllum	2	2	0	BD
Sideroxylon portoricense	2	0	2	BD
Palicourea padifolia	1	1	0	BD
Quercus insignis	1	1	0	AM, TM
Styphnolobium monteviridis	1	1	0	AM
Pouteria reticulata	1	0	0	BD
Ocotea floribunda	1	0	1	BD
Stauranthus perforatus	1	1	0	BD
Cecropia obtusifolia	1	0	1	BD, BT
Croton mexicanus	1	0	1	BL
Sp 1a	1	0	1	?
Sp 2a	1	0	1	?

Table 2. Overall comparison of diversity under the crown of *Ficus* and *Sideroxylon* and comparison of each distance as a function of diversity between *Ficus* and *Sideroxylon*.

Values	t	v	p	H’	
Distance				*Ficus*	*Sideroxylon*
1 m	1.818	85.689	> 0.05	1.0655	0.9248
2 m	1.379	94.559	> 0.05	0.7959	0.6387
3 m	2.704	115.947	**< 0.01**	**0.8826**	**0.6270**
4 m	4.454	115.889	**< 0.001**	**1.0569**	**0.6660**
5 m	1.119	79.850	> 0.05	0.9808	0.8517
6 m	-1.261	64.815	> 0.05	0.8572	0.9562
7 m	-1.970	61.549	> 0.05	0.8020	0.9689
8 m	2.094	83.295	**< 0.05**	**0.8980**	**0.6843**
9 m	1.553	58.321	> 0.05	0.9261	0.7887
10 m	-1.358	36.334	> 0.05	0.7492	0.9042
Overall	4.1767	837.032	**< 0.001**	**1.0880**	**0.9100**

Appendix 1. Field notes on transect and plot conditions for four *Ficus* and four *Sideroxylon*.

Ficus	Trans. (º)	Plot(s)	Notes
#64	120	6	Trunk of tree (#63) through 5% of plot
	240	10	Ends at barbed-wire fence; 3m from road
#77	0	4-10	Entering grassy area; 70% cover with *Cynodon nlemfuensis* (CN)
	120	5-10	Drainage present
	240	5-10	Crown of tree (#77) present
		7	70% CN
		8	80% "
		9	80%"
		10	75%"
#35	0	8	40% herb. cover; 20% trail cover; @ forest edge
		9	40% herb. cover
		10	85% "
	120	7	90% herb. cover; forest edge
		9	100% herb. cover
		10	95% "
#57	0	5	30% "
		6	70% "
		7-10	>95% CN
	120	1-10	Completely through a tree crown
		2-4	Drainage present

Siderox.	Trans. (°)	Plot(s)	Notes
#67	0	7	Armadillo burrow 40%
		8	Stump 50%
		9	50% CN
		10	90% CN
#23	0	2	30% herb.
		3	70% herb. ; 20% trail
		4	70% herb.
		5	40% "
		6	60% tree trunk (#61)
		7	10% "
		9	40% herb.
		10	30% herb.
	120	1-4	Contain tree crown
		2-4	100% herb
		5	80% "
		6	70% "
		7	70% "
		8	60% "
	240	1	>95% "
		2	100% "
		3-5	>95% "
		6	85% "
		8	85% "
		9-10	>95%
#17	0	3-10	Field edge
		5	60% herb.
		6	70% "
		7	80% "
		8-10	>95% "
	240	9	20% tree trunk (#15)
#9	120	6	100% tree trunk (#12)
		7	80% "