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Species richness and composition during sylvigenesis in a tropical dry forest in northwestern Costa Rica

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Abstract: Plant species diversity and composition of life form categories were recorded in a tropical dry forest in northwestern Costa Rica. Nine pairs of spatially separated plots were described representing each of different ages of secondary regeneration ranging from recently cleared and burned to more than 50 years of regrowth. All vascular plants species encountered were recorded during 30 months. The results document great changes in species diversity and composition of plant form categories during sylvigenesis. 328 plant species in 79 families and 247 genera of grasses, herbs, shrubs, lianas and trees were encountered. Species richness was greatest after 15 years and decreased significantly in older plots. The number of non-woody species was highest after three years of succession. Minimum of woody plant species was after one year and increased significantly after five years. Maximum was in the 15 years plots with a slight decrease in older forests.

Resumen: Se registró la diversidad de especies de plantas y la composición de categorías de formas de vida en un bosque tropical seco del noroeste de Costa Rica. Se describieron nueve pares de parcelas separadas espacialmente que representan diferentes edades en la regeneración secundaria, desde algunas recientemente tumbadas y quemadas hasta otras con crecimiento secundario de más de 50 años. Todas las especies de plantas vasculares que se encontraron fueron registradas durante 30 meses. Los resultados documentaron grandes cambios en la diversidad de especies y en la composición de las categorías de formas vegetales durante la silvigénesis. Se encontraron 328 especies de plantas en 79 familias y 247 géneros de pastos, hierbas, arbustos, lianas y árboles. La riqueza de especies tuvo su máximo después de 15 años y decreció de manera significativa en parcelas más viejas. El número de especies no leñosas alcanzó su máximo después de tres años de sucesión. El número más pequeño de especies de plantas leñosas se dio después de solo un año e incrementó significativamente después de cinco años. El máximo correspondió a las parcelas de 15 años y a partir de allí se observó un ligero decremento en los bosques más viejos.

Resumo: A diversidade das espécies de plantas e a composição das categorias de formas de vida foram registadas numa floresta tropical seca no noroeste da Costa Rica. Foram descritas nove pares de parcelas espacialmente separadas representando, cada uma, idades diferentes da regeneração secundária desde as cortadas recentemente e queimadas às de mais de 50 anos de regeneração. Todas as espécies vegetais vasculares encontradas foram registadas durante 30 meses. Os resultados mostram grandes mudanças na diversidade específica e composição das diferentes categorias de plantas durante a sucessão para o estágio florestal. Foram encontradas 328 espécies de plantas de 79 famílias e 247 géneros de gramíneas, ervas arbustos, lianas e árvores. A riqueza específica foi máxima depois dos 15 anos e decresceu significativamente nas parcelas mais velhas. O número de espécies não lenhosas foi máximo depois dos três anos da sucessão. O menor número de espécies lenhosas verificou-se depois de um ano e cresceu significativamente depois dos cinco anos. O máximo verificou-se nas parcelas de 15 anos com um ligeiro decréscimo nas florestas mais velhas.

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Key words: Area de Conservación Guanacaste, Costa Rica, plant species diversity and composition, secondary succession, sylvigenesis, tropical dry forest.

Introduction

Tropical dry forests belong to the most threatened ecosystems on earth. In Central America they once extended more than 550.000 km² but only 0.09% of the original area is under protection (Janzen 1988 a & b). The dry forests especially in the Province of Guanacaste in the northwestern pacific region of Costa Rica are in the same condition. Sader & Joyce (1988) documented the deforestation rates for Costa Rican life zones between 1940 and 1983. Due to this study they found no primary dry forest remaining after 1961. Only trivial amounts of old growth forest parts were left in the Guanacaste Province in northwestern Costa Rica. But now this province contain a large area, where this study was conducted.

Reasons for the immense loss of tropical dry forests are diverse. Precious timber trees like the Meliaceae *Swietenia macrophylla* King (Mahogany, Meliaceae) and the *Dalbergia retusa* Hemsl. (Rosewood, Fabaceae) have been selectively logged for centuries. Most areas were deforested, burned and converted into agricultural land or turned into cattle ranches (Murphy & Lugo 1986). The relative ease of clearing dry forests by fire during the dry season was another aspect forcing the acceleration of deforestation and blocked secondary forest succession (Heinrich & Blancke 1995). There is no evidence of natural fire in the dry forests of Guanacaste, even though early stages of succession can be burned during the drier parts of the rainy season (Janzen pers. comm.). In Central America most species of adult trees are fire intolerant and fire-created habitats are unnatural, though anthropogenic fires are a major blockage to secondary woody succession (Budowski 1966; Janzen 1988 a & b).

A patchwork of disjunct secondary forest fragments remain as islands in the ocean of man-made grassland including some remnants of rare tree species. The landscape of Guanacaste province is widely dominated by the C-4 grass *Hyparrhenia rufa* (Nees) Stapf introduced from Africa as a pasture grass.

Most research on tropical forest succession are focused on tropical rain forests or forest gaps in well-developed forests. The pathway of natural sylvigenesis after clear- cutting in the tropics is concentrated on tree species (e.g. Finegan & Delgado 2000; Kennard 2002; Lykke & Sambou 1998). Exceptional investigations like Killeen *et al.* (1998) documenting the complete life form composition including non-woody species are rare. A number of studies placed great emphasis on treefall gaps in forests (e.g. Fraver *et al.* 1998; Platt & Strong 1989). But natural forest gaps do have their own dynamics because usually they are surrounded by forests. They cannot be compared with the natural sylvigenesis of degraded landscapes being burned almost annually for centuries. In this case the processes of forest restoration are highly unpredictable for any particular site (Janzen 1990).

There is little information about natural recolonization of abandoned fields and the progression of reinvading of plants in degraded tropical dry forests. This study provides detailed basic information about the regeneration of dry forests from degraded fields and pastures to 50 year old secondary forests. To report the dynamics of sylvigenesis nine different ages and stages of natural succession were compared. The results document the species richness of all vascular plants and the changing of the composition of five life-forms categories during the forest recovery.

Methods

Study area

The study area was located in the former Santa Rosa National Park (10°49´-10°53´N and 85°35´-85°37´W), today Sector Santa Rosa of the Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica, Guanacaste Province (Fig. 1). The Santa Rosa Plateau is 300 m of elevation, lying between the Pacific Coast and the Cor-

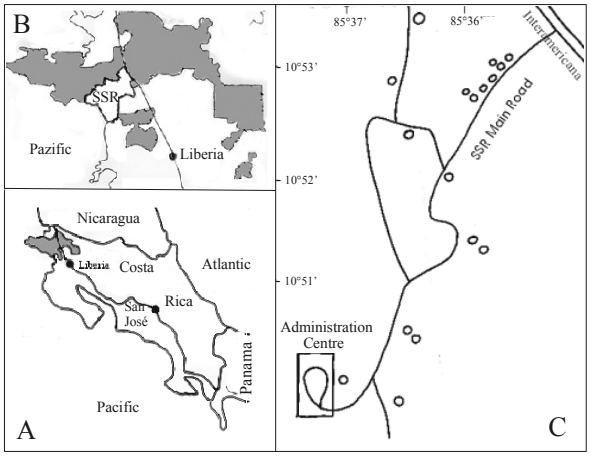

Fig. 1. The study area. A: Map of Costa Rica. B: Map of the terrestical extension (shaded) of the Aera de Conservación Guanacaste (ACG) including the Sector Santa Rosa (SSR). C: Location of the study plots represented by dots.

dillera Guanacaste. The area has been classified as a tropical dry forest (Holdridge *et al.* 1967). Annual precipitation at the Administration Area of Sector Santa Rosa is 1503.3 mm (average over 1980-1997) ranging from 880.1 mm (1991) to 2558.5 mm (1988). Monthly average maximum temperature varies from 31°C to 36°C during dry season (December to April) to 27°C to 33°C in wet season. The soils are weathered nutrient poor entisols, inceptisols or vertisols formed by volcanic eruptions about 1.6 million years ago (Chiesa *et al.* 1996; Gerhardt 1993). Soil depth varies from a few cm to a meter or more (Vasquez 1991).

The degradation of the forests of the Sector Santa Rosa (former Santa Rosa National Park) was documented first in the late 1500´s when the Hacienda Santa Rosa was established (Janzen 1986, 1992). Since that time Santa Rosa was subdivided into several pieces and sold to various owners. Today the Sector Santa Rosa is a mosaic of former farms and cattle ranches gradually abandoned since 1970- 1990 and allowed to regenerate to forest under the protection of the ACG. Today the extension of secondary dry forests (the Sector Santa Rosa included) of the different ages and stages of natural succession, amounts to about 80.000 hectares (Janzen 2001).

Study plots and inventory methods

Eighteen study plots each 1000 m² (20 x 50 m) in size representing nine different ages of succession (0, 1, 3, 5, 10, 15, 20, 30 and more than 50 years) after the last major man-made perturbations (including fire) were established and observed from December 1996 to April 1999. Two separate sites of each age were chosen and combined as pairs for data analysis. The age of some plots were estimated from personal comments by D.H. Janzen. The study plot ages were started on the January of 1997. The pair of zero years old plots was situated in two different wide firebreaks being slashed and burned two times a year. The one-year-old plots were pastures last burned in April of 1996. Each study site was chosen under unique topographic conditions (e.g. plain underground and no streambeds) and situated in the center of its stage of sylvigenesis. Reference specimens are deposited at the herbaria in Santa Rosa and in the University of Osnabrueck. Species identifications are based on Janzen & Liesner (1980) and Gentry (1993). Difficult specimens were determined by taxonomists of the Instituto Nacional de Biodiversidad (INBio), Costa Rica. Nomenclature of species follows that of the Missouri Botanical Garden (w³TROPICOS, http://mobot.mobot.org/W3T/Search/vast.html). All identified plants were classified into five life form categories: grasses (sedges included), herbs (including epiphytes, non-woody vines and ferns), shrubs, woody climbers and trees. The life form classification follows that of Kennard (2002). The seedlings of woody species that could be identified were included and scored as the life form of their adults.

Results

A total of 328 species in 77 families and 247 genera were encountered in 18 plots (each 0.1 ha in size), identified and divided into 5 life form categories: 27 grasses-sedges, 106 herbs, 43 shrubs, 50 woody climbers and 102 trees (Appendix I). This is about 30% of the plant species number for the ACG dry forest. Fabaceae was the species-rich family with 55 species followed by Bignoniaceae (20) and Asteraceae (19).

Plant species richness was not directly or linearly correlated with the age of regeneration of sec-

Table 1. Species richness, life form composition and percentage of woody species of nine pairs (2000m² in size) of second growth stands in years after last anthropogenic disturbance in the sector Santa Rosa of the Area de Conservation Guanacaste, Costa Rica.

Age	Grasses	Herbs	Shrubs	Lianas	Trees	Total	Woody species (%)
0	8	28	3	4	10	53	32.1
1	8	22	4	2	6	42	28.6
3	14	42	8	3	16	83	32.5
5	10	26	13	4	21	74	50.0
10	6	29	16	21	44	116	69.8
15	9	37	20	30	44	140	67.1
20	3	18	21	26	50	118	82.2
30	3	13	11	23	40	90	82.2
50	3	13	17	21	41	95	83.2

ondary forests. Instead, the species richness of the nine pairs of study sites (2.000 m² each pair) varied from 42 after one year to 140 after 15 years decreasing significantly in older sites (Table 1). The 50-year-old secondary forest contained only 95 different vascular plant species. Woody plant species composition differed from 97 taxa after 20 years and to just 12 in the one-year-old pair of study plots. Tree diversity was highest after 20 years (50 species) and lowest after 1 year (six). Lianas had their maximum species diversity in the 15-year-old study sites, while maximum for shrubs and trees was after 20 years.

The percentage of woody species was lowest in one-year-old plots (28.6%) and highest in 50 year-old forest (83.2%). After two decades of natural sylvigenesis the percentage of shrubs, woody climbers and trees stabilizes at 82-84% (Fig. 2).

The non-woody species diversity had its maximum in the youngest secondary growth. Three years after the last clear-cutting 14 grasses or sedges and 42 herbs species were present. This decreased significantly after a second peak in the 15 year old forest (Fig. 3). In the three oldest secondary forests the richness of grasses and sedges was equal (3 species), while 18, 13 and 13 herb species were encountered in the same three pairs of plots. The percentage of non-woody species showed a continuous decrease from recently disturbed areas (71.4% after 1 year) to the oldest sec-

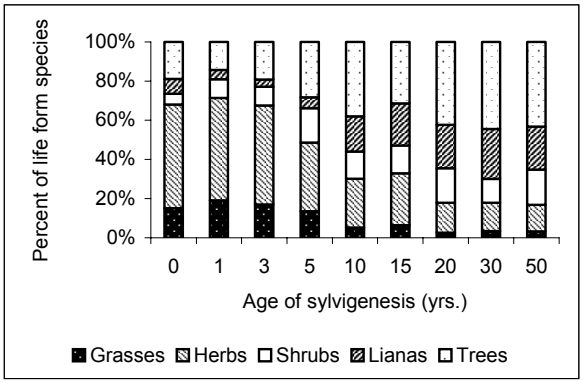

Fig. 2. Percentage of life form distribution of vascular plants in nine pairs of study plots (each 2.000 m² in size) in the sector Santa Rosa of the Area de Conservation Guanacaste, Costa Rica in order of continuance of sylvigenesis in years. Life forms classification: grasses and sedges, herbs (including epiphytes, non woody vines and ferns), shrubs, woody climbers and trees.

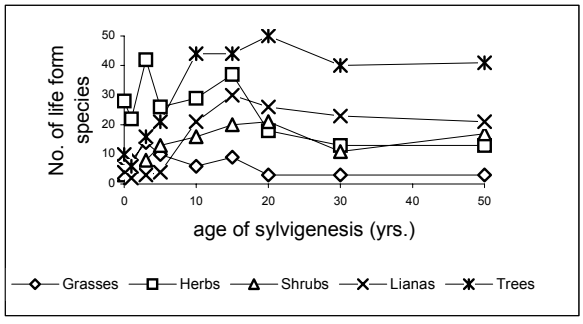

Fig. 3. Number of species of five life form types in nine pairs of study plots (2000 m² in size) of second growth stands after last anthropogenic disturbance in years in the sector Santa Rosa of the Area de Conservation Guanacaste, Costa Rica. Life forms types: grasses and sedges, herbs (including epiphytes, non woody vines and ferns), shrubs, woody climbers and trees.

Table 2. Plants with the highest frequency (recorded in 10 or more of the study plots) in the sector Santa Rosa of the Area de Conservation Guanacaste, Costa Rica in alphabetic order (2X = presence in both sites of the study plot pairs; X = presence in one plot). Life forms categories: G = grasses (including sedges), H = herbs (including epiphytes, non woody vines and ferns), S = shrubs, L = woody climbers and T = trees.

		Age of succession									
Scientific name	Life form	0	1	3	5	10	15	20	30	50	Total
Acacia collinsii	S	X	2X	2X	2X	2X	2X	2X	2X	2X	17
Alibertia edulis	S				X	2X	2X	X	2X	2X	10
Banisteriopsis muricata	L	X		X	2X	2X	2X	X	X	X	11
Bulbostylis tenuifolia	G	2X	2X	2X	2X	X	X				10
Cochlospermum vitifolium	T	2X	2X	2X	2X	2X	2X	X	X		14
Genipa americana	T	X		X	2X	X	2X	2X	2X	2X	13
Gouania polygama	L	2X	2X	2X	2X	X	2X		X		12
Guazuma ulmifolia	T	X		X	2X	2X	2X	2X	2X	X	13
Hyparrhenia rufa	G	2X	2X	2X	2X	X	X	X			11
Lygodium venustrum	H	X		2X	2X	2X	2X	2X	2X	2X	15
Malvaviscus arboreus	S				X	2X	2X	X	2X	2X	10
Randia subcordata	T				X	2X	2X	2X	2X	X	10
Rehdera trinervis	T	2X	2X	2X	2X	X	X				10
Semialarium excelsum	T		X	X	2X	2X	2X	X	2X		11
Tetracera volubilis	L					2X	2X	2X	2X	2X	10

ondary forest site (16.8%).

No species occurred in all 18 study plots but ant-protected *Acacia collinsii* Saff. occurred in 17 plots. Only 15 species were encountered in 10 or more plots (Table 2). Pioneer trees such as *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae) and *Rehdera trinervis* (S.F.Blake) Moldenke (Verbenaceae) were present in all younger plots. The former showed a significant decrease after 15 years and the latter was not present in the plots older than 15 years. Cyperaceae *Bulbostylis tenuifolia* (Rudge) J.F.Macbr. and C-4 Poaceae *Hyparrhenia rufa* were not present in plots older than 20 years but were present in all younger plots. Somewhat shadow-tolerant understory shrubs like *Malvaviscus arboreus* Cav. (Malvaceae) and *Alibertia edulis* (Rich.) A.Rich. (Rubiaceae) were present in almost all five-year-old plots and older. The woody vine *Tetracera volubilis* L. (Dilleniaceae) was present in all secondary forest plots older than 10 years.

Discussion

The results of this study suggest that there was no direct correlation between the age of sylvigenesis without man-made perturbations and the richness of vascular plant species. In the dry forest of the Sector of Santa Rosa the maximum of species diversity is reached after 15 years of regeneration and then gradually declines to some lower level. In 15 year-old stage of succession 140 species were encountered. The number of 94 woody plant species (67.1%) was outdone only by the 20 years old study site (97 species = 82.2%). This should be the age Finegan (1996) called the second phase of secondary succession, the stage when short-lived and the long-lived pioneer species and the first mature forest species are present at the same time. After this time it seems that the short-lived pioneer trees like *Cochlospermum vitifolium* and *Rehdera trinervis* are going to be replaced by long-lived pioneer species like *Guazuma ulmifolia* Lam. (Sterculiaceae) and mature forest species like and *Hymenaea courbaril* L. (Fabaceae). The pres-

ence of the first of the two short-lived species increased significantly after 15 years the second was not present in the plots older than 15 years. Those trees may belong to the part of species which will be locally extinguished or severally distributed during the ongoing process of sylvigenesis. Adult *H. courbaril* was one of the dominant evergreen tree species in the old-growth forest. Those evergreen species are making up 30-60% of the crowns (Janzen 2002).

Herbs are the most diverse life form (106 species) and grasses and sedges (27) took last position among the total number of 328 species. The majority of non-woody species characterizes the first decade of sylvigenesis of abandoned land. The percentage of herbs, grasses and sedges during this phase ranged from 71.4% after 1 year to 50% after five years. During the course of secondary succession the non-woody plants are reduced to a percentage around 15-20% of total species richness in the 20-year-old forests and older. The results of the late three secondary forest stages indicate that the percentage of ca. 80% of woody species could be steady state at least in tropical dry forests. The significant decrease of total species richness after 15 years and woody plant species after 20 years was surprising. In the beginning of this study a constant decrease of woody plant species was expected. Referring to a certain size it seems that the last phases of sylvigenesis (the late secondary dry forests in transition to mature forests) are less species rich but includes a different species composition (e.g. more shade-tolerant species of all life forms). The tree species diversity increases significantly in the first decade and has its maximum after 20 years (50 species) then decreases slightly. This result was confirmed by Kennard (2002) who investigated in secondary forest fallows in a tropical dry forest in Bolivia. Recent studies have found that the secondary successional forests of Sector Santa Rosa contain the highest species richness among six tropical dry forests censured in Central America (Gillespie *et al.* 2000). The diversity of species in old-growth forests of larger size will be higher than this result suggests, but the density will be lower and more distributed. The Sector Santa Rosa is a complex mosaic of different secondary succession stages (Janzen 2002).

The annual growth rates of wood production by many tree species are directly correlated with the monthly and/or annual variation of local precipitation (Enquist & Leffler 2001) and the speed of sylvigenesis is likewise affected. The longer the duration of the rainy season and the higher the amount of annual rainfall the longer the greater is the growth rate of the woody plant species (especially for deciduous species). The smaller the amount of precipitation in the rainy season and the longer the dry season lasts, the higher is the damage of fires to the process of sylvigenesis in ACG dry forests (Janzen 1988 a, b, 2002). Fire reduces diversity and abundance of tree species in tropical dry forests (Miller & Kauffman 1997). Therefore, the ACG developed an effective fire control program to reduce the impact of fires slowing down the progress of dry forest restoration (e.g. Janzen 2000). Fragments of tropical dry forest in Sector Santa Rosa are the source of seeds for woody plant invasion of abandoned farmland and pastures. Compared to other tropical forest types the rate of sylvigenesis in dry forests are among the highest (Kennard 2002). Because of the absence of mature tropical dry forests in Costa Rica, the species composition of a vast old-growth forest covering a vast area is unpredictable, but it will contain all of the species recorded here and many more (D.H. Janzen, pers. comm). The results of this study may help to understand the natural pathway of sylvigenesis of tropical dry forests starting from the first stages of succession in abandoned pastures and fields to old-growth forests.

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Appendix I

Species list of vascular plants encountered in nine pairs of study plots in the Sector Santa Rosa of the Area de Conservation Guanacaste, Costa Rica in alphabetic order (2x = presence in both sites of the study plot pairs; x = presence in one plot). Life forms categories: G = grasses (including sedges), H = herbs (including epiphytes, non woody vines and ferns), S = shrubs, L = woody climbers and T = trees.

Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Acacia collinsii Saff.	Fabaceae/Mim.	S	X	2X	2X	2X	2X	2X	2X	2X	2X
Acacia cornigera L.	Fabaceae/Mim.	S				X					
Acacia farnesiana (L.) Willd.	Fabaceae/Mim.	T	X		X	X					

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Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Acacia tenuifolia (L.) Willd.	Fabaceae/Mim.	L					2X	2X	X	X	
Acacia villosa (Sw.) Willd.	Fabaceae/Mim.	H	X	X	2X						
Acisanthera c.f. quadrata Pers.	Melastomataceae	H	X	X							
Acosmium panamense (Benth.) Yakovlev	Fabaceae/Pap.	T						X	X	X	
Acrocomia aculeata (Jacq.) Lodd. ex Mart. ex	Arecaceae	T					X	X	X		
Adiantum c.f. deflectens Mart.	Pteridaceae	H						X			
Adiantum concinnum Willd.	Pteridaceae	H						X			2X
Aeschynomene sp.	Fabaceae/Pap.	H	X								
Albizia adinocephala (Donn.Sm.) Britton & Rose	Fabaceae/Mim.	T								X	
Alibertia edulis (Rich.) A.Rich.	Rubiaceae	S				X	2X	2X	X	2X	2X
Allophylus occidentalis (Sw.) Radlk.	Sapindaceae	S					2X	2X	2X	2X	X
Amphilophium paniculatum (L.) Kunth	Bignoniaceae	L					2X	X	X	2X	
Andropogon bicornis L.	Poaceae	G			X						
Andropogon leucostachyus Kunth	Poaceae	G				X					
Annona purpurea Lmoc. & Sesse ex Dunal	Annonaceae	T									X
Annona reticulata L.	Annonaceae	T					2X	X			
Apeiba tibourbou Aubl.	Tiliaceae	T					X	X	X		2X
Aphelandra scabra (Vahl) Sm.	Acanthaceae	H					X	X		X	
Archibaccharis schiedeana (Benth.) J.Jacks.	Asteraceae	H			X						
Ardisia compressa Kunth	Myrsinaceae	T						X			
Ardisia revoluta Kunth	Myrsinaceae	T						X	X	2X	2X
Arrabidaea chica (Humb. & Bonpl.) Verl.	Bignoniaceae	L						X			
Arrabidaea conjugata (Verl.) Mart.	Bignoniaceae	L						X			
Arrabidaea molissima (Kunth) Bureau & K.Schum.	Bignoniaceae	L							X		
Arrabidaea patellifera (Schltdl.) Sandwith	Bignoniaceae	L					X	X	X	2X	
Asclepias curassavica L.	Asclepiadaceae	H		X							
Asclepias woodsoniana Standl. & Steyerm.	Asclepiadaceae	H	X		2X						
Asplenium auriculatum Sw.	Aspleniaceae	H									X
Astronium graveolens Jacq.	Anacardiaceae	T					X		2X	2X	2X
Ateleia herbert-smithii Pittier	Fabaceae/Pap.	T								X	
Axonopus sp.	Poaceae	G	X	X	X	2X					
Ayenia dentata Brandegee	Sterculiaceae	H						X	X		
Baltimora recta L.	Asteraceae	H						X	X		
Banisteriopsis cornifolia (Kunth) B.L.Rob.	Malpighiaceae	L					X	X			
Banisteriopsis musicata (Cav.) Cuatrec.	Malpighiaceae	L	X		X	2X	2X	2X	X	X	X
Barleria micans Nees	Acanthaceae	H						X			
Bauhinia ungulata L.	Fabaceae/Caes.	T					2X	2X	X		
Bidens riparia Kunth	Asteraceae	H			X			X			
Blepharodon mucronatum (Schltdl.) Decne.	Asclepiadaceae	H			2X	2X	X	X			
Bombacopsis quinatum (Jacq.) Dugand	Bombacaceae	T								X	
Brassavola nodosa (L.) Lindl.	Orchidaceae	H						X			

Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Briquetia spicata (Kunth) Fryxell	Malvaceae	H					X				
Bromelia pinguin L.	Bromeliaceae	H					X	X	X		
Brosimum allicastrum Sw.	Moraceae	T							X		2X
Buchnera pusilla Kunth	Scrophulariaceae	H				X					
Bulbostylis tenuifolia (Rudge) J.F.Macbr.	Cyperaceae	G	2X	2X	2X	2X	X	X			
Bursera simaruba (L.) Sarg.	Burseraceae	T					2X	2X	2X	2X	X
Bursera tomentosa (Jacq.) Triana & Planch.	Burseraceae	T				X	X	X	X		
Byrsonima crassifolia (L.) Kunth	Malpighiaceae	T	2X	X	2X	2X					
Byttneria aculeata (Jacq.) Jacq.	Sterculiaceae	L						X			
Calea c.f. prunifolia Kunth	Asteraceae	H						X			
Calliandra sp.	Fabaceae/Mim.	T			X						
Callichlamys latifolia (Rich.) K.Schum.	Bignoniaceae	L								X	2X
Calopogonium mucunoides Desv.	Fabaceae/Pap.	H				X					
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	T						2X	X	2X	X
Canavalia brasiliensis Mart. ex Benth.	Fabaceae/Pap.	H			X		X				
Capparis indica (L.) Fawc. & Rendle	Capparidaceae	S					X			X	
Cardiospermum halicacabum L.	Sapindaceae	L	X		X						
Casearia arguta Kunth	Flacourtiaceae	T					X		X	X	
Casearia corymbosa Kunth	Flacourtiaceae	T					X	X		2X	
Casearia praecox Griseb.	Flacourtiaceae	T								X	
Casearia sylvestris Sw.	Flacourtiaceae	T						X	X	X	
Cassia biflora L.	Fabaceae/Caes.	S	2X	X	2X	2X	X	X			
Cassia diphylla L.	Fabaceae/Caes.	H	X	X	2X	2X					
Castilla elastica Sesse	Moraceae	T							X		2X
Cayaponia racemosa (Mill.) Cogn.	Cucurbitaceae	H					X	X			
Cecropia peltata L.	Cecropiaceae	T			X				2X		X
Cedrela odorata L.	Meliaceae	T					X				
Centrosema cf. plumieri (Turpin.) Benth.	Fabaceae/Pap.	H					X	X			
Centrosema macrocarpum Benth.	Fabaceae/Pap.	H							X		X
Centrosema sagittatum (Kunth) Brandegee ex & L.Riley ex	Fabaceae/Pap.	H						X		2X	
Chamaesyce cf. hypericifolia (L.) Millsp.	Euphorbiaceae	H	X		X						
Chamaesyce densiflora (Klotsch & Garcke) Millsp.	Euphorbiaceae	H	2X		X						
Chomelia spinosa Jacq.	Rubiaceae	T					X	X			
Chromolaena odorata (Lam.) R.M.King & H.Rob.	Asteraceae	S		X	2X	2X	X	X			
Chromolaena sp.	Asteraceae	H									X
Cipura cf. paludosa Aubl.	Iridaceae	H	X	X	X						
Cissus rhombifolia Vahl	Vitaceae	L	X			X	2X	X			
Cissus sicyoides L.	Vitaceae	L					X	X	X		
Coccoloba guanacastensis W.C.Burger	Polygalaceae	T									X
Cochlospermum vitifolium (Willd.) Spreng.	Cochlospermaceae	T	2X	2X	2X	2X	2X	2X	X	X	

Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Combretum farinosum Kunth	Combretaceae	L					X		X		
Cordia alliodora (Ruiz & Pav.) Oken	Boraginaceae	T					2X				
Cordia guanacastensis Standl.	Boraginaceae	S	X			X					
Cordia panamensis Riley	Boraginaceae	T					2X	2X	X	X	X
Cornutia grandifolia (Schltdl. & Cham.) Schauer	Verbenaceae	T									X
Coursetia elliptica M.Sousa & Rudd	Fabaceae/Pap.	H								X	
Crescentia alata Kunth	Bignoniaceae	T	2X	2X	2X	2X					
Crescentia cujete L.	Bignoniaceae	T				X					
Crossopetalum parviflorum (Hemsl.) Lundell	Celastraceae	S						X			
Crotalaria sp.	Fabaceae/Pap.	H		X	2X						
Cupania guatemalensis(Turcz.) Radlk.	Sapindaceae	T							X		2X
Curatella americana L.	Dilleniaceae	T		X		2X		X		X	X
Cydista aequinoctialis (L.) Miers	Bignoniaceae	L						2X			
Cydista diversifolia (Kunth) Miers	Bignoniaceae	L					X		2X	2X	2X
Cydista heterophylla Seibert	Bignoniaceae	L					X	2X		2X	
Cyperus cf. rotundus L.	Cyperaceae	G						X			
Cyperus sp.	Cyperaceae	G		X	X						
Dalbergia retusa Hemsl.	Fabaceae/Pap.	T			X	X	X				
Dalea leporina Aiton ex Hemsl.	Fabaceae/Pap.	H		X							
Davilla kunthii A. St.-Hil.	Dilleniaceae	L						X	X	2X	X
Desmodium barbatum (L.) Benth. & Oerst.	Fabaceae/Pap.	H		2X	2X	X			X		
Desmodium sp.	Fabaceae/Pap.	H			X		X				X
Desmopsis bibracteata (Rob.) Saff.	Annonaceae	T									2X
Dilodendron costaricensis (Radlk.) A.H. Gentry & Steyerm.	Sapindaceae	T									2X
Dioclea megacarpa Rolfe	Fabaceae/Pap.	L						X			
Dioscorea convolvulacea Schltdl. & Cham.	Dioscoreaceae	H					2X	2X	2X	2X	X
Diospyrus nicaraguensis Standl.	Ebenaceae	T						2X	X	2X	
Diphysa humilis Oerst.	Fabaceae/Pap.	T			X						
Dodonaea viscosa (L.) Jacq.	Sapindaceae	S						X			
Dorstenia contrajerva L.	Moraceae	H							2X		
Dorstenia drakena L.	Moraceae	H					X		X		
Echinochloa pyramidalis (Lam.) Hitchc. & Chase	Poaceae	G					X	X			
Enterolobium cyclocarpum (Jacq.) Griseb.	Fabaceae/Mim.	T							2X		
Erblichia odorata Seem.	Turneraceae	T									X
Eriosema diffusum (Kunth) G.Don	Fabaceae/Pap.	H			2X	X					
Erythroxylum havanense Jacq.	Erythroxylaceae	S					2X	2X	X	2X	X
Erythroxylum rotundifolia Lunan	Erythroxylaceae	S				X					
Eugenia oerstedeana O.Berg	Myrthaceae	S							X	X	2X
Eugenia salamensis Donn. Sm.	Myrthaceae	T					X				
Eupatorium collinum DC.	Asteraceae	H			X	X	X		X		X
Eupatorium quadrangulare DC.	Asteraceae	H	X			2X		X			X

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			0	1	3	5	10	15	20	30	50
Eupatorium sp.	Asteraceae	H			X						
Euphorbia schlechtendalii Boiss.	Euphorbiaceae	T						X			
Exostema mexicanum A.Gray	Rubiaceae	T					X	X	X	2X	
Faramea occidentalis (L.) A.Rich.	Rubiaceae	S									2X
Fimbristylis sp.	Cyperaceae	G	X	X	X	X					
Fosteronia spicata (Jacq.) G.Mey.	Apocynaceae	L					X	X	2X	2X	
Garcinia intermedia (Pittier) Hammel	Clusiaceae	S									2X
Genipa americana L.	Rubiaceae	T	X		X	2X	X	2X	2X	2X	2X
Gliricidia sepium Cex	Fabaceae/Pap.	T	2X			X	X	X			
Gonolobus barbatus Kunth	Asclepediaceae	H					X				
Gouania lupuloides (L.) Urb.	Rhamnaceae	L							X		X
Gouania polygama (Jacq.) Urb.	Rhamnaceae	L	2X	2X	2X	2X	X	2X		X	
Guazuma ulmifolia Lam.	Sterculiaceae	T	X		X	2X	2X	2X	2X	2X	X
Guettarda macrosperma Donn.Sm.	Rubiaceae	T						2X	2X	X	2X
Habenaria alata Hook. f.	Orchidaceae	H				X					
Habenaria pauciflora (Lindl.) Rchb. f.	Orchidaceae	H			X						
Habenaria quinqueseta (Michx.) Sw.	Orchidaceae	H	X	X				X			
Habenaria sp.	Orchidaceae	H		X							
Hamelia patens Jacq.	Rubiaceae	S				X					
Heliconia latispatha Benth.	Heliconiaceae	H						X	X		
Helicteres baruensis Jacq.	Sterculiaceae	S						X			
Helicteres guazumifolia Kunth	Sterculiaceae	S		X	2X	2X	X	X			
Heteropterys brachiata (L.) DC	Malpighiaceae	L				X					
Heteropterys cf. obovata (Small) Cuatrec. & Croat	Malpighiaceae	L									X
Heteropterys laurifolia (L.) A. Juss	Malpighiaceae	L						X			
Hippocratea volubilis L.	Hippocrateaceae	L							X		2X
Hiraea reclinata Jacq.	Malpighiaceae	L						X		X	X
Hirtella racemosa Lam.	Chrysobalanaceae	S							X		2X
Hymenaea courbaril L.	Fabaceae/Caes.	T					X	X	2X		2X
Hyparrhenia rufa (Nees) Stapf	Poaceae	G	2X	2X	2X	2X	X	X	X		
Hyptis c.f. verticillata Jacq.	Lamiaceae	H			X	X					
Hyptis capitata Jacq.	Lamiaceae	H		X	2X	X					
Hyptis pectinata Poit.	Lamiaceae	H		2X							
Hyptis suaveolens (L.) Poit.	Lamiaceae	H	X	2X	2X	2X					
indet. Asteraceae	Asteraceae	H					X				
indet. Poaceae	Poaceae	G					X	X			
Indigofera hirsuta L.	Fabaceae/Pap.	H		2X	X						
Indigofera suffruticosa Mill.	Fabaceae/Pap.	H				X		X			
Inga vera Willd.	Fabaceae/Mim.	T							X		X
Ipomoea hederifolia L.	Convolvulaceae	H					X				
Ipomoea trifida (Kunth) G.Don	Convolvulaceae	H	2X	X	2X	2X	X	X			

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			0	1	3	5	10	15	20	30	50
Isocarpha atriplicifolia (L.) R.Br.	Asteraceae	H						X			
Ixora floribunda (A.Rich.) Griseb.	Rubiaceae	T									X
Jacquinia pungens A.Gray	Theophrastaceae	S					2X	2X	X	2X	2X
Jatropha curcas L.	Euphorbiaceae	T							X		
Justicia brunneloides Lam.	Acanthaceae	H					X			X	
Karwinskia calderonii Standl.	Rhamnaceae	T				X					
Laelia rubescens Lindl.	Orchidaceae	H								X	
Lantana camara L.	Verbenaceae	S			X		X				
Lasiacis sorghoidea (Desv.) Hitchc. & Chase	Poaceae	G					X	2X	2X	2X	X
Lasiacis sp.	Poaceae	G							X	2X	X
Lasianthaea fruticosa (L.) K.M.Becker	Asteraceae	H	X		2X	2X	X	X		X	
Leptocoryphium lanatum (Kunth) Nees	Poaceae	G			X						
Licania arborea Seem.	Chrysobalanaceae	T							X		2X
Lippia cardiostegia Benth.	Verbenaceae	S				X		X	X		
Lonchocarpus costaricensis (Donn.Sm.) Pittier	Fabaceae/Pap.	T					X	X	X		
Lonchocarpus minimiflorus Donn.Sm.	Fabaceae/Pap.	T					2X		X	X	
Lonchocarpus oliganthus J.F.Herm.	Fabaceae/Pap.	T						X	X		
Lonchocarpus orotinus Pittier	Fabaceae/Pap.	T					X				
Lonchocarpus rugosus Benth.	Fabaceae/Pap.	T					X	X		X	
Ludwigia erecta (L.) H.Hara	Onagraceae	H	X		X						
Ludwigia octovalvis (Jacq.) P.H.Raven	Onagraceae	H	X		X			X			
Luehea candida (DC.) Mart.	Tiliaceae	T							X		
Luehea speciosa Willd.	Tiliaceae	T	X		X	X	X	X	X	X	
Lygodium venustrum Sw.	Schizaeaceae	H	X		2X	2X	2X	2X	2X	2X	2X
Lysiloma auritum (Schltdl.) Benth.	Fabaceae/Mim.	T					X				
Lysiloma sp.	Fabaceae/Mim.	T									X
Macfadyena unguis-cati (L.) A.H.Gentry	Bignoniaceae	L							X	2X	
Machaerium arboreum (Jacq.) Vogel	Fabaceae/Pap.	T							X		
Machaerium biovulatum Micheli	Fabaceae/Pap.	T					2X	2X	X	2X	
Machaerium kegelii Meisn.	Fabaceae/Pap.	L							X		2X
Maclura tinctoria (L.) Donn.	Moraceae	T					2X	X	2X	2X	X
Malpighia glabra L.	Malpighiaceae	S							X		
Malvaviscus arboreus Cav.	Malvaceae	S				X	2X	2X	X	2X	2X
Manilkara zapota (L.) P.Royen	Sapotaceae	T						X	X	X	2X
M*ansoa hymenaea* (DC.) A.H.Gentry	Bignoniaceae	L								X	
Maranta arundinacea L.	Marantaceae	H					X		X	X	
Marsdenia trivirgulata F.A.Bartlett	Asclepiadaceae	L							X		
Mascagnia sp.	Malpighiaceae	L									X
Melloa quadrivalvis (Jacq.) A.H.Gentry	Bignoniceae	L									X
Merremia aegyptia (L.) Urb.	Convolvulaceae	H			X		X	X			
Merremia sp.	Convolvulaceae	H		X							

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			0	1	3	5	10	15	20	30	50
Mikania micrantha Kunth	Asteraceae	L					X				
Mimosa albida Humb. & Bonpl. ex Willd.	Fabaceae/Mim.	H				X		X			
Mimosa pudica L.	Fabaceae/Mim.	H	X		2X						
Mimosa skinneri Benth.	Fabaceae/Mim.	H			X						
Mouriri myrtilloides (Sw.) Poir.	Melastomataceae	S						X			2X
Neptunia plena (L.) Benth.	Fabaceae/Mim.	H	X								
Ocotea veraguensis (Meisn.) Mez	Lauraceae	T									2X
Oncidium cebolleta (Jacq.) Sw.	Orchidaceae	H				X					
Onoseris onoseroides (Kunth) B.L.Rob.	Asteraceae	H						X			2X
Ouratea lucens (Kunth) Engl.	Ochnaceae	S									2X
Pachyrhizus erosus (L.) Urb.	Fabaceae/Pap.	H					X				
Panicum sp.	Poaceae	G					X				
Paspalum botterii (E.Fourn.) Chase	Poaceae	G	X		X						
Paspalum sp.	Poaceae	G	X	X	2X						
Passiflora biflora Lam.	Passifloraceae	H							X	X	
Passiflora pedata L.	Passifloraceae	H	X			X					
Paullinia cururu L.	Sapindaceae	L					2X	2X	2X	2X	X
Paullini*a pinnata* L.	Sapindaceae	L						X			2X
Pavonia cancellata (L.) Cav	Malvaceae	H	X	X	2X	2X					
Pectis sp.	Asteraceae	H		X							
Petiveria alliacea L.	Phytolaccaceae	H									X
Petrea volubilis L.	Verbenaceae	L							X	X	X
Pharus sp.	Poaceae	G									2X
Phaseolus lunatus L.	Fabaceae/Pap.	H						X			
Phoradendron quadrangulare (Kunth) Krug & Urb.	Loranthaceae	H					X	X			
Picramnia quaternaria Donn. Sm.	Simaroubaceae	T									2X
Piper amalago L.	Piperaceae	S							X		
Piper auritum Kunth	Piperaceae	S						X	X		
Piper jacquemontianum Kunth	Piperaceae	S							X		2X
Piper marginatum Jacq.	Piperaceae	S							X		
Piper pseudo-fuligineum C.DC.	Piperaceae	S						X	X		
Piper sp.	Piperaceae	S									X
Pisonia aculeata L.	Nyctaginaceae	T							X	X	
Pithecoctenium crucigerum (L.) A.H.Gentry	Bignoniaceae	L					X	X		2X	
Pleonotoma variabilis (Jacq.) Miers	Bignoniaceae	L							X		2X
Polypodium polypodioides (L.) Watt	Polypodiaceae	H						X			
Prestonia acutifolia (Benth.) K.Schum.	Apocynaceae	L						X	X		
Priva lappulacea (L.) Pers.	Verbenaceae	H							X		
Prockia crucis P.Browne ex L.	Flacourtiaceae	S							X		
Psidium guineense Sw.	Myrthaceae	S			X						
Psychotria horizontalis Sw.	Rubiaceae	S					X	X	X	X	2X

Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Psychotria nervosa Sw.	Rubiaceae	S					X	X	X	X	2X
Pterolepis trichotoma (Rottb.) Cogn.	Melastomataceae	H			X						
Quercus oleoides Schltl. & Cham.	Fagaceae/Pap.	T	X		X	X		X			
Randia aculeata L.	Rubiaceae	T					2X	X	2X	2X	
Randia subcordata (Standl.) Standl.	Rubiaceae	T				X	2X	2X	2X	2X	X
Rauvolfia tetraphylla L.	Apocynaceae	S					X	X	2X		X
Rehdera trinervis (S.F.Blake) Moldenke	Verbenaceae	T	2X	2X	2X	2X	X	X			
Rhynchosia sp.	Fabaceae/Pap.	H						X			
Rhynchospora barbata (Vahl.) Kunth	Cyperaceae	G				X					
Rhynchospora nervosa (Vahl.) Boeck.	Cyperaceae	G	X	X	X	2X					
Rhynchospora sp.	Cyperaceae	G			2X	X					
Richardia scabra L.	Rubiaceae	H	X								
Rourea glabra Kunth	Connaraceae	L						2X	2X	2X	X
Ruellia inundata Kunth	Acanthaceae	H			X		X	X			
Russelia sarmentosa Jacq.	Scrophulariaceae	H			X		X				
Samanea saman (Jacq.) Merr.	Fabaceae/Mim.	T					X			X	
Sapranthus palanga R.E.Fr.	Annonaceae	T							X	X	
Sciadodrendron excelsum Griseb.	Araliaceae	T									X
Scleria cf interrupta Rich.	Cyperaceae	G						X			
Scleria cf. hirtella Sw.	Cyperaceae	G	X								
Scleria microcarpa Nees & Kunth	Cyperaceae	G						X		X	
Scleria setulosociliata Boeck.	Cyperaceae	G				X					
Scleria sp.	Cyperaceae	G		X	X	X		X			
Sebastiana pavoniana Mull. Arg.	Euphorbiaceae	S						X		X	
Securidaca silvestris Schltdl.	Polygalaceae	L					X	X	X	X	
Selaginella horizontalis (C.Presl.) Spring.	Selaginallaceae	H					2X	X	2X	2X	
Semialarium excelsum (Miers) Mennega	Hippocrateaceae	T		X	X	2X	2X	2X	X	2X	
Serjania mexicana (L.) Willd.	Sapindaceae	L					X	X	X	X	2X
Serjania schideana Schltdl.	Sapindaceae	L					2X	X	2X	X	X
Sesbania emerus (Aubl.) Urb.	Fabaceae/Pap.	H	X	2X	X						
Seteria geniculata (Willd.) P.Beauv.	Poaceae	G			X						
Seteria sp.	Poaceae	G			X						
Sida rhombifolia L.	Malvaceae	H			X		X				
Sida sp.	Malvaceae	H	X			2X		X			
Sida urens L.	Malvaceae	H			X						
Sideroxylon capiri (A.DC.) Pittier	Sapotaceae	T					X		2X	X	
Simarouba glauca DC.	Simaroubaceae	T				X	2X	X	X		
Sloanea terniflora (Moc. & Sesse ex) DC. Standl.	Elaeocarpaceae	T									X
Smilax spinosa Mill.	Smilacaceae	L					X	2X	2X	2X	X
Solanum accrescens Standl. & C.V.Morton	Solanaceae	S							X		
Solanum hazenii Britton	Solanaceae	S					X				

Scientific name	Family	Life-form type	Age of succession								
			0	1	3	5	10	15	20	30	50
Spondias mombin L.	Anacardiaceae	T					2X	X	X	X	X
Spondias purpurea L.	Anacardiaceae	T					X				
Stachytapheta frantzii Pol.	Verbenaceae	H	X	2X	X						
Stachytapheta jamaicensis (L.) Vahl	Verbenaceae	H	2X	2X	X	X					
Stemmadenia obovata (Hook.&Arn.) K.Schum.	Apocynaceae	T					2X	X	X	X	X
Sterculia apetala (Jacq.) H.Karst	Sterculiaceae	T									X
Stigmaphyllum ellipticum (Kunth) A.Juss	Malpighiaceae	L						X			X
Swartzia cubensis (Britton & P.Wilson) Standl.	Fabaceae/Pap.	T									2X
Swietenia macrophylla King	Meliaceae	T			X	2X		X			
Tabebuia impetiginosa (Mart. ex) DC. Standl.	Bignoniaceae	T					X				
Tabebuia ochracea (Cham.) Standl.	Bignoniaceae	T			X		2X	X	2X	2X	X
Tabebuia rosea (Bertol.) DC.	Bignoniaceae	T					X		X	X	X
Tectaria sp.	Tectariaceae	H									X
Tephrosia nicaraguensis Oerst.	Fabaceae/Pap.	H				X					
Tetracera volubilis L.	Dilleniaceae	L					2X	2X	2X	2X	2X
Thelypteris sp.	Thelypteridaceae	H									X
Thevitia peruviana (Pers.) K.Schum.	Apocynaceae	T				X					
Thouinidium decandrum (Humb. & Bonpl.) Radlk.	Sapindaceae	T					X			X	
Tournefortia sp.	Boraginaceae	L						X			
Trichilia Americana (Sesse & Moc.) T.D.Penn.	Meliaceae	T								2X	
Trichilia glabra L.	Meliaceae	T						X			
Trichilia trifolia L.	Meliaceae	T							X	X	
Trigonia rugosa Benth.	Trigoniaceae	L		X							
Triumfetta lappula L.	Tiliaceae	H					X	X	X		
Trixis inula Crantz	Asteraceae	H	X		2X		X	X		2X	
Trophis racemosa (L.) Urb.	Moraceae	T									X
Verbesina gigantea Jacq.	Asteraceae	S					2X		X		
Verbesina turbacensis Kunth	Asteraceae	H			X	X			X		
Vernonia argyropappa H.Buek	Asteraceae	H			X	X					
Vismia baccifera (L.) Triana & Planch.	Clusiaceae	S			X	X					
Waltheria glomerata C.Presl.	Sterculiaceae	S			X	2X					
Waltheria indica L.	Sterculiaceae	H	2x	X	2X	2X					
Xanthosoma cf. mexicanum Liebm.	Araceae	H					2X	X	X	X	
Xylophragma seemannianum (Kuntze) Sandwith	Bignoniaceae	L					X		X	2X	
Xylosma anisophylla Standl.	Flacourtiaceae	T				X					
Xylosma flexuosa (Kunth) Hemsl.	Flacourtiaceae	T						X			
Zanthoxylum setulosum P.Wilson	Rutaceae	T					X	X	X		X
Zornia sp.	Fabaceae/Pap.	H	X								
Zuelania guidonia (Sw.) Britton & Millsp.	Flacourtiaceae	T							X		2X