Acta bot. bras. 20(3): 599-613. 2006

Solanaceae composition, pollination and seed dispersal syndromes in Mexican Mountain Cloud Forest[1]

Lidiamar Barbosa Albuquerque[2,4], Alejandro Velázquez[3] and Rafel Mayorga-Saucedo[3]

Received: February 16, 2005. Accepted: February 2, 2006

RESUMO – (Composição de Solanaceae, polinização e síndromes de dispersão de sementes em Floresta Mesófila de Montanha). Neste trabalho a hipótese é que a composição das espécies de Solanaceae e as síndromes de polinização e dispersão de sementes variam de acordo com o grau de perturbação. Assim o objetivo é analisar como a composição de espécies de Solanaceae e suas síndromes de polinização e de dispersão de sementes variam ao longo de um gradiente de perturbação. Este trabalho foi realizado nas Florestas Mesófilas de Hidalgo, México. As Solanaceae foram coletadas ao longo de transectos, dispostos em caminhos ou estradas secundárias. As síndromes de polinização e dispersão de sementes foram caracterizadas a partir das características morfológicas das flores e frutos. Das 500 amostras coletadas, 392 continham Solanaceae, pertencentes a 25 espécies. A similaridade entre as amostras mostrou dois grupos: no grupo I estavam as espécies mais freqüentemente encontradas em áreas menos perturbadas e mais úmidas, enquanto o grupo II apresentava as espécies mais freqüentes em ambientes mais perturbados. A síndrome de melitofilia foi relevante nos dois grupos. No entanto, a ornitocoria (45,8%) prevaleceu sobre a chiropterocoria (37,5%) em áreas menos perturbada e mais úmida do grupo I, enquanto chiropterocoria (50%) foi maior no grupo II.

Palavras-chaves: perturbação florestal, ornitocoria, chiropterocoria, melitofilia, México

ABSTRACT – (Solanaceae composition, pollination and seed dispersal syndromes in Mexican Mountain Cloud Forest). In this work we hypothesised that Solanaceae species composition and pollination and seed dispersal syndromes change according to the degree of disturbance. Hence, the aim of this study is to analyze how the species composition of Solanaceae changes along disturbance gradients of mountain cloud forest, and to establish how Solanaceae pollination and seed dispersal syndromes vary along the same gradients. The study concentrates on the mountain cloud forests in Hidalgo, Mexico. Solanaceae species collection was carried out along transects, laid out alongside paths and secondary roads. Pollination and seed dispersal syndromes for all species were recorded based on floral and fruit morphological traits. From the 500 sample units surveyed, 392 contained 25 Solanaceae species. The (dis)similarity among sample units highlighted a major division: the first group harboured species more commonly found in less disturbed and more humid conditions, whereas the second group contained species more commonly found in contrasting conditions. Melittophily pollination syndromes turned out to be equally relevant in the environmental conditions of both groups. With regard to seed dispersal syndromes, ornithochory (45.8%) prevailed over chiropterochory (37.5%) in group I less disturbed and more humid areas, whereas chiropterochory (50%) prevailed within group II.

Key words: forest disturbance, ornithochory, chiropterochory, melittophily, Mexico

Introduction

The Solanaceae family comprises 90 genera, containing more than 3,500 species (D'Arcy 1986). Its cosmopolitan distribution is best represented in tropical and temperate regions, with Australia and Latin America as major dispersal centres (Barroso *et al.* 1991). The greatest solanaceous species diversity occurs in South America, and this area is recognised as the family's centre of origin (Hunziker 1979).

Solanaceous species are represented in most habits: trees, shrubs, herbs and occasionally as climbers, epiphytes (*Markea* and *Juanulloa*), rhizomateous herbs (*Jaborosa*), and thorny (*Acnistus*, *Grabowskia* and *Solanum*) and thornless (e.g. *Cestrum*) shrubs (Barroso *et al.* 1991). Despite the worldwide distribution and diversity of the group, some taxa are restricted to particular ecological conditions. For example, in Mexico *Lycianthes monziniana* is distributed at elevations above 2000 m in pine-oak forests (Williams 1993), while

---

[1] Part of a PhD thesis of the first Author (Universidade Estadual de Campinas - UNICAMP and Universidad Autonoma de México - UNAM). CAPES scholarship.

[2] Universidade Católica Dom Bosco, UCDB, Campo Grande, MS, Brazil

[3] Instituto de Geografía, UNAM, Aquiles Serdan, 382, Col. Centro, Morelia, Mich. C. Postal 58000, México

[4] Corresponding Author: Rua Moreira Cabral 321, Bairro Planalto, 79009-150 Campo Grande, MS, Brazil (lidiamar98@yahoo.com)

others such as *Solanum iopetalum* are present only in pine forest (Rzedowski & Rzedowski 1985). Yet others are restricted to specific geographical regions (*Physalis tehuacanensis* and *P. queretaroensis*, species endemic to Mexico). Despite the considerable work carried out with this group, little research has been conducted to document its role as a light gap coloniser and coloniser of disturbed areas such as pastures, clearings, roadsides and forest edges (Bohs 1994; Da Silva *et al*. 1996; Miriti 1998; Nepstad *et al*. 1998; Tabarelli *et al*. 1999). Colonisation in open areas depends largely on pollination and seed dispersal processes (Murray *et al*. 2000). These last two processes are crucial to understanding the colonisation role of Solanaceae and, in turn, to comprehending the way colonisation takes place as part of the ecosystem function (Morellato & Leitão Filho 1992; Gorchov *et al*. 1993; Reis *et al.* 1996; Medellín & Gaona 1999).

Solanaceae are well known for the large quantities and variety of secondary metabolites, such as alkaloids, flavanoids and terpenes (Evans 1986). Recently, the ecological importance of *Solanum* alkaloids in limiting frugivory (Cipollini & Levey 1997a; 1997b; 1997c) and as anti-fungal agents (Cipollini & Levey 1997b) has been highlighted. These features, in addition, play a role in herbivory and seed dispersal.

Pollination and seed dispersal processes have been documented within evolutionary (e.g. Herrera 1985; Hegde *et al.* 1991; Tamboia *et al.* 1996) and ecological contexts (Vázquez-Yanes *et al.* 1975; Symon 1979; Howe & Smallwood 1982; Gautier-Hion *et al*. 1985; Fleming & Sosa 1994; Galindo-González 1998). In the present paper, the pollination and seed dispersal processes of Solanaceae are studied within a matrix of forest patches.

This study was conducted in Mexican mountain cloud forest. The vegetation is considered to be transitional, between temperate and tropical forests (Rzedowski 1996). Furthermore, this forest has been drastically disturbed, so forest gaps and openings are common. Colonisation of these forest openings by pioneer species (such as Solanaceae) may therefore play an important role in mountain cloud forest recovery. It has been well documented that disturbance drastically modifies species composition and community structure (Navarro 1992; Velázquez 1994). With this in mind, it is hypothesised that Solanaceae species composition and, consequently, pollination and seed dispersal syndromes vary according to the degree of mountain cloud forest disturbance. Among well-conserved forest patches, the diversity of syndromes may be larger and their proportion more balanced than among disturbed forest patches, where syndromes may differ significantly. Hence, the aim of this study is to analyze how the species composition of Solanaceae changes along disturbance gradients of mountain cloud forest, and to establish how Solanaceae's pollination and seed dispersal syndromes vary along the same gradients.

Methods

Study area – In Mexico, mountain cloud forests reach their most septentrional geographical distribution worldwide. A high diversity (over 3,000 vascular plant species, of which many are endemic) and the remarkable predominance of vascular epiphytes and lianas (Alcantara *et al*. 2002) characterise these ecosystems. Their current distributions form an archipelago-like pattern and cover less than 1% of the Mexican surface (Rzedowski 1996; Luna *et al.* 2001). At such places, heterogeneous ecological conditions prevail (Mayorga *et al.* 1998), which is reflected in large floristic and physiognomic dissimilarities (Rzedowski 1996). Mexican mountain cloud forests comprise dwarf, short, medium and tall forest communities, as well as evergreen and deciduous. This vegetation is subjected to large human disturbances, which have formed a fragmented distribution pattern divided into a matrix of fragments of different sizes and split by trails, secondary roads, crops and pasture lands. Heliophyllous taxa prevail in early successional stages along edges of fragments, among which Solanaceae are conspicuous. These have been poorly studied since most vegetation surveys are biased to sample pristine conditions, so that Solanaceae are rarely found. The role of these as successional facilitators, therefore, has not been documented.

The present research was conducted in nine different areas of Mexican mountain cloud forest located in the Sierra Madre Oriental in the state of Hidalgo (Fig. 1A), within the jurisdiction of the municipalities of Molango, Lolotla, Xochicoatlán and Tlanchinol, and surrounding localities. These areas vary in elevation from 1,380 to 1,800 m. The landscapes vary from hilly to mountainous, with large differences between one slope and another in terms of soils, relief, exposure and sunlight incidence. In turn, forest physiognomy and species composition vary too. Climbers and epiphytes and tree fern types occur regularly in some areas. Table 1 synoptically describes the (dis)similarities among the nine forests studied and provides a detailed profile of the degree of disturbance observed in all areas.

The rainy season is from May to November, with most precipitation falling from June to September. The major landscapes are predominantly mountainous, with steep straight short slopes. Dominant soil types are Cambisol, Regosol, Acrisol and Pheozem. Apart from the vegetation type studied here, pine and subtropical rainforest fragments occur in the region. Nowadays, however, most pristine vegetation types at low altitudes and on moderately steep slopes have been cleared for cropping, livestock production and timbering (Challenger 1998).

Sampling design – Intensive surveys were conducted in the region between April and November 1999 in order to select the cloud forest areas to be sampled. Two selection criteria were applied: a varying degree of disturbance, ranging from low to high, and the presence of paths and secondary roads at least 2 km long (openings) crossing the areas.

The degree of disturbance was estimated by describing the forest structure under the assumption the more pristine, the less disturbed (*sensu* Williams-Linera 1993). Species composition was also considered as an indicator of disturbance. Challenger (1998) provides a detailed list of tree species favoured by disturbance. The abundance of these disturbance indicator species, and their development status were reckoned as indirect measurements of the degree of disturbance. Traces of burning, timbering and grazing were also noted as indicators of the degree of disturbance. In addition, the type of secondary roads crossing each forest patch (for instance, those used by cars or those used by local people only) was also considered as an indirect index of the degree of disturbance (see Table 1).

Overall, nine forest areas were chosen (from different localities). Solanaceae species collection took place along transects (each 1200 m long) lying alongside paths and secondary roads. These nine forest areas were grouped into two disturbance classes, so that transect number was evenly sampled in each group. Each transect was divided into 20 sample units (10 m long and 3 m wide) 50 m apart (Fig. 1B). In total, 25

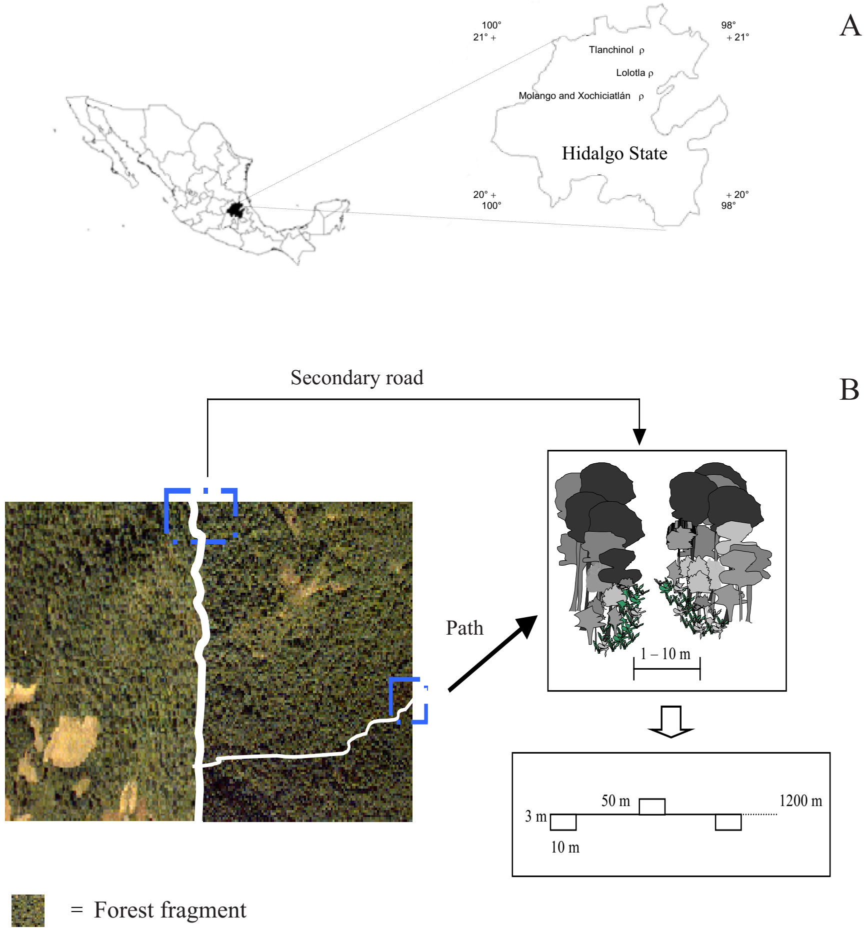

Figure 1. A. Location of study area in Hidalgo State, Mexico. B. Schematic representation of a forest area, layout of transects and sampling units (10×3 m, spaced 50 m apart across sides) along secondary roads and paths.

Table 1. Synoptic characteristics of the nine forest areas (localities) surveyed in Mexican mountain cloud forest in the Sierra Madre Oriental, Hidalgo (Mexico). AMT = mean annual temperature; AMP = mean annual precipitation. Sources: [1]CONABIO/ESTADIGRAFIA (1997a) and Garcia (1981); [2]CONABIO/ESTADIGRAFIA (1997b); [3]SSP (1983).

Forest areas (localities)	Location	Altitude (m)	Climate[1]	AMT[1] (ºC)	AMP[2] (mm)	Soil type(s)[3]
(1) Lontla (road), Highway Pachuca-Tampico. Municipality of Tlanchinol. Pristine forest typified by a canopy 40 m high. Pteridophytes reaching up to 10 m high are abundant. Disturbance: one path used as a walking trail for indigenous people only; no traces of timbering, burning and grazing. The largest area and considered the most conserved.	21°01’34.2”N 98°38’24”W	1380 to 1450	Semi-warm humid (A)C(fm)(i’)gw” Slope exposure: East	18-22	2500	Litosol-Feozem Rendzina, loamy texture
(2) Road to Apantlazol, Highway Pachuca-Tampico 7 km. Municipality of Tlanchinol. Dense forest has a canopy 40 m high. Pteridophyte communities are abundant and short. Disturbance: one secondary road and a path cross the area; traces of timbering, burning and grazing for subsistence purposes were observed. The second largest area and considered well conserved.	20°58’55”N 98°37’1”W	1450 to 1520	Semi-warm humid (A)C(fm)(i’)gw” Slope exposure: East	18-22	2500	Litosol-Feozem-Rendzina, loamy texture
(3) Molango (road chapel, old iron mine), Highway Pachuca-Tampico 130 km. Municipality of Molango. Secondary forest characterised by a canopy 20 m high. Disturbance: an abandoned path used for mining purposes 50 years ago; surrounded by open pasturelands; mowing and grazing were observed along path. No signs of recent timbering or burning were detected. Area of relatively small size.	20°46’41”N 98°43’33”W	1710	Temperate subhumid C(w2) Slope exposure: Southwest / Northeast	12-18	1500	Luvisol-Cambisol, loamy texture
(4) Road to Eloxochitlán. Municipality of Molango. Remnants of secondary forest with canopy 20 m high Disturbance: a secondary road frequently used by trucks; surrounded by open pasturelands. Area of relatively small size.	20°45’04”N 98°45’00”W	1660	Mild humid, with long fresh summer Cb’(m)(f)(1’)g Slope exposure: North	5-12	1500	Luvisol-Cambisol, loamy texture
(5) Road to Jalamelco. Municipality of Xochicoatlán. Secondary forest with canopy 20 m high. Disturbance: one secondary road and a path crossing the area. Relatively medium-size area, considered little disturbed.	20°47’46”N 98°41’48”W	1800	Temperate humid C(m)(f)(e)g Slope exposure: Northeast	12-18	2000	Regosol-Cambisol-Acrisol, deep litic phase, lime texture
(6) Mo-Xo (Molango–Xochicoatlán), Highway Pachuca-Tampico 122 km. Municipality of Molango. The forest varies from dense to semi-dense, with trees reaching from 20 to 30 m. Disturbance: only small trails were observed; traces of timbering, grazing and burning were recorded. The size of the area is medium.	20°44’42”N 98°42’19”W	1450	Temperate subhumid C(w2) Slope exposure: Southeast	12-18	1800	Luvisol-Cambisol, loamy texture
(7) Naopa. Municipality of Lolotla. Open secondary forest with trees from 10 to 20 m. Disturbance: only a secondary road surrounded by pasturelands; texture traces of mowing, grazing and burning were observed. The size of the area is relatively small.	20°51’03”N 98°43’22”W	1510	Temperate humid C(fm)(i’)gw” Slope exposure: Southwest/ Northeast	12-18	2000	Regosol-Cambisol-Acrisol, deep litic phase, loamy
(8) Road to Tianguistengo. Municipality of Xochicoatlán. Secondary forest with trees from 10 to 20 m. Disturbance: a secondary road heavily transited, texture surrounded by pasturelands; mowing, grazing and patches of orchards were observed. The size of the area is relatively medium.	20°45’21”N 98°39’22”W	1380 to 1490	Temperate humid C(m)(f)(e)g Slope exposure: Southeast	12-18	1800	Regosol-Cambisol-Acrisol, deep litic phase, loamy
(9) Lolotla (Highway Pachuca-Tampico, 140 km). Municipality of. Lolotla. Open secondary forest with trees from 10 to 20 m. Disturbance: numerous trails surrounded by pasturelands; grazing, timbering, burning and corn crops	20°51’39”N 98°41’50”W	1400 to 1500	Temperate humid C(fm)(i´)gw Slope exposure: West	12-18	2500	Feozem-Regosol, with deep litic phase, clay texture

transects (including 500 sample units) were surveyed covering the gradient of disturbance. Each sample unit was first characterised on the basis of its environmental condition (degree of disturbance and slope exposure). Then, a complete inventory of all Solanaceae species was carried out at each sample unit. Finally, all individuals per species were counted, their heights measured and their phenological status recorded.

Species composition of Solanaceae – In total, 156 plant specimens were collected in order to verify identification. All specimens were identified at species level in the Herbarium MEXU (Universidad Nacional Autónoma de México) and were deposited in the Herbarium of the Faculty of Sciences (FCME). Bibliographical support from Standley (1924), Standley & Williams (1973), Waterfall (1967), Hunziker (1969), Knapp (1985), Nee (1986; 1993) and Martínez & Hernandez (1999) was needed to achieve the identification process.

Characterisation of pollination and seed dispersal syndromes – In this research, all Solanaceae species were grouped in a pollination (*sensu* Faegri & Van der Pijl 1980) and a seed dispersal syndrome (*sensu* Van der Pijl 1972), based on morphological traits (colour, shape and size) obtained from field observations and herbarium verification. Fruit size was compiled from Waterfall (1967), Hunziker (1969), Knapp (1985), Nee (1986; 1993) and Martínez & Hernandez (1999) and was completed by field observations. Wilson *et al.* (1989) and Akwood *et al.* (1993) alike have conducted comparative studies in other tropical and subtropical regions.

The pollination syndromes characterised in the present study were defined as follows:
a. melittophily: flowers small; white, pale or green in colour; sweet-scented; floral reward mainly pollen;
b. ornithophily: bright reddish-coloured flowers; odourless and tubular corolla; nectar as floral reward;
c. sphingophily: white to pale-yellow colour of flowers; deep corolla tubes; sweet-scented; flowers open late afternoon or just after dark; nectar as floral reward.

The seed dispersal syndromes typified included the following:
d. ornithochory: fruits defined as fleshy berries with bright red, yellow, white, blue and black contrasting colours; usually small and generally without smell;
e. chiropterochory: fleshy berries usually pale green, brown, yellow or black; varying in size and chiefly scented; in addition, some fruits weakly protected;
f. mammaliochory (non-flying mammals): in this study fleshy berries (with smell, inconspicuous colours, in general dropping to the ground at maturity) and fruits with seeds that have to be either protected by a hard coat or by bitter taste or toxic substances. Also fruits inaccessible for bats but likely to be consumed by terrestrial mammals such as rodents and marsupials;
g. autochory: dry, dehiscent fruits (capsules).

Data analysis – Field observations on Solanaceae species, their abundance and the number of individuals per area were entered in a database. First, a complete inventory was made of the species identified, together with their abundance values per sample unit. The abundance value (Ab) was estimated as follows: Abundance (of species x^1 present in locality y^1) = (total number of individuals of species x^1 present in locality y^1/total number of individuals of all species in locality y^1)100.

Species were then organised in order to detect sample units with similar species composition and the abundance values of the same species. The species were then sorted in a table to depict groups of taxa sharing similar statistical performance. The first group comprised differential species, which included exclusive species (defined as those that differentiate one area from the others) and characteristic species (those that show a distinct maximum abundance in certain areas). The second group included constant taxa (defined as those recorded in most sample units; *sensu* Velázquez 1994). This allowed us to depict preliminary groups of sample units sharing comparable species composition. This suggests that these groups share similar ecological conditions (Waite 2000).

In order to quantify the species performance statistically, we used an algorithm of correspondence (TWINSPAN; Hill 1979). Five cut levels were considered sufficient to detect significant differences among groups of sample units. The results were presented in a dendrogram to show the distribution of species groups. These types of multivariate techniques have been recommended for studies of this kind, in order to evenly assess the weight of all species (Terborgh & Robinson 1986). Correspondence analysis (TWINSPAN) performs simultaneously "R" and "Q" classification, giving equal chance to all species and sites to cluster on basis of resemblance index (Waite 2000).

It was expected that species groups would be distributed along a gradient of disturbance. Detrended correspondence analysis (DCA) (McCune & Mefford 1995) was therefore used to statistically relate the results obtained in the dendrogram in order to infer potential attributes that explain the distribution of species groups.

Groups of species (depicting different environmental conditions) detected in the previous analysis were also compared on the basis of their pollination and seed dispersal syndromes. Using G tests (Sokal & Rohlf 1998), significance among group differences was measured from a contingency table (number of groups versus pollination and seed dispersal syndromes). A level of $P<0.05$ was considered as significant throughout the analysis.

Results

Species richness – A clear gradient of disturbance (Table 1) was detected among areas and was reflected in the species composition of Solanaceae. A total of 25 species of Solanaceae were identified. The species *Physalis queretaroensis*, *P. gracilis*, *P. subrepens*, *Solanum rudepannum* and *Witheringia mexicana* were reported in the region for the first time. Abundance values per species per area are shown in Table 2. The most exclusive (stenoecious) species are found at the top (e.g. *Solanum erianthum*, *S. rudepannum* and *Physalis gracilis*), whereas constant (euryecious) species are placed at the bottom (e.g. *Solanum chrysotrichum* and *S. nigrescens*). Characteristic species, represented by *Solanum aligerum*, *S. pseudocapsicum* and *Cestrum oblongifolium*, are found between exclusive and constant species groups. From Table 2, we inferred that Lolotla and Tianguistengo shared similar environmental conditions, which is reflected in the common exclusive species (e.g. *Solanum rudepannum*, *S. erianthum* and *Physalis gracilis*). However, these areas differ from Lontla and Apantlazol, where the exclusive species are *Cestrum elegans* and *Solanum appendiculatum*. Other species such as *Solanum aligerum*, *S. pseudocapsicum* and *Cestrum oblongifolium* occurred within a certain

Table 2. Species of the nine forest areas (localities) surveyed in Hidalgo (Mexico). Abundance (of species x^1 present in locality y^1) = (total number of individuals of species x^1 present in locality y^1/total number of individuals of all species in locality y^1)100. (Tiangui = Tianguistengo; Lolotla; Mo-Xo = Molango-Xochicoatlán; Apan = Apantlazol; Lontla; Molan = Molango; Eloxo = Eloxotitlán; Naopa; Jala = Jalamelco). Legend: ☐ = exclusive species; ▨ = characteristic species; ■ = constant species.

		Abundance (%)								
Species	Spp	Tiang	Lolotla	Mo-Xo	Apan	Lontla	Molan	Eloxo	Naopa	Jala
Solanum nudum Dunal	*Snu*	1.7								
Solanum erianthum D. Don	*Ser*	1.1	0.2	4.9						
Solanum rudepannum Dunal	*Sru*	5.1	24.4	3.2	0.4					
Physalis gracilis Miers	*Pgr*	17.6	2.9				0.7	15.4		
Jaltomata procumbens (Cav.) J.L. Gentry	*Jal*	1.1		1.1				2.6	1.9	
Brugmansia suaveolens (Willd.) Bercht. & Presl.	*Bsu*	2.8			0.4	0.3				
Cyphomandra betacea (Cav.) Sendtner	*Cyb*		2.1							
Physalis queretaroensis M. Martínez & Hernández	*Pqu*		0.3				0.7			
Cestrum sp.	*Csp*			0.7				17.9		
Solanum jasminoides Paxton	*Sja*				0.7					
Cestrum elegans (Brongn.) Schltdl.	*Cel*				5.1	12.0				10.6
Solanum appendiculatum Dunal	*Spe*				1.6	0.3				1.2
Physalis subrepens Waterf.	*Psu*					2.6	2.0		26.7	
Lycianthes aff. *lenta*	*Lyc*					1.3				
Witheringia mexicana (Rob.) Hunz.	*Wit*						2.0	10.3		
Solanum aligerum Schltdl.	*Sal*				28.6	10.7	8.5		8.6	35.3
Solanum schlechtendalianum Wap.	*Ssc*	1.7	16.7	12.0	0.6	0.3				
Solanum umbellatum Mill.	*Sum*	1.1	1.8	6.4	0.7	0.3				
Cestrum oblongifolium Schltdl	*Cob*	28.4	26.0	4.6			7.2		24.8	7.1
Solanum skutchii Corr.	*Ssk*	5.1	0.2	0.4	5.5	10.5		2.6	3.8	
Solanum pseudocapsicum L.	*Sps*	1.7	8.8	40.6	22.7	47.6	72.5		1.0	
Solanum myriacanthum Dunal	*Smy*	0.6	9.7	3.9	13.3	0.8		2.6	11.4	4.7
Solanum aphyodendron S. Knapp	*Sap*	2.3	0.2	6.0	4.8	7.7	4.6	2.6		

range of environmental conditions, although not grouped in a particular set of areas.

Classification and ordination – Of the 500 sample units, 392 comprised Solanaceae species; these were compared and their (dis)similarity was measured. The dendrogram (Fig. 2A) suggests a gradient from the relatively less disturbed and more humid areas, such as Lontla and Apantlazol, towards the more disturbed and less humid areas, such as Lolotla and Tianguistengo (Fig. 2B). The abundance value per species per group was recalculated in order to depict differential species representative of certain environmental conditions (Table 3). The differential species depicting group I were *Solanum pseudocapsicum* and *S. aligerum*, whereas those for group II were *S. rudepannum* and *Cestrum oblongifolium* (Fig. 3).

These two groups were further analysed in order to measure their (dis)similarity along environmental gradients. These gradients were depicted along ordination axes, which in turn allowed us to infer potential environmental attributes that best explain the distribution and abundance of Solanaceae species. The DCA results showed that those sample units forming groups I and II split significantly along axis I ($l_1 = 0.770$; percen-

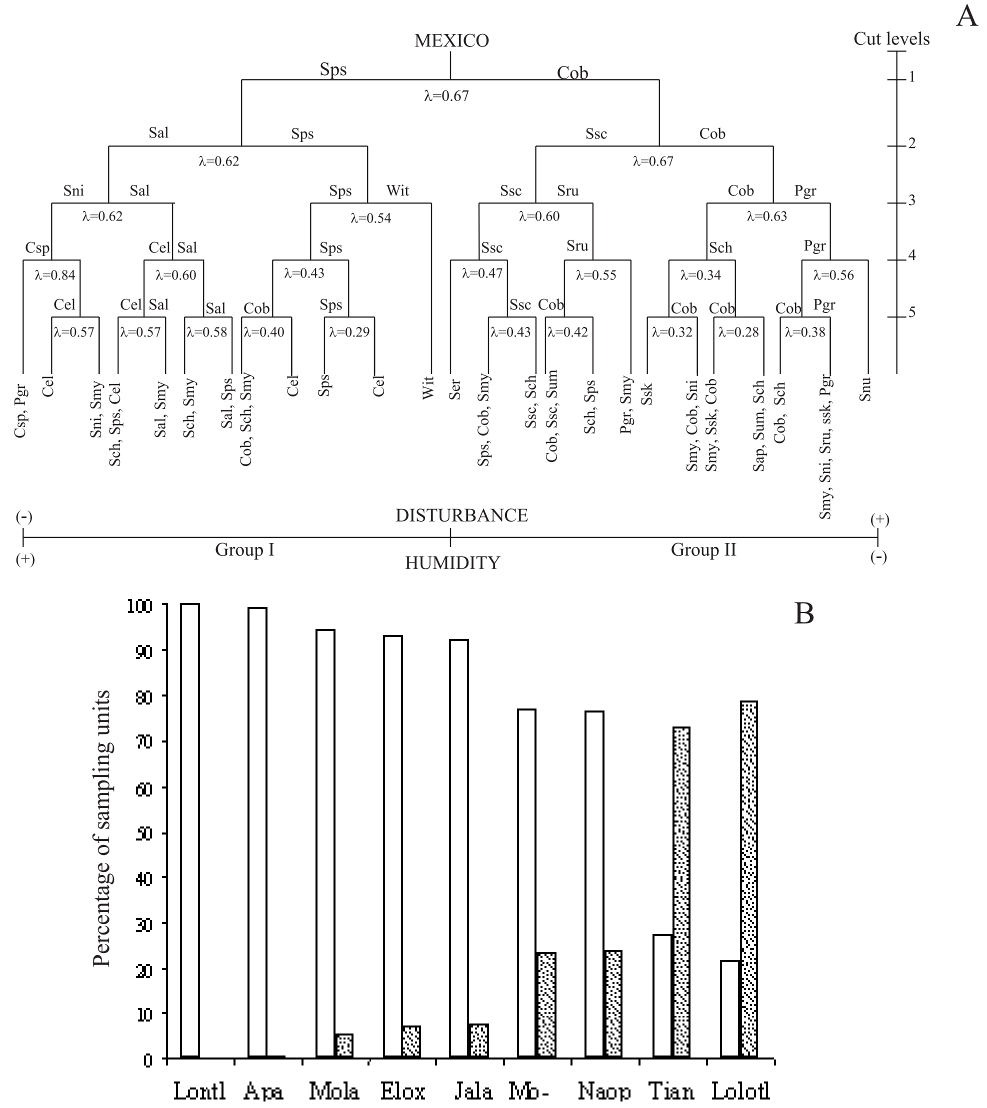

Figure 2. A. Dendrogram (obtained via TWINSPAN) showing the (dis)similarities of the species sampled in the nine Mexican mountain cloud forest fragments. Full names of differential species are given in Table 2 and Figure 4. B. Number of sampling units (expressed in percentage) per area, depicting different environmental conditions represented by group I and/or group II. Group I (□) = less disturbed and more humid; Group II (■) = more disturbed and less humid. Lontla; Apan = Apantlazol; Molan = Molango; Eloxo = Eloxotitlán; Jala = Jalamelco; Mo-Xo = Molango-Xochicoatlán; Naopa; Tiangui = Tianguistengo; Lolotla.

Table 3. Relative abundance of Solanaceae species along a gradient of humidity and disturbance as indicated by groups I and II. The names of municipalities from each group are given in Figure 2B.

Species	Group I Ab (%)	Group II Ab (%)
Brugmansia suaveolens (Willd.) Bercht. & Presl	0.5	
Cestrum elegans (Brongn.) Schltdl.	5.2	
Cestrum oblongifolium Schltdl.	2.1	29.3
Cestrum sp.	0.5	
Cyphomandra betacea (Cav.) Sendtn.	0.1	1.4
Jaltomata procumbens (Cav.) J.L. Gentry	0.4	0.1
Lycianthes aff.*lenta* (Cav.) Bitter	0.3	
Physalis gracilis Miers	0.1	6.9
Physalis subrepens Waterf.	2.3	
Physalis queretaroensis M. Martínez & L. Hernández	0.1	0.3
Solanum aligerum Schltdl.	16.6	
Solanum aphyodendron S. Knapp	5.1	0.5
Solanum appendiculatum Dunal	0.7	
Solanum chrysotrichum Schltdl.	10.4	11.6
Solanum erianthum D. Don	0.6	0.8
Solanum jasminoides Paxton.	0.3	
Solanum myriacanthum Dunal	8.1	5.2
Solanum nigrescens M. Mart. & Gal.	3.6	1.5
Solanum nudum Dunal		0.4
Solanum pseudocapsicum L.	34.9	1.8
Solanum rudepannum Dunal	0.3	21.0
Solanum schlechtendalianum Wap.	1.0	

tage of variance explained 48%). The results showed a major division into two groups. Group I harbours species assemblages that are better distributed in less disturbed forest areas with more humid conditions than the species assemblages from group II (Fig. 4). Along axis II (l_2 = 0.63; percentage of variance explained 29%), species distribution did not show clearly related environmental attributes.

Pollination and seed dispersal – Most types of Solanaceae habits were represented: shrub-like (60%), herb-like (24%), climber-like (12%, including both succulent and woody types) and tree-like (4%). Of these species, 84% were melittophilous (Table 4). This pollination syndrome was found to be equally important in both groups detected in the previous analysis and no substantial differences were found between groups (GI = 83.3% and GII = 93.8%), as shown in Fig. 5A. A detailed characterisation of all species into pollination and seed dispersal syndromes is given in Table 4.

Four seed dispersal syndromes were distinguished, clustered into two types: biotic (comprising three types: ornithochory, chiropterochory and mammaliochory) and abiotic one type (autochory). Overall, 44% of the species were categorised as ornithochoric. Fruits were small, varying in size from 7 to 15 mm, and of these 54.5% were red-orange, 27.3% black and 9.1% white. It was not possible to categorise the remaining 9.1%

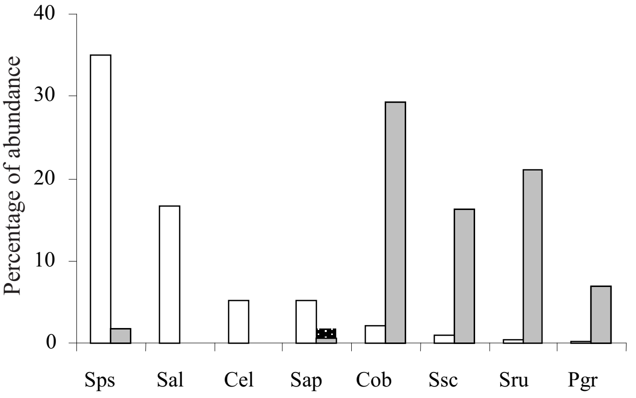

Figure 3. Differential species of contrasting environmental conditions typified by group I and group II (Sps = *Solanum pseudocapsicum*; Sal = *S. aligerum*; Cel = *Cestrum elegans*; Sap = *Solanum aphyodendron*; Cob = *Cestrum oblongifolium*; Ssc = *Solanum schlechtendalianum*; Sru = *S. rudepannum*; Pgr = *Physalis gracilis*). ☐ = Group I; ■ = Group II.

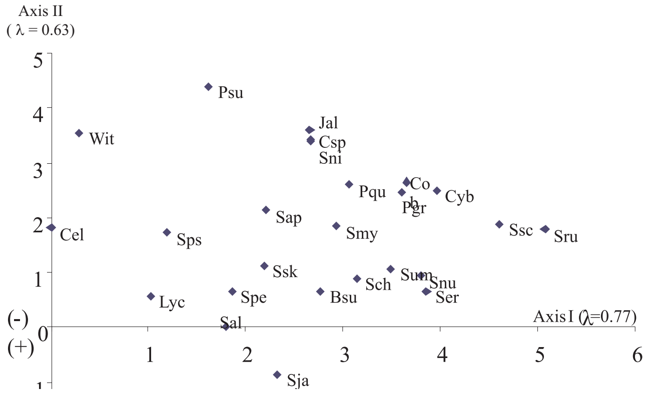

Figure 4. Ordination diagram obtained via DCA, where Solanaceae species distribution infers relation with a gradient of disturbance. The eigenvalues suggest significant differences among species scores. The names of species are: *Snu = Solanum nudum*; *Ser = Solanum erianthum*; *Sru = Solanum rudepannum*; *Pgr = Physalis gracilis*; *Jal = Jaltomata procumbens*; *Bsu = Brugmansia suaveolens*; *Cyb = Cyphomandra betacea*; *Pqu = Physalis queretaroensis*; *Csp = Cestrum* sp; *Sja = Solanum jasminoides*; *Cel = Cestrum elegans*; *Spe = Solanum appendiculatum*; *Psu = Physalis subrepens*; *Lyc = Lycianthes* aff. *lenta*; *Wit = Witheringia mexicana*; *Sal = Solanum aligerum*; *Ssc = Solanum schlechtendalianum*; *Sum = Solanum umbellatum*; *Cob = Cestrum oblongifolium*; *Ssk = Solanum skutchii*; *Sps = Solanum pseudocapsicum*; *Smy = Solanum myriacanthum*; *Sap = Solanum aphyodendron*; *Sch = Solanum chrysotrichum*; *Sni = Solanum nigrescens.*

as regards colour. Concerning the chiropterochoric species (36% of the total), fruit sizes varied from 8 to 35 mm, and 77.8% were green-yellow, 11% black, and the rest were categorised as any colour (Table 4). The mammaliochorous fruits were found at ground level and were usually coriaceous or had an expanded calyx. Comparing these syndromes between groups, it was found that in group I (less disturbed and more humid) ornithochory (45.8%) prevailed over the chiropterochory (33.5%) syndrome (Fig. 5B), whereas within group II, chiropterochory (50%) dominated ornithochory (31.3%). In spite of this, no significant differences were found between the syndromes of groups I and II ($G_{adj} = 0.875 < X^2_{0,05[3]} = 7.815$).

Discussion

Solanaceae composition and disturbance – In the present study, the 25 Solanaceae species reported exceeded the number forecast. Other studies recently conducted in the region recorded between 12 and 20 species, representing 3.6 to 4.6% of all vascular plants in the region (Luna *et al*. 1994; Mayorga *et al*. 1998). Solanaceae therefore represent 7.5% of the vascular plants in the region, which indicates the need for more detailed inventories covering both well-conserved and disturbed areas.

Most of the Solanaceae species in the study area have predominately shrub-like (60%) and herb-like (24%) habits. These species constitute part of the understory, confirming that these layers in the Mexican cloud forest are of Neotropical origin. This understory is shared with the Acanthaceae, Piperaceae, Rubiaceae, Myrsinaceae, Melastomataceae families, as well as with epiphytes and monocotyledonous taxa, coming from low elevations in the Andean region (Gentry 1982; Rzedowski 1978).

Despite the common origin, clear floristic differences in Solanaceae species were observed among the mountain cloud forest areas studied. Table 2 and Fig. 2A show that Solanaceae species were significantly split up to cut level 4, as seen from the large eigenvalues (l) obtained from the classification analysis. Similar floristic patterns have been observed in other groups, so changes in composition may indicate different environmental and ecological conditions (Luna *et al*. 1994; Mayorga *et al*. 1998). In addition to floristic differences, physiognomic discrepancies were also found among the areas. To illustrate this further, the Lontla and Apantlazol areas still retain most of their pristine character, comprising tall tree species (up to *ca*. 40 m in height) of *Magnolia schiedeana*, *Liquidambar macrophylla*, *Podocarpus reichei*, *Pinus patula* and *Cyathea* spp. (Luna *et al*. 1994). The rest of the areas comprised lower tree layers (up to 30 m in height) of *Liquidambar macrophylla*, *Cercis canadensis*, *Pinus patula*, *Dalbergia palo escrito* and *Podocarpus reichei* (Mayorga *et al*. 1998).

Likely environmental attributes to explain Solanaceae composition differences among areas were sought in this study. Of these, degree of disturbance was hypothesised as the major attribute governing Solanaceae species distribution. In this study, the ordination diagram (Fig. 4) showed clear distributions of species along axis I; this was inferred to be related to the degree of disturbance. The species *Solanum aligerum, S. pseudocapsicum* and *Cestrum elegans* were placed on the left side of the ordination diagram and are the differential species in the areas considered well conserved (Lontla and Apantlazol). In contrast, *Solanum rudepannum*, *S. schlechtendalianum* and *Cestrum oblongifolium* are the differential species in the areas categorised as largely disturbed (Lolotla and Tianguistengo) (Table 1) and these were placed on the right side of axis I. This axis, therefore, represents a clear gradient of disturbance.

It was observed that axis I (degree of disturbance) was closely related to a humidity gradient. As disturbance increased, relative humidity decreased, and vice versa. Disturbance (mainly man-made) favours changes in vegetation coverage and species abundance, implying microclimatic changes. Thus, more disturbed areas receive more sunlight and wind exposure, increasing evapotranspiration (Laurance *et al*. 1998), so that relatively less humidity remains. This depends on slope exposure since eastern slopes receive substantially more humidity than western slopes (Luna *et al*. 2001). In brief, both degrees of disturbance and relative humidity explain (48% of variance) the present distribution of Solanaceae in the study area. However, no attribute proved significantly correlated with axis II, so further research is recommended in order to gain insight into the current environmental attributes determining Solanaceae species distribution.

Pollination syndromes – As stated by Faegri & Van der Pijl (1980) and Dafni & Kevan (1997), floral morphological traits such as colour, shape, size and floral rewards are associated with the pollination syndrome and therefore with pollinator type. From the morphological floral traits of the Solanaceae species reported in this study, it was found that melittophily was the main pollination syndrome in all areas (Fig. 5A

Table 4. Morphological features of the Solanaceae species recorded in the Mexican mountain cloud forests of Hidalgo, Mexico. Hb = Habit: H = herb; S = shrub; V = vine; T = tree. Pas (pasture) = pasture edge; Ed = forest and road edges; Re = river edge. Syndromes: Meli. = Melittophily; Orni. = Ornithophily; Sph. = Sphingophily; Chiro. = Chiropterochory; Ornit. = Ornithochory; Mam. = Mammaliochory and Auto = Autochory. The asterisk (*) represents the months when the species was collected with flower and fruit during fieldwork. Flower and fruit orientation: erect (E), pendulous (P), reflexed (R), indistinct (I).

Species		Habitat			Height (cm)	Syndrome		
	Hb	Pas	Ed	Re	min-max	Polin	Disp	Inflorescence
Brugmansia suaveolens (Willd.) Bercht. & Presl	S		x		90-300	Sph.	Auto	Solitary
Cestrum elegans (Brongn.) Schltdl.	S		x	x	30-220	Orni.	Ornit.	Pseudoterminal cymes
Cestrum oblongifolium Schltdl.	S	x	x		20-450	Sph.	Ornit.	Pseudoterminal cymes
Cestrum sp.	S		x		40-50			
Cyphomandra betacea (Cav.) Sendtn.	S		x	x	50-250	Meli.	Chiro.	Lateral umbells
Jaltomata procumbens (Cav.) J.L. Gentry	H		x	x	50-110	Meli.	Ornit.	Lateral umbells
Lycianthes aff. *lenta* (Cav.) Bitter	S		x		80	Meli.	Ornit.	Lateral fascicles
Physalis gracilis Miers	H	x	x			Meli.	Mam.	Solitary
Physalis subrepens Waterf.	H		x	x		Meli.	Chiro.	Solitary
Physalis queretaroensis M. Martínez & L. Hernández	H	x	x			Meli.	Mam.	Solitary
Solanum aligerum Schltdl.	T		x	x	30-1000	Meli.	Ornit.	Pseudoterminal cymes
Solanum aphyodendron S. Knapp	S		x		10-250	Meli.	Chiro.	Lateral
Solanum appendiculatum Dunal	V		x			Meli.	Ornit.	Pseudoterminal cymose-paniculate
Solanum chrysotrichum Schltdl.	S		x	x	20-350	Meli.	Chiro.	Lateral
Solanum erianthum D. Don	S		x		60-200	Meli.	Chiro.	Terminal (at the beginning)
Solanum jasminoides Paxton.	V		x			Meli.	Ornit.	Pseudoterminal
Solanum myriacanthum Dunal	H	x	x	x	20-100	Meli.	Mam.	Lateral
Solanum nigrescens M. Mart. & Gal.	H		x	x	30-100	Meli.	Ornit.	Lateral pseudoumbells
Solanum nudum Dunal	S		x		100	Meli.	Chiro.	Lateral
Solanum pseudocapsicum L.	S		x		20-130	Meli.	Ornit.	Lateral
Solanum rudepannum Dunal	S		x		20-180	Meli.	Chiro.	Pseudoterminal (at the beginning)
Solanum schlechtendalianum Wap.	S		x	x	20-200	Meli.	Chiro.	Pseudoterminal (at the beginning)
Solanum skutchii Corr.	V		x	x		Meli.	Ornit.	Pseudoterminal cymose-paniculate
Solanum umbellatum Mill.	S		x		20-200	Meli.	Chiro.	Terminal (at the beginning)
Witheringia mexicana (Rob.) Hunz.	S		x		100-180	Meli.	Ornit.	Lateral

and Table 4). The prevalence of melittophily as the dominant pollination syndrome in this tropically dominated ecosystem is similar to the results reported in the cloud forests of Michoacán (Hernández & Carreón 1987) and Sierra Madre Oriental (L.M. Godínez, data not published). This corresponds with most tropically dominated environments where 94% of all pollinators are zoophilous (Reis *et al*. 1996; Murray *et al.* 2000).

In descending order, the pollination syndromes melittophily, sphingophily and ornithophily were present in all studied areas, among which no differences were observed (Fig. 5A). Similar pollinator assemblages have been reported elsewhere for Solanaceae (Endress 1994). Pollinators, in general, may influence reproductive success by determining the percentage of seeds set, and eventually influencing the effective size genetically (Fleming & Sosa 1994). It has been widely accepted that this kind of mutualism plays an important role in maintaining the ecosystem function (Howe & Smallwood 1982; Morellato & Leitão Filho 1992; Murray *et al.* 2000).

Seed dispersal syndromes – Fruit morphological traits also play an important role in defining the type of potential disperser (Van der Pijl 1972; Gautier-Hion *et al.* 1985). Solanaceae species in the mountain cloud forest study areas were preferentially characterised as zoochorous (92%). Solanaceae fruits in this study varied from pendulous to erect to reflexed types; colour varied from white to red; fruits from fleshy berries to

Table 4. (continuation) Morphological features of the Solanaceae species recorded in the Mexican mountain cloud forests of Hidalgo, Mexico. Hb = Habit: H = herb; S = shrub; V = vine; T = tree. Pas (pasture) = pasture edge; Ed = forest and road edges; Re = river edge. Syndromes: Meli. = Melittophily; Orni. = Ornithophily; Sph. = Sphingophily; Chiro. = Chiropterochory; Ornit. = Ornithochory; Mam. = Mammaliochory and Auto = Autochory. The asterisk (*) represents the months when the species was collected with flower and fruit during fieldwork. Flower and fruit orientation: erect (E), pendulous (P), reflexed (R), indistinct (I).

Species	Flower (type and orientation)	Fruit (size mm and orientation)	Fruit (colour and type) (⊙ = berry)	Flowering time (Nee 1986, 1993)
Brugmansia suaveolens (Willd.) Bercht. & Presl	Infundibuliform, (P)	100×20, (P)	Dry fruit	Apr-Nov
Cestrum elegans (Brongn.) Schltdl.	Tubular, (E)	8-13, (E)	Red⊙	all the year
Cestrum oblongifolium Schltdl.	Tubular, (E)	10, (E)	White⊙	Dec-Apr
Cestrum sp.				
Cyphomandra betacea (Cav.) Sendtn.	Campanulate, (P)	60-35, (P)	Yellow and/or purple⊙	all the year
Jaltomata procumbens (Cav.) J.L. Gentry	Rotate, (R)	8-12, (R)	Black⊙	all the year
Lycianthes aff. *lenta* (Cav.) Bitter	Rotate, (I)	8, (E)	Red⊙	all the year
Physalis gracilis Miers	Campanulate, (I)	8-15, (R)	Yellow⊙	all the year
Physalis subrepens Waterf.	Campanulate, (I)	8-12, (R)	⊙	Apr-Dec
Physalis queretaroensis M. Martínez & L. Hernández	Campanulate, (I)	5, (R)	⊙	May-Sept
Solanum aligerum Schltdl.	Rotate, (I)	10, (E)	Black⊙	all the year
Solanum aphyodendron S. Knapp	Rotate, (I)	10-12, (I)	Greenish and yellow⊙	all the year
Solanum appendiculatum Dunal	Rotate, (I)	8, (R)	Red⊙	Apr-May
Solanum chrysotrichum Schltdl.	Rotate, (I)	12-15, (I)	Greenish and yellow⊙	all the year
Solanum erianthum D. Don	Rotate, (E)	9-12, (E)	Yellow⊙	all the year
Solanum jasminoides Paxton.	Rotate, (I)	12, (R)	⊙	May*
Solanum myriacanthum Dunal	Rotate, (I)	20-30, (I)	Yellow⊙	Mar-Nov
Solanum nigrescens M. Mart. & Gal.	Rotate, (I)	7-10, (R)	Black⊙	Apr-Nov
Solanum nudum Dunal	Rotate, (I)	8-12, (I)	Yellow⊙	Mar-Nov
Solanum pseudocapsicum L.	Rotate, (R)	10-15, (E)	Orange⊙	Apr-Aug
Solanum rudepannum Dunal	Rotate, (I)	15, (I)	Greenish and yellow⊙	Aug-Apr
Solanum schlechtendalianum Wap.	Rotate, (R)	7-8, (E)	Black⊙	Feb-Oct
Solanum skutchii Corr.	Rotate, (I)	10, (R)	Red⊙	May-Oct
Solanum umbellatum Mill.	Rotate, (E)	8-11, (E)	Greenish and yellow⊙	Apr-Nov (Jul-Sept)
Witheringia mexicana (Rob.) Hunz.	Rotate, (E)	8, (E)	Red⊙	May-Sept*

capsules; sizes were generally small (<15 mm), as shown in Table 4. Van der Pijl (1972), Charles-Dominique (1986), Janson (1992) and Korine *et al*. (1998) have reported similar results.

Ornithochory and chiropterochory were found to be the main seed dispersal syndromes in all areas, where equivalent proportions of each were recorded (Fig. 5B). In general, Solanaceae species (e.g. most species of *Cestrum* and *Solanum*) are well known for their strong leaf scents. This has been recognised as a major bat attraction, favouring fruit consumption and in consequence seed dispersal (Nee 1993). In our study, it was frequently observed that bats dispersed green, yellow and black fruits (e.g. *Solanum rudepannum*, *S. schlechtendalianum* and *S. aligerum*) – colours with strong scents coming from their leaves.

While comparing seed dispersal syndromes among areas, no significant differences were found (Fig. 5B). Ornithochory, however, was detected as the prevailing syndrome in the less disturbed and more humid areas represented by group I (45.8% ornithochory and 33.3% chiropterochory). Conversely, in the more disturbed and less humid areas of group II chiropterochory (50%) prevailed over ornithochory (31.3%). It has been documented that a larger disturbance may be expressed as a clear dominance of chiropterochory in Solanaceae (e.g. Vázquez-Yanes *et al*. 1975; Fleming & Sosa 1994; Da Silva *et al*. 1996; Galindo-González 1998; Medellín & Gaona 1999).

This study showed that birds and bats play an important role in the distribution of Solanaceae, since these are potentially the most likely dispersers. For instance, Da Silva *et al*. (1996) demonstrated that *ca.* 40% of bird species moved some 50 to 150 m away

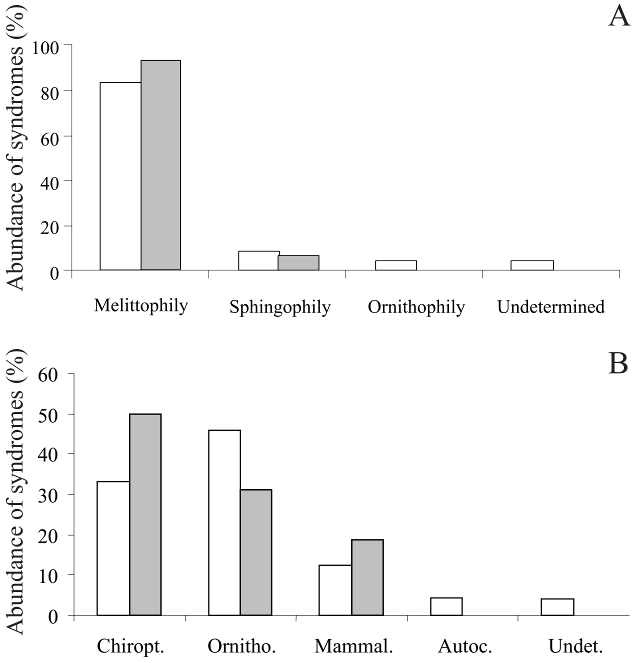

Figure 5. (A) Pollination and (B) seed dispersal syndromes of Solanaceae in the Mexican mountain cloud forest fragments studied (Chiropt. = Chiropterochory; Ornitho. = Ornithochory; Mammal. = Mammaliochory). Group I (☐) = less disturbed and more humid; Group II (■) = more disturbed and less humid.

from forest edges towards pasturelands. At these edges, a particular syndrome may be favoured and as a consequence colonisation may be promoted. Bats too may possibly play an important role in early successional stages, favouring the species establishment of Solanaceae, among other families, along open areas (Willing & Gannon 1996). This is because bats usually feed on Solanaceae and other ruderal species along paths and forest edges, places considered as feeding routes.

It has been documented that zoochory (chiefly ornithochory and chiropterochory) is fundamental in favouring restoration processes in disturbed open areas such as abandoned pasturelands and roads (Bohs 1994; Da Silva *et al*. 1996; Miriti 1998; Nepstad *et al*. 1998). Frugivores diversify their diet by consuming a variety of fruits and, accordingly, spread a pool of seeds over these open areas. In consequence, seed banks are enriched and colonisation and regeneration favoured. This shows that Solanaceae, as a pioneer group, may play a relevant role as colonisers and therefore restoration agents, favouring the establishment of other plants and promoting soil fertility (Baider *et al*. 1999). The large number of habitats and reproductive strategies of Solanaceae observed in the present study confirms their ecological role as colonisers. In this process, Solanaceae are considered as key taxa in open areas. Furthermore, Solanaceae also favour alternative fruit consumption. Once their fruits have been eaten, secondary compounds limit frugivory (Cipollini & Levey 1997a; 1997b; 1997c) and may promote the search for alternative food sources. The medium- and long-term consequences are that consumers eat and disperse a greater diversity of seeds as Solanaceae consumption increases, thus promoting seed-bank enrichment. These effects are yet to be researched in Neotropical solanaceous species.

Implications for management and conservation – Angiosperms have diversified as a consequence of seed dispersal by animals (zoochory) (Tiffney 1984). It has been proved that, compared with pollination, seed dispersal doubles genetic exchange (Hamrich & Nason 1996). Hence, current landscape patterns, to a large extent determined by vegetation communities (Farina 1998), ought to be influenced by seed dispersal (Sinha & Davidar 1992). To illustrate this further, recent studies highlight the lack of seeds in pasturelands compared with forest edges. Da Silva *et al*. (1996) mentioned that animals disperse seeds into small clearings, but seed dispersal decreases as clearing size increases and this retards plant succession. In addition, Tabarelli *et al*. (1999) found that in Atlantic forest (similar conditions to those studied here) Compositae, Euphorbiaceae, Solanaceae and Leguminosae increased as the forest area decreased. When these taxa prevail, a good chance of re-vegetation remains (Rodrigues & Gandolfi 1996). Solanaceae flowers and fruits are available throughout the year, so this family is considered as a trigger group for successional and regeneration processes (Bohs 1994; Da Silva *et al*. 1996; Tabarelli *et al.* 1999). This is especially relevant at landscape level, where birds and bats transport Solanaceae seeds across forest edges.

Birds and bats take an active part in the formation of seed dispersal corridors. Seed dispersal corridor can be defined as a narrow functional belt that limits forest edges, increases connectivity and functions as a route mainly for birds and bats where they spread seed pools within a mosaic. Hence, a seed dispersal corridor allows genetic flow and consequently maintains forest dynamics. Solanaceae in particular offer floral rewards and fruits throughout the year. In the long run, these species favour landscape stability. The threshold for reaching this stage of stability in Mexican mountain cloud forest has yet to be ascertained.

In conclusion, disturbance favours changes in vegetation coverage and species abundance, implying microclimatic changes, as when the disturbance increased, relative humidity decreased. Therefore, the gradients of Solanaceae species' distribution are firstly associated to the disturbance degree and, secondarily, to the humidity gradient. Within these conditions, some species can be considered as indicative of less disturbance and more humidity conditions, as *Solanum aligerum*, *S. pseudocapsicum*, *Cestrum elegans*, while others, for instance, *Cestrum oblongifolium*, *Solanum rudepannum*, *S. schlechtendalianum* are indicative of more disturbance and less humidity. However, the Solanaceae pollination syndromes are not related to the disturbance degree, but to the pattern of tropical species pollination (zoophily). In relation to seed dispersal syndromes among areas, no significant differences were found, although, ornithochory was detected as the prevailing syndrome in the less disturbed and more humid areas. On the other hand, chiropterochory prevailed over ornithochory in the more disturbed and less humid areas. Besides, the tendency that larger disturbances may be expressed as a clear dominance of chiropterochory in Solanaceae has already been documented (e.g. Vázquez-Yanes *et al*. 1975; Fleming & Sosa 1994; Da Silva *et al*. 1996; Galindo-González 1998; Medellín & Gaona 1999).

To summarise, wild Solanaceae species play a relevant role by favouring the colonisation of open areas and, consequently, in forest regeneration processes. In addition, this group attracts wildlife by offering floral rewards and fruits throughout the year. Finally, Solanaceae facilitates connectivity among forest patches by means of seed dispersal corridors. Their conservation is important since a large number of species provide both known and as yet unknown services for human beings. Future research along this line is therefore recommended.

Acknowledgements

We would like to thank to CAPES for the PhD scholarship awarded to the first author. UNAM (Mexico) and UNICAMP (Brazil) provided logistic and academic support throughout the study. We would also like to acknowledge the contribution of R. Dirzo, M. Cipollini and J. Vasconcellos-Neto in improving an earlier version, as well as the editorial comments of I. Luna.

References

Akwood, M.O.; Jurado, E.; Leishman, M. & Westoby, M. 1993. Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. **Journal of Biogeography 20**: 563-572.

Alcantara, O.; Luna I. & Velázquez, A. 2002. Distribution patterns of Mexican cloud forests based upon preferential characteristic genera. **Plant Ecology 161**: 167-174.

Baider, C.; Tabarelli, M. & Mantovani, W. 1999. O banco de sementes de um trecho de floresta atlântica montana (São Paulo, Brasil). **Revista Brasileira de Biología 59**(2): 319-328.

Barroso, G.M.; Peixoto, A.L.; Ichaso, C.L.F.; Costa, C.G.; Guimarães, E.F. & Lima, H.C. 1991. **Sistemática de Angiospermas do Brasil**. v.3. Viçosa, Universidade Federal de Viçosa.

Bohs, L. 1994. **Flora Neotropica. Monograph 63: *Cyphomandra* (Solanaceae)**. New York, The New York Botanical Garden.

Challenger, A. 1998. **Utilización y conservación de los ecosistemas terrestres de México: pasado, presente y futuro**. Mexico, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guinea. Pp. 119-135. In: A. Estrada & T.H. Fleming (eds.). **Frugivory and seed dispersal**. Junk, Dordrecht.

Cipollini, M. & Levey, D.J. 1997a. Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. **Ecology 78**: 782-798.

Cipollini, M. & Levey, D.J. 1997b. Antifungal activity of *Solanum* fruit glycoalkaloids: implications for frugivory and seed dispersal. **Ecology 78**: 799-809.

Cipollini, M. & Levey, D.J. 1997c. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. **American Naturalist 150**: 346-372.

Conabio & Estadigrafia. 1997a. **Carta de climas México. Sistema de Köppen modificado por E. García. Escala 1:1,000,000**. Mexico, CONABIO/ESTADIGRAFIA.

Conabio & Estadigrafia. 1997b. **Mapas de Clima: precipitación total annual México. Escala 1:1,000,000**. Mexico, CONABIO/ESTADIGRAFIA.

Dafni, A. & Kevan, P.G. 1997. Flower size and shape: implications in polinations. **Israel Journal of Plant Scienses 45**: 201-211.

D'Arcy, W.G. 1986. **Taxonomy and biogeography. Solanaceae biology and systematics**. W.G. D'Arcy (ed.). New York, Columbia University Press.

Da Silva, J.M.C.; Uhl, C. & Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. **Conservation Biology 10**: 491-503.

Endress, P.K. 1994. **Diversity and evolutionary biology of tropical flowers**. UK, Cambridge University Press.

Evans, W.C. 1986. **Hybridization and secondary metabolism in the Solanaceae. Solanaceae biology and systematics**. W.G. D'Arcy (ed.). New York, Columbia University Press.

Faegri, K. & Van der Pijl, L. 1980. **The Principles of Pollination Ecology**. New York, Pergamon Press.

Farina, A. 1998. **Principles and methods in landscape ecology**. London, Chapman & Hall.

Fleming, T.H. & Sosa, V.J. 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. **Journal of Mammalogy 75**: 847-851.

Galindo-González, J. 1998. Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. **Acta Zoologica Mexicana 73**: 57-74.

García, E. 1981. **Modificaciones al sistema de clasificación climática de Köppen**. México, D.F., Instituto de Geografía, Universidad Nacional Autónoma de México.

Gautier-Hion, A.; Duplantier, J.M.; Quris, R.; Feer, F.; Sourd, C.; Decoux, J.P.; Dubost, G.; Emmons, L.; Erard, C.; Heckestsweiler, P.; Moungazi, A.; Roussilhon, C. & Thiollay, J.M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. **Oecologia 65**: 324-337.

Gentry, A.H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations or an accident of the Andean Orogeny? **Annals of the Missouri Botanical Garden 69**: 557-593.

Gorchov, D.L.; Cornejo, F.; Ascorra, C. & Jaramillo, M. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. **Frugivory and seed dispersal: ecological and evolutionary aspects**. Pp. 339-349. (T.H. Fleming & A. Estrada, eds.). Belgium, Kluwer Academic Publishers.

Hamrich, J.L. & Nason, J.D. 1996. Consequences of dispersal in plants. In: O.E. Rhodes; R.K. Chesser Jr. & M.H. Smith (eds.). **Population dynamics in ecological space end time**. Chicago, University of Chicago Press.

Hegde, S.G.; Ganeshaiah, K.N. & Shaanker, U. 1991. Fruit preference criteria by avian frugivores: their implications for the evolution of clutch size in *Solanum pubescens*. **Oikos 60**: 20-26.

Hernández, H. & Carreón, Y. 1987. Notas sobre la ecología de árboles en un bosque mesófilo de montaña en Michoacán, México. **Boletin de la Sociedad Botánica de México 47**: 5-35.

Herrera, C. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. **Oikos 44**: 132-141.

Hill, M.O. 1979. *TWINSPAN – a FORTRAN* **Program for arranging multivariate data in an ordered two way Table by classification of the individuals and the attributes**. New York, Cornell University, Department of Ecology and Systematic, Ithaca.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. **Annals Review of Ecology and Systematics 13**: 201-228.

Hunziker, A.T. 1969. Estudios sobre Solanaceae. V: Contribucion al conocimiento de *Capsicum* y géneros afines (*Witheringia*, *Acnistus*, *Athenaea*, Exc.). **Kurtziana 5**: 101-179.

Hunziker, A.T. 1979. South American Solanaceae: a synoptic survey. **The biology of the Solanaceae** (J.G. Hawkes; R.N. Lester & A.D. Skelding, eds.). London, Linnean Society Symposium Series/Academic Press.

Janson, C.H. 1992. Measuring evolutionary constraints: a Markov model for phylogenetic transitions among seed dispersal syndromes. **Evolution 46**(1): 136-158.

Knapp, S. 1985. New species of *Solanum* section *geminata* (G. Don) Walp. (Solanaceae) from South and Central America. **Annals of the Missouri Botanical Garden 72**: 558-569.

Korine, C.; Izhaki, I. & Arad, Z. 1998. Comparison of fruit syndromes between the Egyptian fruit-bat (*Rousettus aegyptiacus)* and birds in East Mediterranean habitats. **Acta Oecologica 19**(2): 147-153.

Laurance, W.F.; Ferreira, L.V.; Rankin-de-Merona, J.M.; Laurance, S.G.; Hutchings, R. & Lovejoy, T. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. **Conservation Biology 12**: 460-464.

Luna, I.; Ocegueda, S. & Alcantara, O. 1994. Florística y notas biogeográficas del bosque mesófilo de montaña del municipio de Tlanchinol, Hidalgo, México. **Anales del Istituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica 65**: 31-62.

Luna, I.; Velázquez A. & Velázquez E. 2001. Los bosques mesófilos de México. Pp. 183-229. In: M. Kappelle & A. Brown (eds.). **Bosques nublados del Neotrópico**. Instituto Nacional de Biodiversidad (INBio), Fundación Agroforestal del Noroeste de Argentina (FUA), World Conservation Union (IUCN), University of Amsterdam (IBED-UvA), Laboratorio de Investigaciones Ecológicas los Yungas de Argentina (LIEY). Costa Rica, INBio Press. Santo Domingo de Heredia.

Martínez, M. & Hernandez, L. 1999. Una nueva espécie de *Physalis* (Solanaceae) de Queretaro, México. **Acta Botanica Mexicana 46**: 77-81.

Mayorga, R.; Luna, I. & Alcantara, O. 1998. Florística del bosque mesófilo de montaña de Molocotlán, Molango-Xochicoatlán, Hidalgo, México. **Boletin de la Sociedad Botánica de México 63**: 101-119.

McCune, B. & Mefford, M.J. 1995. *PC-ORD.* **Multivariate Analysis of Ecological Data, Version 2.0.** USA, MjM Software Design, Gleneden Beach, Oregon.

Medellín, R.A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, México. **Biotropica 31**: 478-485.

Miriti, M.N. 1998. Regeneração florestal em pastagens abandonadas na Amazônia central: competição, predação e dispersão de sementes. Pp. 179-190. In: C. Gascon & P. Moutinho (eds.). **Floresta Amazônica: dinâmica, regeneração e manejo**. Manaus, Ministério Ciência e Tecnologia/INPA.

Morellato, P.C. & Leitão Filho, H.F. 1992. A flora arbórea da Serra do Japi. Pp. 112-141. In: P.C. Morellato (ed.). **História Natural da Serra do Japi: ecologia e preservação de uma Area Florestal no Sudeste do Brasil**. Campinas, São Paulo, Editora da Unicamp/Fapesp.

Murray, K.G.; Kinsman, S. & Bronstein, J.L. 2000. Plant-animal interactions. Pp. 245-302. In: N.M. Nadkarni & N.T. Wheelwright (eds.). **Monteverde: ecology and conservation of a Tropical Cloud Forest**. New York, Oxford University Press.

Navarro, A.G. 1992. Altitudinal distribution of birds in the

Sierra Madre del Sur, Guerrero, Mexico. **The Condor 94**: 29-39.

Nee, M. 1986. **Flora de Veracruz: Solanaceae I**. Mexico, Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa.

Nee, M. 1993. **Flora de Veracruz: Solanaceae II**. Riverside, CA, Instituto de Ecologia, Xalapa, Mexico, and University of California.

Nepstad, D.C.; Uhl, C.; Pereira, C.A. & Silva, J.M.C. 1998. Estudo comparativo do estabelecimento de árvores em pastos abandonados e florestas adultas da Amazônia oriental. Pp. 191-218. In: C. Gascon & P. Moutinho (eds.). **Floresta Amazônica: dinâmica, regeneração e manejo**. Manaus, Ministério Ciência e Tecnologia/INPA.

Reis, A.; Nacazono, E.M. & Matos, J.Z. 1996. Utilização da sucessão e das interações planta-animal na recuperação de áreas florestais degradadas. Pp. 29-36. In: **Recuperação de Áreas Degradadas III Curso de Atualização UFPR**. Curitiba, Fundação de Pesquisas Florestais do Paraná.

Rodrigues, R.R. & Gandolfi, S. 1996. Recomposição de florestas nativas. Princípios gerais e subsídios para uma definição metodológica. **Revista Brasileira de Horticultura Ornamental 2**: 4-15.

Rzedowski, J. 1978. **Vegetación de México**. Limusa, Mexico.

Rzedowski, J. 1996. Análisis preliminar de la flora vascular de los bosques mesófilos de montaña de México. **Acta Botánica Mexicana 35**: 25-44.

Rzedowski, J. & Rzedowski, G.C. 1985. **Flora Fanerogámica del Valle de México**. v. II. Mexico, Instituto de Ecología, A.C.

Sinha, A. & Davidar, P. 1992. Seed dispersal of a wind dispersed rain forest tree in the Western Ghats, India. **Biotropica 24**: 519-525.

Sokal, R.R. & Rohlf, F.J. 1998. **Biometry**. New York, W.H. Freeman.

SPP (Secretaría de Programación y Presupuesto). 1983. **Carta edafológica Pachuca F14-11, Escala 1:250000, México**.

Standley, C.P. 1924. **Trees and shrubs of Mexico**. USA, Contribution of National Herbarium.

Standley, P.C. & Williams, L.O. 1973. **Flora of Guatemala**. Fieldiena, Botany.

Symon, D.E. 1979. Fruit diversity and dispersal in *Solanum* in Australia. **Journal of the Adelaide Botanical Garden 1**: 321-331.

Tabarelli, M.; Mantovani, W. & Peres, C.A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. **Biological Conservation 91**: 119-127.

Tamboia, T.; Cipollini, M.L. & Levey, D.J. 1996. An evaluation of vertebrate seed dispersal syndromes in four species of black nightshade (*Solanum* sect. *Solanum*). **Oecologia 107**: 522-532.

Terborgh, J. & Robinson, S. 1986. Guilds and their utility in ecology. Pp. 65-90. In: J.E. Kikkawa & D. Anderson (eds.). **Community ecology: pattern and process**. London, Blackwell Scientific Publications.

Tiffney, B.H. 1984. Seed size, dispersal syndromes, and the rise of angiosperms: evidence and hypothesis. **Annals of the Missouri Botanical Garden 71**: 551-576.

Van der Pijl, L. 1972. **Principles of dispersal in higher plants**. New York, Editora Springer-Verlag.

Vázquez-Yanes, C.; Orozco, A.; François, G. & Trejo, L. 1975. Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. **Biotropica 7**: 73-76.

Velázquez, A. 1994. Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico. **Journal of Vegetation Science 5**: 263-270.

Waite, S. 2000. **Statistical ecology in practice. A guide to analysing environmental and ecological field data**. England, Prentice Hall.

Waterfall, U.T. 1967. *Physalis* in Mexico, Central America and the West Indies. **Rhodora 69**: 82-329.

Williams, D.E. 1993. *Lycianthes monziniana* (Solanaceae): an underutilized Mexican food plant with "new" crop potential. **Economic Botany 47**: 387-400.

Williams-Linera, G. 1993. Vegetación de bordes de un bosque nublado en el parque ecológico Clavijero, Xalapa, Veracruz, México. **Revista de Biología Tropical 41**(3): 443-453.

Willing, M.R. & Gannon, M.R. 1996. Mammals. Pp. 398-431. In: D.P. Reagan & R.B. Waide (eds.). **The food web of a Tropical Rain Forest**. Chicago and London, The University of Chicago Press.

Wilson, M.F.; Irvine, A.K. & Walsh, N. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. **Biotropica 21**: 133-147.