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Influence of plant abundance on disease incidence in a Mexican tropical forest¹

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Abstract: In this paper we investigate to what extent the occurrence of foliar diseases is affected by plant relative abundance in the understory community of the Los Tuxtlas tropical rain forest, how this changes with season of the year, and how plant species with different life histories present at the understory are affected by disease. To provide a context to these analyses we also include a general description of the floristic composition of the understory community. Using the eight most common species, we found that their relative abundance in each sampling location significantly explained the proportion of diseased plants. Accordingly, using the relative abundance of all plant species, we found that the probability of a host plant species being free of infection showed a significant decrement with abundance. At the plant level, we found that relative abundance had the greatest effect on the variation in leaf area/plant affected by pathogens, although the proportion of explained deviance was only 12%. Seasonality did not affect disease incidence and disease levels per plant. Throughout the year, plant relative abundance was very much lower in lianas, tree seedlings, and palms than in perennial herbs and ferns, and disease incidence was very much higher in the latter two, the most abundant life forms. These results collectively suggest that both intraspecific and interspecific variation in plant relative abundance explain variation in leaf damage by pathogenic fungi in tropical forest understories.

Keywords: leaf pathogens, plant abundance, Los Tuxtlas, tropical rain forest.

Résumé : Dans cette étude, nous avons examiné dans quelle mesure l'abondance relative des plantes en sous-étage dans la forêt tropicale de Los Tuxtlas influence l'incidence de maladies des feuilles. Nous avons aussi examiné si l'incidence de maladies change avec les saisons et comment les espèces de plantes du sous-étage forestier ayant différentes histoires de vie sont affectées par les maladies. Afin de mettre ces analyses en contexte, nous incluons également une description générale de la composition floristique de la communauté du sous-étage forestier. En utilisant les huit espèces les plus communes, nous avons déterminé que leur abondance relative à chaque site d'échantillonnage expliquait de façon significative la proportion de plantes malades. Ainsi, en utilisant l'abondance relative de toutes les espèces de plantes présentes, nous avons observé que la probabilité qu'une plante hôte soit non infectée diminuait significativement avec son abondance. Au niveau de la plante individuelle, nous avons trouvé que c'est l'abondance relative qui avait le plus d'effet sur la variation de la superficie des feuilles par plante infectée par des pathogènes même si la proportion de la variation expliquée était seulement de 12%. La saison n'avait pas d'effet sur l'incidence de maladies et le niveau d'infection par plante. Tout au long de l'année, l'abondance relative des lianes, des semis d'arbres et des palmiers était beaucoup plus faible que celle des herbes pérennes et des fougères et l'incidence de maladies était beaucoup plus élevée chez ces deux dernières formes de vie les plus abondantes. L'ensemble de ces résultats suggèrent qu'à la fois la variabilité intraspécifique et interspécifique dans l'abondance relative des plantes expliquent la variation du niveau de dommage des feuilles par des champignons pathogènes dans les communautés du sous-étage forestier tropical.

Mots-clés : abondance des plantes, forêt tropicale, Los Tuxtlas, pathogènes de feuilles.

Nomenclature: Ibarra-Manríquez & Sinaca-Colín, 1987.

Introduction

Several aspects of the abiotic and biotic environment, acting singly or in combination, have a profound effect on the spatial occurrence and severity of plant diseases (Burdon, Jarosz & Kirby, 1989). For example, soil fungal pathogens kill fewer tree seedlings in gaps than in the shaded understory of a tropical forest (Wenny, 2000). Likewise, biotic factors such as plant density (Burdon & Chilvers, 1982), competition between pathogens (Daamen & Stol, 1990), and the presence of particular plant species (García-

Guzmán & Wennström, 2001) have been shown to influence the incidence of plant diseases in a wide range of natural systems. Surprisingly, the influence of plant abundance and species composition on pathogenic incidence has been poorly explored in natural systems, although a few limited studies indicate that differences in both the number of host plants available for pathogens and host plant spatial distribution affect the establishment and spread of disease among plants in temperate ecosystems (Burdon & Chilvers, 1982).

In species-rich ecosystems, such as tropical rain forests, dispersal of pathogens with some degree of specificity for a host-plant species may be restricted by the low abundance of a potential host-plant species (Burdon, 1978; May, 1991; Gilbert & Hubbell, 1996). However, observations in a species-rich tropical rain forest at Los Tuxtlas, Mexico suggest

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that *ca* 60% of plant species in the understory community exhibit leaf spots caused by fungal pathogens (García-Guzmán & Dirzo, 2001). The floor of this forest is densely covered by extensive carpets of high-density tree seedlings, frequently near parent trees of several species (see Dirzo & Miranda, 1990), or by high-density patches of herbaceous plants (García-Guzmán & Dirzo, 2001). Such high plant seedling density can alter local environmental factors that favour disease development (*e.g.*, increased humidity and temperature) as well as increase disease spread through greater host–pathogen encounter rates (Burdon & Chilvers, 1982). In addition, given that environmental factors such as temperature and humidity change with time of the year, it is possible that the effects of plant density will covary with season of the year. Environmental conditions are known to be particularly favourable for the attack of crop plants by different types of pathogens in the wet season of the year (Waller, 1976; Agrios, 1997), and they may also influence disease incidence in the case of leaf pathogens, but this has not been studied in tropical natural systems. On the other hand, plant life history could be another important source of variation in pathogenic incidence. For example, attack could be lower in short-lived, ephemeral species (*e.g.*, annual herbs) than in long-lived, persistent species (*e.g.*, tree seedlings or lianas). The degree of fungal pathogen dependence on living host plants for reproduction and survival varies among pathogenic species; thus, short-lived plant species might be more affected by pathogens characterized by short life-cycles (like many ascomycetes, rusts, and powdery mildews), while long-lived plant species could also be affected by pathogens with longer life cycles that keep an intimate association with their hosts plants (*e.g.*, obligate fungal pathogens; García-Guzmán *et al.*, 1996). Therefore, variation in plant species composition and relative representation of different plant life histories across seasons could have strong implications for the incidence of infection on plants from tropical understories.

The understory community of the Los Tuxtlas forest is commonly affected by fungal leaf pathogens (García-Guzmán & Dirzo, 2001). In this paper we investigate to what extent the occurrence of foliar diseases is affected by host plant relative abundance (in terms of plant species and life form) and how this changes with season of the year. The specific questions we asked were (*i*) does plant abundance influence the proportion of diseased plants and the amount of per-plant leaf area damaged by pathogens? (*ii*) is there variation in the incidence of disease depending on plant life form? and (*iii*) is there a seasonal effect on the relationships between plant abundance and pathogenic infection? We investigated these questions in the context of possible changes in the floristic diversity of the understory plant community in both seasons of the year in order to assess if the answer to our questions would be influenced by seasonal variation in floristic composition and life form representation.

Methods

STUDY AREA

The study was conducted in the forest of Los Tuxtlas Biological Station, 34 km north of the town of Catemaco

Veracruz, Mexico (18° 34' to 18° 36' N, 95° 04' to 95° 09' W) (see details in Dirzo, González & Vogt, 1997). Mean monthly temperature is 27 °C, ranging from mean temperatures of 17 °C (January) to 29 °C (June). Total mean annual rainfall is 4750 mm, with a relatively dry season from April to the end of May. The rainy season extends from June to mid February (Soto & Gama, 1997). The vegetation of the area, tropical rain forest (Ibarra-Manríquez *et al.*, 1997; Pennington & Sarukhán, 1998), is characterized by the presence of evergreen vegetation with trees exceeding 35 m. The forest understory is composed of herbaceous plants and seedlings and saplings of trees, shrubs, lianas, and palms (Dirzo *et al.*, 1992; Ibarra-Manríquez *et al.*, 1997).

PLANT RELATIVE ABUNDANCE

We assessed the effect of plant relative abundance on the incidence and levels of damage by leaf fungal pathogens in four independent sampling sites in mature forest at Los Tuxtlas. In each site a sampling plot was established using a 50-m north–south straight line. Along the line, 10 points were selected to establish 5-m-long transects, perpendicular to the central line. Their position (right or left of the 50-m line) and distance from the origin were randomly selected. The survey of plants within the transects was carried out using a variation of the point-quadrat technique for sampling species composition and coverage (Greig-Smith, 1983). Along each transect we located 25 points by the random positioning of a descending needle; the first plants or ramets, less than 1 m in height touched by the tip of the needle were recorded, and all their leaves were collected for subsequent analysis of pathogen damage and isolation of the causal agents of damage (Figure 1; García-Guzmán & Dirzo, 2001). The survey was carried out in April (dry season) and November (rainy season), with sampling plots independently established in each season. Relative plant abundance was assessed in terms of cover as the proportion of the total number of random points per site (250 points) intercepted by a species (Greig-Smith, 1983). Sample sizes of plant species were too small to reliably test disease incidence for each transect separately; therefore, abundance analysis are presented for four sites in each season of the year.

ASSESSMENT OF LEAF DAMAGE

Each sampled plant was carefully analyzed to determine evidence of fungal attack (*e.g.*, leaf spots with spores or other fungal structures growing on the surfaces of the leaves). Estimates of the standing levels of area lost to fungal pathogens per plant were determined by assigning leaves of each plant to one of the following categories of damage: 0 = intact; 1 = 1–6%; 2 = 6–12%; 3 = 12–25%; 4 = 25–50%; and 5 = 50–100% of leaf area damaged. The percentage of leaf area damaged was assessed visually, and an index of damage (*ID*) (Kremer & Unterstenhöfer, 1967; Dirzo & Domínguez, 1995) was obtained with the following formula:

$$ID = \sum_{i=1}^5 n_i(C_i) / N$$

where n_i is the number of leaves in i th category of damage, C_i is the midpoint of each category (i.e., $C_1 = 3.5\%$, $C_2 = 9\%$, $C_3 = 18.5\%$, $C_4 = 37.5\%$, and $C_5 = 75\%$ respectively), and N is the total number of leaves per plant. To simplify data presentation, the values of the ID were converted to percentage of leaf area damaged per plant. Phytopathological techniques were used to isolate and identify the causal agents of the observed disease symptoms, based on Koch's principles. Fungi were identified based on morphological characters (see García-Guzmán & Dirzo, 2001 for methods and description of morphotypes).

RELATIONSHIP BETWEEN PLANT ABUNDANCE AND DISEASE INCIDENCE IN RAINY AND DRY SEASONS

The effect of plant relative abundance on disease incidence for eight of the most abundant plant species in the understory community of Los Tuxtlas was analyzed using logarithmic regression analysis. The response variables were the proportion of diseased plants and the proportion of leaf area affected by pathogens per plant. The independent variable was plant relative abundance per transect at the four forest sites in both the dry and rainy seasons.

To assess the effect of abundance and seasonal variation on disease incidence analyses of variance (ANOVA) were used. The response variables, proportion of diseased plants, and proportion of leaf area damaged per plant were arcsin transformed prior to analysis to meet the assumptions of the ANOVA.

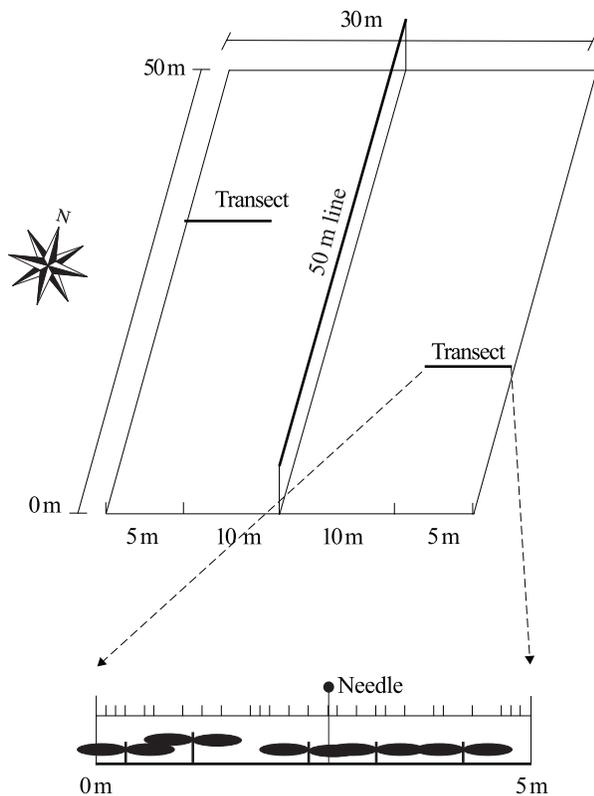


FIGURE 1. Diagram of the sampling protocol used to assess disease incidence at the understory community level in four forest sites of the evergreen rain forest of Los Tuxtlas.

Results

PLANT COMMUNITY

We begin by describing field surveys that analyzed possible changes in plant and species number depending on the season of the year. Throughout the year, herbs from the Araceae family were among the most important components of the understory community (Table I). In the dry season survey, 49 plant species from 23 families and 620 individual plants were observed. In the four forest sites, mean plant relative abundance ranged from 0.4 to 26 plants per site, with *Anthurium flexile*, *Monstera acuminata*, and *Nectandra ambigens* being the most abundant species. During the rainy season survey 57 plant species from 27 families and 483 individuals were found. In this season, mean plant relative abundance ranged from 0.4 to 24.4 individuals per site, essentially the same range as in the dry season. The most abundant species were *Syngonium podophyllum*, *Rhodospatha wendlandii*, and *Anthurium flexile* (Table I). The distribution of the plant species surveyed in both seasons among life forms revealed the presence of ferns, perennial herbs, perennial shrubs, and seedlings of palms, shrubs and trees. Our analysis indicates that 55% of the species surveyed during the year (both seasons) were tree seedlings and 26% were perennial herbs, mainly from the Araceae family (Figure 2), but the relative representation of species among different life forms was not statistically different ($\chi^2 = 1.26$; $P > 0.05$). Therefore, we do not expect that the differences in floristic composition will have an important impact on the incidence of disease.

DISEASE INCIDENCE

Pathogen damage was evident in 64.5% (rainy season) and 65.3% (dry season) of all sampled plant species and in 50.8% (dry season) and 65.4% (rainy season) of all sampled individual plants (Table II). During the dry season, plants were attacked collectively by 53 fungal morphotypes, and in the rainy season a total of 60 fungal morphotypes with morphologically distinguished mycelia and spores were detected. These fungi (Ascomycetes) caused leaf spots of different colours and shapes in their host plants (see García-Guzmán & Dirzo, 2001 for further details).

In both seasons of the year, disease incidence was significantly higher among ferns than in the other plant life forms ($F_{5,48} = 3.39$; $P > 0.01$ and $F_{5,56} = 10.66$; $P > 0.0001$ dry and rainy seasons, respectively; Table III). However, no significant differences in the proportion of leaf area affected per plant among plant life forms were detected ($P > 0.05$).

The statistical analysis showed that of the two variables considered, seasonality and abundance, plant relative abundance had the greatest effect on the proportion of diseased plants ($F_{3,105} = 458.39$; $P > 0.0001$), explaining 79% of the total variance. The season of the year and the interaction term (season \times plant relative abundance) were not significant ($P > 0.05$). Similarly, plant relative abundance had the greatest effect on the proportion of leaf area per plant affected by pathogens ($F_{3,105} = 28.12$; $P > 0.0001$), although this only explained 12% of the total variance. The season of the year and the interaction term (season \times plant relative abundance) were not significant ($P > 0.05$) for this variable either.

TABLE I. List of the plant species sampled during the dry and rainy seasons, including percentage of plant relative abundance, proportion of diseased plants, and leaf area damaged per plant for the dry and rainy seasons.

Plant species	Plant relative abundance (%)	Diseased plants (%)	Leaf area damaged per plant (%)	Plant species	Plant relative abundance (%)	Diseased plants (%)	Leaf area damaged per plant (%)
DRY SEASON							
Acanthaceae				Rubiaceae			
<i>Aphelandra aurantiaca</i>	14.4	1.2	1.085	<i>Faramea occidentalis</i>	2.0	0.4	1.015
<i>Odontonema callistachyum</i>	1.6	0	0	<i>Psychotria faxlucens</i>	1.2	0	0
<i>Schaueria calycobracteata</i>	2.0	0	0	<i>Randia pterocarpa</i>	1.2	0	0
Annonaceae				Sapindaceae			
<i>Cymbopetalum baillonii</i>	4.0	0	0	<i>Cupania glabra</i>	0.4	0	0
Araceae				<i>Paullinia clavigera</i>			
<i>Anthurium flexile</i>	26.0	6.4	2.765	<i>Ulmaceae</i>			
<i>Anthurium pentaphyllum</i>				<i>Ampelocera hottlei</i>	3.2	0.4	3.500
var. <i>bombacifolium</i>	16.8	4.0	2.660	Lomariopsidaceae			
<i>Monstera acuminata</i>	22.0	15.2	2.800	<i>Bolbitis bernoullii</i>	5.2	3.6	2.240
<i>Philodendron guttiferum</i>	0.4	0	0	Violaceae			
<i>Philodendron inaequilaterum</i>	8.0	2.8	3.185	<i>Orthion oblanceolatum</i>	0.8	0	0
<i>Philodendron scandens</i>	2.0	1.2	1.645	Zingiberaceae			
<i>Rhodospatha wendlandii</i>	18.0	10.0	2.030	<i>Costus dirzoi</i>	0.4	0.4	5.250
<i>Spathiphyllum cochlearispathum</i>	6.4	4.4	2.380				
<i>Syngonium podophyllum</i>	14.8	12.8	4.725				
<i>Syngonium schottianum</i>	0.8	0.4	1.155				
Arecaceae				RAINY SEASON			
<i>Astrocaryum mexicanum</i>	11.2	10.0	6.160	Acanthaceae			
<i>Chamaedorea tepejilote</i>	5.2	2.8	3.780	<i>Aphelandra aurantiaca</i>	13.2	1.6	3.150
<i>Reinhardtia gracilis</i> var. <i>gracilior</i>	0.8	0.8	3.500	<i>Odontonema callistachyum</i>	0.4	0.4	5.250
Bombacaceae				<i>Schaueria calycobracteata</i>	0.4	0	0
<i>Quararibea funebris</i>	0.8	0	0	Annonaceae			
Capparaceae				<i>Cymbopetalum baillonii</i>	0.4	0	0
<i>Crataeva tapia</i>	1.6	0.4	3.500	<i>Rollinia jimenezii</i>	0.4	0	0
Clusiaceae				Apocynaceae			
<i>Rhedia edulis</i>	2.0	0	0	<i>Stemmadenia donnell-smithii</i>	0.4	0	0
Commelinaceae				Araceae			
<i>Tradescantia zanonii</i>	0.8	0	0	<i>Anthurium flexile</i> subsp. <i>flexile</i>	18.4	12.4	3.395
Dryopteridaceae				<i>Anthurium pentaphyllum</i>			
<i>Diplazium lonchophyllum</i>	18.4	18.0	2.905	var. <i>bombacifolium</i>	11.6	8.0	2.975
Euphorbiaceae				<i>Dieffenbachia seguine</i>	2.0	2.0	2.345
<i>Acalypha diversifolia</i>	1.2	0.4	4.095	<i>Monstera acuminata</i>	13.2	10.8	1.610
<i>Croton Schiedeanus</i>	2.8	0.4	0.315	<i>Philodendron guttiferum</i>	2.4	1.6	0.945
<i>Omphalea oleifera</i>	2.4	1.6	2.450	<i>Philodendron inaequilaterum</i>	4.4	1.6	0.875
Fabaceae				<i>Philodendron scandens</i>	2.8	2.4	1.680
<i>Inga</i> sp.	1.2	0.4	3.500	<i>Rhodospatha wendlandii</i>	23.2	14.8	1.890
<i>Lonchocarpus</i> sp.	0.4	0	0	<i>Spathiphyllum cochlearispathum</i>	8.8	8.4	1.085
<i>Pterocarpus rohrii</i>	1.6	0	0	<i>Syngonium podophyllum</i>	24.4	20.0	4.340
Hippocrateaceae				<i>Syngonium schottianum</i>	1.6	1.2	2.100
<i>Salacia megistophylla</i>	1.2	0.4	4.095	Arecaceae			
Lauraceae				<i>Astrocaryum mexicanum</i>	2.4	2.0	7.770
<i>Nectandra ambigens</i>	20.4	20.0	3.990	<i>Chamaedorea tepejilote</i>	2.0	0.4	2.345
<i>Nectandra globosa</i>	1.2	0	0	<i>Reinhardtia gracilis</i> var. <i>gracilior</i>	0.4	0	0
<i>Ocotea dendrodaphne</i>	1.2	1.2	0.875	Bignoniaceae			
Meliaceae				<i>Paragonia pyramidata</i>	0.4	0.4	0.805
<i>Guarea glabra</i>	0.4	0.4	1.750	Capparaceae			
<i>Trichilia breviflora</i>	0.8	0	0	<i>Crataeva tapia</i>	0.4	0	0
Menispermaceae				Clusiaceae			
<i>Abuta panamensis</i>	0.8	0.4	7	<i>Rhedia edulis</i>	0.4	0	0
Moraceae				Dichapetalaceae			
<i>Brosimum alicastrum</i>	0.8	0.4	1.330	<i>Dichapetalum donnell-smithii</i>	0.8	0.4	1.400
<i>Pseudolmedia oxyphyllaria</i>	6.0	3.2	1.085	Dryopteridaceae			
<i>Trophis mexicana</i>	10.8	5.6	2.100	<i>Diplazium lonchophyllum</i>	10.8	10.8	4.375
<i>Trophis racemosa</i>	0.4	0.4	4.725	Ebenaceae			
Myrtaceae				<i>Diospyros digyna</i>	0.4	0	0
<i>Eugenia</i> sp.	0.4	0	0	Menispermaceae			
				<i>Abuta panamensis</i>	1.2	0.4	1.75

TABLE I. Continued.

Plant species	Plant relative abundance (%)	Diseased plants (%)	Leaf area damaged per plant (%)
Euphorbiaceae			
<i>Croton Schiedeanus</i>	3.2	1.2	0.875
<i>Omphalea oleifera</i>	0.8	0.8	3.500
Fabaceae			
<i>Dussia mexicana</i>	2.8	0.4	0.245
<i>Inga</i> sp.	0.8	0.4	3.080
<i>Pterocarpus rohrii</i>	0.4	0	0
Flacourtiaceae			
<i>Pleuranthodendron lindenii</i>	2.4	0.8	1.400
Hippocrateaceae			
<i>Hippocratea celastroides</i>	1.2	0	0
<i>Salacia megistophylla</i>	1.6	0	0
Lauraceae			
<i>Licaria</i> sp.	0.4	0	0
<i>Nectandra ambigens</i>	8.0	7.2	3.780
<i>Ocotea dendrodaphne</i>	0.4	0.4	0.875
Loganiaceae			
<i>Spigelia palmeri</i>	0.4	0	0
Meliaceae			
<i>Guarea glabra</i>	0.4	0.4	0.350
<i>Trichilia breviflora</i>	0.4	0	0
Moraceae			
<i>Brosimum alicastrum</i>	0.4	0	0
<i>Poulsenia armata</i>	0.8	0.4	3.010
<i>Pseudolmedia oxyphyllaria</i>	2.8	1.6	1.015
<i>Trophis mexicana</i>	2.0	0.4	2.100
Myrsinaceae			
<i>Parathesis lenticellata</i>	0.4	0	0
Myrtaceae			
<i>Eugenia</i> sp.	0.4	0.4	1.155
Piperaceae			
<i>Piper aequale</i>	0.4	0.4	0.455
Pteridaceae			
<i>Adiantum</i> sp.	2.8	2.4	4.025
Rubiaceae			
<i>Psychotria faxlucens</i>	2.4	1.2	5.600
<i>Psychotria simiarum</i>	0.4	0	0
Sapindaceae			
<i>Paullinia clavigera</i>	1.2	1.2	1.750
Sapotaceae			
<i>Pouteria durlandii</i>	0.4	0.4	3.500
Thelypteridaceae			
<i>Thelypteris rhachiflexuosa</i>	6.8	6.8	1.365
Ulmaceae			
<i>Ampelocera hottlei</i>	0.4	0	0
Violaceae			
<i>Orthion oblancoelatum</i>	0.4	0	0
<i>Rinorea guatemalensis</i>	0.8	0	0

In both seasons of the year, plant relative abundance was very much lower in lianas, tree seedlings, and palms than in perennial herbs and ferns, and disease incidence was very much higher in the latter two life forms ($F_{1,4} = 15.52$; $P < 0.03$ and $F_{1,4} = 41.65$; $P < 0.008$ dry and rainy seasons, respectively). However, there was no significant relationship between relative abundance of each life form and the proportion of leaf area affected per plant.

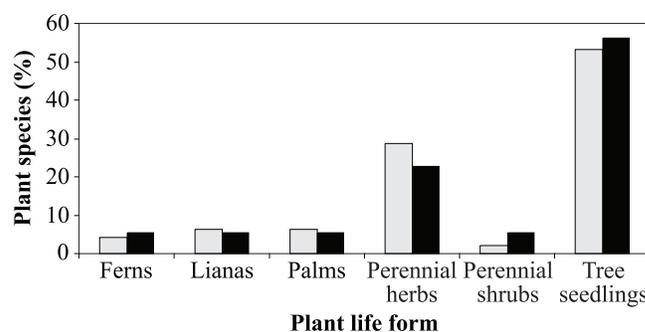


FIGURE 2. Relative representation of plant species of different life forms in the understory community during the dry (grey bars) and rainy (black bars) seasons. The relative representation of the different life forms in the two seasons of the year is not statistically different ($\chi^2 = 1.26$; $P > 0.05$).

TABLE II. Number and percentage of diseased plants (individuals) and species and fungal pathogens collected in four forest sites at the Los Tuxtlas forest during the dry and rainy seasons.

Season	Number of sampled plants (% diseased)	Number of plant species (% diseased)	Number of fungal morphotypes
Dry	620 (50.80%)	49 (65.3%)	53
Rainy	483 (65.4%)	57 (64.5%)	60
Total	1103 (60%)	67 (70%)	53

TABLE III. Average proportion of diseased plants and leaf area damaged per plant for the different plant life forms during the dry and rainy seasons (± 1 SE).

Plant life form	Diseased plants (%)		Leaf area damaged per plant (%)	
	Dry season	Rainy season	Dry season	Rainy season
Ferns	10.80 \pm 7.20	6.67 \pm 2.43	2.57 \pm 0.33	3.26 \pm 0.95
Lianas	0.27 \pm 0.13	0.53 \pm 0.35	3.70 \pm 2.03	1.17 \pm 0.58
Palms	4.53 \pm 2.79	0.80 \pm 0.61	4.48 \pm 0.84	3.37 \pm 2.30
Perennial herbs	4.20 \pm 1.36	6.52 \pm 1.77	2.12 \pm 0.44	2.03 \pm 0.33
Perennial shrubs	-	0.27 \pm 0.13	-	1.90 \pm 1.68
Tree seedlings	1.35 \pm 0.78	0.53 \pm 0.23	1.31 \pm 0.32	1.02 \pm 0.26

According to our survey the most abundant plant species were perennial herbs like *Anthurium pentaphyllum* var. *bombacifolium*, *Monstera acuminata*, *Rhodospatha wendlandii*, *Anthurium flexile* subsp. *flexile*, *Syngonium podophyllum*, and *Aphelandra aurantiaca* and seedlings of the tree *Nectandra ambigens* (cf. Table I). Regression analyses between plant relative abundance per transect for the four forest sites and disease incidence showed different patterns among species. In six plant species a significant relationship was observed between plant relative abundance and percentage of diseased plants in both seasons of the year (Figure 3, Table IV). However, for *A. flexile* plants a positive relationship between disease incidence and plant relative abundance was only detected during the dry season, and for *A. aurantiaca* we did not detect a significant relationship between these two variables in either of the seasons (Figure 3).

In accordance with the changes in leaf infection within each of the eight most abundant species, we found that the likelihood, modelled through binomial probability and generalized linear analysis (JMP, ver.5.0.1.2, Zar, 1999), of a plant

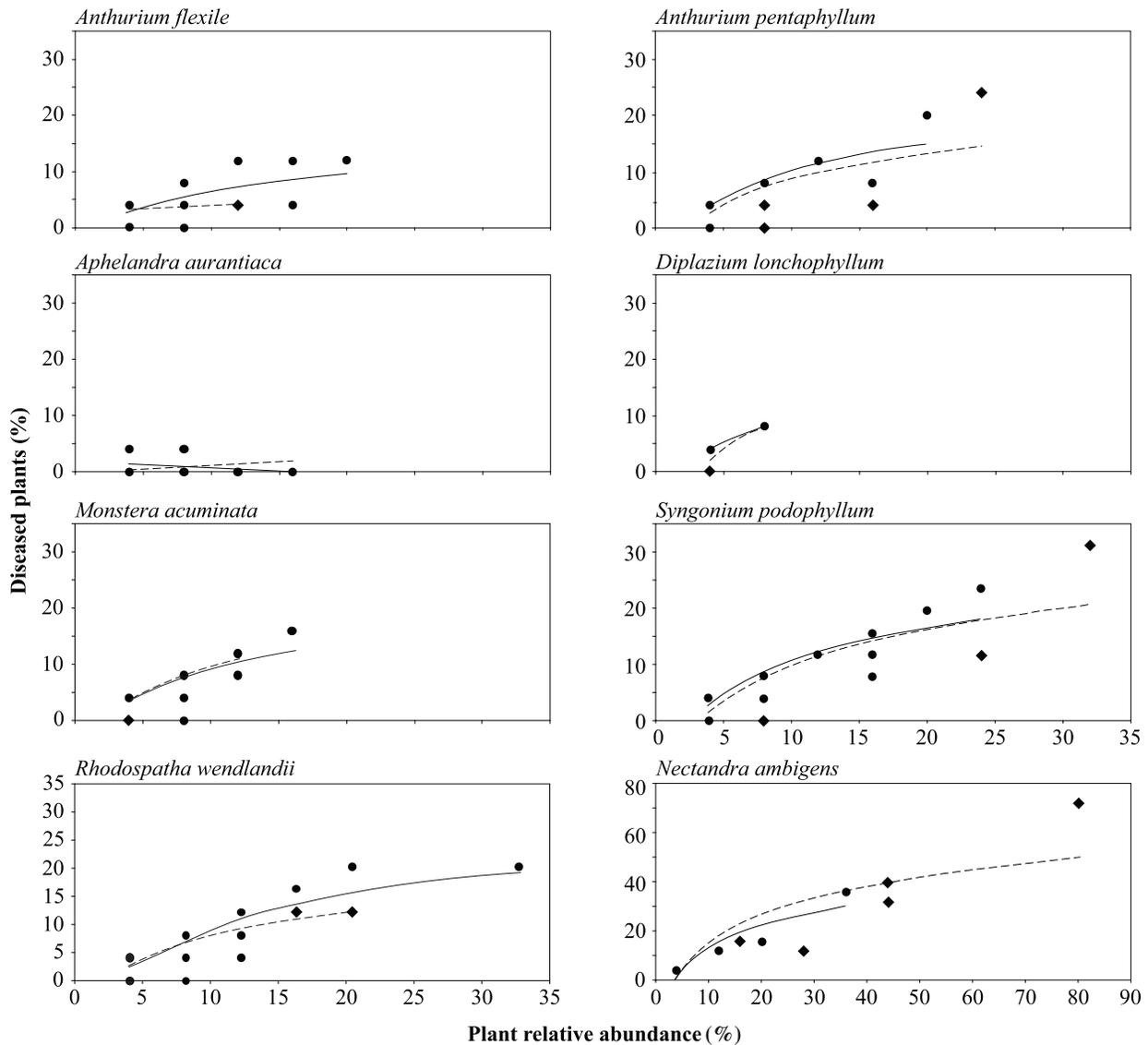


FIGURE 3. Relationship between plant abundance and the percentage of diseased plants per transect for each of the eight most abundant plant species during the dry (circles) and rainy (diamonds) seasons. Note that the scale of both axes is different for *Nectandra ambigens*.

species being healthy (*i.e.*, escaping infection) decreased significantly with relative abundance (Figure 4a and b); this result was consistent in both seasons of the year.

Discussion

Our results suggest that plant relative abundance could be a factor that, at least to some extent, explains disease incidence in the foliage of plants at the Los Tuxtlas understory. We observed an increment in the proportion of diseased plants with plant relative abundance. Similarly, Gilbert, Ferrer, and Carranza (2002) showed that polypore fungi were more commonly found on more abundant hosts, and that the richness of fungi per host species increased with relative abundance of the host. In addition, our data show that the life forms of ferns and perennial herbs included some of the most frequently attacked plant species. Thus, life form seems to be an important determinant of infection, but this pattern is confounded by plant relative abundance.

Pathogens in any plant community have to deal with a variety of plant species, each probably having different patterns of resistance mechanisms. Thus, not all plants at any given time get infected (Burdon, 1978). In tropical forests, the high diversity of plant species may limit the spread of pathogens through physical interference by the presence of non-susceptible plants. However, Gilbert and Hubbell (1996) suggest that high species diversity does not necessarily prevent the spread of diseases, when many, if not most, plant pathogens are not species-specific. To our knowledge nothing is known about the relative representation of damage caused by specialist and generalist leaf fungal pathogens in tropical forests, but there is some evidence for host preference among fungal endophytes in the tropics (Arnold *et al.*, 2000). However, studies on wood-decay fungi in the tropics have shown little host specialization. For example, Lindblad (2000) showed that from 32 common species of polypore fungi, only three were host specific in a Neotropical dry forest. Likewise, Gilbert, Ferrer, and

TABLE IV. Logarithmic regression parameters for the relationship between plant abundance and the percentage of diseased plants per transect for each of the eight most abundant plant species during the dry and rainy seasons.

Plant species	Dry season			Rainy season		
	F	P	r ²	F	P	r ²
<i>Anthurium flexile</i>	12.02	0.003	0.39	0.39	0.55	0.04
<i>Anthurium pentaphyllum</i>	95.09	0.0001	0.80	12.67	0.003	0.46
<i>Aphelandra auratiaca</i>	0.81	0.40	0.07	1.36	0.27	0.12
<i>Diplazium lonchophyllum</i>	96.06	0.0001	0.95	14.44	0.003	0.57
<i>Monstera acuminata</i>	19.33	0.0007	0.60	43.92	0.0001	0.76
<i>Nectandra ambigens</i>	9.58	0.09	0.83	16.64	0.007	0.74
<i>Rhodospatha wendlandii</i>	35.94	0.0001	0.71	18.49	0.002	0.64
<i>Syngonium podophyllum</i>	71.42	0.0001	0.82	36.12	0.0001	0.68

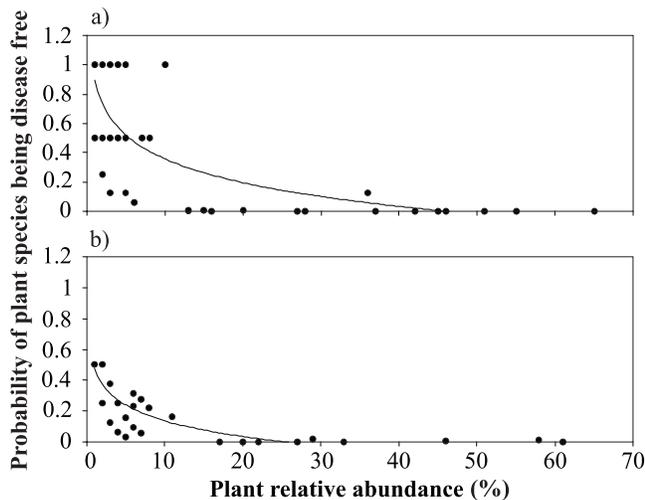


FIGURE 4. Probability of plant species being free of disease, under the assumption that pathogens are host non-selective, plotted against plant relative abundance in four forest sites during the a) dry ($y = -0.2343\ln x + 0.897$, $R^2 = 0.52$) and b) rainy ($y = -0.1469\ln x + 0.4746$, $R^2 = 0.83$) seasons.

Carranza (2002) detected little evidence for host specialization in a lowland moist semi-deciduous forest in Panama. A study by García-Guzmán and Dirzo (2001) suggests that at the Los Tuxtlas rainforest a high proportion of the leaf spots in understory plants are caused by opportunistic fungal pathogens, which take advantage of the wounds caused by herbivorous insects. Although we lack evidence of foliar fungal pathogens being insect vectored in the Los Tuxtlas forest, it is possible that the apparent specificity level of those pathogens is determined by host-specificity of the insect herbivores carrying the fungal spores. Persistence of specialist pathogens in a diverse system depends on the presence of a suitable host species at sufficiently high densities to ensure that the pathogens can infect new individuals. Wild plants in tropical forest understories tend to show aggregated distributions (Hubbell, 1979; Condit *et al.*, 2000). The forest floor at Los Tuxtlas is densely covered by very extensive carpets of tree seedlings, located in the immediate vicinity of reproductive trees of several species (Dirzo & Miranda, 1990). These carpets are local-scale mono-dominated patches, in which the likelihood of infection may be high due to the short distances among co-specific plants. Furthermore, in areas not covered by tree

seedlings, the carpets are replaced by dense mats of herbaceous plants that are also susceptible to leaf pathogens, as shown by this and previous studies (García-Guzmán & Dirzo, 2001). If these pathogens are opportunistic parasites, then the probabilities of infecting several plant species are expected to be high. Clearly, the degree of pathogen specificity is an aspect that warrants investigation to elucidate the underlying mechanisms leading to the abundance–infection relationships we observed.

We found that although a high proportion of the plant species were affected by leaf spots in both seasons of the year, disease levels on a per-plant basis were relatively low and never exceeded 10% of leaf area damaged. We considered an individual plant as diseased even in those cases where only a single leaf was affected by a leaf spot. This method could lead to an underestimate: if diseased leaves fall off the plant, they might be unnoticed in one-time surveys like those of our study. Nevertheless, this bias is unlikely, since leaf abscission by herbivory in seedlings typically occurs when levels of damage are greater than 50% of leaf area damaged—considerably higher than the levels of leaf area affected by pathogens (Núñez-Farfán & Dirzo, 1989). Despite the low proportion of damaged leaf area recorded in our study, the pathogens responsible may have important effects on the physiology and performance of host plants. For example, Mitchell (2003) showed that relatively low levels of infection by foliar fungi in a grassland ecosystem can reduce plant carbon gain and below-ground allocation. Therefore, disease may be playing a larger role in our study than suggested by the relatively low proportion of diseased tissue.

Interactions among pathogens and plants are affected by a variety of environmental factors (Burdon, 1987). Consequently, disease presence and severity in any population, and hence its evolutionary consequences, are determined by the combined effects of abiotic and biotic environmental factors (Burdon, 1993; Jarosz & Davelos, 1995). Our study reveals that plant abundance could be an important factor affecting disease incidence in tropical rainforest plants, but surprisingly, the seasonal variation in rainfall and temperature was not an important determinant of infection. This may be explained by the fact that the seasonality of this forest is not as marked as in other temperate and tropical forests; for example, rainfall during the “dry” months, although lower than in the rainy months, is typically close to 100 mm. Studies in other sites encompassing a gradient of seasonality would be revealing.

Our study presents evidence compatible with previous work in agronomic and temperate ecosystems regarding the importance of plant abundance on disease incidence (Burdon, 1987; Antonovics, Iwasa & Hassell, 1995; Mitchell, Tilman & Groth, 2002) and constitutes one of the few demonstrations of this relationship with tropical plants in a natural setting.

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