Plant Ecology and Evolution 149 (2): 189–198, 2016
http://dx.doi.org/10.5091/plecevo.2016.1150

REGULAR PAPER

Circular distribution of three species of epiphytic orchids in shade coffee plantations, in Soconusco, Chiapas, Mexico

Alfredo García-González[1,*], Anne Damon[1], Frander B. Riverón-Giró[1] & Irene Ávila-Díaz[2]

[1]El Colegio de la Frontera Sur (ECOSUR), Unidad Tapachula. Carretera Antiguo Aeropuerto km 2.5, AP 36, C.P. 30700 Tapachula, Chiapas, México
[2]Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo. Edif. R, planta baja, Ciudad Universitaria, C.P. 58030 Morelia, Michoacán, México
*Author for correspondence: alfredmx22@gmail.com

Background and aims – Cardinal orientation of individuals is one of the least known and understood ecological or demographic factor governing the dynamics of epiphytic orchid populations. The circular distribution of three epiphytic orchids, *Oncidium poikilostalix*, *Oncidium guatemalenoides* and *Lepanthes acuminata*, was studied in shaded coffee plantations in the region of Soconusco, Chiapas, Mexico. A preference for a certain cardinal orientation on the phorophytes was analyzed, using circular statistics.
Methods – Circular distribution tendencies were compared between the three species, two life stages (immatures and adults), and between the microsites (trunk, branch forks, branches, twigs) in which the individual orchids were distributed on the phorophytes.
Results – *Oncidium poikilostalix* was the most abundant species (1,056 individuals). The three orchid species were found growing mainly on twigs of the coffee bushes. For populations in general, and for the life stages and microsites in particular, individuals of *O. poikilostalix* and *O. guatemalenoides* showed a preference for occupying the combination of the cardinal orientations south-southwest-west. Individuals of *L. acuminata* were orientated towards all eight cardinal points, with a slight numerical preference for east.
Conclusions – Cardinal orientation of orchid species can be driven by specific climatic or ecological factors (e.g. direction and speed of prevailing winds; *O. poikilostalix* and *O. guatemalenoides*). These species may show clearer preferences for growing facing certain cardinal orientations. However, many species can be affected by a combination of microclimatic and ecological factors (e.g. humidity in the microenvironments, proximity to water sources, insolation, shade, competition or wind speed and direction; *L. acuminata*), which may influence at such a limited and local scale that orientation patterns may be difficult to detect.

Key words – Cardinal orientation, *Lepanthes acuminata*, *Oncidium guatemalenoides*, *Oncidium poikilostalix*, phorophyte.

INTRODUCTION

Cardinal orientation of individuals is one of the least known and understood ecological or demographic factor governing the dynamics of epiphytic orchid populations, and has given rise to a variety of hypotheses to try to explain its behaviour, with no conclusion to date. Some of these hypotheses suggest that the cardinal orientation of individuals is related to the direction and the speed of prevailing winds, a particular needs of light and humidity of each orchid species, the orientation of sites where the individuals grow on phorophytes and the relation with the other trees around them, humidity, cold air currents, or that distribution may be completely random (González Hernández et al. 2007, Mújica Benítez 2007, Tremblay & Velázquez Castro 2009, Rech et al. 2011, Rodríguez-Cedillo 2012, García-González & Riverón-Giró 2014). In general, cardinal orientation is not considered when designing projects for the reintroduction of epiphytic orchids, despite evidence showing that this may be a determining factor for some species (Tremblay & Velázquez Castro 2009).

In the case of other epiphytes such as bryophytes and lichens, many species are strongly influenced by heavy rainfall, high humidity, shading and geographic position (Busby & Whitfield 1978, Barreno Rodríguez & Pérez-Ortega 2003, Friedel et al. 2006, Proctor 2008, Pérez-Quintero & Watteijne 2009, Root & McCune 2012); then the location of the phorophytes plays an important role (Rudolphi & Gustafsson

All rights reserved. © 2016 Botanic Garden Meise and Royal Botanical Society of Belgium – ISSN 2032-3921

2011). In the northern hemisphere, the greatest abundance of lichens occurs usually on the north side of tree trunks because it is less sunny and retains more moisture (Molina Moreno & Probanza Lobo 1992, Riquelme 2008, Méndez-Estrada & Campos 2015).

Mexico is located on the northern edge of the American tropics and harbours a remarkable orchid diversity, approximately 1,260 species, of which 60% are epiphytes (Hágsater et al. 2005, Soto Arenas et al. 2007). A high proportion of the great diversity of orchids in Mexico takes refuge in shaded coffee plantations, wherein 76 genera and 213 species have been reported, of which 180 (84.1%) are epiphytes (Espejo Serna et al. 2005). The region of Soconusco, situated in the extreme southeast of the state of Chiapas, covers an area of 5,475 km², or 7.2% of the state territory (Sánchez & Jarquín 2008), and harbours 293 orchid species (Damon 2011). In this region coffee plantations occupy more than 70,400 ha (SAGARPA 2015). Despite the fact that coffee plantations are anthropocentric agroecosystems, many species of orchids have managed to colonize the plantations, using the coffee bushes as phorophytes (Espejo Serna et al. 2005). *Oncidium poikilostalix* (Kraenzl.) M.W.Chase & N.H.Williams (fig. 1A), *Oncidium guatemalenoides* M.W.Chase & N.H.Williams (fig. 1B) and *Lepanthes acuminata* Schltr. (fig. 1C) are small to medium-sized, epiphytic orchids, with sympodial growth, that are found in these traditional, shaded plantations of *Coffea arabica* L. (Rubiaceae), in the south of the Soconusco region (Salazar Chávez & Soto Arenas 1996, Espejo Serna et al. 2005, Soto-Arenas & Solano-Gómez 2007, Damon 2011, Solano Gómez et al. 2011, García-González et al. 2013).

Oncidium poikilostalix was reported as species new to Mexico in 2008 (Solano Gómez et al. 2011). Before that, it was only known from Guatemala and Costa Rica (Behar & Tinschert 1998). This taxon apparently shows invasive behaviour in shaded coffee plantations, although its distribution area in Mexico remains restricted (Solano Gómez et al. 2011, García-González et al. 2013). *Oncidium guatemalenoides* is a native species, morphologically very similar to *O. poikilostalix* (Soto-Arenas & Solano-Gómez 2007, Solano Gómez et al. 2011), and also with a restricted distribution in Mexico (Soto-Arenas & Solano-Gómez 2007). *Oncidium guatemalenoides* is considered as threatened (A) in the Mexican Official Standard for threatened flora and fauna (SEMARNAT 2010) and the study area has one of the few populations known in Mexico. On the other hand, *L. acuminata* has a very contrasting situation with respect to the two *Oncidium* species; it is a relatively abundant and widely distributed taxon in southeastern Mexico (Salazar Chávez & Soto Arenas 1996).

In order to test whether the three species of orchids (*O. poikilostalix*, *O. guatemalenoides* and *L. acuminata*) present a uniform circular distribution around the phorophytes, we compared their circular distribution tendencies in the two life stages (immatures and adults) and between microsites (trunk, branch forks, branches and twigs).

MATERIAL AND METHODS

Characterization of the study site

The study was conducted in 2013 and 2014, in two plantations of arabica coffee (*C. arabica*), with commercial polyculture system (Moguel & Toledo 1999), in the communities Fracción Montecristo (FM) and Benito Juárez El Plan (BJ). These two sites are separated by approximately 2.5 km and are aged 20 and 25 years respectively. Both are situated in the buffer zone of the Volcán Tacaná Biosphere Reserve, in the municipality of Cacahoatán, in the region of Soconusco, Chiapas, Mexico. Fracción Montecristo has an elevation of 1,410 m and coordinates 15°5′31.5″N 92°9′57.9″W, and BJ has an elevation of 1,450 m and coordinates 15°5′15″N 92°8′55″W. The area is characterized by the presence of low cloud, variously referred to as mist, or horizontal rain, especially in the afternoon of the rainy season. Annual rainfall and average temperatures in the area are 3,674.4 mm and 20.7°C respectively (SEMARNAT & CONANP 2013).

Data recording

In the FM plantation, the study included populations of *O. poikilostalix* and *O. guatemalenoides*, and in BJ, a population of *L. acuminata.* An area of approximately 2.5 ha was analysed within each coffee plantation (5 ha in total). In this study, the term phorophyte is used exclusively to refer to the shrubs and shade trees (regardless of species) that served as substrates for the three orchid species studied (García-González & Pérez Márquez 2011).

Figure 1 – Epiphytic orchid species studied in two shaded coffee plantations in the region of Soconusco, Chiapas, Mexico: A, *Oncidium poikilostalix*; B, *O. guatemalenoides*; C, *Lepanthes acuminata*.

Dbh and height of phorophyte, and ecological parameters of the three orchid species

The dbh (diameter at breast height; approximately 1.3 m above soil level) of the phorophytes was measured using a diametric tape of 3 m, and the height was estimated using the method employed by García-González et al. (2011). To determine vertical distribution (microsites) of the individuals of the three species of orchids, the classification proposed by García-González et al. (2011) was used, which is specifically designed for coffee bushes and for shade trees. For life stages and cardinal orientation of individuals of each orchid species, methods employed by García-González & Riverón-Giró (2014) were used. The circular distribution of the three orchid species is defined by the location of the populations on the phorophytes, considering the cardinal points (fig. 2). The circular distribution is determined by the cardinal orientations of individuals on the phorophytes (fig. 2A–C).

Statistical analysis

Using the program Oriana (version 1.01), Rayleigh's Circular Uniformity test was applied to the data, with a confidence interval of 95%. The results of the analysis of the circular data were represented graphically using the dispersal frequencies of the angles measured presented in "rose" diagrams. The circular distances were derived from a baseline of 0°, equivalent to magnetic north. Our null hypotheses assume a uniform circular distribution of all three orchid species around the bole of coffee bushes and shade trees. An introduction to circular statistics can be found in Zar (1999). As for all descriptive statistics the mean and standard error were calculated.

RESULTS

Phorophytes, dbh and height

In the coffee plantations, 203 phorophytes were studied (table 1). Only *O. poikilostalix* was found growing on shade

Table 1 – Number of phorophytes, total number of individuals, and number of individuals in each life stage and in each microsite for three epiphytic orchid species, *Oncidium poikilostalix*, *O. guatemalenoides* and *Lepanthes acuminata* (Orchidaceae), in two shaded coffee plantations in the region of Soconusco, Chiapas, Mexico.
I, immatures; A, adults; T, trunk; F, branch forks; B, branches; Tw, twigs.

Species	Number of phorophytes	Number of individuals	Life stages		Microsites			
			I	A	T	F	B	Tw
Oncidium poikilostalix	181	1056	660	396	46	13	200	797
Oncidium guatemalenoides	20	35	8	27	5	0	9	21
Lepanthes acuminata	2	80	46	34	11	0	18	51

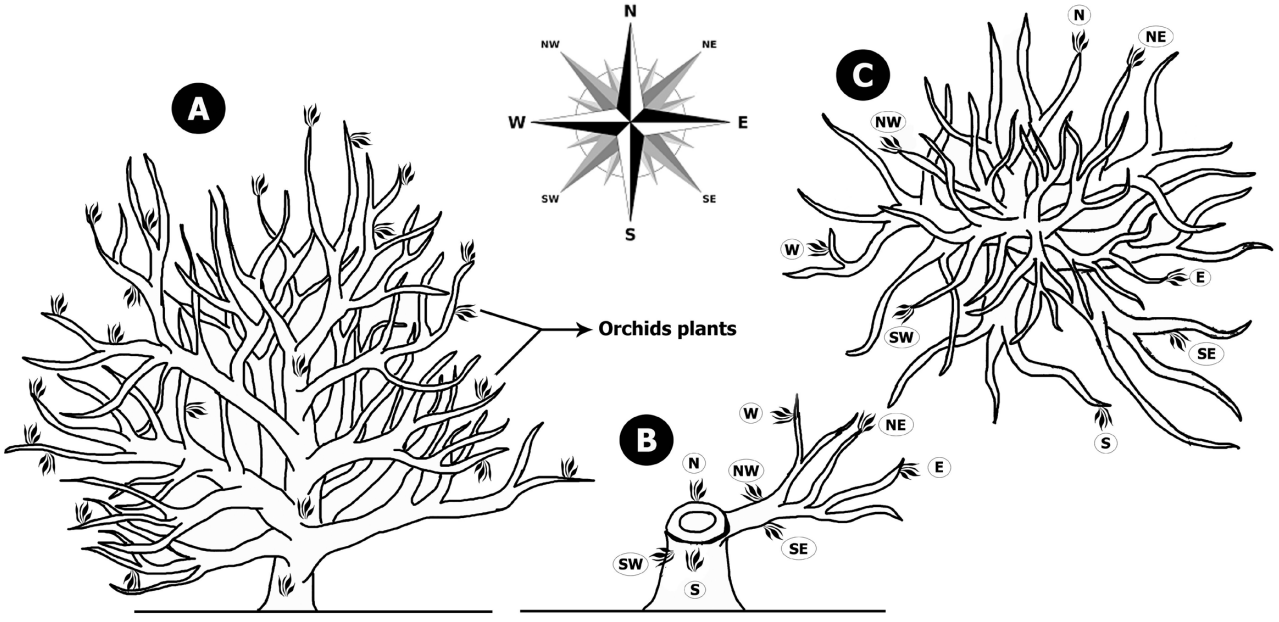

Figure 2 – A, coffee bushes as phorophyte of the epiphytic orchid species *Oncidium poikilostalix*, *O. guatemalenoides* and *Lepanthes acuminata*, in shaded coffee plantations, in the region of Soconusco, Chiapas, Mexico; B, branch and transversal section of the stem, showing the cardinal orientation of the orchid individuals; C, view of the coffee bushes from above, showing the cardinal orientation of the orchid individuals. The cardinal orientation of the individuals is determined by the direction they occupy (considering the cardinal points) on the stem, branch or twigs on the phorophytes. N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west; NW, northwest.

Table 2 – Application of Rayleigh's Circular Uniformity test, using values for population parameters and microsites, to determine the circular distribution of individuals of three species of epiphytic orchids, *Oncidium poikilostalix*, *O. guatemalenoides* and *Lepanthes acuminata*, in two shaded coffee plantations in the region of Soconusco, Chiapas, Mexico.

Population parameters and microsites: No. of individuals	Rayleigh's Circular Uniformity Test	Circular Variance	Circular Standard Deviation	Mean Vector (μ)
Oncidium poikilostalix				
Total population	z = 159.296, p < 0.001	0.612	78.799°	233.068°
Immatures	z = 104.925, p < 0.001	0.601	77.699°	231.257°
Adults	z = 54.831, p < 0.001	0.628	80.564°	236.302°
Trunks	z = 3.801, p = 0.022	0.713	90.474°	235.799°
Branch forks	z = 1.176, p = 0.315	0.699	88.819°	238.334°
Branches	z = 33.696, p < 0.001	0.59	76.462°	230.739°
Twigs	z = 121.377, p < 0.001	0.61	78.601°	233.5°
Oncidium guatemalenoides				
Total population	z = 7.891, p < 0.001	0.525	69.929°	226.036°
Immatures	z = 1.284, p = 0.286	0.599	77.491°	177.774°
Adults	z = 7.983, p < 0.001	0.456	63.248°	235.413°
Trunks	z = 0.879, p = 0.438	0.581	75.555°	191.701°
Branches	z = 2.748, p = 0.06	0.447	62.408°	245.626°
Twigs	z = 4.968, p = 0.006	0.514	68.789°	223.314°
Lepanthes acuminata				
Total population	z = 0.703, p = 0.495	0.906	124.663°	115.714°
Immatures	z = 1.577, p = 0.207	0.815	105.234°	101.871°
Adults	z = 0.139, p = 0.871	0.936	134.327°	226.357°
Trunks	z = 0.894, p = 0.418	0.715	90.764°	168.951°
Branches	z = 1.285, p = 0.28	0.733	93.093°	113.635°
Twigs	z = 0.12, p = 0.887	0.951	140.92°	45°

trees (*Inga micheliana* Harms; Fabaceae) but only 29 individuals were found growing on four shade phorophytes, which was too few to be included in the analysis. All other phorophytes (199 phorophytes) were coffee bushes (*C. arabica*), with an average height of 3.5 ± 5.89 m and with stems averaging 3.57 ± 0.09 cm in diameter.

Number of individuals, life stages and vertical distribution of the three orchid species studied

Oncidium poikilostalix was the most abundant of the three species and was present on the greatest number of phorophytes (table 1). The majority of the 35 individuals of *O. guatemalenoides* were adults (77.14% of individuals), whereas the populations of the other two species consisted of a majority of immature individuals (62.5% of the 1,056 *O. poikilostalix* individuals; 57.5% of the 80 *L. acuminata*; table 1). Regarding the vertical distribution of individuals on phorophytes, the three species were growing mainly on twigs (75.47% of *O. poikilostalix* individuals; 60% of *O. guatemalenoides*; 63.75% of *L. acuminata*; table 1). *Oncidium poikilostalix* was the only species with individuals growing in branch forks, but this represented only 1.23% of the population (table 1).

Circular distribution of the three species of orchids studied

The cardinal orientation of population of *O. poikilostalix* on phorophytes was not uniform (table 2). The individuals were located mainly towards southwest (24.24% of population; 256 individuals; fig. 3A), with 62.4% of the total population (659 individuals; fig. 3A) occupying a combination of the cardinal orientations south-southwest-west. This tendency was maintained when the life stages were analysed separately, immatures (southwest: 24.85% of total individuals in this life stages; combination of south-southwest-west: 63.18%; fig. 3B) and adults (southwest: 23.23% of individuals in this life stages; combination of south-southwest-west: 61.11%; fig. 3C). There were significant differences between the number of individuals in each cardinal orientation for each life stage (table 2).

Significant differences were also found between the numbers of individuals of *O. poikilostalix* growing towards the different cardinal orientation in the trunks, branches and twigs of the phorophytes, not so in the case of individuals growing on branch forks (table 2). Similarly, the combination of the cardinal orientations south-southwest-west was predominant in all microsites (trunk: 52.17% of individuals in this microsite; branches: 64.5%; twigs: 62.6%; fig. 3D–F).

The distribution of cardinal orientation of *O. guatemalenoides* on the phorophytes was also not uniform (table 2). Individuals of this species were also mainly orientated towards the combination of south-southwest-west (65.71% of population; 23 individuals; fig. 4A). However, when the life stages were analysed separately, no significant differences in cardinal orientation was observed for immature individuals, but differences were significant for adult plants (table 2). Of the adult individuals, 70.37% were also orientated towards

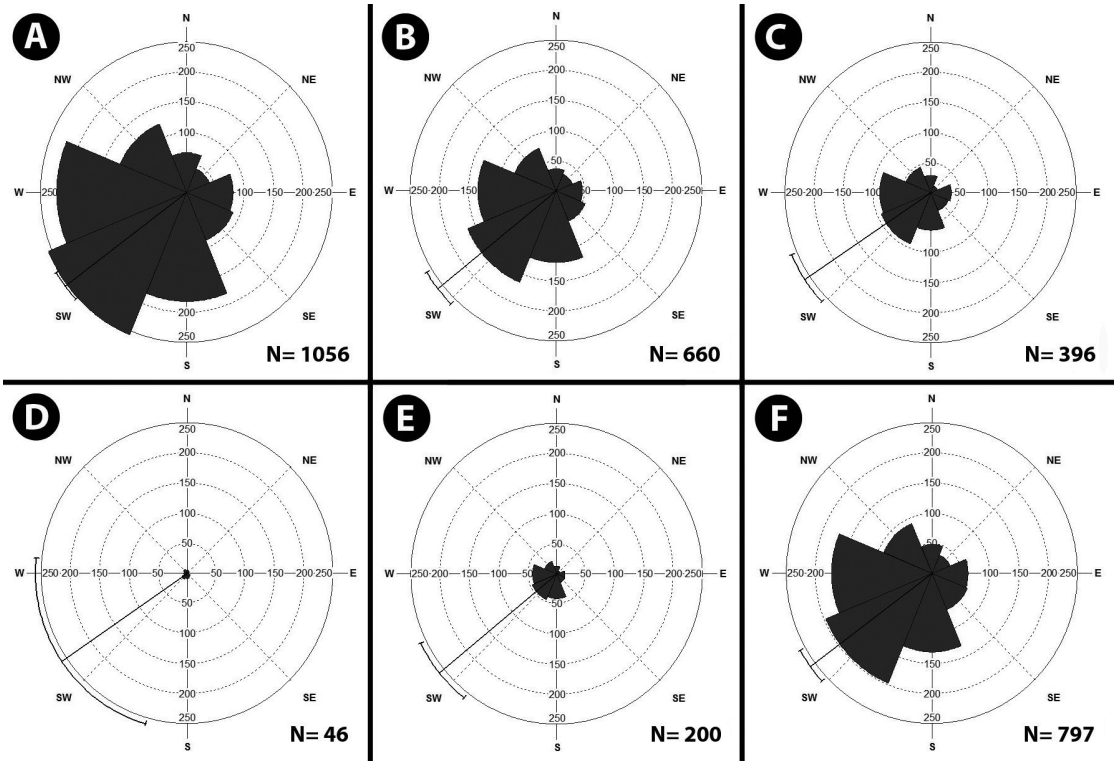

Figure 3 – "Rose" diagrams to show the cardinal orientation of individuals of *Oncidium poikilostalix*: A, total population; B, immature individuals; C, adult individuals; D, trunk microsite; E, branches microsite; F, twigs microsite. The largest "petals" represent the most frequent cardinal orientations. Confidence interval 95%.

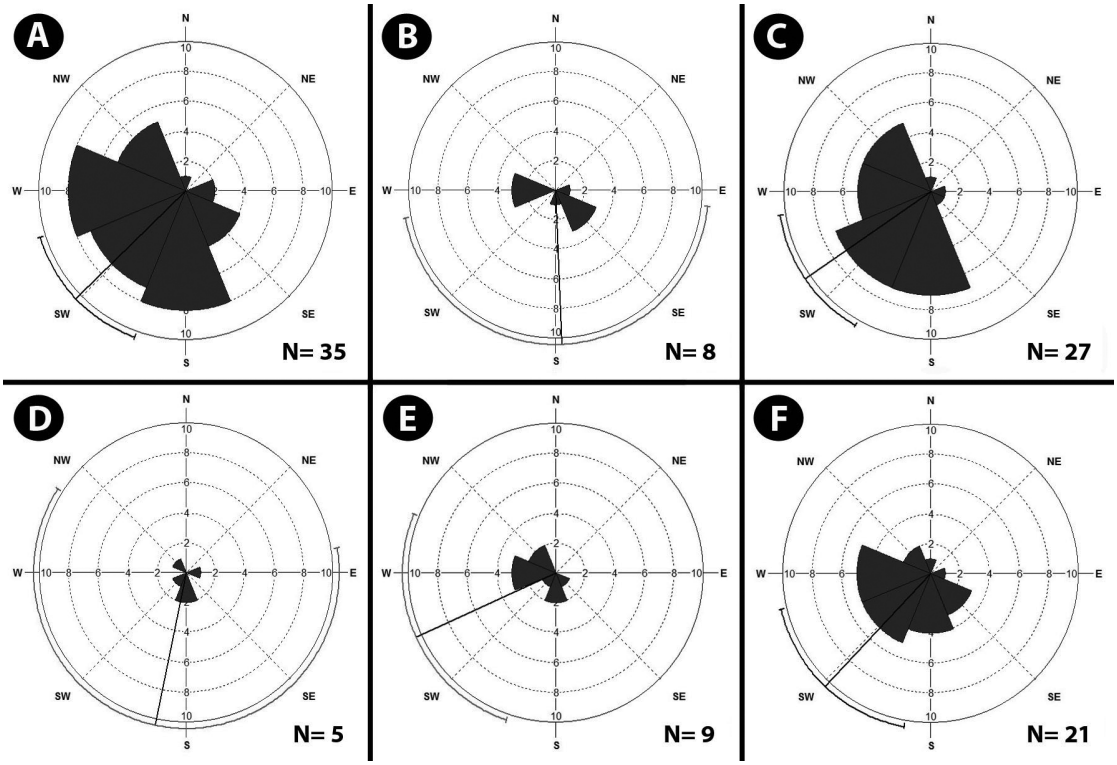

Figure 4 – "Rose" diagrams to show the cardinal orientation of individuals of *Oncidium guatemalenoides*: A, total population; B, immature individuals; C, adult individuals; D, trunk microsite; E, branches microsite; F, twigs microsite. The largest "petals" represent the most frequent cardinal orientations. Confidence interval 95%.

the combination of south-southwest-west, whereas in immature individuals (very few plants) a definite trend was not seen (fig. 4B & C).

Of the three microsites occupied by *O. guatemalenoides*, a significant difference in cardinal orientation was observed only in the case of individuals found growing on the twigs (table 2), with a greater number of individuals orientated towards the combination of south-southwest-west (66.7% of individuals in this microsite; fig. 4F). There was a numerical preference for this same combination of orientations for the other two microsites (trunk: 60% of individuals in this microsite; branches: 66.7%; fig. 4D & E).

The behaviour of the population of *L. acuminata* was different to that of the two species of *Oncidium*, with no significant differences in the distribution of individuals between the cardinal orientations (table 2), and presence in all eight orientations (fig. 5A). However, there was a slight numerical preference for orientation towards the east (25%, 20 individuals; fig. 5A).

When the data for immature and adult plants of *L. acuminata* were analyzed separately, no significant differences between cardinal orientations of individuals were seen (table 2). The same was true when analysing the number of individuals facing towards each cardinal orientation in the three microsites (table 2). However, although it is not statistically appreciated, slight numerical preference was observed for orientation towards the east, particularly in immature individuals, and individuals growing on branches and twigs (immature: 30.43% of individuals in this life stages; branches: 33.33% of individuals in this microsite; twigs: 21.57%; fig. 5B–F).

DISCUSSION

Coffea arabica grows as an understorey plant, and shaded coffee plantations, are one of the perennial cultures that are most similar to the natural forests that they replaced. In these plantations, many elements of the biodiversity of the original forests, including plants, birds, mammals, reptiles, amphibians and insects, can adapt and complete their life cycle (Moguel & Toledo 1999, Sherry 2000, Espejo Serna et al. 2005, Hágsater et al. 2005, Manson et al. 2008). *Coffea arabica* is an exotic plant in Mexico, originating from the southwestern highlands of Ethiopia (Sylvain 1955, Wellman 1961, Baxter 1997, Belayneh et al. 2010). During the approximately 150 years of coffee culture history in the Soconusco region many orchid species have adapted to this new but compatible environment, especially the miniature, twig epiphytes, meaning that presently many of these species are now only found growing on coffee bushes (Damon 2003). These orchids are so called because they have developed adaptations for growing upon the thin, seemingly inhospitable twigs of trees and bushes, which are also areas most prone to damage and with the lowest levels of humidity and accumulation of organic matter as compared to the trunks and branches (Chase 1987, Brown 1990, Hágsater et al. 2005, Mondragón et al. 2007). Coffee bushes in traditional shaded plantations, where moss and epiphytes are not removed, are frequently found to be excellent phorophytes for epiphytes in general and twig epiphytes in particular (Hágsater et al. 2005, Damon & Valle-Mora 2008, Pérez-Hernández et al. 2011), such as the three species of orchids in this study.

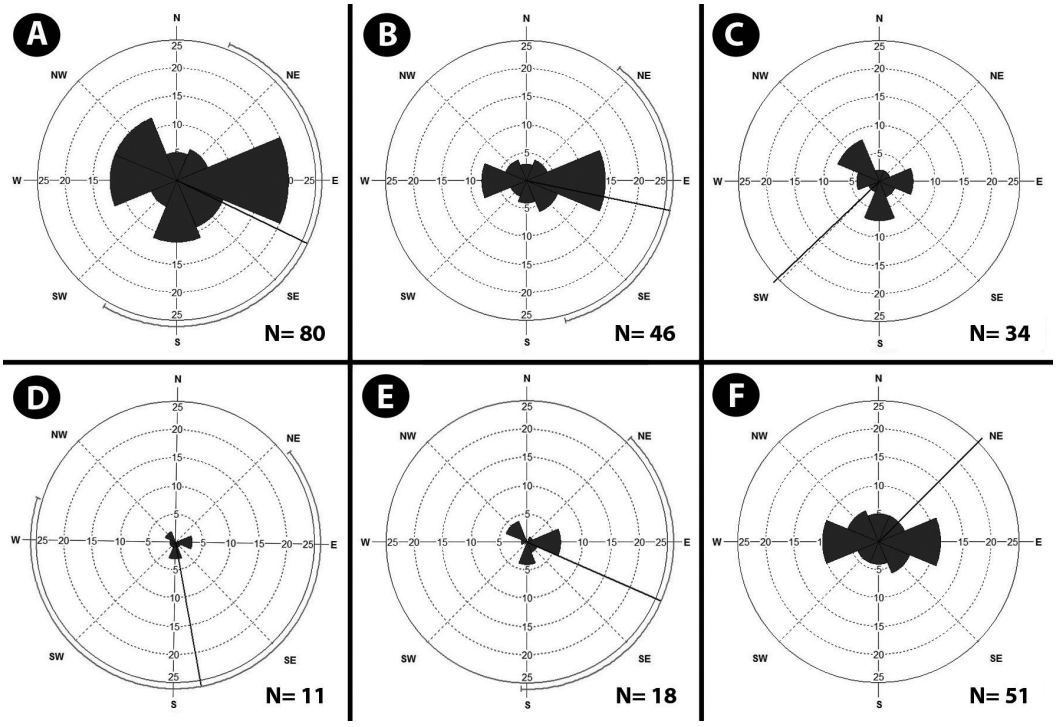

Figure 5 – "Rose" diagrams to show the cardinal orientation of individuals of *Lepanthes acuminata*: A, total population; B, immature individuals; C, adult individuals; D, trunk microsite; E, branches microsite; F, twigs microsite. The largest "petals" represent the most frequent cardinal orientations. Confidence interval 95%.

The microsite (twigs) preferred by the species studied here, is also the one of other orchids, e.g. *Telipogon helleri* (L.O.Williams) N.H.Williams & Dressler, a species found in shaded coffee plantations in the Soconusco region (García-González et al. 2016). The orchids *Ionopsis utricularioides* (Sw.) Lindl., in orange plantation (*Citrus sinensis* (L.) Osbeck; García-González & Riverón-Giró 2014), and *Erycina hyalinobulbon* (La Llave & Lex.) N.H. Williams & M.W. Chase, in pine-oak forests with elements of montane cloud forests (Correa-Soria 2012) and in oak-pine forests (Domínguez 2015) have also been found growing on twigs.

Despite the fact that the three orchid species studied here grow in the same region, and ecosystem, are submitted to same climatic conditions, and mostly occupy the same microsite on the coffee bushes, cardinal orientation coincides for the two *Oncidium* species, but differs for *L. acuminata.* In *O. poikilostalix* and *O. guatemalenoides* the predominant orientation of individuals (a combination of south-southwest-west; in both life stages and all microsites) is probably mainly influenced by the direction and velocity of the dominant winds in the area, as it is the case for *Lepanthes eltoroensis* Stimson in Puerto Rico (Tremblay & Velázquez Castro 2009). The predominant cardinal orientation of *O. poikilostalix* and *O. guatemalenoides* individuals coincides with the direction of the prevailing winds in the Tacaná Volcano area. In this area, during the whole year, winds originating from the Pacific Ocean, come from the southwest, and interfere with superficial winds, which blow from south to north, with velocities lower than 3.5 m/s and a frequency of 25% (SEMARNAT & CONANP 2013). The ocean moist wind probably blows the orchids seeds to phorophyte mostly on its south-southwest-west cardinal orientation where more seeds arrive and seedlings survive.

In *Prosthechea* aff. *karwinskii* (Mart.) J.M.H.Shaw, another species of epiphytic orchid, significant differences were also observed in the number of individuals in the different cardinal orientations. In this case Rodríguez-Cedillo (2012) reported a greater number of individuals orientated towards the east, south and west, and very few were facing the north, northwest and northeast, suggesting that the cold northerly winds do not favor development of this orchid species.

In this study, no clear preference for cardinal orientation was observed for *L. acuminata* wherein individuals were found facing all directions, with only a slight preference for east, similar to the case reported for the other orchid *Cuitlauzina pendula* La Llave & Lex. (Pérez-Decelis 2013). The behaviour of *L. acuminata* can be considered as random, as it was suggested for the abovementioned *I. utricularioides* (García-González & Riverón-Giró 2014), or it is influenced by the combination of various factors, such as wind speeds and directions (González Hernández et al. 2007, Tremblay & Velázquez Castro 2009), the specific requirements of light and humidity of this species of orchid, the orientation of the microsites occupied by the individuals on the phorophytes, the relation to other trees or bushes around them (Mújica Benítez 2007, Damon et al. 2015), and/or the presence of the mycorrhizal fungi essential for the germination of seeds and subsequent development of the orchid plant (Tupac Otero et al. 2004, 2007, Jersáková & Malinová 2007, Mújica Benítez 2007, Chung et al. 2011). Particularly the mycorrhizal association of orchids can be an important factor, but is difficult to evaluate. Some species of orchids are generalists, while others have specificity for individual fungal taxa (Hadley 1970, Tupac Otero et al. 2004, 2007). In general, patterns of dispersion of orchid seeds depend on the spatial distribution of adult plants, the rain and shadows of seeds, while plant recruitment depends on suitability of the microhabitat, including quality of substrate, microclimate and the presence of suitable mycorrhizal fungi (Nathan & Muller-Landau 2000).

In this study, the population of *L. acuminata* was only found on two phorophytes, with the majority of individuals (64 individuals) growing on one of those. To the west of that phorophyte, and at a distance of 2 m, was a young avocado tree (*Persea americana* Mill.; Lauraceae), measuring 3.5 m in height. Towards the south of the phorophyte, at a distance of 60 cm was a plant of *Calathea crotalifera* S.Watson (Marantaceae), measuring 1.5 m of high. Both of these plants could significantly affect the amount of light that reached the phorophyte and the *L. acuminata* individuals, and could also affect factors such as desiccation of the substrate. The second, and less populated phorophyte of *L. acuminata* (sixteen individuals), grows in full sun, with no other trees or shrubs in the close vicinity, so the microclimatic conditions to which individuals are subject, are very different from those of the other phorophyte. In particular, the penetration and distribution of light, and the tolerance to light or shade of each species, determines to a greater extent the distribution of epiphytes in the forest canopy (Arditti 1992, Ferro 2004).

Another very important factor driving the distribution of epiphytes in the canopy is water availability (Callaway et al. 2002). It is interesting to note that the most populated phorophyte was situated near a stream, situated towards the south of the phorophyte, running from east to west. Individuals of *L. acuminata* showed a slight general preference for orientation towards that direction (combination of east-southeast-south-southwest-west: 71.25% of population; 57 individuals; fig. 5A). Possibly this combination of orientations, which are located in front of the stream, permit a slight increase in moisture, which facilitates the recruitment of young plants of this orchid (Rech et al. 2011). The same pattern is likely observed for the abovementioned *Telipogon helleri* in the same region (García-González et al. 2016). Also, in the case of epiphytic lichens, the microclimate influences their abundance. Certain conditions of light, humidity and wind, provides adequate conditions that promotes their growth and development (Molina Moreno & Probanza Lobo 1992).

The presence of bryophytes could be an important factor facilitating the establishment of some species of epiphytic orchids (Kull 1998, Tremblay et al. 1998). Although a direct relation has been shown between the presence of mosses and the development of populations of some other species of *Lepanthes* (Tremblay et al. 1998), in this study the interaction between mosses and *L. acuminata* was not clear as only eleven individuals located on the trunk of the most populated phorophyte were associated with mosses. However, our sampling was too limited to drawn firm conclusions.

The preference of epiphytes for specific cardinal orientations has received little attention and could be an important ecological information, especially for the management

of vulnerable species (Tremblay & Velázquez Castro 2009). Some orchid species are susceptible to specific climatic or ecological factors (e.g. direction and speed of prevailing winds; *O. poikilostalix* and *O. guatemalenoides*), so they show clear preferences for growing towards specific orientations. However, many species can be affected by a combination of microclimatic and ecological factors (e.g. humidity in the microenvironments, proximity from water sources, insolation, shade, competition or wind speed and direction; *L. acuminata*), which may influence at such a limited and local scale that orientation patterns may be difficult to detect. However, it must take into account that in the case of *L. acuminata*, as in *O. guatemalenoides*, few individuals and phorophytes were used in this study, so it would be advisable to extend the sampling effort to other areas, which would allow increase the sample, make comparisons and corroborate the conclusions.

The results presented here could have useful applications for the conservation management of epiphytes in general and epiphytic orchids in particular, for example in the case of reintroduction programs, and for the management of populations for conservation or sustainable exploitation. Epiphytes can also be an important non-timber natural resource for farmers working in agroforestry, agriculture, community woodlands or ecological reserves, with a potential for sustainable, legal exploitation for tourism or the elaboration of crafts using the flowers.

ACKNOWLEDGEMENTS

We are grateful to the coffee growers of the communities Fracción Montecristo and Benito Juárez El Plan, for permitting access to their plantations. The National Council for Science and Technology (CONACYT), funded part of the research. Nelson Pérez Miguel, from the community Benito Juárez El Plan, gave important technical assistance. The organization Idea Wild made possible the completion of this Project, by providing vital equipment. To the editor and anonymous reviewers, for their valuable recommendations.

REFERENCES

Arditti J. (1992) Fundamentals of orchid biology. New York, John Wiley & Sons.

Barreno Rodríguez E., Pérez-Ortega S. (2003) Líquenes de la Reserva Natural Integral de Muniellos, Asturias. Oviedo, Consejería de Medio Ambiente, Ordenación del Territorio e Infraestructuras del Principado de Asturias and KRK Ediciones.

Baxter J. (1997) El libro del café. Madrid, Susaeta Ediciones.

Behar M., Tinschert O. (1998) Guatemala y sus orquídeas. Guatemala City, Bancafé, Grupo Financiero del País.

Belayneh T., Kubicek C.P., Druzhinina I.S. (2010) The rhizosphere of Coffea arabica in its native highland forests of Ethiopia provides a niche for a distinguished diversity of Trichoderma. Diversity 2: 527–549. http://dx.doi.org/10.3390/d2040527

Brown A.D. (1990) El epifitismo en las selvas montañas del Parque Nacional "El Rey", Argentina: composición florística y patrón de distribución. Revista de Biología Tropical 38: 155–166.

Busby J.R., Whitfield D.W.A. (1978) Water potential, water content, and net assimilation of some boreal forest mosses. Canadian Journal of Botany 56: 1551–1558. http://dx.doi.org/10.1139/b78-184

Callaway R.M., Brooker R.W., Choler P., Kikvidze Z., Lortie C.J., Michalet R., Paolini L., Pugnaire F.I., Newingham B., Aschehoug E.T., Armas C., Kikodze D., Cook B.J. (2002) Positive interactions among alpine plants increase with stress. Nature 417: 844–848. http://dx.doi.org/10.1038/nature00812

Chase M.W. (1987) Obligate twig epiphytism in the Oncidiinae and other Neotropical orchids. Selbyana 10: 24–30.

Chung M.Y., Nason J.D., Chung M.G. (2011) Significant demographic and fine-scale genetic structure in expanding and senescing populations of the terrestrial orchid Cymbidium goeringii (Orchidaceae). American Journal of Botany 98: 2027–2039. http://dx.doi.org/10.3732/ajb.1100094

Correa-Soria G. (2012) Listado de las orquídeas epifitas del Área de Ichaqueo y San Miguel del Monte, Michoacán y una aproximación de caracterización ecológica en Bosque Mesófilo de Montaña. Bachelor thesis, Biology School, Michoacan University of San Nicolás de Hidalgo, Morelia, Mexico.

Damon A. (2003) Las epífitas. Ecosistemas y comunidades: procesos naturales y sociales de los bosques. Ecofronteras 18: 1720.

Damon A., Valle-Mora J. (2008) Retrospective spatial analysis of the pollination of two miniature epiphytic orchids with different pollination strategies in a coffee plantation in Soconusco, Chiapas, Mexico. Botanical Journal of the Linnean Society 158: 448–459. http://dx.doi.org/10.1111/j.1095-8339.2008.00857.x

Damon A. (2011) Diversidad y conservación de las orquídeas del corredor biológico Tacaná-Boquerón. Final Project Report. FONDOS MIXTOS-CHIAPAS CHIS-2006-C06-45802. 2007-2010. Mexico, El Colegio de la Frontera Sur (ECOSUR), Tapachula Unit.

Damon A., Almeida-Cerino C., Valle-Mora J., Bertolini V., López-Urbina J.C. (2015) Ravines as refuges for Orchidaceae in southeastern Mexico. Botanical Journal of the Linnean Society 178: 283–297. http://dx.doi.org/10.1111/boj.12278

Domínguez I. (2015) Listado y caracterización ecológica de las orquídeas epifitas del Predio de Tenderio, de la Comunidad Indígena de Santiago Tingambato, Michoacán, México. Bachelor thesis, Biology School, Michoacan University of San Nicolás de Hidalgo, Morelia, Mexico.

Espejo Serna A., López-Ferrari A.R., Jiménez Machorro R., Sánchez Saldaña L. (2005) Las orquídeas de los cafetales en México: una opción para el uso sostenible de ecosistemas tropicales. Revista de Biología Tropical 53: 73–84.

Ferro J. (2004) Efectos de la tala selectiva sobre la estructura y dinámica de la comunidad de epífitas vasculares del bosque semideciduo de la Península de Guanahacabibes, Cuba. PhD thesis, Agroforestry School, "Hermanos Saiz Montes de Oca" Pinar del Río University, Pinar del Río, Cuba.

Friedel A., Oheimb G.V., Dengler J., Härdtle W. (2006) Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany. Feddes Repertorium 117: 172–185. http://dx.doi.org/10.1002/fedr.200511084

García-González A., Pérez Márquez R. (2011) La comunidad orquideológica en la Reserva de la Biosfera Sierra del Rosario, Cuba. Revista de Biología Tropical 59: 1805–1812.

García-González A., Damon A., Esparza Olguín L.G., Valle-Mora J. (2011) Population structure of Oncidium poikilostalix (Orchidaceae), in coffee plantations in Soconusco, Chiapas, Mexico. Lankesteriana 11: 23–32.

García-González A., Damon A., Iturbide F.A., Olalde-Portugal V. (2013) Reproduction of Oncidium poikilostalix (Orchidaceae), potentially invading coffee plantations in Soconusco, Chiapas, México. Plant Ecology and Evolution 146: 36–44. http://dx.doi.org/10.5091/plecevo.2013.674

García-González A., Riverón-Giró F.B. (2014) Organización espacial y estructura de una población de Ionopsis utricularioides (Orchidaceae) en un área suburbana de Pinar del Río, Cuba. Lankesteriana 13: 419–427.

García-González A., Damon A., Riverón-Giró F.B., Aguilar-Romero O., Solís-Montero L., Ávila-Díaz I. (2016) Telipogon helleri (Orchidaceae): population characteristics, new locality in Mexico and risk of extinction. Botanical Sciences 94: 97–106. http://dx.doi.org/10.17129/botsci.280

González Hernández E., Raventós J., Mújica Benítez E., Bonet A. (2007) Estructura y ecología de la población del endemismo cubano Broughtonia cubensis (Orchidaceae), en Cabo San Antonio, Península de Guanahacabibes, provincia de Pinar del Río, Cuba. Lankesteriana 7: 469–478.

Hadley G. (1970) Non-specificity of symbiotic infection in orchid mycorrhiza. New Phytologist 69: 1015–1023. http://dx.doi.org/10.1111/j.1469-8137.1970.tb02481.x

Hágsater E., Soto Arenas M., Salazar Chávez G., Jiménez Machorro R., López M., Dressler R. (2005) Las orquídeas de México. Mexico City, Productos Farmacéuticos, S.A. de C.V., Instituto Chinoin.

Jersáková J., Malinová T. (2007) Spatial aspects of seed dispersal and seedling recruitment in orchids. New Phytologist 176: 237–241. http://dx.doi.org/10.1111/j.1469-8137.2007.02223.x

Kull T. (1998) Fruit-set and recruitment in populations of Cypripedium calceolus L. in Estonia. Botanical Journal of the Linnean Society 126: 27–38. http://dx.doi.org/10.1006/bojl.1997.0141

Manson R.H., Contreras A., López-Barrera F. (2008) Estudios de la biodiversidad en cafetales. In: Manson R.H., Hernández-Ortiz V., Gallina S., Mehltreter K. (eds) Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación: 1–14. Mexico City, Instituto de Ecología, A.C. and Instituto Nacional de Ecología (INE-Semarnat).

Méndez-Estrada V.H., Campos C.A. (2015) Cobertura de líquenes arborícolas y su relación con la orientación cardinal en parques municipales de la Gran Área Metropolitana de Costa Rica. Cuadernos de Investigación UNED 7: 313–317.

Moguel P., Toledo V.M. (1999) Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13: 11–21. http://dx.doi.org/10.1046/j.1523-1739.1999.97153.x

Molina Moreno J.R., Probanza Lobo A. (1992) Pautas de distribución de biocenosis liquénicas epifíticas de un robledal de Somosierra (Madrid). Botanica Complutensis 17: 65–78.

Mondragón D., Maldonado C., Aguilar-Santelises R. (2007) Life history and demography of a twig epiphyte: a case study of Erycina crista-galli (Orchidaceae). Selbyana 28: 137–144.

Mújica Benítez E. (2007) Ecología de las orquídeas epífitas Broughtonia cubensis (Lindley) Cogniaux, Dendrophylax lindenii (Lindley) Bentham et Rolfe y Encyclia bocourtii Mújica et Pupulin en el Cabo San Antonio, Península de Guanahacabibes, Cuba. Análisis espacio-temporal e implicaciones del impacto de un fenómeno atmosférico severo. PhD thesis, Ecology Department, Alicante University, Alicante, Spain.

Nathan R., Muller-Landau H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15: 278–285. http://dx.doi.org/10.1016/S0169-5347(00)01874-7

Pérez-Decelis V.A. (2013) Sistema de apareamiento, caracterización ecológica y propagación in vitro de Cuitlauzina pendula la Llave & Lex. (Orchidaceae). Master Degree thesis, Biology School, Michoacan University of San Nicolás de Hidalgo, Morelia, Mexico.

Pérez-Hernández H., Damon A., Valle-Mora J., Sánchez-Guillén D. (2011) Orchid pollination: specialization in chance? Botanical Journal of the Linnean Society 165: 251–266. http://dx.doi.org/10.1111/j.1095-8339.2010.01109.x

Pérez-Quintero A.L., Watteijne B. (2009) Estructura de una comunidad de líquenes y morfología del género Sticta (Stictaceae) en un gradiente altitudinal. Acta Biológica Colombiana 14: 157–170.

Proctor M.C.F. (2008) Physiological ecology. In: Goffinet B., Shaw A.J. (eds) Bryophyte Biology: 237–268. 2nd Ed. Cambridge, UK, Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511754807.007

Rech A.R., Rosa Y.B.C.J., Rosa-Junior E.J. (2011) Levantamento e características ecológicas de Orchidaceae da mata ciliar do Rio Dourados, Dourados-MS. Revista Árvore (Special edition) 35: 717–724. http://dx.doi.org/10.1590/S0100-67622011000400016

Riquelme F.S. (2008) Evaluación del uso de líquenes como indicadores biológicos de contaminación atmosférica en la Quebrada de la Plata, región metropolitana. Bachelor thesis (Forestal engineer), Forestry Sciences School, Universidad de Chile, Santiago de Chile, Chile.

Rodríguez-Cedillo L.L. (2012) Patrones de distribución de la epifita endémica Prosthechea aff. karwinskii (Orchidaceae) en Michoacán, México. Bachelor thesis, Biology School, Michoacan University of San Nicolás de Hidalgo, Morelia, Mexico.

Root H.T., McCune B. (2012) Surveying for biotic soil crust lichens of shrub steppe habitats in the Columbia Basin. North American Fungi 7: 1–21. http://dx.doi.org/10.2509/naf2012.007.007

Rudolphi J., Gustafsson L. (2011) Forests regenerating after clearcutting function as habitat for bryophyte and lichen species of conservation concern. PLoS One 6: e18639. http://dx.doi.org/10.1371/journal.pone.0018639

SAGARPA (Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, Mexico) (2015) Estadística de la Producción Agrícola 2013. Servicio de Información Agroalimentaria y Pesquera (SIAP). [online]. Available from http://catalogo.datos.gob.mx/dataset/estadistica-de-produccion-agricola-siap/resource/d751a037-2973-40e3-8b46-716e936fb204 [accessed 10 Aug. 2015].

Salazar Chávez G.A., Soto Arenas M.A. (1996) El género Lepanthes Sw. en México. Orquídea (Méx.) 14 (single number). Mexico City, Herbario AMO.

Sánchez J.E., Jarquín R. (eds) (2008) La Frontera Sur. Reflexiones sobre el Soconusco, Chiapas, y sus problemas ambientales, poblacionales y productivos. Mexico City, Senate of Republic.

SEMARNAT (2010) Mexican Official Standard NOM-059-SEMARNAT-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario Oficial de la Federación, second section, December 30, 2010. Mexico City, Secretaria de Medio Ambiente y Recursos Naturales. [online]. Available from http://www.profepa.gob.mx/innovaportal/file/435/1/NOM_059_SEMARNAT_2010.pdf [accessed 25 Jul. 2015].

SEMARNAT, CONANP (2013) Programa de Manejo Reserva de la Biosfera Volcán Tacaná. Mexico City, Secretaría de Medio Ambiente y Recursos Naturales, Comisión Nacional de Áreas

Naturales Protegidas. [online]. Available from http://www.conanp.gob.mx/que_hacemos/pdf/programas_manejo/2014/VOLCAN_DE_TACANA_2014.pdf [accessed 28 Jul. 2015].

Sherry T.W. (2000) Shade coffee: a good brew even in small doses. The Auk 117: 563–568. http://dx.doi.org/10.1642/0004-8038(2000)117[0563:SCAGBE]2.0.CO;2

Sylvain P.G. (1955) Some observations on Coffea arabica L. in Ethiopia. Turrialba 5: 37–53.

Solano Gómez R., Jiménez Machorro R., Damon A. (2011) Two new records and one rediscovery for Orchidaceae of Mexico. Acta Botanica Mexicana 96: 59–72.

Soto-Arenas M.A., Solano-Gómez A.R. (2007) Ficha técnica de Sigmatostalix guatemalensis. In: Soto-Arenas M.A. (comp.) Información actualizada sobre las especies de orquídeas del PROYNOM-059-ECOL-2000. Mexico City, Instituto Chinoin A.C., Herbario de la Asociación Mexicana de Orquideología A.C. Databases SNIB-CONABIO. Project No. W029.

Soto Arenas M.A., Hágsater E., Jiménez Machorro R., Salazar Chávez G.A., Flores González R., Ruiz Contreras I. (2007) Las Orquídeas de México: Catalogo Digital. Mexico City, Instituto Chinoín. CD-ROM.

Tremblay R.L., Zimmerman J.K., Lebrón L., Bayman P., Sastre I., Axelrod F., Alers-García J. (1998) Host specificity and low reproductive success in the rare endemic Puerto Rican orchid Lepanthes caritensis. Biological Conservation 85: 297–304. http://dx.doi.org/10.1016/S0006-3207(97)00163-8

Tremblay R.L., Velázquez Castro J. (2009) Circular distribution of an epiphytic herb on trees in subtropical rain forest. Tropical Ecology 50: 211–217.

Tupac Otero J., Ackerman J.D., Bayman P. (2004) Differences in mycorrhizal preferences between two tropical orchids. Molecular Ecology 13: 2393–2404. http://dx.doi.org/10.1111/j.1365-294X.2004.02223.x

Tupac Otero J., Flanagan N.S., Herre A.E., Ackerman J.D., Bayman P. (2007) Widespread mycorrhizal specificity correlates to mycorrhizal function in the neotropical, epiphytic orchid Ionopsis utricularioides (Orchidaceae). American Journal of Botany 94: 1944–1950. http://dx.doi.org/10.3732/ajb.94.12.1944

Wellman F.L. (1961) Coffee: botany, cultivation and utilization. World crop series. New York, Inter Science.

Zar J.H. (1999) Biostatistical analysis. 4th Ed. New Jersey, Prentice Hall.

Manuscript received 11 Jul. 2015; accepted in revised version 20 Apr. 2016.

Communicating Editor: Tariq Stévart.