Phenotypic plasticity of the basidiomata of *Thelephora* sp. (Thelephoraceae) in tropical forest habitats

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Abstract: Phenotypic plasticity in macroscopic fungi has been poorly studied in comparison to plants or animals and only general aspects of these changes have been described. In this work, the phenotypic variation in the basidiomata of *Thelephora* sp. (Thelephoraceae) was examined, as well as some aspects of its ecology and habitat, using 24 specimens collected in the tropical forests of the Chamela Biological Station, Jalisco, Mexico. Our observations showed that this taxon has clavarioid basidiomata that can become resupinate during development and growth if they are in contact with rocks, litter or live plants, establishing in the latter only an epiphytic relationship. This tropical species may form groups of up to 139 basidiomata over an area of 32.2m^2, and in both types of vegetation (tropical sub-evergreen and deciduous forest) were primarily located on steep (>20°) South-facing slopes. It is found under closed canopy in both tropical forests, but its presence in sub-evergreen forests is greater than expected. Rev. Biol. Trop. 61 (1): 343-350. Epub 2013 March 01.

Key words: *Thelephora*, basidiome, phenotypic plasticity, tropical forest.

The formation of basidiomata constitutes part of the sexual process of Agaricomycotina, and serves the purpose of producing and dispersing spores. The development of these structures is influenced by the interaction of both intrinsic (genetic and physiological) and extrinsic (environmental) factors (Moore-Landecker 1996, Moore *et al.* 2008, 2011). It has been noted that the development of basidiomata of *Coprinus* spp. *Panus fragilis*, *Morchella* sp., *Pleurotus ostreatus* and *Thyphula ishikariensis* is affected by environmental factors including the availability of nutrients, temperature, humidity, light, and pH (Morimoto & Oda 1973, Bujakiewicz 1992, Kost 1992, Boulianne *et al.* 2000, Straatsma *et al.* 2001, Salerni *et al.* 2002, Kawakami *et al.* 2004, Singh *et al.* 2004, Suárez-Duque 2004, Gibertoni *et al.* 2007, Pilz *et al.* 2007, Lodge *et al.* 2008). The shape of the basidiome, however, is genetically determined (Cooke & Whipps 1993, Griffin 1994, Moore 1998, Schmidt 2006, Moore *et al.* 2008), with several basic shapes (corticoid, cyphelloid, clavarioid, dimidiate, effused-reflex and pileate-stipitate), being commonly recognized among different taxa (Corner 1968, Clémençon 1997). Phenotypic plasticity is a mechanism that allows organisms to deal with environmental heterogeneity (Valladares *et al.* 2007). Macroscopic fungi are no exception, having the ability to modify their basidiome morphology in response to varying environmental conditions (McGonigle 1995, Mswaka & Magan 1999). Numerous studies, such as Gottlieb & Wright

(1999), have reported phenotypic plasticity in both micro- and macro-morphological characters of South American species of *Ganoderma*, but without considering their causal factors. In other cases, such as *Pleurotus sajor-caju*, phenotypic variability in the number of concentric lines of the pileus, deformation of the primordia, and reduced growth in response to environmental conditions, particularly temperature and pH, has been observed (Kashangura *et al.* 2006). Similarly, Peabody *et al.* (2003) suggested that some factors are implicated in determining the genetic variability of the number, size, and shape of the basidiomata of *Armillaria gallica*. In the case of clavarioid fungi, morphological variation in response to changes in nutrients, pH, and light has been seen *in vitro* in *Artomyces pyxidatus* and *Pterula echo* (Dodd 1972, McLaughlin & McLaughlin 1972, 1980, James & McLaughlin 1988), but such variation has not been clearly documented in natural conditions.

Worldwide, the genus *Thelephora* includes at least 50 species (Kirk *et al.* 2008), some of which are characterized by the ability to form resupinate, clavarioid, or pileate-stipitate basidiomata (Corner 1968, Sánchez-Jácome & Guzmán-Dávalos 1997). Approximately 28 of these species are found in tropical and subtropical ecosystems, and 10 of them develop clavarioid basidiomata (Corner 1968, Stalpers 1993). One of the notable characters that differentiate species is the macromorphology of the basidiome, but Cunningham (1957) mentioned that variations of form may complicate the characterization of taxa. There are also taxa such as *T. atra* Weinm., *T. dentosa* Berk. & M.A. Curtis, *T. investiens* Corner, *T. japonica* Yasuda, *T. penicillata* (Pers.) Fr., *T. pseudoterrestris* Corner and *T. terrestris* Ehrh. which incrust on inert or living substrates independently of the form of the basidiome (Cunningham 1957, Watling 1996, Corner 1968). Cunningham (1957) did not consider any of the species to be parasitic, but Corner (1968) referred to some species as weakly parasitic because of their propensity to kill plant substrates due to interference with photosynthetic activity.

The environmental conditions and phenotypic plasticity of the basidiomata of *Thelephora* have not been well studied. The objectives of this study were to describe the natural phenotypic variation of the basidiomata of *Thelephora sp.* and to examine aspects of its ecology, spatial distribution, and habitat.

MATERIALS AND METHODS

The study was carried out in the Chamela Biological Station (CBS), located in the Pacific coast of the Mexican state of Jalisco (19°30´N - 105°03´W; Bullock 1988). Vegetation is predominantly deciduous tropical forest, with a smaller area covered by sub-evergreen tropical forest (Lott & Atkinson 2002). The slopes vary between 21-34º, but the elevation does not surpass 580m (Martínez-Yrizar & Sarukhán 1993). Soils are poorly developed young entiosols (or haplic phaeozem) with little organic material and a pH between 6-7 (Solís 1993). Climate is warm sub-humid (Aw_0i), with a marked seasonality (García-Oliva *et al.* 1995, 2002).

Specimens (n=24) of *Thelephora* were collected during the rainy seasons of 2005-2008. Ecological data were also collected, including vegetation type, substrate, canopy cover, orientation and slope, abundance and distribution area of the basidiomata, and the growth form of the basidiome. Habitat orientation and slope were measured with an azimuth compass and a clinometer.

Determination of the specimens was made following normal mycological methods, considering both macro -and microscopic- characters and including reactions with potassium hydroxide and observation of spores using scanning electron microscopy. A number of references were consulted during determination, including Corner (1968, 1976), Ellis & Ellis (1990), Marmolejo *et al.* (1981), Stalpers (1993), and Sánchez-Jacome & Guzmán Dávalos (1997). Evaluation of the relationship of the basidiomata with living substrates was made via observation of rehydrated specimens under a stereoscopic microscope.

A chi-squared test was used to determine if basidiomata were distributed randomly with respect to vegetation type, slope, and orientation. Expected values for the chi-square test were estimated from a sampling of 355 points made every 10m along the trails used to find basidiomata of the clavarioid fungi.

RESULTS

Basidiomata were found to develop in sites beneath a closed canopy, regardless of the level of perturbation at ground level. The relative abundance of basidiomata was 27.9% with respect to other clavarioid fungi found at CBS. The growth form observed was solitary to somewhat gregarious, with between 1-139 basidiomata observed, occupying an area between 0.07-32.2m^2 (Fig. 1A).

The macromorphology of the 24 specimens studied was variable, with 11 of the samples revealing a completely clavarioid form and the rest partially resupinate or a more branched form caused by growth around a physical obstruction; both forms were seen even within a single collection (Figs. 1B-E).

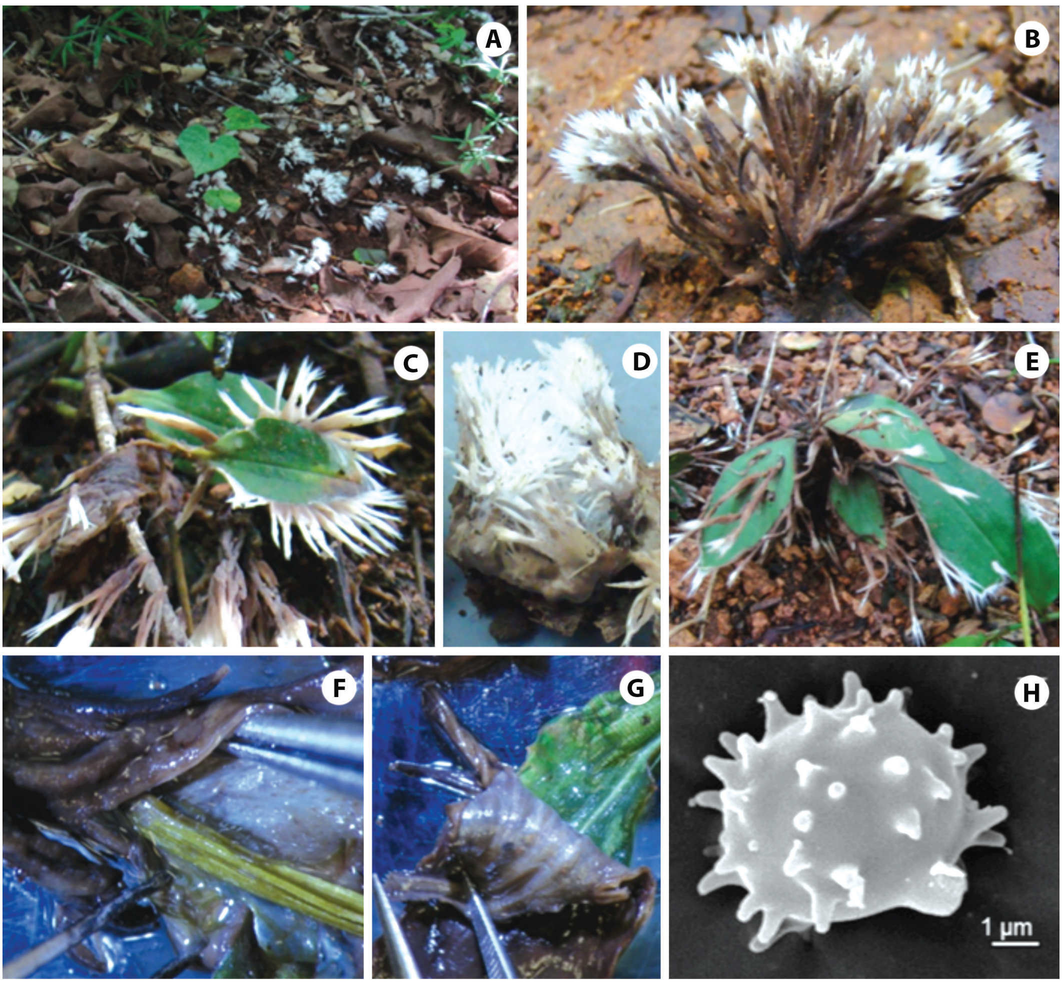

Fig. 1. *Thelephora* sp. (**A**) little gregarious growth of basidiomata on the ground (**B**) clavarioid basidiome well defined. (**C**) resupinated basidiome that return to the clavarioid form. (**D**) resupinated basidiome on a piece of rock. (**E**) leaf lamina crossed by basidiome. (**F-G**) epiphytic relationship on living plants. (**H**) spore by scanning electron microscopy.

Basidiomata were observed growing on plants of the families Convolvulaceae, Sapindaceae, Commelinaceae, Acanthaceae, Asteraceae, Sterculiaceae, Rhamnaceae, Poaceae and Fabaceae. Basidiomata indiscriminately surrounded both stems and leaves (Figs. 1F-G), and occasionally perforated tissue, growing through leaf lamina without causing mortality (Fig. 1E). The fungi were evidently growing as epiphytes, as no penetration of plant tissue was observed, and fungi were easily separated from their substrate (Figs. 1F-G), even in preserved specimens.

The length of the basidiomata varied between 8-145mm, with color ranging from light or reddish brown to dark-violet brown (6D2-16F8; Kornerup & Wanscher 1978) on the base and intermediate part, whereas apices were grey or light yellow to white (2A2-16A1; Kornerup & Wanscher 1978). The hymenium was always smooth regardless of the form of the basidiome.

All specimens showed similar micromorphology and reaction to potassium hydroxide in all tissues. The similarity of size, shape, ornamentation, and type of hylar appendix of the spores observed under scanning electron microscopy confirmed the similarity of all specimens (Fig. 1H). These combined characters and molecular data allowed identification of all the specimens studied as belonging to a new species of *Thelephora*.

Basidiomata were observed after accumulative precipitation surpassed 400mm. Although specimens were found on slopes of varying orientation and inclination (9-41º), South-facing slopes were significantly more common (χ^2=4.9, d.f.=1, $p<0.05$; Fig. 2) as were slopes steeper than 20º (χ^2=72.7, d.f.=1, $p<0.001$; Fig. 3). Finally, specimens of *T.* sp. were found more commonly in the sub-evergreen tropical forest than expected by chance (χ^2=13.5, d.f.=1, $p<0.001$; Fig. 4).

DISCUSSION

Phenotypic plasticity has been widely studied in plants (Palacio-López & Rodríguez-López 2007, Valladares *et al.* 2007) but poorly studied in fungi. This work demonstrates that the unusual growth form found in some basidiomata of *T.* sp. is a characteristic that allows it to fully develop in spite of inert or organic barriers that it may encounter during development.

The observation of basidiomata that adhere to living plant matter has been previously reported for a number of temperate species with stereoid basidiomata such as *Thelephora terrestris* and *T. griseozonata* (Cunningham 1957, Corner 1968, Watling 1996). This process has traditionally been described as incrustation, however, studies demonstrating the type

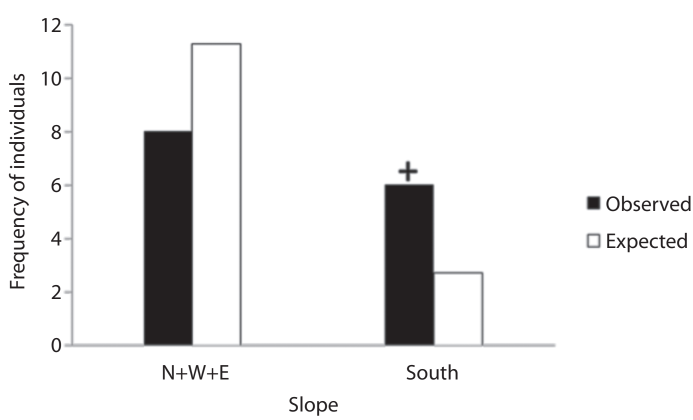

Fig. 2. Frequency of individuals observed and expected of *Thelephora* sp., grouped data from the Northern slopes (N), West (W) and Eastern (E) with respect to the South.

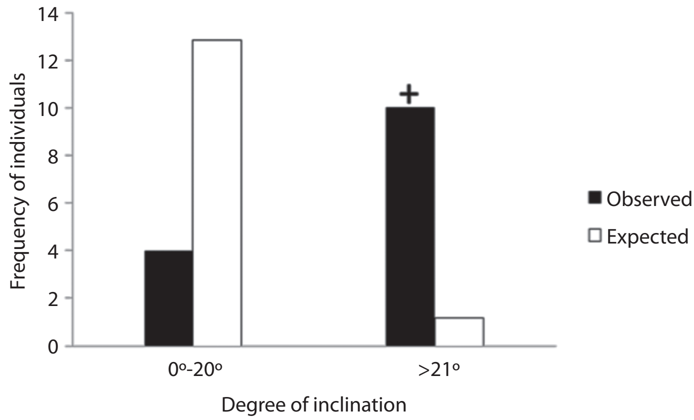

Fig. 3. Frequency of individuals observed and expected of *Thelephora* sp., grouped data from the inclination of 0°-20° and more than 21°.

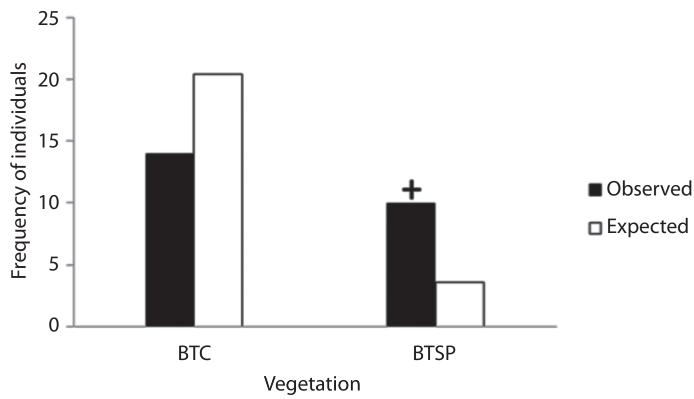

Fig. 4. Frequency of individuals observed and expected of *Thelephora* sp., over the tropical deciduous forest (BTC) and evergreen tropical forest (BTSP).

of interspecific interaction have been lacking. The current study was able to demonstrate that *T.* sp. maintains an entirely epiphytic relationship with the plants to which it adheres, similar to what was proposed by Cunningham (1957) and referred to by Corner (1968) as weak parasitism. Our data show, moreover, that *T.* sp. does not demonstrate specificity towards particular plant parts or taxa. It is important to note, however, that although the growth form of the basidiomata of *T.* sp. is variable, the difference in growth form is temporary, as the basidiomata regain their clavarioid growth as soon as they have surpassed barriers in their path (Fig. 1C).

The particular behavior of *T.* sp. is relevant from several perspectives: (1) biologically, as it indicates that this organism has the capacity to modify the development of its basidiomata and regain its original form; (2) taxonomically, in the interpretation of the observed variation of form as a differentiating character; and (3) ecologically, as a strategy for the species to complete the development of basidiomata in spite of barriers during development.

Among the diversity of clavarioid fungi present in CBS, the taxon studied here presented the greatest abundance of basidiomata, observable in all four of the sampled rainy seasons. Thanks to its leathery consistency, *T.* sp. also lasts for a longer duration than other clavarioid fungi. This abundance suggests the success of the basidiomal growth form of *T.* sp. in these ecosystems that have such marked deciduous seasonality.

Among the extrinsic factors which affect the formation of basidiomata of macroscopic fungi, humidity has been the best studied. A high correlation has been found between humidity and the formation of these structures (Straatsma *et al.* 2001, Salerni *et al.* 2002, Miyamoto & Igarashi 2004, Munguia *et al.* 2006, Gómez Hernández 2009). Although basidiomata of *T* sp. were only found during the rainy season, the ecological data presented here indicate that their distribution is not random, but instead influenced by slope, orientation, and vegetation type.

The high frequency of *T.* sp. specimens found on south-facing slopes suggests that light may be an important factor in the formation and maturation of its reproductive structures. The effect is not likely to be direct, however, as specimens were most commonly found under closed canopies where they reach greater length. Laboratory experiments have shown that the range and duration of light exposure plays an important role in the formation of basidiomata of fungi such as *Coprinus* spp*., Typhula ishikariensis* and *Clavicorona pyxidata* (Morimoto & Oda 1973, James & McLaughlin 1988, Boulianne *et al.* 2000, Kawakami *et al.* 2004).

T. sp. was found predominantly on slopes steeper than 20º, perhaps due to factors related to humidity and nutrient requirements. In samples of mycelia across a gradient from 0-25º, Lodge *et al.* (2008) observed that mycelial coverage was positively correlated with slope, and suggested that the correlation was likely due to improved nutrient uptake on steep slopes with lower humidity but high nutrient availability from runoff.

The data obtained in this study also reveal that basidiomata of *T.* sp. are more frequent than expected in the relatively uncommon sub-evergreen forests of CBS, likely due to canopy coverage. Studies by Lodge & Cantrell (1995), Suárez-Duque (2004), Gibertoni *et al.* (2007) and Lodge *et al.* (2008) have shown a relationship between the extent of canopy coverage and light incidence in tropical zones.

Future studies investigating the roles of conductivity and distribution of nutrients and the structure and type of soils will be necessary for a more detailed understanding of the development and distribution of this species.

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RESUMEN

La plasticidad fenotípica en hongos macroscópicos ha sido poco estudiada en comparación con la de plantas o animales y solo se conocen aspectos generales de estos cambios. En este trabajo se examinó la variación fenotípica en los basidiomas de una especie de *Thelephora* sp. (Thelephoraceae), así como algunos aspectos de su ecología y hábitat a partir del estudio de 24 ejemplares recolectados en bosques tropicales de la Estación de Biología de Chamela, Jalisco, México. Nuestras observaciones mostraron que este taxon presenta basidiomas en forma clavarioide, los cuales pueden modificarse a resupinados si en su proceso de desarrollo se interponen obstrucciones físicas como rocas, restos vegetales o plantas vivas, estableciendo en estas últimas solo una relación epifítica. Esta especie llega a formar conjuntos de hasta 139 basidiomas en un área de 32.2m^2; con localización predominante en laderas orientadas hacia el sur, de pendientes mayores a 20°, bajo doseles cerrados y con presencia mucho más significativa de lo esperado en el bosque tropical subperennifolio.

Palabras clave: *Thelephora*, basidioma, plasticidad fenotípica, bosque tropical.

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