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Leaf shedding and weather in tropical dry-seasonal forest shape the phenology of fungi – Lessons from two years of monthly surveys in southwestern Panama

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ABSTRACT

In the present study, conducted in a secondary dry-seasonal forest in the pacific lowlands of southwestern Panama over 2 years, fungal diversity is linked to plant phenology, litter, and climatic data. Agaricales fungi showed maximum species richness at the beginning of rainy seasons, probably due to the important litter accumulation during the dry season and the increase in humidity favoring fungal growth. Species richness declined during the wet season possibly due to torrential rains, moulds, and decreasing availability of nutrients. Occurrence of foliar pathogenic microfungi correlated negatively with flushing of new leaves at the beginning of the rainy season. Their incidence increased during the wet season and remained high during the dry season. Synchronization of leaf shedding in most tree species significantly reduced the yearly incidence of foliar pathogenic fungi causing an annual turn-over of fungal pathogens that probably contributes to maintain a high diversity of plant pathogenic species.

1. Introduction

Fungi are heterotrophic, mostly immotile organisms and colonize dead or living organic substrata as saprotrophs, parasites, or mutualistic symbionts. They depend on other organisms (e.g., plants, insects) for the uptake of nutrients, for reproduction, and dispersal. Fungal life cycles narrowly correlate with the phenology of these other organisms as well as with abiotic factors. Monitoring the phenology of organisms in natural and disturbed ecosystems is important in the context of global environmental change, since throughout the world the equilibrium of wild and agricultural ecosystems depends on climatic factors (van Vliet, 2010).

Phenology data about macrofungi are available for various temperate regions (e.g., Straatsma et al., 2001; Karasch, 2005; Boddy et al., 2014; and citations therein) but they are scarce for tropical areas (e.g., Lodge and Cantrell, 1995; Watling, 1995; Degreef et al., 1997; Lodge et al., 2004). Fruit body development apparently depends on temperature, precipitation, water availability, soil pH, nutrient availability, CO_2, light, neighboring organisms, and further factors (Watling, 1995; Moore et al., 2008). As shown for southern England for a period of more than 50 years, the phenology of macrofungal fruit bodies is most probably affected by climate change (Gange et al., 2007).

Unusual weather events also influence pathogenic microfungi, possibly jeopardizing food security and human health (Fisher et al.,

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2012). Indeed climatic shifts might be important factors contributing to the spread of fungal epidemics in natural tropical ecosystems (Gilbert and Hubbell, 1996). Seasonal dynamics of plant pathogenic microfungi on non-cultivated plants, however, have only rarely been investigated (Alexander, 1990; Shivas and Hyde, 1997; García-Guzmán and Heil, 2014). On one hand, plant pathogenic microfungi have not been considered in phenological studies of interactions of plants with other organisms, such as pollinators, herbivores, pests, or seed predators (e.g., Sakai, 2001; Williams-Linera and Meave, 2002; Hudson and Keatley, 2010). On the other hand, studies concerning the ecology of plant pathogenic fungi have mostly ignored phenological aspects (e.g., Clay, 1990; Linhart, 1991; Gilbert, 2002; Mordecai, 2011). Burdon (1991, 1993) mentioned seasonality as a cause of fluctuations in the pathogen load of wild vegetation. García-Guzmán and Dirzo (2001) observed that the level of infection by pathogens during the rainy and the short dry season (April–May) was rather similar in an evergreen rainforest in Mexico. The latter forest is a weakly seasonal forest according to Wright and van Schaik (1994). As far as we know, the study by García-Guzmán and Dirzo (2001) is the only publication which includes quantitative phenological data about plant pathogenic fungi on a community level and in a tropical forest.

Species richness and composition of plants and fungi in the study area considered here (a dry seasonal forest located in southwestern Panama) was presented by Piepenbring et al. (2012). In the present study the occurrence of fungi belonging to different systematic and ecological groups was linked to the region's seasonality. Comprehensive data sets about saprobic species of Agaricales and foliar pathogenic microfungi (fpm) were used to answer the following two questions:

(i) At a community level, does the phenology of saprobic agarics (i.e. fruit body production) correlate with precipitation and the availability of substratum (i.e. standing stocks of leaf litter)?
(ii) Is seasonal occurrence of foliar pathogenic microfungi correlated with plant phenology?

2. Materials and methods

2.1. Locality and weather data

The area of investigation (Fig. 1) is located between 8°29.2′ N 82°26.0′ W and 8°29.5′ N 82°25.9′ W, 120–150 m above sea level, in southwestern Panama, about 25 km flight distance from the coast of the Pacific Ocean. It forms part of the valley of the Majagua river and is close to the village of Los Algarrobos, Dolega district, Chiriquí province.

The meteorological station in David, located about 7.5 km south of the study site, reported precipitations of 2322 mm for 2009, and 3624 mm for 2010 (Instituto Nacional de Estadística y Censo, http://www.contraloria.gob.pa/inec/archivos/P3771121-01.pdf, P3771121-02.pdf, P5121121-02.pdf, consulted 29 May 2013). According to these data, the first dry season ended in April 2009 and the rainy season lasted from May to November 2009. The following dry season lasted from December 2009 to May 2010, the rainy season from June to November 2010, and the following dry season from December 2010 to April 2011 (cf. data in Fig. 4).

Two data loggers (DS1923-F5, Maxim Integrated, San Jose, USA) were used to perform our own measurements of temperature and air humidity. They were programmed with the OneWireViewer x64 sofware (version 0.3.15.50) to perform four measurements each day: at midnight, in the morning (6 a.m.), at noon, and in the evening (6 p.m.). The data loggers were fixed in horizontally placed tin cans. One data logger was located in the secondary forest close to the sampling area (8°29.2′ N 82°26.0′ W, cf. Fig. 1C–D) and close to stones almost at soil level. The other data logger was placed about 1 km away from the sampling area (8°29.8′ N 82°26.0′W) as a backup at a safer place.

Relative humidity and air temperature data (arithmetic means of two data loggers) were transformed into vapor pressure deficit (VPD) values following Murray (1967) (Fig. 2) (Supplementary material Appendix A, sheet humidity_temperature, columns K–M). VPD values are ecologically meaningful for plant pathogenic fungi, because VPD indicates how much more water the air can hold, in other words how close it is to saturation (Anderson, 1936; Nieuwolt, 1977; Prenger and Ling, no year). When VPD values decline, the probability of water precipitation (dew) increases. Fungal infection is most damaging below approximately 0.2 kPa (Prenger and Ling, no year). In a forest ecosystem with fluctuating humidity conditions, morning VPD values are the most relevant since they indicate the possibility of dew formation on plant surfaces which might promote fungal spores' germination and infection. Because of this, only morning VPD data were used in our analysis.

2.2. Vegetation

The original vegetation of this area was a seasonally dry forest of evergreen, brevi-deciduous, and dry season deciduous trees (cf. Santiago and Mulkey, 2005). Nowadays the area is mostly used as pasture for cattle. There are remains of riparian gallery forests and some areas are covered by secondary forests.

The sampling area was a 500 m long section of a trail down to the river Majagua, bordered by native tree species (Fig. 1A–B). The lower part of the trail was bordered by an approximately 100 yr old secondary forest (Fig. 1C–D). The vegetation of the path was affected by trampling of cattle and people, occasionally passing cars, by cutting of the vegetation at the borders of the path, the sporadic application of herbicides, and fire during dry season (Piepenbring et al., 2012).

Data on the phenology of trees in tropical seasonal dry forests in Panama are available from Croat (1978) and Santiago and Mulkey (2005). To confirm and complement the latter data by our own observations, the phenology of ten tree species typical for the sampling area was investigated (Supplementary material Appendix B). For each species, five individual trees were analyzed every month from March 31 to August 30 in 2009. Relative frequencies of branches with young leaves were estimated using the following categories: 0 = no branch with young leaves, 1 = 1–25% of the branches with young leaves, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% (Morellato et al., 2010). The Townsend and Heuberger formula (Townsend and Heuberger, 1943) was used to calculate the final percentage of leaf flushing (Supplementary material Appendix B):

$$\%\ \text{leaf flushing} = \left(\sum(v*n)/(i*N)\right)*100$$

where v = category, n = number of trees in the particular category, i = largest category (here 4), and N = total number of trees.

Leaf litter standing stocks (litter input minus decay) were measured in parallel to the monthly surveys. Litter measurements were used here as indicator of dead organic matter available to saprotrophic fungi and as indicator of plant phenology. Leaf litter was sampled in the forest on a monthly basis from three randomly chosen spots (25 × 25 cm^2) having typical litter accumulation for the respective season. Samples were transferred to the laboratory, non-litter debris removed, and the resulting leaf litter samples