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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A B S T R A C T
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.

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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, CO2, 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., 2015).
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, Chiriqui 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 Estadistica 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 software (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% (Morelato 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):

\[
\% \text{ leaf flushing} = \left( \frac{\sum (v*n)}{(*)N} \right) \times 100
\]

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 cm²) having typical litter accumulation for the respective season. Samples were transferred to the laboratory, non-litter debris removed, and the resulting leaf litter samples...
were dried on a Dörrex-desiccator until constant weight. Dried samples were weighed and the weights of three independent samples were summed up for analysis.

2.3. Monitoring of fungi and community analyses

Fungi (fruit bodies, sori, lesions on plants, and molds) were sampled every month from February 2009 to February 2011 on a defined 500 m trail segment of the Majagua valley. All sampling events were performed with similar effort, collecting samples for 2 h, as described by Piepenbring et al. (2012). Even if encountered many times, a fungal species was recorded only once during the 2 h of a sampling event.

Responses to environmental and phenological parameters (rainfall, litter production, VPD, plant phenology) were analysed for Agaricales and foliar pathogenic microfungi (fpm). Values of relative frequency were calculated for these analyses, because the absolute numbers of records were strongly affected by collecting effort and learning effect (cf. Piepenbring et al., 2012). In addition, multivariate analysis (principal coordinate analysis) and permutational multivariate analysis of variance were conducted to assess responses on a community level of all fungi, Agaricales, and fpm to the different parameters. Statistical analyses and graphics were done with R (R Development Core Team, 2015). Input data and the


Fig. 2. Local weather conditions as shown by vapor pressure deficit (VPD) in kPa. (A) Daily VPD values at 6 a.m. (long dashes — — —), noon (dash and dot line — — — ), 6 p.m. (short dashes - - -), and midnight (continuous line — — —) over more than four years. The investigation period is highlighted on the x-axis as dry and rainy seasons. (B) The morning (6 a.m.) values of VPD during the investigation period are shown as 10-d arithmetic means. The gray area above ca. 0.2 kPa VPD indicates generally dry conditions unfavorable for germination of fungal spores and infection of plants by pathogens according to Prenger and Ling (no year).
R-script used here are provided as electronic supplementary material (Supplementary material Appendix D).

3. Results

3.1. Weather and leaf litter

Relative humidity in the investigated area of the Majagua valley (southwestern Panama) was mostly higher than 90%, although it repeatedly dropped below 30% during the dry season (Supplementary material Appendix A). Temperatures recorded in the secondary forest close to the soil oscillated between 20 °C and 32 °C over the year, rarely reaching 35 °C during the dry season, with diurnal differences more pronounced than the variation of daily median values over the year.

The four VPD values recorded over a single day were fairly stable and close to each other during rainy seasons. More variability was observed during the dry season, with the lowest VPD values generally recorded in the morning (6 a.m.; Fig. 2A). Although precipitation was significantly reduced during the dry season, morning-VPD values were often below 0.2–0.3 kPa until March 2010. These values coincided with dew covering the vegetation in the morning during the first part of the dry season (pers. obs.).

The quantity of standing stock of leaf litter on the soil increased from the beginning of the dry season (December) and reached its maximum at the beginning of the rainy season (in April or May; Fig. 4). During the rainy season, leaf litter quantities decreased. This gradually lead to the exposure of bare soil in many places at the end of the rainy season (pers. obs.).

3.2. Diversity and phenology of all fungi

At the end of the sampling period, approximately 311 species of plants and 567 species of fungi (taxonomically named or morphospecies) were known for the area investigated here (Piepenbring et al., 2012). Since then, Hofmann (2013) further identified several species of Aseritera, and Kirschner and Piepenbring (2014) provided new data on cercosporoid fungi. J. Fournier (Xylariales), A. Gieffel (Mycetozoa), R. Lucking (lichens), and other collaborators further identified species from the samples which had been collected (Piepenbring et al., 2012). Overall this results in an updated list of 581 fungal species, including 16 species, which, to the best of our knowledge, had not been recorded earlier in Panama (cf. http://biogeodb.stri.si.edu/fungi; Supplementary material Appendix C).

According to the multivariate analyses, the fungal communities recorded during the first year of the investigation period (2009) significantly differed from those of the second year (2010) (Fig. 3A). The entire fungal community showed strong responses to plant phenology (measured as litter standing stock; Fig. 3B) and climatic parameters (e.g., humidity, temperature, VPD; Fig 3C). Statistical tests confirmed these results (Table 1).

3.3. Phenology of macrofungi

Fruit bodies of species of Agaricales, Geastrales, Hypocreales, and Pezizales were more frequent during rainy seasons, while species of Auriculariales, Polyporales, and Xylariales occurred in comparable frequency during seasons throughout the year. Sample numbers for most groups were rather low except for Agaricales and Polyporales. Because members of Agaricales were the only group of macrofungi showing evident seasonal variation, they were analyzed in detail.

Species of Agaricales exhibited a regular pattern in terms of relative species occurrence in the course of the two years sampling period. In both years a first peak of fruit body formation was observed around June and a second one about four months later in October–November (Fig. 4). The latter period was followed by a period with reduced fruit body development of about 6 months which coincided with the dry season. The highest peak (June 2009) corresponded to high precipitation values and high litter standing stocks. The relative species richness of Agaricales tended to be lower in times of reduced precipitation and/or litter availability.

Ordination (Fig. 5) and statistical tests (Table 1) confirmed a pronounced effect of humidity (as VPD and seasonality) on the occurrence of Agaricales (Fig. 5C). Species composition of both years resembled each other and displayed a strong overlap in the PCO ordination (Fig. 5A) resulting in a non-significant response of the agaric community to this variable (Table 1). The effect of litter quantity on Agaricales was, despite being significant, clearly weaker than the effect of seasonality (Fig. 5B and C).

Numerous species of Agaricales recorded in the context of the present investigation developed small fruit bodies with pilei diameters of less than 2(3) cm and slender stems, e.g., species of Conocybe, Coprinus s.l., Galerina, Marasmius, Mycena, Psathyrella, Tetraprygos, and Xeromphalina (cf. Fig. 6A). These fruit bodies often were ephemeral, developing and sporulating within a single or few days. Leucocoprinus fragilissimus (Fig. 6B) developed rather large, fragile fruit bodies (with pilei up to about 6 cm diam.) that were formed by a minimum of biomass and were abundant only at the beginning of rainy seasons. Mechanically damaged and water soaked fruit bodies covered by hyphomycetes or species of Mucorales (Fig. 6C) or penetrated by insects were observed during periods of frequent, heavy rains.

3.4. Phenology of foliar pathogenic microfungi

The relative species richness of foliar pathogenic fungi increased during rainy and dry seasons reaching maximum relative values mostly during dry seasons with high VPD values (dry conditions), i.e. in March 2009, February and May 2010 as well as in January 2011 (Fig. 7). Maxima of absolute species numbers of foliar pathogenic microfungi were recorded for 2009 in March (16 species), for 2010 in April (35 species) and for 2011 in February (53 species). Increasing values over time are most likely due to an increased efficiency of the investigators in documenting fungal diversity. Towards the ends of rainy seasons relative species richness of foliar pathogenic microfungi decreased slightly in November–December 2009 and in October 2010. Species incidence of foliar pathogenic fungi showed lowest relative values in June–July 2009 and in May 2010, with absolute values of seven - eight species and 18 species, respectively (Appendix C).

At the sampling event in June 2009 which corresponded to the beginning of the rainy season, mainly new leaves without infection by foliar pathogenic microfungi were observed (Fig. 8A). From March 31 to August 30 in 2009, relative species richness of foliar pathogenic microfungi was significantly negatively correlated with the quantity of new leaves (Fig. 8B; ANOVA; p = 0.02; adjusted R-squared = 0.6). Multivariate analyses of the communities of foliar pathogenic microfungi confirmed the significant responses of this fungal group to plant phenology as reflected by standing litter quantities (Fig. 9, Table 1). The factors “sampling year” and to a lesser extent the weather parameters also showed significant impacts.

Hyperparasitic fungi (17 different species) were sporadically found microinfections by leaf pathogenic fungi classified in Asterinaceae, Meliolales, Phylachorales, or Pucciniaceae (e.g., Fig. 6D). Maximum values were recorded at the end of the rainy season at the beginning of October (five different species), beginning of November (six), and beginning of December (six) in 2009 (cf.
species marked by a yellow background in Supplementary material Appendix C). In addition to hyperparasites, lichens, epiphyllous algae, cyanobacteria, other bacteria, and yeasts were also observed on leaf surfaces. Damage by insects and mites was observed frequently, but not quantitatively recorded.

4. Discussion

4.1. Phenology of plants

According to studies from central Panama, published by Croat (1978) and Santiago and Mulkey (2005) and to our data (Supplementary material Appendix B), only a few tree species typical for the seasonal dry forest investigated in southwestern Panama are evergreen (e.g., *Anacardium excelsum*, *Ocotea veraguensis*) or deciduous in the early rainy season with new leaves in the rainy season (*Cordia alliodora*). In our study most tree species were deciduous during the dry season (e.g., *Acacia collinsii*, *Bursera simaruba*, *Cedrela odorata*, *Gliricidia sepium*) or brevi-deciduous in the late dry season/beginning of the rainy season (e.g., *Byrsonima crassifolia*, *Curatella americana*, *Genipa americana*). Accordingly, maxima in the numbers of trees showing new leaves were observed in June at the beginning of the rainy seasons (Fig. 10).

Shrubs and lianas presented seasonal variations similar to those of trees (pers. obs.). Some species of herbs lacked above-ground organs during the dry season while other species exhibited more or less draught resistant leaves.

4.2. Phenology of all fungi

Fungal species were investigated on the ground and in the understory up to a height of approximately 2 m, as well as on branches which had fallen down from the canopy. This strategy probably yielded representative data, since fungi apparently are more...
abundant in the understory than in the canopy (Gilbert and Reynolds, 2005; Gilbert et al., 2007).

Large quantities of dead leaves and other organic material accumulate on the soil during the dry season. This is due to trees shedding their leaves and to draught that inhibits the development of fungi and other decomposer organisms (Wright and Cornejo, 1990; Santiago and Mulkey, 2005; and citations therein). When precipitation intensifies at the beginning of the rainy season, fungal hyphae grow, decompose organic material, and might develop fruit bodies in the case of macrofungi or microfungi with small fruit bodies, as suggested for Agaricales by the question (i) of the introduction.

The importance of standing litter quantities and humidity was confirmed by the principal coordinate analyses (Fig. 3). The significant difference in all fungi observed between the two sampling years is probably due to the incompleteness of the species lists (Piepenbring et al., 2012).

4.3. Phenology of Agaricales

The importance of humidity for the development of Agaricales fruit bodies during the rainy season was exemplified by the significant impacts of humidity, VPD, and seasonality in the principal coordinate analyses (Fig. 3, Table 1). The quantity of standing litter, an important substratum for many Agaricales, had limited impact on the Agaricales communities (Fig. 5B) probably because it might be accessible to fungi only under humid conditions.

Most fruit bodies of Agaricales are relatively small, liberate their spores, and vanish within several hours or few days (Watling, 1995; Piepenbring, 2012). Their small size might reflect limited nutrient availability, especially in the case of fungi growing on leaves and other small pieces of dead organic material, which are quickly decomposed by fungi and bacteria in hot and humid environments (Kost, 2004). Since heavy rainfalls often disrupt the litter layer and cause erosion via surface flow, ephemeral fruit bodies might also
help to minimize losses due to mechanical disturbance. As small fruit bodies quickly develop their spores, they might be able to accomplish spore dispersal before the next rain storm. Prompt sporulation of small, tropical fungal fruit bodies can also help reduce damage by mycetophagous animals and fungicolous fungi that are able to quickly develop under high humidity (Watling, 1995).

During the rainy season, the incidence of fruit bodies of Agaricales diminished probably due to leached soils and low organic material availability. In soils which are flooded due to continuous, heavy rains, the excess of moisture can effectively prevent fruit body production (Lodge et al., 2004). The interruption of the rainy season by short periods of drought (“veranillo”) together with the on-going production of organic debris by vigorous plants might nevertheless allow fungi to produce fruit bodies as observed in the present study (peaks during the rainy seasons, in September 2009 and November 2010).

4.4. Phenology of foliar pathogenic microfungi

When most plants exhibited young leaves at the beginning of the rainy season (June), the incidence of foliar pathogenic microfungi was relatively low (Fig. 7; cf. question (ii) of the introduction). After the particularly severe dry season in 2009 (cf. Fig. 2A), the synchrony of leaf production was more pronounced than in 2010. This resulted in particularly low numbers of foliar pathogenic microfungi.
microfungi at the beginning of the rainy season 2009. In 2010, the dry season was atypical (Fig. 2A) due to interruptions by rainfalls. As a consequence, plant phenology was less synchronized and foliar pathogenic microfungi were less reduced in 2010 than in 2009.

When a plant sheds its leaves, most foliar pathogenic fungi probably survive saprotrophically as mycelium in protected niches or as cells differentiated for survival and dormancy (i.e., resistant spores, immature fruit bodies, sclerotia; Agrios, 2005). This strategy can prove problematic due to wash off by heavy rains and destruction by fire (pers. obs.). A few colonies of foliar pathogenic microfungi might, however, also persist on green leaves of individual host plants that for some reasons (aseasonal rainfall, deeper roots, growth site more humid) do not follow the general pattern of phenology. This has been, for example, described for the grass Panicum maximum, the host of the smut fungus Tilletia ayresii (Piepenbring, 1996). These plants can serve as an above-ground source of fungal inoculum which might be carried by wind or by other vectors to nearby host plants. For several groups of phytopathogenic microfungi, especially for rusts and powdery mildews, the production of dormant structures is observed more rarely in the tropics than in regions with temperate climate (Piepenbring et al., 2011). Apparently, in the tropics these biotrophic pathogens rely on the availability of living host tissue throughout the year.

Following the minimum of foliar pathogenic microfungi observed at the beginning of the rainy season, their occurrence gradually increased during the following months. The slight decreases in incidence of foliar pathogenic microfungi toward the ends of rainy seasons (December 2009, October 2010) can be explained by sori and other fungal structures being washed off by
heavy rain, overgrown by hyperparasites or other epiphytic organisms, or eaten by insects, mites, or snails (pers. obs.; cf. Burdon, 1987; Clay, 1990; Agrios, 2005).

Although plant pathogenic fungi require humidity for germination and infection, in this study the incidence of plant pathogenic species was rather high during the dry seasons (with sometimes high VPD values). This is reflected by only weak correlation of seasonality, VPD, and humidity with fpm community composition as shown by POC analyses (Fig. 9C). The relatively high incidence of fpm during the dry season might be explained by the periodically low VPD values (around 0.2 kPa) especially in the morning, probably due to sporadic rainfalls. Dew allows spores of pathogenic fungi to germinate and to infect host tissues, especially in the mornings during the first part of the dry season (cf. Paul, 1990; Bradley et al., 2003). Once in contact with living plant cells, pathogenic fungi such as mildews, rusts, and smuts receive water from the host plant together with nutrients and become rather independent from environmental moisture (e.g., Paul, 1990; Parbery, 1996).

Seasonal changes in temperature, rainfall, and atmospheric humidity are traditionally considered the most important abiotic factors (proximate cues) influencing the phenology of plants in tropical dry seasonal forests (Morellato et al., 2000; and citations therein). High evaporative demand created by dry-season atmospheric conditions might be one of several cues for leaf fall. However, irrigation during the dry season in a seasonal dry forest in Panama failed to reduce the synchronous shedding of foliage by canopy trees (Wright and Cornejo, 1990) and seasonal variation in solar radiation was proposed as a factor of strong phenological selection (Wright and van Schaik, 1994). Hypotheses concerning ultimate cues for plant phenology refer to maximization of photosynthetic yield as well as to biotic interactions, especially the activity of pests and herbivores, pollinators, and seed dispersers; synchronous shedding of leaves can reduce herbivory and attack by insect pests (Aide, 1993; Coley and Barone, 1996; Sakai, 2001; Williams-Linera and Meave, 2002; and citations therein). Herbivores might be titiated by synchronous leaf production, resulting in relative damage reduction. Herbivores are, therefore, thought to exert selective pressure on the timing of leaf production and to influence patterns of leaf phenology (Aide, 1993). According to data presented in the present publication, synchronized leaf fall also has a strong impact on the incidence of foliar pathogenic fungi and might, therefore, be an adaptation to reduce these pathogens (García-Guzman and Heil, 2014).

Similarly to Parbery (1996) we also ask here how pathogens benefit from their pathosystem. Synchronized leaf shedding might interrupt competition between different fungi and other organisms competing for the same resource. By subsequently colonizing young leaves, pathogenic fungi escape from hyperparasites and other epiphyllous organisms. In addition, young leaves contain fewer endophytes (Scholzysk et al., 2013) which might interfere with infection (Weber and Anke, 2006).

Synchronous leaf fall and subsequent reduction of foliar pathogenic microfungi might also contribute to maintain a high species diversity of phytopathogenic fungi as these processes occur every year and imply a turn-over in pathogen populations. By leaf shedding dominant as well as rare species are reduced, and fresh leaves in a new setting of environmental and biological conditions offer pathogenic fungi new opportunities to test their fitness. This argument is consistent with hypotheses on the maintenance of species diversity by disturbance, for example in the context of gaps in evergreen tropical forests (e.g., Schnitzer and Carson, 2001). A high diversity of pathogenic species might also be preserved because many fungal species might present limited inocula quantities, an argument called recruitment limitation and presented by Hubbell et al. (1999) in the context of the discussion of gap dynamics.

5. Conclusions

Both the development of fruit bodies of saprobic Agaricales and the occurrence of plant pathogenic microfungi depend on the availability of suitable plant material. The occurrence of fruit bodies of Agaricales, however, is mainly influenced by humidity, while seasonal dynamics of plant pathogenic microfungi is shaped in the first place by the availability of susceptible living plant tissues (i.e. biotic interactions). Although the present study is based on more than 1650 records of fungi over 2 yr, this is not long enough to unambiguously decode annual, phenological patterns of fungi (Unserseher et al., 2012). Long-term studies of pathogens in natural vegetation are urgently needed to develop disease control strategies for agricultural crops and for a better understanding of adaptations to changing weather conditions (Dinoor and Eshed, 1984; Burdon, 1987; van Vliet, 2010).

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Supplementary data

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