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Are endophytes an important link between airborne spores and allergen exposure?

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Abstract Grasses represent one of the Earth's most common plant groups, and natural and cultivated habitats dominated by grasses cover about 40% of the land surface. In turn, each grass species hosts multiple fungal species which can behave as endophytes. An analysis of the endophytic taxa identified in surveys conducted in 14 grass species showed that some of the most frequent taxa on each grass were also present across several host grasses. These taxa were *Alternaria*, *Epicoccum*, *Cladosporium*, *Fusarium*, and a few others. A similar analysis of airborne fungi surveyed at 41 different locations throughout the world showed that some of the most geographically widespread, and most locally frequent airborne fungi belonged to the same genera that are dominant endophytes in grasses (i.e. *Cladosporium, Alternaria, Fusarium*, etc.). Therefore, airborne spores of genera that are ubiquitous in grasses are common worldwide and attain high atmospheric concentrations. In addition, spores of the above mentioned fungi are also important respiratory allergens. Direct observation indicates that saprobic colonization and sporulation of non-systemic grass endophytes could become unrestrained when their host plant tissue dies. Subsequently, when appropriate environmental conditions favour sporulation on grass host surfaces, the natural cycle for airborne conidia initiates, and large numbers of these conidia disperse as inoculum for new endophytic infections. Therefore, the cycle of endophytism may be an important link between climate, plant biology and public health.

Keywords Grasses · Airborne spores · Endophytes · *Cladosporium* · *Alternaria* · *Fusarium* · *Epicoccum*

Introduction

Grasses comprise one of the most successful plant families on Earth. The approximately 11000 species of the *Poaceae* are distributed from polar to tropical latitudes, and grass-dominated habitats, like grasslands, represent about 40% of the land surface. In the atmosphere, usually more than 25% of the airborne pollen grains belong to grasses, and in cultivated land, grasses are the most important crops (Strömberg 2011).

In turn, grasses host a very diverse and rich assemblage of endophytic fungi, capable of infecting plant tissues without causing symptoms for most or all of the plant's lifespan (Hyde and Soytong 2008; Rodriguez et al. 2009; Sánchez et al. 2012). Hundreds of species of grass endophytes have been identified in surveys that produced non asymptotic species accumulation curves, indicating that the richness of these mycobiotas was underestimated (Higgins et al. 2011; Sánchez et al. 2012). The endophytic assemblages of grasses, and also of other plants, are usually dominated by a few fungal species having a relatively high prevalence within host populations. Some of the dominant endophytic taxa in grasses are *Alternaria*, *Cladosporium*, *Penicillium* and *Fusarium* (Table 1 references; Stone et al. 2004; Ghimire et al. 2011; Sánchez et al. 2012). Given their ubiquity in grasses, dominant endophytes such as these must produce large quantities of inoculum, facilitating their transmission to new hosts. However, little is known about when and under which circumstances these endophytic species sporulate.

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Table 1 Surveys of fungal endophytes made in thirteen grass species that were used to identify multihost and most frequent fungal taxa

Grass species	Reference
Ammophila arenaria	Sánchez et al. 2008
Botriochloa macra	White and Backhouse 2007
Dactylis glomerata	Sánchez et al. 2007
Elymus farctus	Sánchez et al. 2008
Holcus lanatus	Sánchez et al. 2010
Hypharrhenia hirta	White and Backhouse 2007
Hordeum vulgare	Riesen and Close 1987
Oryza spp	Fisher and Petrini 1992
Panicum virgatum	Kleczewski et al. 2012
Phragmites australis	Wirsel et al. 2001
Stipa grandis	Su et al. 2010
Stipa tenacissima	Peláez et al. 1998
Triticum aestivum	Sieber et al. 1988
Zea mays	Fisher et al. 1992; Pan et al. 2008

Although there are exceptions, like the *Epichloë* species which infect systemically the aerial tissues of their hosts and are seed transmitted, most endophytic fungi in grasses and other plant taxa infect locally host tissues and have horizontal transmission (Saikkonen et al. 1998; Clay and Schardl 2002; Rodriguez et al. 2009). The growth of these non-systemic endophytes is limited in the host plant in what has been hypothesized to be a situation of “balanced antagonism”, where fungal growth is restricted, but not to the point where plant defense mechanisms can eliminate the fungus (Schulz and Boyle 2005).

The completion of the life cycle of non-systemic endophytic species requires sporulation, but this is not likely to occur during an endophytic phase because infections occur in healthy tissues. Sporulation of endophytes could occur in several different scenarios. One possibility is that some endophytes might be latent pathogens that will sporulate in diseased plant tissue. However, pathogens are not a considerable fraction of the endophytic mycobiota of plants, for example, only 15% of the endophytic species identified in *Dactylis glomerata* were known pathogens of this grass (Stone et al. 2004; Sánchez et al. 2007). Another possibility is that some endophytes may be latent saprobes capable of switching to a saprobic lifestyle after host tissue death, and then grow unrestricted on their host and sporulate. Several studies support this possible scenario (Sieber Canavesi and Sieber 1993; Bills and Peláez 1996; Müller et al. 2001; Cannon and Sutton 2004; Osono 2006; Promputtha et al. 2007; Parfitt et al. 2010; Purahong and Hyde 2011; Sánchez et al. 2011; Sun et al. 2011; Bills et al. 2012).

While studying the diversity of the endophytic mycobiota of grasses in Spain (Sánchez et al. 2007; 2008; 2010; 2012), we noticed that some of the most common grass endophytes belong to taxa whose spores have been reported as particle components of the air. Given the abundance of grasses on earth, and their frequent association with endophytic taxa whose spores are also found in the atmosphere, we hypothesized that if dominant endophytic species would produce spores when their host tissue dies, then grass endophytism could be an important source of airborne spores. This sequence would not only represent an important biological cycle affecting plant decomposition and fungal reproduction, but also a potential intervention point for reducing airborne allergen load. To substantiate this hypothesis, we reviewed surveys of the endophytic mycobiota of grasses and of airborne mycobiota, identifying the most prevalent endophytic taxa on each substratum.

Dominant endophytic taxa in grasses

Data was obtained from 15 surveys of fungal endophytes isolated from the aerial organs of 14 different grass species (Table 1). In each survey, the frequency of each reported endophyte was estimated as its number of isolates divided by the total number of fungal isolates reported in that survey. This frequency was expressed as a percentage of the total mycobiota. Only genera representing more than 1% of the total mycobiota of their hosts were considered.

The mean frequency of each endophytic genus in its hosts was estimated as the sum of its frequencies in all grasses where it was reported, divided by the number of host grasses. The total or global frequency in grasses of each endophytic taxon was estimated as the sum of its frequencies on all hosts, divided by 14, the total number of grass species considered. Pearson’s product moment correlation (r) was used to assess the strength of the relationships between variables like mean frequency per host and number of host grass species.

The analysis of endophyte abundance in the set of 14 grass species allowed the identification of the most common genera occurring in this set of grasses. Sixty two different fungal genera, each one representing more than 1% of all endophyte isolates obtained in each survey, occurred in the whole set of grasses. Thirty of these genera were reported in more than one host species (Fig. 1), and *Epicoccum*, *Cladosporium*, *Alternaria, Fusarium* and *Acremonium* occurred in more than half of the grass species analyzed. *Alternaria* was the most frequent endophytic taxon among the selected hosts, on average 22.0% of the endophytes isolated from leaves of host species belonged to this genus. This genus also showed a high multihost capability, being reported in 13 of the 14 host species analysed. *Epicoccum* and *Cladosporium* also occurred in 13 out of 14 grass species; but they were less frequent than *Alternaria* in their hosts (Fig. 1).

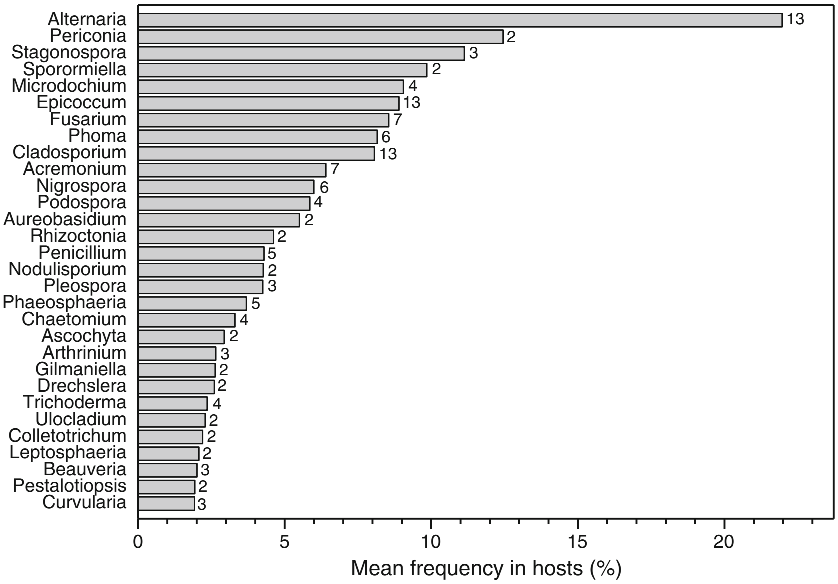

Fig. 1 Mean frequency of endophytic genera of grasses, indicating the mean percentage of the whole endophytic assemblage that each genus represents in its grass hosts. Numbers at the end of bars show the number of grass species, out of a total of 13, where the occurrence of each endophyte genus was reported

Considering the set of endophytes listed in Fig. 1, taxa with a high multihost capability tended to have a high frequency in their hosts ($r=0.59$; $n=30$, $P<0.01$). This positive significant correlation suggests that more host-generalist endophytes tend to have a greater prevalence in their respective hosts than endophytes that are more host-specific. It is likely that these endophytic taxa have very efficient mechanisms for propagation, to infect hosts, and to evade plant defense mechanisms.

In a given environment, the total abundance of an endophyte will depend on its abundance in host populations, and on the number of host species that it infects. An estimation of the total frequency of each endophyte in the whole grass set (Fig. 2) showed that some endophytes having high mean frequencies in their hosts, had a low total frequency in grasses due to their limited host range (i.e. *Periconia, Stagonospora, Sporormiella*). From a global point of view, *Alternaria*, *Epicoccum*, *Cladosporium*, *Fusarium* and *Acremonium* were the most frequent genera. These genera were often among the most prevalent in each survey; for instance, *Alternaria* was one of the three most frequent fungi in all the hosts where it was reported, and *Cladosporium*, was one of the three most frequent in 31% of the grasses where it was reported as an endophyte.

In conclusion, an analysis of endophyte surveys helped to identify fungal taxa achieving a high prevalence among different host grass populations, as well as multihost taxa present in several grass species. Some of the most abundant endophytes were also those with the greatest multihost capability, this is the case of *Alternaria*, *Epicoccum*, *Cladosporium*, *Fusarium* and *Acremonium*. Therefore, considering the abundance of grasses on earth, and the

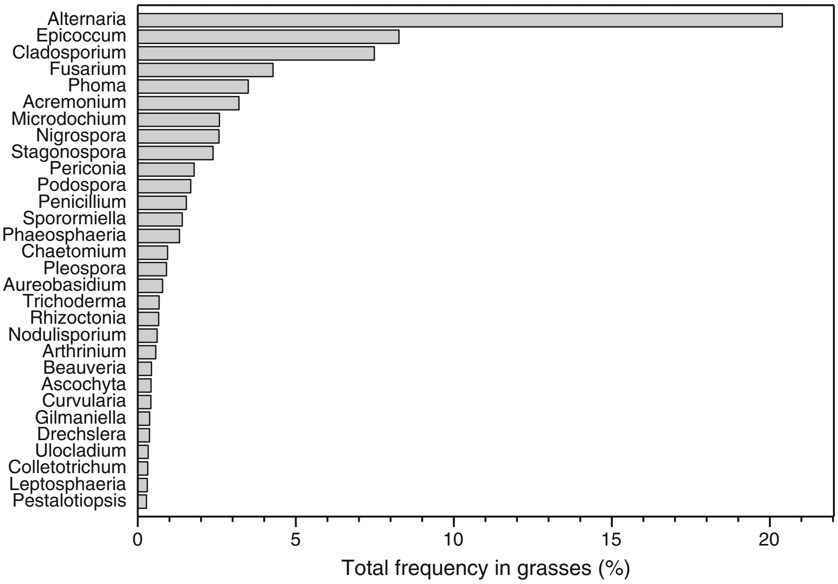

Fig. 2 Total frequency in grasses of multihost endophytic taxa. The total frequency estimates the frequency of each taxon relative to the whole set of 13 grass species considered

apparently ubiquitous relationships of these fungi with grasses, these endophyte taxa can be considered important organisms in grass dominated ecosystems. Furthermore, some of these fungal genera have also been reported as dominant endophytes in leaves of dicotyledonous plant species, like *Arabidopsis thaliana* (García et al. 2012), *Vitis vinifera* (González and Tello 2011), *Cirsum arvense*, *Plantago lanceolata*, *Rumex acetosa* (Wearn et al. 2012), and others.

Relative to other plant families, many species of the *Poaceae* have been surveyed for endophytes; therefore, some common patterns can be discerned. Nevertheless, dominant endophytes occurring in grasses could also predominate in other plant families. However, in conifers, genera like *Lophodermium* seem to be the dominant multihost endophytes, and the above mentioned endophytes, although in some cases were present, they were not as prevalent (Müller et al. 2001; Arnold et al. 2007; Sieber 2007; Yuan et al. 2011; Botella and Díez 2011; Koukol et al. 2012).

Airborne mycobiota

Most surveys of airborne fungi are based on methods where spores are trapped by air sampling devices, and afterwards the spores or the cultures to which they give rise, are identified. To identify the main taxa of airborne fungi and to estimate their abundance, we used data provided by 33 surveys of outdoor airborne fungi, carried out at 41 locations in different continents, countries and habitats (Table 2). Survey locations were defined as urban (n=21), inside cities, and rural habitats (n=20) which included croplands, grasslands, forests and large city parks. For each fungal airborne genus, its frequency at each location (local abundance) was estimated based on its number of samples or propagules (i.e. cfu m^{-3}, number of isolates) relative to the total number of airborne fungal samples recorded at that location. Only the fungal taxa representing more than 1% of the propagules of the total aerial mycobiota at any location were considered. The mean frequency per location of each fungal taxon was estimated as the mean of all locations where it was reported. The global frequency of each airborne fungal species was estimated as the sum of its frequencies at each location where it occurred, divided by 41, the total number of locations. This estimate is related to the spore abundance of a given genus at a random location.

A set of 67 fungal genera resulted from an analysis of the whole set of surveys (Table 2). Thirty five of these genera occurred at more than one location and were considered for the subsequent analyses (Fig. 3). In terms of presence at different geographical locations, *Cladosporium* spores were ubiquitous, being recorded at 95% of the locations analyzed; *Alternaria*, *Aspergillus* and *Penicillium* were found at 65–89% of the locations, and *Fusarium* and *Epicoccum* were found at 25–35% of the locations (Fig. 3). In terms of local frequency, *Cladosporium* was the dominant taxon, representing an average of 40% of the spores detected at each location (Fig. 3). Other taxa that were detected at few locations, like *Aureobasidium* and *Geotrichum*, had high local frequency (21%). However, a significant correlation between the local frequency and the number of locations where each genus was found (r=0.64; n=35; P<0.001), indicated that fungi having a high local frequency tend to be geographically widespread. We did not detect any

Table 2 Surveys of airbone fungi done in 41 urban and rural habitats, in 27 different countries. Urban habitats were inside cities and rural habitats include croplands, grasslands, forests and large city parks

Country	Type of habitat	Reference
Australia	urban	Garrett et al. 1997
Australia	urban	Mitakakis and Guest 2001
Argentina	urban	Mallo et al. 2011
Brazil	urban	Gonzalves et al. 2010
Canada	rural	Li and Kendrick 1995
Chile	urban	Henriquez et al. 2001
China	rural[a] + urban	Fang et al. 2005
Egypt	rural[a] + urban	Awad 2005
Egypt	urban	Abdel Hameed et al. 2007
Egypt	rural	Abdul Wahid et al. 1996
France	urban	Sautour et al. 2009
Greece	urban	Pyrri and Kapsanaki-Gotsi 2007
India	rural	Nayar et al. 2007
India	rural	Uddin 2005
Italy	urban	Airaudi and Marchisio 1996
Italy	rural	Magyar et al. 2009
Japan	rural	Takahashi 1997
Jordanian	rural	Abu-Dieyeh et al. 2010
Kuwait	urban	Moustafa and Kamel 1976
Lithuania	rural	Ulevicius et al. 2004
Lithuania	urban	Lugauskas et al. 2003
Mexico	rural + urban	Calderón et al. 1997
Nigeria	rural	Dransfield 1966
Poland	urban	Kasprzyk and Worek 2006
Portugal	rural	Oliveira et al. 2009
Qatar	urban	Al Subai 2002
Saudi Arabia	rural + urban	Al Suwaine et al. 1999
Singapore	rural	Lim et al. 1998
Spain	rural	Muñoz Rodriguez et al. 2010
Spain	urban	Herrero et al. 2006
Thailand	urban	Reanprayoon and Yoonaiwong 2011
Turkey	rural	Sen and Asan 2001
Turkey	urban	Suerdem and Yildirim 2009
Uganda	rural	Ismail et al. 1999
USA	urban	Shelton et al. 2002

[a] Two different locations studied

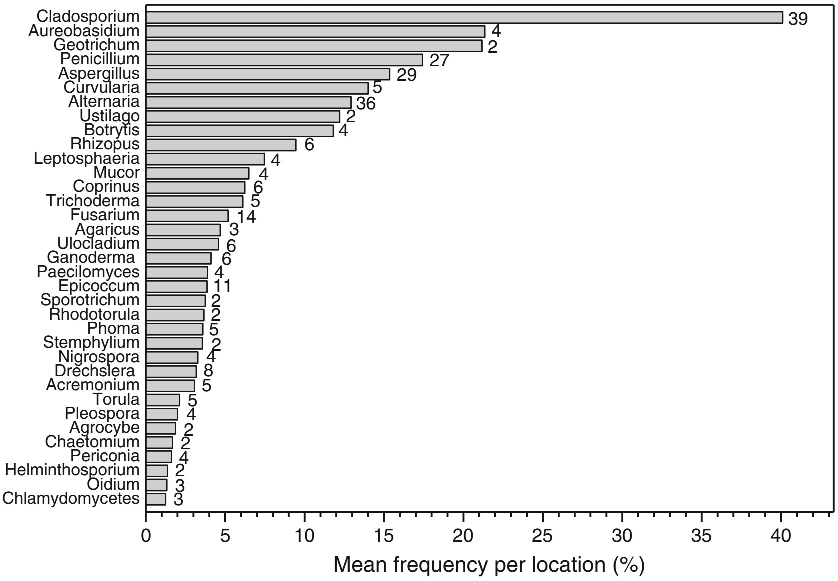

Fig. 3 Thirty five fungal genera that were identified in aerial mycobiota at two or more locations (total number of locations=41). The bars indicate the mean frequency per location, estimated as the mean proportion of the airborne mycobiota that each genus represents at the locations where it was present. The numbers at the end of the bars indicate the number of locations where each genus has been reported

noticeable difference in the most abundant genera between urban and rural habitats (data not shown).

When observed from the perspective of global abundance, *Cladosporium* stands out as an extremely abundant and geographically widespread fungus, representing about 40% of the airborne spores recorded at any location. This taxon was followed distantly by *Penicillium*, *Alternaria* and *Aspergillus* with global frequency values around 12% (Fig. 4). The remaining taxa had very low global abundance values, below 3%.

Airborne spore concentrations and their diversity vary with the time of day, season of the year, geographical region, air pollution, meteorological parameters, presence of local sources, and vegetation types. Our review was based on surveys done at 41 locations around the world, including different climate regions to achieve the highest variability possible. Thus, we found that the most widespread airborne fungi were also the most frequent (*Cladosporium, Penicilium, Alternaria* and *Aspergillus*). This implies that in spite of all of the above factors of variation, these fungal taxa are ubiquitous in the Earth's atmosphere.

Are grasses an important source of airborne spores?

Seventeen of the 30 endophytic genera most common in grasses (Fig. 2) were also present in the list of common airborne genera (Fig. 4). These fungi showing endophytic

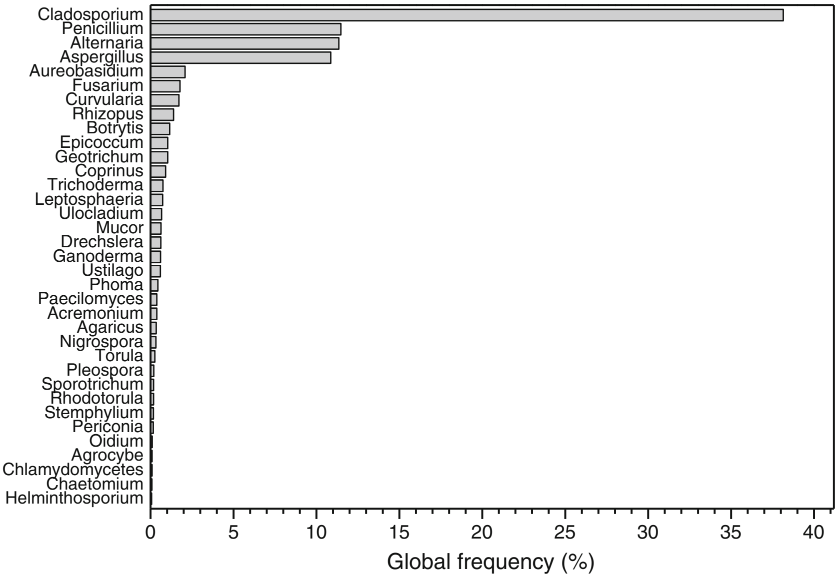

Fig. 4 Global frequency of each airborne fungal taxa. It was estimated for each genus as the sum of its frequencies at all locations where it occurred, divided by the total number of locations

and airborne phases in their life cycles are *Acremonium, Alternaria, Aureobasidium, Chaetomium, Cladosporium, Curvularia, Drechslera, Epicoccum, Fusarium, Leptosphaeria, Nigrospora, Penicillium, Periconia, Phoma, Pleospora, Trichoderma* and *Ulocladium*. In this set of fungi, a trend for increasing multihost capability with increasing frequency in the air was apparent (r=0.72; n=17; P<0.01), and particularly evident in *Cladosporium, Alternaria, Penicillium, Fusarium,* and *Epicoccum* (Fig. 5). These five genera also happened to be some of the most frequent endophytes in grasses and airborne fungi (Figs. 2 and 4). This very interesting coincidence suggests that grasses are an important source of airborne fungi, and leads one to consider whether these dominant grass endophytes may produce at some time of their life cycle spores that become airborne.

One condition contributing to endophyte sporulation is the senescence or death of their host tissue, because some host-imposed constraints on endophyte growth disappear. A switch from an endophytic to a saprobic lifestyle seems to occur in many fungal species (Stone et al. 2004; Hyde and Soytong 2008). Several studies have provided evidence of this transition where endophytes become saprobes in senescent or dead tissue of their host plants (Sieber Canavesi and Sieber 1993; Bills and Peláez 1996; Müller et al. 2001; Cannon and Sutton 2004; Osono 2006; Promputtha et al. 2007; Parfitt et al. 2010; Purahong and Hyde 2011; Sánchez et al. 2011; Sun et al. 2011; Bills et al. 2012). In grasses like *Dactylis glomerata*, *Lolium perenne* and bamboo, spore bearing structures of *Cladosporium, Epicoccum, Alternaria, Phaeosphaeria* and other endophytic taxa have been observed in the early phases of leaf and stem senescence, as well as in dead stems (Webster 1956; Brown 1984; Thomas and Shattock 1986; Wong and Hyde 2001; Zhou and Hyde 2002; Sánchez et al. 2007). In addition, we have observed that after placing surface disinfected fragments of field collected grasses of different species in moist chambers without artificial growth medium, conidia and conidiophores of *Alternaria* and other fungi developed on leaf surfaces (not published). The above observations strongly indicate that some grass endophytes, among them dominant taxa, can sporulate on dead host surfaces. Furthermore, growth and reproduction of endophytes after the death of their host tissue fits well within the theory of balanced antagonism (Schulz and Boyle 2005). Host tissue death would release host-imposed constraints for fungal growth in endophytes able to switch to a saprobic lifestyle.

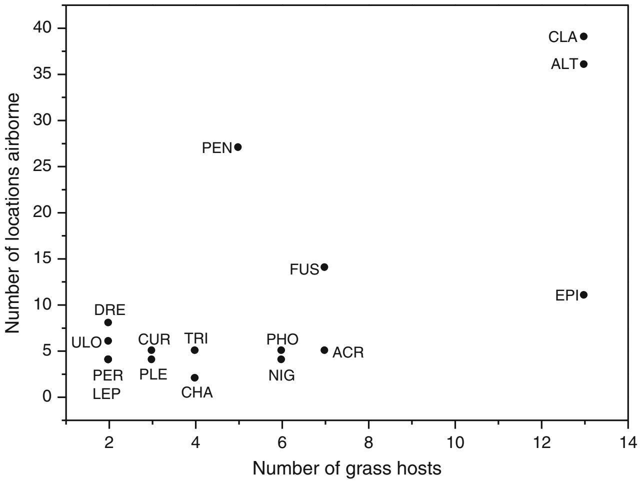

Fig. 5 Relationship between the number of grass hosts where an endophytic taxon has been reported, and the number of geographical locations where it has been reported as an airborne species. The data set (n=17) contains values for taxa that have been reported as grass endophytes and airborne. The species are indicated as: ACR: *Acremonium*, ALT: *Alternaria*, CLA: *Cladosporium*, CHA: *Chaetomium*, CUR: *Curvularia*, DRE: *Drechslera* EPI: *Epicoccum*, FUS: *Fusarium*, LEP: *Leptosphaeria*, NIG: *Nigrospora*, PEN: *Penicillium*, PER: *Periconia*, PLE: *Pleospora*, PHO: *Phoma*, TRI: *Trichoderma*, ULO: *Ulocladium*

A transition from an endophytic to a saprobic phase is likely to bring important changes in the fungus that might allow more mycelial growth and the development of reproductive structures. In this sense, Abdellatif et al. (2009) showed that the morphology of endophytic hyphae, as well as the patterns of root colonization change remarkably in living or dead wheat roots; and several endophytic species, including *Alternaria* and *Epicoccum* are known to produce several cell wall degrading enzymes in vitro or when growing as a saprotrophs (Brown 1984; Sun et al. 2011). Nevertheless, fungi like *Alternaria, Cladosporium, Epicoccum*, *Fusarium* and *Penicillium* often occur as saprobes (Richards 1953; Brown 1984; Fracchia et al. 2000; Thomma 2003; Bills et al. 2004), and they might also colonize other dead substrata besides their previous plant hosts, obviating an endophytic phase in their life cycle.

Based on the above evidence, some grass-associated endophytic genera like *Alternaria, Cladosporium, Epicoccum, Fusarium,* and others might have a life cycle as follows (Fig. 6): 1) These fungi have an endophytic lifestyle in grasses and other plants, having their growth restricted in living hosts. 2) When the plant host tissue dies, the endophytes can grow in the dead tissue as saprobes or remain latent and viable. 3) Given the appropriate environmental conditions (i.e. humidity, temperature) these fungi can grow and sporulate, often over extensive areas of the plant surface, and finally releasing spores to the atmosphere. The seasonality of sporulation observed in taxa like *Alternaria, Cladosporium, Penicillium*, and others support this hypothesis (i.e. Garrett et al. 1997; Henriquez et al. 2001; Stennett and Beggs 2004; Pyrri and Kapsanaki-Gotsi 2007; Oliveira et al. 2009). The spores of these fungi achieve their highest aerial concentrations in the spring and/or fall at locations where rains and mild temperatures, adequate for fungal growth, occur in these seasons. 4) As a result, a huge number of spores produced in dead plant tissue become airborne, and their deposition on live plant tissues represent the inoculum for horizontally transmitted

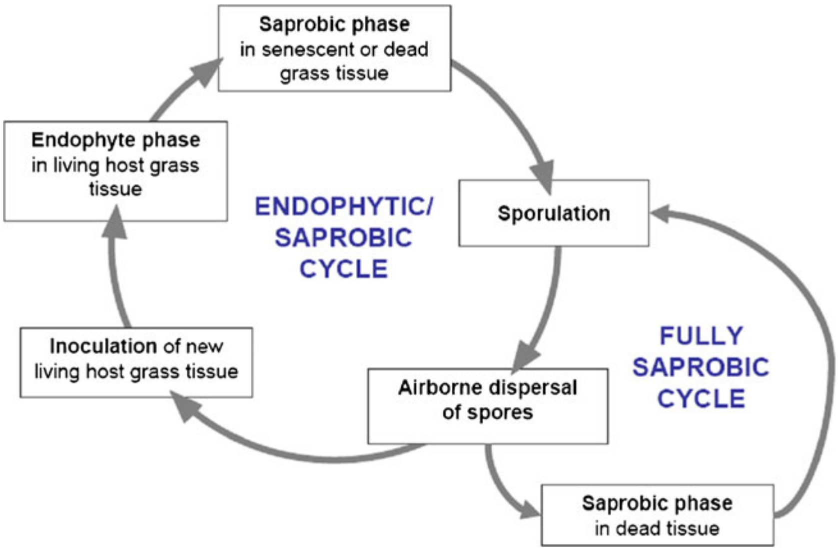

Fig. 6 A hypothetical life cycle of dominant endophytic taxa of grasses that also have been reported as common airborne fungi, such as *Alternaria, Cladosporium, Epicoccum, Fusarium* and *Penicillium*. As a result of a transition from an endophytic to a saprobic lifestyle, spores are produced on dead host tissues, and these spores become airborne

endophytes. These spores might also colonize decaying or newly dead plant tissue.

To test this hypothesis that grass endophytes contribute significantly to airborne spores, further studies are needed. Research aimed at defining species and population level genetic markers in endophytes of genera such as *Alternaria* and *Cladosporium*, and tracking these markers between endophytic and airborne populations will help to determine if species from each substratum are different, or if endophytes are a specific subpopulation among the airborne spores. Studies documenting the continuity of phases in the life cycles of endophytes in grasses will help to support the hypothesis of their sporulation when their host tissue dies, to assess the contribution of endophytes to plant decomposition (i.e. Omacini et al. 2004; Purahong and Hyde 2011; Sun et al. 2011), and to obtain estimates of the amount of spores produced and released to the air per unit of dead plant tissue. Finally, knowledge about the mechanisms that restrict the growth of endophytes in living tissues will be helpful to understand the endophyte-saprobe transition, and might have interesting applications in plant pathology and plant breeding.

Biological relevance of an endophytic-saprobic-airborne cycle

Grasses are very successful plants: thousands of species are distributed throughout many different and contrasting terrestrial habitats, including a major part of the agricultural land. In turn, these grasses are habitats occupied by numerous species of endophytic fungi. In the grass landscape, endophytes belonging to species of *Alternaria, Cladosporium, Epicoccum, Fusarium*, and other genera (Fig. 2) seem to be ubiquitous. After a transition from an endophytic to a saprobic lifestyle, these fungi are likely to play a very important role in nutrient cycling as plant decomposers, as they use nutrients from the dead tissue of their hosts for mycelial growth and sporulation. A similar situation has been reported in trees, where fungal species previously known as dead wood decomposers were found to pre-exist as endophytes in living trees (Parfitt et al. 2010).

The sporulation of dominant grass endophytes on dead plant matter, either on previous endophyte hosts or in new substrata, amplify these fungi into extremely abundant life forms. Some estimations of the *Alternaria* spore concentration in the air range from 10 to 153 spores m^{-3} (Ulevicius et al. 2004; Sautour et al. 2009). Based on these figures, and if the polar circles are excluded from calculations, in the lower 10 m of the biosphere we would expect to find $2\ 10^{16}$ to $2\ 10^{17}$ spores of this taxon. Much larger figures should be expected for *Cladosporium*, the most prevalent airborne taxon.

Another impact of this work is the link with human respiratory allergies. Common respiratory allergy symptoms, such as asthma and rhinitis, can often be a result of exposure to airborne fungi. The main allergens found in outdoor environments are pollen grains and fungal spores, whose concentration might be 100- to 1000-fold that of pollen grains, depending on environmental factors affecting plant and fungal growth (Horner et al. 1995). It has been estimated that about 5% of the general population will suffer at some time an allergy caused by fungi, and about 20–30% of the patients suffering from respiratory allergy are sensitized to fungal spores (Kurup et al. 2000; Gioulekas et al. 2004; Bush et al. 2006). Outdoor exposure seems to be more important than indoor exposure for sensitization to fungal spores, and several studies have shown that the most common airborne genera were found both indoors and outdoors, although outdoor fungal spore concentrations tend to be greater or similar than indoor (Garrett et al. 1997; Lee et al. 2006; Gonzalves et al. 2010). Not all spores are allergenic, but spores of genera like *Alternaria*, *Aspergillus*, *Cladosporium* or *Fusarium* are among the most important allergens, often linked to asthma and rhinitis (Horner et al. 1995; Kurup et al. 2000; Bush et al. 2006; Pulimood et al. 2007). Other allergenic spores are also endophytes in fact, 11 out of 24 fungal genera listed as frequently associated with allergy by Kurup et al. (2000) are also grass endophytes: *Alternaria, Aureobasidium, Cladosporium, Curvularia, Drechslera, Fusarium, Penicillium, Phoma, Trichoderma, Ulocladium,* and *Epicoccum*. Therefore, grasses can be a source of spores of allergenic fungal species, and the knowledge of this situation might be useful to prevent fungal allergies in some environments.

Climate change might affect the future distribution of grasses in some parts of the world. For instance, the predicted reduction in rainfall and increase in temperature in southern Europe may favour grasslands in the grassland-forest equilibrium, because of an increased risk of fires, and also the expansion of heat tolerant C_4 grasses. In addition, increased plant growing seasons in northern Europe might result in more grass biomass production (‘t Mannetje 2007). Thus, climate trends affecting grass growth and distribution might result in increased production of grass tissue available for endophytes, that in turn will sporulate in dead hosts. This could be a factor having an impact in respiratory allergies and other animal diseases caused by fungi (García Solache and Casadevall 2010).

In conclusion, some of the most the abundant spores found in the atmosphere have the capability to interact with plants, where they may become endophytes first and saprobes later. These fungi are extremely abundant as endophytes in grasses and other plant taxa, and are likely to have important roles as saprobes, in plant decomposition and nutrient cycling. Furthermore, the spores of these fungi also interact with human immune systems, being respiratory allergens. Fungi might have had an important impact in the evolution of land animals, as a force of selection for homeothermy (Casadevall 2012), and given the ubiquity and abundance of some important allergenic spores in the atmosphere, these spores might be currently having an impact in the evolution of immune responses to respiratory allergens.

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