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ORIGINAL ARTICLE

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A year-round study on functional relationships of airborne fungi with meteorological factors

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Abstract Air sampling was conducted in Waterloo, Canada throughout 1992. Functional relationships between aeromycota and meteorological factors were analysed. The meteorological factors were, in descending order of importance: mean temperature, minimum temperature, maximum temperature, mean wind speed, relative humidity (RH), rain, maximum wind speed and snow. The most important airborne fungal propagules in descending order were: total fungal spores, unidentified Ascomycetes, *Cladosporium*, *Coprinus*, unidentified Basidiomycetes, *Alternaria* and unidentified fungi. Most airborne fungal taxa had highly significant relationship with temperature, but *Aspergillus/Penicillium*, hyphal fragments and *Epicoccum* did not. *Epicoccum* and hyphal fragments were positively associated with wind speed. In comparison with other airborne fungal taxa, *Leptosphaeria* and unidentified Ascomycetes were more closely correlated with rain and RH during the growing season.

Key words CANOCO · Redundancy analysis (RDA)

Introduction

Air is the most common medium for the dispersal of fungal spores and hyphal fragments (Marchisio et al. 1992). The air is seldom free of fungal spores (Lacey 1981). The composition and concentrations of the airborne fungal spora are largely determined by geographic location, meteorological factors, vegetation, and human activities (Lacey 1981; Lyon et al. 1984). The concentrations of fungal spores in the atmosphere at any particular moment are influenced by the processes involved in their production, release, and deposition (Lyon et al. 1984). The eventual rates of spore deposition and resuspension depend mainly on meteorological factors and on the size and shape of the spores (Lyon et al. 1984).

The relationships between climate and fungi are complex, and should be examined from numerous perspectives (Sneller 1984). Meteorological conditions clearly have a profound influence on the production, dispersal, and deposition of fungal spores. Rain, wind speed, wind direction, humidity, temperature, and flora and fauna in the survey area are among the major factors affecting the populations of airborne fungal spores (Al-Doory et al. 1980). The influence of meteorological factors on the concentrations of airborne fungal spores appears to be additive, not independent (Munk 1981). The relationship might also be multiplicative and non-linear.

Many environmental factors are interrelated and it is often difficult to know which are the most significant (Skre 1981). A better understanding of the relative importance of these factors and their interrelationships would be of help in determining the relationships of airborne spores to allergies caused by airborne fungal spores (Lyon et al. 1984). In order to understand the significance of airborne fungi and to be able to predict the occurrence of airborne fungi, it is critical to elucidate the relationships of airborne fungal spores to meteorological factors. The objectives of the present study were to determine the functional relationships between aeromycota and meteorological factors in Waterloo, Ontario, Canada using redundancy analysis (RDA).

Materials and methods

Outdoor air sampling was conducted from January to December, 1992 at intervals of 5 to 7 days in Waterloo, Ontario, Canada; samples were taken on 58 days. On each sampling date, twelve 10-min samples were taken at 2-h internals with a Samplair-MK1 particle sampler (Allergenco, 403-7834 Broadway, San Antonio, TX 78209, USA). According to the factory calibration, 9 l of air min were drawn into the sampler. Ten-minute sampling gave an appropriate density of spores for counting and identification. Owing to inaccessibility to the roof, the sampling site was located on a northwest-facing balcony on the top floor of a two-storeyed build-

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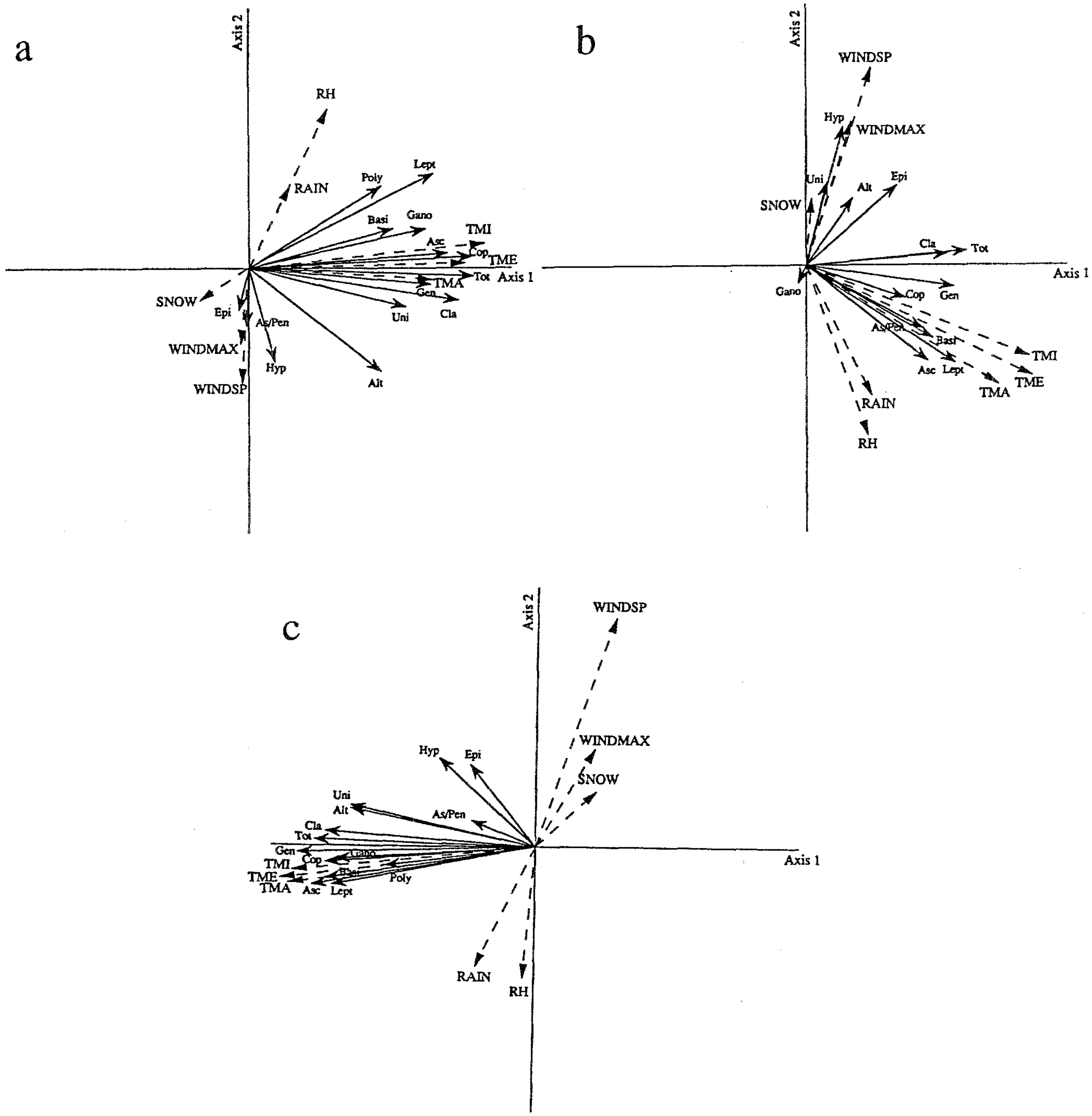

Fig. 1 Redundancy analysis ordination biplots showing meteorological factors (*dashed arrows*), and airborne fungi (*solid arrows*) from May to October (**a**), November to April (**b**) and for the whole of 1992 (**c**). Abbreviations used are as follows: meteorological factors – RH, relative humidity, TMA, daily maximum temperature; TME, daily mean temperature; TMI, daily minimum temperature; WINDMAX, daily maximum wind speed; WINDSP, daily mean wind speed; airborne fungi – Alt, *Alternaria*; As/pen, *Aspergillus/Penicillium*; Asc, unidentified ascospores; Basi, unidentified basidiospores; Cla, *Cladosporium*; Cop, *Coprinus*; Epi, *Epicoccum*; Gano, *Ganoderma*; Gen, No. of genera; Hyp, hyphal fragments; Lept, *Leptosphaeria*; Poly, *Polythrincium*; Tot, total fungal spores; Uni, unidentified spores

ing located near Waterloo park. The balcony was on the external surface of the building. The orifice of the sampler on a 1.8 m high rack was 1 m lower than the roof and 1 m away from the external wall of the building. The Samplair sampler is not waterproof, and therefore, was protected by a 50x50x40 cm baffle/cover during sampling, but there was an opening at a height of 10 cm on the low part of the exhaust outlet side of the sampler to lead exhaust air out. The top cover was 20 cm above the upper edge of the side cover. The exhaust outlet faced the building; this effectively reduced wind velocity over the sampling orifice, and apparently ensured that adequate spore numbers were trapped at all sampling times. The prevailing wind was NW in winter and SW in summer for the Kitchener-Waterloo area in 1992.

The following samples were collected and analysed. (1) (a) Conidia of *Alternaria, Aspergillus/Penicillium, Cladosporium, Epicoccum,* and *Polythrincium*; (b) ascospores of *Leptosphaeria*,

Table 1 Relative importance of meteorological factors in descending order at Waterloo, Ontario

Meteorological factor	Relative importance		
	Growing season	Non-growing seson	Whole year 1992
Maximum temperature	3	3	3
Mean temperature	2	1	1
Minimum temperature	1	2	2
Maximum wind speed	7	6	7
Mean wind speed	5	4	4
Rain	6	7	6
Relative humidity	4	5	5
Snow	Non-significant	8	8

Table 2 Summary of redundancy analysis of airborne fungal spores and meteorological factors at Waterloo, Ontario

Sampling time Axes	Growing season		Non-growing season		Whole year, 1992	
	1	2	1	2	1	2
Eigenvalues	0.545*	0.024ns	0.282*	0.036ns	0.635*	0.008ns
Taxon-environment correlations	0.851	0.679	0.619	0.723	0.854	0.557
Percentage variance of taxon data	54.5	2.4	28.2	3.6	63.5	0.8
of taxon-environment relationship	89.8	3.7	79.2	10.3	98.3	1.7
Length of gradient	1.00		1.08		1.38	

* Significant; ns, non-significant

(c) basidiospores of *Coprinus* and *Ganoderma*; (2) ascospores of other Ascomycetes, and basidiospores of other Basidiomycetes which could not be identified to genus; and (3) hyphal fragments, unidentified spores, total fungal spores and total number of genera. Since the spores of *Aspergillus* and *Penicillium* cannot usually be distinguished under a light microscope, these two genera were recorded as one pooled taxon. Meteorological data were obtained from Waterloo-Wellington 'A' weather station (latitude, 43.27 °N, longitude, 80.23 °W, elevation, 314 m), located 10 km from the sampling site. The following meteorological variables of maximum temperature, mean temperature, minimum temperature, mean wind speed, maximum wind speed, relative humidity, amount of rain and snow, were included in the analysis.

The growing season extended from May to October, the non-growing season from November to April. In the functional relationship study, data for the growing season, the non-growing season, and for the whole year were subjected to RDA using CANOCO software (version 3.12, ter Braak 1992) and CANODRAW (version 2.20) respectively (Smilauer 1991). RDA was chosen because detrended correspondence analysis of fungal spore data from the whole year suggests that the length of the compositional gradients was 1.38 standard deviations, indicating that RDA is appropriate for these data (ter Braak and Prentice 1988). The environmental data were not required to be transformed, but data on biological taxa were squareroot-transformed.

Results

The RDA results are displayed by an ordination diagram in which environmental variables are depicted by dashed arrows and fungal taxa by solid arrows (Fig. 1a; ter Braak 1992). The RDA biplot can be interpreted as follows: each dashed arrow representing an environmental factor determines a direction or axis in the diagram (Fig. 1a); each solid arrow representing a fungal genus determines a direction in the diagram (Fig. 1a, ter Braak 1987). The correlations between fungal genera and environmental factors are displayed by the angles of solid and dashed arrows. Arrows pointing in almost the same direction indicated a highly positive correlation, arrows oriented at right angles indicate nearly zero correlation, and arrows pointing in opposite directions indicate a highly negative correlation (ter Braak and Prentice 1988). Airborne fungal genera and environmental factors with the longest arrows are the most important in the analysis; the longer the arrows, the more confident one can be about the inferred correlation (ter Braak and Prentice 1988).

Crowing season (May–October)

In the growing season, we can deduce from the lengths of the dashed arrows that the meteorological factors, in descending order of importance, were minimum temperature, mean temperature, maximum temperature, relative humidity (RH), mean wind speed, rain, maximum wind speed and snow (Fig. 1a, Table 1). Mean wind speed, rain, maximum wind speed and snow were much less important than temperature and RH. The first axis is defined by temperature, the second axis by RH and wind speed. Canonical axis 1 and axis 2 explained 89.8% and 3.7% of variance in the species-environment relations respectively (Table 2). The eigenvalue of axis 1 is 0.545 and of axis 2, 0.024. Axis 1 was significant as tested by the unrestricted Monte Carlo permutation test, and axis 2 non-significant.

According to the lengths of the solid arrows, the most important airborne fungal propagules in descending or-

Table 3 Relative importance of airborne fungi in descending order at Waterloo, Ontario

Airborne fungi	Relative Importance		
	Growing season	Non-growing season	Whole year 1992
Hyphomycetes			
Alternaria	7	9	9
Aspergillus/Penicillium	Non-significant	10	14
Cladosporium	3	8	4
Epicoccum	Non-significant	7	13
Polythrincium	8	Non-significant	11
Ascomycetes			
Leptosphaeria	4	1	7
Other Ascomycetes	5	3	3
Basidiomycetes			
Coprinus	2	11	5
Ganoderma	6	Non-significant	8
Other Basidiomycetes	10	6	6
Others			
Hyphal fragments	Non-significant	5	12
Unidentified fungal spores	9	12	10
Total fungal spores	1	2	2
Total number of genera	Non-significant	4	1

der of importance were total fungal spores, *Coprinus, Cladosporium, Leptosphaeria*, unidentified ascospores, *Ganoderma, Alternaria, Polythrincium*, unidentified spores and unidentified basidiospores (Fig. 1a, Table 3). Hyphal fragments, *Aspergillus/Penicillium* and *Epicoccum* were non-significant. *Coprinus, Cladosporium*, unidentified ascospores, *Ganoderma*, unidentified spores and unidentified basidiospores had highly significantly positive relationship with temperature, while *Leptosphaeria, Alternaria* and *Polythrincium* had significantly positive relationships with temperature, but hyphal fragments, *Aspergillus/Penicillium* and *Epicoccum* showed no significant relationships with temperature.

The airborne spores of *Polythrincium, Leptosphaeria*, unidentified basidiospores and *Ganoderma* were significantly and positively affected by RH, while hyphal fragments, *Aspergillus/Penicillium* and *Epicoccum* were negatively influenced by RH. Hyphal fragments and airborne conidia of *Aspergillus/Penicillium, Epicoccum* and *Alternaria* were more or less positively related to wind speed.

Non-growing season (November–April)

During the non-growing season, according to the lengths of the dashed arrows, meteorological factors were arranged in descending order of importance as follows: mean temperature, minimum temperature, maximum temperature, mean wind speed, relative humidity, maximum wind speed, amount of rain and snow (Fig. 1b, Table 1). The first axis is defined by temperature, the second axis by wind speed, RH and rain. Canonical axis 1 and axis 2 explained 79.2% and 10.3% of variance in the species-environment relations respectively (Table 2). The eigenvalue of axis 1 is 0.282 and of axis 2, 0.036. Axis 1 was significant as tested by the unrestricted Monte Carlo permutation test, and axis 2 non-significant.

The lengths of the solid arrows showed that the most important airborne fungal propagules, in descending order of importance, were *Leptosphaeria*, total fungal spores, unidentified ascospores, hyphal fragments, unidentified basidiospores, *Epicoccum, Cladosporium, Alternaria, Aspergillus/Penicillium, Coprinus* and unidentified fungal spores (Fig. 1b, Table 3). *Ganoderma* was a non-significant taxon among the common airborne fungal genera.

The relationships between airborne populations of *Leptosphaeria*, unidentified Ascomycetes, unidentified Basidiomycetes, *Aspergillus/Penicillium, Coprinus, Cladosporium*, total fungal spores, on the one hand and temperature on the other were positively or highly significant. Unidentified Ascomycetes and *Leptosphaeria* also had positive relations to rain and RH. The airborne spore counts of *Epicoccum, Alternaria*, unidentified fungi, and hyphal fragments were positively related to mean wind speed and maximum wind speed.

Whole year

For 1992, in accordance with the lengths of the dashed arrows, the ranking of meteorological factors, in descending order of importance, was found to be: mean temperature, minimum temperature, maximum temperature, mean wind speed, relative humidity, rain, maximum wind speed and snow (Fig. 1c, Table 1). The first axis is defined by temperature, the second axis by wind speed, RH and rain. Canonical axis 1 and axis 2 explained 98.3% and 1.7% of variance in the species-environment relations respectively (Table 2). The eigenvalue of axis 1 is 0.635 and of axis 2, 0.008. Axis 1 was significant as tested by the unrestricted Monte Carlo permutation test, and axis 2 non-significant.

In conformity with the lengths of the solid arrows, the most important airborne fungal propagules, in descending order, were: total fungal spores, unidentified Ascomycetes, *Cladosporium, Coprinus,* unidentified Basidiomycetes, *Leptosphaeria, Ganoderma, Alternaria,* and unidentified fungi. Less important fungal taxa were *Polythrincium,* hyphal fragments, *Epicoccum* and *Aspergillus/Penicillium.* Most airborne fungal taxa had highly significant relationships with temperature, though *Aspergillus/Penicillium,* hyphal fragments and *Epicoccum* did not. *Epicoccum* and hyphal fragments were positively associated with wind speed. Although apparently primarily influenced by temperature (Fig. 1c, Table 3), *Leptosphaeria* and unidentified Ascomycetes also showed a somewhat closer association with rain and RH than other airborne genera.

Discussion

Temperature and relative humidity

Temperature was clearly the most important of the meteorological factors, as indicated by the length of the arrows shown in the RDA ordination diagrams. Over the whole year, mean temperature was slightly more important than maximum and minimum temperature, but minimum temperature appeared to be somewhat more influential during the growing season (Fig. 1a). This was probably because minimum temperature was a limiting factor for fungal development.

The virtual absence of any relationship of *Epicoccum* spore numbers to temperature during the growing season suggests that its growth threshold temperature might be low. This could also explain its pattern of occurence later in the season, although such a hypothesis needs to be tested in the laboratory.

For the release of hyphomycete conidia, temperature was less important than wind, but for all basidiospores and ascospores, RH was somewhat more important as indicated by the directions of the arrows of *Ganoderma, Coprinus,* unidentified basidiospores, *Leptosphaeria* and unidentified ascospores. Similar results were observed in other studies (McDonald and O'Driscoll 1980; Beaumont et al. 1985; Halwagy 1989). Basidiospores, prior to their release, form a waterdrop around the hilar area, but whether the drop forms endogenously or exogenously is still in question. It seems that the relation of RH and ascospores reflects the role of RH in ascoma gelatinization, ascus deliquescence or ascus dehiscence, but no explanation or similar observations are to be found in the literature. Ingold (1971) noted that the detailed mechanism of dehiscence of inoperculate asci is not well understood and speculated that possible hydrolysis of material filling the pore is involved. Nevertheless, it is generally agreed that ascus dehiscence mechanisms are basically hydrostatic in nature, depending on water uptake by the ascus of which the contents develop an elevated osmotic pressure by transformation of osmotically inactive carbohydrates into osmotically active sugars. Fungal tissues must therefore be, and remain, hydrated for spore dispersal (Kendrick 1992).

Rain

Spore release by the impact of raindrops may be functional with dry conidia, but is more significant for dispersal of slimy spores, which resist wind dislodgement. Members of the bitunicate Ascomycetes with asci having a gelatinous inner wall, and Ascomycetes with ascoma gelatinization or explosive ascus deliquescence rely on rainfal for spore release (Moore-Landecker 1982). Burge (1986) noted that during rain the ascospore counts of *Leptosphaeria* and *Ophiobolus* increased dramatically. The ascospores of *Leptosphaeria* have a gelatinous sheath and those of some *Ophiobolus* species have a gelatinous terminal appendage (Sivanesan 1984; Hanlin 1990). Although this is not clear in the accompanying figures based on pooled data, we observed a dramatic increase in ascospores of *Leptosphaeria* during rain, as has been documented in a previous publication (Li and Kendrick 1994) and was also demonstrated by Hasnain (1993).

The discharge of ascospores of *Dialonectria (Nectria) galligena* (Bresadola) Petch, *Venturia inaequalis* (Cooke) Wint. and *Cryphonectria (Endothia) parasitica* (Murrill) Barr is closely correlated with rainfall (Ingold 1960). *Venturia* is bitunicate with a thin gelatinous sheath on ascospores of some species (Sivanesan 1984; Hanlin 1990). Asci of *Cryphonectria* are deliquescent (Hanlin 1990). *Nectria* does not undergo ascoma gelatinization or ascus deliquescence, but it does have an apical spore discharge mechanism, as do most other Ascomycetes. More studies are required to elucidate the mechanisms associating spore release with relative humidity for *Nectria* and other similar Ascomycetes: Meredith (1962) noticed that during rain unidentified ascospores in the air increased more than 476-fold.

Wind

Average wind speed was more important than maximum wind speed. The effect of average wind speed operated over a longer time period, while that of maximum wind speed was mainly short-term. Maximum wind speed was probably important for dry spore release and spore resuspension at certain times. The large spores of *Epicoccum* and *Alternaria* require more external energy for release and dispersal; wind speed was important for aerial transport of those spores. Hasnain (1993) noticed that there was a negtive correlation between wind speed and basidiospores of *Ganoderma.* The results from the present studies show that there was almost no correlation between wind speed and *Ganoderma* from May to October, and a negative correlation from November to April. Since the building at which samples were taken produced a partial blocking effect on wind speed due to the position of the sampler, it is difficult to draw general conclusions concerning the importance of wind. Such effects should be carefully minimized in future studies.

Snow

The effect of snow was twofold: (1) it precipitated out airborne spores, reducing the number of spores in the air; and (2) fungal spores were kept covered beneath the snow and thus prevented from resuspension. It is obvious that the effect of snow was negative on most airborn fungi. The positive relations to *Epicoccum, Alternaria,* hyphal fragments and unidentified spores may be due to long distance transport and require further study.

Conclusions

The effects of the meteorological factors varied among seasons. Similar results emerged from a canonical correspondence analysis (CCA) conducted in the Kitchener-Waterloo area (Li and Kendrick 1994). The averages of the meteorological factors were generally more important than maximum and minimum values. Field observations should be combined with controlled experiments in the laboratory to understand better the relationships of airborne fungi with meteorological factors. The effect of environmental factors may not be linear. McCracken (1987) showed that the effect of temperature on spore release of *Paxillus panuoides* was reversed at 37 °C. The relations of airborne fungi to environmental factors should be understood from the perspective of long-term, short-term and instantaneous studies. There are many unanswered questions about the mechanisms of spore release and dispersal requiring intensive study.

Most studies have focused on long-term relationships. Instantaneous and intermediate-term relationships of airborne fungi and meteorological factors are important for understanding of variations in spore populations over short periods, and will repay further study. Both natural and artificial climate play important roles in the initiation and exacerbation of mould-induced allergic symptoms. Yet studies on the functional relationships of airborne fungi with either natural or artificial climatic factors are virtually absent from the literature. It is also essential to conduct studies on functional relationships in indoor environments for improved understanding of indoor airborne fungal dynamics.

ter Braak and Prentice (1988) suggested that the length of the gradient of the first axis in detrended correspondence analysis (DCA) is a useful guide for choosing a direct gradient analysis between CCA and RDA. They proposed that if the length of gradient of the first DCA axis is between 1.5 and 3, both CCA and RDA are appropriate. If the length of the gradient is less than 1.5, RDA is appropriate; while the length of gradient is greater than 3, CCA is appropriate. Since the length of the gradient of the first DCA axis in the present study is less than 1.5, only RDA is an appropriate method of analysis.

Both CCA and RDA are used to explore the relationships of airborne fungal taxa with their environment, but in different ways. RDA shows the relationship by the angle of species and environmental arrows (the cosine of the angle between the arrows of a fungal taxon and an environmental factor is an approximation of the correlation coefficient between the fungal taxon and the environmental factor; Jongman et al. 1987). CCA shows the precise orientation of taxa if a line is projected perpendicularly onto the environmental arrows in the biplot. The RDA lacks an ability to show optimal species positions in a biplot. However, RDA is still a good approach to understanding relationships between species and environmental factors when the variation in the data matrix is not large (length of gradient of first axis<1.5) and CCA is inappropriate to analyse such a matrix.

In order to understand fully the influences of airborne fungi on human allergies, outdoor studies alone are not enough. Indoor studies must be carried out in parallel to elucidate relationships between indoor and outdoor airborne fungi and perhaps also to distinguish their roles in triggering allergies. A further paper derived from our study will describe and interpret the results of our parallel observations.

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