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ORIGINAL PAPER

Distribution of *Ophioglossum reticulatum* L. in South America. A case of long-distance jump dispersal?

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Abstract The objective of this exploratory work is to test the hypothesis that South American populations of *Ophioglossum reticulatum* L. derive from Africa. Spores cross the Atlantic transported by wind and arrive in South America in recurrent migration. Three-dimensional (backward and forward) trajectories of spores between Africa and South America were calculated using the Hybrid Single Particle Lagrangian Integrated Trajectory Model (HYSPLIT4). The model showed possible backward trajectories in the low troposphere arriving in South America with probable origin in Northwestern Africa. The results support the hypothesis of long-distance dispersal of the studied species. Including vertical motion in the model runs allowed obtaining valuable and novel information about the migration routes. The trade winds combined with the South American monsoon could be a dispersal vehicle for the disseminules from Northwestern Africa to the eastern slopes of the Andes. As the monsoon is a periodic regional atmospheric circulation pattern, transcontinental migration can be assumed to be a recurring phenomenon that provides genetic exchange and prevents speciation by reproductive isolation. Modelled forward trajectories connect the neotropics with Africa-Madagascar, but they seem to be less effective due to their travelling altitudes. This hypothesis might explain the absence of infraspecific taxa restricted to different geographic locations.

Keywords Jump dispersal · Recurrent migration · Disseminules · Ferns · Monsoon · Low-level jet

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Introduction

Ferns and lycophytes concentrate in the tropics, although their distribution range extends to extratropical regions in both hemispheres, from sea level to 5,000 m above sea level (m.a.s.l.) in the tropical mountain ranges (de la Sota 1977). Habitat diversity, meteorological and biological factors, as well as physiological adaptations have all been suggested to explain fern richness and distribution (Barrington 1993; Kornas 1993). In addition, this group is apt for long-distance dispersal (LDD) (Smith 1972), which explains the disjoint distribution of many species. Some authors studied LDD and regional-scale transport of different natural aerosols (Johansen and Hafsten 1988; Johansen 1991; Hjelmroos 1991; Cabezudo et al. 1997), but only a few studies reported LDD in Argentina (Bianchi 1994; Pérez 2000; Pérez et al. 2011; Gassmann and Pérez 2006).

Cases were studied in literature of transcontinental LDD of Saharan dust, sea salt, biomass burning, fungi and bacteria. Formenti et al. (2001) documented the transport at low altitudes (below 800 hPa) of wind-blown dust from the Sahara across the North Atlantic Ocean towards Brazil and Suriname using in situ measurements and backward trajectories. Koren et al. (2006) showed that about half of the supply of nutrients to the Amazon basin is emitted from the Bodèlè depression

(Africa), where strong surface winds are responsible for dust emissions on 40 % of boreal winter days. Fabian et al. (2009) analysed the composition of rain and fog water samples on the eastern slopes of the Ecuadorian Andes; the related backward trajectories showed evidence of biomass burning and volcanic particles, sea salt and African dust. Prospero et al. (2005) showed that significant concentrations of viable bacteria and fungi are routinely transported with African dust across the Atlantic during much of the year.

Ophioglossum reticulatum L. (Ophioglossaceae) is a homosporous fern that can be found in tropical and subtropical regions in both hemispheres (Clausen 1938). In America, it grows in southwestern USA, Mexico, Central America and southeastern South America (SESA) (Uruguay, Paraguay, Brazil, Bolivia and Argentina) (Meza Torres 2012), and it is absent in continental Chile (Rodríguez Ríos 1995). The southernmost population in SESA was registered in the Paraná River delta, near 34° 22′ S (Meza Torres et al. 2013). Typically, this fern grows in disturbed or moderately disturbed places, such as shrubby edges, wet grasslands and forest margins, but never in areas with dense tree cover (Meza Torres et al. 2013). In South America, it is often found on pastures dominated by *Andropogon* L. (Meza Torres et al. 2010). *O. reticulatum* lives from sea level to 2,100 m altitude in Lagunas de Yala, Jujuy, Argentina (24° 6′ 20.84″ S, 65° 28′ 40.76″ W) (Meza Torres 2012).

As in most ferns, *O. reticulatum* spores are more likely to be subject to long-distance transport than the heavier propagules of seed plants (Moran 2008). *Ophioglossum* gametophytes, being a homosporous fern, have self-fertilization, which enables colonization from a single spore (Wagner 1972). It forms dense populations which rapidly colonize new places (Meza Torres 2012). This fern produces non-green spores of 32 to 50 μm in diameter (on average 35 μm) (Tryon and Lugardon 1991; Meza Torres 2012). The absence of chlorophyll in the cytoplasm increases their viability period to 3 years on average (Muñoz et al. 2004; Pérez Garcia and Reyes Jaramillo 1993). These features would allow LDD in the low troposphere.

The global monsoon system might act as a dispersal mechanism, carrying spores from Africa to South America. Monsoon systems are characterised by reversal in wind direction and shifts in the rainfall regime—with more rain in summer—from cold to warm seasons. Summer monsoon circulation develops accompanying the seasonal displacement of the Intertropical Convergence Zone (ITCZ). Such circulation is associated primarily to changes in heat distribution from summer to winter. In South America, the major diabatic heat centre is located over the subtropical highland (about 20° S) during austral summers. The South American monsoon (SAM) is driven by a sharp thermal contrast between the subtropical highland and the surrounding oceans, Earth rotation and the relative orientation of mountains and wind. Feedbacks with large-scale circulation and the release of latent heat play an important role as well (James 1995). Zhou and Lau (1998) demonstrated that monsoon perturbation at low levels together with the mean trades travels from the western Sahara to central South America.

According to Nogués-Paegle et al. (2002), the SAM develops over largely varying surface conditions: from the world's largest tropical forest (Amazonia) to high desert (Bolivian plateau). The high Andes Mountains effectively block wind, which is deflected southeastward and reaches the subtropical plains of South America. This wind, known as the South American low-level jet (SALLJ), peaks at 1,500 m.a.s.l. approximately. Previous studies indicate that the SALLJ takes place all year round (Ulke et al. 2012 and references therein), allowing tropical air masses to reach mid-latitudes.

Airborne particles are generally emitted near the surface and are subject to dispersion processes, mainly turbulence in the atmospheric boundary layer (ABL). As a result of this transport mechanism (convection), particles enter the free atmosphere where they are advected over great distances, driven by increasing horizontal wind speed with altitude and deposited far away (Arya 1999).

This is what happens to *O. reticulatum* spores, which have a rather passive behaviour, in contrast to most ferns. Sporangiums remain open to the air until wind incidence promotes an oscillatory movement of the fertile spike which results in the emission and takeoff. The dispersion of the pale-yellowish cloud emitted is easily visible (Meza Torres 2012).

The hypothesis of fern LDD from Africa to South America was suggested by Moran and Smith (2001). These authors presented a list of 114 species that are present in both continents and have floristic affinity. Twenty-seven are the same species and the remaining are species pairs or closely related taxa at the infrageneric level. According to those authors, LDD explains the distribution of those 27 species because they belong to families that appeared during the Paleocene. Muñoz et al. (2004) also suggested that LDD could explain floristic affinities among extratropical Southern Hemisphere landmasses.

The aim of the present study is to show that the SALLJ acts as a regional aerobiological corridor for disseminules of *O. reticulatum*, based on the match of the global distribution of monsoon systems and *O. reticulatum*. Our first approach is to provide elements to support the LDD hypothesis through the analysis of some particular events in which atmospheric circulation favours transcontinental transport.

Materials and methods

The distribution map of *O. reticulatum* was plotted using the works of Clausen (1938) as basis. New localities were added based on examined specimens from the following herbaria: AS, B, BA, BAA, BAB, BAF, BM, BR, CTES, CTESH, E, ESA, FCQ, G, K, LIL, LIV, LP, LPB, M, MO, MVA, MVJB, MVM, NY, P, PY, S, SCP, SI, SGO and UPS. Regional floras, and catalogues also have been consulted (Allan 1961; de la Sota and Ponce 2008; Lichtenstein 1944; Luteyn 1999; Mickel and Smith 2004; Proctor 1985, 1989; Sehnem 1979; Singh et al. 2009; Tryon and Stolze 1989; Wagner 1995; Wheeler 1992).

Horizontal fields of near surface wind (925 hPa, about 800 m.a.s.l.) for the period 1980–2010 (30 years) from reanalyses of the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP-NCAR) (Kalnay et al. 1996) were used to represent global monsoon circulation and the composites of mean seasonal wind. Austral summer and winter were defined as December to February (DJF) and June to August (JJA), respectively. Global monsoon seasonality was represented with difference vectors (JJA minus DJF and DJF minus JJA), and composites, using streamlines (lines tangent to the horizontal wind vector at every point).

Backward trajectories were calculated to link arrival locations in South America with possible fern source regions in Africa. Forward trajectories were obtained to explore potential pathways from South America to Africa-Madagascar. Locations were selected according to the geographical distribution of *O. reticulatum*.

Three-dimensional trajectories were computed using the Hybrid Single-Particle Lagrangian Integrated Trajectory model (HYSPLIT4) developed at the National Oceanic and Atmospheric Administration Air Resources Laboratory (NOAA ARL, USA) (Draxler and Hess 1997, 1998). Vertical velocity was calculated assuming isentropic processes, to preserve quasi-conservative parameters in air mass motion (Carlson 1998). The horizontal flow along an isentropic surface contains the adiabatic component of vertical motion often neglected in conventional vertical reference systems (pressure and height). Moreover, atmospheric variables tend to correlate better along isentropic surfaces than on constant pressure or height surfaces, a relevant feature in LDD.

Atmospheric fields from NCAR/NCEP reanalyses were used to drive the model. Backward (forward) trajectories were calculated for 300 h. The model option that allows slight perturbation at the starting point was applied to control the consistency of modelled trajectories. Days with a high degree of uncertainty were rejected. Several final (initial) altitudes above ground (m.a.g.l.) were considered, but only the results for 1,000 m.a.g.l. are discussed as representative of the arrival (departure) level at the destination (source) region. HYSPLIT4 also provides information on temperature and relative humidity along the trajectory.

Taking advantage of the South American low-level jet experiment that was held in the austral summer 2002–2003, the analysis of SALLJ occurrence in Vera et al. (2005) and references therein, we here calculated backward and forward trajectories for that summer. Additionally, forward trajectories were calculated for the 2003 austral winter.

Although several events were analysed, a reduced sample is presented for brevity. Three arrival locations in SESA were selected for the backward trajectories and two South American coastal sites for forward trajectories. Locations represent regions rather than specific points—for backward trajectories: region 1 representing Buenos Aires (Argentina) with arrival position at 34° S, 58° W; region 2, Santa Cruz (Bolivia) at 18° S, 60° W; and region 3, Alto Paraguay (Paraguay) at 22° S, 58° W. For forward trajectories, the selected sources (region 4) are two points near 22° S, 46° W (Brazil) on the Atlantic coast where atmospheric circulation is more prone to transport spores to Africa-Madagascar.

Results

The northern distribution limit of *O. reticulatum* in the Western Hemisphere is close to 37° N, whilst the southernmost population in South America was found in the Paraná River delta, near 34° 22′ S. In the Eastern Hemisphere, the northern distribution limit is near 34° N, whilst the southern limit is in New Zealand, at about 45° S (Fig. 1).

Only the most relevant features of the 30-year mean low-level circulation for austral winter and summer are described. Figure 2 shows the regional monsoon circulation, which is remarkably similar to the distribution of the fern (Fig. 1). Semi-permanent anticyclonic circulation is present at about 30° latitude in both hemispheres (Fig. 3). From 40° S to 70° S, wind is pre-eminently zonal (west to east) since there is practically no land at these latitudes. In the tropics, circulation is related to the monsoon with the characteristic flow reversal between seasons. Such reversal is not evident in the SAM, where composite wind always has east component, but it can be seen clearly in the difference fields (Fig. 2a, b).

Initially, backward trajectories (Fig. 4a–c) are parallel to the Equator. When the high Andes range blocks the easterly flow, it causes a counterclockwise gyre resulting in a poleward deflection.

Air temperature (Ta) over the trajectories arriving in Argentina varied between 14.5 and 25.8 °C with a mean of 18 and 3 °C standard deviation (sd); relative humidity (RHa) ranged from 60 to 85 %, with a mean value of 67 % (sd=5 %) (Fig. 5a). Initial Ta was 18.4 °C (NW Africa: 5° N, 8.5° W) and decreased slightly when air parcels were advected over the ocean, where it reached the minimum. Over land, RHa varied from 63 to 75 %; the range was smaller (60–68 %) over the ocean. Transport altitude varied from 400 to 1,950 m.a.g.l., with a mean of 1,392 m.a.g.l. (sd=406 m.a.g.l). The highest

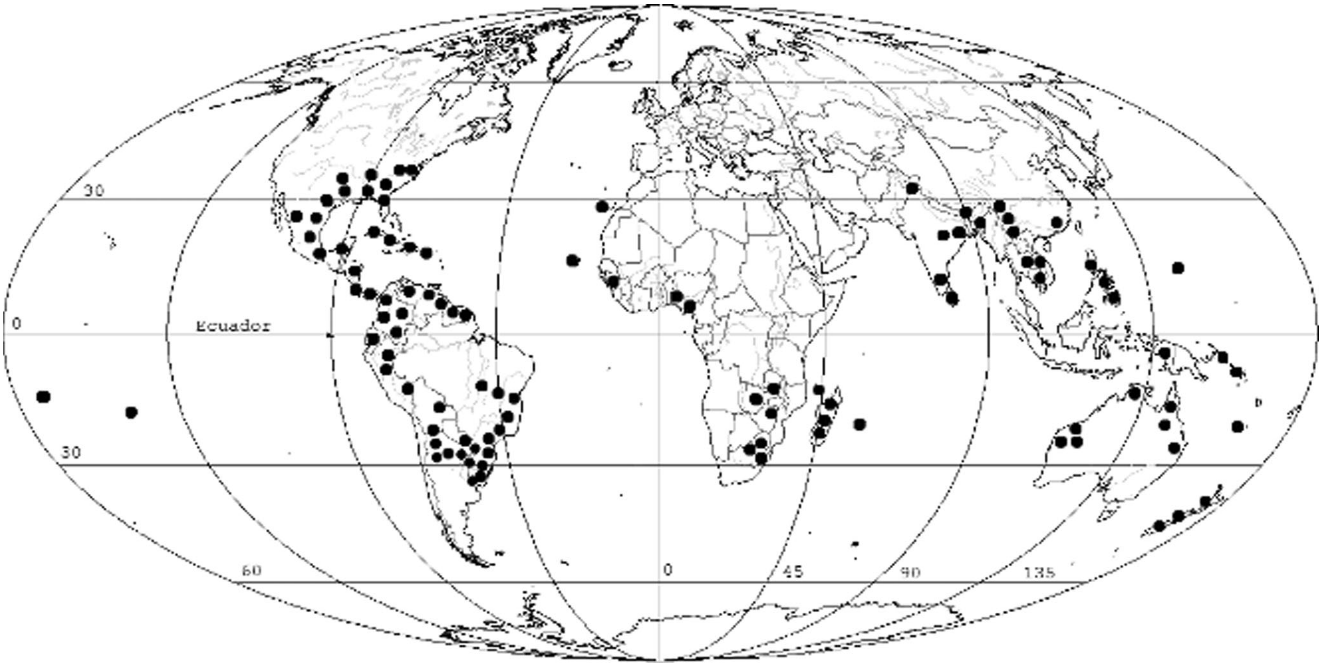

Fig. 1 Global distribution of *Ophioglossum reticulatum*, based on Clausen (1938), updated with the cited regional floras and new collections

trajectory altitude occurred over the ocean (Fig. 5b). After decreasing and reducing its variability over the ocean (hour= −162), Ta warmed over land due to strong summer surface heating. This can be observed in the final part of the trajectory (from hour −45 to −19), at 500 m.a.g.l. (Fig. 5a, b). The noticeable increase in RHa (from hour −162 to −78) was probably associated to local weather and/or strong evapotranspiration processes.

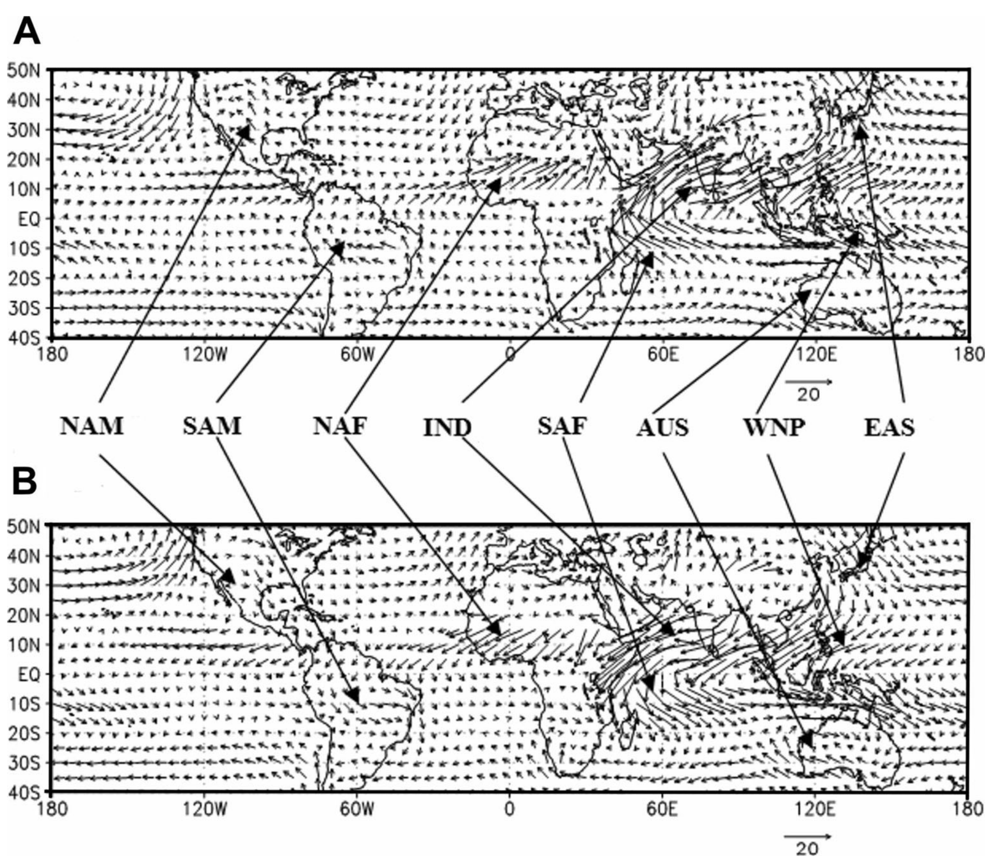

Fig. 2 Seasonal change in lower tropospheric wind (925 hPa) over the tropical monsoon regions **a** JJA minus DJF and **b** DJF minus JJA. The regional monsoons are the North American monsoon (NAM), North African monsoon (NAF), Indian monsoon (IND), East Asian monsoon (EAS), Western North Pacific monsoon (WNP), South American monsoon (SAM), South African monsoon (SAF) and the Australian monsoon (AUS). *Arrows* indicate the wind speed scale in meters per second. Adapted from Wang et al. (2011)

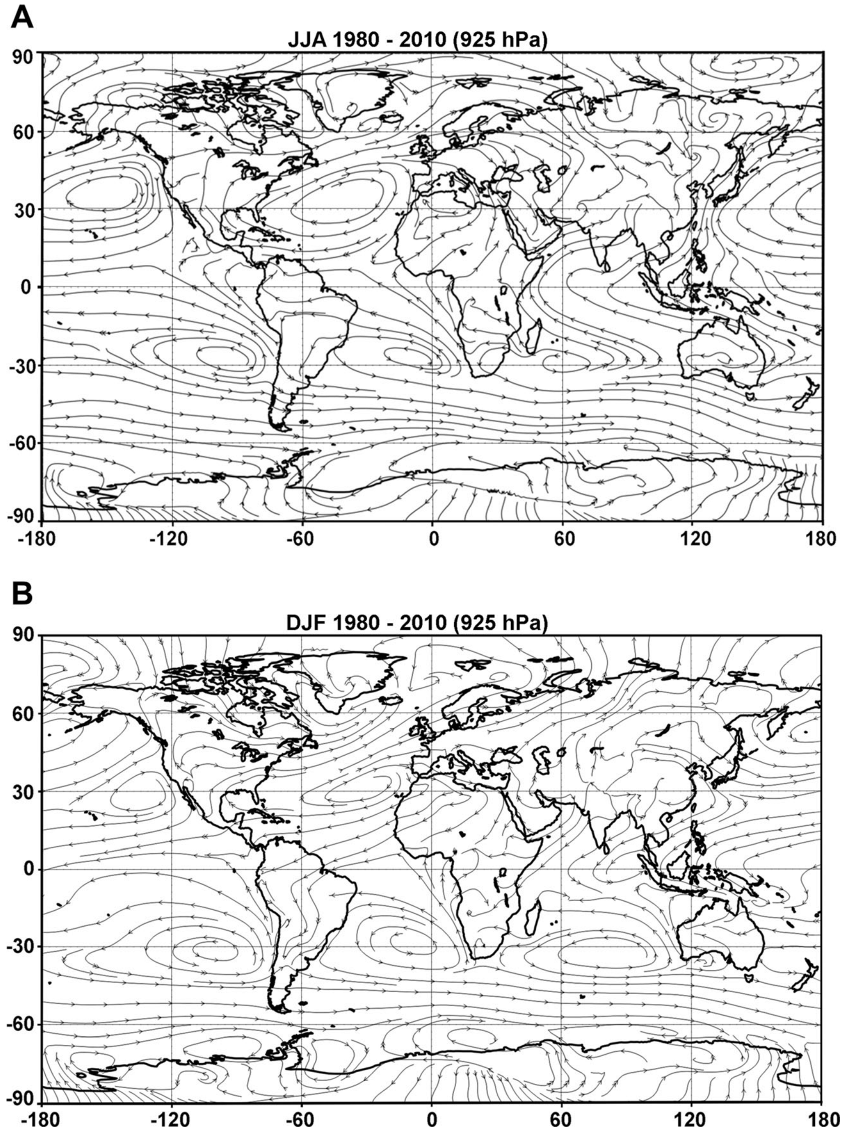

Fig. 3 Streamlines illustrating the 30-year mean horizontal low-level circulation (925 hPa) during **a** austral winter and **b** austral summer

During transit to region 2, Ta ranged from 13 to 23 °C, with a mean of 17 °C (sd=2 °C) (Fig. 6a). RHa varied between 59 and 83 % (Fig. 6a), with a mean of 66 % (sd=6 %). Initial temperature in NW Africa (8.5° N, 2° E) was 19 °C and it decreased continuously until arrival (Brazil: 1.2° N, 45.7° W, hour −96). The progression of RHa over sea shows a similar behaviour. RHa increased markedly over land, with a maximum (83 %, hour −7) close to the arrival point. In this case, transport altitudes ranged from 1,000 to 2,100 m.a.g.l., with a mean of 1,644 m.a.g.l. and sd of 290 m.a.g.l. (Fig. 6b). The increase in Ta over land was much less than on arrival in region 1, because air parcels were at higher altitudes. The sharp increase in RHa over land might be linked to greater water vapour content and to decreased Ta.

For Paraguay, Ta was initially around 18 °C (NW Africa, 5° N, 2° W) and rapidly cooled to 12.5 °C (Fig. 7a). No clear trend was observed after that until air parcels arrived in the continent where Ta increased steadily. Variability of RHa was less over ocean than over land (Fig. 7a). Mean values of Ta and RHa were 15 °C and 65 % and the corresponding sd 1.5 °C and 4 %. Maxima and minima were 22 and 12 °C and 77 and 57 % for Ta and RHa, respectively. Air parcel altitude was always above 1,000 m.a.g.l., particularly over the ocean where it reached 2,000 m.a.g.l. (Fig. 7b). Temperature was cooler and less variable along the trajectory than the previous cases. The jump in RHa at the ocean-land interface and the change in the Ta trend were similar to the former trajectory (Fig. 6a).

Forward trajectories illustrate LDD from the neotropics to Africa-Madagascar (Fig. 8a, b), with a counterclockwise gyre over the South Atlantic Ocean, moving over the ocean south of Africa and arriving in Madagascar. In the summer trajectory, Ta varied from 1 to 24 °C (Fig. 9a), with a mean of 8 °C (sd=5 °C). RHa ranged from 23 to 98 %, with a mean of 56 %

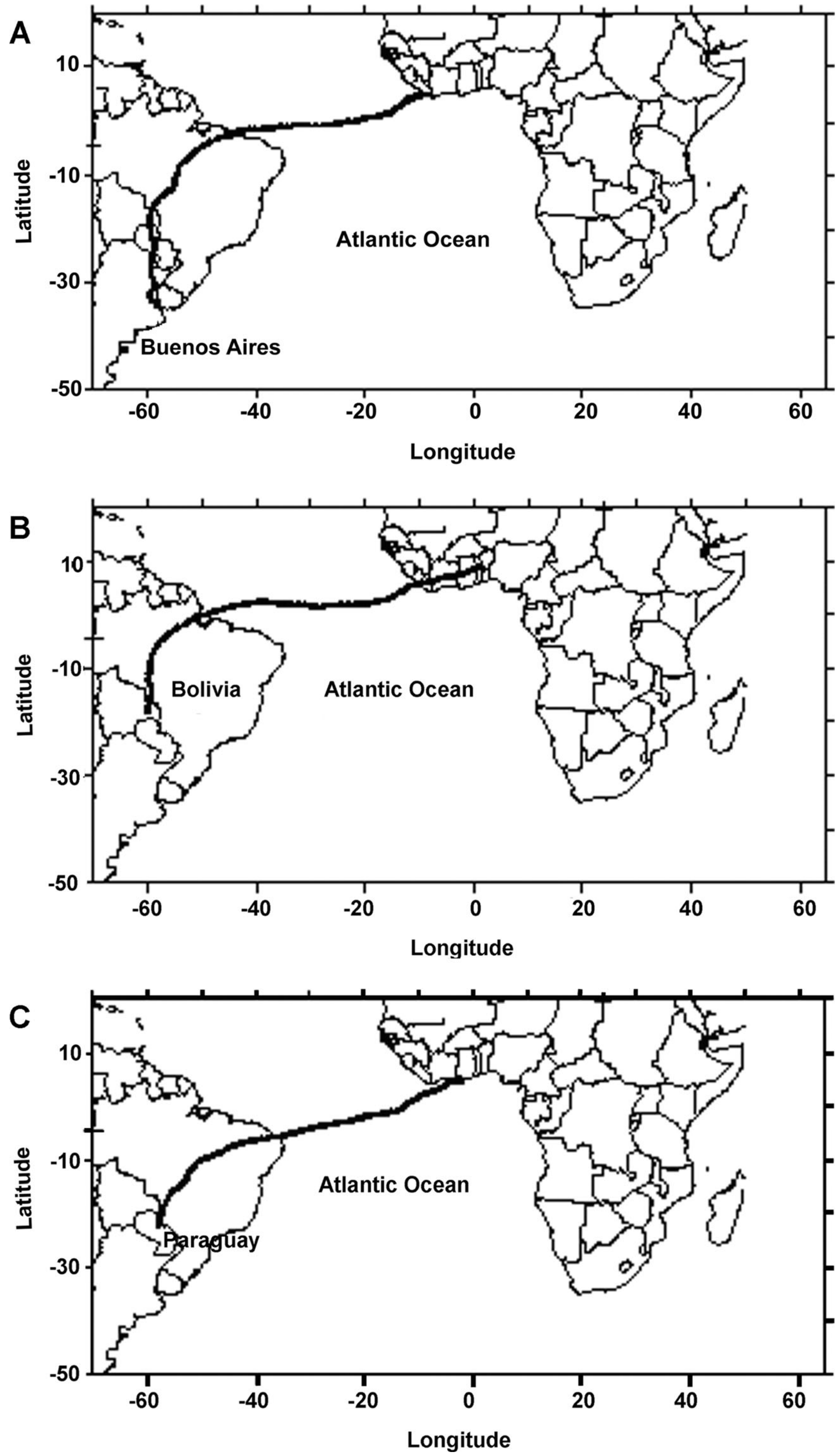

Fig. 4 Three-dimensional backward trajectories arriving in **a** Argentina at 00UTC 6 February 2003, **b** Bolivia at 00UTC 3 February 2003 and **c** Paraguay at 00UTC 3 February 2003 at 1,000 m.a.g.l.

(sd=23 %) (Fig. 9a). The range of transport altitude was 1,000–3,800 m.a.g.l., with a mean of 2,900 m.a.g.l. (sd= 620 m.a.g.l.) (Fig. 9b). Winter trajectory had Ta ranging from −5 to 17 °C with a mean of 5 °C (sd=5 °C) and RHa varied between 12 and 87 %, with mean and sd equal to 44 and 22 %, respectively (Fig. 10a). Transport altitude was similar to summer (maximum 4,000 m.a.g.l., minimum 1,000 m.a.g.l., mean 2,800 m.a.g.l. and sd 550 m.a.g.l.) (Fig. 10b).

Discussion and conclusions

Three-dimensional backward trajectories are strongly linked to global monsoon circulation, which might explain the trans-atlantic part of the proposed LDD. Trajectory altitude ranged from 400 to 2,100 m.a.g.l, where air temperature and relative humidity do not seem to cause thermal or water stress on the transported spores. No data are available about viability and

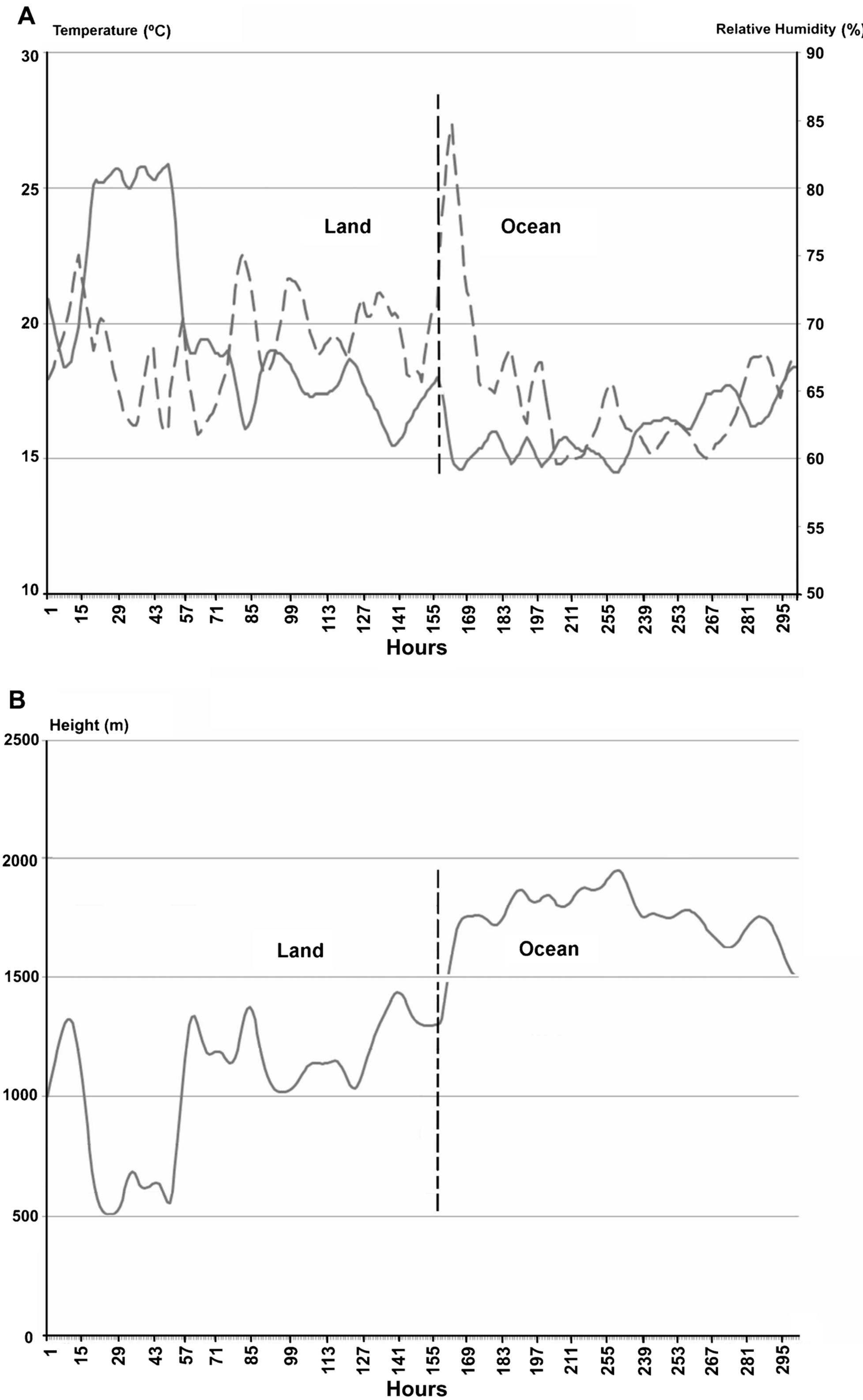

Fig. 5 **a** Temperature (Ta in °C, *full line*) and relative humidity (RHa in %, *dashed line*) and **b** altitude (h in m.a.g.l.) variations in the backward trajectory arriving in Argentina. The *vertical line* indicates the boundary between land and ocean

optimum storage conditions for Ophioglossoid spores; however, viability of spores is preserved at about 7 °C and the optimum germination range is 20–25 °C (Brum and Randi 2002; Khare et al. 2005). Perez-Garcia et al. (1994) found that when stored in dry conditions, non-green spores lose viability faster than when stored water-imbibed.

The three-dimensional forward trajectories revealed that transport occurs at altitudes ranging from 1,000 to

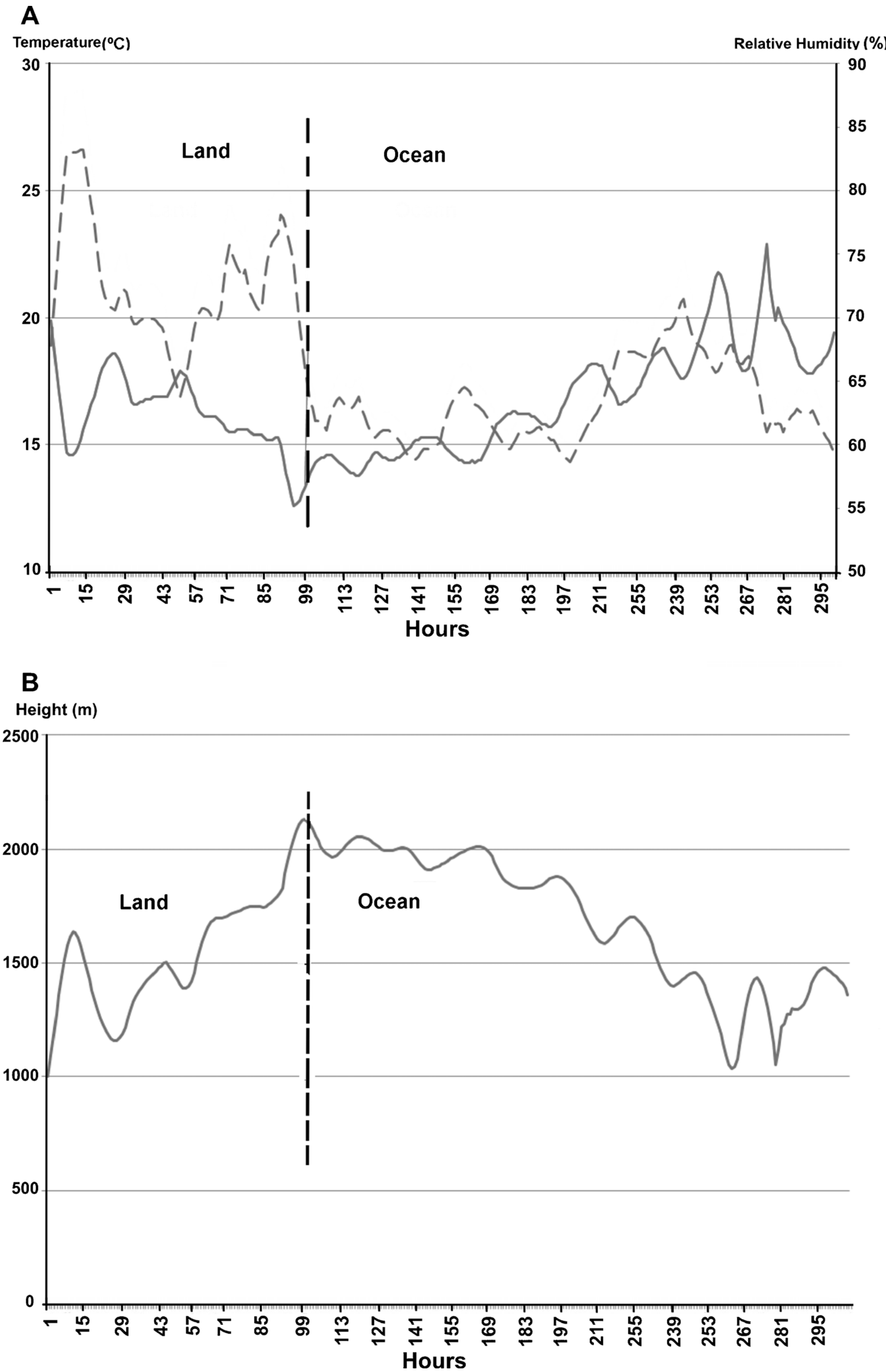

Fig. 6 **a** Temperature (Ta in °C, *full line*) and relative humidity (RHa in %, *dashed line*) and **b** altitude (h in m.a.g.l.) variations in the backward trajectory arriving in Bolivia. The *vertical line* indicates the boundary between land and ocean

4,000 m.a.g.l. At those levels, low temperatures and low relative humidity may put spore viability at risk. The possible effect of UV radiation on spore viability is worth mentioning. Gradstein and van Zanten (2001) tested the sensitivity of fern and bryophyte spores to high levels of UV at high altitudes (9,000 to 12,000 m) and found UV radiation is usually lethal except for a few very widespread or alpine species. They concluded that effective LDD of spores might very well have occurred via birds or air streams at rather low elevations, below 3,000 m.

Importantly, since the resolution of the reanalysis is coarse, the three-dimensional trajectories obtained represent vertical

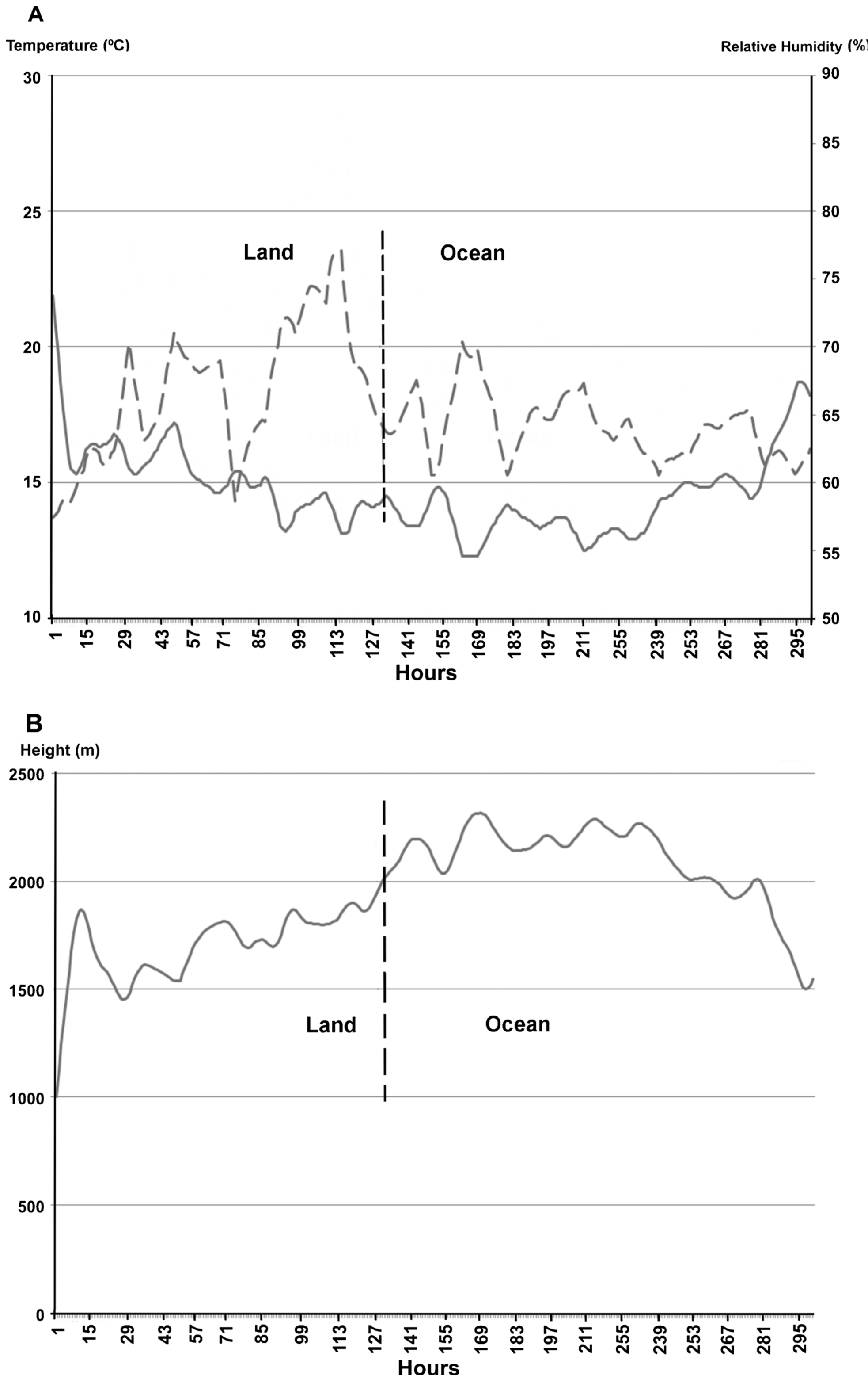

Fig. 7 **a** Temperature (Ta in °C, *full line*) and relative humidity (RHa in %, *dashed line*) and **b** Altitude (h in m.a.g.l.) variations in the backward trajectory arriving in Paraguay. The *vertical line* indicates the boundary between land and ocean

motions only on the synoptic scale, but they do not represent mesoscale or the convective motion within the boundary layer. Backward trajectories show that air parcels over the Atlantic Ocean were lifted above the marine boundary layer owing to large-scale vertical movement. Over South America, air parcels begin to descend and reach the ABL, where downdrafts and deposition processes might cause spores to reach land surface.

Convective movements are also of utmost importance during the takeoff stage. Since the typical habitat of the fern under

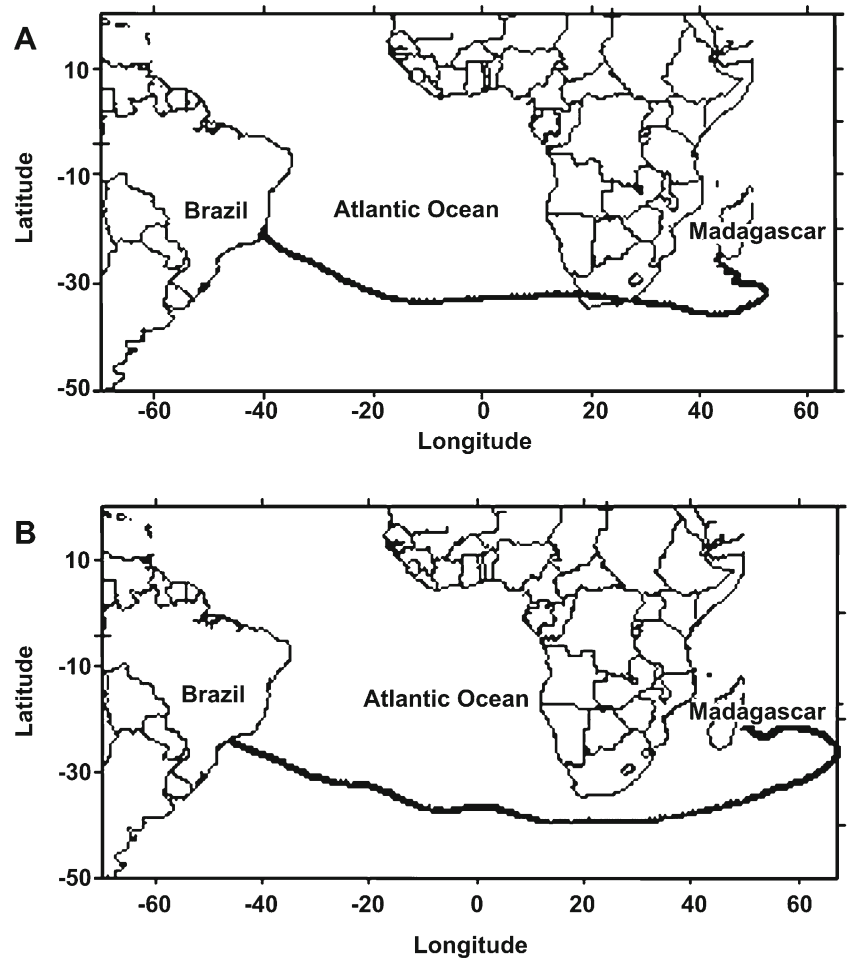

Fig. 8 Three-dimensional forward trajectories departing from the neotropics in **a** austral summer at 00UTC 11 January 2003 and **b** austral winter at 00UTC 8 July 2003

study is wet grassland, fertile spikes are easily exposed to wind. Mechanical turbulence caused by wind-land interaction shakes the fertile spikes very effectively causing them to release the spores. In addition, the local environment, characterised by strong diurnal heating combined with large water vapour content, promotes upward convective movements (thermal turbulence). The vigorous buoyancy of the air surrounding the fern will support the ascent through the ABL.

The present results, which are consistent with existing literature, indicate that large- and small-scale meteorological conditions are important in LDD. Liu et al. (2012) analysed the pathways of transatlantic transport of Saharan dust in the region 45° N to −15° S, −100° W to 30° E. Their results show a strong seasonal shift in source regions and pathways due to meteorological and thermodynamical conditions. The westward transport across the Atlantic is mainly directed to southeastern USA, the Caribbean Sea and South America. In DJF, dust-transporting pathways shift 10° southwards, and after reaching South America, aerosols are transported southwards mostly within 2,000 m.a.g.l. Engelstaedter and Washington (2007) concluded that large-scale convergence favours dry convection and causes an increase in frequency of strong small-scale wind. Updrafts associated with large-scale convergence not only support deep dust layer development, but also increase dust lifetime by reducing sedimentation.

The outcomes of this study support the hypothesis of LDD from Africa to South America and identify the SALLJ as a dispersal corridor towards SESA. Although it is not easy to verify the LDD hypothesis because of lack of observational data in Africa, South America and the Atlantic Ocean, the methodology applied seems to be suitable for capturing the occurrence and features of transcontinental/regional transport. Reanalyses have, by necessity, been taken as reasonable estimate of the real atmospheric state to calculate the trajectories.

The three-dimensional trajectories obtained include synoptic-scale processes (weather systems phenomena) as well as information on the atmospheric conditions during transport. This contributes to advancing the knowledge of LDD as a global mechanism for distribution of *O. reticulatum*.

The SALLJ, a feature of the SAM, could work as a dispersal vehicle of *O. reticulatum* and seems to be responsible for the southward distribution of this fern east of the Andes in SESA. The fern is absent in continental Chile (Rodríguez Ríos 1995), because the SALLJ flows along the eastern tropical and

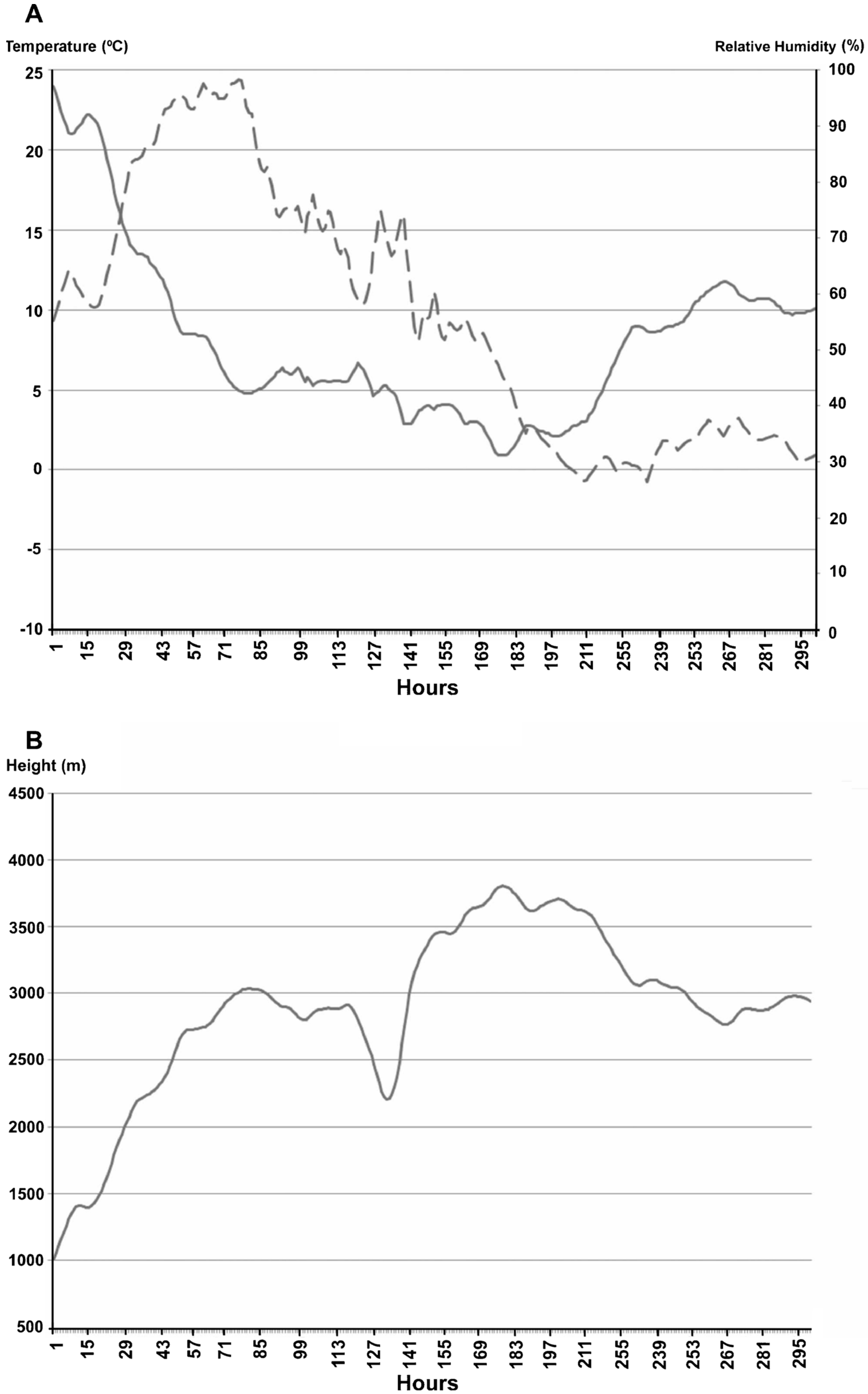

Fig. 9 **a** Temperature (Ta in °C, *full line*), and relative humidity (RHa in %, *dashed line*) and **b** altitude (h in m.a.g.l.) variations in the forward trajectory departing from the neotropics during austral summer

subtropical Andes (above 4,000 m.a.s.l.). South of 40° S, where the mountains are lower (about 1,500 m.a.s.l.) and the westerlies prevail, some pollen types were found to cross the Andes towards Argentina (Pérez et al. 2009).

The periodicity of monsoon systems makes it possible to assume that migration and jump dispersal are recurring phenomena. According to Moran (2008), recurrent migration from source areas maintains gene exchange preventing the

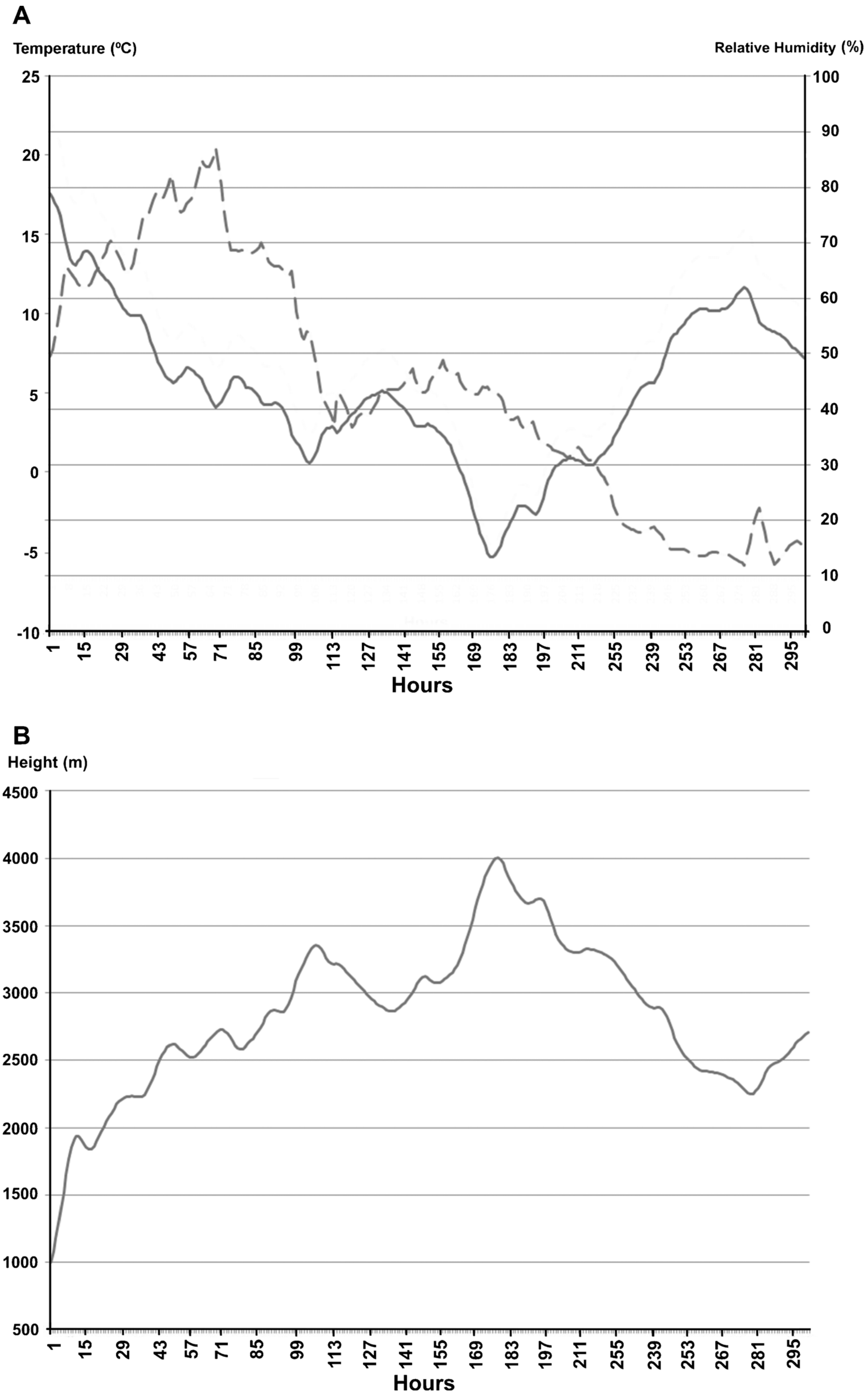

Fig. 10 **a** Temperature (Ta in °C, *full line*) and relative humidity (RHa in %, *dashed line*) and **b** altitude (h in m.a.g.l.) variations in the forward trajectory departing from the neotropics during austral winter

speciation of populations. This assumption could explain the absence of infraspecific taxa in *O. reticulatum*.

To conclude, this study advances the understanding of LDD migration from NW Africa to South America. The trade winds and the SAM could be regarded as a transcontinental/regional dispersal bridge for disseminules, and other taxonomic groups with passive dispersal (e.g. bryophytes, Asteraceae and Poaceae species with fruit or seeds pilose) and other organisms suitable for wind transport in the low troposphere. These results were obtained from a small sample of trajectories; to achieve more conclusive results, more cases need to be analysed in future studies. Phylogeographic studies are planned to provide biological evidence that would support the transport hypothesis. These studies will be based on population samples from Africa and South America. The phylogeography applies analysis of gene genealogies to the study of the evolution of populations and allows to draw conclusions about the sequences of colonization, diversification and extinction of gene lineages in specific areas of specific taxa. Therefore, these studies are appropriate to determine the direction of gene flow between populations from Africa and America in *O. reticulatum*.

Similarly, the global monsoon system might be a dispersal mechanism in other regions. Finally, climate variability and change might affect circulation patterns with possible impacts on LDD and the worldwide distribution of species.

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