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REVIEW

Can zoosporic true fungi grow or survive in extreme or stressful environments?

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Abstract Zoosporic true fungi are thought to be ubiquitous in many ecosystems, especially in cool, moist soils and freshwater habitats which are rich in organic matter. However, some of the habitats where these fungi are found may periodically experience extreme conditions, such as soils in extremely dry, hot and cold climates, acidic and alkaline soils, polluted rivers, anaerobic soil and water, saline soil and water, periglacial soils, oligotrophic soils, tree canopies and hydrothermal vents. It is clear that many ecotypes of zoosporic true fungi have indeed adapted to extreme or stressful environmental conditions. This conclusion is supported by studies in both the field and in the laboratory. Therefore, in our opinion, at least some true zoosporic fungi can be considered to be extremophiles.

Keywords Abiotic factors · Ecotypes · Extreme environments · Stressful environments · Zoosporic true fungi

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Introduction

Extreme or stressful environments are those in which the ranges of one or more abiotic parameters are in excess of what would be considered normal for growth and survival of living organisms. The concepts and definitions of extreme and stressful environments, the primary life strategies adopted by microbes and ecological groupings of microbes in general are thoroughly discussed by Zack and Wildman (2004) and Oarga (2009). Some extreme environments such as substrates near active volcanos and hydrothermal vents are considered to be similar to environments at the time of the origin of life on earth.

Some microbes in each of the three domains (Archaea, Eubacteria and Eukaryotes) have been observed growing in extreme environments (Oarga 2009). Amongst the Eukaryotes some genera of true fungi are considered to be extremophiles (Zack and Wildman 2004). Extremophiles must complete their life cycle under extreme conditions. These groups of microbes were once thought to exclude zoosporic true fungi (or chytrids).

Within the past decade phylogenetic analysis involving ribosomal RNA genes has highlighted the primitive nature of zoosporic true fungi (James et al. 2006). Most zoosporic true fungi produce posteriorly directed uniflagellate zoospores as reproductive structures which are a necessary part of the life cycle. Because these zoospores lack cell walls, are susceptible to mechanical, osmotic and temperature shock, and rely on water in liquid phase for dispersal (Gleason et al. 2008a), we would not expect zoosporic fungi to be able to survive in extreme environmental conditions. However, some recent research has indicated otherwise.

Throughout the twentieth century, much of the ecological research on zoosporic true fungi was conducted in moist and cool freshwater habitats such as along the shores

of Douglas Lake in Michigan (e. g. Sparrow 1960) and Lake Windemere in the English Lake District (e.g. Canter and Lund 1948, 1951; Canter 1967). Yet zoosporic true fungi are thought to be ubiquitous in many other ecosystems, especially in soils and freshwater habitats which are rich in organic matter (Sparrow 1960; Karling 1977; Powell 1993; Barr 2001; Longcore 2001; Shearer et al. 2007). However, some of the ecosystems where zoosporic true fungi are found may periodically experience extreme conditions. For example, moist soils and vernal pools often dry out during a long hot summer without rainfall. In fact, in many ecosystems wide temporal and special fluctuations in abiotic conditions are the rule rather than the exception (Zack and Wildman 2004).

Rather than face extinction under stressful environmental conditions each species of zoosporic true fungi must be capable of slow but continuous growth and reproduction for at least part of its life history (stress-tolerant strategy). At other times each species can persist in the form of resistant structures and then respond quickly to the return to favourable conditions (such as with the input of carbon, rainfall, etc.) with rapid growth (ruderal strategy). Thus, there are two distinct phases in their life history: a growth phase and a quiescent phase. We suggest that microbes which have adapted to periodic wide fluctuations in abiotic conditions should be considered to be a type of extremophile.

Most zoosporic true fungi are placed into four taxonomic groups, three of which are currently recognized as phyla. Many members of the Blastocladiomycota and Chytridiomycota have been isolated into pure culture from substrates in soil and freshwater collected in many parts of the world (Sparrow 1960; Barr 1987, 2001; Bills et al. 2004; Whisler 1987). These fungi can be either saprophytes, which decompose a large number of substrates (Sparrow 1960) or parasites of algae, fungi, animals and plants (Sparrow 1960; Powell 1993; Barr 2001). The fungi in the Neocallimastigomycota are obligate anaerobes and symbionts in the digestive systems of herbivorous mammals (Trinci et al. 1994). The fungi in the genus *Olpidium*, which have not yet been formerly placed into a phylum, are common obligate parasites of plant roots and some small invertebrates in many freshwater ecosystems (Sparrow 1960; Powell 1993; Barron 2004).

In this review we will begin by considering some recently published examples of zoosporic fungi observed in stressful environments in the field. The ranges of some physical and chemical parameters in those environments will be defined. Then we will discuss available information on the capacities of zoosporic fungi to respond to stress under laboratory conditions. Finally, we will predict how zoosporic fungi might respond to stress in natural ecosystems. We will follow the categories for extreme conditions suggested by Zack and Wildman (2004).

Recent studies in extreme environments using culture-dependent and culture-independent methods

Soils in warm and dry climates

Some groups of zoosporic true fungi such as the Spizellomycetales and Rhizophlyctidales have been found in soils in warm and dry climates, for example in grasslands in Colorado (Lozupone and Klein 2002), in desert soils in western North America (Booth 1971a; Barr 1984) and in agricultural soils of northern New South Wales (Australia) (Commandeur et al. 2005), Southeastern North America (Bernstein 1968; Dogma 1972) and many other parts of the world (Letcher et al. 2008a, b; Wakefield et al. 2010). These soils can experience rapid desiccation, fluctuation in osmotic potential and extreme temperature change.

Little is known about the ability of zoosporic true fungi to survive the lack of moisture in soil. However, some studies suggest that it is possible for some zoosporic fungi to survive for long periods of time, even for many years, in dried soil stored in the laboratory or in soils used for cropping in the field (Emerson 1941; Couch 1945; Machlis and Crasemann 1956; Sparrow 1960; Kuznetsov 1981; Campbell 1985; Laidlaw 1985; Whisler 1987; Youatt 1991a, b; Willoughby 2001). For example, *Rhizophlyctis rosea* has been found growing on cellulose baits placed in Petri dishes with soil and water after the soil had been dried and stored in the laboratory for 16 weeks (Willoughby 2001; Gleason et al. 2004). In all of these studies the exact moisture content or water activity of the soil has not been documented and pure cultures were not used.

Also little is known about the ability of zoosporic true fungi to survive high temperatures in soil. In the summer the air temperature near the surface can frequently surpass 40°C during the day in many warm climates, and on hot days the temperature on the surface of dry soils can reach 70°C in Australia (McGee 1989). Furthermore, in some warm and dry climates forest and grass fires are frequent. Microorganisms living in the topsoil are thus subjected to high temperatures periodically which may exceed their maximum temperature for growth.

The recovery of *Rhizophlyctis rosea* was documented in dried soils collected from sites in New South Wales (Australia) which experience warm temperatures in the summer (Gleason et al. 2004). *R. rosea* recovered growth in soil samples from eight different sites after these soils were heated at 90°C for 48 h, then returned to 20°C and baited with filter paper. At 95°C *R. rosea* was recovered from soil samples from five of the eight sites.

Soils in cold climates

Many species of zoosporic fungi have been observed growing on baits or have been detected with molecular techniques in soils from environments where the winter is long and harsh (Sparrow 1960; Booth and Barrett 1971; Barr 2001; Wallenstein et al. 2007; Freeman et al. 2009). Soils in cold climates can repeatedly freeze and thaw, can remain frozen for long periods and then thaw, or can be constantly frozen (permafrost). The Arctic tundra is characterized by long cold winters when microbes remain dormant and a short summer season when rapid microbial growth can occur. Rapid and extreme desiccation and temperature change are frequent in soils at high altitudes in the high mountains of North and South America and Asia where the atmospheric pressure is low.

Therefore, freeze-tolerant ecotypes of chytrids would be expected to dominate chytrid communities in cold climates. Yet, very little is known about the capacity of any of the zoosporic fungi to withstand freezing in the field. Some zoosporic fungi, such as *Synchytrium endobioticum*, can persist in cropping soil for years in cold climates (Laidlaw 1985) indicating that at least some ecotypes have the capacity to tolerate freezing, perhaps existing as survival structures. Anaerobic rumen fungi remained viable in cowpats after several frosts, and they could be isolated from faeces which had been stored in a freezer at −20°C (McGranaghan et al. 1999). Booth and Barrett (1971) isolated many genera of zoosporic true fungi from thawed Artic soils.

Despite the obvious need for freeze tolerance in chytrids from cold climates, it is also possible that they only actually grow during less extreme periods and remain dormant through the coldest periods of the winter. Freeman et al. (2009) speculated that chytrids can dominate snow-covered soils because such soils are often saturated with water during the final weeks or months of snow cover and are thus actually aquatic habitats for much of the snow-melt period. Such conditions would greatly favour chytrids over other fungi and could explain why they are dominant members of the fungal community of some extreme soils of Antarctica, and the Himalayas (Freeman et al. 2009; Bridge and Newsham 2009).

The growth of zoosporic true fungi under the seasonal snow pack could also help explain why rates of soil respiration are especially high under late-season snow packs in areas with snowy winters and very dry summers such as the inter-mountain region of the Western United States (Schmidt et al. 2009a). Thus, chytrids may be previously unappreciated members of the prominent "snow mold" community of such areas (Schmidt et al. 2009a).

Glaciers

Periglacial soils at high altitudes experience wide fluctuations in moisture and temperature and the lack of digestible carbon substrates (Freeman et al. 2009; Schmidt et al. 2009b). Low atmospheric pressure occurs at high altitudes. These soils are increasing in area as glaciers retreat worldwide. Freeman et al. (2009) studied the biodiversity of fungal communities at several of these sites. DNA sequences attributed to zoosporic true fungi were detected in barren soils from the Himalayas Rockies and Antarctica (Bridge and Newsham 2009; Freeman et al. 2009). Also some zoosporic fungi were isolated into pure culture from these soils. Eolian deposited pollen and microbial phototrophs provide carbon for growth of zoosporic fungi. Zoosporic true fungi dominated fungal biodiversity at these sites. Freeman et al. (2009) demonstrated metabolic activity in microbial communities at temperatures below 0°C in free water available under late season snow packs even at the highest "barren" sites studied in the Rocky Mountains. These areas can actually be saturated with free (unfrozen) water under deep snow and ice packs for up to 3 months even when surface air temperatures are well below freezing (Ley et al. 2004; Freeman et al. 2009). Soil temperatures during this period are slightly above 0°C as long as the snowpack is deeper than several meters. Freeman et al. (2009) hypothesized that this long period of water availability under the late season snow pack is what allows the proliferation of such large and diverse communities of zoosporic true fungi in both the high Rocky and Himalaya Ranges. Similar conditions probably prevail under snow and ice packs of Antarctica, but winter-time environmental data comparable to those from high mountain ranges have yet to be collected in Antarctica.

Tree canopies in temperate rain forests

Longcore (2004) isolated 12 species of zoosporic true fungi into pure culture from organic detritus collected from the tree canopies in rain forests of Australia and New Zealand. Most of these species had been previously reported from terrestrial soils. Resistant structures of these zoosporic fungi must be able to tolerate the lack of moisture and high temperatures in the air in tree canopies.

Deep-sea hydrothermal vents

The environment surrounding deep-sea hydrothermal vents is characterized by a wide range of temperatures cooled by ocean water and heated up to 400°C by vent fluid, a lack of dissolved oxygen, a high concentration of reduced compounds such as methane and hydrogen sulphide, strong acidity (pH 2–3), the presence of heavy metals and high

pressure (Le Calvez et al. 2009). DNA samples attributed to zoosporic true fungi have been detected in samples that were collected from various sites in the Mid-Atlantic Ridge and the East Pacific Rise. No species of zoosporic true fungi were isolated into pure culture in this study, although members of other groups of fungi were. Previously unknown clades of zoosporic true fungi were detected in this environment.

Extremely acidic environments

Zoosporic fungi have been observed frequently growing on substrates in habitats with extremely low pH but never with extremely high pH values (Sparrow 1960; Gleason et al. 2010). Water from the Rio Tinto River in Spain is highly polluted with heavy metals from ancient mines and is extremely acidic, with the pH as low as 2. Amaral Zettler et al. (2002) tested water samples from this river with general fungal primers and DNA sequences attributed to zoosporic true fungi were detected. DNA from zoosporic true fungi in the river could indicate either that these fungi grow at low pH values in the river or that thalli could have entered the water from other unpolluted less acidic ecosystems along the river. Zoosporic true fungi have never been isolated into pure culture from the Rio Tinto River (Amaral Zettler et al. 2002), but some ecotypes of these fungi can grow at low pH values (Gleason et al. 2010).

Anaerobic environments

Members of the Neocallimastigales (rumen fungi) are inhabitants of the rumen and hind guts of many herbaceous mammals, and these fungi are considered to be obligate anaerobes (Trinci et al. 1994; Rezaeian et al. 2004). The parts of the digestive systems where these fungi have been found are extremely anaerobic with very low redox potentials (Rezaeian et al. 2004). Addition of reducing agents to the media for growth of these fungi is necessary (Trinci et al. 1994). Recently DNA sequences attributed to rumen fungi have been detected in samples from an anaerobic landfill site in the United Kingdom (Lockhart et al. 2006). Prior to this time rumen fungi had never been isolated or detected outside of the digestive system except in faecal material. Also putative zoosporic true fungi have been found in the extremely anaerobic compartments of the digestive systems of burrowing sea urchins (Thorsen 1999), herbivorous and desert iguanas (Mackie et al. 2004), but the relationship to other zoosporic fungi remains to be determined.

In contrast, most members of the Chytridiomycota and Blastocladiomycota are thought to be obligate aerobes because they have been isolated from aerobic environments (Sparrow 1960). However, a few genera of zoosporic true fungi are known to be facultative anaerobes and are commonly observed growing in stagnant waters (Emerson and Natvig 1981; Whisler 1987).

Laboratory studies using pure cultures

Lack of moisture

Gleason et al. (2004) used a technique to test pure cultures of zoosporic true fungi for survival as desiccated thalli on filter paper. Thalli were placed on filter paper, dried and then inoculated onto fresh growth media. Initially, an incubation period of drying for 7 days at room temperature was selected for comparing the responses of different isolates. Eleven isolates in the Blastocladiales, Rhizophlyctidales and Spizellomycetales survived (Gleason et al. 2004, 2007a), but 16 isolates in the Chytridiales and Cladochytriales did not. The length of the incubation period was then extended. Eight isolates in the Blastocladiales, Rhizophlyctidales and Spizellomycetales (*Catenaria, Spizellomyces, Gaertneriomyces* and *Rhizophlyctis*) survived drying for 16 weeks at 20°C (Gleason et al. 2007a). In a different study pure cultures of *Batrachochytrium dendrobatidis* (Chytridiales) failed to survive drying (Johnson et al. 2003; Piotrowski et al. 2004). Thus, there appears to be significant differences in the ability of zoosporic true fungi to survive lack of moisture in pure culture. However, incubation times of longer than 16 weeks for pure cultures without moisture were not tested. Many isolates of zoosporic true fungi can be stored in the laboratory for long periods, but the length of time and moisture content have not been carefully documented. The long-term effect of lack of moisture under field conditions is not known.

Maximum temperatures for growth

The maximum temperatures for growth of zoosporic true fungi have been estimated in a number of studies in the laboratory. The surveys by Booth (1971a, b), Nielsen (1982), Barr (1969, 1970, 1984), Johnson et al. (2003), Piotrowski et al. (2004), Gleason et al. (2005) and Simmons (2007) clearly indicate that ecotypes of zoosporic true fungi have adapted to different environmental conditions. Some saprophytic zoosporic fungi have maximum temperatures at or below 30°C (Barr 1969, 1970; Gleason et al. 2005; Simmons 2007; Simmons et al. 2009). A number of saprophytic isolates in the Blastocladiales, Chytridiales, Cladochytriales, Rhizophydiales, Rhizophlyctidales and Spizellomycetales have maximum temperatures between 35 and 37°C (Barr 1984; Gleason et al. 2005). Some isolates of *Spizellomyces* (Spizellomycetales)

and *Allomyces* (Blastocladiales) can grow at 40–42°C (Nielsen 1982; Gleason et al. 2010), while some isolates of rumen fungi can grow at 45°C (Lowe et al. 1987; Theodorou et al. 1994). Fungi which grow at or above 35°C may be designated as mesophiles and can grow in soils in the warmer climates of the world or in the digestive systems of mammals, but these fungi are not considered to be thermophiles. In fact Tansey and Jack (1976) found no thermophilic zoosporic true fungi in their survey of sun-heated soil fungi.

Maximum temperatures for survival

After drying at room temperature for 5 days, Gleason et al. (2004) incubated thalli from nine pure cultures from the orders Blastocladiales, Rhizophlyctidales and Spizellomycetales on filter paper at 80 and at 90°C for 48 h before returning them to 20°C and inoculating them on fresh growth media. Six isolates resumed growth after incubation at 90°C for 48 h and three isolates at 80°C (Gleason et al. 2004 and unpublished data).

Sixteen isolates of zoosporic fungi were incubated for 2 days in liquid PYG growth medium at temperatures from 33 to 50°C (Gleason and McGee 2008). These fungi could not resume growth when returned to 20°C if the temperature of incubation was more than a few degrees above the maximum temperature for growth. The maximum temperatures for survival in liquid culture of some zoosporic fungi are probably close to the temperatures reached periodically on the surface of moist soils in warm climates. However, because some zoosporic fungi can survive high temperatures as dehydrated resistant structures, these fungi can be considered to be thermotolerant.

Low temperatures

Gleason et al. (2008b) tested the tolerance to freezing in 21 zoosporic fungi isolated from cropping and natural soils in Australia. Samples of moist thalli grown on solid PYG medium were frozen in a laboratory freezer at −15°C for 7 days, then returned to 20°C and inoculated onto fresh media. Two isolates in the Blastocladiales, six isolates in the Spizellomycetales and one isolate in the Rhizophlyctidales resumed growth quickly. Two isolates in the Chytridiales and one isolate in the Cladochytriales also survived freezing in some tests. None of the nine isolates in the Rhizophydiales survived freezing in any of the tests. Mature zoosporangia were present in the monocentric isolates which survived freezing. Suspensions of encysted zoospores in some isolates also survived freezing. Resistant sporangia or resting spores survived freezing in the polycentric isolates.

These data suggest a widespread distribution of tolerance to freezing among zoosporic fungi, but many of the fungi tested may be ecotypes adapted to cold climates. We would expect that at least isolates of all groups of fungi from the cold environments would have survival structures that enable the fungi to over-winter. In addition, the recent revelation that a wide diversity of zoosporic true fungi occur, and in fact dominate some of the coldest soils on Earth such as the high Himalayas (Freeman et al. 2009) and parts of Antarctica (Bridge and Newsham 2009) is further evidence that many are adapted to either growing or surviving in extremely cold soils.

High osmotic potential

Gleason et al. (2006) tested 20 isolates of zoosporic fungi from soil in the orders Blastocladiales, Chytridiales, Cladochytriales, Rhizophydiales, Rhizophlyctidales and Spizellomycetales for ability to grow on media with high osmotic potentials. All of these fungi grew on complex solid media supplemented with 10 g/l (170 mM) but not with 20 g/l (340 mM) sodium chloride. In a synthetic liquid medium, 4.4 g/l sodium chloride strongly inhibited growth in three of the five isolates, possibly because of the effect of the ions or osmolarity of the solution. The maximum concentration for growth in synthetic liquid medium with different osmotic potentials using polyethylene glycol (PEG) varied considerably amongst the isolates. Nielsen (1982) observed growth of nine isolates of *Allomyces* in complex growth media supplemented with 175 mM and some isolates in media with up to but not over 275 mM sodium chloride. Booth (1971b) observed growth of most isolates of zoosporic fungi in media with sea water diluted to 10 oo/oo (170 mM) and some isolates to 15 oo/oo (255 mM).

From these studies we can conclude that most zoosporic fungi are unable to grow in marine environments (approximately equivalent to 35 g/l or 600 mM sodium chloride). However, a few species of zoosporic true fungi, such as some isolates of *Rhizophydium* (Amon 1984), *Phlyctochytrium* (Amon and Arthur 1981), *Thalassochytrium* (Nyvall et al. 1999) and *Chytridium* (Müller et al. 1999), have adapted for growth as facultative or obligate parasites of macroalgae in marine environments, but it is not known if these fungi can grow in hypersaline conditions.

Most of the fungi resumed growth after return to normal growth conditions following incubation at room temperature for 7 days immersed in complex liquid PYG media supplemented with 35 g/l (600 mM) sodium chloride or 300 g/l PEG. Eight isolates in the Blastocladiales and Spizellomycetales resumed growth after immersion for 7 days in PYG growth media supplemented with 105 g/l

sodium chloride. These data indicate that soil Chytridiomycota can survive various osmotic potentials that may occur during the wetting and drying phases in soils.

Most of the isolates in the studies by Gleason et al. (2006) can be classified as halotolerant fungi, because they resumed growth after immersion in liquid complex growth media with salt at a concentration of approximately equivalent to sea water for 7 days. Furthermore, eight fungi resumed growth after immersion in media supplemented with 105 g/l sodium chloride, hypersaline conditions three times the concentration of sea water. Hypersaline conditions of this magnitude are rarely found in nature (Kis-Papo et al. 2001, 2003) though they presumably occur as soil dries. The capacity of zoosporic fungi to tolerate longer exposure to hypersaline conditions, or even to saline soil or sea water, remains unknown.

Anaerobic environments

Gleason et al. (2007b) tested 22 zoosporic fungi in the orders Blastocladiales, Chytridiales, Cladochytriales, Rhizophlyctidales, Rhizophydiales and Spizellomycetales for ability to grow or to survive under strict anaerobic conditions. These fungi were isolated aerobically from soils in Australia and, not surprisingly, were unable to grow in liquid growth media under strict anaerobic conditions. However, all 22 isolates resumed growth when returned to the air after incubation under these conditions for 7 days, and some for 31 days. Anaerobic conditions can occur periodically in the soil. Three of these isolates produced acid during growth in the presence of air, indicating the capacity for lactic acid fermentation.

Most members of the orders Blastocladiales, Chytridiales, Cladochytriales, Rhizophlyctidales, Rhizophydiales and Spizellomycetales are currently considered to be obligate aerobes. Based on the previous growth studies in the laboratory only two genera in these orders, *Blastocladia* and *Macrochytrium*, can be classified as facultative anaerobes at present (Emerson and Natvig 1981; Gleason and Gordon 1988).

Extremes in pH

Gleason et al. (2010) examined the growth, zoospore release and survival of some zoosporic fungi (Phyla Blastocladiomycota and Chytridiomycota) isolated from the soil in Australia to order to assess tolerance of extremes in pH. Most of the 16 isolates tested could be maintained in culture on solid PYG growth media at pH 4.7 and pH 8.9. One isolate grew at pH 2.9, four isolates at pH 3.3 and four isolates at pH 11.2. In liquid PYG growth media all of the eight isolates tested grew (increased biomass) at pH 5.5 and pH 7.6, most isolates grew rapidly at pH 4.5, some isolates grew at pH 11.2, but none of the isolates grew rapidly, if at all, at pH 2.9. The patterns of release of zoospores broadly reflect the patterns of growth at different pH values.

Twenty-one isolates resumed growth after returning to neutral pH following incubation for 7 days at 20°C in liquid PYG growth media adjusted to pH 4.7, nine isolates at pH 2.9, twelve at pH 9.3, eight at pH 11.2, and three at both pH 2.9 and pH 11.2. Patterns of survival, patterns of growth on solid and in liquid media and relative rates of zoospore release suggest ecotypes which prefer acidic, neutral or alkaline habitats. In general, many zoosporic fungi appear to be well adapted to a wider range of pH values than those found in the environments from which these fungi were isolated, and they quickly recover after brief exposure to extremes of pH. We expect zoosporic true fungi to grow in common acidic and alkaline soils.

Heavy metals

Tomlinson and Faithfull (1979) tested copper and zinc salts as fungicides to kill zoospores of *Olpidium*. These substances appeared to be toxic to zoospores in high concentrations. The effects of heavy metals on other zoosporic fungi are unknown.

Oligotrophic environments

Many genera in the Chytridiomycota can use inorganic sources of nitrogen, and all genera in the Chytridiomycota tested can use inorganic sources of sulphur and phosphorous (Cantino and Turian 1959; Midgley et al. 2006; Digby et al. 2010). In the Blastocladiomycota none of the genera tested are able to use inorganic sulphur, but some can use ammonium salts as nitrogen sources and all can use inorganic phosphorus (Nolan 1985; Midgley et al. 2006; Digby et al. 2010). In the CSM medium used by Midgley et al. (2006), Lilje and Lilje (2008) and Digby et al. (2010) the carbon source, glucose, was the only essential organic constituent required in significant concentrations.

Furthermore, Lilje and Lilje (2008) observed that if the carbon source is deleted from the CSM medium, some zoosporic fungi will continue to produce zoospores for up to 21 days or until the endogenous reserves are exhausted. Gleason (unpublished data) observed the same phenomenon on solid CSM medium. Therefore, we expect that many genera in the Chytridiomycota would be able to grow slowly and survive in extremely oligotrophic environments.

Discussion and conclusions

Monocentric zoosporic true fungi are tiny and have a simple thallus consisting of a sporangium and a few

rhizoids. Polycentric zoosporic fungi have hyphal-like structures which produce multiple sporangia and rhizoids. Fungi are able to occupy niches in stressful environments by adopting different ecological strategies. In all zoosporic true fungi the life cycle is completed rapidly resulting in the release of a large number of asexual propagules (zoospores) under appropriate environmental conditions. In many zoosporic fungi only empty chitin cell walls remain. For example, in natural environments explosive growth rates of zoosporic fungi have often been observed when the temperature becomes warm or when new substrates become available for colonization, such as in the spring in temperate environments (Sparrow 1960, Gleason and Macarthur 2008) and might survive during periods of unfavourable conditions as resistant structures (Sparrow 1960). Since stressful conditions might reduce the number of competitors, some chytrids may escape competition by occurring in conditions which are sub-optimal and hostile for other decomposers (Lee 2000).

Thus, some zoosporic fungi may be considered to be ruderal (R-selected) in their life histories (sensu Dix and Webster 1995). Two other ecological strategies are recognized by Dix and Webster (1995): (1) competitive (C-selected); and (2) stress-tolerant (S-selected). Different strategies may be adopted under different environmental conditions or during different stages in the life cycle of a fungus (Boddy and Wimpenny 1992). The ability of propagules that remain dormant during inclement conditions to recover when conditions become favourable for growth may indicate that zoosporic true fungi can also be S selected.

Marano et al. (unpublished data) assessed the frequency, abundance, number of thalli and density of colonization of *Rhizophlyctis rosea* on lens paper baits after incubation at different temperatures in the laboratory. They observed that *R. rosea* not only resists stressful laboratory conditions (i.e., freezing the soil at −15°C or heating the soil at 80°C prior to incubation at 20°C) but also the number of thalli and the density of colonization of baits increased in comparison to the control. Data from another study suggest that drying is a necessary trigger for completion of the life cycle of *Allomyces* (Youatt 1991b). However, further research is needed to clarify the effects of stress on reproduction within zoosporic fungi.

Soil is often oligotrophic, that is, generally low in nutrients, since nutrients are readily available only for short periods of time (such as following rainfall) or in restricted sites (such as the surfaces of the root tips of an actively growing plants, pollen grains, small pieces of dead plant materials or parts of dead animal bodies). Soil is a highly competitive habitat with highly diverse populations of microbes and small quantities of recalcitrant organic molecules.

Because the abiotic environmental conditions in many ecosystems are rapidly changing, zoosporic true fungi could often be at the mercy of a hostile environment. However, fluctuations in environmental conditions might be beneficial. For example, there is some evidence that alternate periods of drying and wetting can stimulate zoospore release in some species (Sparrow 1960). Fluctuations in environmental parameters might select for ecotypes which can tolerate extremes. As a result large numbers of zoosporic true fungi might be present in some microbial communities. A large number of species of zoosporic fungi have already been described (Sparrow 1960; Shearer et al. 2007). Data obtained from sampling in many ecosystems have revealed considerable diversity in the communities of zoosporic true fungi. In some ecosystems such as periglacial soils zoosporic true fungi even dominate the microbial biota (Freeman et al. 2009). New roles for these fungi in aquatic food webs are presently being proposed (Gleason et al. 2008a). However, our knowledge of the full ecological impact of these fungi awaits the development of better methods for estimating population parameters.

Soils in extremely dry, hot and cold climates, acidic and alkaline soils, polluted rivers, anaerobic soil and water, saline soil and water, periglacial soils, oligotrophic soils, tree canopies and hydrothermal vents are all examples of extreme environments. We have examined the evidence that zoosporic fungi can persist in such environments, in either the growth or quiescent phase from studies both in the field and in the laboratory. It is clear that many ecotypes have adapted to extreme or stressful environmental conditions. Therefore, in our opinion, at least some zoosporic fungi can be considered to be extremophiles.

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