Some *Chytridiomycota* in soil recover from drying and high temperatures

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*Rhizophlyctis rosea* was found in 44% of 59 soil samples from national parks, urban reserves and gardens, and agricultural lands of eastern New South Wales, Australia. As some of the soils are periodically dry and hot, we examined possible mechanisms that enable survival in stressful environments such as agricultural lands. Air-dried thalli of *R. rosea* in soil and pure cultures of *R. rosea*, two isolates of *Allomyces anomalus*, one isolate of *Catenaria* sp., one of *Catenophlyctis* sp. and one of *Spizellomyces* sp. recovered following incubation at 90°C for two days. *Powellomyces* sp. recovered following incubation at 80°C. Sporangia of all seven fungi shrank during air-drying, and immediately returned to turgidity when rehydrated. Some sporangia of *R. rosea* released zoospores immediately upon rehydration. These data indicate that some *Chytridiomycota* have resistant structures that enable survival through periodic drying and high summer temperatures typical of soils used for cropping. Eleven *Chytridiomycota* isolated from soil did not survive either drying or heat. Neither habitat of the fungus nor morphological type correlated with the capacity to tolerate drying and heat.

**INTRODUCTION**

Temperature directly influences the rate of physiological processes of biota, and it affects physicochemical processes in soil. Soils may experience large fluctuations in temperature. Soils used for cropping have a temperature range that exceeds that of soils with a heavy vegetative cover. The temperature of a soil is closely related to its water status (Russell 1973). Thus fungi in cropping soils may be better adapted to rapid change in moisture and temperature than fungi in heavily vegetated soils.

Fungi must have mechanisms that enable survival through conditions unfavorable for growth. For instance, the presence of a wall that is impermeable to water (Sussman 1968) might ensure that resistant structures survive through dry periods. Very little is known about the mechanisms of survival of fungi in the *Chytridiomycota* (herein called chytrids) through periods of environmental stress (Powell 1993). Chytrids may survive fluctuations in temperature and moisture content of the soil as resistant structures (Sparrow 1960). For instance, species of *Allomyces* (Machlis & Ossia 1953, Skucas 1968, Olson 1984, Youatt 1991a) and *Blastocladiella* (Cantino 1969) are reported to survive as resistant sporangia, and *Allomyces* is well known to survive air-drying (Youatt 1991b). Thick-walled sporangia may function as survival structures in *Olpidium* (Campbell 1985, Weber & Webster 2000), and *Synchytrium* is known to form resting spores (Laidlaw 1985, Hampson *et al.* 1994). The survival structures are unknown for *Rhizophlyctis* (Dogma 1974, Willoughby 2001) and rumen chytrids (Davies *et al.* 1993a, b, Theodorou *et al.* 1994) though resting spores of *R. rosea* were illustrated by Dogma (1974).

A few chytrids are thought to be prevalent in soil. *Rhizophlyctis rosea* and several species of *Allomyces* have been reported from around the world (Sparrow 1960, Karling 1977), including Australia (Harder & Gallwitzer-Uebelmesser 1959, Jeffrey & Willoughby 1964, Willoughby 1965, Karling 1988). These fungi were particularly prevalent in soils used for agriculture and horticulture (Weber & Webster 2000). Most of the surveys were limited in extent and results must be viewed as indicative. Recently, *Allomyces* sp. was found once and *R. rosea* only five times in an intensive sampling from native vegetation of the Sydney Basin, Australia (Letcher *et al.* 2004). The fungi may have been uncommon, or inappropriate techniques or timing used for isolation of chytrids.

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In many studies of distribution of chytrids, soil samples were collected and then shipped long distances before analysis. The steps taken to prepare fungi for shipping, and the effect of storage and shipping on the fungi in these soil samples are unknown. A considerable period of time between collection and analysis may result in loss of propagules of sensitive species from the soil sample. Thus these studies may have underestimated diversity of chytrids.

This paper reports the first part of an investigation into the ecology of chytrids in soil. We focused on *Rhizophlyctis rosea* because it is apparently widespread in agricultural soils and is easy to discern microscopically. The main objective of the research was to clarify whether chytrids tolerate high temperatures especially in dry soil.

**MATERIALS AND METHODS**

We first sought to determine whether *Rhizophlyctis rosea* is found in soils that might experience high temperatures. We then tested whether *R. rosea* could tolerate high temperatures. Finally, we compared tolerance of *R. rosea* with a range of other chytrids in culture to determine whether tolerance of heat was widespread among the chytrids.

**Distribution of Rhizophlyctis rosea**

To clarify the distribution of *Rhizophlyctis rosea*, samples of approx. 150 g soil were collected from 59 sites across eastern New South Wales, mostly close to Sydney. Eight sites experience high temperatures, two from under open heath vegetation, and six from fields used to grow cotton. Permission to collect on private lands was granted by the owners. Authorization to conduct research and to collect soil samples on land owned by the New South Wales State Government was granted under scientific investigation license no. A3375 (National Parks and Wildlife Service). Soil was taken from the surface after scraping away any litter, and placed in 17 by 18 cm plastic snap lock bags. Samples were collected and then shipped long distances before analysis. The steps taken to prepare fungi for shipping, and the effect of storage and shipping on the fungi in these soil samples are unknown. A considerable period of time between collection and analysis may result in loss of propagules of sensitive species from the soil sample. Thus these studies may have underestimated diversity of chytrids.

Survival of *Rhizophlyctis rosea*

A soil sample collected from the experimental garden in February was air-dried in a petri dish in the laboratory at 20 °C. After 16 wk, the soil was wetted, and then baited. Baits were examined after 7 d for the presence of *Rhizophlyctis rosea*.

Soil samples from eight sites containing abundant *R. rosea* were air-dried at room temperature. The sites represented undisturbed and highly disturbed soils. Ten g of each air-dried soil was incubated separately in a temperature-controlled oven (Thermoline, Australia) at 70, 80, 84, 90, or 95 °C for 48 h. Incubation at 80 °C was repeated, making six separate experiments. Below 90 °C, samples were incubated in plastic Petri dishes. At 90 °C or above, dry soil was first transferred to aluminum foil dishes prior to heating. After cooling the soil was baited as above, and baits were examined microscopically after 7 d. Only one dish was used for each site in each experiment. We chose 70 °C as the baseline temperature because soil maxima at this level have been observed (McGee 1989).

Soil water solution consisting of approx. 100 g soil from the experimental garden shaken in one L of de-ionized water was passed through a Whatman No. 1 filter paper, bottled and autoclaved. Cultures were established in sterile soil water by transferring pieces of filter paper colonized by *R. rosea* and associated microbes from the experimental garden in petri dishes. Fresh sterile baits were added. After 7–14 d, the newly colonized pieces of filter paper were transferred again to fresh soil water with fresh sterile baits or removed from the water and dried at room temperature in sterile petri dishes. Dried pieces of colonized filter paper were stored at room temperature until further use. A small amount of thallus from a pure culture of *R. rosea* (Table 1: Fungus D; Letcher et al. 2004) growing on PYG agar (Fuller & Jaworski 1987) was placed in the sterile soil water culture with fresh sterile baits and treated in the same way as the isolates from soil.

Air dried pieces of filter paper with thalli of *R. rosea* from the experimental garden and from the pure culture of *R. rosea* were incubated at 70, 80 and 90 °C for 24 h, and then returned to a fresh sterile soil water culture. Small amounts of thallus from cultures on agar were transferred to pieces of sterile filter paper, which were then placed in sterile petri dishes and air-dried. These air-dried thalli on filter paper from the pure
Freshly dried samples of the fungi that survived incubation at 80°C for two days were then tested for survival after heating at 90°C. The experiment was repeated. Further dried fragments of all fungi were incubated on the laboratory bench at 20°C for up to 14 d. Air-dried thalli on filter paper with the fungi attached were transferred to four small pieces of sterile filter paper, which were then placed in sterile Petri dishes. The fungi were then dried to four small pieces of sterile filter paper, which were then tested for survival after heating at 80°C and 90°C for 48 h. After cooling these were transferred to fresh PYG agar and B), Powellomyces sp. (Fungus C), Catenaria sp. (Fungus E), Catenophlyctis sp. (Fungus G) and Spizellomyces sp. (Fungus H) were plated on slides under a coverslip without water, and examined microscopically. To determine whether the sporangia or rhizoids were capable of recovering, de-ionized water was added to the edge of the cover slip, and rehydration was examined microscopically. To determine whether the reaction was possibly due to differences in water potential, 1 M sucrose was added to rehydrated thalli of R. rosea, and the reaction followed. The sugar solution was then replaced by de-ionized water.

**Survival of other chytrids**

Pure cultures of fungi isolated from soil in temperate rain forest, wet sclerophyll forest, dry sclerophyll forest, open heath, or agricultural sites, fungi that were monocentric or polycentric, and fungi originally isolated using various baits, were grown on YPSS/2 agar or PYG agar (Fuller & Jaworski 1987) in Petri dishes at 20°C and 30°C (Table 1). As data were identical, only those from 20°C are reported. Small amounts of thallus from the cultures with or without agar were transferred to four small pieces of sterile filter paper, which were placed in sterile Petri dishes. The fungi were then dried on the laboratory bench for 5–7 d. Air-dried thalli on filter paper were placed back on nutrient agar to determine survival of air-drying. The experiment was repeated. Further dried fragments of all fungi were incubated at 80°C for 48 h and then cooled. The pieces of filter paper with the fungi attached were transferred to fresh solid growth media in Petri dishes and incubated on the laboratory bench at 20°C for up to 14 d. Freshly dried samples of the fungi that survived incubation at 80°C were then tested for survival after heating for two days at 90°C.

**Rehydration of dried thalli**

Air-dried thalli of Rhizophlyctis rosea (from pure culture, Fungus D; and from dried soil from the experimental garden), Allomyces anomalus (Fungi A and B), Powellomyces sp. (Fungus C), Catenaria sp. (Fungus E), Catenophlyctis sp. (Fungus G) and Spizellomyces sp. (Fungus H) were placed on slides under a coverslip without water, and examined microscopically. To determine whether the sporangia or rhizoids were capable of recovering, de-ionized water was added to the edge of the cover slip, and rehydration was examined microscopically. To determine whether the reaction was possibly due to differences in water potential, 1 M sucrose was added to rehydrated thalli of R. rosea, and the reaction followed. The sugar solution was then replaced by de-ionized water.

**RESULTS**

**Distribution of Rhizophlyctis rosea**

Rhizophlyctis rosea was observed on baits from 26 of 59 sites, including 15 of 24 samples from agricultural or horticultural sites, and 11 of 35 soils from undisturbed sites with natural vegetation from private lands, national parks and reserves. R. rosea was isolated from one site that experiences high temperature. The density of sporangia varied on the baits. Sporangia of R. rosea were more easily seen on lens paper than on filter paper because soil particles that stuck to the filter paper obscured sporangia, and because sporangia were deeply embedded in the filter paper. Further, filter paper had sunk to the bottom of the solution, while the lens paper remained on the surface. However, partially decomposed filter paper was easier to manipulate than partially decomposed lens paper. The presence of R. rosea was recorded on samples usually within 7 d, because baits were rapidly digested, and bacteria colonized thalli. Bacteria and protists were commonly present with sporangia. Because of the variable level of

### Table 1. Cultures of chytrids obtained from New South Wales used in the study.

<table>
<thead>
<tr>
<th>No.</th>
<th>Fungus*</th>
<th>Collection site</th>
<th>Vegetation type</th>
<th>Collector*</th>
<th>Form of colony</th>
<th>Substrate used for isolation</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Allomyces anomalus A1</td>
<td>Garrijal National Park</td>
<td>Casuarina</td>
<td>P. Letcher</td>
<td>Hyphal</td>
<td>chitin</td>
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<tr>
<td>B</td>
<td>A. anomalus C/C2</td>
<td>Narrabri</td>
<td>Cotton</td>
<td>Z. Commandeur</td>
<td>Hyphal</td>
<td>keratin</td>
</tr>
<tr>
<td>C</td>
<td>Powellomyces sp. A17</td>
<td>Ourimbah</td>
<td>Rainforest</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>chitin</td>
</tr>
<tr>
<td>D</td>
<td>Rhizophlyctis rosea A13</td>
<td>University of Sydney</td>
<td>Garden</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>cellulose</td>
</tr>
<tr>
<td>E</td>
<td>Catenaria sp. Dec Ad 2-0</td>
<td>Narrabri</td>
<td>Mixed riparian</td>
<td>Z. Commandeur</td>
<td>Polycentric</td>
<td>keratin</td>
</tr>
<tr>
<td>F</td>
<td>Catenophlyctis sp. C/C 4-10</td>
<td>Narrabri</td>
<td>Cotton</td>
<td>Z. Commandeur</td>
<td>Monocentric</td>
<td>pollen</td>
</tr>
<tr>
<td>G</td>
<td>Spizellomyces sp. Mar Ad 2-0</td>
<td>Narrabri</td>
<td>Roadside</td>
<td>Z. Commandeur</td>
<td>Monocentric</td>
<td>pollen</td>
</tr>
<tr>
<td>H</td>
<td>Rhizophlyctis sp. A2</td>
<td>Dharug NP</td>
<td>Wet spongophyll</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>pollen</td>
</tr>
<tr>
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<td>Rhizophlyctis sp. A3</td>
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<td>Wet spongophyll</td>
<td>P. Letcher</td>
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<td>pollen</td>
</tr>
<tr>
<td>K</td>
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<td>Wet spongophyll</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>pollen</td>
</tr>
<tr>
<td>L</td>
<td>Chytrionymyces hyalinus A5</td>
<td>Morton NP</td>
<td>Open heath</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>chitin</td>
</tr>
<tr>
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<td>Wet spongophyll</td>
<td>P. Letcher</td>
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<td>onion skin</td>
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<tr>
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<td>P. Letcher</td>
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<td>P</td>
<td>Rhizophlyctis elynsis A9</td>
<td>Yarramundi</td>
<td>Mud from pond</td>
<td>C. Briggs</td>
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<td>keratin</td>
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<td>Q</td>
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<td>P. Letcher</td>
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<td>pollen</td>
</tr>
<tr>
<td>S</td>
<td>Chytrionymyces hyalinus A14</td>
<td>Ourimbah</td>
<td>Rainforest</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>chitin</td>
</tr>
<tr>
<td>T</td>
<td>Rhizophlyctis sp. A15</td>
<td>Ku-ring-gai NP</td>
<td>Dry spongophyll forest</td>
<td>P. Letcher</td>
<td>Monocentric</td>
<td>pollen</td>
</tr>
</tbody>
</table>

* Identifications putative.

* Voucher cultures are permanently preserved in the collection at the University of Alabama, Department of Biological Sciences.
contamination and difficulty in observing sporangia, sporangia were not quantified.

During a drought in Feb. 2003, R. rosea was abundant in soil samples obtained from the experimental garden, and these samples were used in the subsequent experiments. The fungus was absent on baits for 2 wk following storms in March, but was present when the garden was sampled again in June, when the soil was dry.

**Survival of Rhizophlyctis rosea**

Baits placed in the rehydrated soil samples from the experimental garden that had been stored air-dried for 16 wk became colonized by *Rhizophlyctis rosea*.

*R. rosea* was recovered from soil samples from eight different sites after those soils were heated for 48 h at 70, 80, 84 and 90 °C. At 95 °C, *R. rosea* was recovered from soil of five of the eight sites.

Air dried thalli of *R. rosea* growing in filter paper from a soil water culture survived incubation at 70, 80 and 90 °C for 48 h in three separate experiments. The zoosporangia discharged, and the zoospores colonized fresh filter paper. Thalli of the pure culture of *R. rosea* placed on pieces of filter paper survived incubation at 70 and 80 °C but not 90 °C.

**Survival of other chytrids**

Of the 18 fungi, only two isolates of *Allomyces anomalus*, and one of *Catenaria* sp., *Powellomyces* sp., *Rhizophlyctis rosea*, *Catenophlyctis* sp. and *Spizellomyces* sp. survived drying at room temperature. After drying at room temperature, isolates of *A. anomalus*, *Catenaria* sp., *Rhizophlyctis rosea*, *Catenophlyctis* sp. and *Spizellomyces* sp. also survived incubation at 80 and 90 °C for 48 h. *Powellomyces* sp. survived incubation at 80 °C but not 90 °C.

**Rehydration of dried thalli**

Sporangia of *Rhizophlyctis rosea* from soil appeared shrunken and collapsed after air-drying (Fig. 1a). Sporangia rapidly returned to their normal shape after addition of de-ionized water (Fig. 1b). Hydrated sporangia were slightly plasmolysed by the addition of 1 M sucrose. Subsequent washing with de-ionized water reversed plasmolysis. Addition of water to dry sporangia also resulted in immediate discharge of zoospores in some cases.

Pure cultures of two isolates of *Allomyces anomalus*, *Catenaria* sp., *R. rosea*, *Powellomyces* sp., *Catenophlyctis* sp. and *Spizellomyces* sp. shrunken on drying, and rehydrated rapidly on addition of water. Rehydrated fungi resembled untreated fungi in the light microscope. The survival structures were not elucidated.

**DISCUSSION**

*Rhizophlyctis rosea* was widespread in eastern New South Wales, Australia. The fungus was baited from soils of nearly half of the sites sampled, and was slightly more common in disturbed soils such as those used for horticulture and agriculture. While it was found in only one soil that experiences high temperatures, subsequent extensive sampling at Narrabri found *R. rosea* at low densities in soils of all the sites on the cotton farm (Zoe Commandeur, unpubl.). Thus, while high temperature and disturbance may influence isolation from soil, they appear to be unimportant in the survival of *R. rosea*.

In a few soils, *R. rosea* appeared to be abundant. The factors determining distribution and abundance are unclear. Repeated sampling over 5 m from an experimental garden near the laboratory indicated that abundance of the fungus may be affected by incidence and intensity of rainfall. The fungus was not found on baits placed in soil samples collected immediately after heavy rainfall (data not shown), yet was abundant during an earlier drought period and a later dry period.
(data not shown). Thus, while presence on baits confirms presence of the fungus in a sample, absence does not necessarily indicate absence from the soil.

*R. rosea* is possibly more prevalent than is indicated in this investigation. We did not attempt to collect air-dry soil samples, nor did we air-dry the samples following collection. Apparent absence of *R. rosea* from some soils may have been due to the fungus being in a stage of its life cycle where colonization of baits was unlikely. The relationship between quantity of sporangia on bait and abundance of the fungus in soil must be treated cautiously. For instance, addition of baits to soil stored damp in cool conditions for a long period may result in lower apparent abundance, only because some propagules have exhausted their internal energy supplies. The apparent disparity between abundance and sporangia on baits has implications for ecological studies. If other chytrids have a similar response to soil moisture, then air-dry samples, kept dry are likely to realize a greater abundance and diversity of fungi. The mechanisms regulating changes in abundance require more careful examination, and in part rely on understanding the life-cycle of each chytrid in the soil.

Thalli of *R. rosea* recovered from drying. The walls of the sporangia were clearly permeable, for desiccated sporangia imbibed immediately on exposure to water. Imbibition of water by dried sporangia was immediately followed by release of zoospores in some cases. Thus it might be argued that during periods of dry weather, the fungus survives as dried sporangia in soil, and that zoospores are released soon after adequate rainfall. If so, the fungus will survive if zoospores establish on substrates to form sporangia before the soil dries. Soils were baited with cellulose in these experiments, and colonization was apparent on baits. We do not know what substrate the fungus colonizes naturally in soil.

*R. rosea* was baited successfully on cellulose only, indicating that cellulose might be a good substrate for maintenance and growth of the fungus (Haskins 1939, Stanier 1942, Griffiths & Jones 1963, Dogma 1974, Weber & Webster 2000, Willoughby 2001). It is curious then, that *R. rosea* was not more common in soils where reasonable levels of cellulosic carbon are found. Although not quantified, all of the 59 soils collected in this investigation contained at least some decaying plant material, providing a source of cellulose, and possible nutrients for the fungus. *R. rosea* was observed to co-occur with other microbes on baits; either the fungus was present with many different microbes, or the fungus was absent and other microbes were infrequent. It was unclear whether the diversity of microbes was present because of *R. rosea* or because the absence of *R. rosea* indicated some general antimicrobial factor. The interaction between *R. rosea* and other microbes during colonization of cellulosic substrates in soil warrants further study.

Survival of air-dried *R. rosea* in soil on the lab bench for 16 wk has been observed previously (Willoughby 2001). In our investigation, resistant structures in soil survived temperatures up to 90 °C. Capacity to survive air-drying and high temperatures indicates one mechanism to explain the survival of *R. rosea* in habitats used for cropping that are subject to periodic and frequent summer drought. The air-dried sporangia are also possible dispersal units. They could be carried by wind with soil particles from site to site. These propagules may partly explain the widespread distribution of *R. rosea* in disturbed habitats.

In contrast to Willoughby (2001), sporangia of *R. rosea* became shriveled during drying, and rehydrated to their normal morphology within a few seconds of exposure to water (Fig. 1). Because the sporangial wall appears readily permeable to water, we propose that the cytoplasm itself is resistant to drying and heating when the fungus is in a quiescent state. The mechanism for coping with rapid and cyclic changes in hydration, are unclear. High concentrations of salts or osmoticum may influence metabolic processes within zoospores and the sporangium. Cytoplasmic mechanisms enabling survival warrant further investigation.

Many other fungi tolerate high temperatures (Warcup & Baker 1963, Sussman 1968, Bayne & Mitchener 1979). Indeed, dormancy is broken by heat in some *Ascomycota* (Warcup & Baker 1963). Little is known of heat tolerance in chytrids (Remy 1948, Teakle & Thomas 1985). In our study, air-dried *Allomyces anomalous* (Fungi A and B), *Catenaria sp.*, *R. rosea*, *Powellomyces sp.*, *Catenophlyctis* sp. and *Spizellomyces* sp. survived at 80 °C for 48 h, though not other chytrids from various habitats. Survival is apparently unrelated to morphology of the fungus, habitat from which the fungi were isolated, and the bait on which the fungi were isolated. However, it is interesting to note that *R. rosea* survived sometimes in soil held at 95 °C, indicating that the thermal death point of the fungus is in the range of 90–95 °C.

Many chytrids are subcultured regularly, with consequent potential alteration of the genetic characteristics of these strains in the laboratory. Many of these fungi are difficult to maintain in culture and are lost for no apparent reason. Indeed, different parts of one culture may be at different physiological stages. Several chytrids recovered from air-drying indicating the potential of using air-drying for the long-term storage of these chytrids. Issues that need to be further investigated to clarify the potential of drying for storage include whether the tolerance to drying is induced or staged in soil, the stage of the life-cycle where drying enables quiescence, and the role of nutrients and water during storage and recovery.

The process used to test the survival of extreme temperature by these fungi was direct and presumably harsh. The thalli were placed on filter paper, dried rapidly, and then placed in incubators at very high temperatures. It is unlikely that any protective function could have been induced in the short time allowed. Further, lack of survival at 80 °C need not indicate the
capacity of these fungi to tolerate more realistic rates of drying or soil temperatures, or even to grow when edaphic conditions are amenable. We have clarified one mechanism enabling survival of several chytrids in soil. Other chytrids are found in these soils, and they must have other adaptive mechanisms that enable them to tolerate the soil drying, and exposure to high temperatures. These mechanisms remain to be explored.

*Rhizophyctis rosea* can dry in air, and subsequently survive immediate exposure to prolonged high temperatures. Tolerance of periodic drought and high temperatures are not shared by all soil chytrids, nor does it appear to be related to the environments inhabited by the fungi. The life cycle of *R. rosea* appears to include massive changes in the size of the population associated with inundation of the soil. Population dynamics of other chytrids remain unknown. While *R. rosea* is widespread and relatively easy to identify from soil samples, it appears to have an ecology that differs from many other soil chytrids, and may not provide a good indication of the biology of this poorly studied (Powell 1993) and phylogenetically diverse (Tehler et al. 2003) group.

Techniques to study chytrids are difficult and tedious, yet may result in indications of specificity to edaphic and climatic conditions. As yet, few molecular markers are available (Lozupone & Klein 2002) and applicable to the study of chytrids in the environment. Progress in understanding chytrids will rely on continued use of traditional techniques in tandem with development of our understanding of their molecular genetics. The data presented here indicates that we do not yet understand basic aspects of the biology of this group. Until we do, the importance of chytrids in the environment will remain unclear.

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