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Diurnal temperature fluctuation inhibits the growth of an Antarctic fungus

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ABSTRACT

The surface temperatures of Antarctic soils and bryophyte colonies can fluctuate from close to freezing point to approximately 20 °C under clear skies around solar noon during midsummer. However, whether diurnally fluctuating temperatures influence the growth and metabolic activities of fungi inhabiting these substrates remains unknown. Here, 10 isolates of *Pseudogymnoascus roseus*, an ascomycete that is widespread in Antarctica, were exposed *in vitro* to temperatures fluctuating daily from 2 °C to 15–24 °C. Relative to controls incubated at the constant mean temperature of each treatment, temperatures fluctuating from 2 °C to ≥18 °C inhibited the growth of all isolates by 10–51% at 24 h and 48 h, and by up to 79% for individual isolates. Over a period of 21 days, all fluctuating temperature treatments reduced mean growth rates by between 3% and 48%, but had few effects on specific β-glucosidase activity, a proxy measure for metabolic activity. It is concluded that temperatures fluctuating diurnally to ≥18 °C during summer in mesic Antarctic soils and bryophyte colonies, exacerbated by the occurrence of climate-change associated heatwaves, are likely to inhibit the growth of *P. roseus* and perhaps also other ecologically important fungi.

1. Introduction

Antarctic soils and bryophytes exhibit remarkable diurnal fluctuations in summertime temperatures. With low albedo and an absence of shade from higher plant canopies, the surface temperatures of sun-exposed soils and bryophyte colonies can fluctuate from close to freezing point to approximately 20 °C under clear skies around solar noon in austral midsummer (Newsham, 2010, 2021; Convey et al., 2018; Newsham et al., 2020, 2021a; Misiak et al., 2021). Cold-adapted microbes with growth temperature optima of <20 °C are frequent in polar regions (Zucconi et al., 1996; Robinson, 2001; Ruisi et al., 2007), and it is hence possible that the metabolism of these organisms is inhibited in soils and bryophyte colonies during summer. However, this possibility has rarely been examined, and the effects of fluctuating temperatures on the fungi inhabiting Antarctic soils and other substrates remain poorly defined. Given that fungi attain hyphal lengths in Antarctica of 0.3–8.0 km g^{-1} dry weight of vegetated soil or bryophyte colony (Dowding and Widden, 1974; Hirose et al., 2017; Nagata et al., 2023) and, as in all terrestrial ecosystems, have pivotal roles in the decomposition of organic compounds (Swift et al., 1979), the paucity of information in the literature on how they respond to temperature fluctuations represents a significant gap in current knowledge.

In the only study to have examined the effects of temperature fluctuations on an Antarctic fungus, Misiak et al. (2021) found that the hyphal growth rate of three isolates of *Pseudogymnoascus roseus* Raillo, a member of a species complex widespread in maritime and coastal continental Antarctica (Newsham et al., 2021b; Onofri et al., 2007), is inhibited by temperatures cycling daily from 2–21 °C and 2–24 °C, relative to those cycling from 2–18 °C. However, the growth rate of *P. roseus* in this study was derived from measurements made over periods of up to 10 weeks (Misiak et al., 2021), and it hence remains unknown if the growth of the fungus is inhibited by fluctuating temperatures over durations of a few days, as occur in the natural environment under anticyclonic conditions during austral summer (Longton and Holdgate, 1967; Misiak et al., 2021; Newsham et al., 2021a). Accordingly, the effects of temperatures cycling daily between 2 °C and 15–24 °C are tested here on 10 *P. roseus* isolates from sub- and maritime Antarctica. Exposures over 48 h measured the effects of fluctuating temperatures on growth, while those over 21 days determined treatment effects on growth rate and the synthesis by the isolates of β-glucosidase, an enzyme catalysing the decomposition of cellulose (Béguin and Aubert, 1994), which was used here as a proxy for metabolic activity.

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2. Materials and methods

2.1. Isolation and identification of P. roseus

Isolates of the fungus were obtained from soils sampled from Lewis Pass on South Georgia (54° 15′ 53″ S, 36° 29′ 54″ W) in sub-Antarctica and from The Backslope on Signy Island (60° 42′ 32″ S, 45° 35′ 31″ W), Walton Terraces on Léonie Island (67° 36′ 00″ S, 68° 21′ 28″ W) and Mars Oasis on Alexander Island (71° 52′ 42” S, 68° 15′ 00″ W), each in maritime Antarctica (Fig. 1). Barren fellfield soils were sampled from Lewis Pass, The Backslope and Mars Oasis, and soil from under the darkly pigmented bryophyte *Cephaloziella varians* was collected from Léonie Island (Fig. 1A, inset). The soils were frozen at −20 °C within several hours of collection and were transported to the UK at the same temperature. They were then thawed at 4 °C overnight, sieved (2 mm) and sub-samples (*c*. 4.5 mg fwt) were spread under a sterile hood onto Czapek-Dox agar medium in 90 mm diameter non-vented Petri dishes. Rose Bengal (1:15,000) had been added to the medium in order to slow the growth of rapidly-spreading fungal colonies. The dishes were incubated at 7 °C for 16 days prior to isolations (Misiak et al., 2021). Two isolates of *P. roseus* were each obtained from South Georgia and Signy Island soils (isolates SG1, SG2, S1 and S2, respectively), and three were each obtained from Léonie Island and Alexander Island soils (isolates L1, L2 and L3 and A1, A2 and A3, respectively). Isolates A1, A2 and A3 were the same as those studied by Misiak et al. (2021). The isolates were maintained on half strength potato dextrose agar medium at *c*. 12 °C. Taxonomic placement, based on analyses in the UNITE database (Kõjalg et al., 2005) of ribosomal DNA sequences (deposited in GenBank under accession codes OP036440–OP036446, MT477869, MT477886 and MT477911), indicated species hypotheses for all isolates of *P. roseus*.

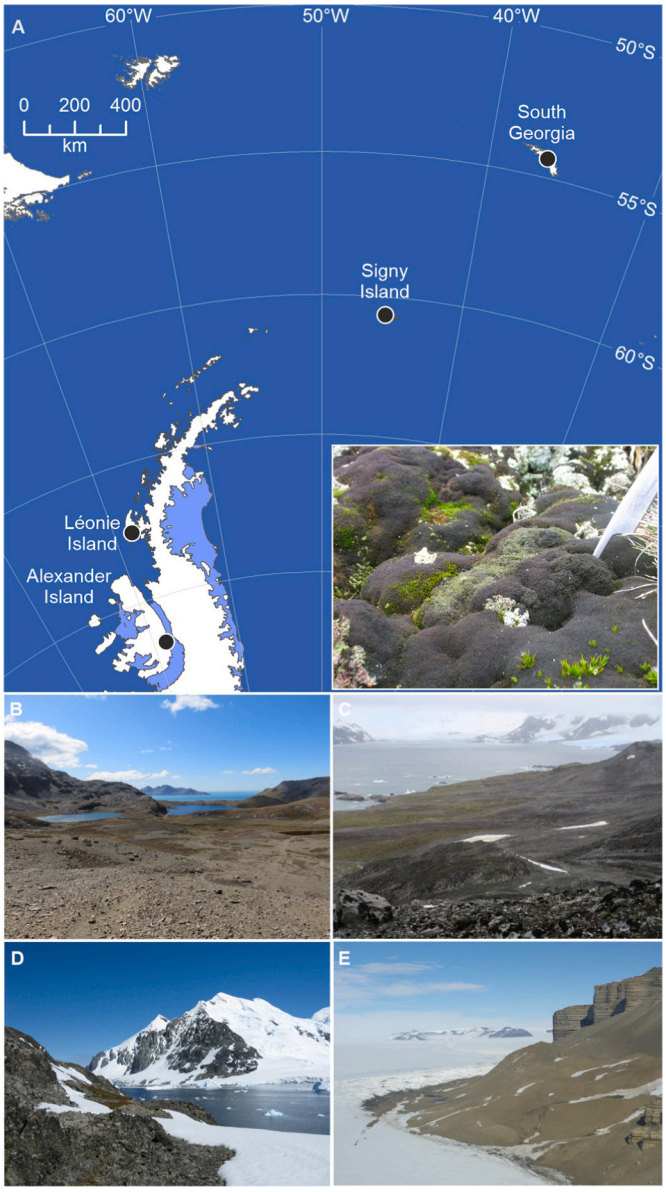

Fig. 1. Sub- and maritime Antarctic sites from which *Pseudogymnoascus roseus* was isolated. (**A**) Map showing the positions of South Georgia, Signy Island, Léonie Island and Alexander Island. Circles show the approximate locations of Lewis Pass, The Backslope, Walton Terraces and Mars Oasis. (**B**) Lewis Pass on South Georgia, (**C**) The Backslope on Signy Island, (**D**) Walton Terraces on Léonie Island and (**E**) Mars Oasis on Alexander Island. Note the dark soil surfaces at the sites. The inset in (**A**) shows a colony of the darkly pigmented bryophyte *Cephaloziella varians* with mosses and lichens on Léonie Island.

2.2. Exposures over 48 h

The isolates were exposed in growth cabinets (MCR-350, Sanyo, Japan) in four separate experiments to diurnally fluctuating and constant temperatures of 2–15 °C and 9.0 °C, 2–18 °C and 10.7 °C, 2–21 °C and 12.0 °C, and 2–24 °C and 13.1 °C, respectively, with 6 h dwells at the highest temperatures in the fluctuating temperature treatments (Fig. 2A). The constant temperature in each experiment was the mean of the fluctuating temperatures (e.g., 9.0 °C was the mean temperature of the 2–15 °C fluctuating temperature treatment), and the amplitudes of the fluctuating temperatures were similar to those measured at the surfaces of Antarctic soils and bryophyte colonies during midsummer (Fig. 2A and B). Fluctuating and constant temperatures deviated from set values by 0.1–0.2 °C (Fig. 2A). The former did not fluctuate to <0 °C as, owing to the zero-curtain effect, in which the phase transition of water to ice is slowed by the release of latent heat (Kelley and Weaver, 1969), the temperatures of maritime Antarctic soils and bryophytes typically remain continuously above freezing point for several weeks during midsummer (Newsham, 2010, 2021; Misiak et al., 2021).

For each experiment, plugs (7 mm diameter) were cut from half-strength potato dextrose agar medium onto which spore suspensions of the isolates had been spread 16 h previously (Misiak et al., 2021). Under a sterile hood, the plugs of each isolate were placed onto sterile soil extract medium in eight 55 mm diameter non-vented plastic Petri dishes. The medium had been prepared by adding Antarctic fellfield soil to natural mineral water (Radnor Hills Mineral Water Co. Ltd., Knighton, Powys, UK) at a ratio of 1:2.5 (v/v). The suspension was shaken vigorously, allowed to settle overnight at 7 °C and was then filtered (0.4 μm). Sucrose (1 g L^{-1}), KH_2PO_4 (0.2 g L^{-1}), yeast extract (0.1 g L^{-1}) and Oxoid no. 1 bacteriological agar (15 g L^{-1}) were added to the filtrate prior to autoclaving at 121 °C for 20 min. The water potential (an expression of biological water availability) of the medium varied between *c*. −1.10 MPa at 2 °C and −0.05 MPa at 24 °C, which was similar to the water potentials of fellfield soil and colonies of *C. varians* with moisture contents of 4% and 84%, respectively (Supplementary Fig. 1). The eight Parafilm-sealed dishes per isolate were inverted and incubated at constant temperatures of 9.0 °C, 10.7 °C, 12.0 °C or 13.1 °C for 7 d, after which colony fronts were marked on dish reverses with a fine blade at × 10–15 magnification (accuracy *c*. 100 μm). Four dishes of each isolate were returned to the cabinets set to constant temperatures of 9.0 °C, 10.7 °C, 12.0 °C or 13.1 °C, and the other four dishes per isolate were transferred to cabinets set to fluctuating temperatures of 2–15 °C, 2–18 °C, 2–21 °C or 2–24 °C, respectively (Fig. 2A). Colony fronts were marked 24 h and 48 h later at × 10–15 magnification and mean radial extension (mm) at each time point was calculated.

2.3. Exposures over 21 days

Plugs (7 mm diameter) of half-strength potato dextrose agar medium

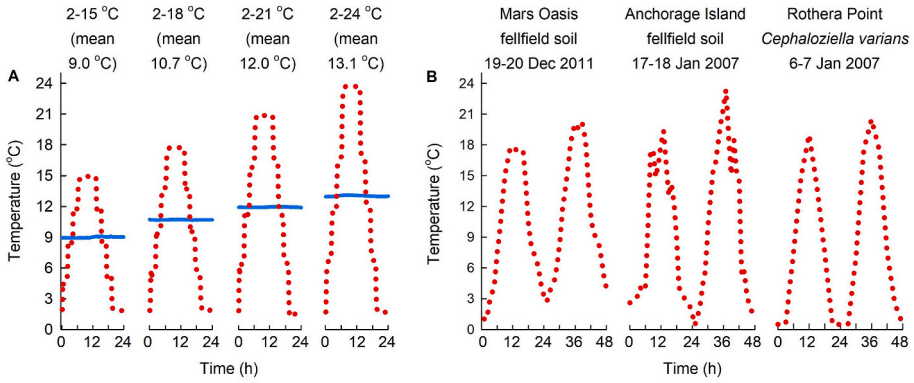

Fig. 2. (**A**) Fluctuating temperature treatments (dotted red lines) and their corresponding constant mean temperature controls (solid blue lines). (**B**) Midsummer temperatures of maritime Antarctic fellfield soils at Mars Oasis on Alexander Island and Anchorage Island (67° 36′ 14″ S, 68° 12′ 33″ W), and of the bryophyte *Cephaloziella varians* on Rothera Point (67° 34′ 05″ S, 68° 07′ 15″ W) on Adelaide Island. Soil and bryophyte temperatures were measured hourly and three-hourly, respectively. Data shown in (**B**) are reported by Convey et al. (2020) and Newsham et al. (2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

onto which the spores of each isolate had been spread in sterile water 16 h previously were placed under a sterile hood onto cellophane (Natureflex 28 NP; Innovia, Wigton, UK) overlaying soil extract medium in eight 90 mm diameter non-vented plastic Petri dishes. As above, the eight Parafilm-sealed dishes were inverted and incubated in cabinets set to constant temperatures of 9.0 °C, 10.7 °C, 12.0 °C or 13.1 °C for 7 d, after which colony radii were measured twice at right angles to each other at × 10–15 magnification. Four dishes of each isolate were then returned to the cabinets set to constant temperatures of 9.0 °C, 10.7 °C, 12.0 °C or 13.1 °C and the remaining four dishes per isolate were placed into cabinets set to fluctuating temperatures of 2–15 °C, 2–18 °C, 2–21 °C or 2–24 °C, respectively (Fig. 2A). Colony radii were measured every 3–5 days over the next 21 days and mean radial extension rates (mm d^{-1}) were then calculated by regressing colony radii against time (all adj. $r^2 \geq 95\%$). At 21 days, the plugs were removed from the cellophane, which was inverted, placed into 10 mM phosphate buffer (pH 7.2) and shaken at 750 rpm for 120 min. Protein concentrations in the buffer were determined (Micro BCA Protein Assay, Thermofisher) and the specific activity of extracellular β-glucosidase was measured and expressed as nmol p-nitrophenol liberated from 4-nitrophenyl-β-D-glucopyranoside min^{-1} μg^{-1} protein using the methods described by Misiak et al. (2021).

2.4. Constant temperature exposures

These exposures determined the constant temperatures at which the isolates exhibited optimum growth. As above, plugs (7 mm diameter) of each isolate were cut from half-strength potato dextrose agar medium onto which spore suspensions in sterile water had been spread 16 h previously. Under a sterile hood, the plugs were placed onto soil extract medium in four 55 mm diameter plastic non-vented Petri dishes that were then sealed with Parafilm, inverted and incubated in cabinets at constant temperatures of 2.0 °C, 5.5 °C, 8.5 °C, 15.0 °C, 18.0 °C, 21.0 °C and 24.0 °C for 7 d, after which colony fronts were marked at × 10–15 magnification on dish reverses with a fine blade. The fronts were marked again in the same way 24 h and 48 h later, and radial extension rate (mm d^{-1}), averaged over 0–48 h, was calculated.

2.5. Statistical analyses

General linear models were used to test the main and interaction effects of fluctuating temperatures and isolate on response variables, with differences between means being tested with ANOVA following Benjamini-Hochberg correction (Benjamini and Hochberg, 1995). All analyses were made in MINITAB (version 19.2020.1).

3. Results

3.1. Exposures over 48 h

Compared with constant temperature controls of 10.7 °C, 12.0 °C and 13.1 °C, temperatures fluctuating from 2–18 °C, 2–21 °C and 2–24 °C inhibited the radial extension of *P. roseus* isolates at 24 h and 48 h by 10–51%, respectively, with the largest reductions in growth rate being caused by the 2–24 °C fluctuating temperature treatment (Table 1; Fig. 3A and B). The 2–15 °C fluctuating temperature treatment did not affect radial extension at 24 h or 48 h (Table 1; Fig. 3B). The significant fluctuating temperature × isolate interactions recorded for the 2–21 °C treatment at 24 h and the treatments fluctuating to ≥18 °C at 48 h (Table 1) indicated that the isolates responded differently to these treatments. Isolates L1, L2 and L3 were particularly sensitive to fluctuating temperatures, with 72–79% reductions in their radial extension caused by exposure to the 2–24 °C treatment at 48 h (Fig. 3B).

3.2. Exposures over 21 days

In contrast with the experiments conducted over 48 h, all fluctuating temperature treatments, including the 2–15 °C treatment, inhibited the mean radial extension rate of all isolates by 3–48% over 21 days (Table 1). The percentage reductions in growth rate caused by the three treatments cycling to ≥18 °C over 21 days were similar to those recorded in the exposures over 48 h (Table 1). The significant fluctuating temperature × isolate interactions for each of the treatments on radial extension rate (Table 1) indicated that they affected the isolates differently. As for the exposures over 48 h, strong inhibitory effects of fluctuating temperatures were recorded on isolates L1, L2 and L3, the growth rates of which were reduced by 75–86% following exposure to the 2–24 °C treatment (Supplementary Fig. 2A). Fluctuating temperatures had no effects on the mean specific β-glucosidase activity of all isolates (range 3.3–84.9 nmol p-nitrophenol min^{-1} μg^{-1} protein) after 21 days (Table 1). The significant fluctuating temperature × isolate interaction for the 2–24 °C fluctuating temperature treatment (Table 1) indicated that the treatment affected the specific β-glucosidase activities of the isolates differently, with it increasing the β-glucosidase activity of isolate SG2 by 1.5-fold and decreasing that of isolate L1 by 78% after 21 days (Supplementary Fig. 2B).

3.3. Constant temperature exposures

The optimum growth temperature of isolates SG1, L1, L2 and L3 was 15 °C (Fig. 4). Each of these isolates exhibited sharp declines in radial

Table 1
F values from general linear models with significance levels (*$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$) showing the main effects of fluctuating temperature treatments and interaction effects of fluctuating temperature and isolate on the radial extension, radial extension rate and specific β-glucosidase activity of the *Pseudogymnoascus roseus* isolates. Arrows indicate the directions of responses to fluctuating temperature treatments, and the percentage differences from constant temperature controls are shown in parentheses.

	Treatment[a]			
	2–15 °C	2–18 °C	2–21 °C	2–24 °C
Radial extension (24 h)				
Fluctuating temperature	2.81	18.44***↓ (10%)	127.37***↓ (28%)	276.49***↓ (42%)
Fluctuating temperature × isolate	0.54	1.21	9.73***	1.24
Radial extension (48 h)				
Fluctuating temperature	0.49	119.83***↓ (13%)	365.35***↓ (32%)	1203.95***↓ (51%)
Fluctuating temperature × isolate	0.88	4.89***	12.50***	9.05***
Radial extension rate (over 21 d)				
Fluctuating temperature	11.46**↓ (3%)	103.43***↓ (14%)	365.20***↓ (25%)	3139.43***↓ (48%)
Fluctuating temperature × isolate	2.28*	8.17***	16.04***	72.53***
Specific β-glucosidase activity (21 d)				
Fluctuating temperature	0.47	0.85	0.07	1.89
Fluctuating temperature × isolate	1.30	1.33	1.48	5.43***

[a] The constant mean temperature controls for the 2–15 °C, 2–18 °C, 2–21 °C and 2–24 °C fluctuating temperature treatments were 9.0 °C, 10.7 °C, 12.0 °C and 13.1 °C, respectively (Fig. 2A). Treatment degrees of freedom for the main effect of fluctuating temperature and the interaction were 1 and 9, respectively, and error degrees of freedom were 56–60. Significant main effects of isolate were recorded in all cases ($F_{9,56–60} = 6.52–248.14$, $P < 0.001$).

extension rate above this temperature, with isolates L1, L2 and L3 failing to grow at 24 °C (Fig. 4). The optimum growth temperature of all other isolates was 18 °C, with marked reductions in the radial extension rates of the isolates at 24 °C (Fig. 4).

4. Discussion

It is evident from the results reported above that short-term temperature fluctuations to, or exceeding, 18 °C most probably inhibit the hyphal growth of *P. roseus*, a widespread Antarctic fungus, in sun-exposed surface soils and bryophyte colonies during austral midsummer. Such events are not infrequent in the natural environment, with the temperatures of surface soils at Mars Oasis on Alexander Island exceeding 18 °C for up to six consecutive hours on between one and seven days each December in 2009–2011, and those of *C. varians* colonies on Rothera Point, 10 km east of Léonie Island, exceeding 18 °C on eight days in December 2007 (Newsham, 2010; Newsham et al., 2020). Inhibited growth and disruptions to metabolism, which similarly occur in temperate regions fungi exposed to temperature fluctuations (e.g., Morton and Eggins, 1977; Rawlings et al., 2022), typically arise from temperatures exceeding an organism's permissive range and nearing its critical thermal maximum, i.e., the temperature at which growth halts (Colinet et al., 2015). This is the likely explanation for the inhibited growth of isolates SG1, L1, L2 and L3 exposed to temperatures fluctuating to ≥18 °C, since these isolates exhibited growth reductions at constant temperatures above 15 °C. However, for the other six isolates, each of which had an optimum constant growth temperature of 18 °C, the growth inhibitions caused by the 2–18 °C treatment most probably arose from physiological stress associated with temperature fluctuation – attributable in *P. roseus* to, e.g., nucleic acid degradation or a lack of membrane integrity (Abu Bakar et al., 2022) – and not from the isolates' optimum temperature for growth being exceeded.

Water potential varies inextricably with temperature in the natural environment. Here, *P. roseus* was exposed to fluctuating temperatures on soil extract medium with water potentials varying between *c.* −1.10 MPa and −0.05 MPa at 2 °C and 24 °C, respectively. These water potentials are similar to those measured in fellfield soils at Mars Oasis shortly after snow melt in early December (Misiak et al., 2021) and in colonies of *C. varians* on Rothera Point, which are continuously hydrated by melt water and consequently have moisture contents of 83–90% throughout austral summer (Newsham, 2021; Newsham et al., 2021a). Given that *P. roseus* inhabits these colonies (Hughes et al., 2003), and, as shown here and elsewhere (Misiak et al., 2021; Newsham et al., 2021b), occurs in soils at Mars Oasis, it is apparent that the fungus is exposed in the natural environment to fluctuating temperatures at water potentials close to those of the medium on which it was grown in the exposures described above. Nevertheless, it is important to note that *P. roseus* is unresponsive to temperatures cycling daily between 2 °C and 21–24 °C at water potentials below −3.6 MPa, which occur in soils at Mars Oasis as they dry during late summer (Misiak et al., 2021). Thus, in dry substrates, although temperatures will increase to a greater extent than in saturated or mesic substrates (Campbell and Gardner, 1971), the response of *P. roseus* to temperature fluctuations will most probably be attenuated.

Climate change in maritime Antarctica has caused minimum daily air temperatures to increase at a faster rate than maximum daily air temperatures, leading to a 0.16 °C per decade decline in diurnal temperature fluctuation in the region since the 1970s (Kejna et al., 2013; Xie et al., 2018). This negligible change to air temperature fluctuation is unlikely to have affected microbial growth. However, the increasing occurrence of Antarctic heatwaves during austral summer (Feron et al., 2021; González-Herrero et al., 2022) is of greater significance for the growth of soil fungi. Heatwaves in Antarctica, associated with long-term summertime warming arising from climate change (González-Herrero et al., 2022), are projected to become more frequent, and to last longer, under only moderate greenhouse gas emission scenarios (Feron et al., 2021). The most severe Antarctic heatwave on record, which lasted for six days in February 2020, caused daily air temperatures to fluctuate by up to 18 °C (Francelino et al., 2021) and rapidly melted snowcover on the northernmost tip of the Antarctic Peninsula (Robinson et al., 2020). As the temperatures of soils in polar regions are consistently several degrees higher than air temperatures during summertime (Lembrechts et al., 2022), it is likely that the growth of *P. roseus*, which is frequent in northern Antarctic Peninsula soils (Newsham et al., 2021b), would have been inhibited by fluctuating soil temperatures during the heatwave.

In contrast with the observations of Misiak et al. (2021), who found that temperatures cycling daily to 2–24 °C for up to 10 weeks inhibited the ability of isolates A1, A2 and A3 to synthesize β-glucosidase, the experiments here indicated that fluctuating temperature treatments applied over 21 days had few effects on the specific activity of the enzyme secreted by *P. roseus*. Following Benjamini-Hochberg correction, the specific β-glucosidase activities of just two isolates of the fungus

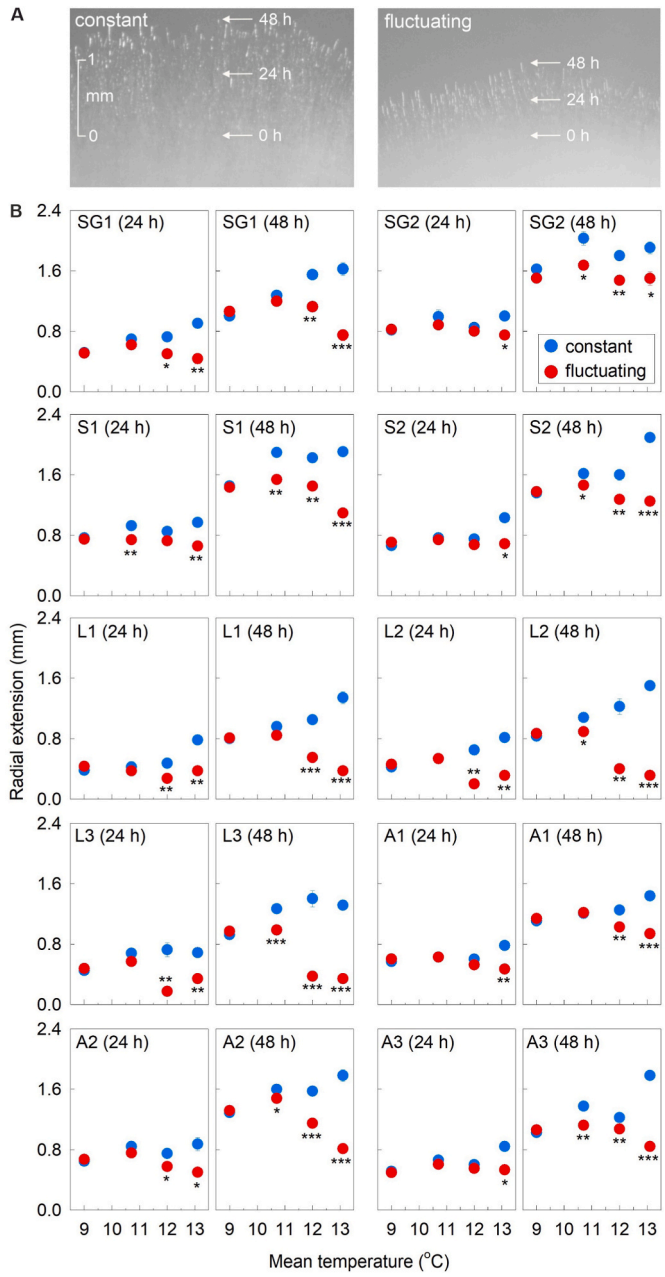

Fig. 3. (**A**) Colony fronts of isolate A1 grown at a constant temperature of 13.1 °C (left panel) and a fluctuating temperature of 2–24 °C (right panel) at 0 h, 24 h and 48 h and (**B**) radial extension of the 10 *Pseudogymnoascus roseus* isolates at 24 h and 48 h following exposure to the fluctuating temperature treatments (red circles) and their corresponding constant mean temperature controls (blue circles). Note that the mean temperatures of the 2–15 °C, 2–18 °C, 2–21 °C and 2–24 °C fluctuating temperature treatments were 9.0 °C, 10.7 °C, 12.0 °C and 13.1 °C, respectively (Fig. 2A). In (**B**), all axes are scaled identically, values are means of four replicates ± standard error and Benjamini Hochberg-corrected differences between pairs of means are denoted by $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$. Note that the circles used to denote the means are typically larger than the error bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

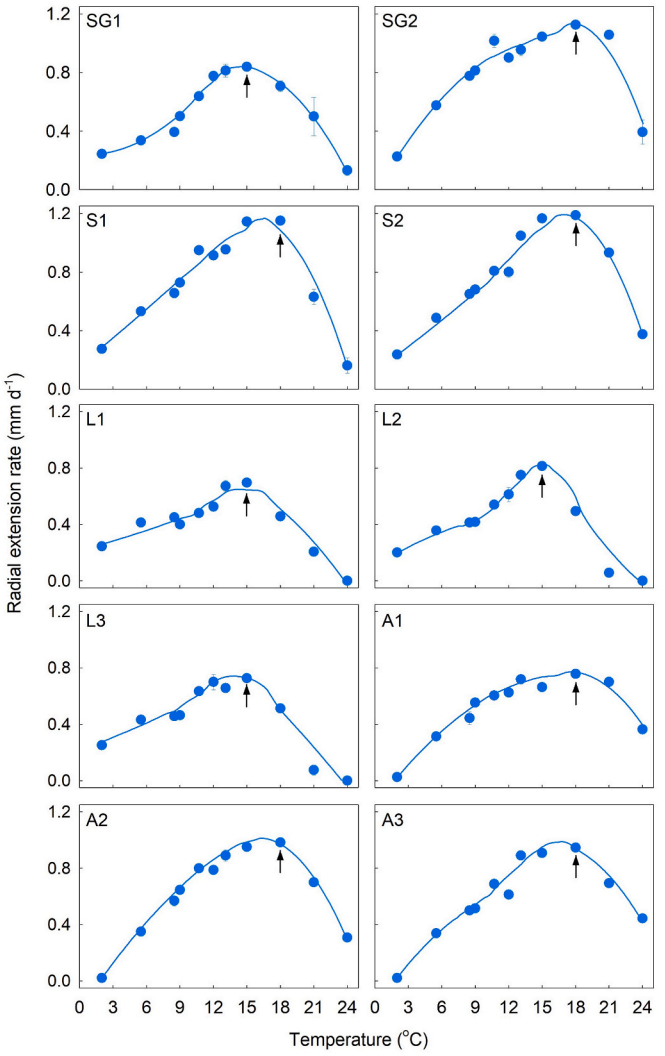

Fig. 4. Radial extension rates of the 10 *Pseudogymnoascus roseus* isolates grown at constant temperatures between 2 °C and 24 °C. The arrows indicate the optimum growth temperature of each isolate. Values, which are rates averaged over 0–48 h, are means of four replicates ± standard error. Those for temperatures from 9.0 to 13.1 °C were derived from the exposures over 48 h. The fits are loess-smoothed (0.7–0.9 sampling proportions and two polynomial degrees). Note that all axes are scaled identically and that the circles used to denote the means are typically larger than the error bars.

responded to the 2–24 °C fluctuating temperature treatment, with one isolate exhibiting decreased, and another exhibiting increased, activity of the enzyme after 21 days. Given that temperatures of 24 °C are only occasionally reached during summer in Antarctic soils and bryophyte colonies (Newsham, 2010, 2021; Convey et al., 2018; Misiak et al., 2021), and the absence of effects recorded here on β-glucosidase synthesis by temperatures fluctuating from 2 °C to 15–21 °C after 21 days, it seems unlikely that temperature fluctuations in the natural environment over periods of several days, even during heatwaves, influence the ability of *P. roseus* to degrade cellulose. Nevertheless, because saprotrophic fungi forage through soil for substrates (Aleklett et al., 2021), it is likely that the inhibitory effects of temperatures fluctuating to ≥18 °C on the hyphal growth of *P. roseus* hamper the ability of the fungus to decompose cellulose by diminishing its effectiveness at locating cellulose-rich substrates in soil.

Previous studies have found reduced abundances of *P. roseus* and other fungi in maritime Antarctic soils that are warmed with open top chambers (Misiak et al., 2021; Newsham et al., 2022). Although similar reductions in the abundances of fungi in experimentally warmed Arctic soils have been attributed to reduced water availability (Allison and Treseder, 2008; Christiansen et al., 2017), further research should address whether they instead arise, at least in part, from the fluctuations in soil temperatures elicited by chambers during summer (Bokhorst

et al., 2013). Further studies should also identify whether fluctuating temperatures inhibit the growth of other fungi that are frequent in Antarctica, such as lichen mycobionts and basidiomycetous yeasts (Newsham et al., 2021b), the former of which inhabit rock surfaces that can heat to 38 °C during austral summer (Smith, 1999). Studies should also focus on the impacts on fungal growth of fluctuating temperatures crossing the freezing point for water, as occur in Antarctic soils during late spring and late summer (Newsham et al., 2020; Misiak et al., 2021), and whether the accumulation of chaotropic metabolites such as glycerol at low temperatures may enable microbes to survive these temperature fluctuations (Chin et al., 2010; Pavankumar et al., 2021). Lastly, since soil temperatures in Arctic and alpine habitats also exhibit wide diurnal variations (Bokhorst et al., 2013; Convey et al., 2018), further research should determine the effects of temperature fluctuations on fungi in these regions, and, given the pivotal roles of these microbes in terrestrial ecosystems (Swift et al., 1979), whether such effects might potentially have ecosystem-level impacts.

5. Conclusions

Short-term experiments under controlled conditions indicated that the growth of the widespread Antarctic fungus *P. roseus* is inhibited by exposure to temperatures fluctuating daily between 2 °C and 18–24 °C. It is evident that temperatures fluctuating to ≥18 °C during austral summer in mesic surface soils and bryophyte colonies, exacerbated by the occurrence of summertime Antarctic heatwaves, are likely to inhibit the growth of *P. roseus* in the natural environment. Further research is necessary to identify whether fluctuating temperatures similarly inhibit the growth of further soil fungi in Antarctica and other cold regions, and to determine the physiological processes responsible for inhibited growth.

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Declaration of competing interest

The author declares no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funbio.2023.12.003.

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