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Will climate warming exceed lethal photosynthetic temperature thresholds of lichens in a southern African arid region?

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Abstract

Predicted elevated temperatures and a shift from a winter to summer rainfall pattern associated with global warming could result in the exposure of hydrated lichens during summer to more numerous temperature extremes that exceed their thermal thresholds. This hypothesis was tested by measuring lethal temperature thresholds under laboratory and natural conditions for four epilithic lichen species (*Xanthoparmelia austro-africana*, *X. hyporhytida*, *Xanthoparmelia* sp., *Xanthomaculina hottentotta*) occurring on quartz gravel substrates at a hot arid inland site two epigeous lichen species (*Teloschistes capensis*, *Ramalina* sp.) occurring on gypsum-rich topsoil at a warm humid coastal site. Extrapolated lethal temperatures for photosynthetic quantum yield under laboratory conditions were up to 4°C higher for lichens from a dry inland site than those from a humid coastal site. Lethal temperatures extrapolated for photosynthetic quantum yield at a saturating photosynthetic photon flux density of $\geq 11,000$ $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ under natural conditions were up to 6°C higher for lichens from the dry inland site than the more humid coastal site. It is concluded that only under atypical conditions of lichen exposure in a hydrated state to temperature extremes at high midday solar irradiances during summer could lethal photosynthetic thresholds in sensitive lichen species be potentially exceeded, but whether the increased frequency of such conditions with climate warming would lead to increased likelihood of lichen mortality is debatable.

Introduction

The unprecedented accumulation of CO₂ and other greenhouse gases in the atmosphere as pre-industrial times has already had a discernible influence on global temperature and is forecast to cause further warming this century (IPCC, 2007). Direct and dramatic biotic responses to global warming are anticipated (Thomas *et al.*, 2004). This expectation is supported by new and increased occurrences of subtropical epiphytic lichen species in Europe, for example in the Netherlands where lichen species preferring colder environments have declined in numbers or disappeared between 1980 and 2001 (Aptroot & van Herk, 2007).

Lichens are recognized as valuable indicators of climate shifts, especially in temperature and precipitation (Insarov & Insarova, 2002), but there are few data on climatic impacts on lichens in arid and semi-arid ecosystems in the southern hemisphere whose diversity is potentially threatened by global climate change, especially in species-rich southern African regions (Zedda *et al.*, 2011). An impact of climatic change on southern African lichens in the arid Succulent Karoo Biome could be a loss of rare and endemic species and a rapid colonization of substrata by globally widespread species, particularly cyanolichens. This will have potentially profound effects on this biome, which is characterized by an extraordinary and peculiar diversity of lichen taxa (Zedda & Rambold, 2009).

Climate simulations for the southern African arid winter rainfall region predict a progressive extension of wetter summer rainfall and drier winter rainfall regions (MacKellar, Hewitson & Tadross, 2007) accompanied by a mean annual air temperature increase of up to 5.5°C towards the end of this century (Hulme *et al.*, 2001). These climatic changes could result in the exposure of hydrated lichens during summer to an increased incidence of temperature extremes that exceed their thermal thresholds.

Methods and materials

Study sites and species

Lichens were examined at two climatically and floristically diverse sites in the South African Western and Northern Cape Provinces. The first hot arid inland site with a mean annual temperature of 25.7°C and annual rainfall of 145 mm was the farm Quaggaskop (31°24.6'S, 18°37.8'E) situated at an elevation ±160 m in the Knersvlakte bioregion 20 km north of the town of van Rhynsdorp (Fig. 1). The second warm humid coastal site with a mean annual temperature of 17.2°C and an erratic low rainfall of 39 mm per annum supplemented by frequent fog measured at 214 mm per annum (Maphangwa *et al.*, 2011) were a large lichen field (28°37'S, 16°30'E) situated south-east of the mining town of Alexander Bay, 3.2 km distant from the Atlantic coast (Fig. 2). The six selected study species were *Xanthoparmelia austro-africana* (Stirt) Hale, *X. hyporhytida* (Hale) Hale, *Xanthoparmelia* sp. (undescribed), *Xanthomaculina hottentotta* (Ach) Hale occurring on quartz gravel substrates at the Quaggaskop site and *Teloschistes capensis* (L.f.) Müll Arg and an undescribed *Ramalina* sp. (often regarded as *R. capensis* Th Fr) occurring on gypsum-rich topsoil at the Alexander Bay site. These four epilithic and two epigeous species were selected for being endemic to the region (Dodge, 1971; Hale, 1990) and for their foliose and fruticose growth forms, which are known to be most sensitive to increased aridness (Nash, 1996).

Laboratory studies

Thirty-five thalli of each of the six lichen species were collected on their original substrates from the two study sites. The 210 lichen thalli were transferred to a growth room and allowed to acclimatize for 8 days at 18°C day per 10°C night at a 16 h daily photosynthetic photon flux density (PPFD)

of 300 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. During the acclimation period, the lichens were hydrated every second day by applying a fine distilled water mist spray to their thalli. Following acclimation, the hydrated lichen thalli were exposed in forced draft ovens for 2-h intervals to temperatures ranging from the laboratory ambient 24–48°C at 4°C intervals. The 2-h oven exposure periods corresponded with diurnal temperature maxima confined to 1-h periods on either side of the solar noon. There were five replicated lichen thalli per species for each of the seven heat treatments.

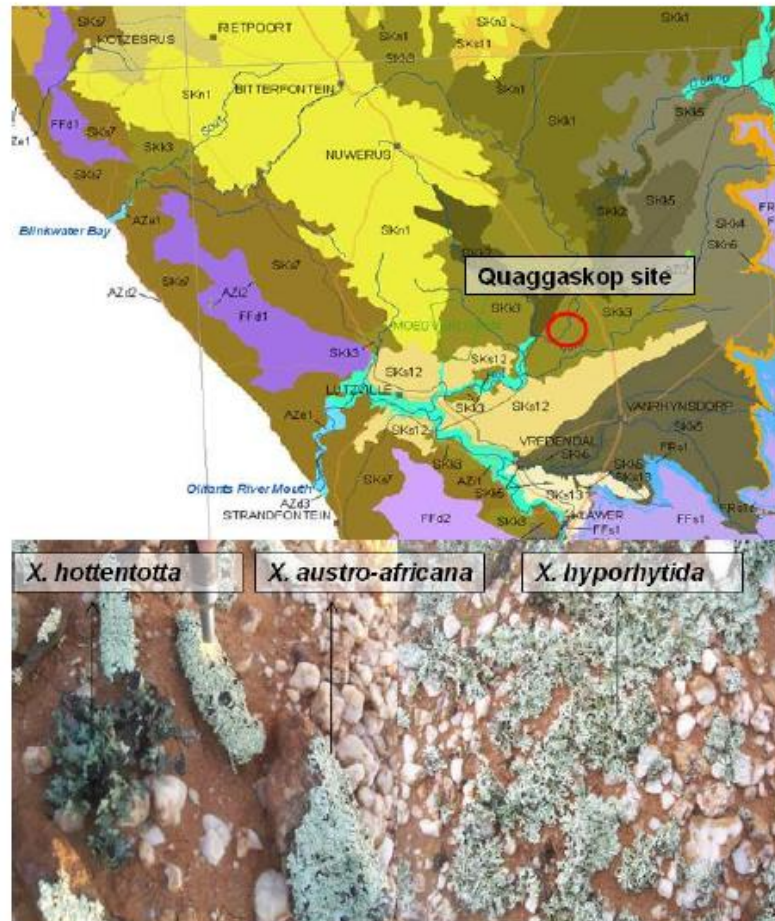


Fig 1 Location of the Quaggaskop experimental site and common lichen species occurring on quartz gravel substrates at the site

Following heat exposure, the lichens were returned to the growth room for an additional 24-h acclimation period after which they were rehydrated with a fine distilled water mist spray and allowed to drain for 1 h in the dark to avoid reported negative impacts of oversaturation by water on lichen photosynthesis, according to Lange, Belnap & Reichenberger (1998). Subsequent measurements of initial (F_0) and maximal (F_m) fluorescence emissions from the dark-adapted, hydrated, heat-treated lichen thalli were taken with a Plant Efficiency Analyser (PEA; Hansatech Instruments Ltd., King's Lynn, Norfolk, UK) following a one-second PPFD of 3500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Three fluorescence measurements were performed on five thalli of each lichen species from each oven exposure temperature. Maximum quantum yields of Photosystem II (PSII)

were computed from the ratios of variable to maximal fluorescence ($F_v/F_m = F_m - F_0/F_m$).

Field studies

Demarcated plots 120 cm in diameter constructed from 40 cm high steel fencing with a five centimetre diameter mesh were installed at random over populations of the four epilithic lichen species at the dry inland site and populations of the two epigeous lichen species at the more humid coastal site (six replicated plots per lichen species per site). Lichen thalli were hydrated with a fine distilled water mist spray and allowed to drain for a 1-h period. Water saturation deficits were measured intermittently in randomly selected samples of lichen thalli 1 h after their artificial hydration using a published formula averaged $30 \pm 10\%$ (Hájek, Barták & Gloser, 2001). These water saturation deficits were in the range of those at which maximum photosynthetic quantum yields have been reported in lichens with plateau and parabolic type photosynthetic responses to thallus dehydration (Hájek, Barták & Gloser, 2001).

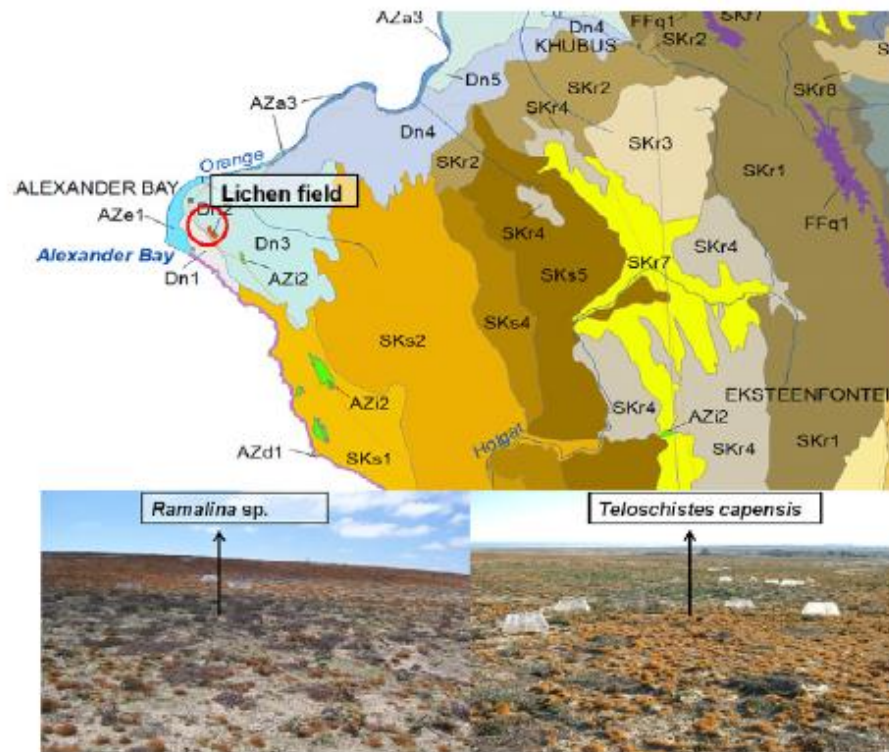


Fig 2 Location and typical lichen topography at the Alexander Bay experimental site

At monthly intervals, five replicated fluorescence measurements were taken hourly between 08 : 00 and 17 : 00 with a portable modulated fluorometer (OSI-F1, Opti-Sciences Inc., Hudson, USA) on four randomly selected thalli of each lichen species at each site following their exposure to an 0.8 s saturating light pulse of $15,000 \text{ lmol photons m}^{-2} \text{ s}^{-1}$. Effective quantum yields of PSII (DF/F_m') were computed from ratios of variable steady state ($F_{ms}-F_s$) to maximum steady-

state (F_{ms}) fluorescence ($\Delta F/F_m' = F_{ms}-F_s/F_{ms}$). Fluorescence measurements were matched with simultaneously recorded ground surface air temperatures and PPFD using radiation-shielded thermocouples as described in Maphangwa *et al.*, 2011.

Statistical analyses

The relationships between oven exposure temperature and measured F_v/F_m in each lichen species were fitted using an iterative nonlinear regression applying an inverse mono-molecular function (Causton & Dale, 1990)

$$y = a(1 - e^{-b-cx}) \quad (1)$$

where $y = F_v/F_m$, x the oven exposure temperature with the coefficients a , b and c derived from the iterative process.

The reverse form of the inverse monomolecular function was applied to extrapolate at which lethal temperature F_v/F_m attained zero:

$$x = -\ln\{[(1 - y/a)b]/c\} \quad (2)$$

Least squares regressions quantified the relationships between field exposure temperature and measured $\Delta F/F_m'$ for each lichen species at a saturating PPFD ($\geq 1100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). A Student's t -test tested the slopes and the intercepts of the linear regressions for significance at $P \leq 0.001$. The regression equations were used to extrapolate the lethal temperatures at which $\Delta F/F_m'$ attained zero.

Results

Laboratory studies

In all six lichen species, relationships between measured F_v/F_m and oven exposure temperature quantified by the inverse monomolecular function (Fig. 3a) had coefficients of determination (r^2) that were statistically significant at $P \leq 0.001$ (Table 1).

Extrapolated lethal photosynthetic temperatures for lichens from the dry inland site (range: 47.1–48.1°C) were up to 4°C higher than those from the humid coastal site (range: 44.1–44.4°C).

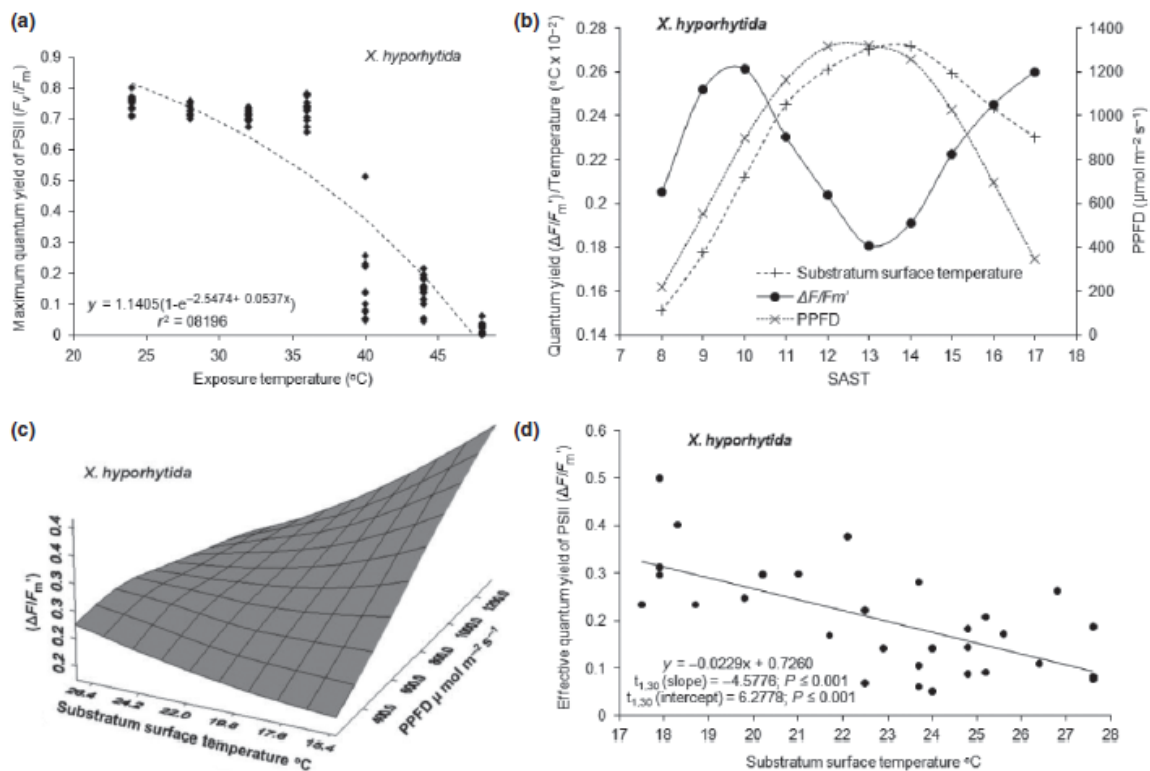


Fig 3 (a) Iterative nonlinear regression (inverse monomolecular function) of F_v/F_m against oven exposure temperature for hydrated *Xanthoparmelia hyporhytida*, (b) two dimensional plot, (c) three-dimensional surface spline plot of $\Delta F/F_m'$ against substrate surface air temperature and photosynthetic photon flux density (PPFD) (annual averages) for hydrated *X. hyporhytida* and (d) linear regression of $\Delta F/F_m'$ at photosynthetic saturating PPF's $\geq 11,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ against substrate surface air temperatures for hydrated *X. hyporhytida*

Field studies

All six lichen species displayed similar diurnal photosynthetic patterns in which $\Delta F/F_m'$ increased with increasing substrate surface air temperature and PPF in the early morning up to about 10 : 00 SAST, depending on season, with DF/F_m' subsequently decreasing with increasing substrate surface air temperature and PPF (Fig. 3b).

Table 1 Laboratory-derived lethal photosynthetic temperatures for hydrated lichen species from two climatically diverse sites (y = maximum photosynthetic quantum yield ' F_v/F_m ' and x = 2-h oven exposure temperature)

Site	Lichen species	Nonlinear regression function	r^2	Lethal photosynthetic temperature °C
Dry inland	<i>Xanthoparmelia</i> sp.	$y = 0.8454(1 - e^{-4.8780 + 0.1013x})$	0.8888***	48.1
	<i>X. austroafricana</i>	$y = 0.7875(1 - e^{-6.3500 + 0.1338x})$	0.8593***	47.5
	<i>X. hyporhytida</i>	$y = 1.1405(1 - e^{-2.5474 + 0.0537x})$	0.8196***	47.4
	<i>Xanthomaculina hottentotta</i>	$y = 1.1024(1 - e^{-2.6885 + 0.0571x})$	0.8439***	47.1
Humid coastal	<i>Teloschistes capensis</i>	$y = 0.9420(1 - e^{-4.1446 + 0.0934x})$	0.8623***	44.4
	<i>Ramalina</i> sp.	$y = 1.1337(1 - e^{-2.6306 + 0.0596x})$	0.8697***	44.1

*** $P \leq 0.001$.

Table 2 Field-derived lethal photosynthetic temperatures for hydrated lichen species from two climatically diverse sites (y = effective photosynthetic quantum yield ' $\Delta F/F_m$ ' at photosynthetic saturating photosynthetic photon flux density (PPFD)'s $\geq 11,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and x = soil surface air temperature)

Site	Lichen species	Linear regression function	t -statistic (slope)	t -statistic (intercept)	Lethal photosynthetic temperature °C
Dry inland	<i>Xanthoparmelia</i> sp.	$y = -0.0236x + 0.7715$	$t_{1,30} = -3.7191^{***}$	$t_{1,30} = 5.2559^{***}$	32.7
	<i>X. austroafricana</i>	$y = -0.0141x + 0.4928$	$t_{1,30} = -3.3056^{**}$	$t_{1,30} = 4.9894^{***}$	34.9
	<i>X. hyporhytidi</i>	$y = -0.0229x + 0.7260$	$t_{1,30} = -4.5776^{***}$	$t_{1,30} = 6.2778^{***}$	31.7
	<i>Xanthomaculina hottentotta</i>	$y = -0.0249x + 0.8112$	$t_{1,30} = -4.5691^{***}$	$t_{1,30} = 6.4515^{***}$	32.6
Humid coastal	<i>Teloschistes capensis</i>	$y = -0.0321x + 0.9282$	$t_{1,24} = -4.5972^{***}$	$t_{1,24} = 5.8057^{***}$	28.9
	<i>Ramalina</i> sp.	$y = -0.0296x + 0.8603$	$t_{1,24} = -5.0461^{***}$	$t_{1,24} = 6.4038^{***}$	29.1

*** $P \leq 0.001$. ** $P \leq 0.01$.

The lowest $\Delta F/F_m'$ values were generally recorded at the highest substrate surface air temperatures and PPFD's around the solar noon (13 : 00 SAST). This was followed by a secondary phase of elevated $\Delta F/F_m'$ with diminishing substrate surface air temperature and PPFD after the solar noon (Fig. 3b). Three-dimensional surface plots revealed linear increases in $\Delta F/F_m'$ with increasing PPFD's at low substrate surface air temperatures and *vice versa* in all six lichen species, but at a PPFD of $\geq 11,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ $\Delta F/F_m'$ decreased linearly with increasing substrate surface air temperature (Fig. 3c).

Least squares regressions of measured $\Delta F/F_m'$ at a PPFD of $\geq 11,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ against substrate surface air temperature (Fig. 3d) had significant ($P \leq 0.001$) slopes and intercepts in all six lichen species (Table 2). Extrapolated lethal photosynthetic temperatures for lichens from the dry inland site (range: 31.7–34.9°C) were up to 6°C higher than those from the more humid coastal site (range: 28.9–29.1°C).

Discussion

The lethal temperature range of 44.1–48.1°C for photosynthetic quantum yield extrapolated for hydrated lichens under laboratory conditions in this study was slightly lower than the lethal temperatures for photosynthetic gas exchange hitherto reported for other lichen species from southern Africa and other regions of the world. Examples include 50°C for hydrated *Umbilicaria mammulata* (Ach.) Tuck. and 55°C for hydrated *Chondropsis semiviridis* (F. Muell. ex Nyl.) Nyl. ex Cromb. (Rogers, 1971), 54°C for hydrated *Lobaria pulmonaria* (L.) Hoffm. (Gauslaa & Solhaug, 1999), 50 and 60°C for hydrated *Ramalina menziesii* Tuck. from cool and hot sites, respectively (Larson, 1989), 50°C for hydrated *Caloplaca elegantissima* (Nyl.) Zahlbr. and 55°C for hydrated *Teloschistes capensis*, *Neofuscelia namibiensis* (Elix & T.H. Nash) and *Xanthoparmelia walteri* M.D.E. Knox (Lalley & Viles, 2006). The slightly lower lethal photosynthetic temperatures measured in this study were likely due to heat-induced reductions in PSII electron transport commencing at temperatures much lower than the threshold for deactivation of the photosynthetic gas exchange enzyme Rubisco (Musil *et al.*, 2009).

Lange *et al.* (2006) concluded that nocturnal moistening by fog or dew in coastal deserts drives a subsequent short phase of peak lichen photosynthetic activity in the early morning hours. The duration of moisture-saturated atmosphere reported to determine the length of photosynthetic activity and distribution patterns of *Teloschistes lacunosus* (Rupr.) Savicz in the Tabernas Desert in Spain (Del Prado & Sancho, 2007). In the Namib Desert, peaks in photosynthetic activity have been reported in *Ramalina maciformis* (Delise) Bory and *Teloschistes lacunosus* in the 3-h period after sunrise, which is complemented by a short second phase of enhanced photosynthetic activity driven by increased humidity in the late afternoon (Lange *et al.*, 1991). These diurnal patterns in photosynthetic activity are typical for crustose and foliose lichens from the Negev Desert (Lange, 1970), for lichens from arid and semi-arid Mediterranean climates (Lange *et al.*, 1985; Kappen, 1988) and for lichens from temperate climates (Lange, 2003). Similarly, in this study, hydrated lichens displayed an increased $\Delta F/F_m'$ in the early morning, which corresponded with increasing substrate surface air temperature and PPFD up to about 10 : 00 SAST with a subsequent decline in $\Delta F/F_m'$ and increasing substrate surface air temperature and PPFD towards the solar noon.

The observed linear decline in $\Delta F/F_m'$ with increasing substrate surface air temperature at a saturating PPFD of $\geq 11,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in all six lichen species examined indicated an additive effect of high PPFD and high temperature on PSII damage. This was evident from the up to 15°C lower extrapolated lethal temperatures for lichen photosynthetic quantum yield at a PPFD of $\geq 11,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ under natural conditions (range: 28.9–34.9°C) than in the dark under laboratory conditions (range: 44.1–48.1°C). Similarly, Gauslaa & Solhaug (1999) reported that a high PPFD of 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ produced about the same reduction in photosynthetic quantum yield in *L. pulmonaria* at 18°C as at 38°C in the dark, and at an irradiance of 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, equivalent to 38°C in the dry lichen thallus, produced more damage to PSII than the same temperature did in the dark. High light intensities have been reported to induce severe and long-lasting photoinhibition in lichens from shaded forest habitats (Gauslaa & Solhaug, 1996, 2000). However, photoinhibition at high light intensities is considered less severe in lichens from sunlit habitats, which display an acclimation of several fluorescence parameters including $\Delta F/F_m'$ to seasonal changes in solar radiation. This acclimation achieved through the regulation of the UV-B-induced sun-screening cortical lichen secondary compound parietin located above the algal layer (Solhaug *et al.*, 2003) in proportion to the seasonally changing sun exposure, the parietin reduces but not entirely eliminates photoinhibition of the photobiont (Solhaug & Gauslaa, 1996).

Comparison of laboratory and field-derived lethal temperature thresholds for lichen photosynthetic quantum yield with a 27-year meteorological record of monthly average daily maximum temperatures and temperature extremes at the two study sites (Fig. 4a,b) revealed that the extrapolated lethal temperatures for lichen photosynthetic quantum yield were appreciably

exceeded only by recorded temperature extremes during summer. Consequently, only under atypical conditions of lichen exposure in a hydrated state to temperature extremes at high midday solar irradiances during summer could lethal photosynthetic thresholds in sensitive lichen species be potentially exceeded, but whether the increased frequency of such conditions with climate warming would lead to increased likelihood of lichen mortality is debatable. This is because in moist lichens, the rate of water loss (Gauslaa & Solhaug, 1998) and consequent evaporative cooling is high so that heat damage is less probable under natural conditions (Hoffman & Gates, 1970). Also, high light-exposed hydrated lichen thalli have been reported to exhibit a rapid recovery of photosynthetic quantum yield in the dark (Gauslaa & Solhaug, 1999).

Further studies are required to establish whether lethal photosynthetic thresholds of lichens from summer rain-fall regions where they are frequently exposed in a hydrated state to high midday temperatures and solar irradiances do exceed those from arid winter rainfall regions.

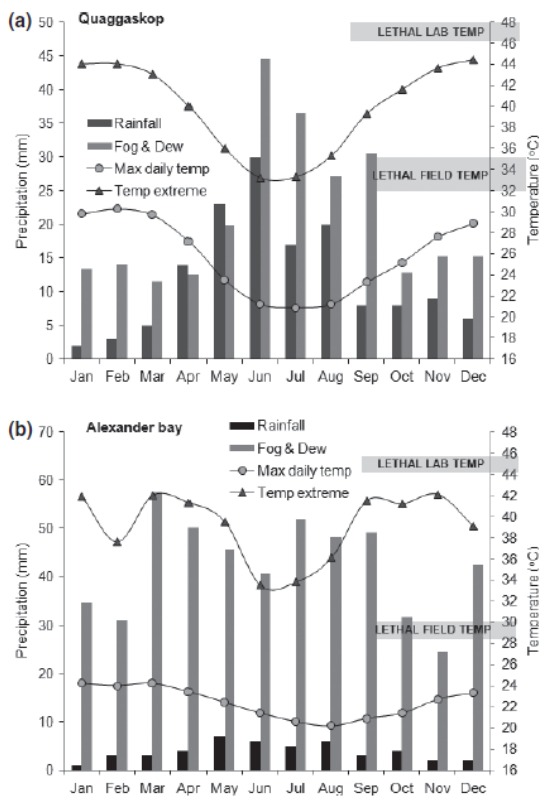


Fig 4 Monthly rainfall, fog and dew precipitation, average daily maximum temperatures and temperature extremes (1957–1984) at (a) dry inland site and (b) humid coastal site. Shaded areas indicate measured lethal photosynthetic temperatures for the dominant epilithic lichens at the two sites under laboratory and field conditions

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