Article

Primary production of lake phytoplankton, dominated by the cyanobacterium *Cylindrospermopsis raciborskii*, in response to irradiance and temperature

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Received 4 August 2014; accepted 5 December 2014; published 3 February 2015

Abstract

We present the first data on the interacting effect of temperature and light on primary production of the toxic cyanobacterium *Cylindrospermopsis raciborskii* in situ. *C. raciborskii* can be a dominant component of the phytoplankton community in tropical and subtropical lakes and reservoirs. We examined the interacting effects of a range of light (0, 2, 7, 17, 30, and 100% of ambient light) and temperature (20, 24, 28, and 32 °C) conditions, in terms of primary production rate and primary production irradiance model parameters, for a *C. raciborskii*-dominated phytoplankton community in a subtropical reservoir. Based on ^{13}C-uptake experiments, phytoplankton preconditioned to temperatures between 24 and 26 °C had highest maximum primary production rates (2.25 ± 0.45 µg C µg Chl-a^{-1} h^{-1}) at 28 °C and lowest at 32 °C (0.58 ± 0.13 µg C µg Chl-a^{-1} h^{-1}). Temperature also had an effect on the response to light conditions. Phytoplankton preconditioned to a shallow euphotic depth (~2.3 m deep) had the lowest half saturation of primary production, I_k, at 28 °C and highest at 32 °C, while the highest temperature treatment also had the highest level of photoinhibition at 100% of ambient light. This suggests that the cyanobacterial community is adapted to a low light environment under optimal temperature conditions for primary productivity. These conditions are consistent with other studies showing that *C. raciborskii* is highly adapted to low light conditions. This work demonstrates the importance of considering temperature when comparing calibrated primary production parameters.

Key words: *Cylindrospermopsis raciborskii*, natural population, P-I curves, primary production, temperature

Introduction

Light and temperature are 2 important parameters determining the abundance of phytoplankton, including cyanobacteria in lakes and reservoirs. Cyanobacteria have high optimal growth temperatures and a preference for low light conditions (Reynolds 2006). Over-supply of nutrients in eutrophic systems causes the biomass in water columns to increase to levels where light is the limiting resource, favouring species suited to lower light conditions (Brauer et al. 2012). This includes cyanobacteria, particularly filamentous species (Scheffer et al. 1997), which can grow at low light levels but are often inhibited a high light levels. A high optimal growth temperature, compared to other phytoplankton members, means that high temperatures can cause cyanobacteria blooms to form (Paerl and Huisman 2008). Unsurprisingly, increases in temperature due to climate change combined with eutrophication are causing an increase in the magnitude of cyanobacteria blooms and an expansion of cyanobacteria species, including toxic species, into new habitats (Paerl and Huisman 2009,

DOI: 10.5268/IW-5.2.778

Brookes and Carey 2011); this is likely to continue. Understanding how temperature and light contribute to high abundances and geographical expansion of cyanobacteria is an important research area for management of these species.

One cyanobacteria species spreading worldwide is *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Subba Raju (*C. raciborskii*; Padisák 1997, O'Neil et al. 2012, Vehovszky et al. 2013). In Australia, *C. raciborskii* is typically toxic, producing cylindrospermopsins, and it blooms periodically in lakes, reservoirs, and weir pools throughout the country but more frequently in the tropics (Byth 1980, McGregor and Fabbro 2000). Toxins produced by *C. raciborskii* have been linked to livestock fatalities (Saker et al. 1999) as well as causing the closure of lakes for recreational swimming due to its potential toxicity to humans. There have also been increased reports of blooms in temperate regions around the world in recent decades, but these are typically nontoxic (Bonilla et al. 2011, Sinha et al. 2012).

C. raciborskii has a preference for high temperatures (Briand et al. 2004) and is a strong competitor for phosphorus (Istvanovics et al. 2000, Posselt et al. 2009) and nitrogen (Sprober et al. 2003, Burford et al. 2006), including being capable of nitrogen fixation. Studies of *C. raciborskii* in lakes, reservoirs, and weir pools have shown highest abundance at higher water temperatures and lower light levels (Fabbro and Duivenvoorden 1996, McGregor and Fabbro 2000, Burford and O'Donohue 2006). Studies have also shown that it exhibits hysteresis of primary production in response to the light climate, possessing a tolerance of low and variable irradiance (O'Brien et al. 2009). The trade-off to all these competitive traits is a low maximum growth rate, only ~0.4 d^{-1} at optimal temperatures (Briand et al. 2004).

It is not yet established how temperature and light interact to affect primary production of *C. raciborskii*. This understanding is needed to predict blooms and also how they might spread or increase in abundance in Australia under future changes in climate. Previous work on the effect of temperature and light on *C. raciborskii* physiology has concentrated mainly on growth rates in laboratory studies and not primary production (Saker and Griffiths 2000, Briand et al. 2004, Mehnert et al. 2010, Bittencourt-Oliveira et al. 2012). The maximum growth rate for *C. raciborskii* in culture conditions has been determined to be between 25 and 32 °C (Saker and Griffiths 2000, Briand et al. 2004, Mehnert et al. 2010) and was similar across strains isolated from different geographical locations (Briand et al. 2004); however, the effect of temperature on primary production has not been determined for natural populations. Previous work in an Australian reservoir (Burford et al. 2006, O'Brien et al. 2009) has confirmed that endemic strains of *C. raciborskii* possess a high affinity for light, but these studies did not consider the effect of temperature on primary production, and hence estimates of common photophysiological parameters. Furthermore, in those studies, there was a mixed phytoplankton community so the response could not be attributable purely to *C. raciborskii*. This study therefore aimed to quantify the interacting effect of temperature and light on primary productivity rates in a phytoplankton community dominated by *C. raciborskii* in a subtropical reservoir.

Methods

Primary production rate experiments were conducted at 4 temperature treatments on field samples of a cyanobacterial bloom dominated by *C. raciborskii*. The data generated from each of the temperature treatments were fitted using a primary production irradiance (P-I) model. The calibrated P-I model parameters were then compared among the different treatments.

Site description

The experiments were conducted at Lake Borumba, a water supply reservoir in southeast Queensland, Australia (Fig. 1; 26°30.6′S, 152°34.8′E). Lake Borumba's waterline at full capacity is 135 m a.s.l. At full capacity, Lake Borumba contains 46 000 ML, has a surface area of 5 km^2, and an average depth of 6.6 m. The lake strongly stratifies on an annual basis and is affected by annual blooms of *C. raciborskii* (McGregor and Fabbro 2000, Leigh et al. 2010). A survey of lakes and reservoirs in Queensland found Lake Borumba had the third highest average mean density of biomass of *C. raciborskii* (1701.1 mm^3 L^{-1}), as well as the highest median concentrations of the toxin cylindrospermopsin (McGregor and Fabbro 2000). The main body of the lake is surrounded by steep terrain, which shields the lake from mixing and reduces the daily insolation.

Primary productivity experiments

Primary production was estimated by measuring ^{13}C-carbon fixation rates as per a previous study by Burford and co-workers (Burford et al. 2011). Carbon fixation rates were determined at a range of temperatures using 2 h incubations using sample collected from a bloom of *C. raciborskii* in Lake Borumba. Due to logistics, the experiments were spread across 3 days: 7 March (20 °C), 8 March (28 °C), and 9 March (24 and 32 °C) in 2008.

Water was sampled using a bucket at the surface of the lake ~200 m from the dam wall at ~11:00 h each day.

 DOI: 10.5268/IW-5.2.778

Water was mixed, and 150 mL subsamples were then poured into each of eighteen 250 mL clear plastic bottles. Incubations were conducted at 6 irradiance levels for 4 different temperature levels (20, 24, 28, and 32 °C). The bottles were placed inside 6 polyethylene shade cloth bags of differing thickness corresponding to 0, 2, 7, 17, 30, and 100% of maximum irradiance, with 3 replicate flask bottles per bag. Incident photosynthetically active radiation (PAR) was logged with 2π PAR sensors (Odyssey, Dataflow Systems Pty Ltd, Harewood, Christchurch, New Zealand), which had been calibrated with a LI-COR (LI-COR Corporate Offices, Lincoln, NE, USA) 2π PAR sensor at the site of the experiment. The shade cloth bags were then placed in baths, with the water temperatures controlled using water chillers, for 30 min in the dark prior to incubation to allow the temperature inside the culture flask bottles to equalise with the water temperature in the temperature-controlled baths.

The temperate baths were then placed in full sunlight, and 95.2 µmol L^{-1} of ^{13}C-sodium bicarbonate solution was added to each bottle. The samples were then incubated for ~2 h either side of local apparent noon, with exact time of incubation recorded. Water samples of 50 mL from each culture flask bottle were then filtered onto precombusted GF/F glass fibre filters (Whatman International Ltd, Maidstone, Kent, England), after which the filters were frozen. Filters were then dried at 60 °C for 24 h before being analysed for $^{13}C/^{12}C$ isotope ratio and percent carbon on a mass spectrometer (GV Isoprime, Manchester, UK). Primary productivity data were compared among the different incubation temperatures by way of a paired t-test using R software (R Core Team 2014), after testing for normality.

Physiochemical parameters

The light profile was measured throughout the water column using an LI-COR 2π PAR sensor. Water subsamples were also taken at the time of sampling for measurement of phytoplankton cell counts, chlorophyll *a*, alkalinity, ammonia-nitrogen, nitrate plus nitrite, and soluble reactive phosphorus. Subsamples of water for phytoplankton cell counts were fixed with Lugol's solution and counted using Sedgewick Rafter cells under a phase contrast microscope (400× magnification). The total biovolume per unit volume was then calculated using 22.44 µm^3 cell^{-1} for *C. raciborskii* and a mean of 10.0 µm^3 cell^{-1} for all other species (G. McGregor, Queensland Department of Environment and Resource Management, June 2010, pers. comm.).

For chlorophyll *a* analysis, known volumes of water were filtered through GF/F (Whatman) filters. The filters were then frozen and returned to the laboratory. Filters were extracted by sonication for 1 min in cold 100% acetone; adjusting the acetone concentration to 90%, the extract was then analysed spectrophotometrically (Lorenzen 1967). Water for alkalinity analysis was stored in plastic vials on ice and analysed by titration using the method of the American Public Health Association (APHA 1995). Ammonia, nitrate/nitrite, and soluble reactive phosphorus were analysed using standard colorimetric methods (APHA 1995). The detection limit for the method is 0.002 mg L^{-1}. Water temperature in the lake was logged throughout the experiment (7–9 March 2008) using HOBO (Onset Computer Corporation, Bourne, MA, USA) temperature loggers deployed at the surface.

Primary production rate model

P-I curves were determined for each of the 4 temperature treatments using a primary production model (Bright and Walsby 2000), hereafter referred to as the primary production model. Models were fit to the mean of each treatment.

The model is defined as:

$$P(I) = P_{max} \times (1 - e^{I/I_k}) - \beta \times I, \quad (1)$$

where $P(I)$ is the rate of carbon fixation (µg C µg Chl-a^{-1} h^{-1}); P_{max} is maximum primary productivity (µg C µg Chl-a^{-1} h^{-1}); β is the photoinhibition parameter (µg C µg Chl-a^{-1} h^{-1} (µmol photons m^2 s^{-1}) $^{-1}$); I_k is light intensity for the half saturation of primary production in absence of photoinhibition (µmol photons m^{-2} s^{-1}); and I is PAR (µmol photons m^{-2} s^{-1}). We chose this model because it allowed comparison with a previous field study on the primary production rates of *C. raciborskii* in southeast Queensland reservoirs (O'Brien et al. 2009).

Results

Weather conditions were similar for all 3 days of the experiment, sunny with occasional cloud cover. The lake was thermally stratified for the entire experimental period. Measured surface irradiance in the treatments was similar for 20, 24, and 28 °C, but 10% higher for the 32 °C treatment (Table 1) due to a 10% higher ambient irradiance on the day that experiment was conducted; the experiments were conducted over 3 days, 7–9 March. The surface temperature in the lake ranged between 24.38 and 26.44 °C across the 3 days of experiments, averaging 24.80 ± 0.60 °C. Chlorophyll *a* concentrations in the lake ranged between 25 and 29 µg L^{-1}. *C. raciborskii* was the dominant algal species, ranging

Table 1. Mean [±SD] measured temperature (°C) and mean irradiance, measured with a 2π PAR sensor, over the 2 h incubation period (μmol photons m^{-2} s^{-1}) for the treatments using Lake Borumba water during the experiments conducted over 3 days in March 2008.

	Temperature (°C) in treatments			
% incident irradiance	20.5 [1.0]	24.5 [0.7]	28.0 [0.6]	32.0 [0.4]
0	0 [0.0]	0 [0]	0 [0]	0 [0]
2	25 [11]	26 [10]	25 [10]	30 [10]
7	66 [28]	68 [26]	65 [25]	77 [26]
17	196 [84]	201 [78]	190 [75]	227 [75]
30	352 [152]	362 [140]	342 [136]	409 [140]
100	1166 [502]	1197 [463]	1133 [451]	1353 [465]

Table 2. Physiochemical parameters measured in sampled surface water at Lake Borumba during 3 days in March 2008. Values in brackets are standard deviation. Values without brackets are single measurements.

Parameter	**7 March 08**	**8 March 08**	**9 March 08**
Alkalinity $CaCO_3$ (mg L^{-1})	76	76	76
Water temperature (°C)	26.44 [0.68]	25.45 [0.24]	24.38 [0.60]
Chlorophyll *a* (μg L^{-1})	29.0 [2.6]	24.5 [0.4]	25.0 [4.7]
Total cell density (cells mL^{-1})	146 000 [2828]	184 000 [41 012]	153 000 [14 142]
C. raciborskii cell density (cells mL^{-1})	91 100 [2687]	105 446 [17 470]	93 353 [17 476]
C. raciborskii (% biovolume)	79 [7]	91 [7]	81 [7]
Soluble reactive Phosphorus (mg L^{-1})	0.002	0.002	0.002
Ammonium (mg L^{-1})	0.009	0.009	0.009
Nitrate + nitrite (mg L^{-1})	0.003	0.003	0.003
Euphotic Depth (m)	2.1	2.6	2.3
Light attenuation (m^{-1})	2.2	1.7	1.9

Table 3. Estimated photosynthetic parameters, half saturation constant, I_k (μmol photons m^{-2} s^{-1}), maximum primary production rate in absence of inhibition (μg C μg Chl-a^{-1} h^{-1}), and inhibition parameter β (μg C μg Chl-a^{-1} h^{-1} (μmol photons m^2 s^{-1}) $^{-1}$) for each temperature treatment.

	Temperature treatment			
Parameter	**20 °C**	**24 °C**	**28 °C**	**32 °C**
I_k	141	104	32	162
P_{max}	1.57	1.28	2.26	0.96
β	3.35e-4	8.30e-5	5.67e-4	7.28e-4

 DOI: 10.5268/IW-5.2.778

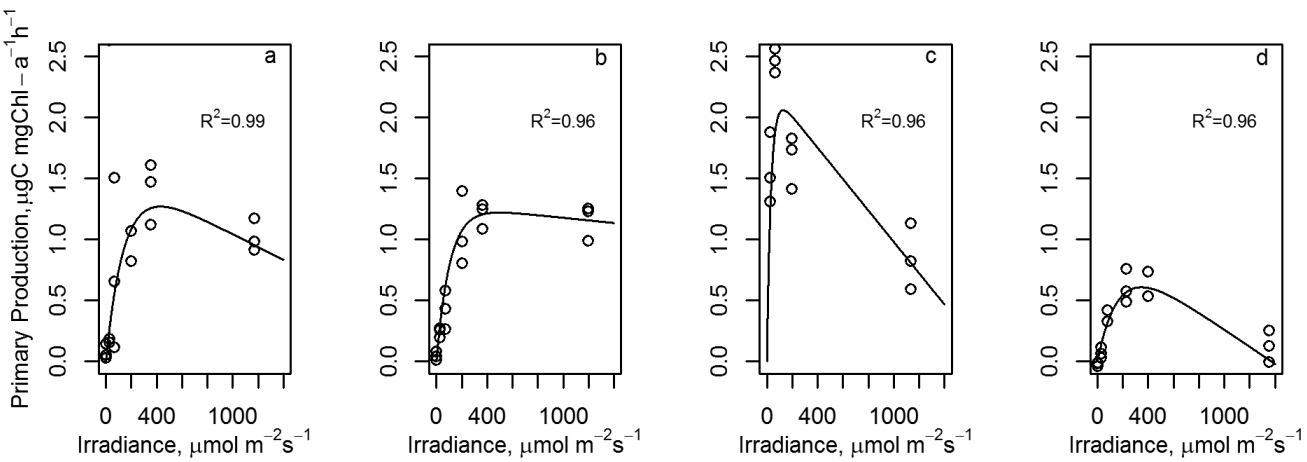

Fig. 1. Measured primary production (µg C µg Chl-a^{-1} h^{-1}) and calibrated model data across a range of irradiance levels (µmol photons m^{-2} s^{-1}) at the 4 temperature treatments: (a) 20 °C, (b) 24 °C, (c) 28 °C, and (d) 32 °C.

between 73 and 98% of the total algal biovolume across the 3 days (Table 2). The only other species at significant densities was the green alga *Monoraphidium*, which averaged 21 000 ± 1200 cells mL^{-1}. The dissolved inorganic nitrogen concentration was 0.012 mg L^{-1}, while soluble reactive phosphorus was at the detection limit (0.002 mg L^{-1}). Nutrient concentrations did not vary among days (Table 2).

Measured primary production rates were highest in the 28 °C treatment, with the exception of the highest irradiance, and lowest at all irradiances in the 32 °C treatment. The 24 °C treatment had the highest primary production rate at 100% irradiance (1.16 ± 0.14 µg C µg Chl-a^{-1} h^{-1}; Fig. 1). Productivity measured in the 20 and 24 °C treatments was not significantly different ($p < 0.05$). Photoinhibition was measured to some degree in all temperature treatments. The percentage decrease was calculated by dividing the mean rate in the 100% light treatment by the mean maximum primary production rate. This showed that the 24 °C treatment (96% of maximum) had the least inhibition, followed by 20 °C (73% of maximum), then 28 °C (38% of maximum), and finally 32 °C (18% of maximum). This pattern was reflected in the calibrated inhibition parameter (β) values for the temperature treatments, which from highest to lowest were: 32, 28, 20, and 24 °C. The primary production model fitted the data well, with coefficients of determination >0.9 for all temperature treatments (Fig. 1). The P-I parameters exhibited variation with temperature (Table 3). Maximum primary production (P_{max}) was also substantially higher at 28 °C compared with the other temperatures, while 32 °C had the lowest P_{max}. The light intensity for half saturation of primary production (I_k) decreased from 24 to 28 °C but then rose to its highest value for the 32 °C treatment.

Discussion

Our results show that the primary production response of *C. raciborskii* at a range of temperatures is qualitatively similar to the growth rate response to temperature shown in Briand et al. (2004), who found that the optimal temperature was between 29 and 31°C regardless of the geographical origin of the strain. Their study found only a minor reduction in growth at 32 °C, however, while our study found substantially lower primary productivity at this temperature. A previous study showed that the surface water temperature in Lake Borumba reaches a minimum of 16 °C in winter and a maximum of 30 °C in summer (McGregor and Fabbro 2000). Algae in this system are therefore not typically exposed to water temperatures as high as 32 °C, and the population in this reservoir may not have been physiologically adapted to higher temperatures. It is possible the short acclimation time in our study meant that there was insufficient time for the cells to adapt to the higher temperature. Mesocosm experiments on the primary production in Lake Stechlin, Germany, found a similar pattern of increasing primary production up to a maximum at 30 °C and then a reduction at 35 °C (Üveges et al. 2012), however, suggesting that perhaps this temperature response is highly conserved within, at least, the Nostocales order of cyanobacteria.

The highest rates of primary productivity per unit chlorophyll in our study, 2.25 ± 0.45 µg C µg Chl-a^{-1} h^{-1}, were comparable with those in a study of a *C. raciborskii*-dominated subtropical reservoir at the same water temperature (O'Brien et al. 2009), despite the typically lower I_k values in our study (32–162 µmol photons m^{-2} s^{-1}) compared to the O'Brien et al. (2009) study (356–390 µmol photons m^{-2} s^{-1}). O'Brien et al. (2009) found that when *C. raciborskii* had a short-term history of low light exposure, it responded with a lower I_k value. The light attenuation recorded in the lake sampled in O'Brien et al. (2009) was 68% of our study (1.36 m^{-1} vs. 1.98 m^{-1}). Furthermore, the chlorophyll *a* concentrations in our study were more than double that of their study (average 12.26 µg L^{-1} vs. average 25.42 µg L^{-1}), so absorption at the chlorophyll *a* wavelengths was higher in our study. Another factor possibly contributing to the photoacclimation of the cyanobacterial community in our study is the orientation and adjacent topography of Lake Borumba. The main part of the reservoir is oriented north–south and is flanked by high steep hills, meaning daily light dose is less than in the lake in O'Brien et al. (2009) study.

Laboratory studies have shown widely varying growth responses of *C. raciborskii* to light. Bonilla et al. (2011) had a mean I_k value of 8.5 µmol photons m^{-2} s^{-1}, and Briand et al. (2004) had values ranging from 15 to 26 µmol photons m^{-2} s^{-1}. A laboratory study of growth rates by Carneiro et al. (2009) had higher growth rates at 100 and 150 µmol photons m^{-2} s^{-1} when compared with growth rates at 50 µmol photons m^{-2} s^{-1}, while Dyble et al. (2006) found maximum growth at 75 µmol photons m^{-2} s^{-1}. These studies were all conducted under different water temperatures. Our study showed that I_k changed with incubation temperature, which may explain the differences in these studies. Mehnert et al. (2010) also found changes in I_k with incubation temperature in laboratory studies of *C. raciborskii*, although the temperatures used in their study were much lower than in our study. At 15 °C, Mehnert et al. (2010) found that I_k ranged from 38 to 70 µmol photons m^{-2} s^{-1}, while at 20 °C it ranged from 80 to 101 µmol photons m^{-2} s^{-1}.

C. raciborskii blooms are associated with high temperatures, high incident light, and high light attenuation (McGregor and Fabbro 2000); our results suggest why. It is established that *C. raciborskii* has as a high optimal growth temperature; however, we have shown that inhibition of primary production at super saturating irradiances is more pronounced at higher than lower temperatures. This would suggest that high water temperature and high incident irradiance would inhibit formation of *C. raciborskii* blooms. *C. raciborskii* blooms occur in midsummer onward, however, when the standing stock of phytoplankton biomass, and hence turbidity, is high. Using the attenuation measured here (~2.0 m^{-1}) would equate to an incident irradiance of 2000 µmol photons m^{-2} s^{-1} being reduced to subsaturating light levels in the first 0.5 m or so. Including the turbulent mixing of cells, it is unlikely that a large proportion of the population experiences supersaturating irradiances for long periods.

Our results add to concerns that *C. raciborskii* will be favoured by anthropogenic climate change and could expand into cooler latitudes in Australia. Mean daytime temperatures in Australia are projected to rise 1.8–3.4 °C (CSIRO 2007) by 2070, which will likely increase the water temperature of lakes and reservoirs in Australia. Given the results here, there is potential for *C. raciborskii* to expand into cooler southern regions of Australia; however, assessing this will require consideration of how traits of *C. raciborskii* interact with other phytoplankton species, and other cyanobacteria in particular. Furthermore, all species traits need to be considered; there is evidence that a high carbon world will not favour *C. raciborskii* (Holland et al. 2012). Future work should look at how all relevant traits of *C. raciborskii* will interact with its environment, including other phytoplankton species, in a changing climate.

In conclusion, we have shown that temperature and light do interact to affect the primary production of *C. raciborskii*, a result that conforms qualitatively with previous laboratory-based studies on the responses of growth to temperature and light. Additionally, this study shows that the interaction between light and temperature in affecting primary production is important to consider when analysing primary productivity measurements and the models fitted to them. There were marked differences in the estimated primary production model parameters across the different temperature treatments. Care should therefore be taken when using published parameters in population simulation models.

Acknowledgements

MK was supported by an eWater CRC scholarship and a UQ School of Engineering new staff start-up scholarship. We wish to thank: staff of SunWater Corporation (Matthew Barrett, Briony Pomplun, Jason Cork, and Len Barsby) for their help with sampling and access to historical data; Emily Saeck and Amanda Posselt from Griffith University; Paul Fisher from The University of Queensland for assistance with primary production rate experiments; and Dr. Glenn McGregor from the Department of Natural Resources and Water (DERM) for field site advice.

 DOI: 10.5268/IW-5.2.778

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 DOI: 10.5268/IW-5.2.778