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PRIMARY RESEARCH PAPER

Xanthophyceaen assemblages during winter–spring flood: autecology and ecophysiology of *Tribonema fonticolum* and *T. monochloron*

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Abstract The autecology and ecophysiology of two selected periphytic species of Xanthophyceae (*Tribonema fonticolum* and *T. monochloron*) were studied from seasonal pools of the inundation area, in the upper part of the Lužnice River (Třeboňsko Biosphere Reserve, Czech Republic) during winter–spring flood. Our studies have shown that these species differ in their ecological requirements (their temperature and light optima; inorganic carbon sources for photosynthesis; and also their ability to survive freezing and desiccation injuries). In our experiments, the optimal growth temperatures for both strains were higher than the temperatures of the water they were collected and isolated from. *Tribonema monochloron* has the rate of photosynthesis several times higher than *T. fonticolum*. In addition, the optimal growth temperatures were about 3–4°C lower for *Tribonema monochloron* than for *T. fonticolum.* From our results, we concluded that both strains of *Tribonema* prefer low intensities of irradiance. Both *Tribonema* strains were determined as CO_2 users, but we revealed the ability of *T. fonticolum* to use HCO_3^- in small amounts. In both *Tribonema* strains, 100% of the cells survived freezing down to −4°C. The cells' viability after freezing at −40, −100 and −196°C was much higher for *T. monochloron* (about 40%) than for *T. fonticolum* (about 4%). With respect to desiccation damages, at temperatures of +4 and +20°C, *T. monochloron* (the species better adapted to low temperatures) did not survive. In contrast, about 80% cells of *T. fonticolum* survived desiccation at both temperatures.

Keywords *Tribonema* · Growth conditions · Temperature · Inorganic carbon · Desiccation and freezing

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Introduction

River floodplains provide examples of highly specialised inland ecosystems, which can be viewed as ecotones somewhere between terrestrial and aquatic environments (Holland et al., 1991). Due to both habitat instability and water level fluctuation, the river floodplain ecosystems are usually comparable in their functioning to that of tidal zones. Spatial and temporal heterogeneity is evidenced by the presence

of a mosaic of both micro- and meso-habitats, including a network of pools and oxbows in river inundation areas (Prach et al., 1996). The floodplain ecosystem in the upper part of the Lužnice River (Třeboňsko Biosphere Reserve, Czech Republic) includes a variety of pools and river oxbows; they are either perennial or seasonal. The seasonal pools are frequently shallow and emerge only during winter–spring and summer flood events. They persist only for a limited time (from a few days to a few months). At the time of the winter–spring floods, the periphytic cyanobacteria and algae produce a high biomass and thus, play an important role in the inundation zone, through both inorganic carbon assimilation in photosynthesis and the removal of other nutrients such as nitrogen and phosphorus (Pithart et al., 1996). Similar winter–spring periphyton mass developments have been recorded in a variety of shallow wetlands (Gudleifsson, 1984; Elster, 1991). Species diversity of cyanobacterial and algal communities is characterized by a limited number of species. However, during seasonal rises of water temperature, the species dominance changes (Elster et al., 2002). Chrysophyceae, Synurophyceae, Xanthophyceae and Bacillariophyceae are the dominants at the beginning of flood events (February and the beginning of March). At this time period, the rapidly growing periphyton is exposed to low temperatures and fluctuations in water levels (freezing and drying injury), and its growth is limited neither by competition for light and nutrients from vascular plants nor by grazing pressures. Water from melted snow is rich in mineral nutrients. Later, in the second half of flood events (April–May), cyanobacteria and green algae (Chlorophyta) become dominant. Altogether, 42 periphytic species were determined to be in these seasonal winter–spring alluvial pools in the upper part of the Lužnice River in 2001 (Elster et al., 2002).

In both the European and world literature, there are only very limited numbers of papers on periphytic algal ecology and ecophysiology of these temporary, shallow water bodies. In the Czech Republic, several studies were performed in inundation river areas (e.g. the middle Elbe River, Frič & Vávra, 1901; Hrbáček & Novotná-Dvořáková, 1965), along the Dyje river (Ošmera, 1973) and in the Lužnice River floodplain (Pithart & Pechar, 1995; Pechar et al., 1996; Pithart, 1999). However, all of these studies were performed in permanent pools and oxbows, and were focused on zooplankton, phytoplankton ecology and water chemistry. None of them dealt with periphyton ecology and the ecophysiology in temporary pools, which persist only during the winter–spring flood events. The aim of this work is to clarify some details of the autecology and ecophysiology of two selected species of Xanthophyceae under wide range of conditions that occurred in natural environment during spring flood (wide range of temperature and irradiance, the stresses of low temperature, desiccation and cryoinjuries). Strains were chosen because of their morphological distinctness (*T. fonticolum* is a robust filamentous alga, while *T. monochloron* is a fine filamentous alga), high abundance in precultivated samples, easy isolation and cultivation.

Materials and methods

Locality description and field periphyton precultivation

Algal samples were precultivated in the Upper Lužnice River floodplain (Třeboňsko Biosphere Reserve, Czech Republic), which includes the meandering riverbed and a diverse system of both permanent and periodic backwater pools and oxbows. Study site is located close to the bridge crossing the river between the villages Dvory nad Lužnicí and Halámky (48°51′N, 14°55′E, 450 m a.s.l.). For more details, see Prach et al. (1996). During the 2001 winter–spring flood period, five temporary pools from the river inundation area (from the floodplain boundary up to the Lužnice River) were selected for periphyton species precultivation and collection. Periphytic communities were precultivated in two ways: (1) on fibreglass net strips (10 cm × 10 cm, cut from a commercial window-screen material); and (2) on rubber plugs holding microscopic slides. The fibreglass nets and the plugs with slides were fixed to the pool bottoms and/or were kept close to the water surface by a polystyrene float. The nets and slides were installed on February 16, and collected and transported to the laboratory between March 6 and April 27, 2001. During the precultivation period, the pool and river water temperature fluctuated between 2 and 15°C.

Isolation and cultivation of algal strains

Once every 2 weeks, samples of periphyton were collected from the pools and taken to the laboratory (Institute of Botany, Culture Collection of Autotrophic Organisms, Třeboň) in 250 ml polyethylene bottles filled with the pool/river water. Periphyton were brushed out from the nets and slides and transferred onto Petri dishes filled with agar (solid media with 1.5% agar, containing mineral nutrient medium Z; (Staub, 1961) or BG-11 (Bischoff & Bold, 1963). The dilution plate method was used for the isolation and culturing of algae and cyanobacteria (Elster et al., 1999). This method for isolation of unialgal strains was repeated several times. All experimental materials in the Petri dishes were cultivated in an illuminated (30 μmol m^{-2} s^{-1}), kept in refrigerator (temperature 5–8°C) with a light regime of 18 h of light (fluorescent tubes White Dove, Wattbrighter F 30 T8, Fluora, Germany), 2 h of UV radiation (germicide lamp), and 4 h of dark (the irradiance was measured by PU 550 Lux-meter (USA) and temperature was regulated by a digital omega thermometer (USA). The germicide lamps sterilized the cultivation box repeatedly (UV-B light did not penetrate through the glass bottles).

The field observations have shown that the periphyton community had high species diversity. Altogether 36 species of cyanobacteria and algae were isolated (Table 1; Machová, 2002). Algae from the group Xanthophyceae, especially the *Tribonema* genus, predominated as the most common component of the community. Two strains of *Tribonema*, that were isolated from natural periphyton assemblages, were used for the experiments. These two species are important in respect to periphyton biomass production. *Tribonema fonticolum* Ettl is a single filamentous alga (Fig. 1). Its filaments are 5–8 μm wide, rough, consisting of isodiametric cells. In liquid medium, the filaments made tufts. There is one parietal chromatophor in the cells, either ribbon- or channel-like. This strain was isolated from a natural sample collected (March 12, 2001) from a pool at a water temperature of 2°C. It is a common species occurring in shallow wetlands. *Tribonema monochloron* Pascher et Geitler forms short, thin filaments which are 3–4 μm wide (Fig. 2). Cells are 8–12 μm long with one parietal

Table 1 List of strains of cyanobacteria and algae isolated during spring flood in 2001

Cyanobacteria
Komvophoron skujae Anagnostidis
Oscillatoria tenuis Agardh ex Gomont
Phormidium sp.
Phormidium cf. *ambiguum* Gomont ex Gomont
Phormidium cf. *interruptum* Kützing ex Gomont
Phormidium cf. *vulgare* [Kützing] ex Anagnostidis
Pseudanabaena galeata Böcher
Bacillariophyceae
Navicula atomus (Kützing) Grunow
Nitzschia sp.
Peronia cf. *fibula* (Brébisson) Ross
Xanthophyceae
Xanthonema bristolianum (Pascher) Silva
Xanthonema debile (Vischer) Silva
Xanthonema exile (Klebs) Silva
Xanthonema hormidoides (Vischer) Silva
Tribonema aequale Pascher
Tribonema ambiguum Skuja
Tribonema fonticolum Ettl
Tribonema monochloron Pascher et Geitler
Tribonema pyrenigerum Pascher
Tribonema vulgare Pascher
Euglenophyceae
Lepocynclis cf. *texta* (Dujardin) Lemmermann
Euglena sp.
Chlorophyta
Coenocystis subcylindrica Korshikov
Chlorococcum infusionum (Schrank) Menenghini
Keratococcus bicaudatus (A.Braun) J.B.Petersen
Monoraphidium contortum (Thuret) Komárková-Legnerová
Monoraphidium griffithii (Berkeley) Komárková-Legnerová
Monoraphidium minutum (Nägeli) Komárková-Legnerová
Scenedesmus acuminatus (Lagerheim) Chodat
Scenedesmus acutus Meyen
Desmodesmus communis (Hegewald) Hegewald
Desmodesmus subspicatus (R.Chodat) Hegewald et A.Schmidt
Klebsormidium flaccidum (Kützing) Silva, Mattox et Blackwell
Stichococcus cf. *bacillaris* Nägeli
Stichococcus cf. *dubius* Chodat
Stigeoclonium sp.

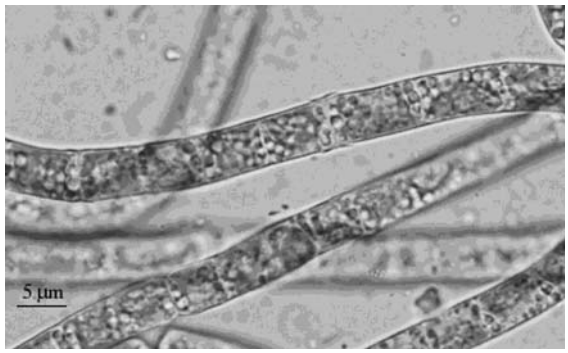

Fig. 1 *Tribonema fonticolum* Ettl

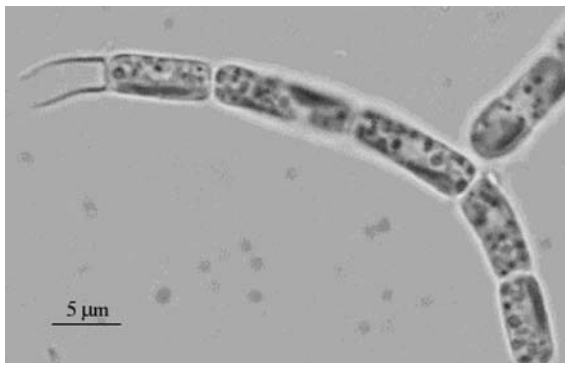

Fig. 2 *Tribonema monochloron* Pascher et Geitler

chain-like chromatophor, which is often irregularly lobed. This strain was isolated from a pool at a water temperature of 6°C, on March 26, 2001. It is a common species occurring in shallow Central European wetlands.

Growth rate measurements

In order to find the temperature and light demands of the two strains, method of cross gradients of temperature and light was used as described by Kvíderová & Lukavský (2001). Irradiances ranged from 4 to 40 µmol m^{-2} s^{-1} PAR and temperatures from 2 to 35°C. The irradiance gradient was chosen according to conditions that occurred during the flood period when the average irradiance in a water column is 40 µmol m^{-2} s^{-1} PAR (Elster, unpubl.). In total, 45 Petri dishes with agar plates, solidified with Z medium, were prepared. One millilitre of algal suspension (chlorophyll *a* content was 3.8 mg l^{-1} for *T. monochloron* and 1.7 mg l^{-1} for *T. fonticolum*) was pipetted onto agar plates and placed on the cross-gradient desk. The cultivation lasted for 12 days. Chlorophyll *a* content of the algal suspension at the beginning and at the end of cross-gradient experiment was estimated spectrophotometrically on Whatman GF/C filters. For chlorophyll *a* extraction, a mixture of 90% acetone and methanol (5:1, by volume) was used (Pechar, 1987).

Photosynthetic measurements

The rate of net photosynthesis (P_N) and dark respiration (R_D) were measured as an oxygen production or consumption. Algal suspension was placed into a magnetically stirred, thermostatically controlled (±0.1°C) closed chamber (8.2 ml); and a Clarke-type oxygen sensor (Labio, Prague, Czech Rep.) was used. The rate of oxygen production and/or consumption was recorded by using a TZ 4200 linear chart recorder (Laboratory instruments, Prague, Czech Rep.—for details see Adamec, 1997). Before measurements, the suspension of *Tribonema monochloron* (content of chlorophyll *a* was 1.1 ± 0.5 mg l^{-1}) was centrifuged (3,000 rpm, 4°C, 15 min) and then transferred to a working solution (0.88 mM $NaHCO_3$ + 0.05 mM KCl; Allen & Spence, 1981; Adamec & Ondok, 1992). Tufts of *T. fonticolum* (content of chlorophyll *a* was 2.1 ± 0.7 mg l^{-1}) were transferred using tweezers, washed in the solution and then put into the chamber. Initial pH of the working solution was set to 6.92, and corresponded to 0.25 mM CO_2. The concentration of CO_2 in the solution was high enough to prevent CO_2 limitation during the P_N measurements. Moreover, this corresponded roughly to the CO_2 concentrations at which the algae were grown in the field (Elster, unpubl.). A 55 W halogen lamp provided a constant irradiance 300 µmol m^{-2} s^{-1} in the experimental chamber (the irradiance reaching the water surface in a sunny day in spring was measured between 180 and 360 µmol m^{-2} s^{-1}—Elster, unpubl.). The light was homogenized by a neutral dispersion filter. First, the dark respiration rate was measured for about 20 min; and afterward the photosynthetic rate in the same algal sample was measured, within about the next 20 min. After each individual measurement, the concentration of chlorophyll *a* was estimated using

the same method mentioned above. The P_N and R_D were measured at five different temperatures (3, 8, 14, 20, 26°C) to find the temperature curve for photosynthesis.

In addition, P_N was measured at various irradiances. Seven irradiances (0, 20, 80, 150, 300, 600, 1,000, 1,500 μmol m^{-2} s^{-1}) were used at three temperatures of 3, 14, 20°C for *T. monochloron* and 3, 14, 26°C for *T. fonticolum*, respectively (the highest temperature was chosen as the temperature of the highest rate of photosynthesis in previous measurements). Four parallel measurements (chlorophyll *a* content of each sample was 2 mg l^{-1}) were performed for each combination of temperature and irradiance. Photosynthetic parameters were estimated with a photosynthetic model according to Platt et al. (1980).

For graph constructions program SigmaPlot (ver. 9.1; Systat Software, Inc., USA, 2004) was used.

To estimate inorganic carbon sources for photosynthesis, a pH-drift technique was used (Allen & Spence, 1981; Adamec & Ondok, 1992; Adamec, 1993). Five parallel samples (chlorophyll *a* content was 2 mg l^{-1}) of algae of each species, in 10 ml glass tubes in the working solution, were exposed to a temperature of 14 ± 0.5°C and an irradiance of 310 μmol m^{-2} s^{-1} (fluorescent light) for 6 h. The initial pH was 7.3–7.6. The final pH of each sample was also measured (combined pH electrode). An air bubble of about 1 ml was left inside the tubes to reduce the final oxygen concentration (Adamec, 1997). Tubes were mixed several times during the exposures. Values of the final pH and total alkalinity were used for calculation of the final concentration of CO_2 and HCO_3^- (Helder, 1988). The possibility of HCO_3^- use was concluded from ratio values of total carbon (c_T) and alkalinity (Maberly & Spence, 1983).

Freezing and desiccation

For viability testing after freezing and desiccation, both algal species were precultivated in a refrigerator at a temperature of 5–8°C and 30 μmol m^{-2} s^{-1}. A dense suspension of algae in 2 ml cryovials was then placed into a Planer Kryo 10 programmable freezer (Planer, UK) and exposed to several freezing regimes (Table 2), simulating natural and near-natural freeze-thaw cycles. In freezing experiments, algae were exposed to following temperatures: −4°C represented the temperature which usually occurred in natural condition in spring, −40°C is a temperature which causes complete freezing of the cells and stops all metabolic processes; but cells that are able to survive freezing should be able to survive (in our case, we assume that algae that occurred in temperate zone are able to survive freezing), −100 and −196°C as possible temperatures for cryostorage. Two aliquots were desiccated within a desiccator, both at +4 and +20°C.

Viability evaluations were based upon the controlled cultivation of the algal colonies on agar plates in Petri dishes (Lukavský, 1975). After exposures to the described regimes, the cryovials with the algae were either quickly thawed in a water bath at 40°C for ca. 2–5 min (if frozen), or resuspended in ca. 0.5 ml of liquid medium (if desiccated). This algal inoculum (0.1 ml) was then uniformly spread by use of a glass rod onto a 2% agar plate with nutrient solution Z. The agar plates were maintained in an illuminated refrigerator, as mentioned above, for 3 days. After that, the viability was evaluated. Viability is expressed in % as a percentage in comparison with nonfrozen and nondesiccated controls.

Results

Growth on cross-gradient apparatus

The results of *Tribonema fonticolum* and *T. monochloron* 12 days experimental cultivation in temperature and irradiance gradient is showed in Fig. 3. The highest biomass production (chlorophyll *a* content) of *T. fonticolum* was recorded at temperatures between 19 and 27°C, when the chlorophyll *a* content was 49–66 mg l^{-1}. At temperatures from 12 to 19°C and from 27 to 30°C, there was a very small biomass production. At temperatures below 6°C and above 30°C, no algal growth was recorded. The highest *T. monochloron* biomass was produced at temperatures from 15.5 to 23.5°C, when the final chlorophyll *a* content was 98–168 mg l^{-1}. At temperatures below 10°C, the production of biomass was minimal, while a loss of initial algal biomass occurred at temperatures above 26°C, when the cells died. The maximal production of *T. monochloron* was almost three times higher than *T. fonticolum*.

Table 2 Regimes used in freezing and desiccation (Stibal & Elster 2005—modified)

Starting temperature (°C)		20	20	20	20	20	20
Final temperature (°C)		−4	−40	−100	−196	4	20
Phase 1	T_{start} (°C)	20	20	20	20	20	20
	T_{final} (°C)	0	0	0	−196	4	20
	Rate (°C min^{-1})	−4	−4	−4			
	Time	5 min	5 min	5 min	120 min	8 days	8 days
Phase 2	T_{start} (°C)	0	0	0	−196		
	T_{final} (°C)	−4	−40	−40	20		
	Rate (°C min^{-1})	−5	−5	−5			
	Time (min)	1	8	8	5		
Phase 3	T_{start} (°C)	−4	−40	−40			
	T_{final} (°C)	−4	−40	−100			
	Rate (°C min^{-1})	0	0	−12			
	Time (min)	5	5	5			
Phase 4	T_{start} (°C)	−4	−40	−100			
	T_{final} (°C)	40	40	−100			
	Rate (C min^{-1})			0			
	Time (min)	5	5	5			
Phase 5	T_{start} (°C)			−100			
	T_{final} (°C)			40			
	Rate						
	Time (min)			5			
Times repeated		3	3	3	1	1	1

T_{start}, starting temperature of given phase; T_{final}, final temperature of given phase

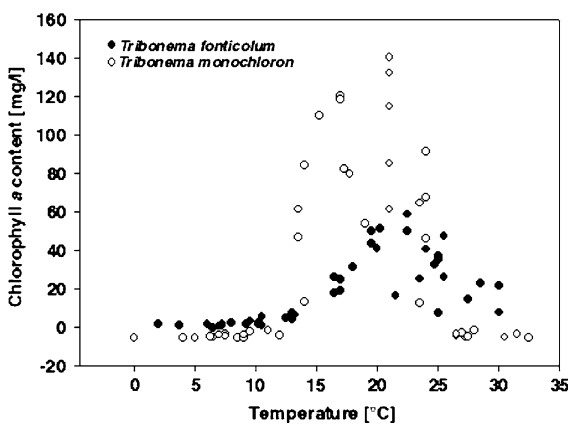

Fig. 3 Chlorophyll *a* content of both *Tribonema* strains after 12 days of cultivation on cross gradients

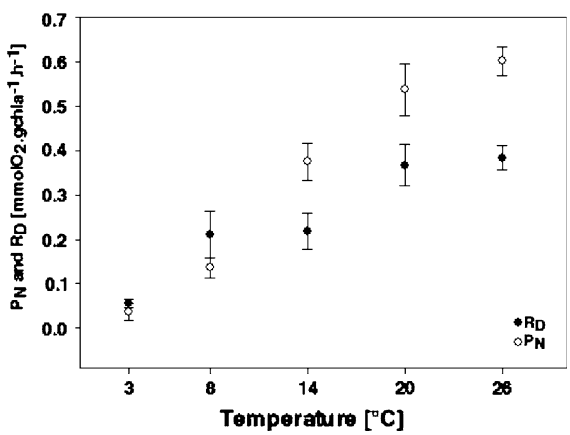

Fig. 4 *Tribonema fonticolum*—Rate of P_N and R_D dependent on temperature (irradiance 300 µmol m^{-2} s^{-1}; means ± SE)

Dependence of photosynthesis and dark respiration on temperature

The rates of net photosynthesis and dark respiration for *T. fonticolum* are shown in Fig. 4. P_N and R_D of *T. fonticolum* both increased with temperature. At lower temperatures (3 and 8°C), the P_N was lower than that of the R_D. However, as the temperature rose, the P_N increased faster, and extended the rate of R_D. The highest P_N occurred at 26°C (0.6 ± 0.03 mmol

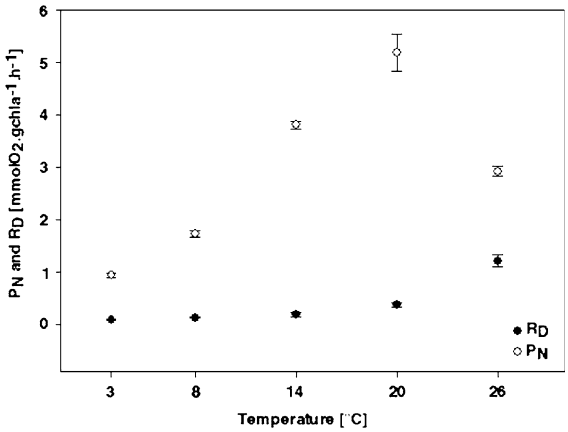

Fig. 5 *Tribonema monochloron*—Rate of P_N and R_D dependent on temperature (irradiance 300 µmol m^{-2} s^{-1}; means ± SE)

O_2 g chl a^{-1} h^{-1}). The rates of P_N and R_D of *T. monochloron* are shown in Fig. 5. The dependence of P_N and R_D on temperature in *T. monochloron* differed greatly from that in *T. fonticolum*. Within the whole temperature range, P_N was higher than that of R_D, and both rates increased with higher temperatures. The highest P_N value was at 20°C (5.4 ± 0.35 mmol O_2 g chl a^{-1} h^{-1}). The R_D rose much more slowly. Chlorophyll-based P_N values in *T. monochloron* were ten times higher than those in *T. fonticolum*; while R_D values were similar for both strains. P_N/R_D ratio is shown in Fig. 6. P_N/R_D ratio was the highest for both strains at a temperature of 14°C, but this ratio was ten times higher for *T. monochloron* than for *T. fonticolum*.

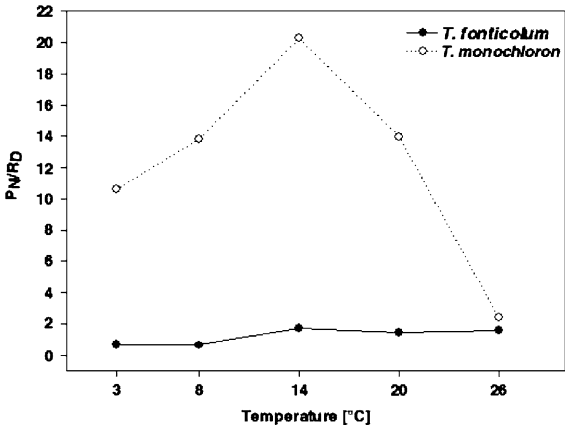

Fig. 6 P_N/R_D of both *Tribonema* strains (irradiance 300 µmol m^{-2} s^{-1})

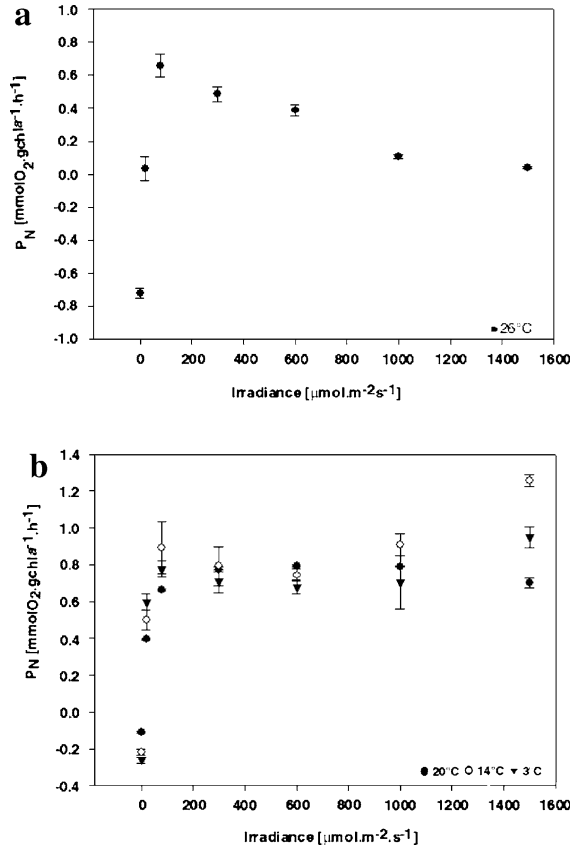

Fig. 7 Rates of P_N, dependent on irradiance—*Tribonema fonticolum* (**a**), *Tribonema monochloron* (**b**); (means ± SE)

The light curve for *T. fonticolum* shows that the P_N was only positive at 26°C, while it was negative (or zero) at 3 and 14°C, at any irradiance used (Fig. 7a). At 26°C, photosynthesis was the highest at the irradiance of about 80 µmol m^{-2} s^{-1} and a marked decrease of P_N occurred at higher irradiances. The estimated photosynthetic parameters were: P_{max} = 1.064 ± 0.097 mmol O_2 g chl a^{-1} h^{-1}, α = 0.051 ± 0.018, I_C = 14.26 ± 0.034 µmol m^{-2} s^{-1}, I_S = 20.9 ± 0.029 µmol m^{-2} s^{-1}. A similar pattern for P_N was also evident at lower temperatures (not shown). For *T. monochloron*, the shapes of the light curves for P_N were different at different temperatures (Fig. 7b). At 20°C, the P_N increased with irradiances between 300 and 600 µmol m^{-2} s^{-1}; P_N was saturated at higher ones, and a mild photoinhibition occurred at 1,500 µmol m^{-2} s^{-1}. The estimated photosynthetic parameters for 20°C were: P_{max} = 0.853 ± 0.026 mmol O_2 g chl a^{-1} h^{-1}, α = 0.028 ± 0.0004, I_C = 3.75 ± 0.267 µmol m^{-2} s^{-1}, I_S = 30.46 ± 0.652

μmol m^{-2} s^{-1}. At temperatures of 3 and 14°C, P_N was saturated at only 80 μmol m^{-2} s^{-1}, but it increased distinctly again at the highest irradiances. The estimated photosynthetic parameters for 14°C were: P_{max} = 1.136 ± 0.102 mmol O_2 g chl a^{-1} h^{-1}, α = 0.042 ± 0.006, I_C = 5.14 ± 0.519 μmol m^{-2} s^{-1}, I_S = 27.05 ± 0.728 μmol m^{-2} s^{-1} and for 3°C were: P_{max} = 1.24 ± 0.123 mmol O_2 g chl a^{-1} h^{-1}, α = 0.057 ± 0.008, I_C = 4.56 ± 0.315 μmol m^{-2} s^{-1}, I_S = 17.97 ± 0.589 μmol m^{-2} s^{-1}. From these photosynthetic parameters, we concluded that both strains of *Tribonema* are shade-adapted species.

Final values of pH, after 6 h, were used to calculate the concentration of inorganic carbon and the compensation points of CO_2 and HCO_3^- (Table 3). *T. fonticolum* was able to raise the pH of the bicarbonate medium to a final value of 9.58, while *T. monochloron* to 9.09. These results show that both strains of *Tribonema* utilised free CO_2 as their main carbon source for photosynthesis, but only the former strain could use HCO_3^- also at low affinity rates (HCO_3^- compensation concentration 0.648 mmol l^{-1}).

Freezing and desiccation experiments

The ability to survive freezing and desiccation stresses was different in both strains of *Tribonema* (Table 4). Viability was expressed in % (as a percentage, in comparison with the nonfrozen and nondesiccated controls). Viability after freezing (−4, −40, −100 and −196°C) was higher for *T. monochloron*, and reached more than 40% in all cases. However, *T. monochloron* did not survive desiccation (desiccated in temperature +4 and +20°C). *T. fonticolum* reacted to freezing and desiccation damage differently, compared with *T. monochloron*. Only a minor part of the population survived temperatures between −40 and −100°C. After cultivation, the biomass was yellow to white; chromatophores were brown and smaller, and most of the cells in filaments died. However, this species showed a high percentage of survival at temperatures of −4°C, in −196°C (liquid nitrogen) and also under desiccation stress, respectively. The observed filaments and chromatophores in *T. monochloron* were green and vital. Akinete formation was recorded during cultivation on agar plates after freezing treatments (except during direct freezing in N_2).

Discussion

Autecology and ecophysiology of two selected species of Xanthophyceae (*Tribonema fonticolum* and *T. monochloron*) were studied. These species are important components of periphytic communities that produce a high biomass in the seasonal pools of the inundation area of the upper parts of the Lužnice River (Třeboňsko Biosphere Reserve) during the winter–spring floods (Pithart et al., 1996). In the flood period, algal assemblages are exposed to low temperatures and fluctuations in water levels (freezing and drying injuries), and play an important role by fixing their carbon and trapping of nutrients delivered by the floodwaters. Detailed knowledge of the autecology and ecophysiology of these species could better help us understand the ecological role of the periphytic communities during winter–spring flood events, and also could tell us about the ecological and physiological features of the class Xanthophyceae. Measurements of *Tribonema*

Table 3 Final values of pH, total inorganic carbon concentration (c_T), compensation points of HCO_3^- and CO_2 at the end of pH-drift experiment (means ± SE)

	Tribonema fonticolum	*Tribonema monochloron*
Initial pH	7.55 ± 0.098	7.65 ± 0.077
Initial total amount of carbon (mmol/l)	0.938 ± 0.063	0.926 ± 0.029
Initial CO_2* concentration (mmol/l)	0.06 ± 0.002	0.05 ± 0.0013
Initial HCO_3^- concentration (mmol/l)	0.877 ± 0.049	0.876 ± 0.033
pH after 6 h	9.58 ± 0.107	9.09 ± 0.097
Total amount of carbon c_T (mmol/l)	0.752 ± 0.056	0.833 ± 0.074
HCO_3^- compensation point (mmol/l)	0.658 ± 0.023	0.791 ± 0.039
CO_2* compensatin point (mmol/l)	0.41 ± 0.012	1.55 ± 0.08
c_T/Alkalinity	0.854 ± 0.041	0.946 ± 0.032

Table 4 Viability (in %—expressed as a percentage proportion in comparison with non-frozen and non-desiccated controls), after exposure to freezing and desiccation experiments in *Tribonema fonticolum* and *T. monochloron*

	Frozen −4°C	Frozen −40°C	Frozen −100°C	Liquid N_2	Dessicated 4°C	Dessicated 20°C	Control
T. fonticolum	100.0	3.4	4.1	76.8	81.0	83.0	100.0
T. monochloron	100.0	49.0	40.0	88.0	0.0	0.0	100.0

fonticolum and *T. monochloron* showed that the two species differed from each other on the following parameters: temperature effects on growth; use of the cross-gradient method for evaluating the chlorophyll *a* concentration; rate of net photosynthesis (P_N); dark respiration (R_D); freeze-thaw cycles; and desiccation.

Studies comparing the ecological requirements of temperature and light for periphytic algae, isolated from winter–spring flood rivers inundation areas, had not been previously performed, although these dependences (on temperature and light) upon the growth of individual algal species had been described (e.g. Tang et al., 1997; Kvíderová & Lukavský, 2005; Stibal & Elster 2005, etc). The cross-gradient experiments, and photosynthesis rate plus dark respiration measurements, showed that both *Tribonema* strains have their optimal growth temperatures at higher temperatures than that of the water from which they were collected and isolated (*T. fonticolum* from temperature 2°C and *T. monochloron* from 6°C, respectively). Similar results were introduced by e.g. Tang et al. (1997), Tang & Vincent (1999), Kvíderová & Lukavský (2005), Stibal & Elster (2005) and many others. So, for example, in the article by Tang et al. (1997) it was shown that among 27 isolates of the Arctic and Antarctic mat forming cyanobacteria, the optimal growth rate temperature ranged from 15 to 35°C, with an average of 19.9°C; which are all much higher than that in their ambient environments.

Tribonema fonticolum is a filamentous alga which occurs in bulky tufts, with the highest growth rate (measured as concentration of chlorophyll *a*) at temperatures between 19 and 27°C with an average of 23°C. Outside this range, at temperatures from 12 to 19°C and from 27 to 30°C (as well as below 6°C and above 30°C) there is scarcely perceptible, or no growth. This can be explained by acclimation to the low temperatures, because the algae were precultivated in 12°C after isolation. However, in contrast, in the upper temperature range (higher than 30°C), alga quickly died. Castenholz & Schneider (1993), Tang et al. (1997) studied the acclimation of Antarctic cyanobacteria to low temperatures. They showed that in their experiments (at 5°C) they detected no increase in growth rate and photosynthetic activity cultivation at 5°C over a 2–3 week period. P_N and R_D measurements and their ratio followed temperature limits of growth measured in the cross-gradient experiment. Both cultures of *Tribonema* contained bacteria of unknown densities. We think that these bacteria were responsible for a high proportion of measured values of R_D that were very high and caused negative values of P_N. In nature, we observed during the spring flood microbial vegetation bloom that was connected with high dead biomass of vascular plants in pools. Moreover, we assume that these bacteria are acclimated or adapted to low temperatures and we were not able to remove them when we isolated and cultivated strains of *Tribonema*. The high R_D that made the P_N negative also was in discrepancy with observed algal growth in temperatures that according to values of P_N indicated no growth. However, with respect to our data for P_N and R_D, it should be mentioned that there exist acclimation strategies, which help them to flourish in a low temperature environment. Raven & Geider (1988) discussed evidence that cells can allocate resources away from the photosynthetic light reaction components and towards those enzymes that control dark fixation. The light curve showed that the P_N was only positive at 26°C, while it was negative (or zero) at 3 and 14°C, at the irradiance used (Fig. 7a).

We assume that the negative values P_N were caused by bacteria that consumed the oxygen produced by algae during the measurement. At 26°C, photosynthesis was saturated at the irradiance of 80 μmol m^{-2} s^{-1} and marked decrease of P_N occurred at higher irradiances. A similar pattern for P_N was also evident at lower temperatures. It is well known that algae tend to be more sensitive to photoinhibition at low temperatures, as well as temperatures above the optimum (Graham et al.,

1995; Ibelings, 1996). Our measurements confirm these results. In respect to growth rate and photosynthesis, it can be concluded that *Tribonema fonticolum* is a psychrotrophic—sciophilous species, which grows over a wide temperature range (typically 20°C); preferring lower doses of irradiance (shade-adapted species). The growth rate is low, even at optimal temperature and light conditions. The species can be characterized as a typical K-strategist.

Tribonema monochloron is an epiphytic filamentous alga producing soft tufts in seasonal pools of the upper part of the Lužnice River floodplain. The cross-gradient experiments and photosynthesis rate measurements (P_N/R_D ratio) showed that *T. monochloron* has the rate of photosynthesis several times higher than *T. fonticolum*. The highest growth rate (measured as concentration of chlorophyll *a*) was recorded at temperatures from 15.5 to 23.5°C, with an average of 19.5°C. The net photosynthetic rate was highest at 20°C (5.4 mmol O_2 g chl a^{-1} h^{-1}) and it followed nicely the growth rate experiments. The optimal growth temperatures were lower (by about 3–4°C) for *T. monochloron* than for *T. fonticolum*. However, with respect to *T. monochloron* it seems that this species increases growth only at lower temperatures; but above the optimal temperature range the growth and photosynthesis rate fell quickly. As has already been mentioned, Tang et al. (1997) studied temperature optima for the growth of 27 isolates of mat-forming cyanobacteria from the Arctic, sub-Arctic and Antarctic regions. They found that there was a wide spectrum of genotypes, with different temperature growth rate optima. Our results confirmed these findings and showed that even two species isolated from one habitat type arising during the winter–spring flood events were occupied by different species, with respect to their temperature and light requirements. In addition, Tang et al. (1997) also compared the temperature growing curves of strains studied with the theoretical parabolic function. Of these isolates, 75%, with a 90% level of confidence, fit the parabolic function. Both strains we studied had growing curves that fit to a parabolic function (Figs. 5 and 6). The light curve's shape for *T. monochloron* was different at different temperatures (Fig. 7b). At lower temperatures (3 and 14°C), P_N was saturated at 80 μmol m^{-2} s^{-1}; but it increased again at irradiances of 1,500 μmol m^{-2} s^{-1}. This trend was not observed at 20°C. It is not easy to explain the rise of P_N at the highest irradiances, at 3 and 14°C, in the former strain. The dynamic characteristics of photosynthesis are associated with three different time scales: rapid photoresponse (min), photoinhibition (h) and photoadaptation (days) (Falkowski, 1992; Han et al., 2000). In our experiments, R_D and P_N were measured within 20 min. During the rapid photoresponse, photosynthesis usually reaches a steady state with a time lag of several minutes, and is nearly constant afterward (Han et al., 2000). In respect to photoadaptation, an ecological differentiation of P_N was found in a fishpond population of *Cladophora fracta* (Eiseltová & Pokorný, 1994). Photosynthesis of samples collected from the water surface (sun-adapted algae) was saturated at the irradiance 460 μmol m^{-2} s^{-1}; while photosynthesis of samples collected from the bottom (shade-adapted algae) at the irradiance of only 200 μmol m^{-2} s^{-1}. Judging from the light P_N curves of both *Tribonema* strains (Fig. 7a, b), it might be suggested that *T. monochloron* tolerates higher irradiance than *T. fonticolum*, although the saturation irradiances of photosynthesis are comparable.

In respect to growth and photosynthesis rate, *T. monochloron* is a fast-growing psychrotrophic (shade-adapted species), which are characterized by quick growth and photosynthesis rate at low temperatures. It can be characterized as a typical fast growing opportunistic R-strategy species.

From our measurements of inorganic carbon sources for photosynthesis, it can be concluded that both *Tribonema* strains use mainly free CO_2 for photosynthesis (Table 4). When the coefficients of final total carbon to total alkalinity ratios were estimated (for *T. fonticolum* 0.854, for *T. monochloron* 0.946, respectively), both strains were determined to be strict CO_2 consumers (Maberly & Spence, 1983). However, when the final HCO_3^- concentrations were taken into account, and compared with the usual HCO_3^- compensation concentrations reported for various higher aquatic plants and algae (Maberly & Spence, 1983), the slowly growing *T. fonticolum*, with its HCO_3^- compensation concentration of 0.648 mmol l^{-1}, may be regarded as an inefficient and weak HCO_3^- user. Strict use of CO_2 (in respect to our study, *T. monochloron*) requires less energy and, thus, it may also grow at lower irradiances (e.g. Jones, 2005). On the contrary, in warmer environments with a higher competition of submerged plants or algae,

and where the pH is higher and less free CO_2 is available due to intense photosynthesis, it is beneficial for the plants and algae to have the ability to use HCO_3^- (Maberly & Spence, 1983; Sand-Jensen, 1987). In the cold environments of shallow temporary pools at the beginning of the spring flooding period, when the competition and irradiance were lower, the strict CO_2 use did not prevent the production of *T. monochloron* algal biomass. At higher temperatures, that are optimal for the growth of *T. fonticolum*, an ability to use HCO_3^- is advantageous, because of the higher competition for sources of inorganic carbon.

The winter–spring shallow seasonal pools last only for a limited time (from a few days to a few weeks) and are subjected to diurnal (and/or seasonal) freezing temperatures and cellular dehydration. Periphytic communities, which produce a high biomass during short flood events, must withstand both freeze-thaw and desiccation periods. The phase transition from liquid water to ice and dehydration poses a number of osmotic and mechanical stresses. In addition, the seasonal pools frequently last only for the winter–spring flood period and after this, all of these shallow pools mostly dry-up. Periphytic species occupying temporal pools in inundation areas need to remain viable during periods of diurnal and seasonal freezing temperatures, and also during prolonged seasonal desiccation.

In our experiments, 100% of cells of both *Tribonema* strains survive freezing down to −4°C. In seasonal Lužnice River pools there is frequently a decrease of temperatures down to −4°C as a result of diurnal temperature fluctuations (Elster et al., 2002). Similar results (Hawes, 1990) have been recorded for the Antarctic alga *Zygnema* sp. during repeated overnight exposures to temperatures of down to −4°C, where the algal photosynthetic capacity was maintained without any cryoinjury effect. In addition, Hawes (1990) also demonstrated that during the Antarctic summer, diurnal temperature changes are slow. Temperature changes ($0.5°C\ min^{-1}$) avoid intracellular ice nucleation. However, at temperatures greater than or equal to −40°C, homogenous ice nucleation occurs and all cell's liquid water freeze-up (Convey, 2000; Elster & Benson, 2004). This formation of ice usually destroys membranes, particularly if the crystals are formed intracellularly (Fuller, 2004). Our experiments confirmed these results because the viability of tested strains fell dramatically at temperatures of −40, −100°C and in liquid nitrogen. However, the cells' viability after freezing at −40, −100 and −196°C was much higher for *T. monochloron*, and reached more than 40%. As discussed already, *T. monochloron* prefers lower temperatures in comparison with *T. fonticolum* (the growth temperature optima for *T. monochloron* are lower by about 3–4°C than for *T. fonticolum*). Low temperatures exert an obvious dampening effect on all metabolic processes, although the magnitude of this cold inhibition varies greatly among species. The molecular responses of algae cells to a low temperature environment was divided into two steps (e.g. Friedmann et al., 1993; Sato, 1995; Murata & Los, 1997; Wall & Virginia, 1998; Elster & Benson, 2004; Singh & Elster, 2007): (1) the cold-induced desaturation of fatty acids in membrane lipids (which fluidizes membranes to compensate for decreases in membrane fluidity at low temperatures); and (2) the cold-induced synthesis of certain enzymes that are involved in transcription and translation. Such enzymes compensate for the decrease in the efficiency of transcription and translation at low temperatures. These molecular responses to low temperature are also closely associated with biochemical cryoprotection strategies. These strategies alter the formation and pattern of ice crystallization, which involve: (a) the manipulation of cellular osmotic status via the synthesis of sugars, sugar alcohols and polyols; (b) manipulation of ice nucleation; and (c) the production of antifreeze proteins (Elster & Benson, 2004).

Tribonema fonticolum reacts to desiccation damage differently when compared to *T. monochloron* (desiccated in temperatures +4 and +20°C). Fast growing *T. monochloron* did not survive desiccation at either temperature. In contrast, about 80% cells of *T. fonticolum* (slow-growing and a shadow-adapted species) survived desiccation at both temperatures. Water deficiency (desiccation) includes both osmotic and mechanical stresses (cell shrinkage and decrease of cell turgor; Reed & Walsby, 1985; Elster, 1999). Both species of *Tribonema* studied which occurred in temporal pools during the winter–spring flood, should have created a variety of strategies to minimise the osmotic and mechanical stresses. The most common adaptation for survival under desiccation is the production of compatible solutes

(Mackay et al., 1984) that reduce the osmotic effects. This effect has been examined in the mat-forming cyanobacteria species in the cold environments of the McMurdo Ice Shelf (de los Ríos et al., 2004). The species studied form copious quantities of mucopolysaccharides (exopolymeric substances, EPS). This material, likely, slows the flow of liquid water during freeze-up and desiccation. Experiments on *Nostoc commune* indicate that EPS is critical to surviving desiccation, as well as freeze-up (Tamaru et al., 2005).

One of the prerequisites for life in seasonally occurring shallow wetlands within river inundation areas is the ability to maintain viability until the next flood period. Both strains of *Tribonema* studied formed akinetes during freezing treatments. Generally, akinetes are formed to survive unfavourable conditions. Akinete formation in *T. bombycinum* was studied in Japan (Nagao et al., 1999). This strain was isolated from a small pond that freezes in winter. Akinete formation has been recorded to occur after experimental freezing, as a result of desiccation, and from lack of some important nutrients (N, S).

Conclusions

In the cold environment of winter–spring pools, which arise during flood events, *Tribonema fonticolum* probably does not produce a high biomass. Its success in this type of environment is more likely a result of its resistance to mortality (stress factors such as freeze-thaw cycle, desiccation), its ability to growth in wide temperature ranges (psychrotrophic), as well as in low light environments (shade-adapted)—than a high gain in biomass. It is probably only an accompanying species of the winter–spring mass development of periphyton of the seasonal pools, which arise during flood events. *Tribonema monochloron*, in the contrary, is a fast-growing soft tuft epiphytic alga even at suboptimal temperatures (mean optimal temperature is about 19.5°C). This species is also adapted to use higher doses of irradiance, which support its growth rate. It is a typical fast-growing species, which produces a high biomass during flood events and thus plays an important role in the inundation zone through both inorganic carbon assimilation in photosynthesis and the removal of other nutrients such as nitrogen and phosphorus. However, this species is sensitive to damage caused by the drying of these temporary habitats.

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