Competition between a planktonic diatom and a dinoflagellate during enclosure experiments in a mountain lake

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INTRODUCTION

The classical theory of nutrient-determined succession postulates that one species is superior in growth at low nutrient concentrations, but that some other species are superior at a higher concentration, so that the two (or potentially more) species partition natural gradients in the availability of the nutrient (e.g. Dugdale 1967). Tilman’s research on competition has been presented in several papers, including Tilman (1976, 1977) and Tilman & Kilham (1976). His mechanistic theory of competition is fully developed in Tilman (1982). The mechanistic models assume that competition will occur only if nutrients are limiting. Moreover, the N:P and Si:P supply ratios are fundamental axes along which the phytoplankton community structure varies (Kilham 1986). Therefore, silica availability can affect algal community composition, interspecific competition and succession.

According to Wetzel (2001) there is a great diversity in tolerances to variations in temperature among algae. In particular, what is frequently observed is a prominent role of diatoms at colder temperatures and an increasing variety of other algae as the waters warm. Temperature influences growth and mortality rates, coupled to limiting nutrients resources able to determine phytoplankton succession, that is, capable of altering the outcome of competitive interactions affecting the maximal growth rate of a species. Among several species of algae (e.g. A, B and C), the species with the lowest R* (R* sensu Tilman) should be the superior competitor at a given temperature, and, as a result, species A should dominate at low temperatures, followed by species B and C as temperature increases (Mechling & Kilham 1982; Wetzel 2001). Huisman & Weissing (1994) showed that Tilman’s theory is applicable to the light resource as well, although light competition is conceptually a more complex issue than nutrient competition (Tilman 1990).

Classical competition experiments are carried out in cultures using one or more species under controlled nutrient conditions (e.g. Kilham 1986). To analyse the factor causing differences in spatial and temporal distribution of certain phytoplankton species in the natural environment, enclosure studies are the best choice. Enclosures methodology is perhaps more complex to interpret (e.g. Bloesch et al. 1988), but also more realistic because all other factors are maintained. For an exhaustive survey of this field experimental technique see Berg et al. (1999) and Cantonati et al. (2002) for comments on the performances of different types of enclosures used in this study. This is in agreement with modern limnological approaches, which highlight the importance of addressing systems as a whole.

The purpose of this research was to describe and interpret the main ecological characteristics and the competition mechanism of two species that are dominant in the summer phytoplankton of Lake Tovel:

- *Glenodinium sanguineum*. This dinoflagellate was described with this binomial by Marchesoni in 1941. Until 1964 these algae accumulated in the SW-part of Lake Tovel (Red Bay) and reached densities of about 3–4 millions cells per litre. High densities and cells with large amounts of carotenoids in the cytoplasm (identified as astaxanthin by thin layer chromatography by Gerosa in 1961), induced the reddening phenomenon. For morphological and ecological observations on *G. sanguineum* and for reddening mechanism description see Baldi (1941), Marchesoni (1941, 1955, 1959), Miola & Trevisan (1982) and Dodge et al. (1987). The forms with (red) and without (green) carotenoids were believed (Baldi 1941 and following cited scientists) to be ecophysiological stages of the same species. The dinoflagellates that developed within our enclosures all matched the overall description of the green form. However, there were slight differences such as cell size (in average slightly larger than the dimensions supplied for *G. sanguineum* by Marchesoni, 1941) and epichene-ipochene shape (both rounded and poorly differentiated between each other). These observations are important because taxonomic work, based on ultrastructural, bioorganic and genetic evidences, is in progress within the SALTO-Project and will sure-
ly produce useful data to clarify the taxonomy of the two forms of G. sanguineum and other dinoflagellate taxa of Lake Tovel. For simplicity we will keep on referring to the dinoflagellates proliferating in the enclosures as G. sanguineum. Present day maximum densities of G. sanguineum (sum of green and red forms) are 10–100 times lower than those recorded at the time of the reddening. No recent evidence (macrosopic and microscopic observation and bioorganic chemistry analyses) of a presence of astaxanthin in the cells we collected are available (the sole exception being represented by the cysts (G. Guella, personal communication).

- *Fragilaria tenera* (W. Smith). Lange-Bertalot is a cosmopolitan diatom, frequently found in mountain lakes and cold waters with low to medium mineral content. In Lake Tovel it shows a high cellular size variability (Table 1) and notable differences in average length among years. F. tenera has always been recorded as one of the major constituents of Lake Tovel phytoplankton [as *Synedra acus var. radians* (Kützing) Hust]. In fact, this diatom was always mentioned as an abundant taxon of the phytoplankton community of Lake Tovel by the investigators who studied G. sanguineum, both before and after 1965 (Baldi 1941; Marchesoni 1955, 1959; Arrighetti & Siligardi 1977; Paganelli et al. 1981; Paganelli 1992). Most recently, this alga has indeed been observed to be the main competitor of G. sanguineum and it is often dominant during the whole summer Corradini et al. 2000).

Based on experimental studies, more reliable hypotheses suggest that the decline of G. sanguineum resulted from the decreased phosphorus input, due to changes in the husbandry of the cattle burns in the valley (Cantonati et al. 2003), and to recent modifications in the local climate [late-spring rainfall and summer-humidity increase with shorter water renewal times that lead to water cooling (Paganelli et al. 1981)].

This paper deals with part of the results of out last investigations that were focusing on the ecological factors influencing dinoflagellate blooms. The aims of the study were to identify the environmental factors regulating the competition between G. sanguineum and F. tenera both in ‘natural’ conditions and in situations forced by phosphorus additions, and to identify a parameter describing the competition between the two species to be able to predict which taxon will profit from phosphorus additions.

### MATERIAL AND METHODS

#### The study environment

Lake Tovel (1178 m a.s.l., *z* <sub>max</sub> = 39 m) is a temperate, meromictic, oligotrophic (P limiting) mountain lake. The limnion shows a dimictic behaviour. It is renowned for red blooms due to the dinoflagellate G. sanguineum, which suddenly ceased in 1964. Among the most complete descriptions of Lake Tovel are the monographs by Baldi (1941) and Marchesoni (1959). Phosphorus was shown to be the factor limiting primary production already by Cordella et al. in 1981.

#### Enclosure experiments

Enclosures used are of two types: cylindrical and bag enclosures. Both are in polyethylene, but the cylinders have a diameter of 3 m, a depth of 3.5 m, are opened at the top and even at the bottom and the capacity is 25 m<sup>3</sup>; instead, bag enclosures have a diameter of 0.7 m and a volume of about 0.4 m<sup>3</sup>. Experimental modifications are described in Table 2. In each experiment one of the enclosures was not modified in any way and sampled as control. At least at the beginning and the end of each experiment samples were taken also in the open water to get an estimate of the effects on the phytoplankton due to the sole presence of the experimental structures (enclosure effect).

The results considered for this contribution were selected from data obtained during in situ experiments carried out in 2000, 2001 and 2002. Phosphorus enrichments were obtained adding concentrated Na<sub>2</sub>HPO<sub>4</sub> solution, whereas nitrogen addition was obtained using a Mg(NO<sub>3</sub>)<sub>2</sub> solution. For the experiment in 2002, which was conducted in a bag-shaped enclosure, Red Bay phytoplankton composition was monitored daily in order to identify the dinoflagellate/diatom biovolume

### Table 1. Experimental design: period and experimental modifications carried out during the years 2000, 2001 and 2002 in the enclosures in Lake Tovel.

| Year | Period | Structure | Number of enclosure and labels | Experimental modifications |
|------|--------|-----------|--------------------------------|-----------------------------|
| 2000 | 03 Jul.–27 Jul. | cylinders | 2; A and B | P B: + 20 µg l<sup>-1</sup> | 03 Jul. and 13 Jul. |
| 2001 | 13 Jul.–24 Aug. | cylinders | 2; A and B | N B: + 200 µg l<sup>-1</sup> | 13 Jul. |
| 2002 | 22 Aug.–23 Aug. | cylinders | 2; A and B | P B: + 20 µg l<sup>-1</sup> | 23 Jul. and 16 Aug. |
| 2003 | 16 Aug.–31 Aug. | bag | 1 | P + 20 µg l<sup>-1</sup> | 16 Aug. and 22 Aug. |
|      |         |           |                               | N + 200 µg l<sup>-1</sup> | 22 Aug. |

| Table 2. Correlation coefficients between the biovolumes of the two species, the biovolumes of the two species and temperature and *Fragilaria tenera* biovolumes and silica concentrations during the years 2000, 2001 and 2002 in the enclosures in Lake Tovel. |
|-------------------------------------------------|-----------------|-----------------|
| Variables                                      | Glenodinium sanguineum | Fragilaria tenera |
| Glenodinium sanguineum                         | temperature (°C) | −0.371 | 0.01 |
| Glenodinium sanguineum                         | silica (mg l<sup>-1</sup>) | 0.308 | 0.05 |
| Fragilaria tenera                              | temperature (°C) | −0.299 | 0.05 |
| Fragilaria tenera                              |                | −0.067 | NS |

*P (V = 46)*
ratio. Phosphorus was then added to the ‘bag’ only when the dinoflagellates became clearly dominant.

Field work, phytoplankton counts and data processing

Before collecting samples (always between 10:00 and 12:00 AM), we always recorded the main physical and chemical parameters by means of a multiprobe (Hydrolab H20). Water samples for chemical and biological analyses were taken with a Patalas-Schindler sampler at constant depth of 1.0 m. Chemical analyses, including pH, alkalinity, major ions and nutrient concentrations, were carried out following I.R.S.A.-C.N.R. (1994). Phytoplankton counts were performed according to Utermöhl (1958) after sedimentation in glass chambers. At each magnification, at least 100 individuals of the most frequent taxon were counted, which corresponds to a maximum statistical error of 20% (Lund et al. 1958). Biovolumes of the different taxa were calculated approximating the cell shape to simple geometrical shapes (Rott 1981). Size variability of F. tenera was described considering three length-classes (‘small’, ‘medium’ and ‘long’). We determined the correlations between algae biovolumes, temperature and silica on the one side, and t-tests on mean water temperatures among years on the other. Surface/volume ratio of the two species were estimated according to Hillebrand et al. (1999).

Redundancy analyses (RDA) were performed using CANOCO 4.5 (Ter Braak & Šmilauer 2002) and multiple regression analyses using STATISTICA (StatSoft Italia srl). Statistical significance of the RDA axes was checked with Monte-carlo Permutation tests at a 5% significance level.

RESULTS

During the three years investigated (2000–2002), summer phytoplankton was composed mainly of G. sanguineum and F. tenera (other algae represented only between 5% and 18% of the total phytoplankton biovolume). In 2000 (Fig. 1) both species coexisted in the control enclosure, whereas in the nutrients-enriched ones G. sanguineum became dominant after the first N-addition and the second P-addition (13 July), reaching biovolumes higher than 7.5 mm³ l⁻¹. On the contrary, no clear effect occurred in consequence of the first P-enrichment carried out at the start of the experiments (Fig. 1). In 2001 F. tenera dominated the control until the end of the experiment, whereas G. sanguineum was able to prevail in the enriched one only after the second P-addition (26 July). Both in 2000 and in 2001, silica reduced more in the enriched enclosures (B), reaching the lowest concentrations measured (= 0.14 mg l⁻¹; Fig. 1). In 2002 both species coexisted at the beginning of the experiment, but P-enrichment favoured F. tenera that became dominant by 2 August; after this date, the diatom population declined and silica reduced from 0.6 to 0.18 mg l⁻¹, from 29 July to 1 August). After the decline of the diatoms, G. sanguineum increase slightly, but it did not reach a clear dominance.

Linear correlations were calculated for the three summers (Table 3): F. tenera and silica concentration showed a negative correlation (r = -0.299; P < 0.05); a significant negative correlation was also found (r = -0.37; P < 0.01) between the two species. Moreover, G. sanguineum and temperature showed a positive correlation (r = 0.31; P < 0.05). It is possible to note that G. sanguineum tends to be more abundant at temperatures higher than about 12°C, whereas at lower temperatures F. tenera tends to be dominant (Figs 2, 3). The mean water temperature recorded in summer 2002 (14°C) is significantly different from the one measured in summer 2000 (10°C) (t = 5.71, P < 0.001), but it does not differ in a statistically significant way from the mean water temperature of summer 2001 (10°C) (t = -1.32, P = 0.20). Dinoflagellate and diatom proportions in the natural environment (out) in summer 2002 are displayed in the left part of Fig. 4. Dinoflagellates become dominant in the Red Bay only in the first half of August. A phosphorus addition carried out on a bag-shaped enclosure on 16 August resulted in a G. sanguineum biovolume as high as 18 mm³ l⁻¹ (density = 2.7 millions cells l⁻¹; right part of Fig. 4); this bloom occurred with an exponential growth rate (r = 0.495).

As regards the results of the multivariate analyses, we initially calculated a detrended correspondence analyses (DCA) in order to evaluate the linear or unimodal response of our species (Hill & Gauch 1980). The first axis calculated by DCA has a length of 1.4 s revealing that our data showed a linear context. For this reason, we chose to carry out a RDA (Fig. 5). The RDA produced an ordination in which the first four axes were temperature, silica, nitrate (NO₃⁻) and total phosphorus (TP) with eigenvalues of 0.293, 0.102, 0.393 and 0.211, respectively. The Monte Carlo Permutation tests calculated for all variables showed that temperature additional variance to the model was significant (P = 0.016), as well as that of nitrate (P = 0.002) and even of silica (P = 0.054); TP, on the contrary, was not significant (P = 0.81). The ordination diagrams are useful both to outline some patterns and to uncover correlations between the two algal species and the environmental variables. G. sanguineum shows a high positive correlation with temperature and a high negative correlation with nitrate, whereas F. tenera presents a negative correlation with silica (Fig. 5). Multiple regression analyses carried out on the same data used for RDA and in which the dependent variable was F. tenera provided R² = 0.48 (v = 3.37, P = 2.1 × 10⁻⁵). In these analyses G. sanguineum, nitrogen and silica concentrations had significant beta values (P < 0.05) of −0.31, −0.69 and −0.94, respectively. Instead if G. sanguineum was chosen as the dependent variable, R² = 0.41 (v = 3.37, P = 2.2 × 10⁻⁴) and F. tenera, temperature and nitrogen concentrations had a significant (P < 0.05) beta values of −0.34, 0.42, −0.24, respectively.

Because specific data on nutrient uptake efficiency were not available, we calculated the surface/volume ratio (S/V) according to Smith and Kalff (1983). This cell features (Table 1) help to explain the different nutrient uptake efficiencies: in fact, species with higher S/V ratios usually display higher uptake efficiencies.

DISCUSSION

The parameters considered to be relevant in predicting the algal response to a pulsed addition of a limiting nutrient are uptake rate, storage ability and maximum growth rate. Although the maximum initial uptake rate is a major characteristic for storage (Turpin & Harrison 1979), the duration over
Fig. 1. Temperature, *Glenodinium sanguineum* and *Fragilaria tenera* biovolumes, silica and reactive phosphorus concentrations in the control and enriched enclosures during 2001, 2002 and 2003 in Lake Tovel. Arrows indicate nutrient enrichments.

Table 3. Mean biovolumes and surface/volume ratio of *Glenodinium sanguineum* and of three size-ranges of *Fragilaria tenera* during 2000, 2001 and 2002 in the enclosures in Lake Tovel.

| Species                  | Mean biovolume (μm$^3$) | S/V ratio |
|--------------------------|-------------------------|-----------|
| *Fragilaria tenera* (short) | 813.9 ± 85.7            | 1.16      |
| *Fragilaria tenera* (medium) | 1685.8 ± 224.5          | 0.97      |
| *Fragilaria tenera* (long)  | 4217.8 ± 1145.0         | 0.73      |
| *Glenodinium sanguineum*   | 7192.9 ± 1213.0         | 0.12      |

which elevated uptake rates are maintained during a P-pulse is also important in competition (Suttle *et al.* 1987). In phytoplankton, generally two uptake strategies are distinguished (Lean 1984). The smaller-sized species, with a high cellular surface to volume ratio (see Table 1) appear to have a higher affinity for the uptake of a limiting nutrient (Smith & Kalff 1983). Under a continuous, stringent limitation they will outcompete larger-sized species. Also in our experiments we noted that, after P-addition, the diatom was a stronger competitor than the dinoflagellate. In this regard, the different sizes that *F. tenera* displayed during the three years of experiments may have influenced the competition with the dinoflagellate. It
must, however, be remembered that smaller sizes could be a consequence of growth under silica limitation (Tilman et al. 1986).

The coexistence between *G. sanguineum* and *F. tenera* in Lake Tovel during the summer months over the last century is documented by all authors who studied the phytoplankton community of the lake (cf. references quoted in the Introduction). For example, paleolimnological studies on cores taken in the deepest part of the lake (Guilizzoni et al. 1992) show that, during the last 20–30 years, the astaxanthin concentration (in Lake Tovel considered a marker for *G. sanguineum*) had a negative correlation with fucoxanthin (accessory pigment characteristic of diatoms and chrysophytes).

Individual taxa in natural assemblages often do not respond in a uniform way to nutrient enrichments and large differences in response can occur even among taxa coexisting in the same biological and chemical environment (Stoermer et al. 1978). During the three years of our study, the first P-enrichment was always followed by a different response; the second one, instead, favoured generally *G. sanguineum* in conditions of silica deficiency. Silica reduction below about 0.5 mg l\(^{-1}\) is known in the literature (e.g. Wetzel 2001) to be one of the major factors contributing to the decline of planktonic diatom production. Kilham (1971) showed that progressive enrichments with phosphorus and nitrogen can lead to a rapid biogenic reduction in silica levels so that diatoms cannot effectively compete and are replaced by nonsiliceous phytoplankton.

R* can be defined also as the concentration of available resource that a species requires to survive in a habitat. Our data showed silica decreases which continued until this element became limiting (0.15–0.18 mg l\(^{-1}\); Fig. 1). This silica concentration is probably approaching the R* value. Some observations referring to summer 2003 support this hypothesis: silica concentrations reached the threshold; after that it becomes limiting (F. Corradini, personal communication); and indeed *F. tenera* was absent. Moreover, *F. tenera* was re-
placed by *Cyclotella* spp. and this Fragilariaeaceae/Centrales shift is well known from the literature to be regulated primarily by the Si:P ratio (Tilman & Kilham 1976). Kilham (1986) reported that in natural community experiments the most P-limiting cases were dominated by some species of *Syndra*. In our experiments *F. tenera* (= *Syndra radians var. acus*) showed a good P-uptake and storage ability in the first days of enclosures experiments, when silica is available. However, if silica concentration never becomes limiting during summer (e.g. because of a rainfall increase) that causes a continuous silica input from the catchment, Paganelli *et al.* (1981), then the diatom can compete and win against the dinoflagellate. It must, however, be remembered that eventual silica reductions at the beginning of the summer are reported in the literature to be related not only to a decrease in rain events and lixiviation, but also to the climate conditions during the winter (type and thickness of ice-cover) conditioning the possibility of winter blooms of diatoms capable of silica bioreduction.

When silica is available, temperature seems to control the competition between the two species (usually under 12°C *F. tenera* is dominant), whereas temperatures above 12°C favour *G. sanguineum* (this temperature is the mean of the values recorded along the whole water column in the Red Bay). Multiple regression analyses show that temperature (and *F. tenera* density and nitrogen concentration as well) is a variable that significantly regulates *G. sanguineum* densities. In agreement with Tilman (1981), a species may be a superior nutrient competitor only within a precise temperature range. Because the competitive abilities of the algae depend upon temperature, variations in temperature can potentially determine which of them will become dominant. In fact, the highest mean temperature was registered in summer 2000, during which *G. sanguineum* was coexistent in the control enclosure and dominant in the enriched one. In fact according to multiple regression analyses results temperature seems an environmental factor which affects in a marked way *G. sanguineum* than *F. tenera*.

The RDA analyses confirmed the dependence of *F. tenera* upon Si concentration (negative correlation) and uncovered a positive correlation between *G. sanguineum* and temperature. The RDA also pointed out an inverse correlation between *G. sanguineum* and nitrate. Nitrate concentrations are never limiting in Lake Tovel, but in the experimental environment and following P addition, nitrogen would be severely consumed, particularly during the *G. sanguineum* bloom. Owing to sudden P uptake by the phytoplankton, it is difficult to determine the relationships between P addition and other parameters. Inorganic phosphorus added to the enclosures is suddenly assimilated and therefore is not found by chemical analyses. Instead, total phosphorus has a steady trend, but does not show any clear relation in both RDA analysis and multiple regression. Our previous results (Cantonati *et al.* 2003) suggested that water temperature, more than being a determining environmental variable in itself, could be relevant as an expression of light and climate conditions. Wetzel (2001) stated that the ecological effects of light and temperature on the photosynthesis and growth of algae are inseparable because of the interrelationships between metabolism and light saturation. Response to light intensity, however, is species-specific, and in many cases, a considerable degree of adaptation to changing light intensities occurs (Tardio *et al.* 2003).

The competition for the interactively essential resources can generate competitive exclusion with a winner that depends on the initial conditions, if species consume most of the resources for which they are strong competitors (Huisman & Weissing 2001). Phosphorus additions in a natural community have different effects on the individual populations according to the previously discussed parameters, but the ratio between the abundances of the populations is fundamental too. In fact, dominant populations have the largest "population uptake rate". This situation is well described by the results obtained in the summer 2002, when we added P only in presence of a clear dominance of *G. sanguineum*. Following this enrichment, the dinoflagellate became superior to the diatom and dominated the phytoplankton community for a restricted period, after which the abundance dropped. Sudden dinoflagellate bloom crashes have been observed both in marine (e.g. Smayda 2002) and in freshwater systems (e.g. Taylor & Polingher 1987), that is, bloom conditions will become stressful, and the blooming organism may become a victim of its own success. In enclosed systems, this effect is enhanced by the impossibility of dispersal and could lead to a more rapid bloom breakdown.

In conclusion after three years of field studies in Lake Tovel the competition between *G. sanguineum* and *F. tenera* and possible implications referring to the disappearance of the dinoflagellates’ blooms may be synthesised as follows:

i. Phosphorus is the limiting nutrient in Lake Tovel and the two species dominate alternatively following seasonal trends. Water temperature (light climate?) seems to be an important environmental factor regulating the competition between the two taxa. In particular, dinoflagellate dominance was correlated with higher water temperatures in contrast to the diatom.

ii. In experimental conditions, the two species coexist in the control enclosure, with P-enrichment it usually favours the diatom, at least at the beginning. However, after this initial advantage, silica concentration decreases under resource requirements (about 0.15–0.18 mg l⁻¹) and this bioreduction can favour the dinoflagellate that might become dominant.

iii. The phosphorus addition, carried out when *G. sanguineum* biovolumes were clearly higher than those of *F. tenera*, determined a prompt and marked increase of the dinoflagellate. This outcome suggested that the ratio between the two competing species is a useful parameter to predict which taxon will benefit from the nutrient additions.

iv. The balance that assured dinoflagellate summer blooms and the patterns of seasonal dynamics changed. Probably the pattern before 1965 was (1) at the beginning of summer, with low temperature and P availability, the diatom biomass increased and the silica concentration reduced under R² and (2) during summer, with an increase in water temperature and constant input of P, the dinoflagellate may have successfully competed and red blooms occurred. At present the typical dynamic succession is the lack of input of P and an increase in rainfall increase (that causes major inputs of silica and cooling of the water), which allows diatoms to compete strongly with dinoflagellates throughout the summer. However, in exceptionally dry summers, silica may become limiting, but dinoflagellates cannot grow because they are limited by phosphorous concentrations.
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