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Development and ecological importance of phytoplankton in a large lowland river (River Meuse, Belgium)

Jean-Pierre Descy & Véronique Gosselain
Unité d'Ecologie des Eaux Douces, Département de Biologie, FUNDP, rue de Bruxelles 61, B-5000, Namur, Belgique

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Abstract

The ecological importance of the River Meuse phytoplankton with regard to carbon and nutrient transport has been examined in two reaches of the Belgian course of the river.

Field measurements of total particulate organic carbon (POC), particulate organic nitrogen (PON) and particulate phosphorus (PP) show that the large autochtonous production of organic matter strongly affects the carbon and nutrient budget of the aquatic system. During the growing season, phytoplankton accounts for nearly 60% of the POC and dominates the PON. Calculations of the carbon and oxygen budget in the upper reach of the Belgian Meuse demonstrates that the ecosystem is autotrophic, *i.e.* that autochtonous FPOM (fine particulate organic matter) production is the major carbon input. This suggests that in large lowland rivers, primary production (P) may exceed community respiration (R), *i.e.* P:R>1, whereas they are assumed to be heterotrophic (P:R<1) in the River Continuum concept.

The question of maintenance of phytoplankton in turbid mixed water columns is also addressed, and the case of the River Meuse is treated on the basis of studies of photosynthesis and respiration (ETS measurements). The results suggest that the potamoplankton may show some low-light acclimation, through an increase of chlorophyll *a* relative to biomass, when it comes to deep downstream reaches, and that algal respiration rate may be reduced. A simulation of the longitudinal development of the algal biomass shows the different phases of algal growth and decline along the river and brings support to the 'importation hypothesis' for explaining maintenance of potamoplankton in the downstream reaches.

Introduction

When considering phytoplankton dynamics in large lowland rivers, aspects other than specific composition and the factors involved in longitudinal and temporal community changes must be acknowledged. One of these aspects pertains to the effect of the potamoplankton development on the carbon and nutrient budget of the aquatic ecosystem. In this respect, the term 'large lowland river', which is commonly used for rivers of quite different size, might be properly defined according to the River Continuum concept (Vannote *et al.*, 1980) and related considerations (Wetzel, 1983). A 'large river' may then be defined as a flowing water body transporting a large amount of FPOM (fine particulate organic matter), *which may include a significant contribution of autochtonous organic material produced by a well-developed phytoplankton.* However, according to this theory (Vannote, 1981), large rivers (of order 9 to 12) are characterised by a tendency to be dominated by heterotrophic processes (R), as the primary production (P) becomes limited by reduced light penetration and/or increased water depth. Conversely, autotrophy (P/R>1) is supposed to be attained in mid-river reaches (order 3–6, see Billen *et al.*, this volume) dominated by benthic primary producers. Nevertheless, when looking more closely at the carbon budget of large river ecosystems, a phytoplankton-dominated river may be predominantly autotrophic, exporting new, autochtonous organic matter. This has been well shown in eutrophied rivers, either by *in situ* measurements (e.g. R. Rhine, Admiraal *et al.*, 1992), or by modelling the balance of carbon fluxes in particular reaches (e.g. R. Meuse, Descy *et al.*, 1987, and below). We present thereafter a dataset containing measurements of C, N and P forms in the River Meuse, which tends to confirm the profound changes brought about by the phytoplankton development in a lowland river ecosystem. These data also allow us to verify the carbon to chlorophyll ratio often used in primary production models, as well as to approach the nutrient status of the potamoplankton through sestonic C:N and C:P ratios.

Another question to be addressed, and one which is closely connected to the autotrophic production of FPOM, is directly related to the development of phytoplankton in a turbid water column undergoing a relentless turbulent mixing. The problem, already discussed by other authors (e.g. Cole *et al.*, 1991, 1992; Loehr, 1987) is 'how to explain the maintenance of a potamoplankton despite low water transparency and deep mixing ?'. As a matter of fact, if mixing occurs below the critical depth (Kirk, 1983), the plankton algae circulating in the mixed layer should experience negative net production rates. A first hypothesis, as stated by Cole *et al.* (1991), explains potamoplankton development in large rivers and estuaries by physiological adaptation, *i.e.* low light acclimation of the algae. A variant, which would account for algal growth in mixed turbid systems without any change in the photosynthetic efficiency, invokes enhanced photosynthesis of the plankton algae, as they are repeatedly moved in a strong gradient of light, *i.e.* up from darkness to full subsurface irradiance and down back to lower light. However, evidence for strongly increased photosynthetic rates arises from mathematical calculations (Loehr, 1987; Imboden, 1992) and from field measurements, which however yielded variable results in several cases (see e.g. Dokulil, this volume). Contradictory results may be explained by the difficulty to find the right experimental design: moving bottles up and down, even by a seemingly elaborated system (*i.e.* Mallin & Paerl, 1992), may neither reproduce the right frequency of vertical entrainment in turbulent eddies (see Reynolds, this volume), nor the complexity of a cell's movement in the mixed layer, which entails discontinuous fluctuations of the light experienced by the phytoplankton (MacIntyre, 1993). Furthermore, the result of a fluctuating light field in terms of algal production could also depend of the extent of the euphotic zone, as the probability of depressed photosynthesis by photoinhibition is greater in a well-lit water column (Gallegos & Platt, 1982) than in a turbid one. Of course, the observed response of the algal community depends upon its photoacclimation too.

Other hypotheses put forward to account for the presence and growth of phytoplankton in the downstream reaches of a large river are: (i) reduced loss rates, *i.e.* grazing and sedimentation, and (ii) importation of the biomass from upstream productive reaches. As shown below, some support to the latter idea can be obtained from simulations of the longitudinal development of the potamoplankton, based on a mathematical model previously designed for the River Meuse (Descy *et al.*, 1987; Descy, 1992).

In addition, we attempt to test the adaptation or acclimation hypothesis by reference to some studies carried out in the river Meuse during the period 1987–1992. They deal with algal photosynthesis and respiration, the latter being based on measurements of the activity of the respiratory electron transfer system (ETS; Devol & Packard, 1978; Rai, 1984, 1988). Indeed, algal respiration is a key physiological process in algal growth, yet it has been seldom directly measured in natural samples. If some estimates may be derived from cultures, usually by measurements of oxygen consumption by axenic algal strains, the range of values is quite large, varying with the taxa and the physiological state of the cells, and can hardly be extrapolated to simulations of natural communities. For example, the ratio between the respiration rate per unit chlorophyll *a* (r_{chla}) and the photosynthetic capacity (P_{opt}), varies in the literature between 0.05 and 0.5 (Pourriot *et al.*, 1982) or between 0.04 and 0.15 in healthy growing cells (Daneri *et al.*, 1992), and it may even reach 0.67 under extreme nutrient limitation (Reynolds *et al.*, 1985). As a result, instead of being determined from measurements on natural assemblages, the respiratory activity of the phytoplankton is often 'adjusted' by the routines of mathematical models, in order to account for a net photosynthesis which matches observed algal biomass or growth rate. Such a procedure may lead to errors in estimating the other loss processes.

Description of the sites studied

The data used herein are from the R. Meuse, which has been described previously (e.g. Descy, 1987; Descy

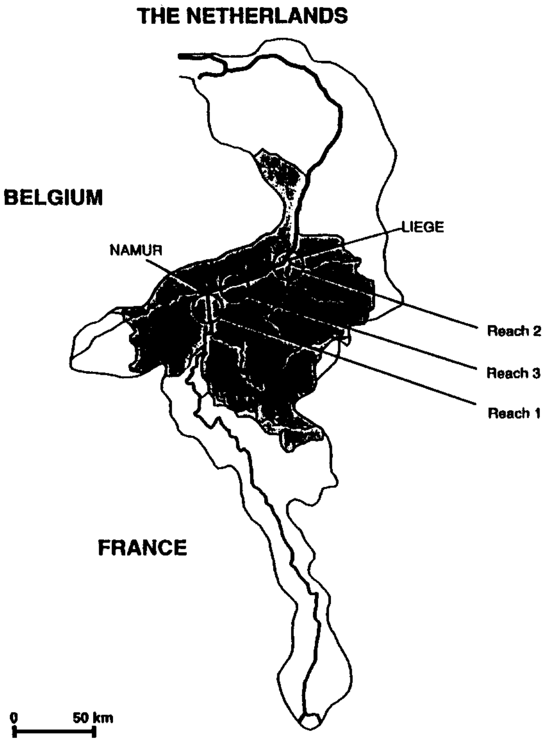


Fig. 1. Map of the River Meuse basin; the grey area is the Belgian part of the catchment (about 40% of the total area).

et al., 1987, 1988). One of the important features of the Belgian part of the R. Meuse (*ca* 200 km, see Fig. 1) is that it has been heavily regulated for navigation. So, the depth of the river channel (3 to 6 m) and the low water transparency (usual range of the vertical extinction coefficient: 1.5–3.5 m^{-1}) do not allow any significant benthic primary production and the barely developed benthic vegetation is restricted to the banks. On the other hand, a large phytoplankton biomass develops in favourable weather and flow rate conditions (see Descy, 1987 and Gosselain & Descy, this volume), showing a successional pattern that is driven mostly by external physical factors.

The data were collected from two main parts of the Belgian section (Fig. 1): reach 1, upstream of Namur, around km 535 from the source, and reach 2, in the vicinity of Liège, between km 580 and km 600. Although being eutrophied, the first site presents a rather good water quality by the usual standards, whereas the second reach is subject to heavy inputs of industrial and domestic sewage, particularly from the city of Liège. A third site, located slightly downstream of reach 1, was sampled in 1992: one of the main features of this 'reach 3' is its increased depth (6 m) relative to reach 1 (3.5 m).

Material and methods

Samples were usually taken with a 3-l Van Dorn bottle and brought back to the laboratory, in a cooled dark container, within a few hours of collection. Carbon, nitrogen and phosphorus were measured on filtered water samples (using precombusted Whatman GF/C filters; a comparison with Millipore 0.45 μm filters showed no significant difference in SRP concentrations). Standard analytical procedures were used for measuring N-NO_3^-, N-NO_2^-, N-NH_4^+ and SRP (soluble reactive phosphorus) on filtered samples. On the same samples, DOC (dissolved organic carbon) was measured with a Dohrman DC-80 analyser. Analyses of the seston were made after drying the filters carrying the particulate material overnight at 60 °C and using a persulphate digestion followed by orthophosphate determination (Wetzel & Likens, 1979) for particulate phosphorus (PP), and a NA1500 Carlo Erba elemental analyser for particulate organic carbon (POC) and particulate organic nitrogen (PON). Chlorophyll *a* measurements were also carried out on the seston collected on GF/C filters, according to the technique described by Péchar (1987), *i.e.* a hot extraction in a solvent made of 5:1 acetone 90%-pure methanol, followed by measurements of absorbance at 665 nm before and after acidification with HCl 0.03 M in the extract.

Methods for photosynthesis and respiration measurements have been described in detail elsewhere (Descy *et al.*, in press). In short, photosynthesis measurements were based on the ^{14}C technique, using, in both the field and in the laboratory, a simple incubator. This permits exposure of the water samples to a range of fixed relative light intensities (6 to 100% of subsurface irradiance). Irradiance data were obtained *in situ* by monitoring surface PAR with a Licor 190SB sensor or from data of total incident radiation (Royal Meteorological Institute, Belgium). Light in the water column was calculated from the vertical extinction coefficient of light, obtained by immersion of a photocell fitted with red, green and blue filters at various depths; calculations of the mean coefficients were made according to Vollenweider (1974). Photosynthetic parameters were determined by the fit of the observed values to the Vollenweider equation.

Respiration was determined from measurements of ETS activity of the seston retained on GF/C filters, with the techniques described by Christensen & Packard (1979), Rai (1984), Packard (1985). As the samples were prefiltered through a 63 μm plankton net, most of the zooplankton was excluded from the seston; furthermore, water samples preincubated with antibiotics showed no significant difference from untreated samples. Thus, it was assumed that most of the ETS activity measured resulted from algal respiration. The entire procedure was first applied to cultures of a diatom (*Cyclotella meneghiniana* Kütz.) and of a green alga (*Dictyosphaerium ehrenbergianum* Näg.), both originally isolated from the River Meuse, in order to define the various analytical steps, which were afterwards routinely applied to natural samples. In particular, a sonication time of 3 min was applied to the filters carrying the algal material and immersed in a homogenization buffer; the homogenates were kept under 4 °C throughout the sonication. Then, the homogenates were treated as in Rai (1984) *i.e.* incubated 10 min with INT at the field temperature, at saturating levels of the substrates, NADP and NADPH. Calculations of the ETS activity were made from the absorbance of the formazan produced by the reduction of INT, according to Rai (1984). The respiration rate was expressed as mg O_2 (mg chl*a*)$^{-1}$ h^{-1}, taking a R:ETS ratio of 0.17 (Packard, 1985). The data presented here are a synthesis of photosynthesis measurements, mostly in the upstream reach of the Belgian Meuse, from 1987 to 1992; however, some data from reaches 2 and 3 have been included for comparison. The respiration data were collected in 1991 and 1992, only in the upstream part of the river (reaches 1 and 3).

The simulations of the longitudinal potamoplankton development were calculated by the PEGASE mathematical model, developed at the 'Centre Environnement', University of Liège, Belgium. The phytoplankton submodel is largely based on the Meuse ecological model presented in Descy *et al.*. (1987), which was also used to calculate the daily phytoplankton production, integrated over time and depth, from field incubations. The PEGASE model takes into account inputs of C:N:P forms from the watershed and from domestic and industrial releases, and simulates the evolution of the algal biomass in stationary conditions, *i.e.* at defined values of temperature, light and discharge conditions at a reference site. These variables are calculated for the whole course of the river, and are used to determine the physical factors and processes which control phytoplankton growth and biomass, including the mean velocity of flow and the dilution rate, depending of the river morphometry and of the watershed structure. These last characteristics were known with some detail for the Belgian course but were described more simply for the French section.

Results

Effect of the potamoplankton on the C:N:P budget

A fairly complete picture of the fluctuations in the amount and share of the organic carbon in the Meuse is presented in Fig. 2, which shows concentrations and distributions of DOC and POC. The DOC is only twice as high as POC (mean DOC:POC ratio 2.2, range 0.93–11.3), which resulted both from the large input of untreated sewage, that influenced both dissolved and particulate carbon, and from the phytoplankton development. If the contribution of the algal biomass to POC is estimated using a C:chl*a* ratio of 37 (determined from measurements in the river, see below), an average fraction of 1/3 of the particulate matter comprised phytoplankton, the remaining being detrital carbon (Fig. 3). However, the contribution of algal C was quite variable over the growing season. Dissolved inorganic nitrogen forms (concentration range 2–4 mg l^{-1} mostly nitrate and ammonia, largely dominated over particulate nitrogen (mean DIN:PON ratio 10, range 3.1–22.1). The situation was more variable for phosphorus, as an important industrial release influenced the results, so that SRP (up to 1.6 mg l^{-1}!) often overwhelmed particulate phosphorus (PP).

This situation can be compared to that of the upper reach of the Belgian Meuse, which is much less influenced by domestic and industrial inputs. In this reach:

(i) DOC:POC ratio was 2.3 on average over the growing season (range 0.9–12.3); DOC was quite constant all over the year, which indicates that a large fraction of this dissolved carbon was refractory, originating from soil leaching in the watershed (the concentrations were similar to that of unpolluted rivers, see Meybeck, 1993); POC was variable and was mostly dependent on the contribution of living algae to particulate carbon, which was even higher than in the lower Meuse (Fig. 4); the mean percentage of algal C to total POC was 56.8% (range 12.5–92); of course, the largest amount of algal carbon coincided with the periods of blooms, in April, May, June, depending on weather and hydrodynamic conditions;

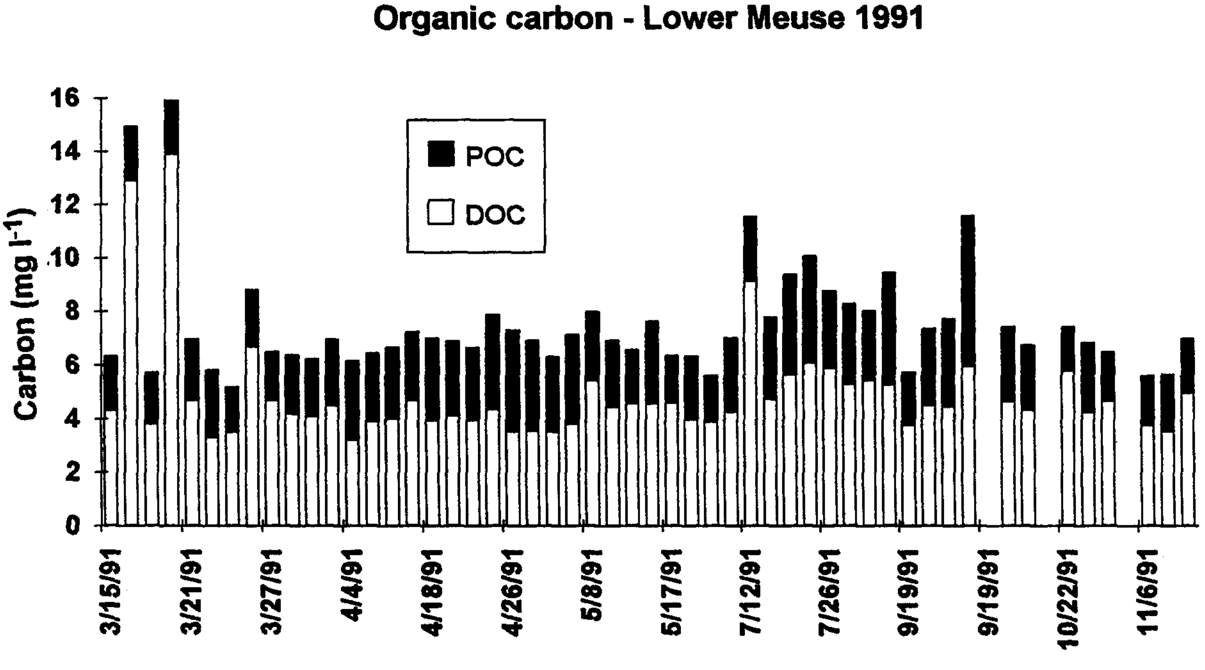


Fig. 2. Organic carbon in the lower Belgian Meuse (reach 2 in the text), measured at four sites at each sampling date, during the year 1991; POC: particulate organic carbon; DOC: dissolved organic carbon.

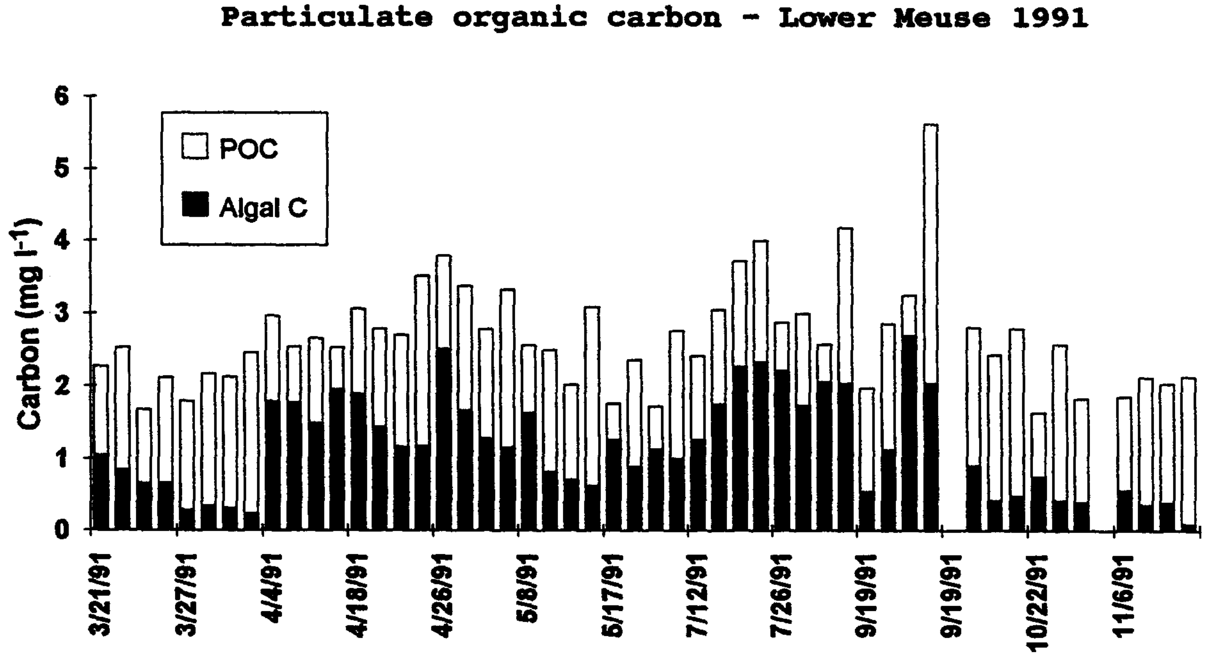


Fig. 3. Particulate organic carbon in the lower Belgian Meuse (reach 2 in the text), measured at four sites at each sampling date, during the year 1991; POC: particulate organic carbon; algal carbon was calculated from chlorophyll *a* concentration, using a C:chl*a* ratio = 37.

(ii) for nitrogen, the balance between dissolved and particulate forms was similar to that of the downstream reach (mean DIN:PON ratio 10.1); nitrate was the main dissolved form, while ammonia and nitrite reached much lower concentrations;

(iii) particulate phosphorus exceeded, most of the time, dissolved inorganic phosphorus, and the potamoplankton development strongly affected the relative abundance of the two forms, as a large fraction of the PP comprised algae which had taken up the SRP.

The carbon to chlorophyll *a* ratio, calculated from a linear regression of POC on chlorophyll *a* (Fig. 5) varied between 35 (lower Meuse) to 45 (upper Meuse), when the data of the two reaches were analysed separately. The regression on the data of the two reaches together gave a ratio of 37 (s.d. = 2.6, $n = 108$, $r^2 = 0.65$), despite the variable contribution of the detrital carbon, mainly in the downstream polluted reach. This C:chl*a* ratio is quite in the expected range of eutrophic water bodies (Riemann *et al.*, 1989). The mean detrital carbon concentration, given by the Y-intercept (Fig. 5), is 1.3 mg l^{-1}.

A similar regression analysis of the POC:PON and POC:PP data, carried out for the upstream Belgian reach (Fig. 6), gave the following results:

(i) a very good correlation between POC and PON (Fig. 6, A), showing the quite constant N content of the seston, with a C:N ratio of 7.9; the very low Y-intercept shows that almost all particulate nitrogen was contained in the phytoplankton; the C:N ratio (6.3) of the phytoplankton can be approached by regression of algal carbon, calculated from chlorophyll *a*, on PON; this value, very close to the Redfield ratio, is expected for algae growing in a N-saturated environment;

(ii) a more variable relationship between POC and PP (Fig. 6, B), which may result from the presence of variable amounts of phosphorus adsorbed on non-living suspended material; the regression of calculated algal C on particulate P gives a C:P ratio of 82, which is lower than the Redfield ratio and indicates that, most of the time, the phytoplankton was not P-limited.

Photosynthesis and respiration of the potamoplankton

A brief summary of the data on temperature, light, phytoplankton biomass and photosynthetic parameters obtained from measurements in the River Meuse during the period 1988–1992 is presented in Table 1.

The two parameters of the photosynthesis-light curve, P_{opt} and I_k, were plotted against temperature and light in the water column, respectively (Figs 7–8). P_{opt} values varied between 1.7 and 8.1 mg C (mg chl*a*)$^{-1}$ h^{-1}, over the whole range of water temperature, but unlike the one previously obtained (Descy *et al.*, 1987), the relation between photosynthetic capacity and temperature is not satisfactory. The large scattering may result (i) from the temperature *and* light dependence of P_{opt} and (ii) from the varying composition of the phytoplankton community. For instance, the P_{opt} values of the 'small *Stephanodiscus*'-dominated community (which occurred mostly below 15 °C) reached at times the typical summer values. A similarly scattered plot was obtained for the I_k parameter: its range was large (see Table 1) but most values fell between 50 and 150 μE m^{-2} s^{-1}. Because of the variability of the weather and light conditions, the plot of I_k *vs* mean daily light in the water column (calculated assuming continuous mixing down to the mean depth of the channel) also showed an important scattering, but most values were below 100 μE m^{-2} s^{-1}. Compared to literature data, values for P_{opt} and I_k were in a common range for temperate waters and showed no particular low light adaptation (Harris, 1978; Reynolds, 1984). Nevertheless, the initial slope of the photosynthesis-light curve, α, was on average in the range of published values for coastal waters and estuaries: Keller (1988, in Cole *et al.*, 1992) reported a range from 8.5 to 16.7 mg C (mg chl*a*)$^{-1}$ E^{-1} m^{-2}, with a mean of 12.

The respiration rate (r_{chla}) of the phytoplankton of the R. Meuse, measured by the ETS activity of the seston, was comprised between 0.08 and 0.62 mg C (mg chl*a*)$^{-1}$ h^{-1} and are only weakly temperature-dependent (Descy *et al.*, in press). On the other hand, respiration rate was rather well correlated with P_{opt} ($r = 0.65$), and the mean r_{chla}:P_{opt} ratio, was 0.066 (s.d. = 0.021). This ratio may allow calculations of the algal respiration rate as a fraction of P_{opt}, as proposed by various authors (e.g. Coveney *et al.*, 1977) or, according to Straskraba & Gnauck (1985), by a linear regression equation, where the slope is the r_{chla}:P_{opt} ratio, permitting calculation of an 'active', light-dependent, respiration, the Y-intercept being a 'passive' component, temperature dependent, acting in the dark. In the present case (Fig. 9), the equation is:

$$r_{\mathrm{chla}} = 0.046 * P_{\mathrm{opt}} + 0.073 \ (r^2 = 0.42; n = 39)$$

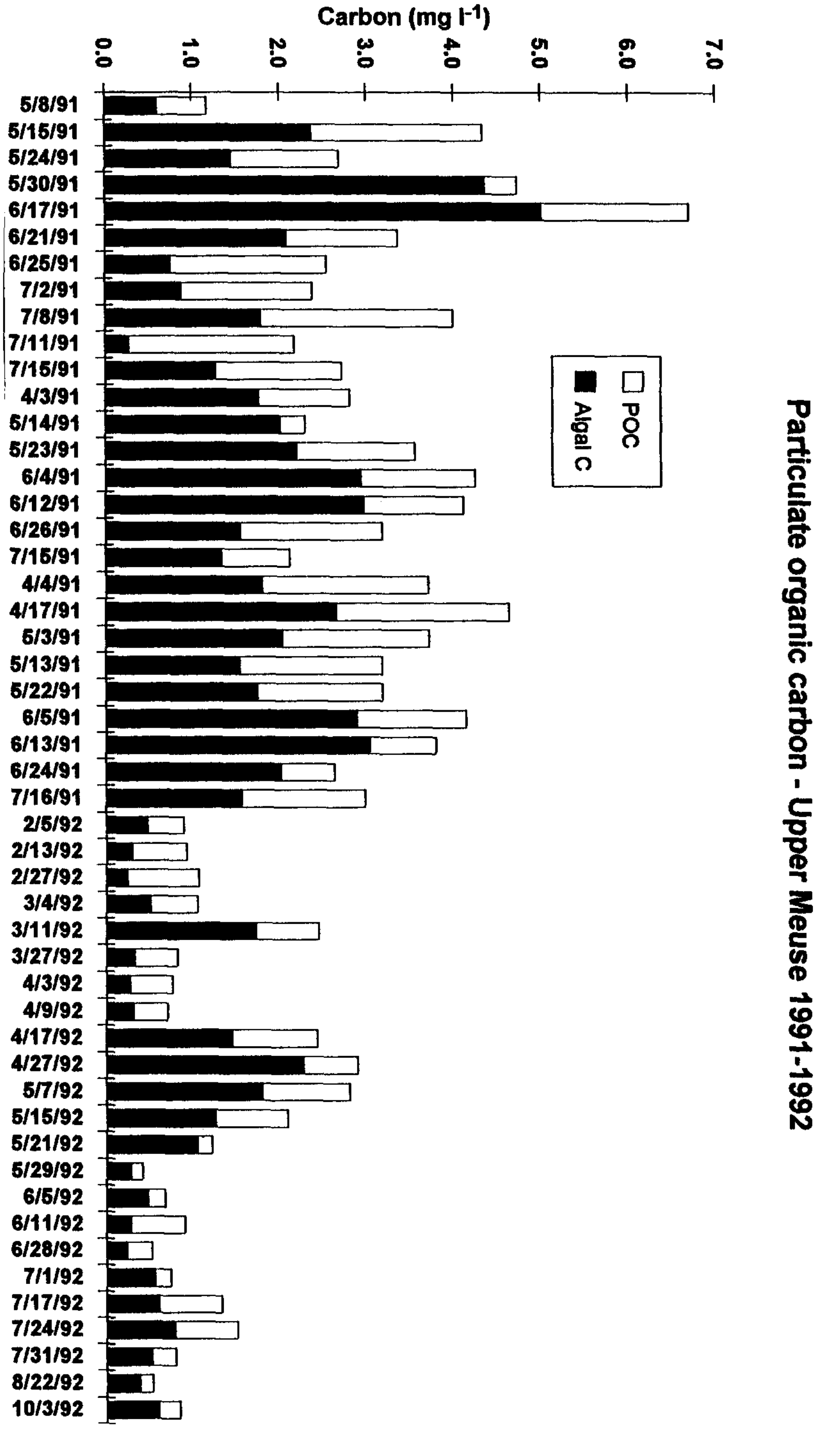


Fig. 4. Particulate organic carbon in the upper Belgian Meuse (reach 1 in the text), measured at one site at each sampling date, during the growing seasons 1991 and 1992; POC: particulate organic carbon; algal carbon was calculated from chlorophyll *a* concentration, using a C:chl*a* ratio = 37.

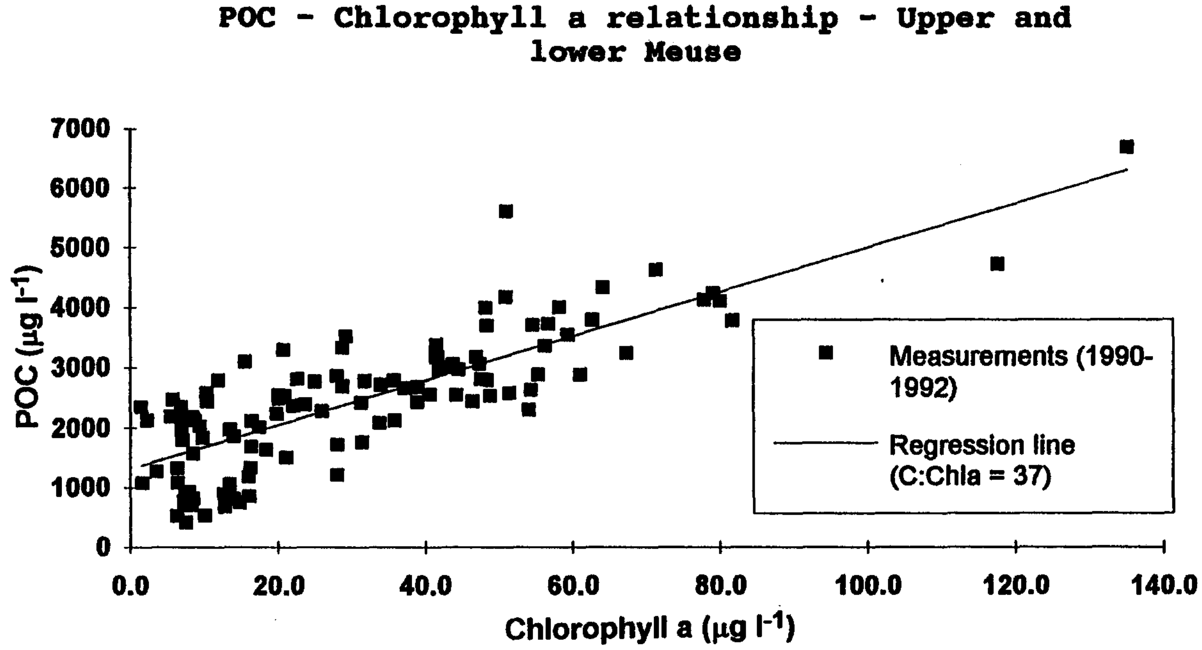


Fig. 5 a. Plot of POC (particulate organic carbon) *vs* chlorophyll *a* concentrations in the River Meuse, from measurements during the growing seasons of the period 1990–1992; A: all data included; B: data from the upper Belgian Meuse (reach 1 in the text) only.

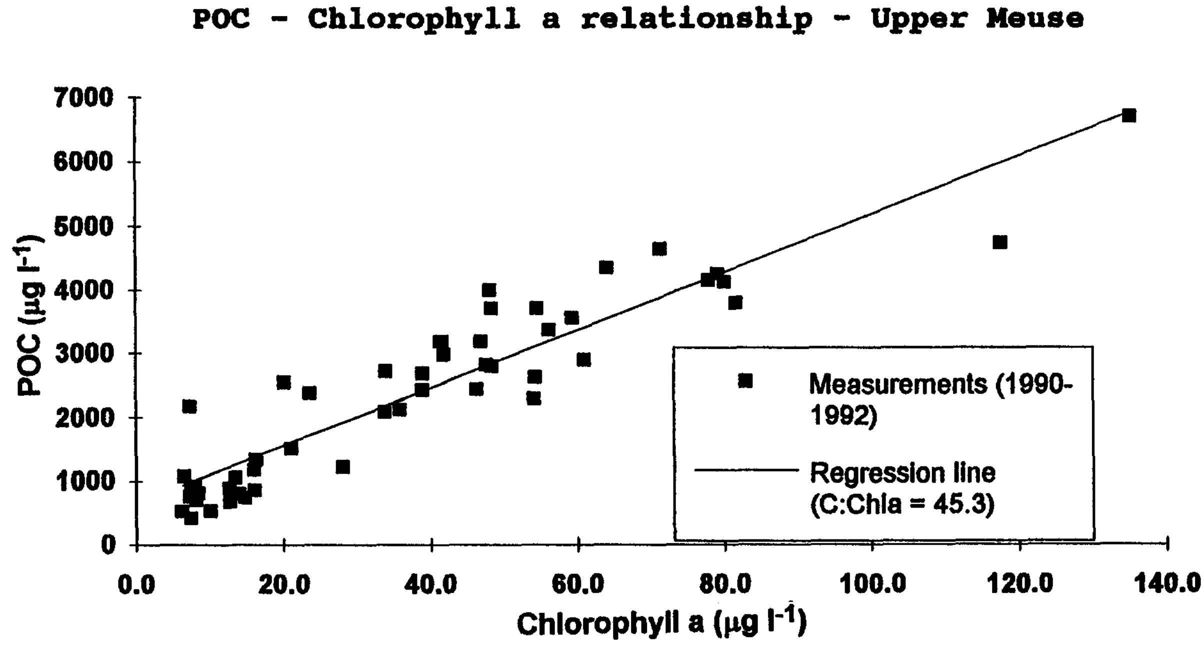


Fig. 5 b.

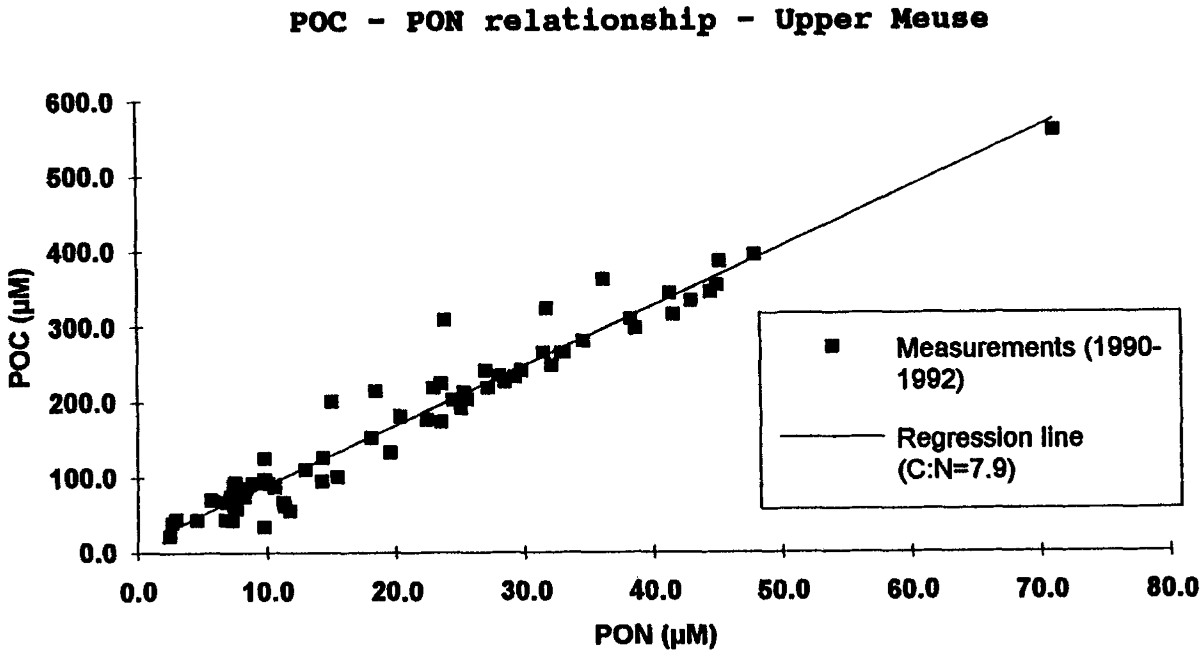


Fig. 6 a. Plot of POC (particulate organic carbon) *vs* PON (particulate organic nitrogen, A) and *vs* PP (particulate phosphorus. B) concentrations in the River Meuse, from measurements during the growing seasons of the period 1990–1992; data from the upper Belgian Meuse (reach 1 in the text).

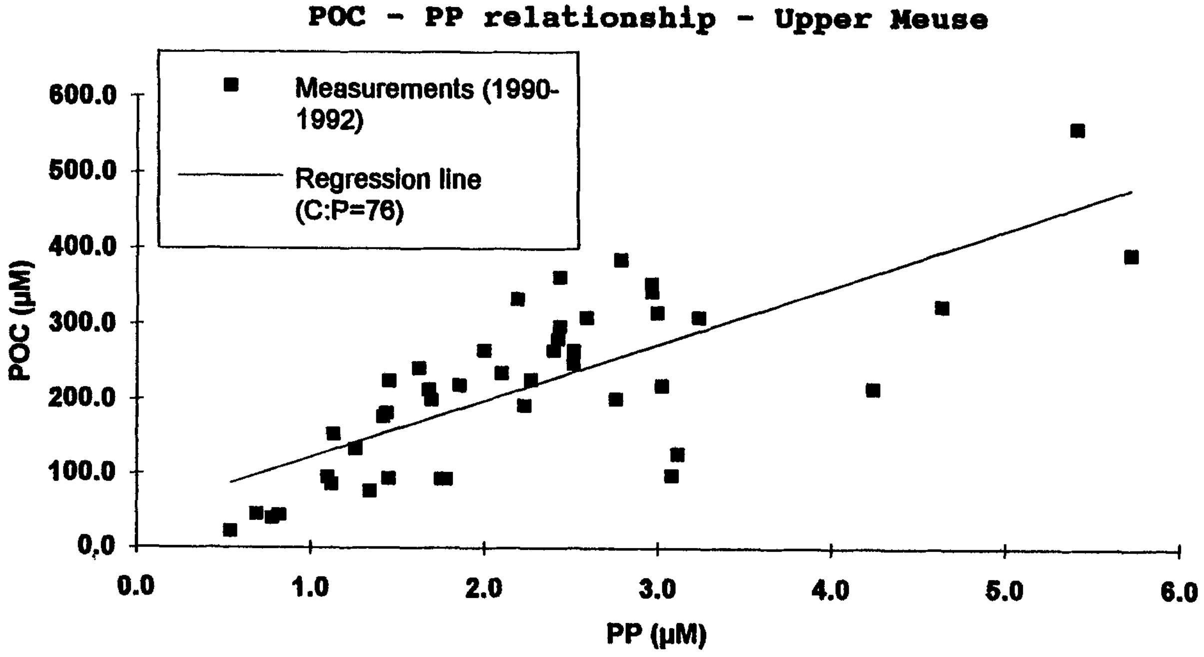


Fig. 6 b.

Table 1. Summary of the data of temperature, phytoplankton biomass, photosynthetic parameters and light, obtained from measurements in the River Meuse during the period 1988-1992 (n = 66). In each column, in descending order, mean, standard deviation, minimum, maximum; k is the vertical attenuation coefficient of light and PAR is the mean daily photosynthetically active radiation.

Temperature °C	Chl*a* mg m^{-3}	Ik $\mu E\ m^{-2} s^{-1}$	P_{opt} mg C (mg chl*a*)$^{-1}$ h^{-1}	α mg C (mg chl*a*)$^{-1}$ $E^{-1}\ m^{-2}$	k m^{-1}	PAR $\mu E\ m^{-2} s^{-1}$
16.7	53.7	97.8	4.1	15.4	2.35	391
4.2	35.2	52.3	1.4	9.4	0.62	245
8.0	7.2	26.0	1.7	2.7	1.46	77
24.7	153.5	245	8.1	49.6	3.89	1175

where r_{chla} is the respiration rate of the algae and P_{opt} their photosynthetic capacity, both expressed as mg C (mg chl*a*)$^{-1}$ h^{-1}.

The photosynthesis and respiration data also allowed us to calculate the net production and potential maximal growth rate of the algae, taking into account full mixing of the water column and assuming that short ^{14}C incubations measured gross photosynthesis. The results are given in Table 2, for reaches 1 and 3, which differ by their mean depth (3.5 m *vs* 6 m). They show the effect of increased depth on the daily net production (NP), equivalent to potential growth rate, of the algae. In the shallowest reach, the phytoplankton experienced NP>0.1 d^{-1} five times over the 11 series, while in the deepest reach, they reached this level only once, despite the lower respiration rate of the algal community. There was indeed a difference in the respiration activity between the two sites: the r_{chla}:P_{opt} ratios were significantly different at the 0.95 probability level.

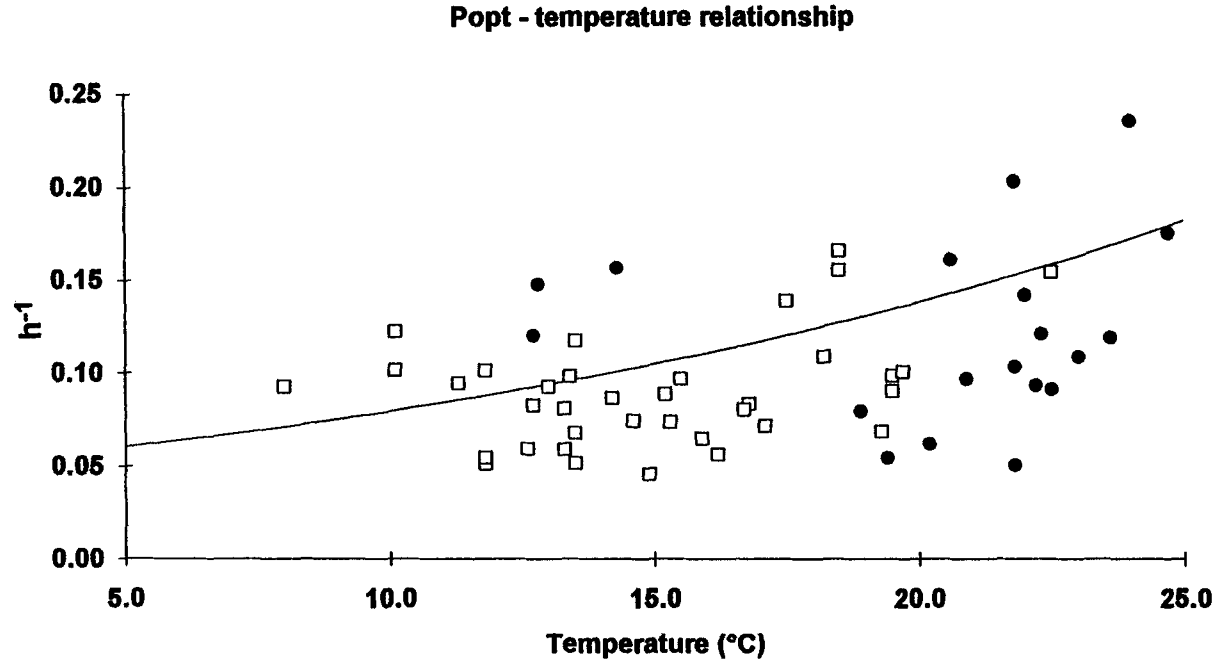
Development of the phytoplankton along the river and ecosystem P:R ratio of the Belgian Meuse

Figure 10 presents the simulated phytoplankton biomass along the French and Belgian course of the river. In the simulated conditions, which are typical of a summer situation, *i.e.* high irradiance and low discharge, the phytoplankton algae begin to develop a significant biomass from about 200 km from the source. Then, they achieve their full growth, peaking at 5 g C m^{-3} (135 μg chl*a* l^{-1}) within less than 200 km. Downstream, the potamoplankton decline to about half of their maximum biomass, by the combined action of (i) dilution by lateral water inputs (*i.e.* tributaries) and (ii) reduced growth due to increasing depth. Whether or not such a profile might characterise other large rivers is discussed below, yet it can be mentioned that a similar longitudinal pattern of growth and decline of the potamoplankton has been already reported by Welch (1952, p. 429–430) for several rivers in the world but the loss processes involved were not identified.

The oxygen budget of the River Meuse in the uppermost Belgian section has been calculated for the years 1983–1984 (Billen *et al.*,, 1985; Descy *et al.*, 1987) and is summarised in Table 3. According to these calculations, the P:R ratio of the river in its upper Belgian reach characterised a fully autotrophic status (P:R = 1.2 on a yearly basis, 1.5 over the growing season). This also implies that a large fraction of the primary production is exported downstream, which accounts for a major part of the algal biomass found in the lower deep reaches of the river.

Discussion and conclusions

The data collected in the Belgian Meuse on the C:N:P concentrations in the particulate and dissolved phase confirms the observations on other large eutrophied rivers, reviewed by Admiraal *et al.* (1992). In particular, the contribution of the potamoplankton to particulate carbon and nitrogen was very high, at least in the upstream reach of the R. Meuse. The average value of 58% of algal carbon in the total POC (range 12.5–92, over the growing season) can be compared to the 15–65% for the lower Rhine (The Netherlands), the estimated 55% for the R. St. Laurent (Canada) and for the R. Ebro (Spain), the 50% for the R. Loire (France). As for the R. Rhine, such data can be used for assessing the transformations of elements along a river and the inputs to the sea, but they also demonstrate



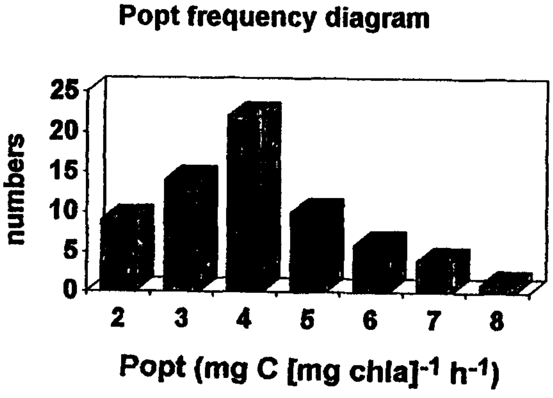


Fig. 7. Photosynthetic parameters of the River Meuse phytoplankton. A: plot of P_{opt}, the light-saturated rate of inorganic carbon uptake, *vs* temperature, for the data of the upper Belgian Meuse (squares) and of the lower Belgian Meuse (black dots); the curve is the relationship found for the years 1983–1984, used in the Meuse ecological model (Descy *et al.*, 1987); the frequency plot of the P_{opt} values is also presented.

that the theoretical view of the heterotrophic large river according to River Continuum concept should be somewhat amended. Clearly, many large lowland rivers produce an amount of FPOM which exceeds the input from upstream, as far as hydrodynamics and morphometry allow a planktonic net primary production to take place. So, these rivers are actually autotrophic systems in a part of their course, and only become heterotrophic (*i.e.* receive their FPOM mostly from upstream) where net primary production is offset by increased depth and turbidity. So, there is indeed a continuous variation from the autotrophic, non light-limited midreaches to the heterotrophic, strongly light-limited downstream reaches, the transition between these two extremes being the lowland river supporting an important phytoplankton production. Such a transi-

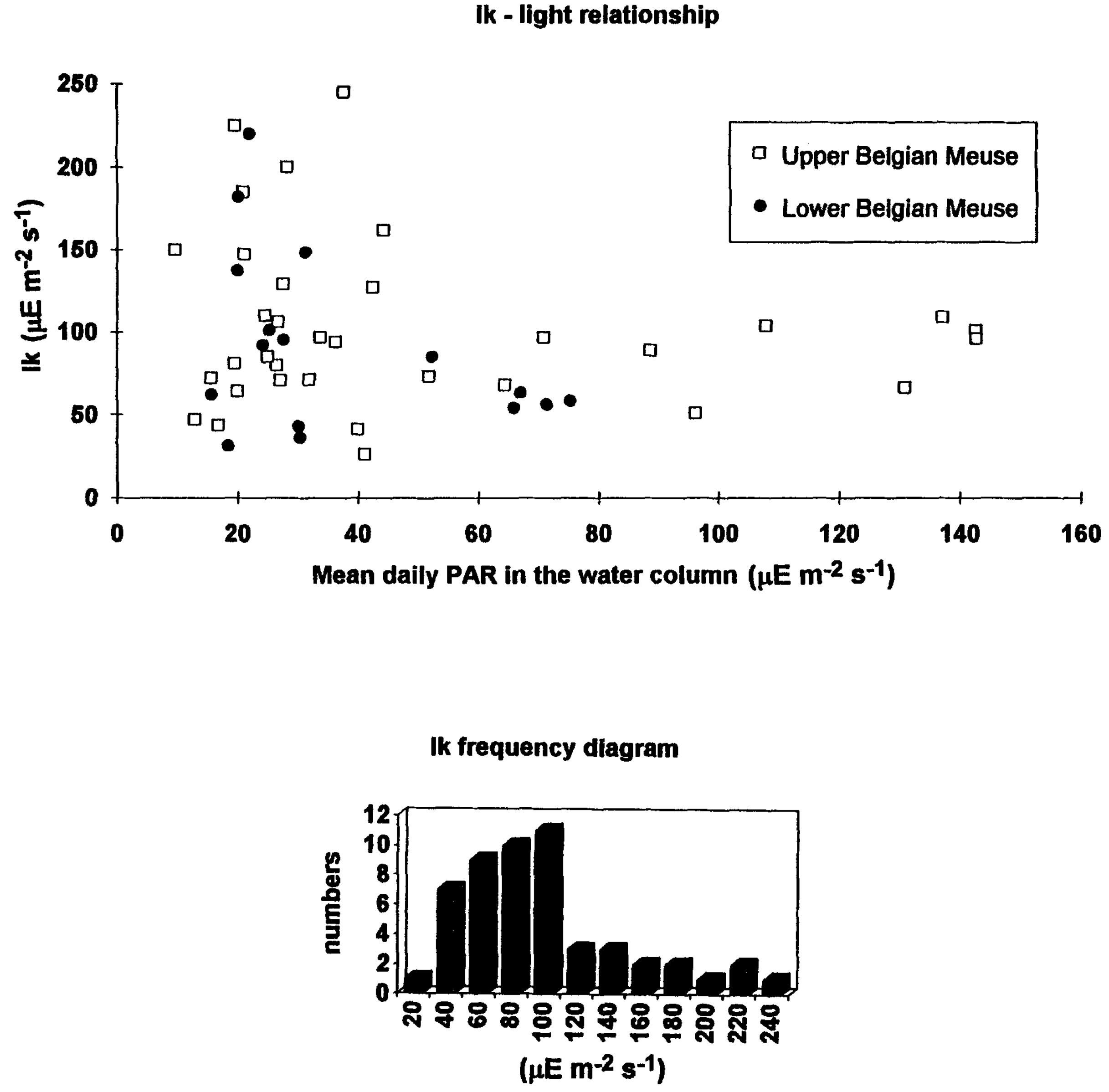


Fig. 8. Photosynthetic parameters of the River Meuse phytoplankton. A: plot of Ik, the irradiance at the onset of light saturation, *vs* mean daily light in the water column, for the data of the upper Belgian Meuse (squares) and of the lower Belgian Meuse (black dots); the frequency plot of the Ik values is also presented.

tion from benthic primary production (in macrophytes-dominated rivers) to planktonic primary production (phytoplankton-dominated rivers) is consistent with the view of a river continuum, yet it depends less on the *stream order* and related attributes than on *local properties* of the channel (turbidity, depth, slope, pattern of discharge and flow velocity).

As mentioned above, an autotrophic status has been well demonstrated for the upper Belgian Meuse where P:R>1, thanks to a gross primary production (GP) which is in the range of 500–600 g C m^{-2} y^{-1}. Such a high productivity is encountered in other large rivers (see e.g. Descy *et al.*, 1988, for European rivers), but contrasts with the much lower values found in estuaries, where GP is lower than 100 g C m^{-2} y^{-1} (Cole

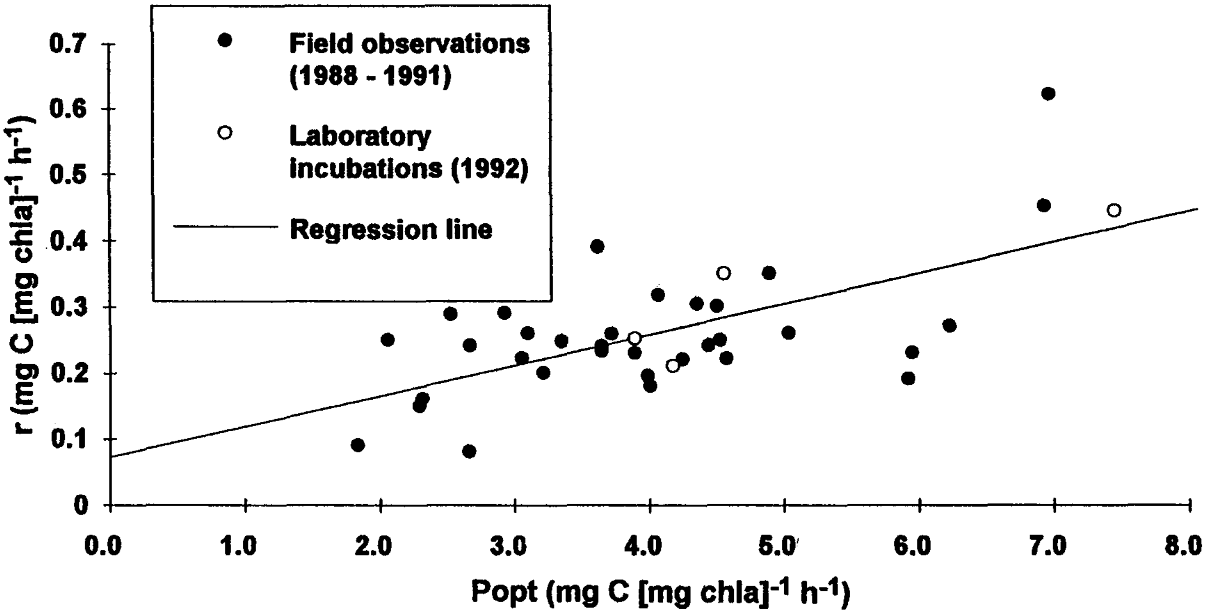


Fig. 9. Plot of the respiration rate (r) *vs* the light-saturated rate of photosynthesis (P_{opt}) of the phytoplankton of the River Meuse; measurements were made during the growing periods of the years 1988, 1991 and 1992.

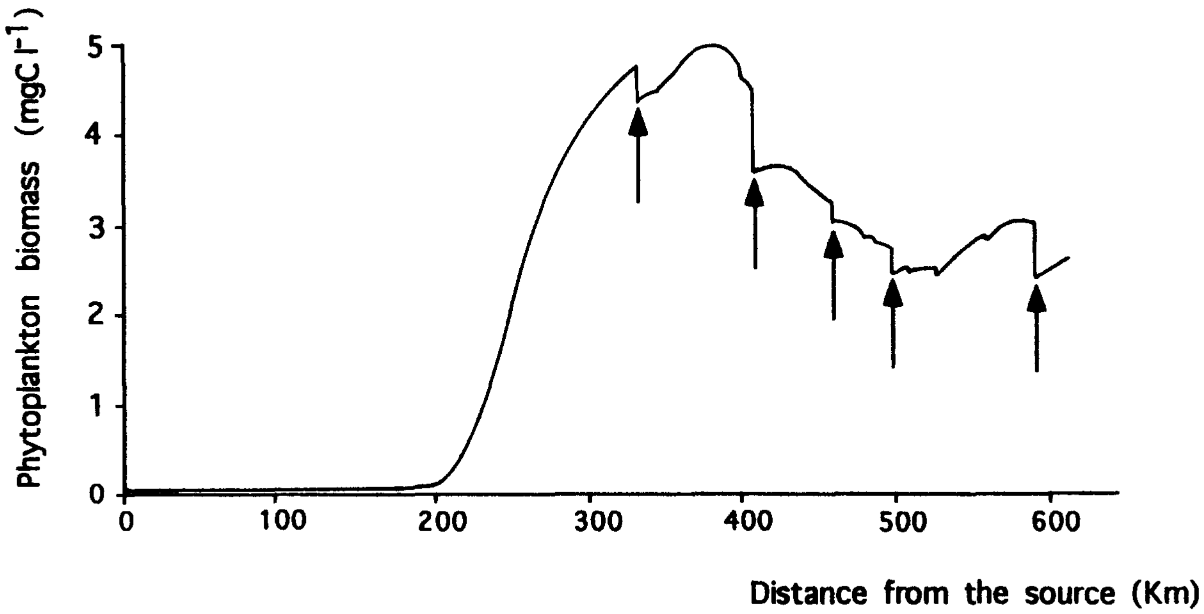


Fig. 10. Simulation of the phytoplankton biomass (g C m^{-3}) from the source of the R. Meuse in France to the Belgian-Dutch border, according to the PEGASE model (Centre Environnement, University of Liège, Belgium); the external variables correspond to a typical summer situation, *i.e.* water temperature 20 °C, daily irradiance 380 W m^{-2}, discharge 50 m^3 s^{-1} at Tihange, km 580; the arrows indicate the outlet of main tributaries.

Table 2. Measurements and calculations of biomass, respiratory activity and daily production of the phytoplankton of the River Meuse, at two sites of the Belgian course; r_{chla} was determined by ETS measurements and Ra is daily respiration of the algae, assuming constant respiration over 24 h; growth rate is equivalent to the net production rate, regardless of the loss processes.

Reach 1 (mean depth = 3.5 m)	Chl *a* $\mu g\ l^{-1}$	*r* mg C (mg Chl*a*)$^{-1}$h^{-1}	Ra g C m^{-2} d^{-1}	Resp. rate d^{-1}	GP g C m^{-2} d^{-1}	GP rate d^{-1}	growth rate d^{-1}
13-Sep-90	64.1	0.390	2.099	0.27	1.991	0.25	−0.01
19-Oct-90	135.2	0.080	0.909	0.05	1.354	0.08	0.03
3-Apr-91	47.6	0.221	0.884	0.15	2.442	0.42	0.27
16-Apr-91	70.1	0.160	0.942	0.11	1.196	0.14	0.03
30-Apr-91	66.9	0.241	1.354	0.17	0.893	0.11	−0.06
14-May-91	54.1	0.250	1.136	0.17	1.456	0.22	0.05
23-May-91	59.3	0.290	1.445	0.20	2.251	0.31	0.11
4-Jun-91	79.1	0.350	2.326	0.24	3.851	0.40	0.16
12-Jun-91	80.1	0.270	1.817	0.19	3.457	0.35	0.17
26-Jun-91	41.6	0.620	2.167	0.43	3.594	0.710	0.28
15-Jul-91	35.8	0.450	1.353	0.31	0.978	0.22	−0.09
Reach 2							
(mean depth = 6 m)							
14-Sep-90	39.0	0.230	1.292	0.16	1.758	0.21	0.06
10-Oct-90	117.7	0.090	1.525	0.06	0.743	0.03	−0.03
4-Apr-91	48.4	0.300	2.091	0.21	2.41	0.24	0.03
17-Apr-91	71.4	0.220	2.262	0.15	1.201	0.08	−0.07
3-May-91	54.6	0.150	1.179	0.10	0.605	0.05	−0.05
13-May-91	41.4	0.230	1.371	0.16	2.09	0.24	0.08
22-May-91	46.9	0.260	1.756	0.18	3.472	0.35	0.17
5-Jun-91	77.9	0.240	2.692	0.16	3.844	0.23	0.07
13-Jun-91	81.7	0.200	2.353	0.14	1.732	0.10	−0.04
24-Jun-91	54.3	0.180	1.407	0.12	0.969	0.08	−0.04
16-Jul-91	41.9	0.190	1.146	0.13	1.298	0.15	0.02

et al., 1991; Lara-Lara *et al.*, 1992). To some extent, river regulation and management, as well as nutrient inputs, have favoured potamoplankton development. However, potamoplankton is not restricted to regulated rivers, as shown by some examples, e.g. in French (e.g. River Loire, see Meybeck *et al.*, 1988) and British rivers (e.g. River Severn, Reynolds & Glaister, 1993) but changes of morphometry and regulation of flow certainly have profound influences on the phytoplankton dynamics and the metabolism of the river system. Accordingly, Vannote *et al.* (1980) predicted that 'unnatural disturbances' (including impoundment and nutrient enrichment) could be regarded as 'reset mechanisms which cause the continuum response to be shifted (either) toward the headwaters or seaward'.

The analysis of the photosynthetic and respiratory response of the whole algal community leads to the following conclusions:

(i) the current river models which treat the phytoplankton as an homogenous community need improvement, in order to take into account the diverse ecophysiological responses and requirements of some important components of the community; for instance, more attention should be devoted to cell-specific rates of photosynthesis, growth and losses;

(ii) the potamoplankton of the R. Meuse does not seem to show a particular low light acclimation, as far as the parameters of photosynthesis are considered; however, distinct values of the C:chl*a* ratio were

Table 3. Oxygen budget in the River Meuse in the upper Belgian reach (around km 500), for the years 1983-1984 (from Billen *et al.*, 1985). Units are kg O_2 m^{-1} y^{-1}

Gross primary production	206.6
Reaeration	−37.7
Respiration of phytoplankton	−30.9
Respiration of zooplankton	−44.6
Consumption by bacterioplankton	−72.0
Benthic consumption	−24.0
Total consumptions	−171.5
P:R	1.2

obtained in the two studied reaches of the Meuse, which may indicate an increase of the cell-specific chlorophyll content related to the deepening channel as going downstream; similarly, a significant reduction of the algal respiration rate with increasing depth was found, which was likely the result of a stronger light limitation; this interpretation is supported by the coupling between photosynthesis and respiration, as respiration rates adjust to the rate of substrate supply by photosynthetic carbon fixation (Falkowski & LaRoche, 1991); accordingly, Daneri *et al.* (1992) found a control of respiration by growth irradiance in marine phytoplankton, and a corresponding decrease of r_{chla}:P_{opt} with decreasing growth irradiance; moreover, the mechanistic explanation of reduced respiration at low light may be found in Reynolds *et al.* (1985) who interpret enhanced respiratory losses as a regulatory process depending on the size of the fixed carbon pool which is not used for growth: for instance, phytoplankton going down the River Meuse and coming to our 'reach 3' (see Table 2) could not obtain much excess carbon from their photosynthesis!

These observations, coupled to mathematical models simulations (see Fig. 10) help to understand the development of potamoplankton in a river system:

- so far as no nutrient limitation occurs, growth takes place in the upstream, shallow part of the river, *as soon as growth rate exceeds dilution rate* (see Descy *et al.*, 1987 and Billen *et al.*, this volume);
- the biomass produced is exported toward the lower deepening reaches; growth of this biomass is maintained until increasing depth, together with decreasing light availability, prevents positive net production; the maximal attainable biomass level in given river is strongly dependent of turbidity and depth, which explains differences of maximal chlorophyll *a* concentrations observed among rivers of similar carrying capacity (Descy *et al.*, 1988);
- further downstream, the biomass declines, as a result of dilution by tributaries and of several loss processes: grazing, mortality, sedimentation.

Dead zones or better 'storage zones' in river channels (Reynolds, 1988; Reynolds *et al.*, 1991; Reynolds & Glaister, 1993) can play a role in these dynamics, as far as they act as 'nurseries' and may be sources of phytoplankton which will develop in productive reaches. As a matter of fact, the above 'model' is based on an experience of a regulated river, that has a sufficient 'retentivity' through the flow regulation. Moreover, the above reasoning does not account for the inoculum of algal populations, which, as so nicely demonstrated by Reynolds & Glaister (1993), originates within the river. Similarly, new inocula or renewed development of some populations may occur in shallow arms located in the main river channel, which can explain increases of biomass and diversity of potamoplankton in downstream sections of large rivers (Stoyneva, this volume).

Then, coming back to the discussion by Cole *et al.* (1991) about how to explain the presence of a large phytoplankton biomass in the lower R. Hudson, we would retain primarily the 'importation hypothesis', *i.e.* an origin of the biomass from upstream productive reaches. The 'production hypothesis' does not receive much support, as there is little experimental evidence for photosynthetic acclimation by improvement of the photosynthetic efficiency of algal cells, at least when rates are expressed per unit chlorophyll *a*. Also, the possibility of enhanced photosynthesis in changing light (Loehr, 1987; Imboden, 1992) cannot presently be ruled out, but it should be investigated further, as it has not yet received convincing experimental support, at least in turbid systems.

The 'removal hypothesis', based on the reduction of losses by grazing and sedimentation, should be further examined, particularly for zooplankton grazing. As stated by Reynolds *et al.* (1990) and Reynolds (1992), sedimentation is certainly reduced in well-mixed and sufficiently deep water columns. Reduction of settling losses as depth increases in rivers may account for maintaining in suspension algae susceptible to this process. Concerning grazing by zooplankton or benthic animals, the common assumption is that the process is negligible in rivers, as the development of the most efficient grazers, the large crustaceans, is limited by the short residence times. Nevertheless, evidence arises, both from observations and models, that grazing may be a significant loss factor during the low flow periods. For instance, as shown by other contributors (Billen *et al.*, this volume), most models fail to represent rapid biomass declines often encountered in summer conditions: an explanation might be that the effect of biotic interactions on the phytoplankton dynamics in large lowland rivers have been so far largely overlooked. As a matter of fact, some observations (Descy, 1993; Gosselain *et al.*, this volume) seem to show that in rather stable physical conditions, which are usually occurring in the summer period in most temperate large rivers, biotic interactions may exert some influence on the phytoplankton biomass and composition. Information, based on *in situ* measurements, on such a 'biotic control' of potamoplankton is still relatively scarce, but experimental evidence may be provided by data from ongoing studies.

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