1.6

Macrophytes and Algae in Running Waters

Georg Janauer and **Martin Dokulil**

1.6.1 MACROPHYTES

1.6.1.1 Ecological Relevance of Macrophytes in Rivers

Most authors consider "macrophytes" as genuinely aquatic (hydrophytes) and amphibious plants (amphiphytes) and that in most cases species determination

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needs no microscope (Westlake, 1974; Wetzel, 2001). This covers large algae (e.g. Charophytes), bryophytes and vascular plants. In running water environments, macrophytes contribute to the oxygen budget and to the autochthonous carbon pool. Roots, stems and leaves of macrophytes provide structural elements in an otherwise unstructured water column, thus enhancing spatial diversity in the aquatic ecosystem. Microbes, invertebrates and vertebrates (Jeppesen *et al.*, 1998; Kornijow and Kairesalo, 1994) live on the surface of, and in spaces between, organs of aquatic plants. Fish prey, and fish, use aquatic plant stands as a nursery, feeding ground, or seek shelter in dense vegetation (Lillie and Budd, 1992; Ombredane *et al.*, 1995). The spatial functioning of macrophytes is influenced by the growth form of each species. The most simple scheme follows Sculthorpe (1967): emergents (helophytes), floating-leaved, free-floating (pleustophytes (Luther, 1949)) and submerged species. Submerged plants with small leaves and growing in dense stands, provide ample structure, whereas floating-leaved plants and pleustophytes provide little submerged surface, but support animals such as amphibians and water birds. As a consequence, aquatic macrophytes are one of the essential ecological components wherever they occur in running waters.

1.6.1.2 The role of river reach, catchment geology and river morphology on macrophyte development

Springs are the sources of running waters. Wherever water collects in pools or small lakes before it starts its run down the river, algae, bryophytes and even vascular plants grow. The limited nutrient load in spring ecosystems usually prevents the development of large plant mass. Few species are reported to grow in springs, e.g. macroalgae like *Nitella* species, oligotrophic *Chara* species, bryophytes like *Cratoneuron commutatum*, *Scapania undulata* and *Drepanocladus exannulatus*, and vascular plants like *Cardamine amara* or *Nasturtium officinale*.

In the upper reach, where rivers are still small and often close to their natural ecological status, two main parameters control the growth of macrophytes. The speed of water flow is often too fast and/or run-off too irregular to allow for the development of vascular plants in mountain rivers, but bryophytes (e.g. *Scapania undulata*, *Marsupella emarginata* (Lottausch *et al.*, 1980)) inhabit the hard and stable substrates found there. In the upper reach of lowland rivers, where bushes and trees grow next to the river, shading can prevent any macrophyte growth. Wherever the gradient decreases, or more light reaches the river, stands of vascular plants will develop.

In the middle and lower reaches, rivers create a system of secondary channels, meanders and oxbows. In situations where water flow is slow enough (for most vascular species < 0.8 m s^{-1}) and the width of the water body prevents heavy shading, macrophytes will become abundant. Downstream changes usually reflect an increase in species preferring higher trophic states (Kohler *et al.*, 1971; Kohler and Zeltner 1974; Holmes and Whitton, 1975, 1977a; Haslam, 1978, 1987; Janauer, 1981). Successive surveys in the same river (e.g. Fritz *et al.*, 1994; Würzbach *et al.*, 1977;

Kohler *et al.*, 2000; Veit and Kohler, 2003) clearly showed recuperation effects following, e.g. enhanced sewage treatment and phosphorus stripping in river catchments, and successful regrowth of macrophytes after severe floods (Henry *et al.*, 1994; Janauer and Wychera, 2000).

Water flow velocity is a dominant environmental parameter. In the river corridor of the Danube (original data, MIDCC database, 2003), *Potamogeton filiformis* and *Potamogeton nodosus* were associated with still water. *Myriophyllum spicatum*, *Potamogeton pusillus* and *Potamogeton natans* were indicative of water flow less than 30 cm s^{-1}. Intermediate flow (30–65cm s^{-1}) was characterized by the occurrence of *Potamogeton pectinatus*. For higher flow velocities, no statistically significant occurrence of vascular species was detected, but the absence of *Ceratophyllum demersum* and *Potamogeton perfoliatus* was significant ($p = 0.05$). In smaller rivers, *Ranunculus* species are often dominant in fast-flowing water.

In the centre of the main stem of large rivers, high flow velocities and moving sediment material prevent macrophyte growth. Near to the banks, the flow is lower, but plants rarely grow in water deeper than 1.5 m. This phenomenon is caused by shading due to either inorganic suspended material or phytoplankton growth (Westlake, 1975). However, permanent stands of plants even without roots, like *Ceratophyllum demersum*, were found in the main stem of the Danube in sheltered habitats, e.g. behind groynes (Janauer and Stetak, 2003).

Catchment geology is a prime factor in determining the occurrence of macrophyte species (Zander *et al.*, 1992; Grasmück *et al.*, 1993; Thiébaut *et al.*, 1995). Bryophytes like *Hygrohypnum ochraceum*, *Nardia compressa* and *Marsupella emarginata*, amphiphytic *Juncus* species, and hydrophytic *Myriophyllum alterniflorum*, *Potamogeton polygonifolius*, and *Ranunculus peltatus* are indicators of silicate rock areas with acidic water (Kohler and Tremp, 1996). In many cases, acidic rivers are also low in nutrient content and the occurrence of a specific species may indicate a combination of environmental factors. Bogs and mires tint streams and rivers with humic substances. The growth of submerged macrophytes is then suppressed, but species with floating leaves like water lilies, or spreading out from the bank like *Menyanthes trifoliata*, dominate the river. Typical species for rivers in regions dominated by calcareous rock are, e.g. Charophytes, *Fontinalis antipyretica*, *Cinclidotus fontinaloides*, *Callitriche obtusangula* and *Potamogeton coloratus*.

Substrate is another important factor. Rocks and hard, immobile substrates (rip-rap) are most closely associated with bryophytes, no matter what the elevation above sea level is for a certain location. Typical species on gravel are *Potamogeton perfoliatus* and *P. crispus*, but *Najas marina* is never found there. Pure sand forms the basis of many *Cyperus* stands, but is never found below *P. lucens* and *P. pectinatus*. The latter species is predominantly associated with fine inorganic sediments, together with *Phragmites australis* and *Typha angustifolia* (original data, MIDCC project). It is clear that all classification of sediment type based on field surveys is only accurate to the extent that the surveyor's eye determines the essential fraction. In many cases, small volumes between large stones or gravel contain fine sediment in which the plants actually root. Useful collections of physical and chemical habitat factors are the compilations by Haslam (1978, 1987) and the concise review by Bayerisches Landesamt (1998).

1.6.1.3 Regional distribution and abundance

The remarkable study of running water vegetation in EC states by Haslam (1987) is still a valuable source of basic information. Three main reasons for diminished aquatic plant growth were listed: highlands, where the water flow has high force, pollution and river straightening in regions with low or medium elevation above sea level throughout Europe. *Ceratophyllum demersum*, *Elodea canadensis*, *Myriophyllum spicatum*, *Nuphar lutea* and *Sparganium emersum* were found in more eutrophic habitats, and *Potamogeton crispus* in semi-eutrophic reaches. *Potamogeton pectinatus* was concentrated in polluted areas. *Callitriche hamulata* and *Myriophyllum alterniflorum* were frequent in oligotrophic and dystrophic habitats. This general picture is still valid for most regions in Europa, but as only Western European countries were included different patterns of dominance and habitat preference should be expected in other regions.

The Atlantic zone can be characterized by examples from the United Kingdom and North-Western France. In the River Tweed system (UK), the upper reach was dominated by *Hygrohypnum ochraceum*, *Scapania undulata*, *Myriophyllum alterniflorum* and *Ranunculus aquatilis* agg. In the lower reach, *Potamogeton lucens*, *P. perfoliatus*, *P. pusillus*, *P. pectinatus*, *Ranunculus fluitans* and *Zannichellia palustris* were found. Following the course of the Tweed and its tributary, Teviot, the dominance of bryophytes decreased, and that of vascular species increased with distance from the source. However, bryophytes like *Eurhynchium riparioides* or *Hygroamblystegium fluviatile*, as well as vascular plants like *Elodea canadensis*, *Potamogeton crispus* or *Ranunculus penicillatus*, occurred throughout the whole length of the river (Holmes and Whitton, 1975). The importance of bryophytes within the macrophyte assemblage is also mirrored by other rivers in this region (Holmes and Whitton, 1977b, 1977c; Haslam, 1978).

In the Bretagne (France), Haury (1996) recorded more vascular species, e.g. *Ranunculus hederaceus*, than bryophytes in the upstream parts of Kernec Brook. However, several bryophytes (e.g. *Leptodictyum riparium*) were found next to *Ranunculus pseudofluitans* in the lower reach. Studies on the relationship of species to environmental factors show the importance of bryophytes as part of macrophyte communities in Western France (Haury *et al.*, 1995; Ombredane *et al.*, 1995, Haury, 1996).

In Sweden, the rivers Kävlinge and Björka were studied by Kohler *et al.* (2000). The slightly eutrophic Kävlinge River was dominated by *Potamogeton perfoliatus* in its upper reach, while further down its course *Potamogeton pectinatus*, several *Potamogeton* hybrids and *Ceratophyllum demersum* reached high abundance, and near the mouth *Myriophyllum spicatum* and *Zostera marina* dominated the species pattern. *Potamogeton lucens*, *Nymphaea alba* and *Sagittaria sagittifolia* were among the most widespread species. As a characteristic of many northern European rivers, 46 % out of 65 aquatic species were of amphiphytic character. In the eutrophic Björka River, amphiphytes dominated (56 % of all species) and were most abundant throughout the whole river. With little variation, Lemnids, *Elodea canadensis* and *Nuphar lutea* were dominant among the hydrophytes. Very few truly aquatic bryophytes were found. In the humic River Bräkne (Kohler *et al.*, 1996) 57 % of all species were amphiphytes, and the floating leaved species *Nuphar lutea* and *Nymphaea alba* dominated the submerged *Myriophyllum alterniflorum*. Similar to the macrophyte assemblages in England and Western France, bryophyte species were as numerous as the vascular macrophytes, and *Fontinalis antipyretica* showed medium to high abundance throughout the whole river course.

The head waters of the Portuguese River Divor were characterized by the vascular aquatic species *Callitriche stagnalis*, *Zannichellia palustris* and *Potamogeton pectinatus*. In the middle course, *Utricularia australis*, *Myriophyllum spicatum* and *Ceratophyllum demersum* occurred, but fringing herbs and helophytes became increasingly dominant. In the lower reach, *Myriophyllum aquaticum* prevailed between emergent species. Bryophytes represented only 3 % of the listed species (Ferreira, 1994). Quite similar assemblages of macrophytes were found in other Iberian rivers and in drainage channels (Ferreira *et al.*, 1998a,b).

The Danube River crosses Europe from West to East over a course of over 2800 km and its catchment is highly complex. The Alps, the Carpathians and the Balkan Mountains dominate much of its run-off regime in the upper and middle part where constrained reaches and wide fluvial plains alternate, until the river reaches the lowlands of Romania, Moldavia and the Ukraine. Hydropower regimes dominate most of the river in Germany and Austria. In the head water streams Breg and Brigach, which form the Danube, several bryophytes and *Callitriche hamulata* dominate the upper parts. In the lower reach of the Brigach, *Fontinalis antipyretica* is the only bryophyte, but vascular plants occur with high abundance. In the Breg, bryophytes, as well as vascular species, are less abundant. In the Danube, bryophytes are confined to the upper reach (Germany, Austria). In the middle and lower reaches, vascular species reach high abundance in sheltered habitats, even in the main channel. Floodplain water bodies and the canals in the Danube delta rival for the maximum in species richness and abundance (Janauer, 2003b).

1.6.1.4 Macrophytes in flood plain water bodies

Fluvial corridors in Europe clearly reflect the human impact since the mid-19th Century: the larger rivers are confined to a regulated main channel and former side channels and meanders are oxbows and relict waters with reduced, or missing, permanent connection with the main stem today. Several studies (Rhone (Bornette and Amoros, 1991; Bornette *et al.*, 1994, 1998), Rhine (Buchwald *et al.*, 1995; Robach *et al.*, 1997, Fritz *et al.*, 1998; Greulich and Tremolières, 2002), Danube (Janauer, 2003a; Sarbu, 2003; Janauer and Stetak, 2003; Otahelova and Valachovic, 2003; Janauer *et al.*, 2003; Rath *et al.*, 2003)) have dealt with macrophytes in floodplain waters. In general, an increase in species richness was detected where the direct influence of the river was lower and where groundwater influence increased. In the Danube floodplain waters, species richness did not always correspond to disturbance frequency in a uniform way, but the total amount of hydrophytic vegetation clearly decreased with enhanced disturbance (Janauer, 2003a). In Hungary, a very pronounced increase in species richness was detected between the main stem of the Danube, floodplain waters, and man-made irrigation and drainage channels, where the most constant hydrological and hydraulic regime prevailed in the last category (Janauer and Stetak, 2003). In a statistical analysis (PCA, DA, sign test, $p = 0.05$) of the Danube and its secondary water bodies, the absence of *Elodea canadensis* from the main channel, of *Potamogeton perfoliatus* from large secondary channels and of *Potamogeton crispus* from small side-arms, and the presence of *Potamogeton pectinatus*, *Myriophyllum spicatum* and *Pharagmites australis* in these respective cases, were characteristic and indicative (Filzmoser and Janauer, original data). Aside from the examples presented here, many studies did not distinguish between the contribution of amphiphytes and helophytes to total species richness. Therefore, the final picture of macrophyte reaction to differences in connectivity is certainly more complex than pointed out so far. One conclusion can be drawn without any reservation: river regulation, urban development and intensive agriculture restricted wetlands, water courses and fluvial corridors to their very limits of spatial extension in almost every river catchment in Europe. The remaining floodplain water bodies are the last and most essential species refuges for aquatic vegetation in modern landscapes.

1.6.1.5 Macrophytes and pollution

Pollution can be defined as man-made impacts on water quality. Annex VIII, Indicative List of the Main Pollutants, of the Water Framework Directive (WFD, 2000), the most recent work dealing with all aspects of pollution, lists organohalogens, organophosphorus and organotin compounds, carcinogenic and mutagenic substances, persistent and bioaccumulating hydrocarbons and organic toxic substances, cyanides, metals and arsenic and their compounds, and biocides and plant protection products, suspended solids, substances causing eutrophication (nitrate, phosphate) and substances influencing the oxygen balance. Eutrophication and sewage impact are the most common threats to water quality. With regard to nitrogen compounds, the ammonium concentration is the more discriminating feature as compared to nitrate. The importance of aquatic macrophytes in supporting natural pollution reduction processes was recognized a long time ago (Liebmann, 1940). General aspects of different types of pollution and some pollution-related indices have been discussed by Haslam, (1987).

Some mosses (*Marsupella emarginata*, *Cratoneuron commutatum*) occur predominantly in oligotrophic water (Lottausch *et al.*, 1980), but Fontinalis antipyretica grows well in eutrophic conditions, too. The same is true for Charophytes: *Chara aspera* indicates predominantly oligotrophic conditions, whereas *Chara vulgaris* is most abundant in eutrophic water (Bayerisches Landesamt, 1998). Vascular plants exhibit a wider range related to plant nutrients, which differs with respect to geographical region, river type and adaptation of a species. *Isoetes* species, *Potamogeton polygonifolius* (acidic water), *Potamogeton coloratus* (carbonate-rich rivers) and *Juncus subnodulosus* indicate nutrient-poor water. On the other end of the scale, *Ceratophyllum demersum*, *Potamogeton crispus*, *Potamogeton pectinatus*, *Sparganium erectum* and *Sagittaria sagittifolia* become most abundant in eutrophic and eu-polytrophic conditions, but are found in oligo-meso- or mesotrophic water as well. The most extreme range is reported for *Zannichellia palustris*, which survives oligotrophic conditions as well as polytrophic water. Clear relations between macrophyte abundance and phosphate and ammonium content in running waters were summarized by Kohler (1978). The negative influence of fish farms on small acidic rivers was extensively studied in Western France (Daniel and Haury, 1995, 1996). Changes in macrophyte composition caused by eutrophication were also studied with multivariate statistical methods, e.g. by Monschau-Dudenhausen (1982) and Filzmoser *et al.* (2003). With regard to geographic regions, macrophytes may react differently to trophic levels. Three ways of assessing the trophic state of water bodies using macrophytes were developed in Europe: the "Mean Trophic Rank" (MTR in the UK, Holmes *et al.*, 1999), the "Trophic Index of Macrophytes" (TIM in Germany, Schneider *et al.*, 2001; Kohler and Schneider, 2003) and the "Indices Biologiques macrophyte en rivrière" (IBMR in France, Haury *et al.*, 2002). All calculations of the indices in a survey unit include the abundance of the species present, and the focus of occurrence of those species with regard to phosphorus concentration in their environment. When applying these indices, their indicative power should be re-estimated as it may deviate from the relation between macrophytes and nutrients found in the geographic region where the indices were developed.

One consequence of eutrophication, as well as of organic pollution, can be increased turbidity, which reduces light intensity in the water. This and the deposition of silt and/or bacteria and algae on the leaves may reduce macrophyte growth to a great extent. Low and intermediate organic pollution *per se* does not seem to influence macrophytes too much, but alpha-saprobic conditions usually limit the growth of mesotrophic species.

The toxicity of detergents (Westlake, 1975; Labus, 1979) was studied in some detail. Special interest focused on bryophytes (Miller *et al.*, 1983; Say and Whitton, 1983; Wehr and Whitton, 1983; Tremp, 1991; Rath, 1995; Samecka-Cymerman and Kempers, 1998; Zhihong *et al.*, 1998) and their application for heavy-metal passive monitoring. In most cases, acidification impact parallels with heavy-metal toxicity and the same bryophyte species function as indicators. Regarding salinity tolerance, Olsen (1950) is still a valid source of information. Several limnic macrophytes like *Potamogeton natans*, *Sagittaria sagittifolia*, *Elodea canadensis*, *Lemna trisulca* and *Nuphar lutea* withstand oligohaline conditions (< 0.3 % salinity) and *Potamogeton pectinatus*, *Najas marina*, *Ranunculus baudotii* and *Zannichellia palustris* prevail under β-mesohaline conditions (Luther, 1951; Gessner, 1959). Most species tolerating high trophic levels survive enhanced salinity levels. Good examples are *Potamogeton pectinatus*, *Myriophyllum spicatum* and *Ceratophyllum demersum* which recently showed progressive growth in shallow lakes with high ionic concentrations, e.g. Lake Balaton (Hungary) and Neusiedler See/Lake Fertö (Austria/Hungary, Dinka *et al.*, 2004; Richter, 2004).

Other man-induced impacts on rivers are changes in flow regime and connectivity caused by river regulation or construction of hydroelectric power plants, and changes in man-induced turbidity. Such changes are readily mirrored in the composition of the aquatic vegetation. Despite their rather wide amplitude of habitat preference, macrophytes react to environmental stress and resulting changes in species composition and abundance are easily observed. For the assessment of ecological conditions in surface waters, e.g. with regard to Water Framework Directive monitoring, aquatic macrophytes are an indispensable tool in modern environmental control and research.

1.6.2 ALGAE

1.6.2.1 Algal vegetation, geology and river morphology

Algae are an essential part of river vegetation. As a polyphyletic group they are intermediate in size and generation time between smaller micro-organisms and higher plants. River algae can belong to any freshwater algal group, with Cyanobacteria (blue-green algae), Bacillariophyceae (diatoms) and Chlorophyceae (green algae) being usually most prominent. Their morphological variability ranges from unicellular, to colonial, to filamentous. Some are motile (Table 1.6.1). For taxonomic and life-cycle details, consult Ettl (1980) or Van den Hoek *et al.* (1995).

River algae grow in a multitude of heterogeneous habitats along the river corridor from springs, through brooks to large rivers. In smaller streams, algae are almost

Table 1.6.1 Morphology in the divisions of benthic algae (adapted from Stevenson, 1996)

	Unicellular[a]		Colonial[a]		Filamentous[a]		
Taxon	Mot	n-m	Mot	n-m	Mot	n-m	Motility by
Cyanobacteria (blue green algae)		•		•	•	•	Sheaths
Rhodophyta (red algae)						•	
Chrysophyta (chrysophytes)	•	•	•	•		•	Flagella pseudopods
Xantophyta (xantophytes)						•	
Phaeophyta (phaeophytes)					•	•	Sheaths
Bacillariophyta (diatoms)	•	•		•		•	Raphe
Chlorophyta (green algae)	•	•	•	•		•	Flagella
Euglenophyta (eugleoids)	•						Flagella
Pyrrophyta (dinoflagellates)	•	•		•			Flagella
Cyryptophyta (cryptomonads)	•						Flagella

[a] Mot, motile; n-m, non-motile.

exclusively attached to a wide variety of substrates as *Periphyton* ('*Aufwuchs*'). Microscopic-sized algae are often macroscopically visible. In oligotrophic waters, they appear as coloured incrustations of less than 1 mm in thickness, while in more nutrient-rich waters, periphyton assemblages form matrices of several centremeters in thickness. These *biofilms* can be differentiated from macroscopical filamentous aggregates often more than a metre long by using the term *benthic algae* which otherwise is used synonymous with periphyton (Stevenson, 1996). On the same substratum type, however, macroalgae are in very different habitats than microalgae, because they extend farther into the water. A common criterion for habitat is the substratum type (refer to Stevenson (1996) for a detailed discussion) which is also important for the various interactions between benthic algae with their substrata, including *endolithic* algae (Burkholder, 1996). Structure and stability/instability of the substrata are crucial factors for benthic algal growth. Both factors depend on the position within the fluvial corridor and the hydrological regime affecting flood disturbance.

In more protected areas, algal aggregates can develop which are not directly attached to substrata, nor are they freely suspended in the water column. This *Metaphyton* comes in many forms and may have many origins. Usually, metaphyton are clouds of filamentous algae, like *Spirogyra, Mougeotia,* or assemblages of filamentous cyanobacteria, but can often originate from other submerged substrata as well when they become detached (Stevenson, 1996).

Larger rivers contain algae in the free-flowing water as river phytoplankton or *Potamoplankton* which prolifically reproduce in rivers, often achieving high biomass (Reynolds, 1988). River phytoplankton is usually dominated by diatoms and a variety of green algae, particularly during summer (Dokulil, 1991, 1996). Other algal groups are suppressed by the current but may become more distinct where currents are reduced. Much of the phytoplankton community, however, may derive from attached forms (*Meroplankton*) or originates from lake surface outflow, and outlets of streams and rivers. Survival is accomplished by a variety of water-retentive mechanisms, most importantly by backwater 'dead zones' (Reynolds and Descy, 1996).

Algal communities in streams and rivers can be seen as *ecotones* mediating between different habitats. Biofilms link the substratum with the overlaying water. River plankton acts as a mega-ecoton connecting the river with the floodplain (Dokulil, 2003a). Through this lateral connectivity, flood-plain waters exchange algal taxa and nutrients with river communities (e.g. Dokulil and Janauer, 1990).

1.6.2.2 Algal vegetation and environmental factors

The ability of river algae to grow and prosper, especially on substrata in streams, is the outcome of complex interactions between hydrology, water quality and biotic factors which, in turn, reflect the topography, slope, land-use and vegetation of catchments, among others. Broad-scale patterns of benthic algae in different geographic areas, and between years, reflect the geology, climate and human activity of their watersheds

(Biggs, 1996). Resources, particularly nutrients and light, are the main factors regulating algal growth in streams. In addition, temperature influences metabolic rates.

In areas of negligible anthropogenic disturbance, nutrient concentrations mainly depend on the geochemical background which, in turn, is related to geology. The main differences arise from carbon availability which is linked to the pH value, and silica concentrations, a potential limiting element which is essential for cell-wall formation, especially in diatoms and Chrysophyceae. Similarly, sulfate and chloride concentrations, which are important parameters for species composition, are dependent in undisturbed streams on the geological underground (Rott *et al.*, 1999).

Light environments of the benthos are highly variable and may range from near zero to full sunlight. In addition, considerable temporal variability is observed from very short 'sun spots' to seasonal or inter-annual long-term changes. Terrestrial streamside vegetation reduces the light intensity, alters the spectral distribution and creates considerable heterogeneity. As light impinges on and penetrates into the water column, both the quantity and the spectral composition are altered. Part of the impinging radiation is reflected. The penetrating part is attenuated exponentially which, in addition, is selective because of various suspended and dissolved components in the water. The importance of light attenuation increases in running waters with stream size because of greater depths and more likely effects from phytoplankton and suspended particles. When light finally reaches the benthic community, it is further reduced by the matrix of the biofilm and associated inorganic particles. Additional effects come from UV irradiation penetrating considerably into clear waters or affecting algae on river banks (Hill, 1996).

Light intensity affects biomass, productivity and taxonomic composition of benthic algal species. When grazing pressure is low, algal biomass and productivity often correlate with the amount of stream-side vegetation. When grazing pressure is high, biomass is not correlated to light. Turbidity from inorganic particles substantially reduces the light available for photosynthesis for both plankton and benthic algae in larger streams and rivers. Differences in light response of the major taxonomic categories of algae have been suggested, although large interspecific variability is observed. Diatoms, cyanobacteria and rodophytes in general, grow better than most of the chlorophytes under low-light conditions. Motile benthic taxa, such as raphe-bearing diatoms, have a distinct advantage over non-motile taxa because they may regulate their light environment through phototaxis. The effects of light quality are much less clear than those from variation in light intensity. Most authors, however, conclude that light quantity is much more important than spectral distribution. Many benthic species are either highly resistant against high light intensities and UV irradiation or have protective mechanisms against the detrimental effects of UV exposure (Hill, 1996). These mechanisms include mycosporine-like amino acids, the sheath pigment scytonemin or carotenoids (reviewed by Castenholz and Garcia-Pichel, 2000).

Temperature is one of the most important environmental factors because it affects biochemical reactions. Water temperature is primarily determined by direct solar radiation. On a large spatial scale, temperature regimes depend on latitude, elevation, continentality and morphometry. Water temperature also varies with long-term climatic cycles which recently are increasingly influenced by anthropogenic changes in global climate. As the temperature increases, dominance of algal classes shifts from diatoms to green algae to cyanobacteria. Concomitantly, biodiversity and biomass increases to an upper limit at around 20–25°C, both decreasing at higher temperatures. Community structure and biomass of the very specialized flora on sand (*epipsammic*) are less affected by temperature than other periphyton assemblages. Temperature is not limiting in most natural communities but the degree to which primary productivity is limited by factors such as light, nutrients and grazing depends on temperature. A more complete understanding of temperature effects, especially autecological responses of (benthic) algae, is required to make accurate predictions of periphyton response in a 'warmer world' (De Nicola, 1996).

Abundance, biomass and seasonality of algal vegetation

Development of benthic algal communities in streams and rivers is governed by a complex array of factors and interactions. In addition, different sampling and analytical techniques, as well as the use of artificial substrates, which may be highly selective (e.g. Schagerl and Donabaum, 1998), make generalizations difficult. Available data, however, permit us to conclude that benthic chlorophyll-a values in streams can span four orders of magnitude and ash-free dry mass three orders in the course of a year (Biggs, 1996). Some of the variation is accounted for by the degree of enrichment, vegetation cover, development of the water-shed and depends on the type and quality of the river (Table 1.6.2). Filamentous green algal communities can have particularly high chlorophyll-concentrations (> 600 mg m^{-2}) and ash-free dry mass (> 200 g m^{-2}).

The temporal pattern of short-term benthic algal accrual is clear and generally universal (Figure 1.6.1). It starts off as a linear process by immigration/colonization, followed by exponential growth. Accumulation of biomass slows down when the loss

Table 1.6.2 Algal biomass range in rivers of different qualities (adapted from Marker and Collett, 1991)

River type	NO_3-N (mg l^{-1})	PO_3-P (mg l^{-1})	biomass range, minimum (g m^{-2})	chl-a, maximum (mg m^{-2})
Soft water, pH 4–5	0.06–0.35	< 1	26	92
Soft water, pH 6–7	0.5	1–2	40	178
Head water chalk stream	4–5	10–30	50	200
Chalk stream	4–5	30–50	15–25	150–300
Hyper-eutrophic stream	5–15	1000–3000	25–50	150–250

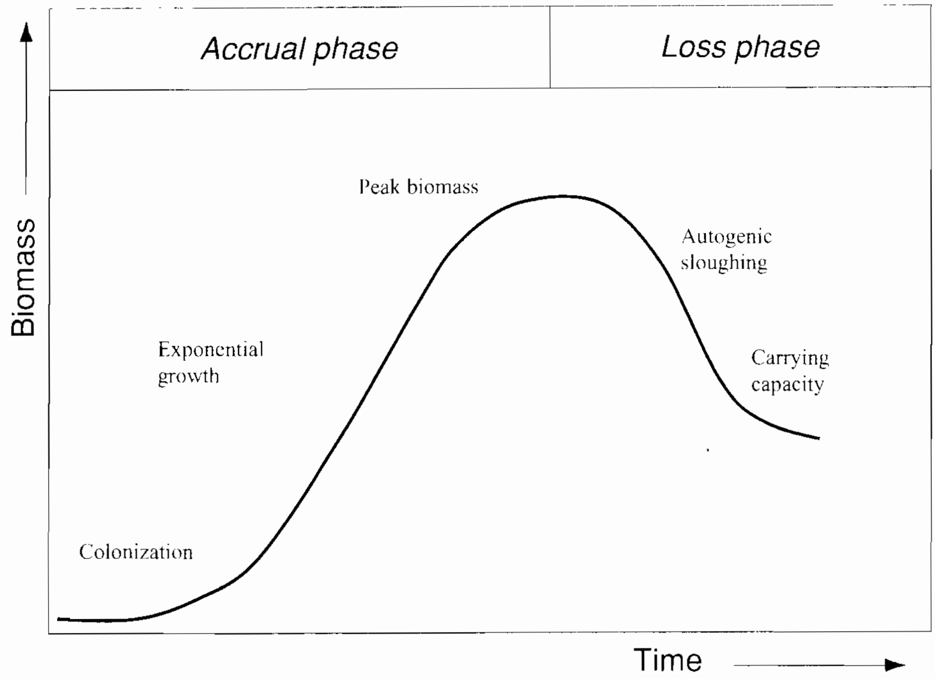

Figure 1.6.1 Idealized accumulation curve of benthic algal biomass, showing different phases (adapted from Biggs, 1996)

rates approach accrual rates, finally reaching the carrying capacity when both processes balance. Long-term or seasonal patterns of biomass can usually be classified into one of the following:

(1) more or less constant, low biomass when streams are frequently disturbed;

(2) accrual and sloughing cycles in rivers experiencing moderate or seasonal flood disturbance;

(3) seasonal cycles in community development are mediated by:

  (a) seasonality in disturbance regimes if nutrient resources are adequate;

  (b) seasonality in grazer activity when flood disturbances are rare;

  (c) seasonality in light regimes when neither (a) nor (b) are important.

Spatial patterns in the distribution of river benthic algae occur on a wide range of scales, from single sand grains to across continents. Micro-scale patterns on substrates vary according to species preference, some living in depressions or crevices while others prefer more exposed positions. Biomass is often greater on larger substrata because of higher stability. Communities on boulders are structured in zones with increasing depth (Blum, 1956). In gravel streams, algae may live as deep as 1 m within the hyporheic interstitial substrate. Assemblages on more mobile substrata are more frequently disturbed and set back to early successional stages (Peterson, 1996). Meso-scale distribution within a catchment can occur in pool, run and riffle habitats. In general, benthic algal biomass increases progressively downstream from head water to mid-catchment reaches. When river channels become wider and deeper, biomass is predicted to decrease again in lower reaches as a function of light attenuation (Vannote *et al.*, 1980). Gradients are also formed by increased nutrient loading downstream leading to severe changes in benthic algal composition. Large-scale regional (inter-catchment) patterns reflect differences in geology, flow pattern, flood regime, land-use and associated nutrient enrichment (Biggs 1996).

1.6.2.3 Ecological relevance of algal vegetation

The role of benthic algae in river and stream environments is manifold. As primary producers, algae are the basis of any food web. River algae are important components in both *macroscopic* and *microscopic* food webs (Lamberti, 1996; Bott, 1996). As *producers*, benthic algae serve as the food basis for many *consumers*, particularly for herbivores, detritivores and decomposers. Depending on the size and the reach of the river, periphyton may contribute varying amounts of *autochthonous* organic carbon to the overall energy budget. In small-order streams (order 1–2), autotrophic production may be as small as < 1 % when most organic carbon is derived from external sources (*allochthonous* carbon) but may reach as much as > 60 %. The degree of river autotrophy is related to stream size and biome type. In arid regions with limited riparian vegetation, for instance, carbon budgets are dominated by autotrophic production. In most streams, there is a delicate interplay between production and consumption. Plant–herbivore interactions are central to food web structures and energy flow. Streams may be, however, at the extreme of the environmental constancy spectrum because of their frequent disturbance. Benthic food webs therefore have fewer links and lower connectance than in other ecosystems. Such food webs may also be more easily disrupted by global environmental changes.

At the other, microscopic end, benthic algae are important because their excreted organic substances (~ 10 % of total photosynthate) support heterotrophic organisms, particularly bacteria. Both algae and bacteria are ingested by a variety of organism groups, such as protists, which have an amazing diversity of energy acquisition, rotifers, copepods, nematodes, etc. Few, if any, of these taxa are strictly algivorous or bacterivorous. Other food, such as *detritus* fungi, and other animals, is used as well.

Benthic algae also contribute significantly to nutrient cycling in stream ecosystems directly by increasing nutrient supplies, uptake of nutrients and back-release to the river water. Through the formation of boundary zones, benthic algae alter the hydraulic characteristics of the river bottom and therefore contribute to nutrient cycling indirectly, because the probability for remineralization increases before nutrients are transported downstream. In addition, interactions between periphyton and herbivores can have positive or negative effects on nutrient cycling in streams depending on the relative importance of algal biomass (negative) or remineralization (positive).

Algae, both benthic and planktonic, positively influence the oxygen budget of streams and rivers through oxygen evolution during photosynthesis. This is especially important in rivers carrying larger pollution loads, resulting in oxygen depletion due to bacterial respiration during mineralization.

River algae as ecological indicators

Benthic algae are primarily used for ecological monitoring of streams. Phytoplankton is used in larger rivers when conditions are appropriate. The rationales, methods and techniques of bioindication and biomonitoring using algae have recently been summarized by Dokulil (2003b).

Benthic river algae possess several attributes to make them ideal organisms for water quality monitoring (Lowe and Pan, 1996):

(1) Benthic algae are primarily autotrophic and are positioned at the interface between environmental and biotic components of the food web.

(2) Benthic algae are sessile and cannot avoid pollution through migration.

(3) Benthic communities are usually species-rich and therefore represent an information-rich assemblage ideal for environmental monitoring.

(4) Many benthic algae have relatively short life cycles, thus allowing rapid response to shifts in environmental conditions. Many species, however, live long enough to integrate impacts over certain periods of time.

Historically, benthic algae have been used for monitoring organic pollution of streams and rivers, by applying the concept of *saprobity* (Rott *et al.*, 1997). More recently, the emphasis has changed to direct nutritional effects using algae for trophic classification because algal growth is usually limited by a single substance (Rott *et al.*, 1999). As a consequence, structure and abundance of phytoplankton and periphyton is now included in the EC-Water Framework Directive (WFD, 2000) for water quality assessment and monitoring. Benthic algae can be used for *active monitoring* by using the reactions of individual species or assemblages to trace environmental changes, but may also be used in *passive monitoring* when species accumulate substances such as heavy metals from the surroundings. Summaries of algal usage for river monitoring in individual countries can be found in Whitton *et al.* (1991), Whitton and Rott (1996) and Prygiel *et al.* (1999).

Among the various algal groups in streams and rivers, diatoms are most universally used in freshwaters (e.g. Dokulil *et al.*, 1997; Rott *et al.*, 2003; Poulíčková *et al.*, 2004) because many species are very sensitive indicators of changes in the surrounding environment over short (days to weeks) or even very long time periods (palaeoecology). Diatoms can be used to trace changes in trophy, organic pollution, acidification, salinity or climate (summarized in, e.g. Schönfelder. 2000). However, several different methods are in use. If amalgamated, unified and tested, diatoms could form the basis for a classification system across lakes and rivers. Diatoms can be easily identified by their shells which are highly resistant and can readily be preserved as permanent mounts. In many cases, however, identification is also possible from inspection of live cells, at least at higher taxonomic levels (Cox, 1996). Diatoms, like many other algal groups, are sensitive indicators for inorganic chemical stress (Genter, 1996), toxic organic substances (Hoaglund *et al.*, 1996) or the effects of acidification (Planas, 1996). Benthic algal biomass and production may not be drastically altered in response to organic toxicants. At the community level, however, shifts in species composition and structure are common. A variety of organic toxicants, particularly herbicides, produce dramatic impacts to benthic algal communities at concentrations already below the $\mu g\ l^{-1}$ range (Dokulil, 2003b; Fent, 2003). During acidification of streams and rivers, carbon may become limiting, metals, especially aluminium, become toxic. nitrogen becomes more available, and microbial–algal interactions are altered. As a result, species composition will change and affect herbivore structure. In contrast to most algal groups which are sensitive to toxicants, cyanobacteria are potential producers of cyanotoxins which can be detrimental for fish, insects and mammals. In some instances, human health might be affected as well (Dow and Swoboda, 2000). All of these effects may become more pronounced and deleterious through food-web disrupture when global environmental changes impact on fresh waters.

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