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综述

STRESS OF FERTILE SEDIMENT ON THE GROWTH OF SUBMERSED MACROPHYTES IN EUTROPHIC WATERS

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富营养水体中肥沃底质对沉水植物生长的胁迫

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Submersed macrophytes are real water plants because they are rooted in sediment and can complete their growth and reproduction inside the overlying water. Providing a linkage between water and sediment, they have the closest interaction with water environment. This interaction is very complicate partly because sediment are not only served as a base of physical attachment. Recent attention has focused on the effects of submersed macrophytes on sediment redox, nutrient statues and the effects of sediment organic composition on macrophyte growth. This line of investigation has been thoroughly reviewed by Barko et al. (1991).

Long-term ecological records of the decline of submersed macrophytes in the progress of eutrophication have suggested that sediment may play an important role for the decline due to its close relations to macrophyte growth and distribution. Therefore, more concerns should be given to the inhibitory effects of fertile sediment on submersed macrophytes when nutrients are excessive for their growth. However, this line of investigation and experiments are relatively weak up-to-date.

In this review the author synthesize available information of the inhibitory effects of

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fertile sediment on the growth of submersed macrophytes to suggest possible mechanism referred. Speculative views are made to test in the further researches. The aim is to contribute to the restoration and management of submersed vegetation in eutrophic waters.

1 General impacts of eutrophication on macrophytes

Eutrophication caused by increased loading of nutrients to the waters from its catchment areas either through point source effluent or non-point source surface runoff, which affects submersed macrophyte community as a kind of exogenous disturbance. In shallow lakes, eutrophication generally comprises two factors: 1. High availability of nutrients, especially nitrogen and phosphorus, and 2. Enhanced accumulation of organic mater by accelerated primary production of the water column. Impacts of eutrophication on rooted submersed macrophytes generally include shading by phytoplankton and epiphytes (Jupp and Spence, 1977; Phillips et al. 1978; Sand-Jensen and Borum, 1984), DIC stress by the photosynthesis of dense phytoplankton (Jones et al., 1983; Twilley et al., 1985; Vadineanu et al., 1990); phytotoxin formed in low redox sediment due to high content of organic substances and their decomposition (Barko and Smart, 1986; Barko et al., 1991; Chamber and Kalf, 1985; Delaune et al., 1984), carbohydrate starving due to increased tissue nutrient loading and anaerobic respiration of roots (Brandle and Crawford, 1987; Cizkova-Koncalova et al., 1992; Sorrell and Dromgoole, 1987), reproductive failure (Twilley et al., 1985) and combined effects of eutrophication (Moss, 1983). In this sense, the stress of fertile sediment, as it directly affects macrophyte growth, carbohydrate reserve and even survive, may be the important contributing factor in the decline of submersed vegetation in the process of eutrophication.

2 Effects of sediment physics

It has been suggested that influence of sediments on the growth of submersed macrophytes might be due to physical properties rather than chemical compositions (Sculthorpe, 1967). Texture, for example, can be important in relation to the rooting depth of species with different abilities to physically penetrate sediments (Denny, 1980). Texture is generally related to sediment trophic statues. Extremely sandy or otherwise coarse-textured sediments of oligotrophic or running waters can be considered as nutritionally poor substrata for macrophyte growth, while fine-textured sediment containing high level accumulations of organic matters in productive standing water is fertile substrata. Sediment texture is related to its bulk density. Sandy and muddy sediments have high and low densities respectively. Reduced macrophyte biomass growth was found to occur in the both ends of the density spectrum. Low density sediment-related macrophyte growth reduction was also suggested due to nutrient limitation caused either by increased diffusion resistance of nutrients for the plant to uptake (Barko and Smart, 1986), or by low nutrient bulk content on the basis of decreased sediment density (Delaune et al., 1984). However, this explanation cannot apply to the reduction of submersed macrophyte growth in eutrophic waters for the sufficient nutrient supply in water column.

3 Effects of organic content

Aquatic macrophyte beds serve as effective traps for inflowing dissolved and particulate materials (Wetzel, 1979; Carpenter, 1981). It has been reported that under condition of eutrophication, sedimentation of epiphytes and filamentous algae can provide considerable amount of organic materials to sediment (Howard-Williams, 1981; Moeller and Wetzel, 1988). It is increasingly evident that macrophyte community composition and the spatial distribution of individual species have been correlated with sediment organic matter content (Macan, 1977). There is an apparent association during lake aging between increasing sediment organic matter and the decline of rooted submersed aquatic vegetation (Wetzel, 1979; Carpenter, 1981). This in turn influences ecosystem dynamics on a broad scale.

It is suggested that the effect of sediment on submersed macrophytes may be in part related to sediment organic mater content. In experimental investigation, addition of low level of organic matter in nutritionally poor sediment can stimulate the growth of macrophytes (Barko et al., 1991), while additions of organic matter to a fine textured inorganic sediment can substantially reduce the growth of submersed macrophytes (Barko and Smart, 1983). The causal mechanisms involved remains unknown.

However, in wetland species, addition of organic matter to muddy and fertile substrate had no effect on plant growth, while the combined treatment of organic addition and excessive nitrogen had resulted in a decline of the growth (Cizkova-Koncalova et al., 1992). This suggests that the organic matter may not directly inhibit the plant growth, it may enhance other existed growth stresses instead.

4 Effects of excessive loading of nutrients in sediment on macrophyte growth

Nutrient contents in sediment interstitial water are closely related to the exogenous nutrient loading in the eutrophic water column. The ratio of dissolved reactive phosphorus (DRP) in the sediment interstitial water to that in the open water exceeds about 4 (Patterson and Brown, 1979). Therefore, sediment has much higher P supply for macrophytes than does eutrophic open water. In fertile sediment or eutrophic waters, submersed macrophytes are characteristic of luxury consumption of nutrients and thus accumulate excessive nutrients in their tissue (Wetzel, 1983). Decreased macrophyte biomass growth at tissue luxury nutrient contents has not yet been reported in literature. However, in an earlier experiment (Ni, 1999, unpublished), reduced biomass growth of four submersed macrophytes at their tissue luxury N and P contents has been observed. It has been clear in terrestrial plants that accumulation of large amount of minerals in the tissues has resulted in smaller cell size with thicker walls and slower growth rate than normal plants (Marschner, 1986). This regularity should be applicable to aquatic macrophytes. The critical N and P reported for growth requirement of submersed macrophytes are low: 13mg N g^{-1} DW and 3mg P g^{-1} DW, respectively (Gerloff, 1969).

5 Effects of excessive nutrients on macrophyte carbohydrate reserve

Photosynthetic assimilated carbohydrate is subsequently allocated to different sinks such as: supply for respiration; synthesis of enzymes; synthesis of structural materials; synthesis of storage compounds like starch. Among these sinks, storage carbohydrate is particularly important for the survival of macrophytes. The main functions of the reserve are to support seasonal regrowth and recovery after disturbance such as grazing and shading, and before photosynthetic carbohydrate supply can commence (Cizkova-Koncalova et al., 1992). It has been reported that carbohydrate reserves are also related to macrophyte tolerance to limited oxygen availability in reducing sediment of eutrophic water (Brandle and Crawford, 1987). This is because anaerobic respiration (fermentation) of roots occurred under reduced condition is much less efficient in carbohydrate use.

Thus, the carbohydrate budget includes three important steps: carbonate assimilation in plant photosynthesis, carbohydrate partition among different sinks and consumption of stored carbohydrates. The macrophyte nutrient supplies are considered to affect the carbohydrate partitions (Cizkova-Koncalova et al., 1992).

Low carbohydrate reserve at high nutrient supply has been widely observed. In wetland species, it was pointed out by Cizkova-Koncalova et al. (1992) that high nitrogen supply acted as the main predisposing factor for reed decline. In rooted submersed macrophytes, Ni (1999, unpublished data) observed that three species grown on unfertile sediment had higher carbohydrate contents than on fertile one when their tissue P content at unfertile sediment was lower than the critical value required for growth (P limit condition). It has been well documented for root and tuber crops that excessive nitrogen supply decreased accumulation of carbohydrate reserves in storage organs (Marschner, 1986). It was also reported that decreased reserve carbohydrate accumulation at excessive nutrient supply coincided with a delayed switch from vegetative to generative phase of macrophyte growth (Kuhl and Kohl, 1992).

Even not further affected by excessive tissue nutrient accumulation, carbohydrate reserve of submersed macrophytes in eutrophic waters is already at very low level. Compare to the ranges from 5—30% DW in low trophic waters (Best, 1977), carbohydrate of submersed macrophytes only ranges from 2—9% DW in high trophic water or fertile sediment (Ni unpubliched data). This low level is caused by decreased photosynthetic assimilation at intensive shading and DIC depletion from water column by phytoplankton; decreased reserve allocation at high nutrient supply; and increased consumption of carbohydrate by anaerobic fermentation of roots. The extremely low reserve carbohydrate caused by the combined effects of eutrophication is very critical for macrophyte to survive under disturbing environment.

6 Effects of reducing sediment

Sediment redox potentials (Eh) were reported to decrease with increasing organic substance and increased loading of nutrient into sediment in productive eutrophic waters. Sedimentation of the organic materials results in high oxygen demanding and low Eh of sediment. Recent investigation shows a decrease of Eh at increasing extractable P loading of sediment (Andersen and Jensen, 1992; Sondergaard, M., 1990). Its mechanism may be closely related to regeneration of sedimentary P at reducing condition. Reduced sediment in eutrophic water of high productivity was potentially phytotoxic (Ponnamperuma, 1972; Sanderson and Armstrong, 1980). Although submersed macrophytes are reportedly capable of adapting low Eh to certain extent by transporting photosynthetic originated oxygen through the intercellular lacunae to their roots (Amstrong, 1978), or by formation of nontoxic end products in root' s anaerobic fermentation (Penhale and Wetzel), this mechanism seems to be ineffective in fertile sediment of eutrophic waters (Carpenter et al., 1983; Chen and Barko, 1988).

In low Eh sediment, biomass growth was reported to reduce due to high concentration of soluble reduced iron manganese and sulfides (Jones, 1975), organic acids and other organic substances such as methane, ethylene, phenols and alcohol (Yoshida, 1975), and by indirect effects of organic contents on sediment density (Barko and Smart, 1983).

According to more recent studies (Barko and Smart, 1986; Barko et al., 1986, 1991), however, reduced macrophyte biomass in fertile sediment was related more to high organic content than directly to sediment redox potential.

Influences of macrophyte roots on sediment Eh are considered to be ineffective in eutrophic water (Carpenter et al., 1983). This influence is determined by amount of radical oxygen losses from plant lacunae to rhizosphere. Lacunae oxygen is photosynthesis generated. It was stated by Barko et al. (1991) that oxygen release rates appeared to be similar (in unit root mass) across a broad range of submersed macrophyte taxa in different trophic waters. This fact can explain what observed by Wigand et al. (1979) that rhizosphere Eh of deep-rooted submersed macrophyte species was significantly higher than that of shallow-rooted and rootless species. However, as reported in many marine and freshwater macrophytes that oxygen release rates are several times greater in the light than in the dark (Sand-Jesen et al., 1982; Carpernter et al., 1983; Smith et al., 1984; Thursby, 1984), lacunae oxygen supply is expected to decrease in eutrophic water due to increased shading of both phytoplankton and epiphytes. In addition, increasing oxygen demanding of root respiration will also consume considerable amount of lacunae oxygen reserve. These might cause decreased macrophyte root oxygen release in eutrophic waters.

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