



The interaction between water movement, sediment dynamics and submersed macrophytes

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Abstract

Water movement in freshwater and marine environments affects submersed macrophytes, which also mediate water movement. The result of this complex interaction also affects sediment dynamics in and around submersed macrophyte beds. This review defines known relationships and identifies areas that need additional research on the complex interactions among submersed macrophytes, water movement, and sediment dynamics. Four areas are addressed: (1) the effects of water movement on macrophytes, (2) the effects of macrophyte stands on water movement, (3) the effects of macrophyte beds on sedimentation within vegetated areas, and (4) the relationship between sediment resuspension and macrophytes. Water movement has a significant effect on macrophyte growth, typically stimulating both abundance and diversity of macrophytes at low to moderate velocities, but reducing growth at higher velocities. In turn, macrophyte beds reduce current velocities both within and adjacent to the beds, resulting in increased sedimentation and reduced turbidity. Reduced turbidity increases light availability to macrophytes, increasing their growth. Additionally, macrophytes affect the distribution, composition and particle size of sediments in both freshwater and marine environments. Therefore, establishment and persistence of macrophytes in both marine and freshwater environments provide important ecosystem services, including: (1) improving water quality; and (2) stabilizing sediments, reducing sediment resuspension, erosion and turbidity.

Introduction

The aquatic environment is vastly different from the terrestrial environment with which we are more familiar. Compared to air, water is a more viscous medium, a better solvent, and more stable thermally, but it also transposes more force and reduces diffusion rates. These properties of the aqueous environment have direct and indirect effects on aquatic macrophytes. Conversely, aquatic macrophytes modify the aquatic environment through their development and metabolic activity.

A simple conceptual model illustrates the complexity of the interactions among submersed macrophytes, water movement and sediment dynamics (Fig. 1). Submersed macrophyte growth is light-limited in most aquatic environments (Barko et al., 1986), with turbidity being a significant factor limiting light availability. Fast currents increase sediment resuspension in sparsely vegetated areas, which further reduces light available for the growth of rooted submersed macrophytes. Increased current velocity can also physically affect the ability of macrophytes to colonize or survive in a certain area (Biggs, 1996).

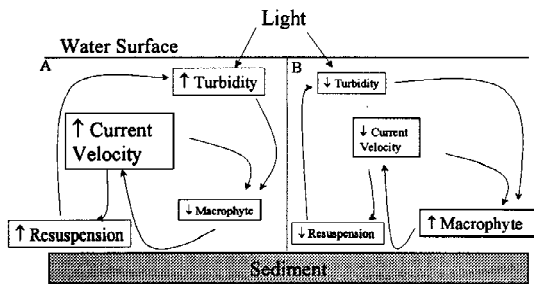


Figure 1. Conceptual model of the interactions among water movement, sediment, and aquatic macrophytes. When or where macrophytes are sparse (A), current velocity is affected only slightly, sediment resuspension is relatively high and turbidity and light attenuation are also high. In contrast, when or where macrophytes are abundant (B), currents are strongly attenuated, leading to reduced sediment resuspension, turbidity, and light attenuation.

Once established, however, aquatic macrophytes can reduce turbidity levels by increasing the sedimentation rate, mostly through a localized reduction in current velocity (Petticrew & Kalff, 1992).

The purpose of this paper is to review the complex interactions among submersed macrophytes, water movement and sediment dynamics. Submersed aquatic macrophytes encompass a variety of plants ranging from freshwater to marine, and from only a few centimeters to several meters tall. In this paper, we consider submersed freshwater, estuarine, and marine flowering plants that colonize soft sediments (e.g. sand and silt).

Within the submersed macrophytes, two major groups of plants can be distinguished: those that form meadows *versus* those that form canopies. Meadow formers have a basal meristem, and their biomass is either equally distributed over depth, or with a higher proportion of biomass allocated towards the base of the plant. Seagrasses (marine macrophytes such as *Zostera*, *Halodule* and *Thalassia*) are meadow formers, as well as some freshwater and estuarine macrophytes, such as *Vallisneria*. Canopy formers have an apical meristem, with their biomass disproportionately concentrated near the surface or top of the canopy. These plants occur in estuarine and freshwater environments (e.g., *Hydrilla verticillata* and *Myriophyllum spicatum*). The distinction between these two growth forms is important because they have significantly different effects on water flow and sediment dynamics. In this paper, we review the effects of water movement on aquatic macrophytes, and conversely, the effects of aquatic macrophytes on water move-

ment, turbidity, and sedimentation with the aim of identifying areas that need further research.

Effects of water movement on macrophytes

Water movement has long been recognized as a prime factor regulating the growth and distribution of submersed aquatic macrophytes. As early as the 1920s, Butcher (1933) recognized that changes in water flow or velocity could alter the biomass and species composition of submersed aquatic macrophytes in streams and rivers. Physiological studies have shown that photosynthetic rates of freshwater macrophytes are positively correlated with current velocity at low levels (0–0.10 m s⁻¹), the range likely to occur within dense macrophyte beds (Westlake, 1967; Madsen & Søndergaard, 1983). However, biomass is often negatively correlated with stream current speeds above this range (Bilby, 1977; French & Chambers, 1996). In contrast, the stagnant flow conditions that in marine environments may occur only in protected areas during slack tide (Koch, 1993a) can limit photosynthesis of seagrasses (Koch, 1994; Van Keulen 1997). In these environments, intermediate currents favor maximum aquatic macrophyte growth. High currents and wave energy can also limit the distribution of seagrasses, but their tolerance to wave energy and current flow is higher than that for freshwater and estuarine macrophytes (Koch, 1993a, 1996).

Physical effects

Water flow can affect river macrophytes both directly, due to stretching, breaking and mechanical damage; and indirectly, due to changes in gas exchange and sediment characteristics. The force acting on the rooted macrophyte under field conditions is significantly related to water velocity and plant biomass according to:

$$F = k * V^{l * Bm}, \quad (1)$$

where F is the force in Newtons, V is the velocity in m s⁻¹, B is the biomass in kg fresh weight per macrophyte; with k , l and m being coefficients specific to season and macrophyte species (Dawson & Robinson, 1984). This force is the tension expressed to the stem securing the shoot to the roots. Measurements using tensiometers on whole macrophytes in a river showed that for *Ranunculus pseudofluitans*, the velocity constant (k) was higher and the biomass constant (m)

Table 1. Approximate force (N) acting on whole macrophytes within their beds in streams, as calculated for different species, using Equation 1. Biomass values range from 0.1 to 0.25 kg fresh weight m^{-2} and a water velocity of $1.0 m s^{-1}$ (as reported in Dawson & Robinson, 1984)

Species	Force (N)
<i>Ranunculus pseudofluitans</i> (Dumort.) Bab.	2–4
<i>Potamogeton pectinatus</i> L.	5
<i>Elodea canadensis</i> Michx.	5
<i>Potamogeton X zizii</i> Koch ex. Roth	6
<i>Myriophyllum spicatum</i> L.	7

lower during the summer when the macrophytes have long, buoyant stems and diffuse growth (and, therefore, more force is exerted) as compared with autumn when the macrophytes have short, less buoyant stems and more compact growth (with the result of lower force exerted on shoots). Fewer data are available for other species, but similar relations between force and velocity are evident (Table 1).

Macrophyte orientation (i.e. angle to the sediments) is also important in determining the force acting upon them, and hence, their resistance to damage (Dawson & Robinson, 1984). Flume experiments conducted with model macrophytes showed that, at typical summertime velocities (approximately $0.30 m s^{-1}$), the force acting on the deepest half meter of the plants was reduced by at least half when the plants were at angles of $40\text{--}70^\circ$ to the sediment, as compared with a vertical orientation. A similar response was observed for the seagrass *Zostera marina* (Fonseca & Kenworthy, 1987). Thus, canopy drag also can be reduced by the bending of the blades in the direction of flow. Macrophytes also become streamlined in areas with strong current in order to minimize drag (Koehl, 1986; Gerard, 1987; Kraemer & Chapman, 1991; Dudgeon & Johnson, 1992; Hurd et al., 1996, 1997).

Few studies have examined the mechanical properties of freshwater macrophytes that provide resistance to drag, although this has been a topic of considerable study for marine macroalgae (but not marine seagrasses) (Koehl & Wainwright, 1977; Koehl, 1984; Denny, 1988). Brewer & Parker (1990) reported that the tensile strength (force per cross-sectional area that a stem can withstand before breaking, measured in $MN m^{-2}$) for seven freshwater macrophytes ranged from 2 to $34 MN m^{-2}$; and extensibility (the distance a stem will stretch before breaking relative to its initial

length, measured in % of total length) ranged from 3 to 13%. Species associated with deep water were less strong ($8.8 MN m^{-2}$) but more elastic (8.7%) than shallow water species ($18 MN m^{-2}$ and 5.5%, respectively). Dawson & Robinson (1984) also reported that the drag force exerted on macrophytes in a stream varied among species, among macrophytes of different size for the same species, and among macrophytes of different growth form yet of the same size and species. Given that complexity, the relationship of species composition and biomass to the mechanical forces in the aquatic environment is presently unknown. Moreover, there is no information on the role of toughness (the product of tensile strength and extensibility) in determining freshwater macrophyte distribution. However, it is interesting to note that tensile strength is generally greater and extensibility lower for freshwater macrophytes than for many seaweeds (e.g. 6.2 versus $0.7 MN m^{-2}$ and 6.5 versus 38% for seaweeds; Delf, 1932; Koehl & Wainwright, 1977). This may reflect the fact that the prevailing current to which riverine macrophytes are exposed tends to be unidirectional and constant and, as a result, tends to stretch macrophytes more than in nonflowing conditions. In the marine environment, however, the oscillatory motion of waves and tides does not impose a constant force in one direction. Thus, toughness for riverine macrophytes may be conferred more by tensile strength than by extensibility. In contrast, toughness of seaweeds (which are typically very long and exposed to oscillatory flows) may be due to greater extensibility than tensile strength.

Wave energy also can cause damage to aquatic macrophytes. For instance, increasing wave heights from 0.1 m to 0.3 m dramatically increased breakage of the canopy former, *Myriophyllum spicatum*, although not to the extent to cause mortal injury (Stewart et al., 1997). In fact, since stem fragments of this species are viable, this might actually aid in the spread of *M. spicatum*. In the same flume study, increased wave height caused significant damage to the inflorescences of the meadow former, *Vallisneria spiralis*, and some tangling and breakage of leaves. Wave action also can cause uprooting of seagrasses (Fonseca & Kenworthy, 1987) and littoral zone macrophytes (Madsen et al., 1996), but little is known about the maximum wave exposure tolerated by most plants. In stream communities, increased current velocity rather than wave action causes uprooting of stream vegetation (Haslam, 1978). In contrast, in the marine environment, currents and waves tend to limit the dis-

tribution of seagrasses to certain areas. Therefore, it is very difficult to address the effect of currents or waves alone.

Macroalgae are known to become streamlined as water flow increases (Koehl, 1986). Almquist & Kautsky (1995) observed that shoots of *Potamogeton pectinatus* in wave exposed areas were shorter than those in more quiescent waters. Streamlining has been observed by several investigators studying seagrasses, but few data have been published; in contrast to many studies on marine macroalgae documenting this phenomenon (Koehl, 1986). Epiphytic growth (which can contribute to drag, current velocity reduction and rescaling of turbulence) has also been found to be inversely proportional to wave exposure (Strand & Weisner, 1996). Rescaling turbulence is the conversion of turbulence from one magnitude or intensity to another. For example, the turbulence that reaches a seagrass bed has relatively low frequency of oscillations (or large eddies) but the vegetation breaks these low frequency oscillations (or eddies) down forming high frequency oscillations (or small eddies). Streamlining is both an effect of greater force exerted on the plant profile, and a morphogenetic response as the plant grows in response to these forces. Streamlining and other morphological responses may also impact other factors, such as light transmission through the canopy (Dennison, 1979; Short, 1980). In order to construct a holistic model of the interactions between water movement and submersed macrophytes, more empirical research is required to develop the relationships between flow velocity and direction, and plant response, including drag and the creation of turbulent flow.

Physiological responses

Current velocity can benefit aquatic macrophyte growth by enhancing CO₂ and nutrient supply, or be detrimental to growth due to mechanical stress. In addition to the physical stresses imparted by moving water, macrophyte metabolic and uptake processes, including photosynthesis, are affected by water movement. Gases diffuse 10 000 times more slowly in water than air, so diffusive processes are limiting steps to macrophyte metabolism. In addition, the boundary layers through which gases and nutrients must diffuse are typically substantially larger in water than in air, so this distance is a key factor to metabolic activity. Laboratory experiments have generally shown positive relationships between photosynthesis or nutrient

uptake and flow rates for very slow current velocities ($\leq 0.01 \text{ m s}^{-1}$ for freshwater species and ≤ 0.02 to 0.06 m s^{-1} for marine species), presumably due to a greater flux of solutes resulting from reduced thickness of the diffusion boundary layer (Westlake, 1967; Wheeler, 1980; Madsen & S ndergaard, 1983; Koch, 1993b, 1994). In experiments conducted at concentrations of CO₂ and oxygen expected to saturate photosynthesis and dark respiration, Madsen et al. (1993) showed that net photosynthesis of eight freshwater macrophyte species decreased as current velocity increased from 0.01 to 0.086 m s⁻¹. However, when shoots and leaves were fixed so that they could not flutter in the current, net photosynthesis was not affected by increasing current speed, suggesting that physical stress (agitation or stretching) had a negative effect on photosynthesis. These findings are consistent with studies of terrestrial macrophytes which have shown that physical disturbance can retard their growth (Jaffe, 1976). Thus, slow currents appear to enhance the growth of freshwater macrophytes by increasing the flux of CO₂ or nutrients across the diffusive boundary layer, whereas only slightly faster currents constrain growth due to mechanical stress.

Net photosynthetic responses in marine and estuarine macrophytes occur at higher current velocities than freshwater plants. At velocities $< 0.02 \text{ m s}^{-1}$, photosynthesis is limited by the thickness of the diffusive boundary layer, and reaches a maximum between 0.02 and 0.06 m s⁻¹ (Wheeler, 1980; Koch, 1993b, 1994; Gonen et al., 1995; Hurd et al., 1996). For the more polyhaline species, photosynthesis is not limited by current velocity, but by the enzymes responsible for carbon fixation (Koch, 2000). Jumars et al. (2000) provides a review of mechanisms by which aquatic macrophytes deal with limiting diffusive boundary layers. For marine macrophytes, no inhibition of photosynthesis by high current velocities has been observed, but strong currents are detrimental when excessive drag dislodges the plant.

Current speed also can affect the growth of macrophytes indirectly by determining the particle size of sediments. The particle size that can be eroded and transported is a function of current velocity. Thus, sand particles are most easily eroded (critical erosion velocity of about 0.20 m s⁻¹), whereas larger particles require faster current speeds to initiate movement (about 1.0 m s⁻¹ for coarse gravel). Although having a smaller grain size than sand, silts and clays require greater critical erosion velocities because of their cohesiveness. Organic particles, due to their low dens-

ity, tend to erode easily. Therefore, coarse substrates, which are characteristic of strong flow areas, generally lack organic matter and are nutrient-poor (Chambers et al., 1991; French, 1995). Because rooted macrophytes obtain most of their needed phosphorus and nitrogen from the sediments, current velocity, through its effect on sediment particle size and organic content, have the potential to constrain macrophyte growth (Barko & Smart, 1981, 1986; Anderson & Kalff, 1986). In addition, it may be difficult for macrophytes to root firmly into coarse sediments.

Conversely, the settling of particles has a significant impact on macrophyte growth. Initially, low rates of settling will stimulate growth through the influx of more nutrients in the sediments. However, at some point, the flux of settling particles will become too great, resulting in shading of photosynthetic surfaces and burial of the plant.

The growth of some aquatic macrophytes may be aided by the influx of nutrients in groundwater (Lodge et al., 1989). Mineral nutrition in rivers may be aided by hyporheic flow, or the flow of stream water through the interstices of bottom sediment particles, specifically in coarse sand and gravel sediments. In addition to the increased mineral nutrients, the flow of groundwater around roots increases the uptake rate by reducing boundary layer around root surfaces. Hyporheic flow moves the nutrients into the water column and, therefore, the increased availability of nutrients in the water column and decreased diffusion boundary layers of leaves in flowing waters may enable a shift in nutrient source from the sediment to the water column (Carignan, 1982).

Ecological responses to water flow

In situ studies of aquatic macrophytes have generally shown that community biomass decreases with increasing current velocity. For example, Chambers et al. (1991) reported that biomass of freshwater macrophytes in a western Canadian river decreased linearly with increasing current velocity up to 1 m s^{-1} , after which macrophytes were no longer present. *In situ* experiments in which *Potamogeton pectinatus* was grown at three sites differing in current velocity (0.17, 0.45 and 0.73 m s^{-1} average velocity) also showed that increased current velocity coincided with a decrease in biomass (total, shoot, root and rhizome) and shoot density (Chambers et al., 1991). *Ranunculus* spp. and many marine macrophytes appear to be exceptions to this pattern, and show increasing biomass with in-

creasing velocity up to some critical velocity (Dawson & Robinson, 1984). Submersed bryophytes are typical dominant plants in fast-flowing habitats (Butcher, 1933; Sirjola, 1969; French & Chambers, 1996). Many bryophytes have rhizoids that allow them to attach to rock surfaces and colonize fast-flowing water, providing bed movement is minimal. In contrast, vascular aquatic macrophytes root in finer material and out-compete bryophytes in these substrates. Thus, water movement also may favour certain species, thus altering community composition. Selection may operate on features such as leaf shape (Madsen, 1991), growth form (Keddy, 1982) or stem tensile strength (Brewer & Parker, 1990).

A conceptual framework for the effects of current velocity on submersed macrophytes in streams is presented in Figure 2, as adapted specifically for macrophytes from a more general model for all aquatic plants by Biggs (1996). In rivers with minimal flow variation during the growing season, increasing current speed over the range $0\text{--}0.90 \text{ m s}^{-1}$ is expected to decrease biomass and species richness, and favour species characterized by tough stems (i.e. stems that are very extensible, have a high tensile strength, or both). In contrast, the effects of current velocity on macrophytes in rivers characterized by regular floods or spates during the growing season is less well known, although research is being undertaken on this subject (Barrat-Segretain & Amoros, 1995, 1996; Henry et al., 1996). Presumably, the effects of a rapid short-lived increase in flow would depend upon the timing and magnitude of the event. Events occurring early in the growing season might simply delay the onset of growth whereas events late in the growing season might remove biomass or, at least, result in reduced net production.

Effects of macrophytes on water movement

Macrophytes reduce flow velocities within their beds in rivers and streams (Madsen & Warncke, 1983; Marshall & Westlake, 1990; Machata-Wenninger & Janauer, 1991; Newall & Hughes, 1995), as well as in marine environments (Fonseca & Kenworthy, 1987; Gambi et al., 1990; Koch, 1993a; Worcester, 1995). Likewise, wave energy and current velocity are reduced within beds in the littoral zone of lakes (Losee & Wetzel, 1988, 1993) and coastal areas (Heller, 1987; Fonseca & Cahalan, 1992; Koch, 1996). This reduction in waves and currents not only increases sed-

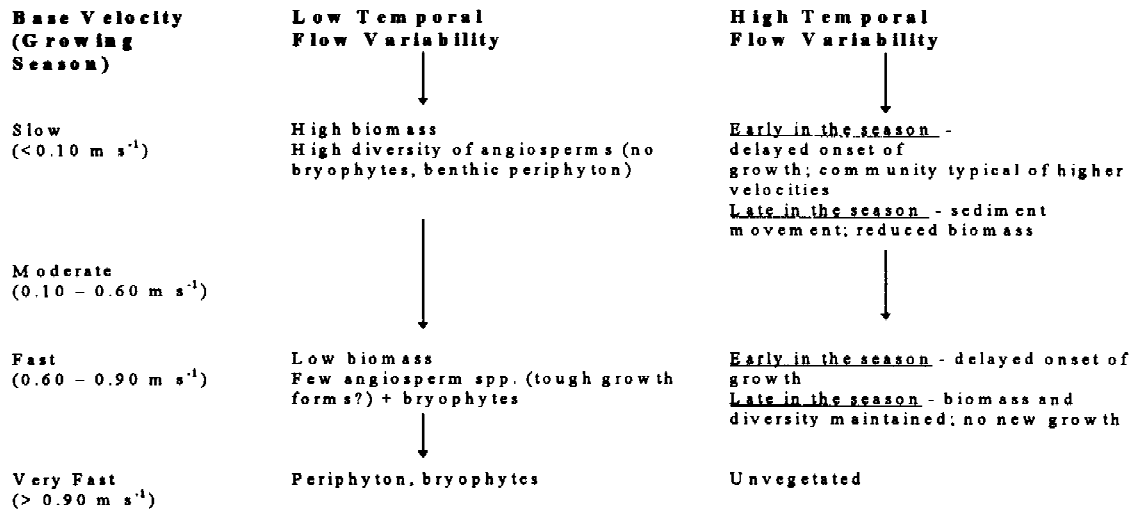


Figure 2. Conceptual model of the effects of current velocity on biomass and species composition of submersed freshwater macrophytes in streams and rivers adapted from a more general model for all aquatic plants by Biggs (1996). Aquatic environments are classified as having slow, medium, fast or very fast current velocities, and those having either low or high variability of flows or stages over the growing season. In environments with high variability in flow, this variability can occur either early or late in the growing season.

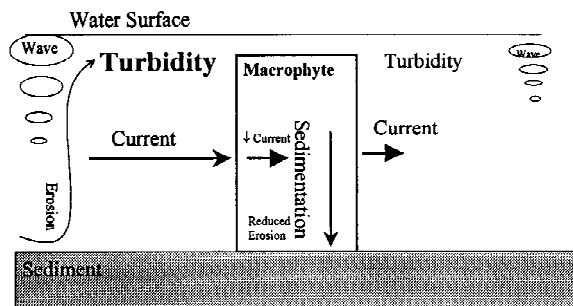


Figure 3. Conceptual model of direct and indirect effects of macrophytes on water movement.

imentation rates within macrophyte beds (Figure 3) (Eleutrius, 1975; Haslam, 1978; Harlin et al., 1982; Almasi et al., 1987; Fonseca, 1996), but also decreases the potential for resuspension (James & Barko, 1991; 1995; Fonseca & Cahalan, 1992). Increased sedimentation rates and reduced resuspension rates will reduce turbidity and increase light availability, which in turn promote further growth and reproduction of macrophytes (Doyle, 2000).

Hydraulic resistance

Knowledge of the effects of aquatic plants on water flow is very limited despite the need for information on channel roughness in engineering operations for irrigation, water supply, river channelization and floodwater management. The effects of aquatic macrophytes

on the flow of rivers are routinely interpreted through the roughness coefficient (n) in Chezy-Manning type equations. However, the choice of roughness values for inclusion in streamflow models is largely based on subjective experience, rather than objective measurements.

Dawson & Robinson (1984) studied hydraulic roughness in vegetated rivers of southern England, and found that Manning's n (a measure of hydraulic roughness) varied between 0.03 and 0.3 with biomass and discharge. Because of seasonal variation in both biomass and discharge, the relationship was difficult to de-couple, however, the removal of 1.0 and 1.5 kg fresh weight m⁻² in late spring resulted in a decrease in n by approximately 0.02 and 0.04, respectively. In general, there was a constant inverse relation between discharge and n except during major discharge events. The change in n after high discharge was attributed to the removal of biomass, the redistribution of sediments and changes in macrophyte bed morphology.

Studies have also shown the importance of seasonal growth, species composition and stand shape and structure, to the roughness coefficient. Westlake & Dawson (1988) studied the relationship between discharge and water levels along 30 km of a densely vegetated stream. The stream studied usually has dense populations of a water buttercup (*Ranunculus* sp.) which grows in a clumped distribution. Vertical distribution of biomass in these beds as homogeneous in depths of up to 1 m, after which the beds tended to

form a top-heavy canopy of plants, with lower biomass underneath. Shortly before macrophytes were cut, n was very sensitive to changes in discharge, which was presumed to relate to changes in macrophyte bed morphology. After macrophytes were cut, n decreased from about 0.2 to about 0.1 due to the reduction in vertical force (drag) by the plants.

The Chezy-Manning equation is strictly applicable only to steady uniform flow, which can only be assumed to apply over long reaches of rivers. This standard method for analyzing river flow and the effects of obstacles is unlikely to be easily applicable to the irregular distribution of close, flexible, and permeable clumps of vegetation. For example, Marshall & Westlake (1990) found that there was no significant correlation between n and biomass. Depths, velocities and turbulence at any point were influenced by the streamlines set up by neighboring conditions as well as by the local cross-section and resistance. Similarly, Gregg & Rose (1982) and Marshall & Westlake (1990) could not show significant or consistent relations between clump biomass and velocity reduction. Newall & Hughes (1995) also found it difficult to generalize this relationship, although they found a close relationship between velocities and biomass for individual clumps. Turbulence can be decreased by increasing the density of macrophytes, or altered by different species with different morphologies or biomass distributions (Newall & Hughes, 1995).

Sediment resuspension within and outside macrophyte beds

Sediments in freshwater and marine systems are derived from river inputs, suspension of bottom sediments, shoreline erosion and dead organic material. For sediment to be resuspended, it first needs to be eroded. Erosion occurs when the forces exerted by the moving water (drag and lift) overcome gravitational and frictional forces (Middleton & Southard, 1984). The velocity at which sufficient force is exerted to initiate motion of a sediment particle is called critical friction velocity (u_{*crit}). The Shields diagram is commonly used to determine the shear stress, τ , needed to move particles of a certain size resting on a flat bed ($u_*^2 = \tau/\rho$ where ρ is the density of the water). In submersed macrophyte beds, the sediment is not well sorted and the surface has roughness elements. Therefore, the determination of u_{*crit} is more difficult. To determine u_{*crit} of a (flat) sediment mixture

(a variety of grain sizes), the mixture can be exposed to controlled u_* levels in microcosms with homogeneous bottom stresses (Gust & Muller, 1997), the water column sampled for suspended sediment over a period of time while u_* (friction velocity) levels are increased. The number of particles in suspension increases exponentially when u_{*crit} is reached. This method also could be used to determine the effect of roughness elements on u_{*crit} .

Resuspension of particles also depends on the fraction of the water column that is occupied by the submersed macrophyte bed. When the submersed macrophytes occupy the entire water column, current velocities are efficiently reduced (Ward et al., 1984; Fonseca & Fisher, 1986) and sediments tend to accumulate. In contrast, when the water depth is larger than the maximum canopy height, wave attenuation is less efficient and sediment is resuspended (Ward et al., 1984).

Once a particle is eroded from the bottom and is in suspension, whether the particle will settle again or remain in suspension, depends on the settling velocity (downward motion) of the particle and the turbulent energy (upward motion; see Middleton & Southard, 1984). Although the settling velocity of the particles and the friction velocity of the water near the sediment surface (indicator of turbulence) are essential parameters in sedimentary processes, few studies have calculated the friction velocity in or above submersed macrophyte beds.

Sediment is deposited in macrophyte beds due to their capacity to reduce current velocities and attenuate wave energy. In relatively shallow streams (0.25–0.75 m) and coastal areas, fine sediments accumulate in areas associated with macrophyte stands (Minckley, 1963; Ladle & Casey, 1971; Grady, 1981; Gregg & Rose, 1982; Posey et al., 1993). For marine macrophytes, sediment accumulation in the beds decreases the height of the overlying water column, which in tidally influenced areas leads to more frequent, prolonged exposure of the macrophytes to air during low tide and accelerated currents over the macrophyte bed. If the bed area accretes enough to be exposed at low tides, intertidal macrophytes like mangroves or marsh plants may take over and continue the accretion process, ultimately leading to the formation of an island. If the submersed macrophyte area does not become intertidal, the higher friction velocities and erosion rates will gradually increase to the point that sediments are removed, increasing the depth of the macrophyte bed. A similar process occurs for stream

macrophytes (Dawson et al., 1978). Studies on chalk streams have shown that as the clumps of submersed macrophytes grow, vegetation expands and the flow is directed into low biomass areas between the clumps. In these areas, the velocities increase as the channels get narrower due to the expansion of vegetation. Since macrophyte biomass increases sedimentation, the low biomass areas either have low sedimentation or active resuspension, while the dense beds are areas of high sedimentation.

Organic matter is accumulated more in submersed macrophyte beds than in adjacent unvegetated areas (Kenworthy et al., 1982). Continuous accumulation of organic matter may lead to the death of macrophytes. Koch (2000) showed that more than 5% organic matter in the sediment may lead to the loss of marine macrophytes, while a similar limitation of freshwater macrophyte growth by sediment organic content was found in laboratory tests by Barko & Smart (1983, 1986). Resuspension events may be beneficial to the plants due to the removal of some of the organic matter deposited in the submersed macrophyte beds (Dauby et al., 1995). Therefore, the deposition/erosion cycle may be necessary for the health of submersed macrophyte beds.

Resuspension and nutrient availability

Resuspension of sediment from within or outside submersed macrophyte beds has the potential to release nutrients into the water column (Wainright, 1990). This mechanism can provide up to 94% of the N and 83% of the P required by phytoplankton (Cowan et al., 1996). According to Fanning et al. (1982), if a storm resuspends as little as 1 mm of sediment, the local productivity could be augmented by as much as 200%. Therefore, resuspension of sediment will not only contribute to light attenuation by the increased particles, but also by increased phytoplankton growth due to enhanced nutrients in the water column.

Marine macrophytes

Normal conditions

The deposition and resuspension of sediment within marine macrophyte beds depends on the hydrodynamic conditions to which the macrophytes are exposed (Koch & Gust, 1999). Under tide-dominated conditions, the blades tend to lean over in one direction for several hours before changing direction with the tidal currents. This forms a relatively sealed environ-

ment between the blades, leading to strong reductions in current velocity within the vegetation (Koch, 1993a). The water tends to flow over the canopy transferring high friction velocities from the sediment surface to the top of the canopy (Fonseca & Fisher, 1986). In contrast, in wave-dominated environments, the blades are constantly flapping back and forth, changing direction in a matter of seconds. A constant opening and closing of the canopy then occurs, with more interaction between the submersed macrophyte bed and the water column (Koch & Gust, 1999). As a result, currents are attenuated to a lesser degree and friction velocity (u_*) values at the sediment surface within the bed can be as high as in unvegetated areas. Therefore, sediment resuspension is higher in submersed macrophyte beds colonizing wave-dominated environments than those in tide-dominated environments (Koch & Gust, 1999).

In seagrass meadow species, the lower part of the shoots is held together by a sheath, which results in less area occupied by the macrophytes at the bottom than at the top of the canopy resulting in less drag near the sediment. Consequently, in seagrass meadows, currents may be intensified near the sediment surface (Koch, 1993a, 1996). This flow intensification is observed in other macrophyte systems with the same type of vertical biomass *versus* drag distribution (Oliver, 1971; Shaw, 1977; Leonard & Luther, 1995). If water flow is intensified by the presence of aquatic macrophytes with sheaths, sediment erosion and resuspension will also be enhanced (Koch, 1999).

Fonseca & Fisher (1986) calculated the friction factor ($f = 8 (u_* / u)^2$, where u is velocity) at the top of the meadow of four seagrass species in a flume, under unidirectional flow conditions. The flat-bladed species (*Thalassia testudinum*, *Zostera marina* and *Halodule wrightii*) had similar f values whereas those for the round-bladed seagrass, *Syringodium filiforme*, were lower, showing that leaf shape and cross-section are important components to friction.

The seagrass species mentioned above form meadows (i.e. macrophyte biomass distributed predominantly towards the plant base), sometimes reaching the water surface, whereas several other submersed macrophyte species form canopies (i.e. macrophyte biomass concentrated near the water surface). Hydrodynamic differences between these two types of submersed macrophyte beds must be taken into consideration for purposes of modeling hydrodynamic and sediment dynamics with macrophyte beds (Best et al., 2001). For example, in marine environments, wave

attenuation by kelp forests (canopies) has been found to be insignificant (Elwany et al., 1995; Mork, 1996) when compared to that of seagrass meadows. These hydrodynamic differences are likely to generate different u_* and turbulence conditions within the bed, which will in turn affect sediment erosion and resuspension.

The attenuation effects of seagrasses on waves and currents have not yet been explained. Fonseca & Fisher (1986) and Gambi et al. (1990) suggest that density is not a determining factor for current velocity reduction and turbulence generation, based on flume work, whereas the opposite conclusion was reached by Ward et al. (1984), Koch (1996) and Van Keulen (1997), based on field work. This contentious point obviously has to be clarified before deciding whether or not plant density must be included in a seagrass model used to simulate interactions between vegetation and environment.

Turbulence in marine macrophyte beds is not well understood. In studies using a variety of techniques in flumes and in the field, the presence of vegetation versus unvegetated areas has caused increased (Gambi et al., 1990; Grizzle et al., 1996), decreased (Ackerman & Okubo, 1993) or no change (Worcester, 1995) in turbulence. Turbulence within these beds can be generated where laminar flow occurs, as well as rescaled, where the flow is already turbulent. (Gambi et al., 1990; Ackerman & Okubo, 1993; Koch, 1996). The generation of turbulence in submersed macrophyte beds can occur through the low-amplitude movement of leaves in meadows. Additionally, a region of high turbulence is created at the interface of the submersed macrophyte bed and the overlying water; whereas turbulence near the bottom is reduced but still higher than in unvegetated areas (Gambi et al., 1990). Further research on turbulence in submersed macrophyte canopies and meadows is needed.

Sedimentation and resuspension aspects important for underwater light climate and the modeling aspects of current velocity are presented by Teeter et al. (2001) and Van Duin et al. (2001) in this issue. Consequences of changes in underwater light climate to submersed macrophytes and related modeling aspects are illustrated by Best et al. (2001) in this issue.

Extreme events

Studies on sediment dynamics in seagrass beds have focused mainly on depositional processes (Fonseca, 1996). Few studies describe the mechanisms of resuspension in these macrophyte-dominated environments; and the few that analyze this topic focus

on extreme events. Preen et al. (1995) observed the decimation of 1000 km² of seagrasses after a flood-cyclone-flood sequence. The floods increased the volume discharged from rivers and the cyclone resuspended sediments and eroded the coastline. The authors attribute the decline in seagrasses to decreased light availability after the events due to increased suspended sediment concentrations. In contrast, the passage of hurricane Andrew over south Florida in 1992 increased turbidity and nutrient loading, yet the seagrasses in the region suffered little (Tilman et al., 1994; Dawes et al., 1995). The difference in macrophyte response during and after these two events is likely related to the duration of the turbid or low light conditions. When submersed macrophytes are growing under extremely low light levels (late in the season when days become shorter, in deep waters or high turbidity environments), a short-term high turbidity event can result in the loss of the macrophyte population. The disappearance of seagrasses at 20 m depth but not in shallower waters following a late season storm (Williams, 1988) is an example of the interdependence of light availability and sediment resuspension events.

The loss of submersed macrophytes may lead to the resuspension of large amounts of sediment. For example, the recent loss of large areas of seagrasses in Florida Bay resulted in the resuspension of the fine carbonate sediments giving the water a milky appearance (Roblee et al., 1991).

Freshwater macrophytes

Limnological conditions in shallow lakes and reservoirs are strongly influenced by sediment resuspension processes that promote high turbidity, enhanced nutrient recycling, low water clarity and dominance by nuisance phytoplankton (Dillon et al., 1990; Maceina & Soballe, 1990; Hellström, 1991; Søndergaard et al., 1992). The magnitude of sediment resuspension, and its frequency of occurrence are controlled to a large extent by sediment composition and associated critical shear stresses at the sediment surface in relation to wave energy (Håkanson, 1977; Carper & Bachmann, 1984; Bengtsson & Hellström, 1990, 1992; Kristensen et al., 1992; Hamilton & Mitchell, 1996). Typically, the critical shear stress of soft sediments is easily overcome as deepwater waves touch the sediment surface. Thus, resuspension can occur frequently in shallow lakes if the water column depth is less than one-half the wavelength of deepwater waves (Carper & Bachmann, 1984). Submersed aquatic macrophytes

can reduce sediment resuspension by dampening wave energy and redirecting currents (Gregg & Rose, 1982; Madsen & Warncke, 1983; Dieter, 1990), thereby increasing the wind velocity required to exceed critical shear stresses at the sediment interface.

A good example of the interactions between freshwater macrophytes and sediment resuspension comes from a study conducted in Marsh Lake, Minnesota (USA). Marsh Lake is a shallow (maximum depth of approximately 1.2 m) impoundment on the Minnesota River that is susceptible to frequent periods of sediment resuspension (James & Barko, 1994). For winds blowing from any direction, over 80% of the lake bed can be disturbed by wave activity at critical wind velocities ranging between 10 and 15 km h⁻¹ (Carper & Bachmann, 1984; James & Barko, 1994). Sediment resuspension dynamics were examined when submersed macrophyte biomass was absent (1992), and when the entire lake was densely vegetated with *Potamogeton pectinatus* (1996). When macrophytes were absent (1992), total phosphorus (P) concentrations in the water column increased substantially when wind velocity exceeded approximately 12 km hr⁻¹ (Figure 4A). Based on the wind record for 1992 (James & Barko, 1994), resuspension of P occurred > 30% of the time during the summer. During 1996, there was an absence of sediment resuspension above nominal P levels, even at high sustained wind velocities (Figure 4B). These patterns clearly indicate that macrophytes can play a very important role in reducing the occurrence of sediment resuspension and the release of nutrients from the sediments. As P is an important nutrient for phytoplankton growth in shallow eutrophic systems, management tools need to be developed for reducing sediment resuspension.

Submersed aquatic macrophytes may be an effective management tool for limiting wind-driven sediment resuspension in shallow water systems. In other shallow water systems, the occurrence of macrophytes coincides with high water transparency and low phytoplankton biomass (Hosper, 1989; Dieter, 1990; Scheffer, 1990), due to macrophyte regulation of sediment resuspension. Thus, the establishment and maintenance of aquatic macrophyte communities should, perhaps, be encouraged to improve water quality in shallow water systems (Hosper & Jagtman, 1990; Hanson & Butler, 1994).

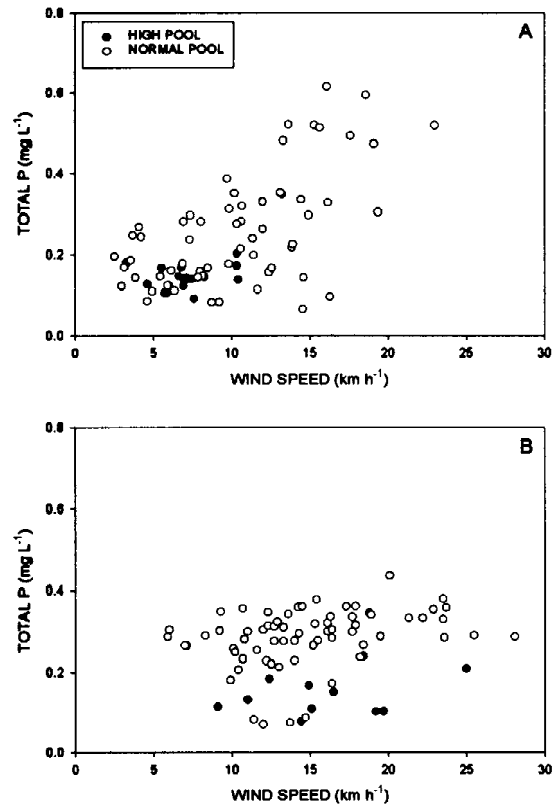


Figure 4. (A) Mean daily wind velocity versus total P concentrations in Marsh Lake, WI (U.S.A.) during a year when vegetation was absent (1992), and (B) Mean daily wind velocity versus total P concentrations in Marsh Lake during a year when vegetation was present (1996). The solid and open circles represent points in which the reservoir water levels are either at normal or high levels, respectively.

Conclusion

The interaction between hydrodynamics, sediment dynamics and macrophytes is complex. By a multitude of interactions, the hydraulic environment and sedimentary environment affect macrophytes, which in turn have direct effects on the physical environment. Despite this complexity, most of the basic interactions have at least been conceptualized at both the individual plant and stand levels. However, there are only limited studies that provide numerical data to quantify the conceptual relationships. In several instances, results from field or laboratory are not only disparate in numerical value, but also often contradictory in result. Major efforts in quantification are required to build coefficients for even simple models of the interactions between hydrodynamics, sediment dynamics and macrophytes. On a more reassuring note, this review has

shown that, although some differences are observed among marine, estuarine and freshwater macrophyte communities in these interactions, for the most part, the communities are more similar than different. In fact, freshwater and marine macrophyte studies in some instances provide complementary results. This should encourage more efforts to compare and contrast studies of seagrass communities with estuarine and freshwater macrophyte communities, which all too often are pursued in isolation, presented in separate professional meetings or sessions, and published in separate journals.

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