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Review

A systematic review of mechanistic models of riverine macrophyte growth

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ABSTRACT

Riverine macrophytes play diverse and foundational ecological roles, directly influencing ecosystem properties from local biodiversity to flows of water, energy, nutrients, and sediment, many of which in turn are central to river management. Numerical modeling is thus a crucial tool for understanding macrophyte and ecosystem responses to environmental, ecological, or management changes. However, riverine macrophytes have received relatively limited modeling attention compared to plants in many other aquatic or terrestrial systems. We conducted a systematic review of riverine macrophyte growth models, focusing on mechanisms of macrophyte growth, biomass loss, and feedback effects on river ecosystems. Processes such as light availability, thermal tolerance, nutrient limitation, and mortality were widely included in almost all models meeting the review criteria. However, models varied widely in their inclusion of processes such as shading, scour, and the roles of macrophytes in stream nutrient cycles. There has been relatively little consideration of factors such as dispersal, carbon sources, herbivory, burial, desiccation, and competition for space or nutrients, indicating directions for future modeling work. In light of this, we present a conceptual framework to help guide future macrophyte growth modelers through a thorough consideration of macrophytes' myriad interactions with their ecosystems. We also emphasize the importance of modularity and accessibility toward improving efforts to model, and in turn manage, riverine ecosystems.

1. Introduction

Riverine macrophytes are plants that spend at least some of their life cycle submerged, emergent, or floating in rivers. These plants often serve highly consequential ecological roles such as providing food and habitat for higher trophic levels (Argentina et al., 2010; Nelson and Scott, 1962), sequestering carbon and nutrients (Clarke, 2002; Conde-Álvarez et al., 2011; Hyldgaard and Brix, 2011; Mebane et al., 2014), intercepting suspended sediment (James and Barko, 1994), and altering hydraulic roughness and flows at multiple spatial scales, with implications for flood management (Dodds and Biggs, 2002; Kang et al., 2018; Sand-Jensen and Mebus, 1996). From a management perspective, some macrophyte species are declining and/or endangered (Chappuis et al., 2011; Poole and Bowles, 1999; Takafumi et al., 2015), while others may become invasive and threaten other species (Carniatto et al., 2020, 2014; Hardy et al., 2016), or interfere with human water uses such as extraction (Murphy, 1988), hydropower generation (Gómez et al., 2014), and navigation or recreation (Chambers et al., 1999). Resulting management actions have included planting desired macrophytes (Hardy et al., 2016; Nguyen et al., 2021) and/or removing unwanted macrophytes either physically (Bickel and Closs, 2009; He et al., 2019), chemically (Caudill, 2019; Kovalenko et al., 2010), or both (Madsen et al., 2015), with varying success. The influence of aquatic macrophytes on their ecosystems is often proportional to their biomass, but may also depend on species identity and local physicochemical factors (Best and Boyd, 1999).

Because riverine macrophytes play central roles in mediating diverse physical and ecological processes, it is often essential to model their growth under different environmental conditions and management scenarios. Models are crucial tools for developing and refining our

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understanding of biological systems for applied and fundamental research purposes (Rykiel, 1996). Conceptual models can help synthesize and communicate qualitative relationships (Fischenich, 2008) and numerical models can quantitatively interrogate hypotheses and simulate possible future scenarios (Grimm and Railsback, 2012; Wang et al., 2018). This is as true for rivers as it is for other ecosystems, but models of riverine macrophyte growth are relatively scarce compared to vegetation growth models in other systems. Often, modeling frameworks designed for one system can be applied to another relatively simply, such as by re-parameterizing or altering coding structure. For example, inland dunefield models have been applied to coastal or lacustrine systems, and forest models have been applied to mangroves (Piercy et al., 2023). However, due to the unique constraints of unidirectional water flow in rivers, models from other systems such as lakes (Trolle et al., 2008; Wang et al., 2016) or coastal marine habitats (Berger et al., 2008; Wang et al., 2013), or even more generalizable terrestrial models (Hudiburg et al., 2013; Luo et al., 2008), are often insufficient for meaningfully simulating the growth of riverine macrophytes. Effective modeling of riverine macrophytes necessitates river-specific models.

Although several models of riverine macrophyte growth have been developed, efforts to integrate or compare them have been sparse. This in turn can create a bottleneck for both model use and advancement (Rykiel, 1996). To address this, we performed a systematic literature review of efforts to model riverine macrophyte growth. Our objectives were to compile existing approaches and identify both the state of the science and key challenges. Using this information, we then developed a practical conceptual framework to help guide the development and application of future riverine and aquatic macrophyte growth models.

2. Methods

We followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA, http://www.prisma-statement.org/) framework for systematic literature review (Gurevitch et al., 2018), omitting categories such as effect measures that apply only to quantitative meta-analysis. We searched for English-language publications that included models simulating macrophyte growth over time in riverine systems. Thus, models of macrophyte growth in lakes, estuaries, floodplains, coastal zones, wetlands, irrigation channels, and ditches were excluded from this analysis, as were models that were set in rivers but only simulated the growth of algal primary producers such as phytoplankton.

2.1. Literature search

To identify models, we performed the following search in Web of Science on November 23, 2021: (ALL=(river OR lotic) AND (ALL=(plant grow* OR plant biomass OR plant produc* OR macrophyte grow* OR macrophyte biomass OR macrophyte produc*)) AND (ALL=(numerical model OR simulation model OR quantitative model)) AND (ALL=(mechanis* OR Michaelis-Menten OR physics-based OR dynamic))). This search yielded 344 results, listed in Table S1. We also included several models from "gray literature" (mainly government reports) personally known to the authors, and used the snowball technique to include river vegetation growth models cited by studies already identified (Wohlin, 2014).

All identified studies were screened in a two-step process. First, article titles and abstracts were screened to remove studies that clearly did not fit the eligibility criteria (e.g., studies not set in rivers, or studies not including vegetation or models). Studies that passed this initial screening were then examined in more detail to confirm whether they fit the eligibility criteria of modeling river macrophyte growth over time.

2.2. Data collection

For each study meeting the eligibility criteria, the lead author (LHD) analyzed the structure and function of the macrophyte growth model, with spot-checking by co-authors. We focused our analysis on three fundamental groups of processes: macrophyte growth, macrophyte biomass loss, and feedback effects on river ecosystems (Table 1).

- Macrophyte growth includes processes by which macrophytes might colonize a new area such as germination, establishment, and dispersal, alongside macrophyte requirements for light, temperature, nutrients, and carbon.
- Biomass loss includes mortality, senescence, and potentially nonlethal processes such as respiration, herbivory, competition, scour, burial, and desiccation.
- Feedback effects include effects of macrophyte biomass on hydraulic flow or stream nutrient concentrations, luxury nutrient uptake, and formulations of stream elemental cycling or spiraling, dissolved carbon and oxygen availability, and suspended sediment dynamics.

We also recorded model metadata including citation information, geographic setting, spatiotemporal scale, intended macrophyte species or growth form(s), data inputs and outputs, and logistics associated with accessing or using the model. Details of extracted data and our rationale for considering them are available in Table 1.

3. Results

3.1. Models meeting review criteria

Our Web of Science search returned 344 studies, of which 49 passed our initial screen (Table S1). We performed a more thorough screening on these 49 studies, potentially relevant studies cited therein, and "gray literature" studies identified separately. We grouped closely related models with strong functional similarities into single model families. For example, HYDRIL, MILFO, POTAM, and VALLA (Best et al., 2011, 2001; Best and Boyd, 2003, 2007, 2008) were developed by the same research group and share largely identical model structures, so we will refer to them as the "Best et al. models." Similarly, our treatment of AQUATOX (Clough, 2018; Park et al., 2008; Park and Clough, 2014, 2018; Sourisseau et al., 2008), will implicitly include its direct predecessors CLEAN, CLEANER, LAKETRACE, MACROPHYTE, PEST, TOXTRACE, and PART, cited in (Park and Clough, 2018). We ultimately identified 13 models or families thereof (Table 2).

3.2. Model characteristics

The structure and function of the 13 models are summarized in Tables 2–3 and presented in more detail in Table S2. The models vary widely in their levels of complexity and the processes included. Here, we present them in rough order of increasing complexity and spatial scale..

Of the models identified, Gurnell et al. (2012) offer perhaps the simplest macrophyte growth formulation, in a model designed for riparian systems. If groundwater is below the bed surface, plants undergo logistic growth, but if groundwater is above the bed surface, plant biomass decreases, presumably due to shear stress, uprooting, and root anoxia. We include this model as an edge case, as it can technically simulate the biomass of plants in rivers, but it does not allow plants to increase in biomass when submerged. Thus, it cannot realistically simulate the growth of submersed or emergent aquatic macrophytes.

The model of Hilt et al. (2011) represents another interesting edge case, as it simulates rivers not as continuous bodies of water but as chains of lakes with a user-specified rate of water flushing from one to the next. This model was designed to assess the circumstances under which macrophyte dominance and high water transparency versus phytoplankton dominance and high water turbidity represent alternate stable states in lakes and rivers. Macrophyte cover here is modeled here as the result of a simple relationship with the rate of vertical light attenuation (Hilt et al., 2011).

Table 1
Summary of data gathered from models, and associated rationale.

Type of Data	Data Field	Description	Rationale
Citation	Model	Name of model or model family. Citation information was used if a model name was not available.	Necessary for discussion of models.
	Abbreviation	Abbreviated model name for use in Table 3.	Make Table 3 easier to read and interpret.
	Reference(s)	Literature reference (s) for model.	Provide clear reference and attribution to model developers.
Geography	Biome	Biome in which model was originally developed.	Relevant to potential efforts to apply models to new systems, and to assess the generality of conclusions based on this review.
	Continent	Continent on which model was originally developed.	
	Country	Country in which model was originally developed.	
	Region	Region in which model was originally developed.	
	River	River(s) in which model was originally developed.	
	Macrophyte species	Macrophyte species for which model was originally developed.	
	Growth forms	Macrophyte growth form(s) for which model was originally developed.	
Model Setup	Spatial structure	Denotes whether model allows growth to vary over space (spatial structure included), or simulates macrophyte growth in a single homogeneous patch (spatial structure not included).	Spatial structure and dynamics are important to some model applications, but significantly increase model complexity.
	Time Step	Temporal resolution of the model; i.e., how frequently the model generates simulated macrophyte biomass values.	Temporal resolution is a fundamental consideration in model development and depends on desired applications. Compared with shorter time steps (minutes to hours), longer time steps (weeks to months) simplify computation but limit sophisticated consideration of factors such as light or temperature that vary substantially within a day.
	Number of independent input data sets	Describes the amount of external data needed for the model to function.	Greater amounts of input data allow a model to consider more processes, but may make it more difficult for a model to be applied to a new system.
	Number of state variables	The number of state variables included in the model.	An indicator of model complexity.
	Number of Parameters	The number of parameters included in the model.	
	Number of outputs	The number of output variables produced by the model.	
Logistics	Programming Language	Language in which the model was programmed.	Important to potential model users.
	Institutional Support	Denotes whether any institution, such as a university or government agency, is involved in providing access, maintenance, or technical support to the model.	
	Versions	Denotes the most recent version of a model, if available.	
Plant growth	Macrophyte germination, establishment, or dispersal	Shows whether model includes the processes of germination, establishment, or dispersal.	These are the processes by which macrophytes may establish populations in a new habitat and/or move among habitats, which can be especially important in models considering multiple populations, spatial structure, or other situations in which recruitment or immigration are significant components of population growth.
	Light availability at water surface	Denotes whether model considers the availability of light at the river surface.	Light is the energy source required for photosynthesis, so its availability is an important component of many models.
	Light attenuation in water column	Denotes whether the model allows light to be attenuated as it passes through the water column to the depth of the simulated macrophyte leaves.	Light is the energy source required for photosynthesis, so its availability at the depth of macrophyte leaves is important for mechanistic simulation of macrophyte growth.
	Temperature limitation of growth	Denotes whether macrophyte biomass growth is limited by temperature; this is typically done by assuming that growth is optimized at a specific	Temperature (departure from optimum) is one of the principal factors that can limit macrophyte growth.

(continued on next page)

Table 1 (*continued*)

Type of Data	Data Field	Description	Rationale
		temperature and defining a function to reduce growth based on departures from that temperature optimum	
	Nutrient limitation of growth	Denotes whether macrophyte biomass growth is limited by the availability of one or more nutrients; this is frequently done by using Michaelis-Menten kinetics to determine a factor by which the most limiting nutrient reduces growth rate.	Nutrient scarcity is one of the principal factors that can limit macrophyte growth.
	Carbon source	Denotes whether model considers availability of carbon source(s) for photosynthesis.	Macrophyte growth may be limited by carbon, which they may assimilate as CO2 and/or HCO3-, so macrophyte preferences for these carbon sources and their availability may pose important constraints to macrophyte growth.
Biomass loss mechanics	Temperature affects biomass loss	Denotes whether model allows temperature to affect biomass loss mechanisms.	The rates of biomass loss processes such as respiration, herbivory, or competition may vary with temperature.
	Respiration	Denotes whether model includes macrophyte respiration.	Respiration associated with growth and tissue maintenance is a major component of plant carbon budgets, and thus may be important to include as a sink of carbon assimilated during photosynthesis.
	Mortality	Denotes whether the model includes biomass loss by macrophyte mortality.	Mortality, including senescence, is often an important component of biomass loss in any population, including macrophytes.
	Herbivory	Denotes whether the model includes biomass loss by herbivory.	Herbivory is often an important component of macrophyte biomass loss and elemental cycling in rivers.
	Intraspecific competition for light (self-shading)	Denotes whether the model includes self-shading, or competition for light among individuals of the same macrophyte species.	Competition for light, including self-shading, may substantially reduce photosynthetic rates especially in deeper water and/or denser populations.
	Intraspecific competition for space	Denotes whether the model includes competition for space separately from light among individuals of the same macrophyte species.	Competition for space, in particular substrate area, may substantially reduce macrophyte growth or dispersal.
	Interspecific competition for light	Denotes whether the model includes competition for light between the modeled macrophyte and other primary producer species.	Competition for light, including self-shading, may substantially reduce photosynthetic rates especially in deeper water and/or denser populations. This process may overlap with light attenuation in the water column by suspended algae.
	Interspecific competition for space	Denotes whether the model includes competition for space separately from light between the modeled macrophyte and other primary producer species.	Competition for space, in particular substrate area, may substantially reduce macrophyte growth or dispersal.
	Scour	Denotes whether the model includes macrophyte biomass loss by scour.	Scour, or biomass loss associated with high hydraulic flows, may be an important source of stochasticity and biomass loss for many macrophytes.
	Flow effects on macrophytes other than scour	Denotes whether the model includes effects of hydraulic flow on macrophyte biomass by processes other than scour.	Flow effects on macrophytes other than scour may also play important roles in macrophyte growth and biomass loss in rivers.
	Burial	Denotes whether the model includes reductions in biomass or growth due to macrophytes becoming buried by moving sediments.	Burial may be an important component of macrophyte biomass loss, or at least cause severe reductions in photosynthesis while macrophytes are buried.
	Desiccation	Denotes whether the model includes biomass loss due to desiccation.	Desiccation may be an important component of macrophyte biomass loss.
Feedbacks and other stream processes	Macrophytes affect hydraulic flow	Denotes whether the model allows macrophyte biomass to feed back to affect hydraulic flow.	These are among the principal ways in which macrophyte biomass is thought to affect river ecosystems.
	Macrophytes affect stream nutrient concentrations	Denotes whether the model allows macrophyte biomass to feed back to affect stream nutrient concentrations.	
	Macrophytes capable of luxury nutrient uptake	Denotes whether the model allows macrophytes to engage in luxury nutrient uptake, that is, nutrient uptake beyond	The dynamics of macrophyte nutrient uptake, including the possibility of luxury nutrient uptake, represent an important

(continued on next page)

Table 1 (*continued*)

Type of Data	Data Field	Description	Rationale
		stoichiometric minima.	component of potential macrophyte contributions to river nutrient cycles or spirals.
	Stream nutrient cycling	Denotes whether the model includes components of stream carbon and nutrient cycles apart from macrophyte growth.	Simulating stream nutrient cycles is often a central application of river macrophyte growth models.
	Dissolved oxygen	Denotes whether the model includes dissolved oxygen availability.	Dissolved oxygen is an important component of stream metabolism and water quality, and responds strongly to diel cycles in photosynthesis and respiration.
	Suspended sediment	Denotes whether the model includes suspended sediment concentrations.	Suspended sediment dynamics are often an important component of water quality and a central consideration in river management.

The model of Wright and McDonnell (1986) is the simplest model we identified which mechanistically simulates aquatic macrophyte growth. It simulates a single biomass pool which increases by photosynthesis and decreases by respiration, mortality, and an optional advective loss term. Photosynthesis and respiration are assumed to reach their maximum rates at 20 °C, and decrease as ambient temperature deviates from that optimum. Photosynthesis is also limited by light and nutrient availability. Light availability encompasses day-to-day variation in incident light, the fraction of light available as photosynthetically active radiation (PAR), attenuation in the water column, and species-specific density-dependent shading by macrophytes. For nutrient availability, P is assumed to limit growth by Michaelis-Menten kinetics (Wright and McDonnell, 1986).

Several models expand on the framework of Wright and McDonnell (1986). Garbey et al. (2006) recombined multiple mathematical formulations of photosynthesis, respiration, plant architecture, and scour to make 54 different models. They compared the ability of these models to simulate a single macrophyte biomass pool. Their results highlighted light, temperature, and flow velocity as key environmental parameters, photosynthetic temperature optima and maximum physiological rates as highly sensitive constants, and plant plasticity in response to environmental change as a factor strongly influencing biomass predictions (Garbey et al., 2006).

Lázár et al. (Lázár et al., 2010, 2016) and the Kennet model (Wade et al., 2001, 2002a, 2002b, 2004) both focus on communities dominated by a single macrophyte species. Both use a single pool of biomass for each species, but also incorporate shading by other producers. Lázár et al. (2016) simulate epiphyte and phytoplankton biomass and allow them, along with suspended organic matter, to attenuate light and shade macrophytes. In contrast, the Kennet model does not include shading by phytoplankton, but simulates competition with epiphytes using a Lotka-Volterra predation model. Epiphytes are treated as predators and macrophytes are treated as prey, such that greater epiphyte abundance increases macrophyte mortality (Wade et al., 2001, 2002a, 2002b, 2004).

Davis and McDonnell (1997) and Best et al. (Best et al., 2001, 2011; Best and Boyd, 2003, 2007, 2008) incorporate variation among plant tissues and times of year. Davis and McDonnell (1997) accomplish this implicitly by dividing their macrophyte population into growing, mature, senescent, and dormant pools, and allowing transition rates among these groups to either vary over time or respond to environmental conditions. The Best et al. models explicitly partition macrophyte biomass among multiple tissues such as leaves, stems, roots, and tubers, which may vary in photosynthetic activity and metabolic costs. The relative proportions and activities of these different tissues vary over time, with transitions among phenological stages governed by degree-days (number of days times number of degrees above a threshold). Interestingly, while Best et al. (Best et al., 2001, 2011; Best and Boyd, 2003, 2007, 2008) use a formulation of light availability for photosynthesis similar in complexity to Wright and McDonnell (1986), Davis and McDonnell (1997) use a much simpler form, only taking as an input light availability at the water surface. Davis and McDonnell (1997) allow a single nutrient of the user's choice to limit plant growth by Michaelis-Menten kinetics, but the models of Best et al. (Best et al., 2001, 2011; Best and Boyd, 2003, 2007, 2008) do not yet account for nutrient limitation or negative biotic interactions beyond shading.

Compared to the aforementioned models, CASM (Bartell et al., 1999, 2020; Nair et al., 2015) is broader in scope because it embeds macrophyte growth in the context of stream nutrient cycles. In CASM, the growth of floating or suspended macrophytes and algae may be limited by dissolved N, P, and Si, and uptake by primary producers removes nutrients from dissolved pools. However, rooted macrophytes are assumed not to be nutrient-limited because they take up nutrients from nutrient-rich sediments. Macrophytes and other producers take part in stream C and nutrient cycles, which take a mass balance approach to follow C and nutrients between biological, particulate, and dissolved forms. Macrophyte biomass also contributes to a food web that can accommodate multiple species of producers and consumers. Despite this broader ecosystem scope, CASM uses the simpler light availability formulation of Davis and McDonnell (1997), considering only light availability at the water surface (Bartell et al., 1999, 2020; Nair et al., 2015).

Models such as CE-QUAL-W2 (Berger and Wells, 2008; Wells, 2021), WASP (Ambrose et al., 1988; Ambrose and Wool, 2017; DiToro et al., 1983; Martin et al., 2017), and AQUATOX (Clough, 2018; Park et al., 2008; Park and Clough, 2014, 2018; Sourisseau et al., 2008) accommodate additional complexity by including multiple macrophyte species and growth forms, which may respond differently to temperature, light, and nutrient availability. These models embed macrophyte growth in complex carbon and nutrient cycles within spatially explicit model domains. Flow and sediment dynamics are either included or linked from other models. Competition within and among species for light and/or space are also considered. AQUATOX and WASP further incorporate macrophytes into food webs. Each of these models also offers a feature unique among the models identified in this study: AQUATOX allows users to simulate the fate and effects of environmental toxicants, CE-QUAL-W2 allows macrophyte biomass to have feedback effects on hydraulic flow, and WASP is the only model we identified that simulates the equilibrium between dissolved CO_2, HCO_3, and CO_3^{-2} as potential plant carbon sources.

As a last category, the Patuxent Landscape Model (Voinov et al., 2007a, 2007b, 2007c, 2007d) considers aquatic macrophytes along with terrestrial plants in an attempt to simulate landscape processes at larger scales. This model divides plant biomass into three pools (aboveground photosynthetic, aboveground nonphotosynthetic, and belowground nonphotosynthetic), uses degree-days to dictate phenological transitions among plant growth stage, and uses other modules to simulate environmental factors such as temperature, light, nutrient availability, and hydrology. Most growth mechanics are conserved between terrestrial and aquatic plants, but a water limitation function accounts for taxon-specific tolerances of submergence and desiccation. Perhaps in exchange for its complexity in simulating terrestrial and aquatic ecosystems together, this model does not include relationships between macrophyte biomass, flow velocity, and stream sediment dynamics.

Table 2
Baseline information on the 12 models or model families identified, including citations, (A) geographic setting, (B) model inputs and outputs, and (C) logistics associated with access or reuse. Variables in the "Model setup" category may vary substantially among different applications of a single model, depending on features such as which modules are used and how many taxa are included. For models that can simulate the growth of multiple macrophyte species simultaneously, we estimated these values based on the case of modeling a single species. The ranges of values provided here attempt to capture central tendencies, but they are approximate and subject to exceptions.

A

Citation			Geography						
Model	Abbreviation	Reference (s)*	Biome	Continent	Country	Region	River	Macrophyte species	Growth Forms
AQUATOX	A	1–5	NA	North America	USA	NA	NA	NA	Rooted macrophytes, free floating macrophytes, and bryophytes
CASM	B	6–8	Temperate	North America	USA, Canada	Developed for use in Quebec but since used more broadly	NA	NA	NA
CE-QUAL-W2	C	9–10	Temperate	North America	USA	Various	Various; calibrated in Columbia Slough, Oregon, USA	Not specified; can accommodate multiple species at once; calibrated for *Ceratophyllum demersum*, *Elodea canadensis*, *Lemna minor*, *Potamogeton crispus*, and *Callitriche stagnalis*	Submerged, floating
Davis and McDonnell (1997)	D	11	Temperate	North America	USA	Central Pennsylvania	Spring Creek, PA	*Elodea canadensis*, *Potamogeton crispus*	Submerged
Garbey et al. (2006)	E	12	Temperate	Europe	France	Northeastern France	NA	*Ranunculus peltatus*	Emergent
Gurnell et al. (2012)	F	13	Temperate	Europe	England, France, Italy	Southern England, southern France, and northeastern Italy	Rivers Blackwater, Frome, Tech, and Tagliamento	Aquatic *Ranunculus* sp. and riparian *Sparganium*, *Populus*, *Salix*, and *Alnus* species	Emergent, riparian
Best et al. (HYDRIL, MILFO, POTAM, VALLA)	G	14–18	Temperate to tropical	North America	USA	Midwest USA	Upper Mississippi River	*Hydrilla verticillata*, *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Vallisneria americana* (individually)	Submerged
Kennet model	H	19–22	Temperate	Europe	UK	Southern England	Kennet River	Predominantly *Ranunculus penicilatus* var. *calcareous*, also *Callitriche obtusangula* and *Rorippa nasturtium-aquaticum*	Emergent
Lázár et al. (2016)	I	23–24	Temperate	Europe	UK	Southern England	River Frome	Predominantly *Ranunculus penicillatus*	Emergent
Patuxent Landscape Model	J	25–28	Temperate	North America	USA	Maryland	Patuxent River and watershed	NA	NA
WASP	K	29–33	NA	North America	USA	Mississippi and Georgia	NA	NA	Top floating, subsurface floating, submersed canopy forming, and benthic mats
Wright and McDonnell (1986)	L	34	Temperate	North America	USA	Central Pennsylvania	Spring Creek, PA	NA	NA
Hilt et al. (2011)	M	35	Temperate	Europe	Germany	Northeastern Germany	River Spree	NA	NA

B

Citation			Model Setup					
Model	Abbreviation	Reference (s)*	Spatial structure	Time Step	Number of independent input data sets	Number of state variables	Number of Parameters	Number of outputs
AQUATOX	A	1–5	Yes	Hourly to daily	> =9	> 20	> 100	21–50
CASM	B	6–8	No	Daily for 1 y	5–8	11–20	51–100	21–50
CE-QUAL-W2	C	9–10	Yes	Variable	5–8	> 20	> 100	> 100

(*continued on next page*)

Table 2 (*continued*)

B

Citation			Model Setup					
Model	Abbreviation	Reference (s)*	Spatial structure	Time Step	Number of independent input data sets	Number of state variables	Number of Parameters	Number of outputs
Davis and McDonnell (1997)	D	11	No	Input weekly, output daily	1–4	1–4	10–20	1–20
Garbey et al. (2006)	E	12	No	Hourly to monthly	1–4	5–10	21–50	1–20
Gurnell et al. (2012)	F	13	No	Continuous	1–4	1–4	1–20	1–20
Best et al. (HYDRIL, MILFO, POTAM, VALLA)	G	14–18	No	Daily	1–4	10–20	21–50	21–50
Kennet model	H	19–22	No	Daily	> =9	5–10	21–50	1–20
Lázár et al. (2016)	I	23–24	No	Daily	5–8	5–10	51–100	1–20
Patuxent Landscape Model	J	25–28	Yes	Variable	> =9	10–20	51–100	51–100
WASP	K	29–33	Yes	Hourly to daily	> =9	> 20	> 100	> 100
Wright and McDonnell (1986)	L	34	No	Daily	1–4	1–4	1–20	1–20
Hilt et al. (2011)	M	35	Yes	Continuous	1	2	9	2

C

Citation			Logistics		
Model	Abbreviation	Reference(s) *	Programming Language	Institutional Support	Versions
AQUATOX	A	1–5	Pascal and Delphi	US EPA	3.2
CASM	B	6–8	Fortran	Steven M Bartell, Cardno, Greenback TN USA	NA
CE-QUAL-W2	C	9–10	Fortran	Portland State University	4.5
Davis and McDonnell (1997)	D	11	NA	NA	NA
Garbey et al. (2006)	E	12	NA	NA	NA
Gurnell et al. (2012)	F	13	NA	NA	NA
Best et al. (HYDRIL, MILFO, POTAM, VALLA)	G	14–18	Fortran	USACE-ERDC-EL	3.0
Kennet model	H	19–22	NA	NA	NA
Lázár et al. (2016)	I	23–24	Fortran	NA	NA
Patuxent Landscape Model	J	25–28	Spatial Modeling Environment, STELLA, and C+ +	NA	NA
WASP	K	29–33	C+ + and Fortran	US EPA	8.32
Wright and McDonnell (1986)	L	34	NA	NA	NA
Hilt et al. (2011)	M	35	MATLAB	NA	NA

*References: 1- Park et al. (2008); 2- Sourisseau et al. (2008); 3- Park and Clough (2014); 4- Clough (2018); 5- Park and Clough (2018); 6- Bartell et al. (1999); 7- Nair et al. (2015); 8- Bartell et al. (2020); 9- Berger and Wells (2008); 10- Wells (2021); 11- Davis and McDonnell (1997); 12- Garbey et al. (2006); 13- Gurnell et al. (2012); 14- Best et al. (2001); 15- Best and Boyd (2003); 16- Best and Boyd (2007); 17- Best and Boyd (2008); 18- Best et al. (2011); 19- Wade et al. (2001); 20- Wade et al. (2002a); 21- Wade et al. (2002b); 22- Wade et al. (2004); 23- Lázár et al. (2010); 24- Lázár et al. (2016); 25- Voinov et al. (2007b); 26- Voinov et al. (2007c); 27- Voinov et al. (2007d); 28- Voinov et al. (2007a); 29- DiToro et al. (1983); 30- Ambrose et al. (1988); 31- Martin et al. (2017); 32- Langeveld et al. (2013); 33- Moreno-Rodenas et al. (2017); 34- Wright and McDonnell (1986); 35- Hilt et al. (2011).

3.3. *Reporting biases*

We note that all of the studies analyzed come from rivers in temperate North America and Europe, consistent with known biases in research funding and English-language publication (Culumber et al., 2019; Di Marco et al., 2017). As a result, although they contain a wide range of temperate latitudes and ecosystems (Table 2) and we have striven for generality in our analysis, some caution is warranted in applying these models and conclusions to non-temperate (e.g., tropical, boreal) ecosystems. This also highlights a clear need for collaborations in performing new studies and sharing existing knowledge across languages and biomes.

4. Discussion

4.1. *Summary of processes included*

The 13 models or model families we identified varied widely in their coverage of the growth, biomass loss, and environmental feedback mechanisms we investigated (Tables 2–3). Considering macrophyte growth processes, almost all (10−11) of the models included light availability at the water surface as well as nutrient and temperature limitation of growth, and nine included light attenuation in the water column. Relatively few (3−4) accounted for macrophyte germination, establishment, or dispersal into a habitat, or carbon availability for photosynthesis. Four models explicitly considered macrophytes of multiple growth forms, while five considered just one growth form and four did not specify a growth form. Models varied more widely in their incorporation of biomass loss mechanics. All 13 models included some form of plant mortality, and many (8−9) included respiration, temperature effects on biomass loss, competition for light within and among species, and scour. Relatively few models (1−4) included biomass loss by herbivory, competition for space, or flow effects other than scour, and none simulated burial or desiccation. As for environmental feedbacks, a majority of models (8) included some form of stream nutrient cycling, six of which allowed macrophytes to affect stream nutrient concentrations. Six models also included a feedback mechanic on the role of macrophytes in reducing suspended sediment concentrations. However, few (1−4) models allowed macrophytes to perform luxury nutrient uptake, or to affect dissolved oxygen or hydraulic flow.

The processes that do not yet occur in many riverine macrophyte growth models to our knowledge represent clear future directions for the

Table 3
Processes included or excluded from each model. Model abbreviations follow Table 2. Shaded cells marked with X indicate processes included in models; blank cells indicate processes not included. For rows involving nutrients or carbon sources, the nutrients or carbon sources involved are specified. DIC stands for dissolved inorganic carbon.

	Model process	A	B	C	D	E	F	G	H	I	J	K	L	M	Number of models that include process
Plant growth	Macrophyte germination, establishment, or dispersal	X			Optional						Optional				3
	Light availability at water surface	X	X	X	X	X		X	X	X	X	X	X		11
	Light attenuation in water column	X		X		X		X		X	X	X	X	X	9
	Temperature limitation of growth	X	X	X		X		X	X	X	X	X	X		10
	Nutrient limitation of growth	C, N, P [1]	N, P, Si [1]	C, N, P	P	P			P	N, P	N, P	N, P	P		10
	Carbon source	CO_2		DIC				CO_2				H_2CO_3, HCO_3^-, CO_2			4
Biomass loss mechanics	Temperature affects biomass loss	X	X	X	X	X		X				X	X		8
	Respiration	X	X	X	X	X		X			X	X	X		9
	Mortality	X	X	X	X	X	X	X	X	X	X	X	X	X	13
	Herbivory	X	X							X		X			4
	Intraspecific competition for light (self-shading)	X		X		X		X	X	X		X	X		8
	Intraspecific competition for space						X	X							2
	Interspecific competition for light	X	X	X				X	X	X			X	X	8
	Interspecific competition for space											X			1
	Scour	X			X	X	X		X	X		X	X		8
	Flow effects on macrophytes other than scour						X	X						X	3
	Burial														0
	Desiccation														0
Feedbacks and other stream processes	Macrophytes affect hydraulic flow			X											1
	Macrophytes affect stream nutrient concentrations	X	X	X					X		X	X			6
	Macrophytes capable of luxury nutrient uptake	X										X			2
	Stream nutrient cycling	C, N, P	C, N, P, Si	C, N, P					C, P, B	C	C, N, P	C, N, P, Si	X [2]		8
	Dissolved oxygen	X		X								X	X [2]		4
	Suspended sediment	X		X		X			X	X		X			6

1. Specified nutrients limit growth of floating but not rooted macrophytes.
2. Model itself does not contain this variable, but is later linked with an in-stream oxygen model to investigate effects of P input reductions on water quality.

field. Technical innovations in high-resolution modeling of hydraulic flow and sediment dynamics (Kang et al., 2018; Kuhn et al., 2019) may soon facilitate detailed modeling of processes such as burial, desiccation, and feedback effects of macrophytes on flow and sediment dynamics. These processes are also currently absent from models of marine macrophytes like seagrasses (Piercy et al., 2023), so their absence is not unique to riverine models. There is also abundant room for future work in the characterization of processes such as scour, herbivory, and competition, the latter two of which are more common in terrestrial vegetation models, but widely absent from SAV models in other systems (Piercy et al., 2023). For example, scour may necessitate different mathematical formulations depending on whether scour in a given system tends to break, knock over, or uproot the study macrophyte (e.g., Pollen-Bankhead et al., 2011). Similarly, the models identified here variously characterize herbivory using relatively simple functions of biomass (Ambrose et al., 1988; DiToro et al., 1983; Lázár et al., 2016; Martin et al., 2017), an ecological predation model (Clough, 2018; Park et al., 2008; Park and Clough, 2014, 2018), or an entire river food web (Bartell et al., 1999, 2020; Nair et al., 2015). Furthermore, these formulations do not include other herbivory mechanisms identified in empirical studies such as velocity-mediated herbivory (Wood et al., 2019).

These processes suggest two main priorities for future macrophyte research and modeling. The first concerns improving our understanding and model representation of connections and feedbacks between macrophytes and their ecosystems. Models such as AQUATOX, CASM, CE-QUAL-W2, the Kennet model, Lázár et al. (2016), the Patuxent Landscape Model, and WASP have made substantial advances connecting macrophyte growth with carbon and nutrient cycling. We see strong opportunities for similar advances in modeling macrophyte interactions with flows of water and sediment that shape riverine and riparian hydrogeomorphology; such work could be widely applicable to ongoing challenges in the management of hydraulic flows and sediment loads (e.g., Cornacchia et al., 2023; Kang et al., 2018). Better situating riverine macrophytes within the webs of biotic interactions that occur in and adjacent to rivers is another opportunity for models to improve their applicability, in this case, to understanding river ecology and preserving biodiversity. As a second main priority for future work, we note that model parametrizations can easily outpace empirical understandings of the study species' physiology, necessitating difficult-to-validate assumptions about plant responses to changes in factors such as light, temperature, nutrient availability, and the biotic environment. This may be particularly challenging in efforts to apply models to species for which they were not originally developed, or to use models that do not

Table 4
Conceptual framework for future model development.

Category	Feature	Examples
Nature of growth	Growth characteristics	Biomass, cover, extent, roughness
	Natural history	Variation among tissues, life stages, species, or seasons
	Population ecology	Recruitment, growth, reproduction, senescence, mortality
	Spatial scales	Reach-scale, grid size, mesh size
	Temporal scales	Hourly, daily, monthly, yearly
Requirements for growth	Light availability	Sources of attenuation in atmosphere and water column
	Plant responses to light	Max photosynthetic rate, response to non-optimal light availability
	Nutrient availability or limitation	Identity of limiting nutrient(s), shape of uptake and growth response
	Carbon sources and availability	CO2/HCO3- equilibrium and preferences
	Substrate	Size, texture, stability, carbon and nutrient contents
Factors affecting growth and survival	Climate	Temperature, flow regime, seasonality, probabilities of extreme weather events
	Water quality	pH, dissolved oxygen, turbidity, suspended sediment, pollutants
	Biotic interactions	Competition, herbivory, mutualism, facilitation, parasitism, pathogenicity
Feedback effects on environment	Hydraulic flow	Hydraulic roughness
	Water quality	Intercepting nutrients, sediments, or toxins, or releasing dissolved oxygen
	Nutrient spiraling	Carbon fixation and sequestration, nutrient uptake and transformation

specify a study species (Table 2), and models can be highly sensitive to physiological parameters (e.g. Garbey et al., 2006). The field of river vegetation modeling would thus benefit from increased collaboration with empiricists toward improved understandings of the physiology, ecology, and natural history of the macrophytes under investigation.

The diversity of processes included in these 13 models highlights the interdisciplinary nature of riverine macrophyte modeling. Depending on the goals of a given model, it may be necessary to incorporate expertise in the natural history, physiology, and ecology of the study species, the climate, hydrology, and geomorphology of the study region, and/or the biogeochemistry of nutrients and potential toxicants in the study system. This may become even more complex for models simulating multi-species macrophyte communities or food webs, large geographic areas, or detailed nutrient dynamics. This complexity will likely necessitate collaboration not only across scientific disciplines, but also with managers and other stakeholders who may offer valuable local knowledge and benefit from models being user-friendly and producing interpretable results (Riddick et al., 2017).

4.2. Model structure and development

There appears to be a tradeoff between specificity and generality in macrophyte models, in which efforts to model one system in greater detail tend to make it more difficult to apply that model to another system. More generally, there is a clear tradeoff between simplicity and complexity in model development. Ideally, models achieve parsimony, including just enough detail to effectively characterize desired processes without becoming unnecessarily complex (Larsen et al., 2016). This is difficult to achieve and generalize across complex systems, due in part to increasing numbers of parameters to estimate and potential differences in qualitative relationships among key ecosystem processes. Modularity can help address this challenge by allowing modelers greater flexibility to select processes for a given study or application. This occurs in many of the existing tools. For example, later versions of the Best et al. models give users the option of including effects of flow velocity and epiphyte cover on macrophyte growth (Best and Boyd, 2007), while WASP (Ambrose et al., 1988; Ambrose and Wool, 2017; DiToro et al., 1983; Martin et al., 2017) and Garbey et al. (2006) allow users to choose between multiple formulations of processes such as photosynthetic response to light and temperature. At a larger scale, Patuxent Landscape Model has separate modules including temperature, solar radiation, nutrient availability, and water availability (Voinov et al., 2007a, 2007b, 2007c, 2007d). Some models achieve a related goal by allowing links to other models via inputs and outputs. For example, the Kennet model has been linked to a model of stream oxygen and phosphorus (Wade et al., 2001, 2002a, 2002b, 2004), and AQUATOX and CE-QUAL-W2 allow linkage to an external sediment diagenesis model (Berger and Wells, 2008; Clough, 2018; Park et al., 2008; Park and Clough, 2014, 2018; Sourisseau et al., 2008; Wells, 2021).

We emphasize accessibility and reproducibility as additional future directions for river vegetation modeling. Public availability is key to the continued development, refinement, and widespread application of models; however, to date, only five of the 13 models analyzed here appeared to be publicly available. Modularity tends to make models more accessible from an open science perspective as well (Hampton et al., 2015), and allows users to tailor model complexity to their specific application. We urge future modelers to follow open science principles as their situations avail, and note the utility of platforms such as R packages, R Markdown, and GitHub for making programs and code accessible (Shaw and McKay., in preparation). Database approaches may also make modeling more accessible across models or programming languages (Mooij et al., 2014; Van Gerven et al., 2015).

4.3. Macrophyte modeling across systems

Development of riverine-based macrophyte models has varied over time. The earliest riverine macrophyte model meeting the review criteria was developed in 1986 (Wright and McDonnell, 1986), though AQUATOX cites precursors dating back to 1974 (Park et al., 1974). The field then saw a relative uptick in model development in the early 2000s. This timeline closely matches the timing of model development surrounding seagrass beds, riverine macrophytes' marine 'cousin' for whom many modeling concerns may be most similar. The first process-based model for seagrass beds was developed in 1980, and then this model field saw a considerable boom in research effort (i.e., number of models developed) in the early 2000s (Piercy et al., 2023). This increase in seagrass bed model development coincides with global declines in their habitat extent due to worsening water quality (Duarte et al., 2013). Recognition of poor water quality, together with advances in computing technology, may help explain the concomitant increase in riverine macrophyte models as well. Like seagrass models, riverine models to date lack thorough and consistent means of simulating variation in water quality (e.g., pH, dissolved oxygen, turbidity, suspended sediment, nutrient concentrations, pollutant contamination), which may have species-specific impacts.

Riverine macrophyte models possess noteworthy similarities and differences to models in other systems. Many of the models reviewed here use a mass-balance approach for primary productivity, simulating standing biomass over time as a function of biomass gain from gross photosynthesis and biomass loss from respiration (Carr et al., 1997; Piercy et al., 2023). This approach also occurs in models of crop plants (Teh, 2006) and in the recent coastal dune model DOONIES (Charbonneau et al., 2022). Irradiance is a critical component of these calculations, and sub-routines such as ASTRO (Goudriaan, 1986) for calculating day length and instantaneous irradiance are common in many systems (Charbonneau et al., 2022; Piercy et al., 2023; van Nes et al., 2003), including many of the riverine models examined here (Table 3, S2). While burial via sediment erosion and deposition is relevant for many riverine macrophytes (Table 1), it is absent from all models in this review (Table 3, S2). In contrast, many terrestrial coastal dune and marsh models simulate burial, but coastal and seagrass models do not. The physics of these terrestrial interface models likely will not translate directly to rivers, but different modeling frameworks for elevation change (grid-based, point-based, or grain-based) may be applicable (Piercy et al., 2023). Existing coastal frameworks could also serve as a starting point for including sea level rise in models of tidally influenced rivers, another important future direction (Piercy et al., 2023). Overall, riverine models will likely remain specific to rivers because the constraints imposed by unidirectional water flow, but lessons can still be learned from existing models in other systems.

4.4. *Framework for future model development*

To help guide future development of riverine macrophyte growth models, we propose a conceptual framework based on four components: (1) the specific nature of macrophyte growth, (2) macrophyte requirements for growth, (3) external factors affecting macrophyte growth and survival, and (4) feedback effects of macrophytes on their environment. This is not a one-size-fits-all set of prescriptive instructions for developing a macrophyte growth model, as the best model for a given task will always depend on the research question or management application at hand, as well as the resources available. Our goal in providing this framework is to help modelers from a wide range of disciplines systematically consider the processes most relevant to macrophyte growth and its ecological consequences in their particular study system.

By the specific nature of macrophyte growth, we mean to ask what characteristics of macrophyte growth are most important to a given modeling study. At coarse scales this could be as simple as cover, stem length, or biomass, but at finer scales it may be necessary to consider variation among individual plants, plant tissues, life stages, species, or seasons. The growth form(s) of the macrophytes being modeled can strongly affect their responses to environmental conditions and will thus be highly relevant here. Processes underlying macrophyte population ecology such as recruitment, growth, reproduction, non-fatal biomass loss, and mortality may also be relevant. Decisions about whether to include the above processes in a model will likely depend strongly on the desired spatial and temporal scale for simulation, which may depend in turn on the extent and resolution of available input data.

For macrophyte requirements for growth, we urge users to consider the various resources and conditions a macrophyte may need in order to grow. Most broadly, these are water, light, nutrients, carbon, and substrate. Water availability rarely limits aquatic plant growth, but may be important in the forms of depth, velocity, and desiccation. For light, many models already contain thorough characterizations of light availability at the water surface and attenuation through the water column, but the details of macrophytes' optimum light levels, ability to tolerate deviation from these optima, and effects of epiphyton on light availability, may make these projections more sophisticated if they are known. Similarly, many existing models could serve as guides for formulating macrophyte responses to nutrient availability, and there are abundant opportunities for future work to incorporate processes such as nutrient co-limitation and luxury uptake. As for carbon sources, while terrestrial plants fix carbon from atmospheric CO_2, aquatic plants vary in their ability to take up dissolved CO_2 and/or HCO_3^-, the equilibrium between which varies with pH (Hussner et al., 2016; Maberly and Spence, 1983; Pedersen et al., 2013). This has received relatively little attention in macrophyte growth models to date, but has been shown to be important in some systems (Power and Doyle, 2004). The availability of suitable substrates is another central component of macrophyte growth in a given reach: macrophytes that root in fine sediments will not thrive on bare rock, and macrophytes that adhere to hard substrates will struggle to grow in silt or sand.

Many environmental and anthropogenic factors affect macrophyte growth and survival, and identifying which of these factors is most important in a given system may represent a significant ecological challenge. Climate is the most central component of this category, and may include many scales of variation in water temperature or hydraulic flow relative to macrophytes' preferences or tolerances, as well as changes in seasonality or the probabilities of extreme weather events. Many components of water quality may be relevant here as well, including pH, dissolved oxygen, turbidity, suspended sediment, or pollutants. This category also includes a diversity of biotic interactions such as competition, herbivory, parasitism, mutualism, facilitation, or pathogenicity. Anthropogenic factors are frequently central components of macrophyte growth models and will surely continue to be; these may include impacts of river management actions on flow or water quality (Bhattacharjee et al., 2019; Marcinkowski et al., 2018; McKay and Fischenich, 2011), direct planting or removal of macrophytes (Kovalenko et al., 2010; van Nes et al., 2002), or land use changes in the surrounding watershed (Dorotovičová, 2013). Modeling tools are not substitutes for empirical or controlled studies; however, they can serve valuable roles in developing understanding and predicting combinations of factors that would be infeasible in empirical models.

Finally, we urge modelers to consider feedback effects of macrophytes on their environment. Just as macrophytes respond to changes in their environment, so too can they shape environmental features. This may include affecting downstream hydraulic flow via changing the hydraulic roughness of the streambed, altering water quality by producing dissolved oxygen, intercepting sediments and toxins, providing habitat structure for consumers, or shaping nutrient spirals by sequestering nutrients in biomass and/or sediments (Mebane et al., 2014).

4.5. *Notes on practice*

No model exists in a vacuum. Models of riverine macrophyte growth are developed to be used toward any number of goals, some of which may include helping plan efforts to remove invasive macrophytes, restore endangered macrophytes, understand macrophytes' roles in biogeochemical cycles from rivers to landscapes, help prioritize potential management actions, and test, constrain, and generate hypotheses about macrophyte biology. This diversity of potential goals is reflected in the diversity of model structures and functions observed here. As the field continues to advance, we emphasize that a river macrophyte model is just one of many tools, information sources, or forms of knowledge at the disposal of modelers, empiricists, and practitioners. We call for sustained, equitable, and interdisciplinary collaboration between these three groups and those affected by model results, with the goals of tailoring models to the questions at hand and maximizing their ability to produce realistic and usable results.

5. Conclusions

Riverine macrophytes play foundational roles in numerous ecosystem processes, functions, and services. It is thus often important to model their growth under changes in environmental conditions or management strategies. However, riverine macrophyte growth has received less modeling attention than plant growth in other habitats, despite the fact that models developed in other habitats seldom characterize the unique physical implications of growth in rivers. In this systematic review, we traced existing efforts to model riverine macrophyte growth with varying levels of complexity. We identified several features widely included among these models, including light availability, nutrient and temperature limitation of growth, and mortality. We also identified several promising future directions for river vegetation growth modeling, including dispersal, carbon sources, herbivory, scour, burial, and desiccation, as well as feedbacks to ecosystem processes such as nutrient spirals, hydraulic flow, and sediment dynamics. There is no single best way to model riverine macrophyte growth, and we urge future modelers to incorporate principles of accessibility and modularity so that new models can build more easily and effectively on past work. Finally, we present a conceptual framework to guide future model development, focusing on the specific nature of macrophyte growth, macrophyte requirements for growth, factors affecting growth and survival, and feedback effects of macrophyte growth on environmental conditions. We aim for this framework to help future modelers thoroughly conceptualize the multitude of ways in which macrophytes interact with their environments so that users can choose which processes are most important to specific applications.

CRediT authorship contribution statement

Lee H. Dietterich: Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Suhey Ortiz Rosa:** Conceptualization, Investigation, Writing – review & editing, Visualization. **Bianca R. Charbonneau:** Conceptualization, Investigation, Writing – review & editing. **S. Kyle McKay:** Conceptualization, Methodology, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2023.103724.

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