A Recalibrated Simulation Model (Version 3.0) on the Competition for Light by American wildcelery and Sago pondweed at High and Low Nutrient Availability

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PURPOSE: This technical note describes an ecological modeling framework that can be used to explore relationships between species of submersed aquatic vegetation (SAV) communities, environmental conditions, and each other. The framework is based on an earlier version and was recalibrated for species characteristic responses to nutrient limitation. The framework was used to evaluate the feasibility of competition for light at various nutrient availability levels by two SAV species, which play quantitatively important roles in shallow water bodies.

BACKGROUND: Submersed aquatic vegetation may play important roles in aquatic ecosystems: (i) roles attributed to 'desirable' species are: stabilization of sediment, amelioration of transparency and regulation of nutrient availability in the water column and serving as habitat and food source for invertebrates, fish and waterfowl; (ii) roles attributed to 'nuisance' or 'invasive' SAV species, however, are: excessive biomass production interfering with human utilization of freshwater resources or displacing desirable indigenous communities. Distribution and abundance of SAV in the Upper Mississippi River System (UMRS), USA, have changed since the Mississippi River was impounded (Rogers 1996). A succession of species has occurred in the upper Navigation Pools since the late 1930s, with the floating-leaved *Polygonum amphibium* L. occupying many newly created habitats and eventually being replaced by pondweed species (Green 1960). Navigation pools (pools) are impoundments that develop in rivers upstream of newly constructed dams. *Vallisneria americana* Michx. (American wildcelery) occurred throughout the Upper Mississippi Refuge by 1960 and was reported common and widespread in the upper pools along with several pondweeds (Korschgen and Green 1988). In 1991, large-scale declines in SAV occurred, with areas vacated by *V. americana* being colonized by other species (Fischer and Claflin 1992). Currently, *V. americana* has returned in several pools, coexists with pondweeds and other species at some sites, but is replaced by *Potamogeton pectinatus* L. (sago pondweed; current taxonomic name *Stukenia pectinata* L. according to Crow and Hellquist (2006)) at other sites. *V. americana* is a desirable species and *P. pectinatus* an invasive species. Direct relationships between potential persistence of *V. americana* and *P. pectinatus* and light climate in a River Pool of the Illinois River, just north of its confluence with the Mississippi River, were recently evaluated through simulation modeling, with results indicating that altered water level, decreased light availability, and altered flow negatively impacted sites for potential colonization and persistence by SAV and that *P. pectinatus* was better suited to colonize and persist under the extant conditions (Best et al. 2008). Relationships between potential persistence of these plant species, light climate, nutrient limitation, and interactions with each other, however, remain to be elucidated.

Although physical and chemical environmental factors greatly affect a plant's performance, another important factor that may shape its environment is other plants. One of the most active debates in ecology focuses on the unresolved question of the mechanisms by which plants interact with one another (Lambers et al. 1998). Plant-plant interactions range from positive (facilitation) to neutral to negative (competition) effects on the performance of neighbors (Bazzaz 1996). Competition occurs most commonly when plants use the same pool of growth-limiting resources (resource competition). The question of which species wins in competition depends strongly on the time scale of the study. Short-term experimental studies of competition often depend on rates of resource acquisition and growth, whereas equilibrium persistence of a species in a community is affected by rates of resource acquisition, tolerance of ambient resource availability, efficiency of converting acquired resources into biomass, and retention of acquired resources (Goldberg 1990).

The competitive ability of a species depends on the environment. There are no 'super species' that are competitively superior in all environments. Rather, there are some trade-offs among traits that are beneficial in some environments, but which cause plants to be poor competitors in other environments. For a plant to compete successfully in a particular environment, it must have specific ecophysiological traits that allow effective growth in that environment. Traits that are important for competitive success at an early stage of succession may differ greatly from those that are pertinent in later stages. Similarly, plant characteristics that determine the outcome of competition in short-term experiments may differ from those that give a species a competitive edge in the long run. Ultimately the effect of competitors on reproductive output — the number of vegetative propagules or seeds — is also important. In most cases, competitive coexistence of multiple species in a community is not simply a function of capacity to tap a unique resource or to draw down a single resource (Tilman 1988; Tilman and Wedin 1991). Rather, it involves a wide range of traits and subtle differences in resistance to different environmental circumstances. Important traits are propagule size, growth rate, tissue turnover, allocation pattern, growth form, tissue mass density, and plasticity (Spencer and Rejmanek 1989; Lambers et al. 1998). Strong competition for light seldom coincides with strong competition for belowground resources. In the aquatic environment, those submersed macrophytes that are effective competitors for light are plants that allocate most of their biomass as a canopy close to the water surface (Spencer and Bowes 1990). Canopy formers may intercept a substantial portion of the light available for those submersed macrophytes that allocate most of their biomass close to the sediment surface (meadow formers). Submersed macrophytes are all physiologically shade plants in that leaf photosynthesis is saturated at less than half full-sunlight, but the degree of tolerance to light level is species-characteristic. This shade nature of submersed plants may represent a compromise with the massive constraint on photosynthesis imposed by the resistance of water to dissolved inorganic carbon diffusion (Bowes 1987). Besides light, nitrogen (N) and phosphorus (P) are generally believed to be the most important limiting elements in freshwater systems (Hutchinson 1975), but there have been few substantiated reports of nutrient-related growth limitation of submersed plants in natural systems. Relationships between biomass nutrient concentrations and nutrient limitation are complex. Biomass nutrient concentrations tend to be positively correlated with nutrient supply when all other resources are sufficiently available (Guesewell and Koerselman 2002). A low concentration of N in plant biomass should reflect a low availability of N to this plant and, therefore, indicate that additional supply of N would increase the plants' biomass production. By definition, this means that N is limiting (Vitousek and Howarth 1991). If two or more nutrients, e.g., N and P, are in short supply, their availability relative to each other is

likely to determine which of them is limiting. Therefore, the ratio of N:P, rather than the individual concentrations, should indicate limitation (Koerselman and Meuleman 1996) with tissue N:P ratios less than 14, indicative of N-limited growth in terrestrial plants (Aerts and Chapin 2000). Results of short-term (one-growth season) fertilization experiments indicate that critical N:P ratios in SAV may vary with species, ranging for N limitation from ≤5.7 to 9.8, and for P limitation from ≥8.4 to 10.5 (Sytsma and Anderson 1993; Best et al. 1996; Spencer and Ksander 2003).

Simulation models, which include descriptions of SAV responses to changes in physical and chemical conditions in various climates as well as plant responses to each other, can be valuable tools for water resource managers. These models can be used to evaluate key environmental conditions in which SAV would persist or produce excessive biomass, with ensuing consequences for the systems in which they grow, either affected or not affected by management scenarios (Carr et al. 1997; Best et al. 2001). This note summarizes a dynamic simulation modeling approach to submersed plant biomass formation, with light and temperature as driving variables, and including descriptions of plant responses to current velocity, nutrient limitation, and human influences such as management measures (changes in turbidity, mechanical harvesting, grazing, flooding). Listings of earlier versions of this modeling approach for *V. americana* and *P. pectinatus* are provided by Best and Boyd (2001, 2003), updated and detailed descriptions by Best and Boyd (2007, 2008), while the new framework created to enable modeling competition for light between these species under potentially nutrient limiting conditions is outlined and used in the present paper. The modeling approach is mathematical similar to other models for freshwater SAV, such as that developed for *Myriophyllum spicatum* L. (Titus et al. 1975; Collins and Wlosinski 1985), *P. pectinatus* (SAGA; Hootsmans 1991, 1994), and generic (MEGAPLANT, Scheffer et al. 1993; Herb and Stefan 2003), in that it describes plant morphology and biomass formation in relative detail, but it differs in that it relates ecophysiological processes to developmental cycle, enabling use of the model to simulate plant communities in different climates. In the model, CO_2 availability is assumed to be typical for hard water with an alkalinity between 0 and 300 mg L^{-1} and a circumneutral pH; effects of changes in CO_2 availability are not included. The model species are *V. americana* and *P. pectinatus*, both plants being similar in growth strategy but significantly different in morphology and physiology. The model versions have been calibrated, tested for sensitivity, and validated against field data (Best and Boyd 2007, 2008). Important physiological differences are that *V. americana* has a lower potential photosynthetic rate at light saturation, species-characteristic light extinction coefficient, epiphyte cover, sensitivity to current velocity, and a higher relative tuber growth rate than *P. pectinatus*, with both species differing in critical N:P ratios. These are characteristics which, besides having most of its biomass close to the sediment surface, make *V. americana* a species that thrives in clear water and grows less in turbid water, whereas *P. pectinatus* grows well in both clear and turbid water. In addition, *V. americana* tubers exhibit innate dormancy whereas *P. pectinatus* tubers sprout as soon as temperature permits. Both plant species over-winter through tubers in the sediment that are depleted and disintegrate in the summer following the season in which they were formed. As a result, their populations are expected to respond to annual changes in environmental conditions. Therefore, the described ecological model type provides an ideal means to investigate the effects of relatively short-term changes in environmental conditions on the potential persistence of these two SAV species in shallow water bodies, such as river pools, as part of restoration plans, provided detailed information on environmental conditions is available.

In the present study, two aspects of the relationship between important species of SAV communities, environmental conditions, and each other were investigated using a dynamic ecological modeling approach: (i) competition for light without nutrient limitation; and (ii) competition for light under potential growth limitation by N and P.

ECOLOGICAL MODELING APPROACH: This ecological model type simulates the carbon flow mass balance of a typical SAV vegetation in a 1-m^2 water column (Figure 1). Central features of the model are (1) the link between species-characteristic phenological cycle, physiological processes, and environmental conditions, and (2) the state variable equation determining instantaneous gross photosynthesis. The responses of plant species to each other are included in a framework in which two ecological models run, the first one pertaining to *V. americana* and the second one to *P. pectinatus*, while sharing and influencing one common light climate within the water column (Figure 2).
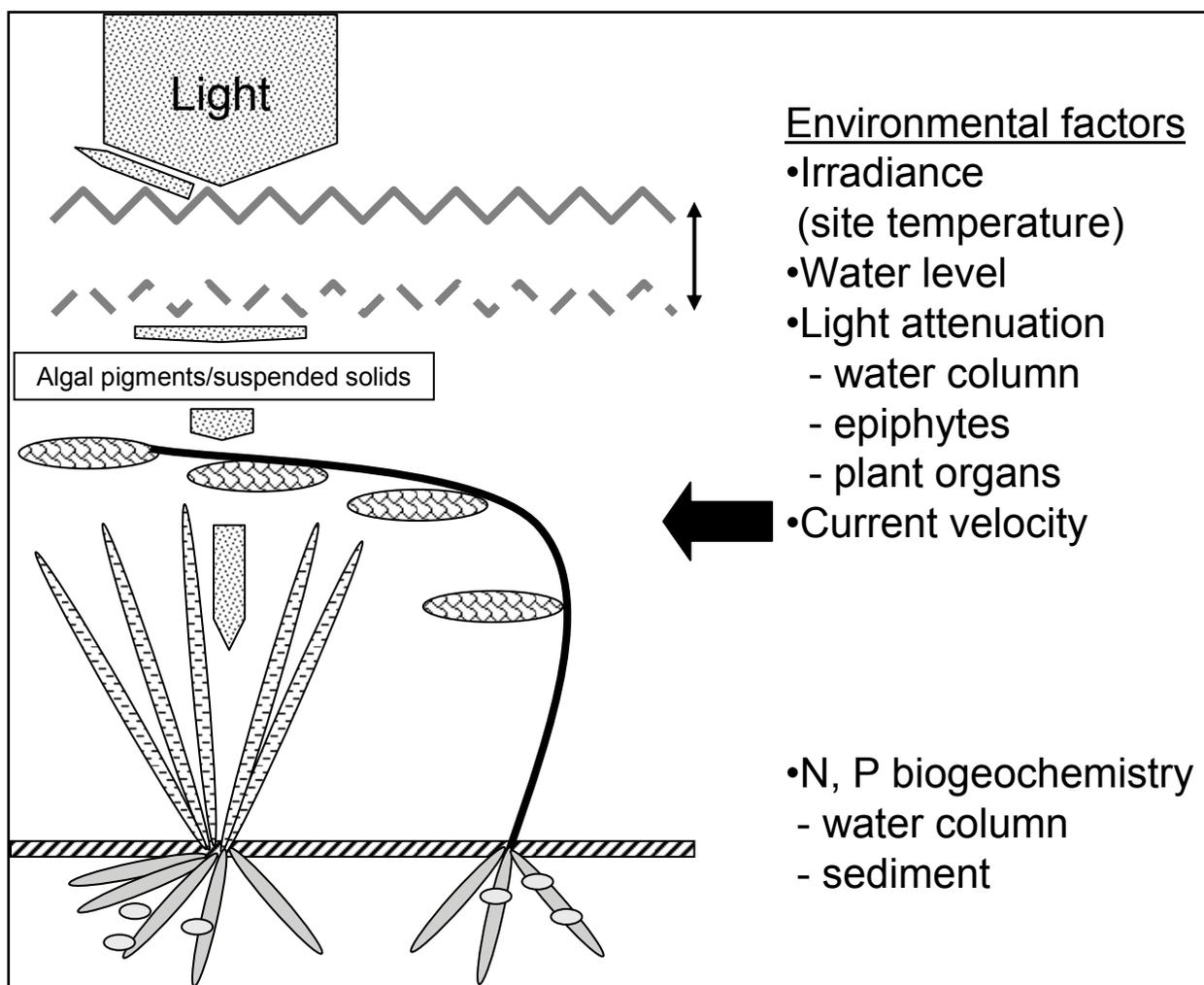

Figure 1.   Relationships between two meadow-forming and canopy-forming submersed plant species and their environment.
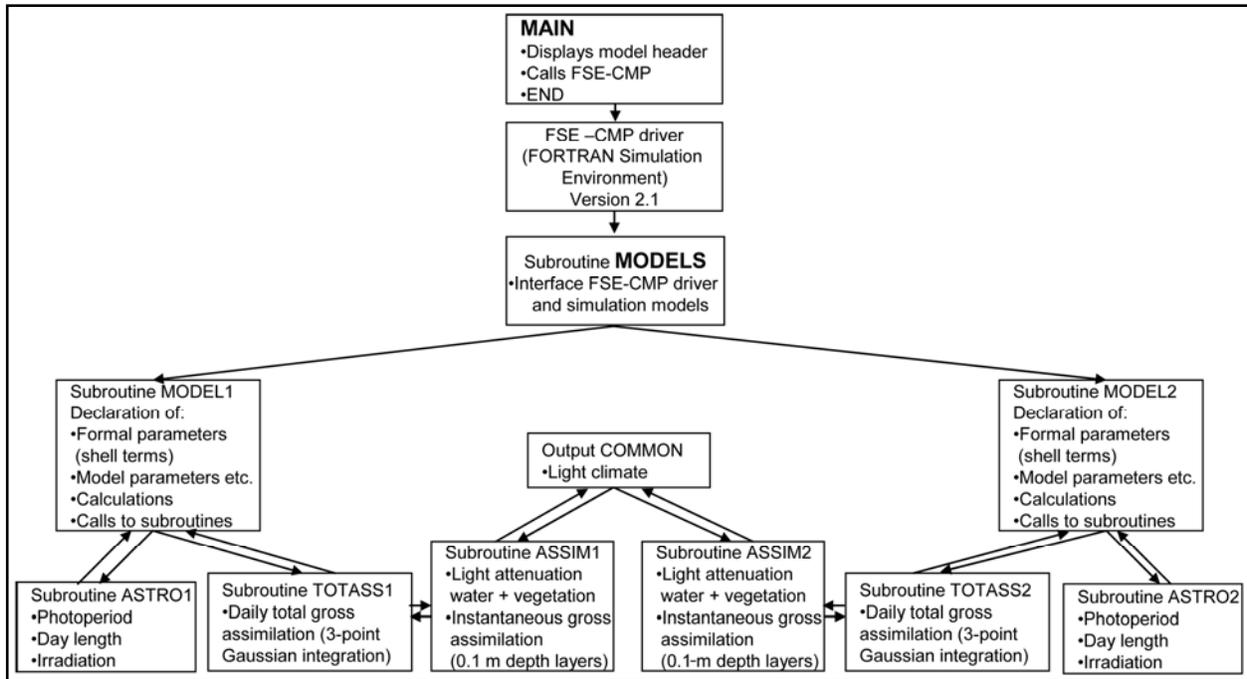
Figure 2. Relational diagram illustrating the organization of each model, its subroutines, and the common light climate output file in combination with the FSE shell.

Growth is considered as the plant dry matter accumulation including subterranean tubers, in an environment where N and P may be limiting under the prevailing weather conditions. At least one plant cohort waxes and wanes per season in different climatological regions, varying from temperate to tropical. The rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. The rate of CO_2 assimilation (photosynthesis) of the SAV community depends on the radiant energy absorbed by the canopy. The daily rate of gross CO_2 assimilation of the community is calculated from the absorbed radiation, the photosynthetic characteristics of individual shoot tips, and the pH-determined CO_2 availability. Calculations are executed in a set of subroutines added to the model (Figure 2). A portion of the carbohydrates produced is used to maintain the existing biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the conversion process, part of the weight is lost in respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors, defined as a function of the phenological cycle of the community. The dry weights (DW) of the plant organs are obtained by integration of their growth rates over time. The plant over-winters through tubers in the sediment without or with biomass present. Tubers are depleted and disintegrate in the summer following the season in which they were formed. All calculations are performed on a square meter basis. Since environmental factors and plant growth characteristics vary with depth, in the model the water column and associated growth-related processes have been partitioned in 0.10-m depth layers. Seed formation has not been included in the model, because its role in maintaining existing SAV communities in a temperate climate is minimal.

Species-characteristic phenological cycle. The phenology of the plant community, for which the development phase can be used as a measure, quantifies physiological age and is related to morphological appearance. It is modeled as a sequence of processes that take place

over a period of time, punctuated by more or less discrete events. Development phase (DVS) is a state variable in the models. The DVS is dimensionless and its value increases gradually within a growing season. The development rate (DVR) has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase. The response of DVR to temperature in the model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990). Calibration according to this hypothesis allows use of the model for the same plant species at various sites differing in climate (temperature regime). The relationships between the development phase, the day of year and 3 ^{o}C day-degree sum for a temperate climate are presented in Table 1. Each simulation starts at the first Julian day (i.e. 1 January, when the DVS has the value of 0.0), using a selected tuber bank density and individual tuber weight as initial values. Initiation of growth activity occurs by sprouting of the tubers at a DVS between 0.292 and 0.875 in *V. americana*. Sprouts of the first plant cohort develop through remobilization of carbohydrates until the tubers are depleted. If the first plant cohort does not succeed in becoming self-supporting and DVS is less than 0.875, a second cohort sprouts from the tuber bank. The DVS values of the phenological processes in *V. americana* differ from those in *P. pectinatus* (Table 1).

Table 1
Relationship between plant development phase (DVS), day of year, and 3°C day-degree sum in a temperate climate[1] (DVRVT= 0.015; DVRRT= 0.040; at a reference temperature of 30 ^{o}C)

Plant Developmental Phase	*V. americana*			*P. pectinatus*		
Description	DVS value	Day number	3°C Day-degree sum	DVS value	Day number	3°C Day-degree sum
First Julian day number → tuber sprouting and initiation elongation	0 → 0.291	0 → 105	1 → 270	0 → 0.210	0 → 77	1 → 193
Tuber sprouting and initial elongation → leaf expansion	0.292 → 0.875	106 → 180	271 → 1215	0.211 → 0.929	78 → 187	194 → 1301
Leaf expansion → floral initiation and anthesis	0.876 → 1.000	181 → 191	1216 → 1415	0.930 → 1.000	188 → 195	1302 → 1434
Floral initiation and anthesis → induction of tuber formation, tuber formation and senescence	1.001 → 2.000	192 → 227	1416 → 2072	1.001 → 2.000	196 → 233	1435 → 2077
Tuber formation and senescence → senesced	2.001 → 4.008	228 → 365	2073 → 3167	2.001 → 4.033	234 → 365	2078 → 3193
Senesced	4.008	365	3167	4.033	365	3193

[1] Calibration was: for *V. americana* on field data on biomass and water transparency from Chenango Lake, New York, 1978 (Titus and Stephens 1983) and climatological data from Binghamton (air temperatures) and Ithaca (irradiance), New York USA, 1978; for *P. pectinatus* on field data on biomass and water transparency from the Western Canal near Zandvoort, 1987 (Best and Boyd 2003) and climatological data from De Bilt, The Netherlands, 1987.

Instantaneous gross photosynthesis. Light availability is an important factor controlling the distribution and abundance of SAV. In aquatic systems a small part of the irradiance can be reflected by the water surface, and further attenuation occurs by water and its suspended solids and by SAV itself, either covered or not covered by epiphytes. Measured daily total irradiance (wavelength 300-3000 nm) is used as input in the model. Only half of the irradiance reaching the water surface is considered to be photosynthetically active and is, therefore, used as a base for the calculation of CO_2 assimilation. Part of the irradiance (6 percent) is reflected by the water

surface. The subsurface irradiance is attenuated by dissolved substances and particles (in mg L^{-1}) within the water column, resulting in a site- and season-specific water extinction coefficient (Appendix A, Equation 1). The remaining radiation may be further reduced by epiphyte shading (Appendix A, Equation 2). The vertical profiles of the radiation within the SAV layers are characterized also. The absorbed irradiance for each horizontal SAV layer is derived from these profiles (Appendix A, Equation 3). The SAV light extinction coefficient, *K*, is plant species-characteristic and assumed to be constant throughout the year. The incoming irradiance is attenuated by the shoots, part of which is absorbed by the photosynthetic plant organs, i.e., the leaves. Instantaneous rates of gross assimilation are calculated from the absorbed light energy and the photosynthesis light response of individual shoots, here used synonymously to leaves. The photosynthesis-light response of leaves is described by Equation 4 in Appendix A. In the photosynthesis-light response equation, the value of potential photosynthetic activity at light saturation (*AMX*) is species-characteristic and the initial light-use efficiency (*EE*) typical for C$_3$ plants. *AMX* is affected by temperature via a fitted, relative function, *AMTMPT*, accounting for the measured effect of daytime temperature, and enabling the calculation of the actual photosynthesis rate (*AMAX*). *AMAX* is affected by tissue N:P ratio via a species-characteristic, fitted, relative, function *NPREDF*, accounting for the measured effect of tissue N:P ratio on plant biomass production, here used synonymously for photosynthesis (Figure 3). *AMAX* may also be affected by current velocity via a species-characteristic, fitted, relative, function *REDAM1*, accounting for the measured effect of current velocity on *AMX*. Senescence and daily changes in pH and oxygen concentrations may affect *AMX*. Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer. The instantaneous rate of gross assimilation over the height of the vegetation is calculated by relating the assimilation rate per layer to the species-characteristic biomass distribution and by subsequent integration of all vegetation layers. The daily gross assimilation rate is calculated by using the Gaussian integration method. A portion of the carbohydrates formed is respired in maintenance of existing plant components and during the formation of new plant components (i.e. growth). After flowering, tubers are induced and formed under a specific combination of temperature and day length, and senescence sets in. The model for *V. americana* has been calibrated on data pertaining to a *V. americana* vegetation in Chenango Lake, NY, USA (Titus and Stephens 1983). The model for *P. pectinatus* has been calibrated on data pertaining to a *P. pectinatus* vegetation in the Western Canal near Zandvoort, The Netherlands (Best and Boyd 2003). The models simulated the dynamics of plant and tuber biomass and tuber numbers for the calibration and validation sites well over a period of one to five years. The models have been used to simulate plant and tuber biomass and tuber numbers for other sites with temperate and tropical climates as well. Key model equations dealing with photosynthesis and nutrient limitation are provided in Appendix A, and parameters, variables, and constants are provided in Table 2. More detailed descriptions of the equations involved and model applications can be found in Best and Boyd (2007, 2008). Executable versions of the models are available at *http://el.erdc.usace.army.mil/products.cfm?Topic=model&Type=aquatic*.
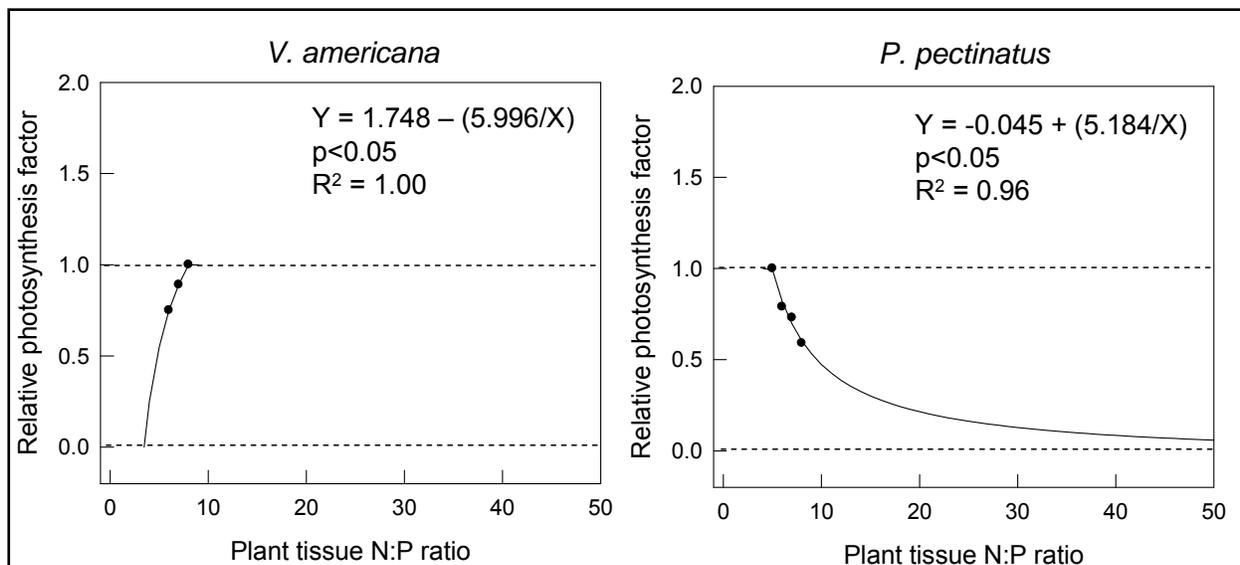
Figure 3. Relationship between tissue N:P ratio and relative photosynthesis factor (*NPREDF*). Values between 0 and 1 have been used for model calibration. Symbols indicate values measured in plant classes (W.F. James, USACE Eau Galle Laboratory, Spring Valley, WI, unpublished results, 2003).

Table 2
Parameters, variables and constants, grouped according to model processes

Var/Constant	c/v[a]	Value, Va	Value, Pp	Unit	Description	Source, Va	Source, Pp
Phenological cycle and development							
FLV(T)	v (tab)	0.718	0.731	Unitless	Fraction of total dry matter increase allocated to leaves as function of DVS	1, 2	3, 4
FST(T)	v (tab)	0.159	0.183	Unitless	Fraction of total dry matter increase allocated to stems as function of DVS	1, 2	3, 4
FRT(T)	v (tab)	0.123	0.086	Unitless	Fraction of total dry matter increase allocated to roots as function of DVS	1, 2	3
DDTMP	v			^{o}C	Daily average temperature (field site)		
DVRV(T)	v (tab)	0.015	0.015	d^{-1}	Development rate after flowering as function of temperature	Calibr.	Calibr.
DVRR(T)	v (tab)	0.040	0.040	d^{-1}	DVR prior to flowering as function of temperature	Calibr.	Calibr.
DVS	v			Unitless	Development phase	Calibr.	Calibr.
Wintering, sprouting, and growth of sprouts to water surface							
NPL	c	30	30	m^{-2}	Plant density	1	3, 5
NDTUB	v	233	240	m^{-2}	Dormant tuber density	6	3
INTUB	c	0.090	0.083	g DW tuber^{-1}	Tuber size	6, 7	3
RDTU	c	0.018	0.026	d^{-1}	Relative tuber death rate (on number basis)	1	8
NTUBD	v			N m^{-2}	Dead tuber number		
NTUBPD	v			N m^{-2}	Dead tuber number previous day		
NGTUB	v			N m^{-2}	Sprouting tuber number		

Var/Constant	c/v[a]	Value, Va	Value, Pp	Unit	Description	Source, Va	Source, Pp
REMOB	v			g CH_2O m^{-2} d^{-1}	Remobilization rate of carbohydrates		
ROC		0.0576	0.0576	g CH_2O g^{-1} DW d^{-1}	Relative conversion rate of tuber into plant material	9	9
RCSHST	c	12	12	m g^{-1} DW	Relation coefficient tuber weight-stem length	9,10	9, 10
CRIFAC	c	0.0091	0.0076	g DW $layer^{-1}$ $plant^{-1}$	Critical shoot weight per 0.1-m depth layer	6, 7	11, 12
SURPER	c	23	27	d	Survival period for sprouts without net photosynthesis	10, 13	3
TWGTUB	v			g DW m^{-2}	Total dry weight of sprouting tubers		
Photosynthesis, maintenance, growth, and assimilate partitioning							
SC	c			J m^{-2} s^{-1}	Solar constant corrected for varying distance sun-earth	14	14
TL	c	0.1	0.1	m	Thickness depth layer		
IABS(i)	v			J m^{-2} s^{-1}	Total irradiance absorbed by depth layer i		
IABSL(i)	v			J m^{-2} s^{-1}	Total irradiance absorbed by shoots in depth layer i		
IRZ(i)	v			J m^{-2} s^{-1}	Total photosynthetically active part of irradiance on top of depth layer i		
SC(i)	v			g DW m^{-2}	Shoot dry matter in depth layer i		
K(T)	v (tab)	0.0235	0.095	m^2 g^{-1} DW	Plant species specific light extinction coefficient as function of DVS	16	3
EPISHD	V (tab)	0-0.43	0-1.0	Unitless	Fraction of irradiation shaded by epiphytes	17	17
AMX	c	0.0165	0.019	g CO_2 g^{-1} DW h^{-1}	Potential CO_2 assimilation rate at light saturation for shoots	16	18
AMAX	v			g CO_2 g^{-1} DW h^{-1}	Actual CO_2 assimilation rate at light saturation for shoots		
EE	c	0.000011	0.000011	g CO_2 J^{-1}	Initial light use efficiency for shoots	14	14
NPRAT	v (tab)	6-8	5-8	Unitless	Plant biomass N:P ratio	15	
NPREDF(T)	v (eq)	0-1	0-1	Unitless	Relative AMX factor to account for nutrient limitation	15	
REDF(T)	v (tab)	1	1	Unitless	Relative reduction factor for AMX to account for senescence plant parts	User def.	User def.
REDAM	c	1	1	Unitless	Relative reduction factor to relate AMX to water pH and oxygen level	User def.	User def.
REDAM1	v (tab)	0-1	0-1	Unitless	Relative reduction factor to relate AMX to water current velocity	17	17
AMTMP(T)	v (tab)	0-1	0-1	Unitless	Daytime temperature effect on AMX as function of DVS	19	3
FGL	v			g CO_2 m^{-2} h^{-1}	Instantaneous CO_2 assimilation rate per vegetation layer		
GPHOT	v			g CH_2O m^{-2} d^{-1}	Daily total gross assimilation rate of the vegetation		
DMPC(T)	v (tab)	0-1	0-1	Unitless	Dry matter allocation to each plant layer	16	3
ASRQ	v			g CH_2O g^{-1} DW d^{-1}	Assimilate requirement for plant dry matter production		
FL(T)	v (tab)	0-1	0-1	Unitless	Leaf dry matter allocation to each layer of shoot as function of DVS	1, 2	3
GLV	v			g DW m^{-2} d^{-1}	Dry matter growth rate of leaves		
GST	v			g DW m^{-2} d^{-1}	Dry matter growth rate of stems		

Var/Constant	c/v[a]	Value, Va	Value, Pp	Unit	Description	Source, Va	Source, Pp
GRT	v			g DW m^{-2} d^{-1}	Dry matter growth rate of roots		
GTW	v			g DW m^{-2} d^{-1}	Dry matter growth rate of the vegetation (excl. tubers, rhizomes)		
TWLVG	v			g DW m^{-2}	Total dry weight live leaves		
TWSTG	v			g DW m^{-2}	Total dry weight live stems		
TWRTG	v			g DW m^{-2}	Total dry weight live roots		
TGW	v			g DW m^{-2}	Total live plant dry weight (excl. tubers, rhizomes)		
MAINT	v			g CH$_2$O m^{-2} d^{-1}	Maintenance respiration rate vegetation		
MAINTS	v			g CH$_2$O m^{-2} d^{-1}	Maintenance respiration rate vegetation at reference temperature		
Upper biomass limit	c	496	1,952	g DW m^{-2}	Maximum plant biomass	2	20
Flowering, translocation, senescence, and formation of wintering organs							
RTR	c	0.247	0.190	g DW tuber^{-1} d^{-1}	Maximum relative tuber growth rate at 20 $^{\circ}$C	7, 19, 21	3
RTRL	v			g DW tuber^{-1} d^{-1}	Relative tuber growth rate at ambient temperature		
CVT	c	1.05	1.05	Unitless	Conversion factor for translocated dry matter into CH$_2$O	14	14
NINTUB	c	5.5	8.0	N plant^{-1}	Tuber number concurrently initiated per plant	21	3, 12
TWCTUB	c	14.85	19.92	g DW m^{-2}	Total critical dry weight of new tubers	1,6, 21	3, 5
NNTUB	v			N m^{-2}	New tuber number		
RDR(T)	v (tab)	0.021	0.047	d^{-1}	Relative death rate of leaves as function of DAVTMP (on DW basis)	1	3
RDS(T)	v (tab)	0.021	0.047	d^{-1}	Relative death rate of stems and roots as function of DAVTMP (on DW basis)	1	3
TEFF(T)	v (tab)			Unitless	Relative effective temperature function accounting for temperature effect on maintenance respiration, remobilization, maximum tuber growth and death rates as function of temperature	Calibr.	
TRANS	v			g CH$_2$O m^{-2} d^{-1}	Translocation rate of carbohydrates		

1. Titus and Stephens 1983; 2. Haller 1974; 3. Best and Boyd 2003; 4. Sher Kaul et al. 1995; 5. Van Wijk 1989; 6. Korschgen and Green 1988; 7. Korschgen et al. 1997; 8. Best and Boyd 1996; 9. Bowes et al. 1979; 10. Best and Boyd 2007; 11. Spencer 1987;12. Spencer and Anderson 1987; 13. Titus and Adams 1979a; 14. Penning de Vries and Van Laar 1982; 15. Unpublished results. 2003. W.F. James, USACE Eau Galle Laboratory, Spring Valley, WI; 16. Titus and Adams 1979a; 17. Best et al. 2005; 18. Van der Bijl et al. 1989; 19. Donnermeyer 1982; 20. Howard-Williams 1978; 21. Donnermeyer and Smart 1985.

[a] c indicates that the parameter is a constant. v indicates a variable. eq and tab indicate that the parameter is implemented in the model as an equation and a table, respectively . Abbreviations: Va = *V. americana*; Pp = *P. pectinatus*.

METHODS SIMULATION STUDIES: The competition model composed by the framework, in which the ecological models VALLA (for *V. americana*) and POTAM (for *P. pectinatus*) were run simultaneously, requires daily values of the following environmental variables as inputs: water depth, water transparency, temperature (water or air), and irradiance. Among the required inputs, data on water depth can be derived from local and regional stage observations available via a web-based database. Data on water transparency can be derived from Secchi disk

observations also available via a web-based database using the relationship of Giessen et al (1990). According to Giessen et al. (1990), the light extinction coefficient (L), required as input for these ecological models, can be derived from measured Secchi disk depths following L (m^{-1}) = 1.65/ Secchi disk depth (m). The latter relationship is valid for turbid, shallow water only. Both water depth and water transparency data can also be generated from hydrodynamic and sediment transport model results (Best et al. 2008). Data on irradiance and air temperature can be obtained from local or regional weather stations.

In the present simulation studies the following environmental data were used as inputs: (i) a constant water depth of 0.5 m (Table 3; 0.5-m depth is typical for shallow water bodies such as river pools, but in addition usually daily and seasonal fluctuations occur as documented by Best and Boyd (2008)); (ii) light extinction coefficients, either typical for clear water such as in an oligotrophic lake (of 0.43 m^{-1}) or typical for turbid water such as river pools and peat lakes (of 2.0 m^{-1}; Table 3); (iii) weather data, either typical for the Mississippi River site of interest with a temperate climate, i.e., La Crosse, WI, for a year in which field data on *V. americana* and *P. pectinatus* distribution were collected (2001), or typical for a near subtropical climate where both species also abundantly grow but descriptions of wax, wane, and coexistence are still lacking, i.e., Davis, CA, 1990 (Table 3).

Table 3
Variables and constants, grouped according to field site characteristics and management

Var/Constant	c/v[a]	Value, Va	Value, Pp	Unit	Description	Source, Va	Source, Pp
Field site characteristics[b]							
DPT(T)	v (tab)	0.5	0.5	m	Water depth (field site)	User def.	User def.
WTMP(T)	v (tab)			^{o}C	Daily water temperature as function of day no. (field site)	User def.	User def.
L(T) - clear	v (tab)	0.43	0.43	m^{-1}	Water type specific light extinction coefficient as function of day no. (field site)	1, User def.	1, User def.
L(T) - turbid	V(tab)	2.0	2.0	m^{-1}	Water type specific light extinction coefficient as function of day no. (field site)	2, User def.	2, User def.
WVEL	v (tab)	0-100	0-100	cm s^{-1}	Water type specific current velocity as function of day no. (field site)	3, User def.	3, User def.
TGWM(T)	v (tab)			g DW m^{-2}	Total live dry weight measured as function of day no. (field site)	3, User def.	3, User def.
NTM(T) -Va	v (tab)	233	240	N m^{-2}	Tuber density measured as function of day no. (field site)	1, User def.	4, User-def.
Management (harvesting)							
HAR	c	0 or 1	0 or 1		Harvesting switch (0=off, 1=on)	User def.	User def.
HARDAY	c	1-365	1-365	d	Harvesting day number	User def.	User def.
HARDEP	c			m	Harvesting depth (measured in 0.1-m increments from water surface)	User def.	User def.

1. Titus and Stephens 1983; 2. Best et al. 1985; 3. Best et al. 2005; 4. Best and Boyd 2003.
[a] A c indicates that the parameter is a constant. A v indicates a variable and a tab indicates that the parameter is implemented in the model as a table. Abbreviations: Va = *V. americana*; Pp = *P. pectinatus*.
[b] Temperate field site: La Crosse, WI (lat 43° 10'N, long 91° 30'W); weather file 2001
Near subtropical field site: Davis, CA (lat 38° 22'N, long 121° 47'W); weather file 1990

The competition model also has options to include epiphyte shading, current velocity, and plant tissue N:P ratio governed nutrient limitation in the simulations. By activating these options, the models either use the default values of the input file or new measured values (that have to be inserted in the input file). Among the optional inputs, data on current velocity can be derived from local observations available via a web-based database or generated from hydrodynamic model results (Best et al. 2008). In contrast, data on epiphyte shading and on tissue nutrient N:P ratio are usually not easy to obtain, and should be determined. Epiphyte shading was determined in both plant species at the site of interest in Pool 8 of the Mississippi River, intercepting up to 43 percent of light in *V. americana* (usually 10 percent on mature plants) and up to 100 percent in *P. pectinatus* at the end of the growth season (Best et al. 2005). Tissue N:P ratio, and its relationship with biomass production, was determined experimentally by a one-season fertilization experiment in outdoor ponds, including 44 units for each plant species.[1] Results indicated that this relationship differed greatly in *V. americana* and *P. pectinatus*, with a certain N:P ratio indicating nutrient limitation in one species but not in the other, and vice versa. Biomass production in *V. americana* increased parabolically with increasing N:P ratio between 3.43 and 8.02, while in *P. pectinatus* it decreased hyperbolically with increasing N:P ratio ≥ 4.96. The relationship between tissue N:P ratio and biomass production was used as synonymous to the relationship between tissue N:P ratio and photosynthesis for model calibration. In the predecessor of the present modeling framework (Best and Boyd 2004), the calibration of the relationship between tissue N:P ratio and photosynthesis was based on published responses of two SAV species occupying niches similar to those of *V. americana* and *P. pectinatus*, i.e., *Zannichellia palustris* and *Elodea canadensis* (Spencer and Ksander 2003). Because responses to nutrient limitation turned out to be species-characteristic, the modelling framework was recalibrated. In the present simulation studies the following optional data were used as inputs: (i) epiphyte shading not activated, or activated using light interception increasing from 0 to 10 percent at the end of the growth season in *V. americana* and increasing from 0 to 100 percent at the end of the growth season in *P. pectinatus*; (ii) current velocity not activated; (iii) tissue N:P ratio-based nutrient limitation not activated, or activated using the experimentally determined species-characteristic regressions as photosynthesis-limiting factors (between 0 and 1) in the models (Figure 4) and chosen N:P ratios of interest in the input files.

Simulations were run to determine the effects of (i) competition for light without nutrient limitation under environmental conditions when *V. americana* and *P. pectinatus* occur in monotypic and mixed stands; and (ii) competition for light under potential limitation by N and P.

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[1] Unpublished results. 2003. W.F. James, USACE Eau Galle Laboratory, Spring Valley, WI.
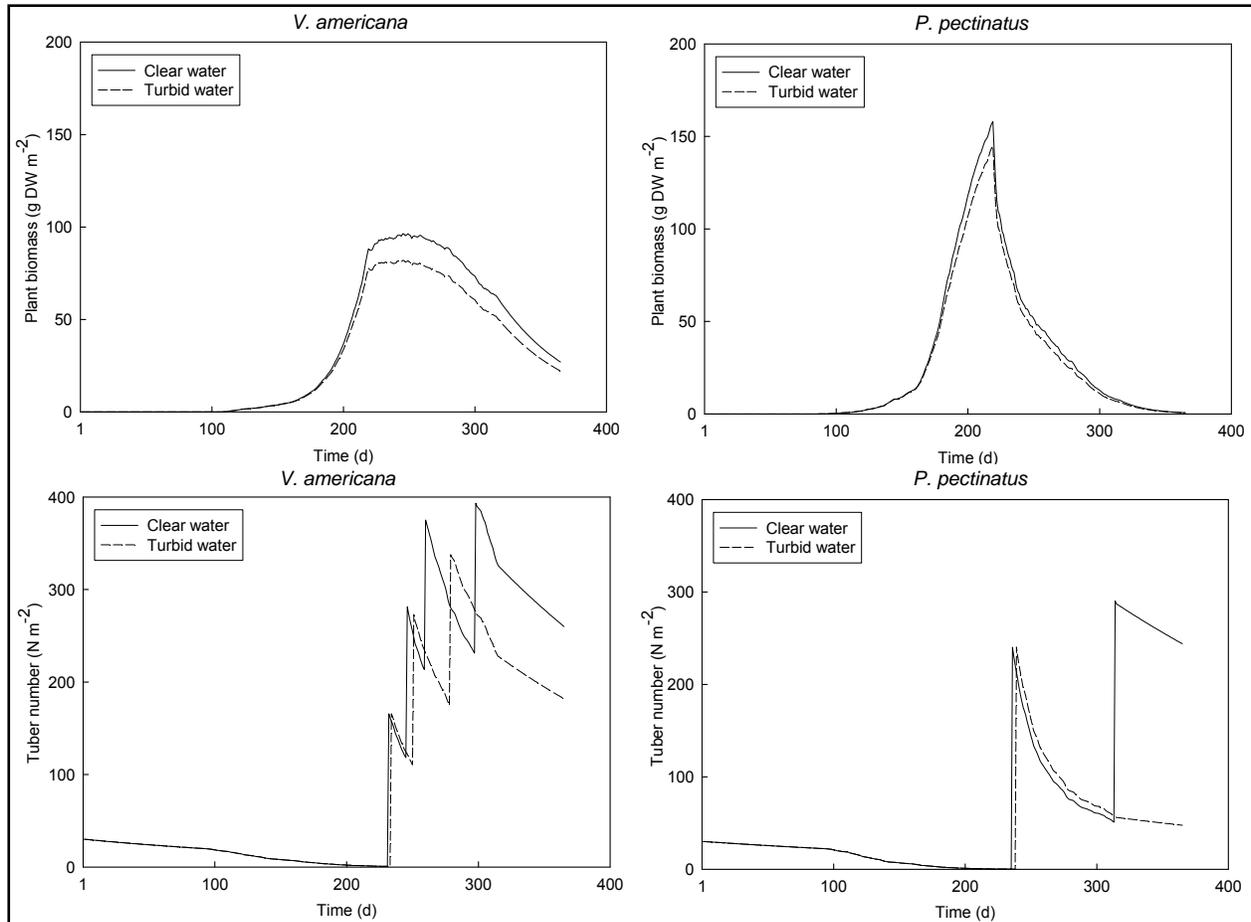
Figure 4. Simulated plant biomass and tuber numbers of monotypic *V. americana* and *P. pectinatus* communities in Pool 8 of the Upper Mississippi River, WI, USA.

RESULTS SIMULATION STUDIES:

Competition for light without nutrient limitation. The main objective of this part of the study was to identify environmental and vegetation density conditions, using a combination of irradiance, water level, water transparency, epiphyte shading, and plant density, that would favor colonization and persistence of *V. americana* and *P. pectinatus*, and enable coexistence of both species, without taking potential nutrient limitation into consideration.

Simulations by the model indicated that environmental conditions representative for Pool 8 of the Upper Mississippi River (0.5-m depth, turbid water, and a climate observed in 2001 at nearby La Crosse, WI) were conducive to the persistence of both plant species in monotypic stands, starting from 30 tubers/m^2 and growing at a plant density of 30 plants/m^2, since considerable biomass and at least one tuber class were produced (Figure 4). Peak biomass was less but maximum tuber number a factor of 1.3 greater in *V. americana* than in *P. pectinatus*. Simulated peak plant biomass was within the range of measured plant biomass for *V. americana* and was a factor of 3 higher than measured for *P. pectinatus*, with the simulated maxima lagging somewhat behind the observed ones (Best et al. 2005). The overprediction of plant biomass for *P. pectinatus* was attributed to the fact that modeled biomass was generated from a tuber bank

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density of 30 m^{-2}, while heavy grazing by waterfowl may have depleted tuber bank densities to far lower numbers in Pool 8 (Kenow et al. 2004). Under simulated clear water conditions, plant biomass increased only by 5 to 10 percent, but tuber number to a far greater extent, providing tuber bank densities of 280 m^{-2} to *V. americana* and of 260 m^{-2} to *P. pectinatus* at the end of the year (Figure 4).

The completion of at least one tuber class is a prerequisite for persistence in both species, which lose their entire plant biomass at the end of the growth season under temperate conditions, and initiate growth the subsequent season from tubers. The completion of more tuber classes provides more opportunities for persistence, e.g., enabling initiation of growth from a second cohort of tubers when the first cohort has depleted its carbohydrate reserves prior to becoming self-sufficient plants under unfavorable environmental conditions in spring. Because tubers are relatively short-lived (<one year), tuber production is a good indicator of persistence potential for these plants, and, therefore, the maximum tuber number was used as the main parameter to evaluate persistence potential in the present study.

Conditions under which intraspecific competition for light occurred were first explored using the model. This was done by simulating the behavior of monotypic stands with plant densities increasing from 1 to the typical density of 30 plants/m^2 found in stable macrophyte beds under natural conditions (Titus and Stephens 1983; Best and Boyd 2003; Van Wijk 1989). The effects of low and high light levels on plant persistence in monotypic stands were also explored. Large differences in light levels were introduced into the simulations by exposing the model plants to typical temperate and near subtropical climates. Effects of subtropical and tropical climates were not included in these simulations, because in the latter climatological conditions the effects of light level by itself become confounded by those of day length and temperature on tuber initiation and production. Smaller differences in light levels were introduced by exposing the model plants to water transparencies characteristic of turbid and clear waters, without and with typical shading by epiphytes.

In monotypic *V. americana* stands, intraspecific competition for light occurred at plant densities ≥25 plants/m^2 in both climates, when the linear increase in maximum tuber number with plant density leveled off in turbid as well as clear water (Table 4). Persistence potential was less in turbid than in clear water, and less in a temperate than in a near subtropical climate. Low epiphyte shading increased persistence potential in clear but not in turbid water in a temperate climate, and decreased persistence in turbid but not in clear water in a near subtropical climate (Table 4). In monotypic *P. pectinatus* stands, intraspecific competition for light occurred at plant densities ≥25 m^{-2} in turbid water, >27 m^{-2} in clear water in a temperate climate, and not at all in a near subtropical climate (Table 4). As with *V. americana*, persistence potential was less in turbid than in clear water, and less in a temperate than in a near subtropical climate. High epiphyte shading completely prevented the completion of tubers at plant densities ≥15 m^{-2} in a temperate climate, at densities of ≥25 m^{-2} in turbid water, and of ≥30 m^{-2} in clear water and in a near subtropical climate (Table 4). Thus, epiphyte shading may play an important role in regulating *P. pectinatus* persistence.

Table 4
Simulated maximum tuber number in monotypic stands of *V. americana* and *P. pectinatus* in relation to plant density at sites differing in climate, water transparency, and epiphyte cover (= EC). [N] = maximum equals initial tuber number

Plant Density (N m⁻²)	Maximum Tuber Number (N m⁻²)							
	Temperate Climate				Near Subtropical Climate			
	Turbid Water	Clear Water	Turbid Water	Clear Water	Turbid Water	Clear Water	Turbid Water	Clear Water
	No EC	No EC	EC	EC	No EC	No EC	EC	EC
V. americana								
1	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]
2	27	30	29	36	48	58	52	68
5	70	81	73	94	114	144	122	163
10	137	156	141	179	194	246	203	265
15	187	228	202	253	250	323	248	331
20	242	292	242	304	302	366	299	366
25	292	344	292	365	324	388	317	388
26	301	356	302	379	334	399	330	399
27	310	366	310	394	342	411	333	411
28	321	377	321	404	346	423	349	423
29	332	383	326	397	363	434	342	424
30	337	393	336	409	356	436	348	436
P. pectinatus								
1	[1]	[1]	[1]	[1]	[1]	[1]	[1]	[1]
2	[2]	[2]	[2]	[2]	101	125	32	41
3	142	156	27	31	122	134	47	58
4	159	180	32	38	134	147	59	69
5	164	190	40	46	149	168	61	79
7	182	199	56	56	178	176	79	86
10	195	220	80	80	164	208	80	111
15	231	243	[15]	[15]	190	231	120	120
20	241	249	[20]	[20]	236	240	160	160
25	272	293	[25]	[25]	236	287	[25]	200
27	216	306	[27]	[27]	269	291	[27]	216
30	240	290	[30]	[30]	270	305	[30]	[30]

Conditions under which interspecific competition for light occurred were subsequently explored using the model. This was done by simulating the behavior of mixed stands maintaining total plant density at 30 m⁻², the density that would be expected in an established plant stand composed of either species, and varying the plant density ratio of *V. americana* relative to *P. pectinatus* (Va : Pp) between 30:0 and 0:30, and varying the light availability to the mixed stands following the same approach as for monotypic stands. In mixed stands, *V. americana* outcompeted *P. pectinatus* only at Va:Pp density ratios ranging from 29:1 to 28:2 without epiphyte shading, and ranging from 29:1 to 20:10 with epiphyte shading (Table 5). *P. pectinatus* outcompeted *V. americana* in the absence of epiphyte shading at ratios ranging from 24:6 to 1:29. The competitive ability of *P. pectinatus* was greatly diminished by epiphyte shading,

particularly in a temperate climate where it only persisted and outcompeted *V. americana* in clear water at a Va:Pp density ratio of 20:10 (Table 5). Coexistence occurred only in a narrow ratio range, i.e. at Va:Pp density ratios ranging from 27:3 to 25:5 in a temperate climate with turbid water providing better opportunities for coexistence than clear water, and ranging from 28:2 to 25:5 in a near subtropical climate with no difference between clear and turbid water conditions being apparent. No coexistence occurred in the presence of an epiphyte cover (Table 5).

Table 5
Simulated maximum tuber number in a mixed stand of *V. americana* and *P. pectinatus* in relation to plant density ratio at sites differing in climate, water transparency, and epiphyte cover (= EC). [N] = maximum equals initial tuber number. Coexistence cases shaded

Plant Density Ratio (N_{Va} : N_{Pp})	Maximum Tuber Number (N m^{-2})							
	Turbid Water				Clear Water			
	No EC Va	Pp	EC Va	Pp	No EC Va	Pp	EC Va	Pp
Temperate climate								
30 : 0	337	[0]	336	[0]	393	[0]	409	[0]
29 : 1	332	[1]	326	[1]	383	[1]	397	[1]
28 : 2	321	[2]	321	[2]	377	[2]	404	[2]
27 : 3	310	29	310	[3]	366	40	394	[3]
26 : 4	298	41	298	[4]	356	49	379	[4]
25 : 5	290	40	290	[5]	[25]	190	370	[5]
24 : 6	[24]	180	280	[6]	[24]	196	361	[6]
20 : 10	[20]	195	242	[10]	[20]	220	[20]	80
15 : 15	[15]	231	[15]	[15]	[15]	243	[15]	[15]
10 : 20	[10]	241	[10]	[20]	[10]	249	[10]	[20]
5 : 25	[5]	272	[5]	[25]	[5]	293	[5]	[25]
0 : 30	[0]	240	[0]	[30]	[0]	290	[0]	[30]
Near subtropical climate								
30 : 0	356	[0]	348	[0]	436	[0]	436	[0]
29 : 1	363	[1]	342	[1]	434	[1]	424	[1]
28 : 2	346	38	349	[2]	423	46	423	[2]
27 : 3	342	37	333	[3]	411	57	411	[3]
26 : 4	334	45	330	[4]	399	64	399	[4]
25 : 5	324	45	321	[5]	388	166	388	[5]
24 : 6	[24]	142	311	[6]	[24]	173	381	[6]
20 : 10	[20]	164	[20]	299	[20]	208	[20]	111
15 : 15	[15]	190	[15]	120	[15]	231	[15]	120
10 : 20	[10]	236	[10]	160	[10]	228	[10]	160
5 : 25	[5]	263	[5]	[25]	[5]	287	[5]	200
0 : 30	[0]	270	[0]	[30]	[0]	305	[0]	[30]

Competition for light under potential limitation by N or P. In typical, relatively dense, SAV communities with 30 plants/m^2, as modeled in the present study, light availability is often limiting (see above), and, thus, competition for light occurs. When light is not limiting the whole

growth season or part of the season, nutrients can be limiting, and in these cases the outcome of competition for light is difficult to predict in two plant species with different sensitivities to potential nutrient limitation that are able to coexist under conditions in which nutrients are not limiting. In the present study, interspecific competition for light under potential nutrient limitation was explored using the model by conducting runs at the same plant density ratios at which coexistence was observed in the simulations when nutrients were not limiting (Table 5). Model runs were conducted in which the following tissue N:P ratios were assigned to both plant species (i) 3.5, indicative for severe N limitation and limiting the AMAX by a factor of 0.03 in *V. americana* (not in *P. pectinatus*), (ii) 6.0, indicative for moderate N limitation and limiting the AMAX by a factor of 0.75 in *V. americana* (not in *P. pectinatus*), and (iii) 8.0, indicative of moderate P limitation and limiting the AMAX by a factor of 0.6 in *P. pectinatus* (not in *V. americana*; Figure 4). Simulation results indicated that coexistence was completely eliminated by nutrient limitation, with *P. pectinatus* winning the competition at tissue N:P ratio's ≤ 6.0 and *V. americana* winning at a tissue N:P ratio ≥ 8.0 in cases where coexistence occurred in the absence of nutrient limitation (Table 6).

Table 6
Simulated maximum tuber number in a mixed stand of *V. americana* and *P. pectinatus* in relation to plant density at sites differing in climate and water transparency, at tissue N:P ratios associated with nitrogen and phosphorus limitation. [N] = maximum equals initial tuber number. Coexistence cases shaded

Plant density ratio (N_{Va} : N_{Pp})	Tissue N : P ratio	Maximum tuber number (N m^{-2})							
		Temperate climate				Near subtropical climate			
		Turbid water		Clear water		Turbid water		Clear water	
		Va	Pp	Va	Pp	Va	Pp	Va	Pp
28 : 2	NA	321	[2]	377	[2]	346	38	423	46
27 : 3	NA	310	29	366	40	342	37	411	57
26 : 4	NA	298	41	356	49	334	45	399	64
25 : 5	NA	290	40	[25]	190	324	45	388	166
28 : 2	3.5	[28]	[2]	[28]	[2]	[28]	96	[28]	125
27 : 3	3.5	[27]	142	[27]	156	[27]	122	[27]	134
26 : 4	3.5	[26]	159	[26]	180	[26]	134	[26]	147
25 : 5	3.5	[25]	164	[25]	190	[25]	149	[25]	168
28 : 2	6.0	[28]	[2]	[28]	[2]	[28]	26	[28]	27
27 : 3	6.0	[27]	41	[27]	70	[27]	38	[27]	52
26 : 4	6.0	[26]	79	[26]	93	[26]	38	[26]	72
25 : 5	6.0	[25]	95	[25]	110	[25]	65	[25]	90
28 : 2	8.0	321	[2]	372	[2]	346	[2]	423	[2]
27 : 3	8.0	310	[3]	364	[3]	342	[3]	411	[3]
26 : 4	8.0	298	[4]	354	[4]	334	[4]	399	[4]
25 : 5	8.0	290	[5]	342	[5]	324	[5]	388	[5]

DISCUSSION: Competition for light proved to be a far more important determinant of potential persistence and species composition of SAV than the availabilities of N and P. This outcome supports the explanation for the general decline in SAV in the UMRS provided by Rogers (1996), i.e., attributable mainly to decreased light availability due to increased turbidity from

runoff, erosion and navigation activities, with decreased nutrient availability due to depletion of sediment nutrients, toxification due to increased agricultural herbicide use, and grazing contributing also. However, the outcome of the present modeling study contrasts with those of two experimental studies on other SAV species. Results of a field experiment at sites varying in sediment nutrient availability in which neighbor plants were selectively removed, suggested that interspecific competition between naturally coexisting submersed plant species is small, and that spatial heterogeneity or differential utilization of abiotic resources promotes species diversity in SAV communities (Chambers and Prepas 1990). In addition, results of a competition experiment in *Myriophyllum spicatum* L. and *Najas marina* L. indicated that growth inhibition at increased plant density in mixed cultures exceeded inhibition in monocultures, and was attributed to depletion of resources other than light (Agami and Waisel 2002).

In the present modeling study, intraspecific competition for light occurred in stands of both plant species at different plant densities, in *V. americana* at 25 m^{-2} and in *P. pectinatus* at 25 to >27 m^{-2} in a temperate climate and not at all in a near subtropical climate. Persistence potential generally decreased with the capturable light quantity: it was less in turbid than in clear water, and less in a temperate than in a tropical climate. Epiphyte shading at levels typical for Upper Mississippi River Pools barely affected persistence in *V. americana* but greatly diminished persistence in *P. pectinatus*. Interspecific competition for light greatly affected the species composition in mixed stands. *V. americana* outcompeted *P. pectinatus* at Va:Pp density ratios of 29:1 to 28:2, *P. pectinatus* outcompeted *V. americana* at ratios ranging from 24:6 to 1:29 in the absence of epiphyte shading but to a far lesser extent when covered by epiphytes. Coexistence of both species occurred only in a narrow ratio range of 27:3 to 25:5 in a temperate climate and 28:2 to 25:5 in a near subtropical climate. At the low tuber densities of *P. pectinatus*, as occur in coexistence cases, any tuber removal may shift the SAV vegetation into predominance by *V. americana* the subsequent year, and, thus, this may explain between-year fluctuations in coexistence of both species and replacement of one species by the other observed in river systems. Such a case is illustrated in Figure 5, where simulated plant biomass and tuber number in a mixed stand with a Va: Pp plant density ratio of 26:4 under temperate climatological conditions are presented. Under these conditions both plant species coexisted in turbid and clear water and showed persistence potential since both completed tuber classes, while only *V. americana* persisted in the presence of epiphyte shading. However, without any tubers being inactivated by processes other than senescence, e.g., grazing, heavy sedimentation or scouring, the mixed plant stands were expected to be completely dominated by *P. pectinatus* during the subsequent year, since the end-of-year tuber number of the latter species was on the order of 20 tubers/m^{-2}. Nutrient limitation eliminated coexistence completely, with *V. americana* winning at a tissue N:P ratio $\geq$ 8.0 in cases where the absence of nutrient limitation coexistence occurred and *P. pectinatus* winning the competition at tissue N:P ratio's $\leq$ 6.0.
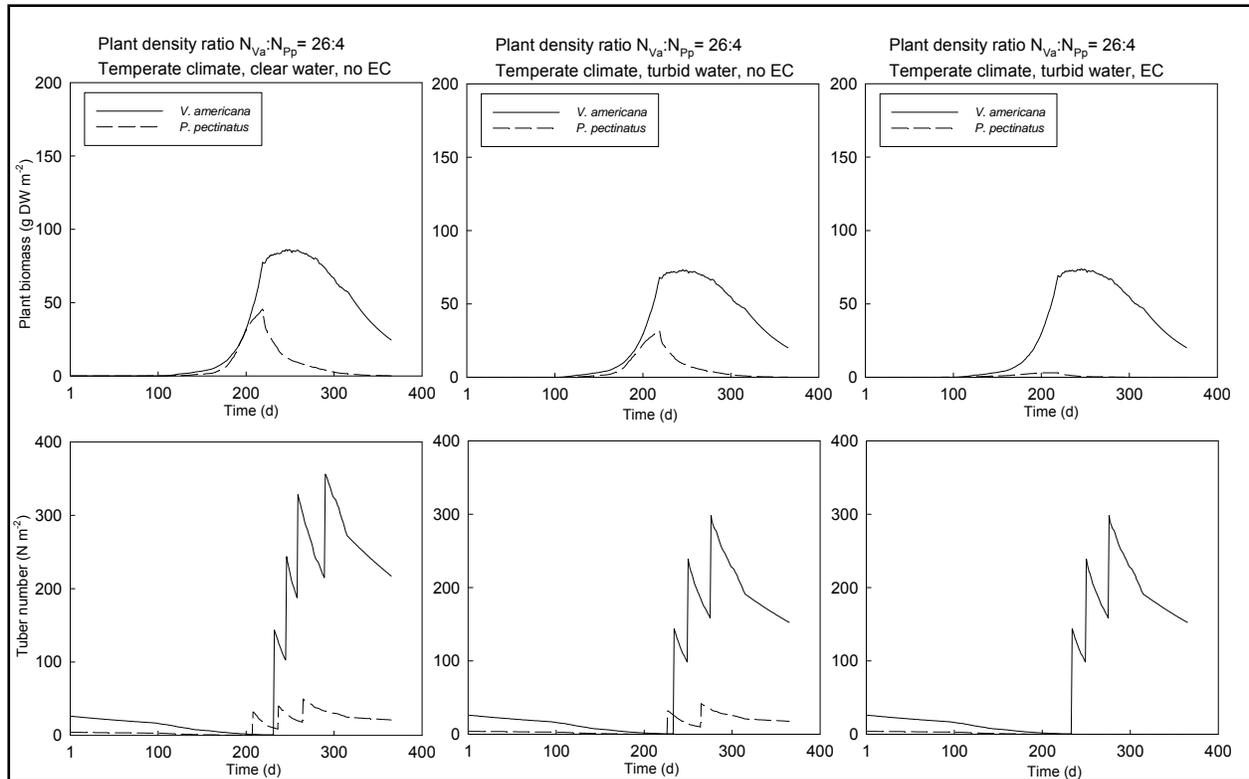
Figure 5. Simulated plant biomass and tuber numbers of a mixed plant community composed by *V. americana* and *P. pectinatus* at a Va : Pp plant density ratio of 26 : 4 in Pool 8 of the Upper Mississippi River, WI, USA.

The results of the present modeling study may indicate that *P. pectinatus* has a high potential of replacing *V. americana* when allowed to colonize gaps in dense *V. americana* stands. N limiting conditions strengthen and P limiting conditions weaken the competitive potential of *P. pectinatus* relative to that of *V. americana*, while higher N and P availabilities enhance the potential for coexistence between both species. This may provide a basis for management and restoration of SAV with a desired species composition.

SUMMARY: Management and restoration of shallow water bodies to promote growth of submersed aquatic vegetation (SAV) with a desired species composition requires knowledge of the environmental factors affecting SAV growth, persistence, and species interactions, and a means to predict the success of SAV reestablishment under different management scenarios to improve these conditions. A dynamic ecological modeling approach was used to relate SAV responses to changes in physical and chemical conditions, and to each other. Competition for light proved to be a far more important determinant of potential persistence and species composition of SAV than the availabilities of nitrogen (N) and phosphorus (P). Intraspecific competition for light occurred in stands of both plant species at different plant densities. Persistence potential generally decreased with the capturable light quantity: it was less in turbid than in clear water, and less in a temperate than in a tropical climate. Epiphyte shading at levels typical for Upper Mississippi River Pools barely affected persistence in *V. americana* and greatly diminished persistence in *P. pectinatus*. Interspecific competition for light greatly affected the species composition in mixed stands. *V. americana* outcompeted *P. pectinatus* at Va:Pp density

ratios of 29:1 to 28:2, *P. pectinatus* outcompeted *V. americana* in the absence of epiphyte shading at ratios ranging from 24:6 to 1:29. Coexistence of both species occurred only in a narrow ratio range of 27:3 to 25:5 in a temperate climate and 28:2 to 25:5 in a near subtropical climate. Nutrient limitation eliminated coexistence completely, with *V. americana* winning at a tissue N:P ratio ≥ 8.0 in cases where coexistence occurred in the absence of nutrient limitation *and P. pectinatus* winning the competition at tissue N:P ratios ≤ 6.0. The results of the present study indicate that *P. pectinatus* has a high potential of replacing *V. americana* when allowed to colonize gaps in dense *V. americana* stands. N limiting conditions strengthen and P-limiting conditions weaken the competitive potential of *P. pectinatus* relative to that of *V. americana*, while higher N and P availabilities enhance the potential for coexistence between both species. This may provide a basis for management and restoration of SAV with a desired species composition.

PRODUCT DEVELOPMENT AND AVAILABILITY: Aquatic plant growth models are available to both U.S. Army Corps of Engineers (USACE) and non-USACE interested parties. The 3.0 versions can be downloaded from the following URL: *http://el.erdc.usace.army.mil/ products.cfm?Topic=model&Type=aquatic*. Model descriptions and user manuals can be downloaded from the same web page.

POINTS OF CONTACT: This technical note was prepared by Dr. Elly P. H. Best and William A. Boyd, research biologists at the U.S. Army Engineer Research and Development Center, Environmental Laboratory. The upgrading of the model was conducted as an activity of the ecological model development work unit of the System-Wide Water Resources Program (SWWRP). For information on SWWRP, please contact *https://swwrp.usace.army.mil/* or contact the Program Manager, Dr. Steven L. Ashby, at *Steven.L.Ashby@usace.army.mil*. Questions about this technical note may be addressed to Dr. Best at 601-634-4246; *Elly.P.Best@usace.army.mil*. This technical note should be cited as follows:

> Best, E. P. H., and W. A. Boyd. 2009. A recalibrated simulation model (Version 3.0) on the competition for light for American wildcelery and Sago pondweed at high and low nutrient availability. ERDC TN-SWRRP-09-5, Vicksburg, MS: U.S. Army Engineer Research and Development Center. *https://swwrp.usace.army.mil/*

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Appendix A

Equation 1

$$IRZ_{i+1} = \frac{\left(-TL \times L - K \times SC_i\right)}{IRZ_i \times e} \tag{1}$$

$$IABS_i = \frac{\left(IRZ_i - IRZ_{i+1}\right) \times SC_i \times K}{\left(K \times SC_i + TL \times L\right)} \times \left(1.0 - EPISHD\right) \tag{2}$$

$$IABSL_i = IABS_i \times FL \tag{3}$$

$$FGL = SC_i \times NPREDF \times AMAX \times \left(1 - \exp\left[\frac{-EE \times IABS_i \times 3600}{AMAX \times SC_i}\right]\right) \tag{4}$$