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Aquatic Plant Control Research Program

A Simulation Model on the Competition for Light of Meadow-forming and Canopy-forming Aquatic Macrophytes at High and Low Nutrient Availability

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ABSTRACT:

A simulation model has been developed that focuses on the ability of two competing submersed macrophytes, meadow-forming and canopy-forming, to maintain their biomass under different environmental conditions. *Vallisneria americana* (American wildcelery) serves as the example for meadow-forming plants and *Stuckenia pectinata* (until recently known as *Potamogeton pectinatus* or sago pondweed) for canopy-forming plants. The model can be used to predict changes in species composition of submersed vegetation as a result of changes in the availability of resources in shallow freshwater bodies.

In the model, the two plant species compete for light and exhibit different species-specific relationships between plant tissue nitrogen (N):phosphorus (P) ratio and plant biomass production. The latter species-specific relationships have not been determined in *V. americana* and *P. pectinatus*, and, therefore, for calibration of the model, the specific relationships between plant tissue N:P ratio and reduction in plant biomass production of *Zannichellia palustris* and *Elodea canadensis* were used. The latter species have habitat preferences similar to those of *V. americana* and *P. pectinatus*.

Competition for light proved to be a far more important determinant of species composition than the availabilities of N and P in the sediment.

Intraspecific competition for light did not occur in *V. americana* in a temperate climate, but it was observed at densities $\geq$ 8-9 plants m^{-2} in a more southern climate. It occurred in *P. pectinatus* at plant densities $\geq$4-5 plants m^{-2}.

Coexistence of both species occurred only at *V. americana*:*P. pectinatus* plant density ratios of 28:2 to 26:4 plants m^{-2} in the absence of N and P limitation of growth, irrespective of climate (temperate and more southern climates tested). At density ratios higher than 28:2, *V. americana* excludes *P. pectinatus*, and at density ratios lower than 26:4, *P. pectinatus* excludes *V. americana*. The density ratio range at which coexistence was possible increased with water turbidity between extinction coefficients of 0.43 and 2.00 m^{-1}. Light interception by epiphytes at a level of 25 percent of observed maxima in the Upper Mississippi River allowed coexistence in clear water but prevented it in turbid water in a more southern climate. Under N limiting conditions for both species, *P. pectinatus* displaced *V. americana*, but under P limiting conditions for *P. pectinatus*, *V. americana* won the competition. Coexistence was expanded by fertilization with both N and P.

These results 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 advantage of *P. pectinatus* relative to that of *V. americana*, while raised N and P availabilities enhance the potential for coexistence of both species. These notions can be used as a basis for management of submersed macrophytes.

It is recommended to verify/determine the species-specific relationships between plant tissue N:P ratio and plant biomass production of *V. americana* and *P. pectinatus* and validate the model coexistence results by comparison with outcomes from plant competition experiments.

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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit Number 33308. The APCRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Research and Development Center (ERDC) under the purview of the Environmental Laboratory (EL), Vicksburg, MS. Funding was provided under Department of the Army Appropriation 96X3122, Construction General. Mr. Robert C. Gunkel, Jr., EL, ERDC, was Program Manager for the APCRP. Program Monitor during this study was Mr. Timothy R. Toplisek, HQUSACE.

This study was conducted and the report written by Dr. Elly P. H. Best, Dr. Gregory A. Kiker, and Mr. William A. Boyd, Ecosystem Processes and Engineering Division (EPED), EL, ERDC. Dr. David Spencer, U.S. Department of Agriculture – Agricultural Research Service, Weed Science Program, University of California, Davis, CA, provided an external technical review. The report was reviewed internally by Dr. David M. Soballe and Dr. Linda Nelson, EPED, EL.

This investigation was conducted under the direct supervision of Dr. Lance D. Hansen, Chief, Environmental Risk Assessment Branch, and the general supervision of Dr. Richard E. Price, Chief, EPED, EL, and Dr. Beth Fleming, Acting Director, EL.

Commander and Executive Director of ERDC was COL James R. Rowan, EN. Director was Dr. James R. Houston.

1 Introduction

Competition

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. Indeed, Grime's triangle would suggest that in highly disturbed or very harsh environments, competition may not be an important process.

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 seeds or vegetative propagules, is also important. However, it may not be measured often in short-term studies.

Relationship of Plant Traits to Competitive Ability

Evidence from field studies, laboratory experiments, and ecological theory has converged on the conclusion that species from high-resource environments exhibit high relative growth rates (RGR), whereas species from low-resource

environments will compete most effectively by minimizing tissue loss (greater tissue longevity) more than by maximizing resource gain. The ecological advantage of a high potential RGR seems straightforward; fast growth results in the rapid occupation of a large space, which leads to the preemption of limiting resources (Grime 1977). A high RGR may also facilitate rapid completion of the life cycle of a plant, which is essential for plant species that occur in highly-disturbed but non-stressful environments (ruderals), whose habitat does not persist for a long time. In growth analyses and in short-term competition experiments carried out at a limiting nutrient supply, potentially fast-growing species grow faster and produce more biomass than do slow-growing ones (Lambers and Poorter 1992).

The question arises then why plants with a high potential RGR do not become dominant at nutrient-poor sites. It has been demonstrated that the low tissue mass density of fast-growing species is associated with a more rapid turnover of their leaves and a shorter mean residence time of nutrients. Turnover of plant parts causes loss of about half of the leaf nutrients from the plant and reduces the mean residence time of the nutrients (Reich 1993). Although rapid growth may therefore lead to a competitive advantage in the short term, even when the nutrient supply is severely limiting, there is a penalty associated with this trait in the long run (Tilman 1988). That is, the losses associated with tissue turnover become so large that they can not be compensated for by uptake of nutrients from the nutrient-poor environment. As a result, the fast-growing species are not as competitive as slower-growing species, once the time scale of the experiment is long enough that differences in tissue loss and mean residence time influence the outcome of the competition (Aerts and Van der Peijl 1993).

Another reason for shorter nutrient residence times in faster-growing plant species at a low nutrient supply is that species differ in the manner in which they respond to a limitation of nutrients in the environment. The typical response of a fast-growing species upon sensing nutrient shortage is to promote leaf senescence and thus withdraw nutrients from older leaves and use these for its newly developed tissues. A slow-growing species that occurs naturally on nutrient-poor sites may slow down the production of new tissues, with less dramatic effects on leaf senescence and allocation pattern. Slow-growing species have been suggested to grow closer to their optimum than fast-growing species in an adverse environment (Chapin 1980). This explanation suggests that allocation or other aspects of the plant's physiology at a low nutrient supply is closer to the optimal pattern for inherently slow-growing species than it is for fast-growing ones. Thus, environmentally-induced senescence may be far stronger in faster-growing species, causing relatively more nutrient loss, than it is in slower-growing species. Information on the pattern of allocation, however, indicates that both fast-and slow-growing species allocate their carbon and nitrogen in a manner that will maximize their relative growth rate (Van der Werf et al. 1993).

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, as suggested by Tilman for terrestrial grasses (Tilman 1988; Wedin and Tilman 1990; Tilman and Wedin 1991). Rather, it involves a wide range of traits and subtle differences in resistance to different environmental circumstances (Lambers et al. 1998). Important traits in this respect are: propagule size,

growth rate, tissue turnover, allocation pattern, growth form, tissue mass density, and plasticity, while traits associated with competition for the specific resources of light and nutrients are outlined below. Vegetative propagule size proved to influence competition between two submersed macrophytes also (Spencer and Rejmanek 1989).

Traits Associated with Competition for Specific Resources

Light and carbon gain

Strong competition for light seldom coincides with strong competition for belowground resources for two reasons. First, high availability of belowground resources is an essential prerequisite for the development of a leaf canopy dense enough to cause intense light competition, which is strongest under conditions where water and nutrients are not limiting to plant growth. Second, trade-offs between shoot and root competition constrain the amount of biomass that can be simultaneously allocated to acquisition of above- and below-ground resources (Tilman 1988). Those plants that are effective competitors for light are, in the terrestrial environment, trees with a high above-ground allocation, but in the aquatic environment, submersed macrophytes are able to allocate over 60 percent of their aboveground mass in the upper third of the water column (Spencer and Bowes 1990). In the aquatic environment, the water itself supports the plants through its high density. The species that most strongly reduce light availability are not necessarily the species that are most tolerant of low light. Terrestrial species that are tall and have a high leaf area index have the greatest impact on light availability, whereas understory and late-successional species are generally the most shade-tolerant. Submersed macrophytes are all physiologically shade plants in that leaf photosynthesis is saturated at less than half full-sunlight (Bowes 1987). 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 (DIC) diffusion (Bowes 1987). However, water is also a strong absorber of photosynthetically active radiation, so submersed macrophytes are almost always ‘in the shade’ regardless of the DIC levels. Because light is such a strongly directional resource, competition for light is generally quite asymmetric, with the taller species having greatest impact on the shorter species, with often little detectable effect of understory species on the overstory, at least with respect to light competition.

Nutrients

What evidence is there that species growing in infertile environments deplete resources below levels needed by potential competitors, and what might be the processes responsible for this resource drawdown? From a multiple-year field experiment with perennial prairiegrasses on soils of differing fertilities (Wedin and Tilman 1990; Tilman and Wedin 1991), it was demonstrated that the traits associated with competitive success were a high allocation to root biomass and low RGR. High allocation to roots was the plant trait that correlated most

strongly with the nitrogen draw-down. The low RGR reduced loss rates and enhanced tolerance of low supply rates. No such long term experiments have been published for submersed aquatic macrophytes. Moreover, unlike terrestrial plants, submersed aquatic plants can also obtain some nutrients from the water column.

Other nutritional traits are also involved in competition for nutrients. The uptake kinetics of plant species from infertile soils are unlikely to result in low soil solution concentrations. These species typically have a lower maximum rate (I_{max}) of nutrient uptake and do not differ consistently in affinity (of the protein that transports the nutrient ion into the cell, K_m) from species that grow on fertile soils. The influence of uptake kinetics on the soil solution should be greatest for dissolved, mobile nutrients (e.g. nitrate) and less pronounced for adsorbed constituent cations (e.g. ammonium) and phosphate.

The most likely cause of nutrient draw-down by species in infertile soils is microbial immobilization of nutrients. In isolated, often terrestrial sites, this may be caused by the low litter quality of local plant species adapted to infertile soils (Wedin and Tilman 1990). Litter from these plant species has low concentrations of nitrogen and phosphorus, leading to low net mineralization rates. In addition, a large proportion of the litter is produced by roots, which typically have lower tissue nutrient concentrations than leaves and which are dispersed in the same soil area from which the nutrients are taken up. In open, often aquatic sites, the quality of local plant litter may be important, but the influx and quality of imported sediment and detritus are also determinants of the nutrient pools (Rogers et al. 1995; Barko and James 1997).

Typical Behavior of *Vallisneria americana* and *Potamogeton pectinatus* in the Upper Mississippi River System

Distribution and abundance of native submersed macrophytes in the Upper Mississippi River System (UMRS) have been changing since the Mississippi River was impounded (Rogers 1996). A succession of species has occurred in the upper pools since the late 1930s, with *Polygonum amphibium* occupying many newly created habitats, eventually being replaced by pondweed species (Green 1960). *Vallisneria americana* (*V. americana*) occurred throughout the UMRS refuge by 1960, and was reported to be common and widespread in the upper pools along with several pondweeds (Korschgen and Green 1988). In 1991, large-scale declines in submersed macrophytes occurred, with areas vacated by *V. americana* being colonized by other submersed plant species (Fischer and Claflin 1992). Currently, *V. americana* has returned in several pools, where it coexists with pondweeds and other species at some sites, and is replaced by *Potamogeton pectinatus* (sago pondweed; since 2000 known as *Stuckenia pectinata* (Crow and Hellquist 2000)) at other sites. Throughout this report, the name *P. pectinatus* is used to facilitate comparison of results with historical data. The following factors have been identified as potentially contributing to the general decline in submersed macrophytes: increased water turbidity, depletion of sediment nutrients, increased navigation activities, increased agricultural herbicides,

and grazing (Rogers 1996). Competition between plant species is another process that potentially contributed to the wax and wane of selected submersed macrophytes in the UMRS and is the topic of the current modeling study.

Objectives

The current study aims at elucidating whether resource competition for light at varying nutrient availability levels may explain the behavior of selected submersed macrophytes that are major constituents of the submersed vegetation of the UMRS. In this report, a simulation model is presented that focuses on the ability of two submersed macrophyte species to maintain their biomass when they compete for light at high and low nitrogen and phosphorus availabilities. *Vallisneria americana* serves as an example of meadow-forming plants and *P. pectinatus* for canopy-forming plants.

2 Concepts of the Competition Model

General

The current model describes the competition for one resource, i.e. light, between two submersed macrophyte species, at high and low availabilities of nitrogen and phosphorus. This study focuses on the persistence of a species in a relatively short amount of time, i.e. 1 to 2 years.

Physical and Chemical Factors Governing Submersed Macrophyte Persistence and Production

Submersed aquatic macrophytes are important components of the littoral zone of inland water bodies. They range from sparse inhabitants of a narrow zone along steep-sloped deep lakes and rivers to dense mats dominating many shallow waters. The variation in biomass of these plants is large (0.1-1500 g DW m^{-2}; Sculthorpe 1967), as is the list of proposed controlling factors (Wetzel 1983). A schematic diagram illustrating the influence of the various physical and chemical factors on submersed macrophytes is presented in Figure 1.

Light and water movements

Irradiance limits the maximum depth of colonization (Spence 1976; Chambers and Kalff 1985). Only a fraction of the total irradiance reaches the plants' photosynthetic tissues. A small portion (6-10 percent) is reflected at the water surface, and usually larger portions are absorbed by the water column (Kirk 1983; Van Duin et al. 2001) and epiphytes (23-43 percent; Sommer 1977; Sand-Jensen and Sondergaard 1981; Best et al. 2001; Best et al. in preparation). Exposure to wave action appears to have an effect opposite to that of light penetration on the depth at which maximum biomass occurs; the stronger the wave action the deeper the maximum biomass (Spence 1976). Current velocities in the range of >0 to 0.04 m s^{-1} may stimulate photosynthesis, reach an optimum in the range of 0.04-0.08 cm s^{-1} (Madsen and Sondergaard 1983), decrease submersed plant biomass by a factor of 2 at 0.45 m s^{-1}, and eliminate entire vegetation types at

velocities > 0.73 m s^{-1} possibly by mechanical damage (Chambers et al. 1991; Best et al. in preparation).

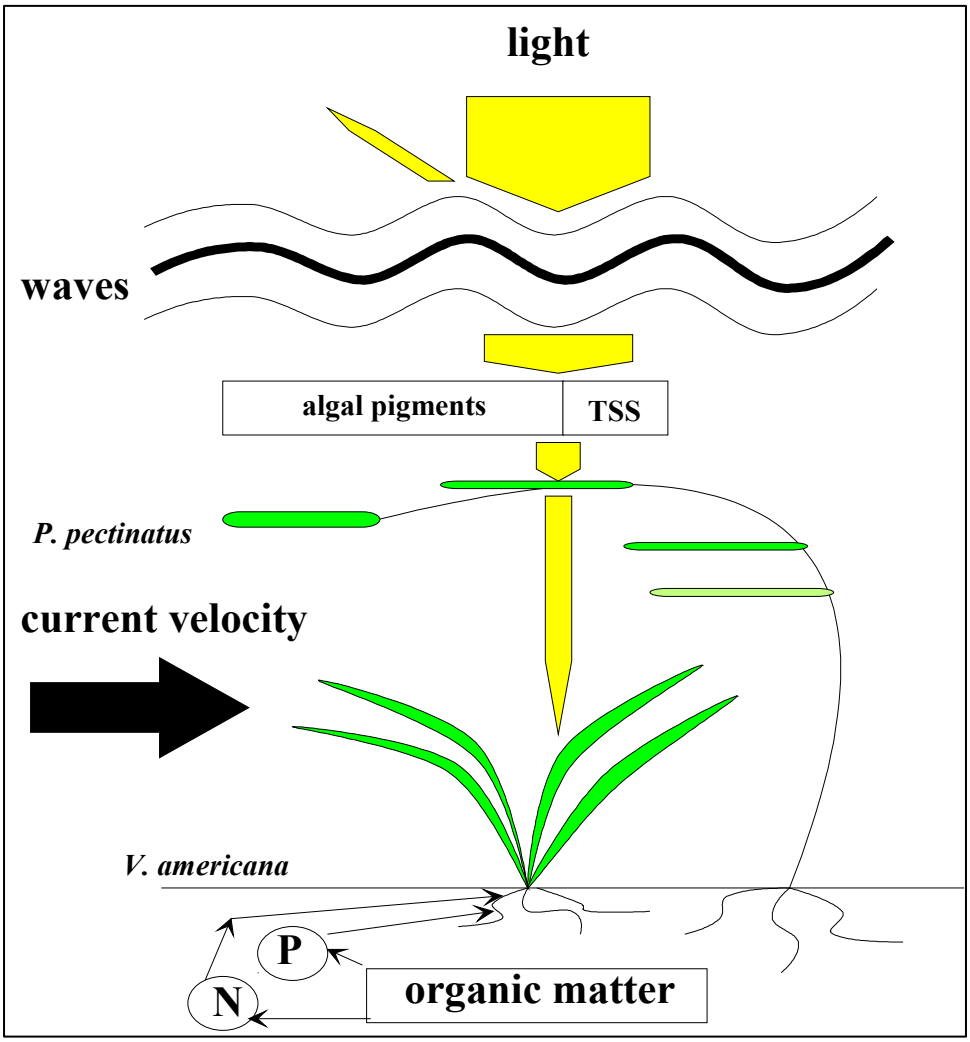

Figure 1. Relations among two submersed plant species and their environment

Nutrients

Although rooted submersed macrophytes have access to nutrients in ambient water and sediment, it is generally agreed that they obtain almost all of their nutrients from the sediment (Toetz 1974; Nichols and Keeney 1976; Carignan and Kalff 1980; Barko and Smart 1980, 1986; Barko 1982; Huebert and Gorham 1983). Three mineral nutrients, nitrogen (N), phosphorus (P), and potassium (K), are required in the greatest quantities by most higher plants, including aquatic macrophytes (Rawlence and Whitton 1977), and they have most often been demonstrated to limit growth in terrestrial plants (Brady 1974; Chapin 1980).

N and 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 (Sytsma and Anderson 1993). Results of mesocosm fertilization experiments indicate that N rather than P limited growth of *Myriophyllum spicatum* (Anderson and Kalff 1986), *Elodea nuttallii* (Best et al. 1996), *Zannichellia palustris,* and *Elodea canadensis* (Spencer and Ksander 2003), while results of a field study indicated that submersed plant biomass across a trophic gradient was most closely correlated with potassium availability (Anderson and Kalff 1988).

Although considerable information on the nutrition of submersed plants is available, it remains difficult to predict submersed plant growth based on sediment nutrient availability alone. It appears that tissue N:P ratios rather than tissue-N or tissue-P concentrations are determinants of submersed plant growth (Best et al. 1996; Spencer and Ksander 2003).

Aquatic Plant Growth Models as Basis for the Competition Model

Both plant species to which the current competition model pertains, *V. americana* and *P. pectinatus*, are rooted, submersed aquatic macrophytes native to the United States, and important phases in their phenological cycles are similar. The plants usually perennate by tubers in the sediment, initiate growth in spring by developing sprouts that elongate within the water column, and their formation of biomass depends on climate and water quality. Flowering occurs in early summer, and seeds are formed, but short-term plant propagation is largely vegetative through subterranean tubers. Seed viability appears to be low. The two species differ greatly in their growth habits in terms of the vertical distribution of biomass within the water column. *V. americana* has a basal rosette of leaves that may extend to the water surface, with over 60 percent of its biomass distributed in the lower 0.3-m water layers of the water column. *P. pectinatus* is a typical canopy-former with over 60 percent of its biomass distributed in the upper 0.5 m of the water column. Both species typically occur in circum-neutral fresh to slightly saline water. *V. americana* is known to tolerate alkalinities ranging from 0-300 mg $CaCO_3$ L^{-1} and prefers mesotrophic systems, while *P. pectinatus* prefers an alkalinity of ≥ 1.2 60 mg L^{-1} and pH >6 (Spence and Maberly 1984) and usually occurs in eutrophic systems. However, these species may also co-occur. Both plant species have similar development rates (Best and Boyd 2001a,b; Best and Boyd 2003a,b), but *V. americana* tubers undergo true dormancy in winter, which prevents sprouting, while *P. pectinatus* tubers do not become truly dormant.

In the competition model, competition for light is based on the assumption that both species occupy the same 1 m^2 of substrate and the overlying water column at a total density of 30 plants m^{-2}, thus sharing and influencing a common light climate. Both plant species may wax and wane species-specifically in monotypic or mixed stands with variable relative density ratios. Various types of shading can be introduced, i.e. self-shading, shading by the competing species, and shading by epiphytes. Effects of nutrient limitation are introduced as species-specific photosynthesis-reducing factors related to tissue N:P ratios.

The competition model is a FORTRAN program that simultaneously runs two individual aquatic plant growth models, VALLA (pertaining to *V. americana*) and POTAM (pertaining to *P. pectinatus*), and stores the light climate results in a common file from which the program allows each model to read the light climate three times per day.

Both aquatic plant growth models have been published elsewhere (Best and Boyd 2001a,b; Best and Boyd 2003a,b). VALLA has been calibrated on field data pertaining to Chenango Lake, NY (Titus and Stephens 1983), and validated using historical plant biomass data pertaining to Lake Mendota, WI (Titus and Adams 1979), Ft. Lauderdale, FL (Haller 1974), and the UMRS (Donnermeyer 1982). POTAM has been calibrated on field data pertaining to the Western Canal, The Netherlands, which is at a latitude similar to that of Maine, USA (Best et al. 1987), and validated using historical plant biomass data pertaining to Lake Veluwe, The Netherlands (Van Dijk et al. 1992; Van Dijk and AchterBerg 1992), the Byrne Canal, CA (Spencer, unpublished 2001; Dr. David Spencer, U.S. Department of Agriculture - Agricultural Research Service, University of California, Davis, December 2001), and Lake Ramgarh, India (Sahai and Sinha 1973). The models have recently been expanded with equations describing effects of epiphytes on light interception and effects of current velocity on plant biomass formation, and they have been revalidated using field data of both plant species collected in 2001 and 2002 (Best et al. in preparation).

3 Model Formulation

Both original versions of the aquatic plant growth models used as the basis for the current competition model (Versions 1.0; Best and Boyd 2001a,b; Best and Boyd 2003a,b) have been modified recently (Versions 2.0; Best et al. in preparation). The models may be used to explore the effects of the following environmental factors: climate (site irradiance and air temperature), water depth, transparency, temperature, epiphyte shading, current velocity, and grazing. The parameter values of these models are presented in Appendix A, Tables 1 and 2**.** Both models are summarized below and yet unpublished descriptions of light interception by epiphytes and inclusion of effects of tissue N:P ratio on photosynthesis are presented.

The individual models simulate growth of a monotypic (single species) submersed plant community, including roots and tubers, under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions, unless stated otherwise. Competition for light can be introduced by forcing both species to use the same $1m^2$ sediment with the above-standing water column. Limitation of growth by low nutrient availability can be introduced as a species-specific photosynthesis-reducing factor (see "Photosynthesis and N:P effects"). At least one plant cohort waxes and wanes each growth season in climates ranging from temperate to tropical. The modeled rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. Light attenuation by epiphytes is incorporated. The rate of CO_2 assimilation (photosynthesis) of the plant community depends on the radiant energy absorbed by the canopy, which is a function of incoming radiation, reflection at the water surface, attenuation by the water column by epiphytes, by macrophyte material, and leaf area of the community. 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. The model does not account for daily fluctuations in pH.

A fraction of the carbohydrates produced is used to maintain the existing plant biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the process of conversion, part of the mass is lost as respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors defined as a function of the plants' phenological cycle. The dry mass of the plant organs is obtained by integration of the growth rates over time. The plants winter either as a system composed by rooted plants and subterranean tubers or tubers alone. Environmental factors and plant

characteristics vary with depth. Therefore, the model partitions the water column and the associated plant-related processes into 0.1-m depth layers. All calculations are performed on a m^2 basis.

The models are equipped with input files in which standard physiological properties, initial plant and tuber biomass, and water temperature are given. These input files can be changed by the user to apply to the study site. The models run at daily time steps for periods of 2 to 5 years.

Development and Phenological Cycle

The phenology of the plant community, for which the development phase is used as a measure, is modeled as a sequence of processes which take place over a period of time, punctuated by more or less discrete events. Development phase (DVS) is a state variable in the models. 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 development rate to temperature in the model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990a). Calibration according to this hypothesis allows for use of the model for the same plant species at other sites differing in climate (temperature regime). The relationships between the development phase, the day-of-year, and 3 ^{o}C degree-day sum for a temperate climate are presented in Appendix A, Table 3 for *V. americana* and in Table 4 for *P. pectinatus*.

Wintering and Sprouting of Wintering Organs, and Growth of Sprouts to Water Surface

Modeled plant growth is initiated at a certain developmental phase, and a fixed number of plants develop through conversion of carbohydrates from hibernating organs (tubers, plants, or both) into plant material. The developmental phase and plant density are species characteristics (Appendix A, Tables 3 and 4). Plant density is presumed to be constant throughout the year. This presumption is based on estimates of the density of adolescent plants in the field, which indicate narrow density ranges for both species (Titus and Stephens 1983, Doyle 2000, Best and Boyd 2003a, Van Wijk 1989). It is possible that late in the growing season, density increases somewhat through emergence of rosettes or shoots from stolons, but the role of these organs in biomass production and population survival is deemed negligible due to their low carbon gain (shaded by neighbor plants) and absence or low production of small-sized tubers. Small-sized tubers have low survival value for both species. The period in which the tubers do not grow is considerably longer in *V. americana* (true dormancy) than in *P. pectinatus* (growth inhibition by low temperature), providing a relatively longer period for new plant establishment for *P. pectinatus*. Remobilization proceeds until the tubers are depleted. Once a specified plant height has been reached (1.2 m or the water surface in *V. americana*; the water surface in *P. pectinatus*), plant mass is distributed following a fixed pattern with a species-characteristic shape. Given the initial tuber mass, sprouts can only elongate a certain distance on these

reserves. If net photosynthesis after this elongation period is negative for 23 consecutive days in *V. americana* or for 27 days in *P. pectinatus*, the sprouts are presumed to die. The next tuber class can sprout subsequently, provided floral initiation has not yet been reached and temperature is within the range of 5-25^{o}C in *V. americana* and DVS>0.211 in *P. pectinatus*. In the elongation phase, shoot biomass is distributed equally over the successive 0.1-m depth layers, with each layer growing after the preceding layer achieves a minimum shoot biomass. After reaching maximum shoot height, biomass is distributed according to the species-characteristic spatial distribution (pyramid-shaped in *V. americana*, umbrella-shaped in *P. pectinatus*). A relational diagram illustrating wintering and sprouting of tubers is presented in Figure 2.

Light

The measured daily total irradiance (wavelengths of 300-3000 nm) and maximum and minimum temperatures of the site are used as input for the model in the form of a separate weather file. Only half of the irradiance reaching the water surface is presumed photosynthetically active radiation (PAR), and 6 percent of the remaining PAR is presumed to be reflected by the water surface.

In the models, daily irradiance in the water column is attenuated following the Lambert-Beer law. Although subsurface irradiance is attenuated by both color and particles within the water column, no distinction between either of these factors has been made, and one site-specific light extinction coefficient accounts for subsurface attenuation. The vertical profiles of light within the vegetation layers also are characterized, and the light absorbed by each horizontal vegetation layer is derived using these profiles. The plant community-specific extinction coefficient, K, is presumed to be constant throughout the year and is 0.0235 m^2 g dry weight^{-1} (DW) for *V. americana* and 0.095 m^2 g DW^{-1} for *P. pectinatus* (Titus and Adams 1979, Best and Boyd 2003a).

Shading by epiphytes is introduced into the models as an equation reducing the light interception by plants with a relative factor accounting for light interception by epiphytes. Light interception by epiphytes varies with plant species and development stage via a relative, dimensionless factor (≤ 1) and may have a maximum value that varies with maximum epiphyte cover.

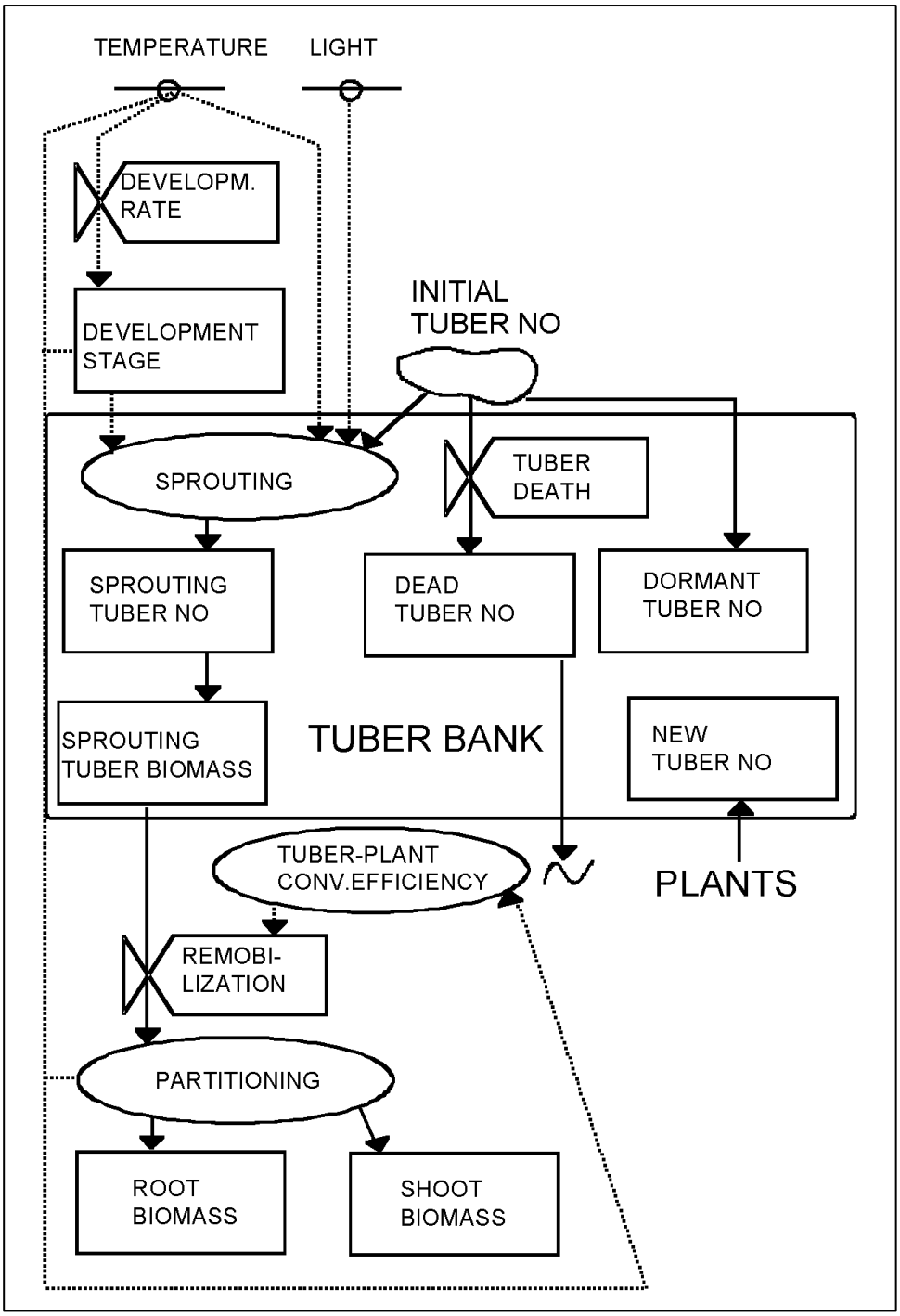

Figure 2. Relational diagram illustrating the wintering and sprouting of tubers

Total irradiation on top of stratum I is described by the following equation:

$$IRZ_{i+1} = IRZ_1 \times \exp^{(-TL \times L - K \times SC_i)} \quad (1)$$

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

where:

$EPISHD$ = epiphyte shading effect on light interception by the plant as function of DVS, used in calculation source code (-, -)

$IABS_i$ = total irradiance absorbed per depth layer containing plant material (J m^{-2} s^{-1})

IRZ_i = total irradiance on top of depth layer I (J m^{-2} s^{-1})

K = plant species specific light extinction coefficient (m^2 g^{-1} DW)

L = water type specific light extinction coefficient (m^{-1})

SC_i = shoot dry matter in depth layer I (g DW m^{-2} $layer^{-1}$)

TL = thickness per depth layer (m)

The relationships between development phase and relative epiphytic light interception are presented in Figure 3. In these functions, epiphytic light interception increases linearly from 0 at the beginning of the year to a maximum value (0.43 for *V. americana* and 1.0 for *P. pectinatus*) at the development phase of 2, when plant senescence sets in, and decreases subsequently very slowly to 0 at the end of the year. This curve describes the typical behavior of tuber- and turion-forming submersed plants. These plants hibernate as tubers and/or turions, usually completely covered by silt and epiphytes, sprout and strongly elongate in early spring, losing their epiphytic cover, flower and successively senesce, becoming increasingly covered by epiphytes and silt (Best and Visser 1987). The maxima of these curves have recently been measured in Pool 8 of the Mississippi River (Best et al. in preparation).

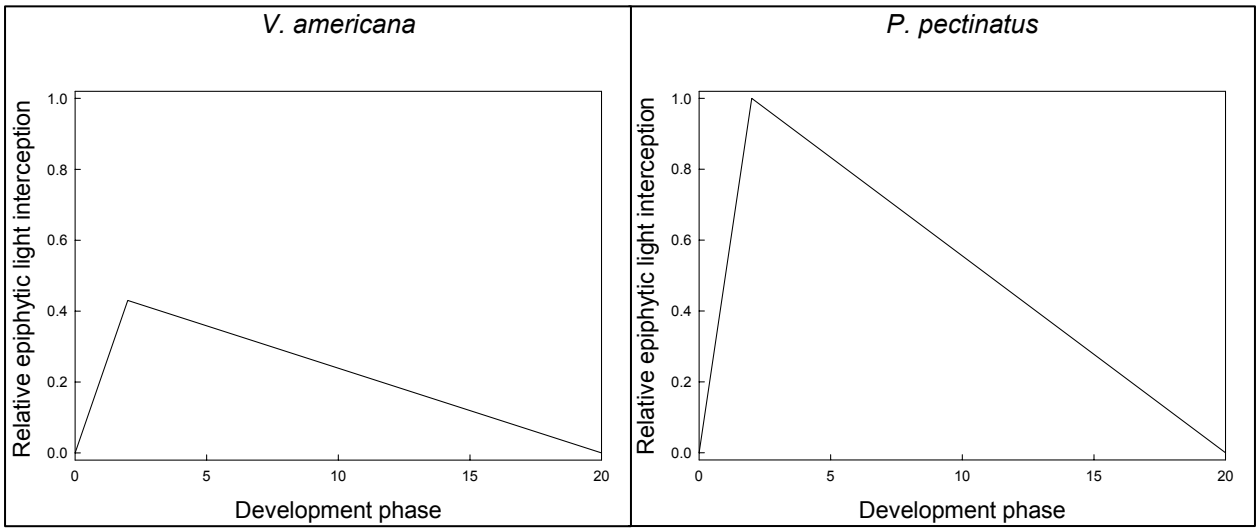

Figure 3. Relationship between development phase and relative epiphytic light interception used for model calibration

The variable listing and available output parameters of Version 2 of the plant growth models are presented in Appendix B; the input files are presented in Appendix C. Examples illustrating calculations needed for runs with changed default values are described in Appendix D.

Photosynthesis and N:P Effects

Instantaneous gross photosynthesis (*FGL* expressed in g CO_2 m^{-2} h^{-1}) in the models depends on the standing crop per depth layer i (SC_i in g DW m^{-2} layer $^{-1}$), the photosynthesis light response of individual shoot tips at ambient temperature (*AMAX* in g CO_2 g DW^{-1} h^{-1}), the initial light use efficiency (*EE* in g CO_2 J^{-1} absorbed), the absorbed light energy (*IABSL* in J m^{-2} s^{-1}), and temperature (*AMTMPT,* in degrees C). It can be reduced by a plant tissue N:P dependent factor NPREDF (≤1). The relationships between plant tissue N:P ratio and relative photosynthesis reduction have not been determined for *V. americana* and *P. pectinatus*, but were presumed to be similar to those found in *Zannichellia palustris* and *Elodea canadensis* that have similar habitat preferences (Batiuk et al. 1992). These relationships were derived from experiments in which monocultures of *Z. palustris* and *E. canadensis* were fertilized with N, P, and N+P (Spencer and Ksander 2003). Exponential quadratic equations fitted the measured biomass production best: $Y=Y_0 \exp (a_1X-a_2X^2)$, in which Y is the photosynthesis reducing factor, and X is the plant tissue N:P ratio (Thornley and Johnson 1990b). The relationships used for calibration of the current model are presented in Figure 4. A value of 0.15 for Y_0 would yield values of 0.14452 for a_1 and 0.00273 for a_2, in *Z. palustris*. A value of 0.15 for Y_0 would yield values of 0.35677 for a_1 and 0.01622 for a_2 in *E. canadensis*. Plant tissue N:P ratios under natural conditions may have values that vary seasonally with sediment and water quality.

The photosynthesis light response of leaves is described by the exponential function

$$FGL = SC_i \times NPREDF \times AMAX\left[1 - \exp\left(\frac{-EE \cdot IABSL_i \cdot 3600}{AMAX \cdot SC_i}\right)\right] \qquad (3)$$

where

AMAX = actual CO_2 assimilation rate at light saturation for individual shoots (g CO_2 g DW^{-1} h^{-1})

EE = initial light-use efficiency for shoots (g CO_2 J^{-1} absorbed)

FGL = instantaneous gross assimilation rate per depth layer (g CO_2 m^{-1} h^{-1})

$IABSL_i$ = total irradiance absorbed per depth layer containing plant material (J m^{-2} s^{-1})

NPREDF = N:P ratio dependent relative factor that reduces FGL by a factor ≤1 (-)

SC_i = shoot dry matter in depth layer i (g DW m^{-2} $layer^{-1}$)

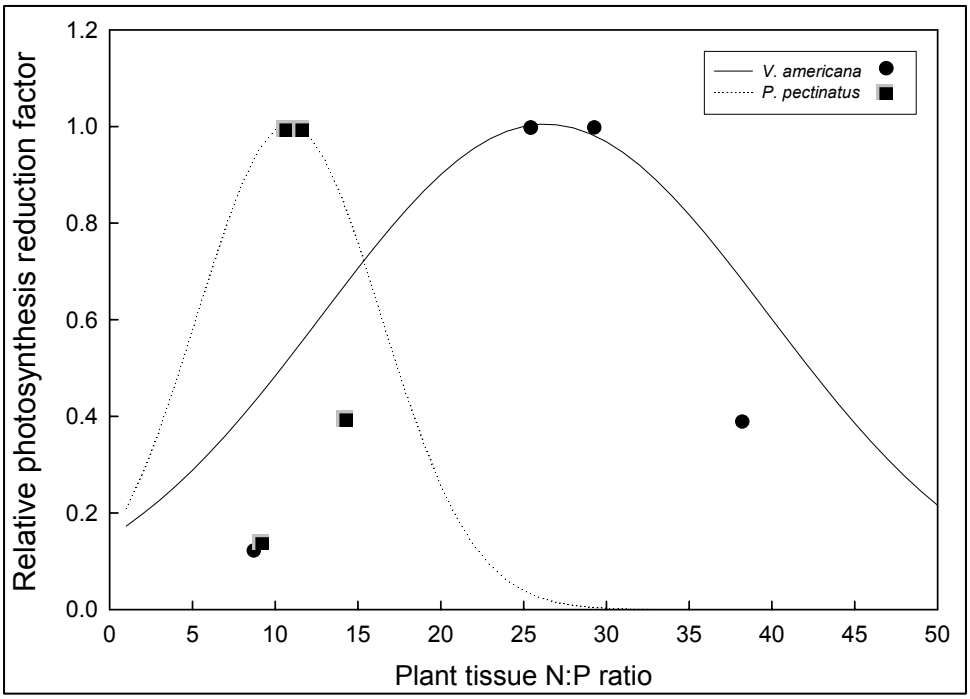

Figure 4. Relationship between tissue N:P ratio and relative photosynthesis reduction factor used for model calibration. Symbols indicate values measured by Spencer and Ksander (2003)

For photosynthetic activity at light saturation and optimum temperature (*AMX*), the values of 0.0165 g CO_2 g DW^{-1} h^{-1} for *V. americana* and 0.019 g CO_2 g DW^{-1} h^{-1} for *P. pectinatus* were used (Titus and Adams 1979; Van der Bijl et al. 1989). The photosynthetic activity at ambient temperature (*AMAX*) is calculated proportionally from the photosynthetic activity at optimum temperature using a relative function fitted to data for *V. americana* (Titus and Adams 1979) and *P. pectinatus* (Best and Boyd 2003a). For photosynthetic light use efficiency (*EE*), a value of 11.10^{-6} g CO_2 J^{-1}, typical for C_3 plants, is used (Penning de Vries and Van Laar 1982). Substituting the appropriate value for the absorbed PAR 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 community-specific biomass distribution and by subsequent integration of all 0.1-m-high vegetation layers. The daily rate of gross assimilation is then computed using a 3-point Gaussian integration method (Goudriaan 1986; Spitters 1986).

Respiration and Growth

Maintenance costs are calculated based on the chemical composition of plant organs, usually ranging from 0.010 to 0.016 g CH_2O g ash-free dry $weight^{-1}$ (AFDW) (Penning de Vries and Van Laar 1982). Maintenance costs for the tubers are negligible. A temperature increase of 10 ^oC is assumed to increase

maintenance respiration by a factor of about two (with a reference temperature of 30 °C; Penning de Vries and Van Laar 1982).

Assimilates in excess of maintenance costs are converted into structural plant material. Growth efficiency and concomitant CO_2 evolution (growth respiration) are accounted for using the assimilate requirement for growth. The assimilates required to produce one unit weight of plant organ are calculated from its chemical composition, and typical values are 1.46 g CH_2O g DW^{-1} for leaves, 1.51 for stems, and 1.44 for roots (Penning de Vries and Van Laar 1982; Griffin 1994). The more recently determined construction costs for several submersed plant species using a different method (Williams et al. 1987) are generally lower, ranging from 0.99 to 1.11 (Spencer et al. 1997). However, some of the latter plants are relatively poor in nitrogen, and transport costs have not been included. Both are factors which may have contributed to the lower cost found.

As summarized in Equation 4 below, plant growth (*GTW* expressed as g DW m^{-2} d^{-1}) equals remobilized carbohydrates (*REMOB* in g DW m^{-2} d^{-1}, converted to g glucose m^{-2} d^{-1} by multiplication with CVT, a conversion factor of translocated dry matter into glucose) augmented with gross photosynthesis (*GPHOT*) and decreased by downward translocation (*TRANS*) and maintenance respiration (*MAINT*), all expressed as g glucose m^{-2} d^{-1}, divided by the assimilate requirement for plant biomass production (*ASRQ* expressed as g glucose g DW^{-1}).

$$GTW = \left[\left(REMOB \times CVT\right) + GPHOT - TRANS - MAINT\right] / ASRQ \qquad (4)$$

where

ASRQ = assimilate requirement for plant dry matter production (g CH_2O g DW^{-1})

CVT = conversion factor of translocated dry matter into CH_2O (-)

GPHOT = daily total gross assimilation rate of the vegetation (g CH_2O m^{-2} d^{-1})

GTW = dry matter growth rate of the vegetation (plants excluding tubers; (g DW m^{-2} d^{-1})

MAINT = maintenance respiration rate of the vegetation (g CH_2O m^{-2} d^{-1})

REMOB = remobilization rate of carbohydrates (g CH_2O m^{-2} d^{-1})

TRANS = translocation rate of carbohydrates (g CH_2O m^{-2} d^{-1})

The assimilate allocation pattern in plants (excluding tubers) is proportional to the biomass distribution pattern and depends on the physiological age. The typical patterns are followed when shoots have reached their maximum height and are 72 percent to leaves, 16 percent to stems, and 12 percent to roots in *V. americana* (Haller 1974, Titus and Stephens 1983), and 73 percent of the total to leaves, 18 percent to stems, and 9 percent to roots in *P. pectinatus* (Best et al. 1987).

The vertical biomass distribution within the water column follows typical patterns, being pyramid-shaped in *V. Americana*, with 78 percent of the shoot biomass in the lower 0.5 m of the water column (Titus and Adams 1979), and umbrella-shaped in *P. pectinatus,* with 78 percent of the shoot biomass in the upper 0.5 m of the water column (Best and Boyd 2003a). This entails the distribution of shoot biomass in the lower (*V. americana*) or upper (*P. pectinatus*) five 0.1-m vegetation layers according to a specific fitted function (*DMPC*) based on the respective species-characteristic shapes, followed by equal distribution of the remaining biomass over the remaining 0.1-m layers, up to a total biomass share of 5 percent per layer and proportional distribution of the then-remaining biomass over all 0.1-m vegetation layers. A species-characteristic share of the total biomass is allocated to the roots, presumed to be situated in the upper 0.1 m of the sediment. The vertical biomass distribution pattern is recalculated and redistributed by the models when a rooting (water) depth other than the nominal one is chosen. A relational diagram illustrating photosynthesis, respiration, biomass and tuber formation, and senescence in the plants is presented in Figure 5.

Flowering, Translocation, and Senescence

Flowering affects metabolic activity of the modeled plants by initiating substantial downward translocation of assimilates to form tubers in both *V. americana* and *P. pectinatus*. Translocation and tuber formation have been formulated similarly for both species, but the parameter values are species-specific. In *V. americana*, translocation occurs after flowering is initiated, at a day length <14.7 hours and at a temperature between 5 and 25 ^{o}C (Titus and Stephens 1983; Donnermeyer and Smart 1985). *V. americana* tubers grow at a maximum rate of 24.7 percent of net production per day (Donnermeyer and Smart 1985). Translocation continues as long as plant biomass is greater than zero. In *P. pectinatus*, translocation occurs after flowering is initiated, at a day length < 16 hours (Best and Boyd 2003a) and in a temperature between 5 and 25 ^{o}C (Spencer and Anderson 1987). *P. pectinatus* tubers grow at a maximum rate of 19 percent of net production per day (Wetzel and Neckles 1986), with remaining assimilates available for other processes.

Tuber production is based on the hypothesis that plants produce the largest possible tubers at their ambient light levels, because large tubers have the largest potential to survive future adverse low temperatures, low irradiance, and a short growth season. This hypothesis is supported by field data on *P. pectinatus* (Van Dijk et al. 1992) and experimental data on *V. americana* and *P. pectinatus* (Spencer 1987; Doyle 2000). The variation in tuber size found in the field is attributed to the inability of the plants to complete the last tuber class with such a large tuber size. In the models, after reaching a given tuber size, all concurrently initiated tubers of that class are added to the tuber bank, and a new tuber class is initiated. A fixed, linear relationship was found in both species, indicating that the tuber number concurrently initiated increases with tuber size, with a smaller range for *V. americana* than for *P. pectinatus* (Figure 6).

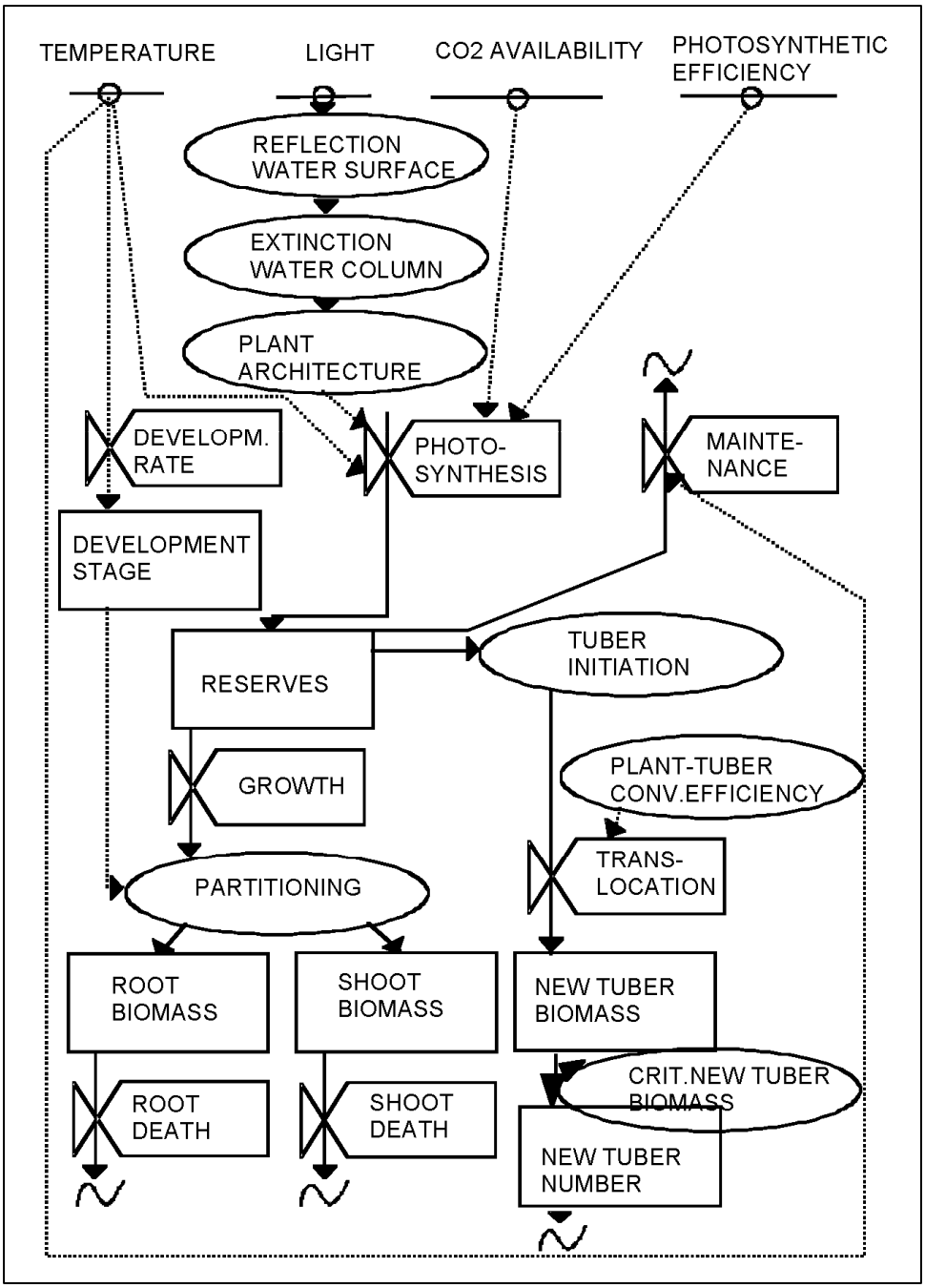

Figure 5. Relational diagram illustrating photosynthesis, respiration, biomass and tuber formation, and senescence

Senescence is modeled by defining a death rate as a certain fraction of plant biomass per day when the conditions for growth deteriorate. The timing and values of relative death rates of plants have been derived from field observations on shoot biomass for *V. americana* by Titus and Stephens (1983) and for *P. pectinatus* by Best and Boyd (2003a). The timing was found by running the models repeatedly with different development rates, and base- and reference-temperatures, until a realistic timing for decreasing shoot biomass occurred.

Values for the relative death rates were found by applying the same differential equation that is commonly used for simple exponential growth to describe exponential decrease in biomass after flowering, with a negative specific decrease rate (Hunt 1982; Thornley and Johnson 1990b). Following this approach, relative death rates of 0.021 g DW g DW^{-1} d^{-1} for *V. americana* and of 0.047 g DW g DW^{-1} d^{-1} for *P. pectinatus* were calculated. The timing and values of relative death rates for the tubers were derived similarly from published data on tuber bank dynamics (Titus and Stephens 1983, Van Wijk 1989). Figure 5 illustrates translocation, tuber formation, and senescence in the models.

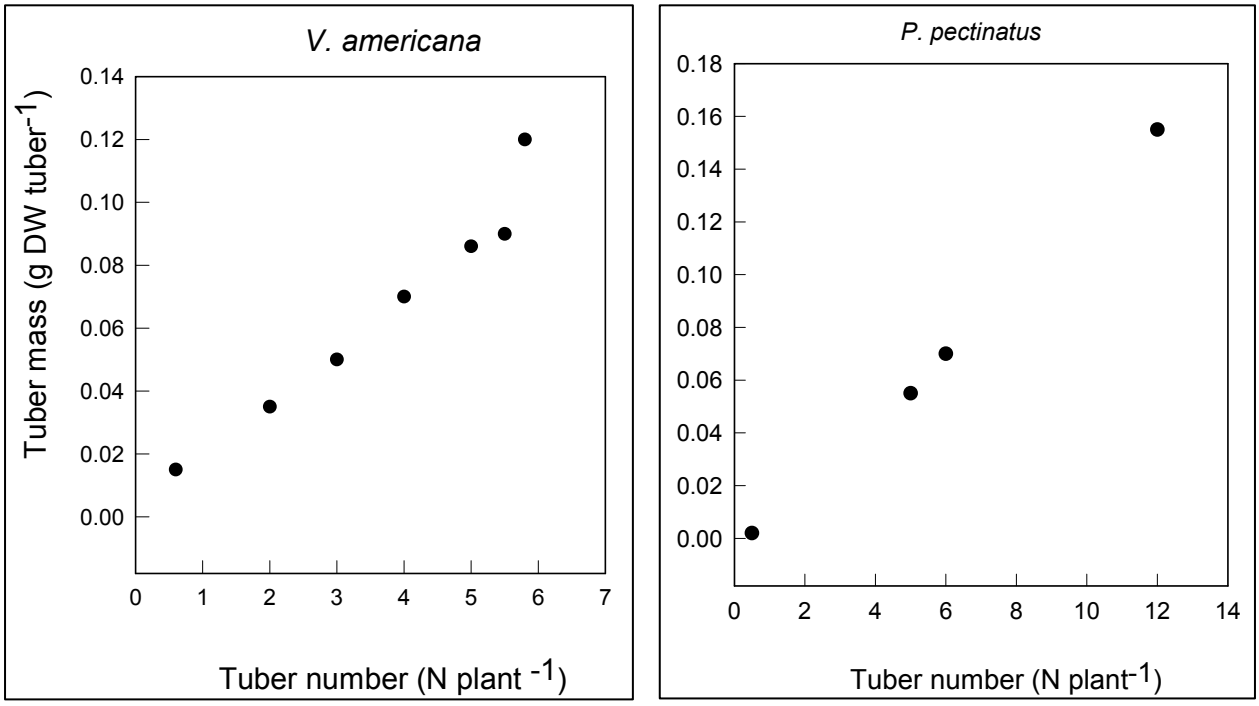

Figure 6. Relationship between tuber number concurrently initiated per plant and tuber mass

Typical Model Results for the Upper Mississippi River System

The model was applied to an area in Pool 8 in the UMRS where *V. americana* and *P. pectinatus* beds occurred in 2001 and 2002. It was utilized to simulate plant biomass and tuber number in monotypic stands using site-specific data on water depth, water transparency, current velocity, and climate (temperate at La Crosse, WI, 2001) as inputs, and field data on biomass for verification (Best et al. in preparation). Model results indicated that simulated peak plant biomass was within the range of measured plant biomass for *V. americana* and was a factor of three higher than measured for *P. pectinatus*, with the simulated maxima lagging somewhat behind the observed ones (Best et al. in preparation). The overprediction of *P. pectinatus* biomass was attributed to the fact that modeled biomass was generated from a default tuber bank density of at least 30 tubers m^{-2}, while heavy grazing by waterfowl may have depleted tuber bank

densities to far lower numbers (Kenow et al. 2003). The typical behavior of *V. americana* and *P. pectinatus* stands under UMR-mimicking conditions is presented in Figures 7 and 8 (0.5-m rooting depth, current velocity 0 m s^{-1}). Results from these simulations indicate that *V. americana* would produce twice as many tubers as *P. pectinatus* in the shallow water at this site when the model is run for turbid water conditions and started from default tuber bank densities, assuming default combinations of tuber size/concurrently initiated tuber number for each species (*V. americana*: tuber size 0.09 g DW $tuber^{-1}$, 5.5 tubers $plant^{-1}$; *P. pectinatus*: tuber size 0.083 g DW $tuber^{-1}$, 8 tubers $plant^{-1}$). When run for clear water conditions, *V. americana* would produce about three times as many tubers as *P. pectinatus*.

Model Sensitivity

A sensitivity analysis of a simulation model is required to assess the parameters most likely to strongly affect model behavior. This analysis has been conducted on both original versions of the aquatic plant growth models VALLA and POTAM, used as the basis for the current competition model (Versions 1.0; Best and Boyd 2001a; 2003a). In this report, the results of the sensitivity analysis will be repeated.

These analyses are based on the effect of a change in one parameter when all other parameters are kept the same. As a reference level, the nominal parameter values with which VALLA and POTAM 1.0, respectively, were calibrated were chosen. The tables with calibration parameters for VALLA and POTAM are presented in Appendix A. For VALLA, environmental conditions mimicked those in Chenango Lake, New York, 1.4-m water depth. In a one-year simulation starting with a tuber size of 0.09 g DW and a tuber bank density of 233 m^{-2}, the value of the parameter under study was changed. The results were compared with those of a nominal run. Each parameter was once increased by 20 percent and once decreased by 20 percent. As summarized in Equation 5 below, the relative sensitivity (RS) of a parameter was then defined as the relative change in the variable on which the effect was tested divided by the relative change in the parameter (Ng and Loomis, 1984). The effects of ten parameters on two variables, representing plant biomass aspects, were tested. A model variable is considered sensitive to a change in the value of a parameter at RS>0.5 and <-0.5. The current sensitivity analysis was performed over a one-year period.

$$RS = \frac{\left(yield_i - yield_r\right)/\, yield_r}{\left(param_i - param_r\right)/\, param_r}$$

where

RS = relative sensitivity of a parameter

$yield_i$ = value at parameter value i;

$yield_r$ = value at reference parameter value;

$param_i$ and $param_r$ as above

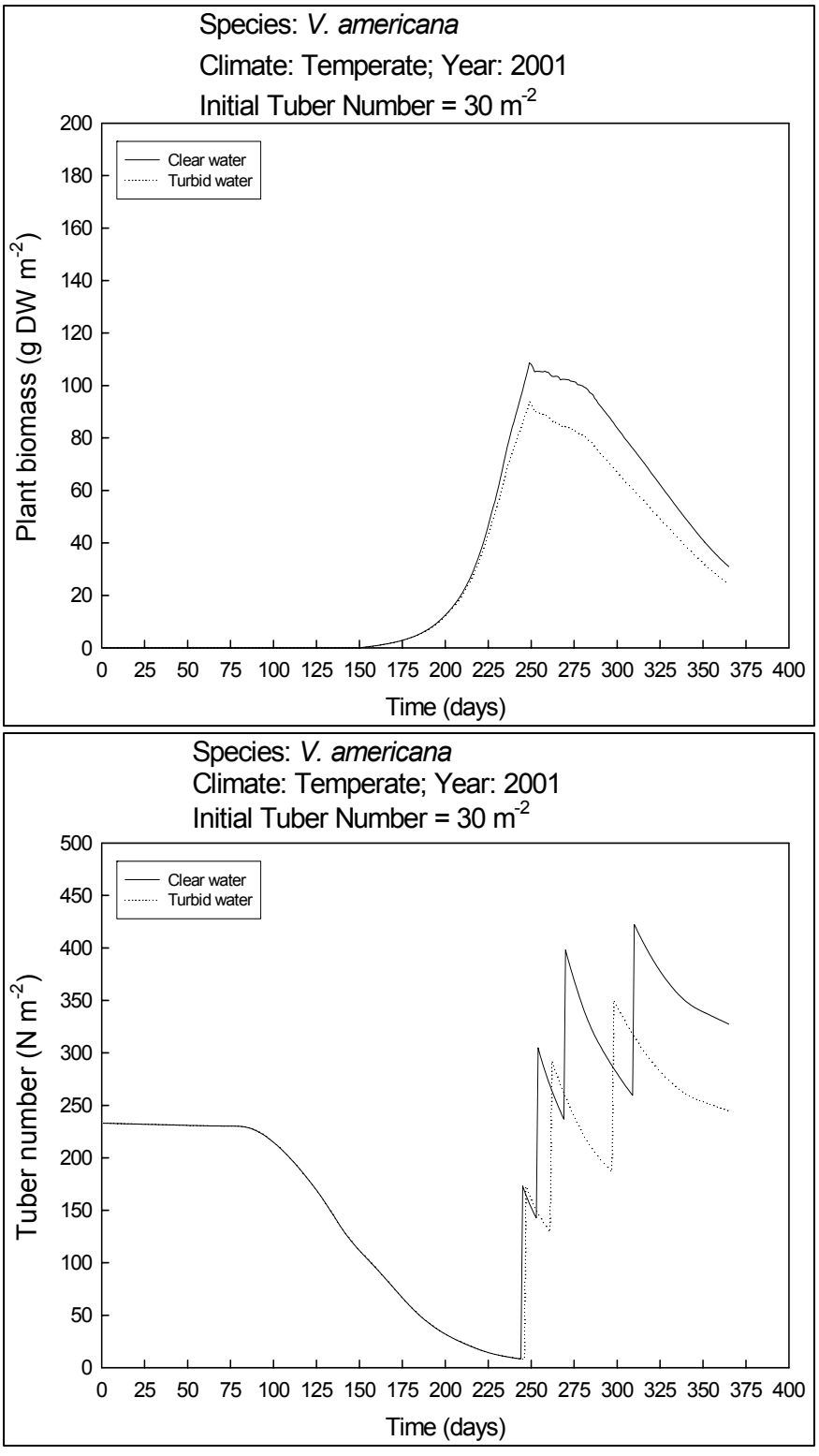

Figure 7. Typical simulated biomass of plants and tubers of a *V. americana* community in Pool 8 of the Upper Mississippi River, WI, USA. Nominal run. Climatological data 2001, La Crosse, WI (longitude 91º30'W, latitude 43º10'N); water depth 0.5 m; light extinction coefficient clear water 0.43 m^{-1}, turbid water 2.0 m^{-1}

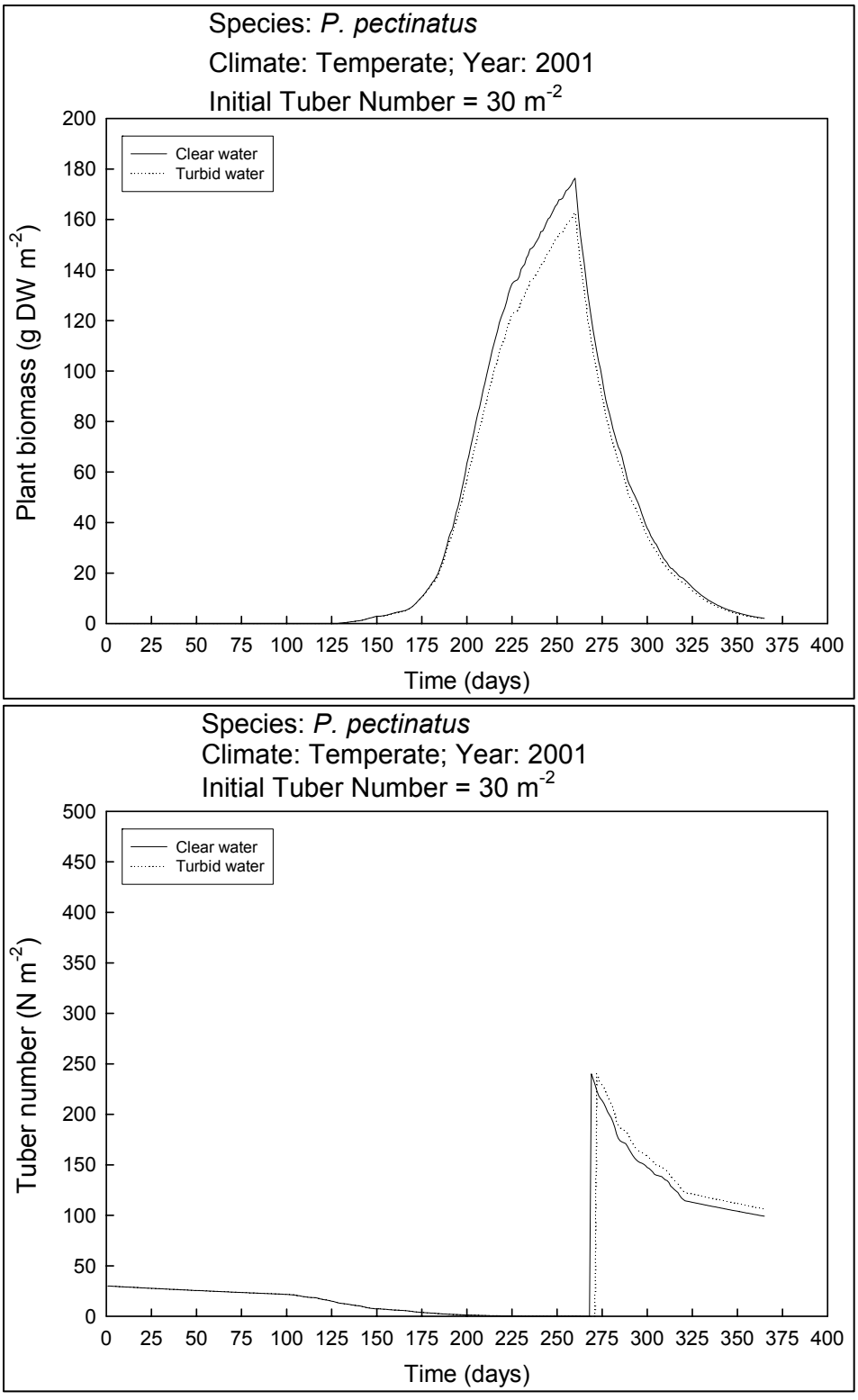

Figure 8. Typical simulated biomass of plants and tubers of a *P. pectinatus* community in Pool 8 of the Upper Mississippi River, WI, USA. Nominal run. Climatological data 2001, La Crosse, WI (longitude 91º30'W, latitude 43º10'N); water depth 0.5 m; light extinction coefficient clear water 0.43 m^{-1}, turbid water 2.0 m^{-1}

In VALLA, maximum plant biomass proved most sensitive to changes in potential CO_2 assimilation at light saturation for shoots, but not to changes in light use efficiency (Table 1). Maximum biomass was also strongly affected by changes in plant density, but less than by photosynthetic activity at light saturation. Maximum biomass was more strongly influenced by pre-anthesis than by post-anthesis development rate, and it was strongly influenced by individual tuber weight and relative death rate of shoots and roots. Effects of changes in relative conversion rate of tubers into plant material and of relative tuber growth rate were in the same order of magnitude, and lower than those of changes in the other parameters.

Table 1
Relative Sensitivity of Two Model Variables in VALLA Version 1.0 to Deviations in Parameter Values from Their Nominal Values as Presented in Appendix A (Results were obtained in a 1-year simulation under Chenango Lake, New York, 1978 conditions, starting from 233 tubers m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity	
		Maximum Live Plant Biomass	End-of-Year Tuber Number
Potential CO_2 assimilation rate at light saturation for shoot tips	0.0165		
	0.0200	5.00	4.46
	0.0149	3.02	2.04
Light use efficiency	0.000011		
	0.000013	0.50	-0.73
	0.000008	0.56	1.44
Relative death rate leaves, stems, and roots	0.021		
	0.025	2.25	0.71
	0.017	-3.03	0.22
Individual tuber weight	0.090		
	0.108	3.25	-1.79
	0.072	-0.92	-0.03
Relative conversion rate of tubers into plant material	0.0576		
	0.069	2.65	-0.43
	0.046	-1.37	2.33
Relative tuber growth rate	0.247		
	0.296	1.76	-0.77
	0.198	-2.62	2.19
Plant density	30		
	36	3.39	-0.01
	24	-0.82	2.71
Pre-anthesis development rate	0.015		
	0.018	0.56	-2.5
	0.012	-6.04	-1.39
Post-anthesis development rate	0.040		
	0.048	0.98	-2.47
	0.032	-2.19	0.24

In general, the same parameter changes that influenced maximum plant biomass were important determinants of the end-of-year tuber numbers, with potential CO_2 assimilation at light saturation, development rates, and plant density exhibiting the largest effects. This illustrates the utmost importance of the tubers for local survival and biomass production of *V. americana*.

For POTAM, environmental conditions mimicked those in the Western Canal, The Netherlands, 1.3-m water depth. In a one-year simulation starting with a tuber size of 0.083 g DW and a tuber bank density of 240 m^{-2}, the value of the parameter under study was changed. The results were compared with those of a nominal run. Further, the same procedure was followed as for VALLA. In POTAM, maximum plant biomass proved most sensitive to changes in potential CO_2 assimilation at light saturation for shoots, but not to changes in light use efficiency (Table 2). It was also strongly affected by changes in pre-anthesis development rate. Maximum plant biomass proved to be insensitive to changes in the other parameters tested.

End-of-year tuber number was sensitive to seven out of the nine parameters tested. Sensitivity was greatest to changes in pre-anthesis development rate, followed by changes in relative tuber growth rate, potential assimilation rate, light use efficiency, post-anthesis development rate, plant density, and relative death rate of the plants. End-of-year tuber number was insensitive to changes in individual tuber weight and relative conversion rate of tubers into plant material. This illustrates the importance of the tubers for local survival and biomass production of *P. pectinatus*, just as of *V. americana*.

Earlier or later flowering biotypes are suited to different environments. The effect of flowering date can be tested with the model by varying the development rate of the vegetation. Slower rates represent later biotypes, and faster rates represent earlier biotypes. Development rate slower or faster than the nominal rate leads to lower biomass. Faster development leads to a shorter growing season and less vegetative dry matter, incomplete light interception, and lower carbohydrate availability for organ formation. At the same time, however, the rate of organ formation increases, but the duration of each organ formation shortens. Therefore, intuitive prediction of biotype behavior under such highly variable climatic conditions is hazardous. The model shows promise in being able to reproduce some of these complex responses of the vegetation and may be useful in evaluating long term implications of differences in development rate. Although no publications are known to exist on what the temperature requirements of aquatic plants are to traverse development from anthesis to senesced state, differences in post-anthesis development rates for several wheat and rice cultivars are known to be small and have little effect on yield (Van Keulen 1976).

In VALLA, maximum plant biomass proved to be sensitive to changes in development rate except to an increased pre-anthesis development rate, while end-of-year tuber number was sensitive to changes in all development rates except a decreased post-anthesis development rate (Table 1). In POTAM, maximum plant biomass was sensitive to pre-anthesis development rate, while end-of-year tuber number was sensitive to all changes in development rate except an increased post-anthesis development rate (Table 2).

Table 2
Relative Sensitivity of Two Model Variables in POTAM Version 1.0 to Deviations in Parameter Values from their Nominal Values as Presented in Appendix A (Results were obtained in a 1-year simulation under Western Canal, The Netherlands, 1987 conditions, starting from 240 tubers m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity	
		Maximum Live Plant Biomass	End-of-Year Tuber Number
Potential CO_2 assimilation rate at light saturation for shoot tips	0.019		
	0.0228	1.720	-1.577
	0.0152	1.941	5
Light use efficiency	0.000011		
	0.000013	0.245	-0.832
	0.000008	0.324	-3.095
Relative death rate leaves, stems and roots	0.047		
	0.0564	0	0
	0.0376	0	-2.931
Individual tuber weight	0.083		
	0.0996	0.246	0
	0.0664	0.341	0.192
Relative conversion rate of tubers into plant material	0.0576		
	0.069	0.092	0
	0.046	0.136	0
Relative tuber growth rate	0.19		
	0.228	-0.103	-2.153
	0.152	-0.102	5
Plant density	30		
	36	0.276	1.204
	24	0.346	1.140
Pre-anthesis development rate	0.015		
	0.018	-1.360	-3.363
	0.012	-0.913	4.914
Post-anthesis development rate	0.040		
	0.048	-0.392	-0.426
	0.032	-0.451	-3.123

4 Simulations Using the Competition Model

Competition for Light in the Absence of Growth Limitation by N or P

Intraspecific competition

First, the model was used to explore intraspecific competition for light. This was done by simulating the behavior of monotypic stands with plant densities increasing up to the typical default densities of 30 plants m^{-2}, found in stable macrophyte beds under natural conditions (Titus and Stephens 1983; Best et al. 1987; Van Wijk 1989). All simulations were conducted for plant stands in a 0.5-m water column, over one year, and generated daily values of plant biomass and tuber production. The maximum tuber number m^{-2} was used as a parameter for species persistence rather than plant biomass, because the tubers are the main plant propagules.

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 more southern climates. Smaller differences in light levels were introduced by exposing the model plants to water transparencies typical for clear and turbid waters, with and without typical shading by epiphytes. Typical climates used were for temperate conditions, daily irradiance, and air temperature measured at La Crosse, WI (latitude 43° 10'N, longitude 91° 30' W) in 2001, and for more southern conditions as measured at Davis, CA (latitude 38° 32'N, longitude 121° 47' W) in 1990. Effects of subtropical and tropical climates were not included in these simulations, because in these climatological conditions, the effects of light level by itself become confounded by those of daylength and temperature on tuber initiation and production. Typical water transparencies used were: for clear water 0.43 m^{-1}, as measured in oligotrophic Chenango Lake, NY (Titus and Stephens 1983); and for turbid water 2.0 m^{-1}, as measured in the eutrophic Loosdrecht Lakes, The Netherlands (at a latitude similar to ME; Best et al. 1984). Shading levels by epiphytes were increasing from zero at the start of the simulation to one quarter of the maximum measured on mature plants in the UMRS in 2002 (i.e. 11 percent for *V. americana* and 25 percent for *P. pectinatus*; Best et al. in preparation).

In *V. americana*, intraspecific competition for light did not occur in a temperate climate, and maximum tuber number continued to increase almost linearly in turbid as well as clear water (Figure 9, upper). Persistence was lower in turbid than in clear water. At higher irradiance, in a more southern climate, competition for light occurred at plant densities ≥ 8-9 plants m^{-2} (Figure 9, lower). Low epiphyte shading generally decreased persistence (Figure 10).

In *P. pectinatus*, intraspecific competition for light occurred at plant densities ≥4-5 plants m^{-2} in both temperate and more southern climates (Figure 11). Persistence was lower in plant communities growing in a temperate climate than in a more southern climate. Water turbidity did not affect persistence in plant communities at the default plant density of 30 m^{-2} (Figure 11). The lower maximum tuber number produced at a plant density of 20 m^{-2} compared to that formed at a plant density of 18 m^{-2} is explained by the higher self-shading at 20 plants m^{-2}, leading to a later completion of the first tuber class and prevention of finalizing a second tuber class (Figure 12). Low epiphyte shading generally decreased persistence (Figure 13).

Interspecific competition

Interspecific competition for light was explored by maintaining total plant density at 30 m^{-2}, the density that would be expected in an established plant stand composed by either species, and varying the plant density ratio of *V. americana* relative to *P.pectinatus* (Va:Pp) between 30:0 and 0:30 and exposing the mixed stands to low and high light levels following the same approach as for monotypic stands.

At Va:Pp density ratios of 29:1 and 30:0, *V. americana* replaced *P. pectinatus*, but at a Va:Pp ratio of 26:4 and lower, *P. pectinatus* replaced *V. americana* (Table 3; Figure 14). Coexistence occurred only in a narrow ratio range, i.e. at Va:Pp density ratios 28:2 and 27:3 in clear water, and at Va:Pp ratios of 28:2, 27:3, and 26:4 in turbid water. Thus, at most density ratios *P. pectinatus* won, but in turbid water, coexistence with *V. americana* was possible over a somewhat larger Va:Pp ratio range than in clear water. In Figure 15, plant biomass and tuber production in both coexisting species at a Va:Pp ratio of 26:4 is presented. Without any tubers being inactivated by processes other than senescence, e.g. grazing, heavy sedimentation, or scouring, this mixed plant stand should be completely dominated by *P. pectinatus* during the subsequent year, since the end-of-year tuber number of the latter species exceeds 30 tubers m^{-2}. Epiphyte shading increased the Va:Pp range for coexistence for clear water situations in both climates, but eliminated coexistence in turbid water in a more southern climate (Table 4; Figure 16). In Figure 17, plant biomass and tuber production at Va:Pp of 26:4 and 24:6, respectively, are presented. At a density of 26:4, *V. americana* develops enough plant mass early in the growth season to start tuber production. In contrast, at a density of 24:6 enough light is intercepted directly at the water surface to completely prevent tuber production in *V. americana.*

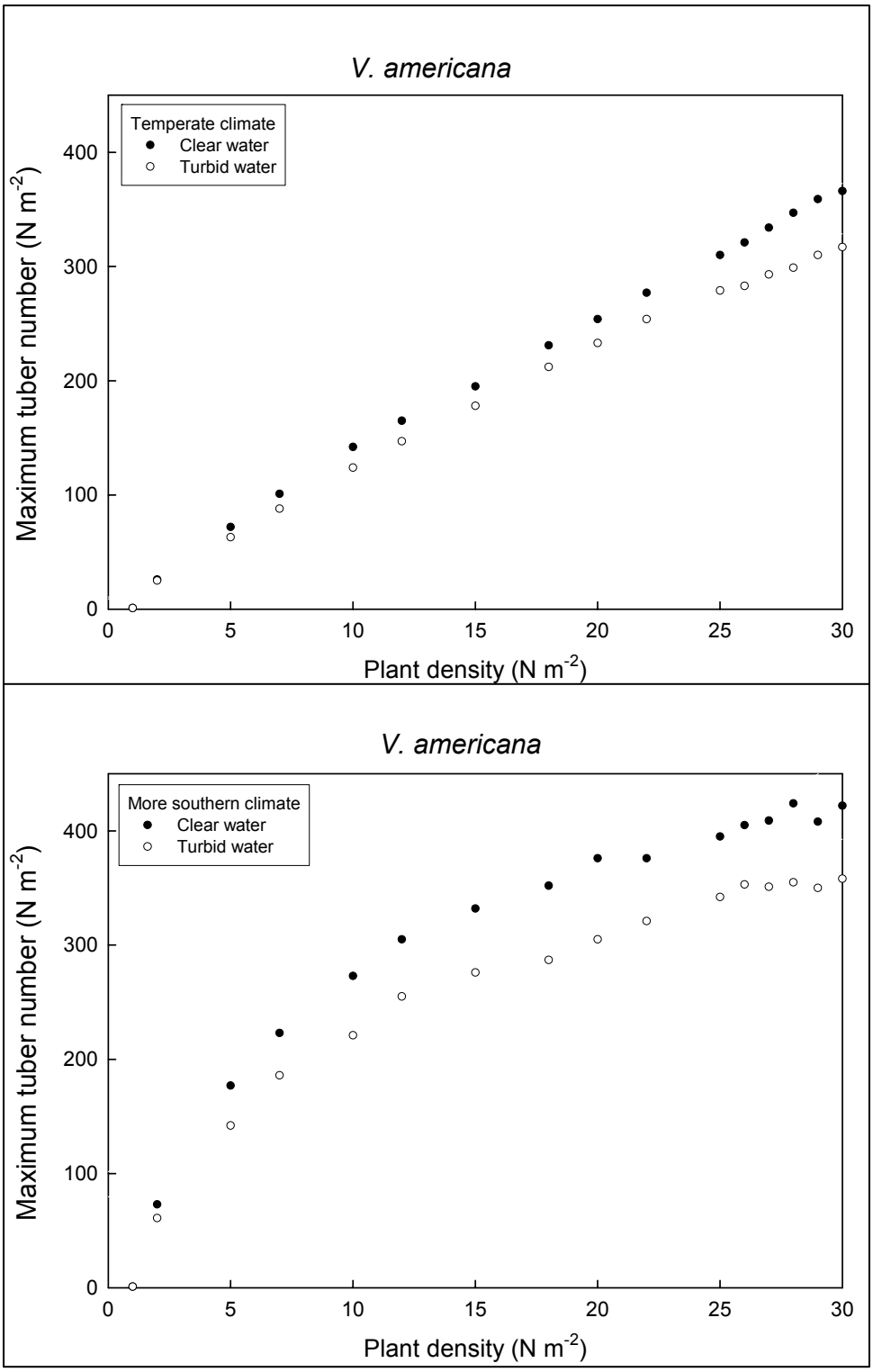

Figure 9. Simulated maximum tuber number, in relation to plant density of a *V. americana* community, at sites differing in latitude (temperate versus more southern) and water transparency (clear versus turbid)

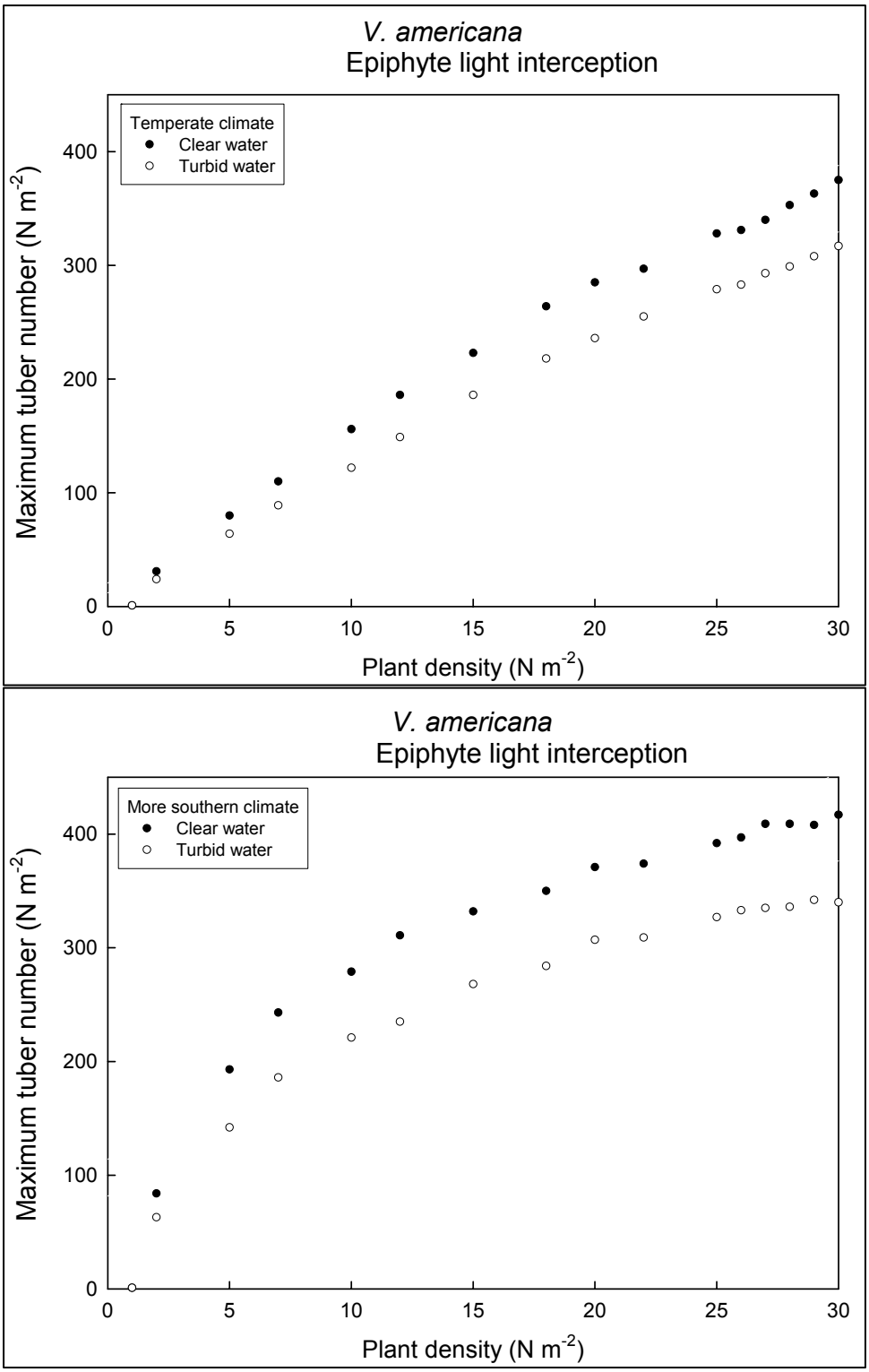

Figure 10. Simulated maximum tuber number, in relation to plant density of a *V. americana* community, at sites differing in latitude (temperate versus more southern) and water transparency (clear versus turbid), with epiphyte cover (light extinction of 11 percent at plant maturity)

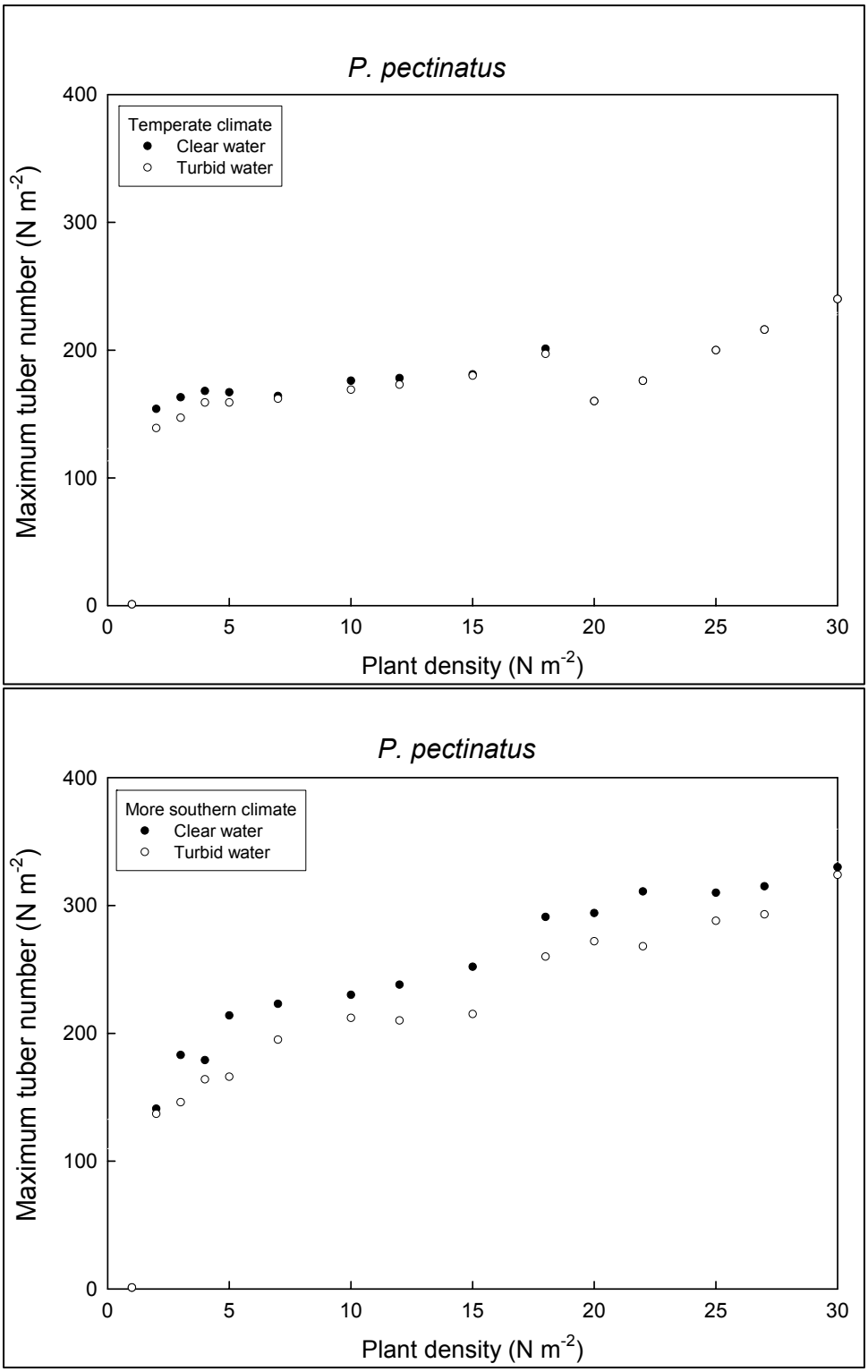

Figure 11. Simulated maximum tuber number, in relation to plant density of a *P. pectinatus* community, at sites differing in latitude (temperate versus more southern) and water transparency (clear versus turbid)

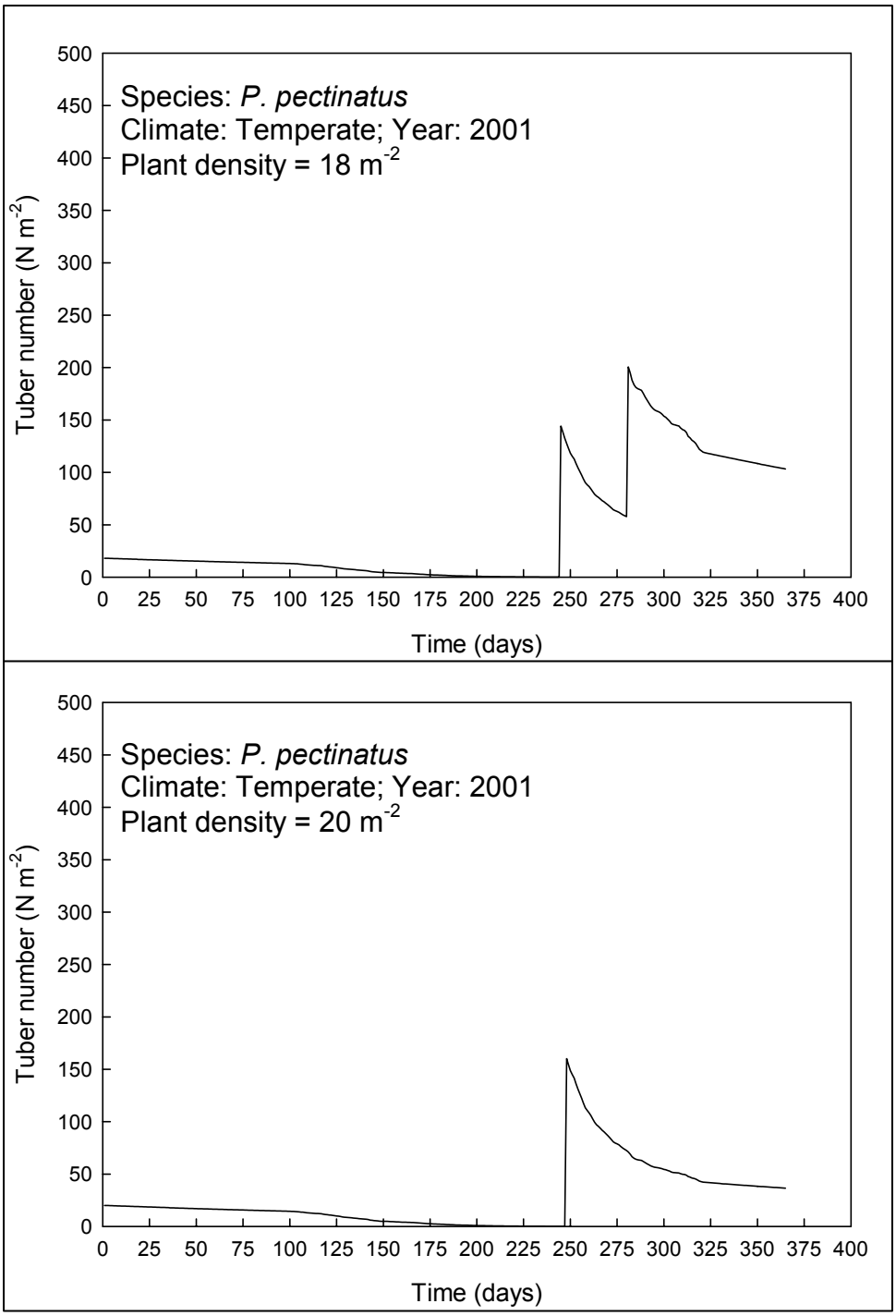

Figure 12. Simulated tubers of *P. pectinatus* communities, with different plant densities, in Pool 8 of the Upper Mississippi River, WI, USA. Climatological data 2001, La Crosse, WI (longitude 91°30'W, latitude 43°10'N); water depth 0.5 m; light extinction coefficient clear water 0.43 m^{-1}

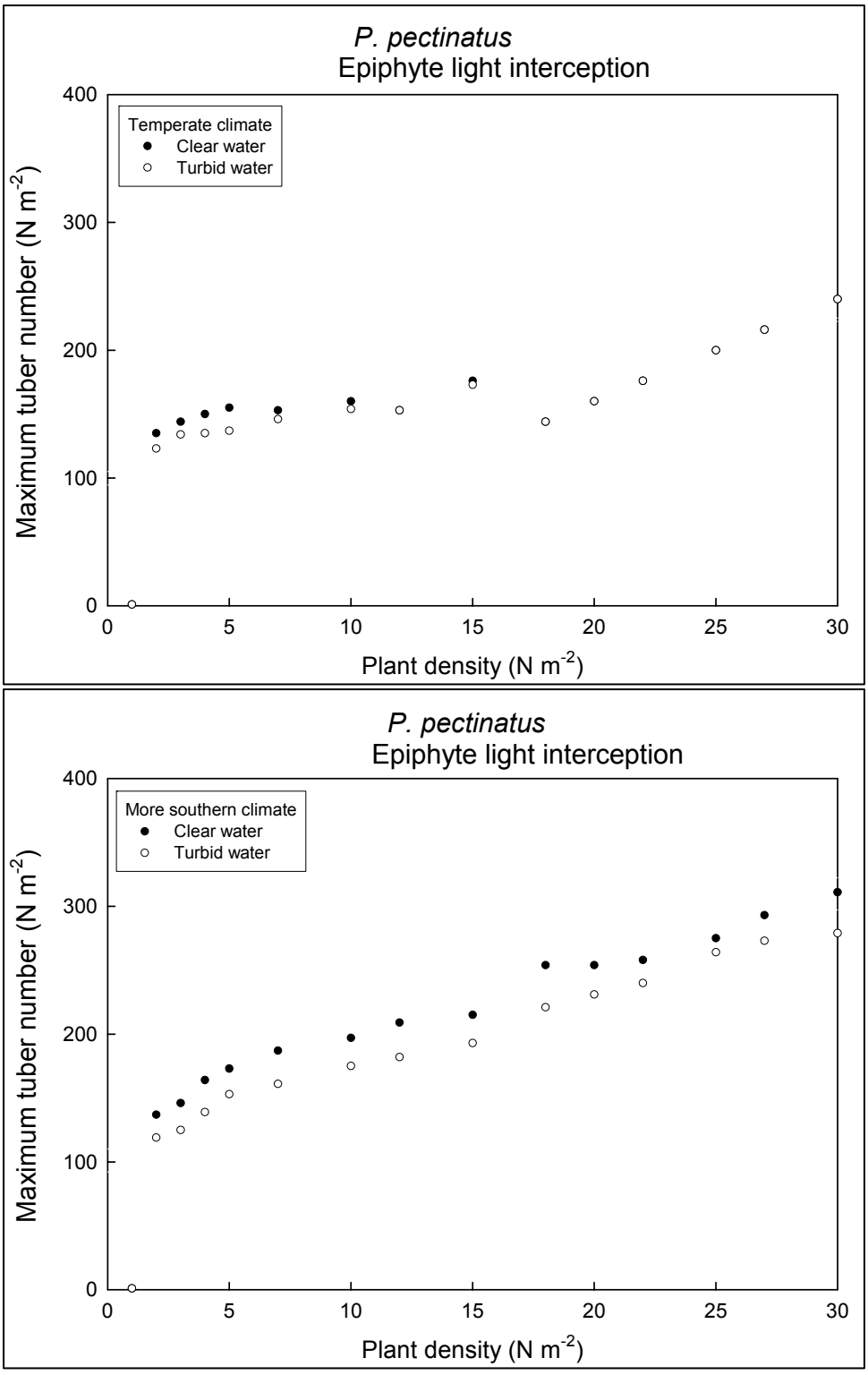

Figure 13. Simulated maximum tuber number, in relation to plant density of a *P. pectinatus* community, at sites differing in latitude (temperate versus more southern), water transparency (clear versus turbid), with epiphyte cover (light extinction of 25 percent versus 100 percent at plant maturity)

Table 3
Simulated Maximum Tuber Number for *V. americana* (Va) and *P. pectinatus* (Pp) in Relation to Plant Density at Sites Differing in Latitude (Temperate Versus More Southern) and Water Transparency (Clear Versus Turbid). Cases of Coexistence Between Va and Pp are Bold and Underlined

Plant Density Ratio $N_{Va}:N_{Pp}$	Maximum Tuber No (N m^{-2})							
	Temperate Climate				More Southern Climate			
	Clear		Turbid		Clear		Turbid	
	Va	Pp	Va	Pp	Va	Pp	Va	Pp
30 : 0	366	0	347	0	422	0	358	0
29 : 1	359	1	310	1	408	1	350	1
28 : 2	**347**	**40**	**299**	**33**	**424**	**21**	**355**	**19**
27: 3	**334**	**41**	**293**	**38**	**409**	**25**	**351**	**25**
26 : 4	26	168	**283**	**43**	26	179	**353**	**32**
25 : 5	25	167	25	159	25	214	25	173
24 : 6	24	158	24	159	24	194	24	190
15 : 15	15	181	15	180	15	252	15	215
10 : 20	10	202	10	160	10	294	10	272
5 : 25	5	200	5	200	5	310	5	288
0 : 30	0	240	0	240	0	330	0	324

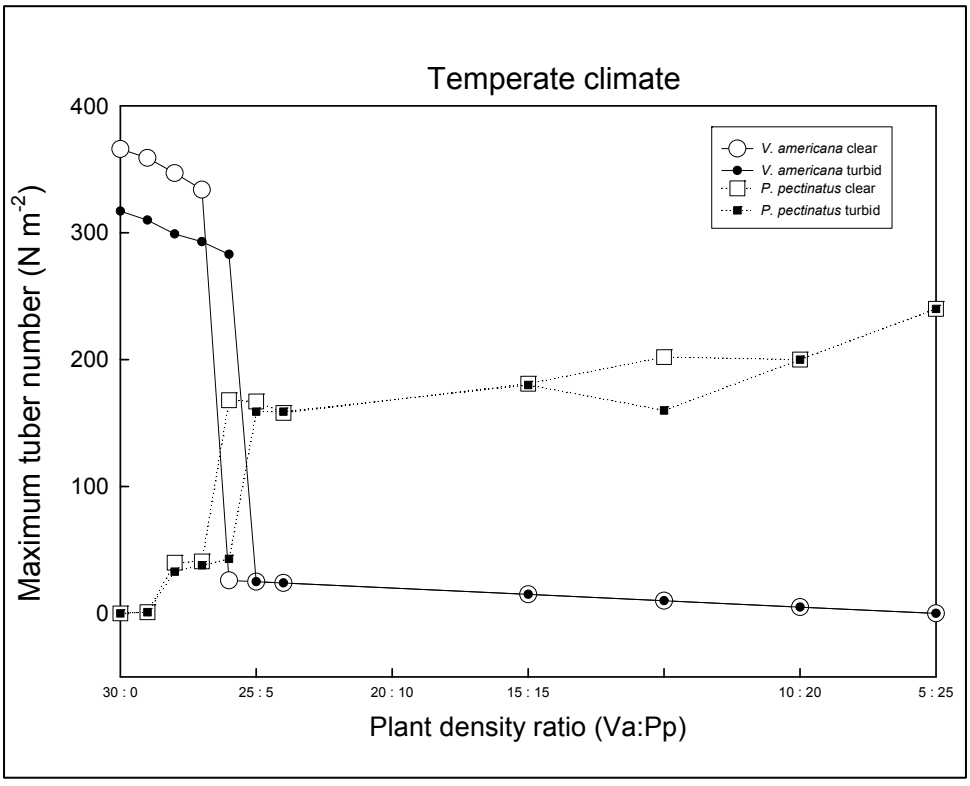

Figure 14. Simulated maximum tuber number, in relation to plant density ratio of a mixture of *V. americana* and *P. pectinatus*, at a temperate site

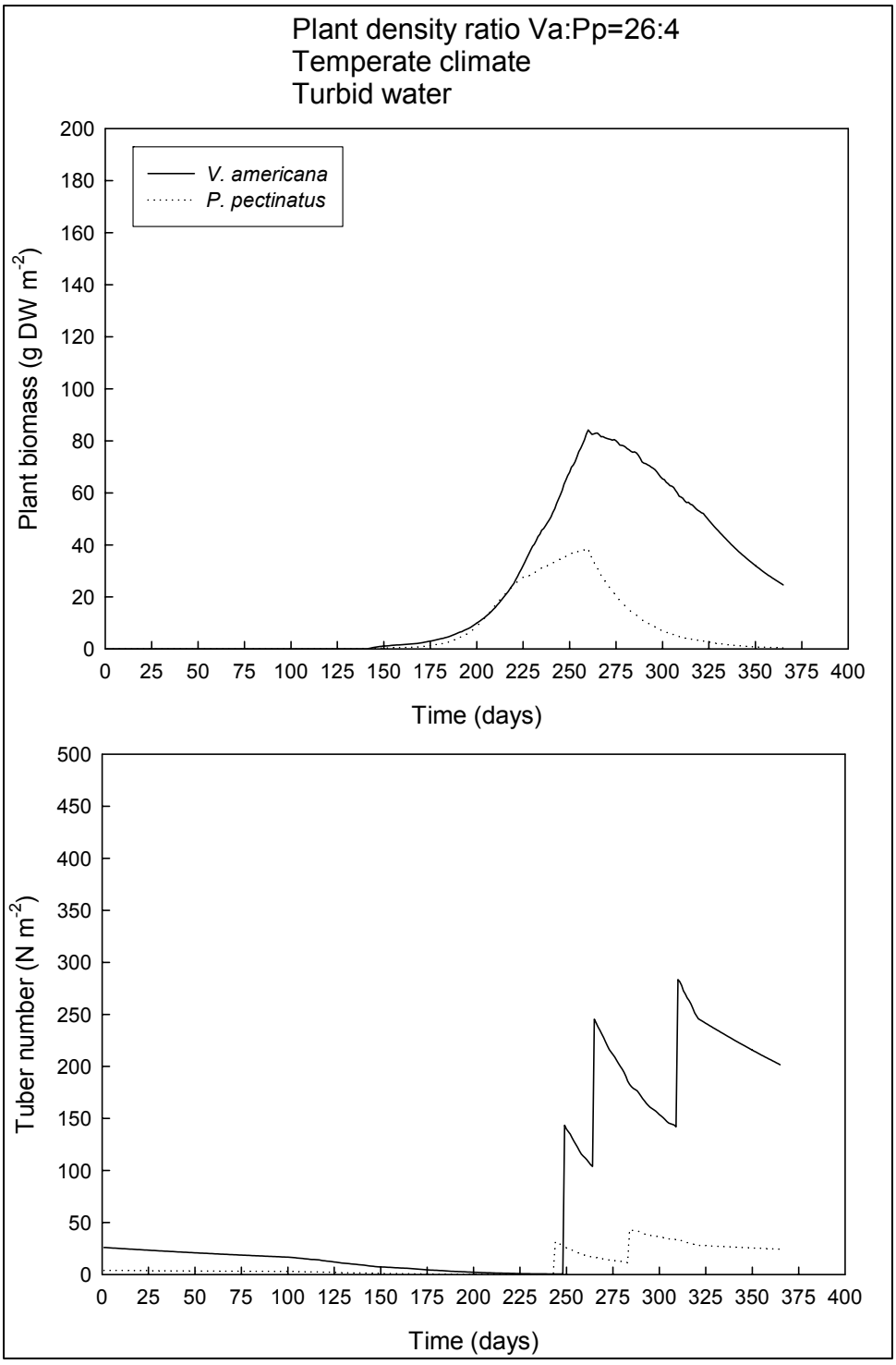

Figure 15. Simulated plant biomass and tuber number of a plant community composed of a mixture of *V. americana* and *P. pectinatus* at a Va:Pp plant density ratio of 26:4, in Pool 8 of the Upper Mississippi River, WI, USA. Climatological data 2001, La Crosse, WI; water depth 0.5 m; light extinction coefficient turbid water 2.0 m^{-1}

Table 4
Simulated Maximum Tuber Number for *V. americana* (Va) and *P. pectinatus* (Pp) in Relation to Plant Density at Sites Differing in Latitude (Temperate Versus More Southern) and Water Transparency (Clear Versus Turbid) When Epiphyte Cover on Plants is Significant (Light Extinction of 11 percent for Wildcelery and 25 percent for Sago Pondweed at Plant Maturity). Cases of Coexistence Between Va and Pp are Bold and Underlined

Plant Density Ratio $N_{Va}:N_{Pp}$	Maximum Tuber No (N m^{-2})							
	Temperate Climate				More Southern Climate			
	Clear		Turbid		Clear		Turbid	
	Va	Pp	Va	Pp	Va	Pp	Va	Pp
30 : 0	375	0	317	0	417	0	340	0
29 : 1	363	1	308	1	408	1	342	1
28 : 2	**353**	**24**	**299**	**16**	**409**	**16**	336	2
27: 3	**340**	**24**	**293**	**24**	**409**	**24**	335	3
26 : 4	**337**	**32**	**287**	**32**	**397**	**32**	333	4
25 : 5	25	155	281	5	25	173	328	5
24 : 6	24	155	24	143	24	164	329	6
20 : 10	20	161	20	154	20	197	20	175
15 : 15	15	176	15	173	15	215	15	193
12 : 18	12	144	12	144	12	254	12	221
7 : 23	7	184	7	184	7	266	7	250
2 : 28	2	224	2	224	2	310	2	280
0 : 30	0	240	0	240	0	311	0	279

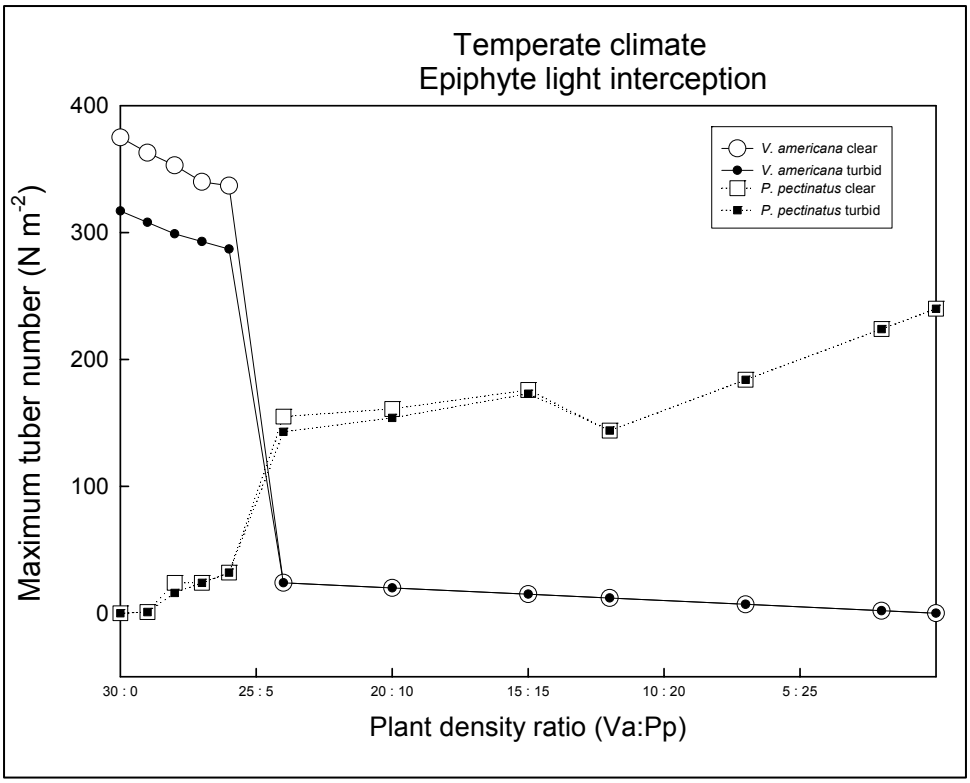

Figure 16. Simulated maximum tuber number, in relation to plant density ratio of a mixture of *V. americana* and *P. pectinatus*, at temperate sites differing in water transparency (clear versus turbid) and epiphyte cover (light extinction of 11 percent for wildcelery and 25 percent for sago pondweed at plant maturity)

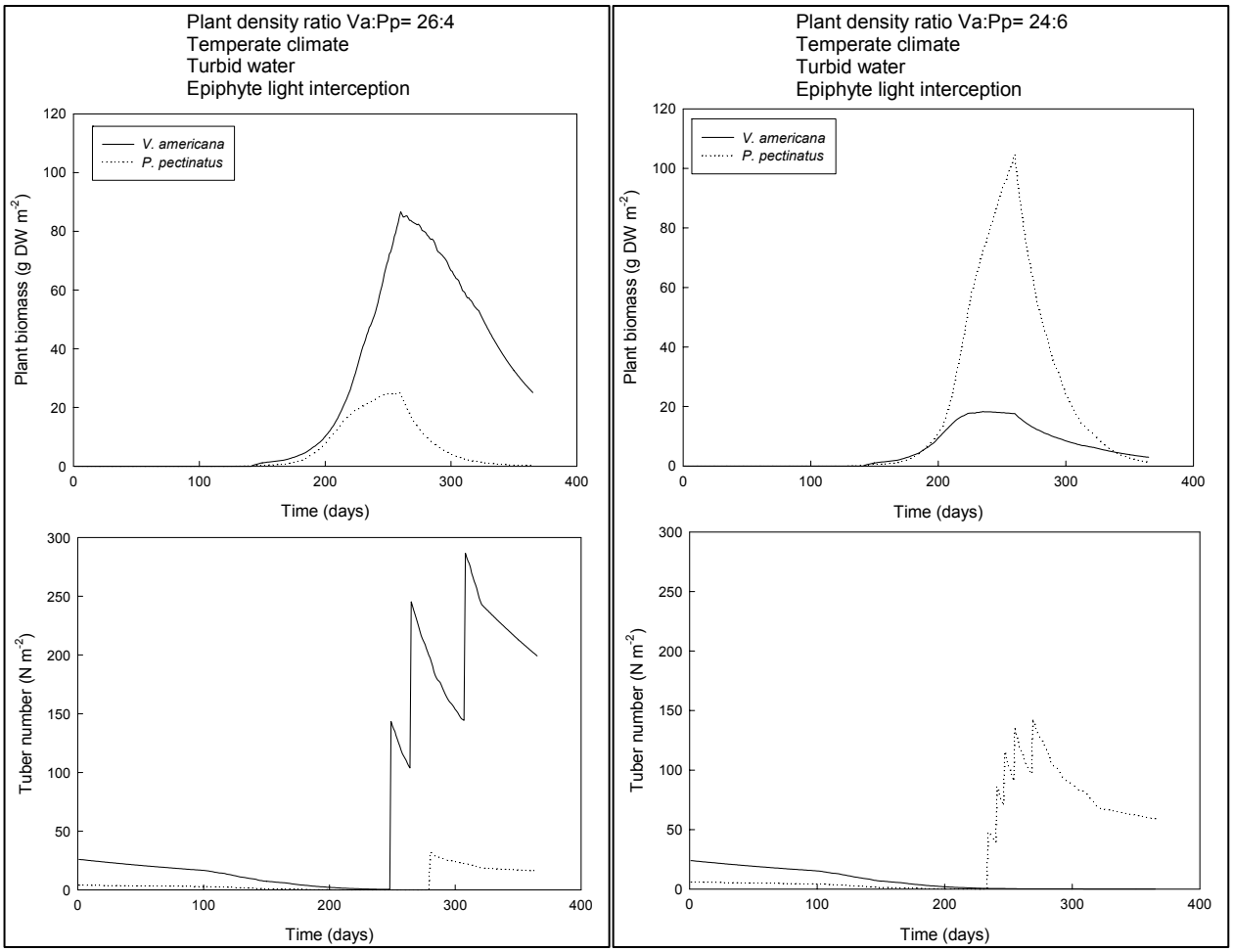

Figure 17. Simulated plant biomass and tuber number at Va:Pp plant density ratios of 26:4 and 24:6, respectively, in Pool 8 of the Upper Mississippi River, WI, USA. Climatological data 2001, La Crosse, WI (longitude 91°30'W, latitude 43° 10'N); water depth 0.5 m; light extinction coefficient clear water 0.43 m^{-1}

Simulations using (a) the measured epiphyte shading levels of 43 percent at maturity for *V. americana* and 100 percent at maturity for *P. pectinatus* were also conducted, as were simulations for (b) half of the measured values. Results of the latter simulations indicated that no coexistence of the species occurred (results not shown).

Interspecific Competition for Light under Potential Growth Limitation by N or P

Several simulations were carried out to explore how potential nutrient limitation (expressed in plant species-specific tissue N:P ratio and their consequent effects on photosynthesis) changed the plant density ratio range over which coexistence of both *V. americana* and *P. pectinatus* would occur. The simulations were done for the Va:Pp density ratios of 28:2, 27:3, 26:4, and 25:5, in temperate and more southern climates, and in clear and turbid water conditions.

The assignment of tissue N:P ratios of 2:7 and 5:4, indicative of severe growth limitation by N in both species, and an N:P ratio of 1:0, indicative of growth limitation by N in *V. americana* but not in *P. pectinatus* (see Figure 4), allowed *P. pectinatus* to win in all cases. In contrast, the assignment of tissue N:P ratios of 2:5 and 3:0, indicative of severe growth limitation by P in *P. pectinatus* but not in *V. americana* (see Figure 4), allowed *V. americana* to win in all cases. Coexistence was only found to be possible under conditions where nutrients were not limiting, i.e., simulations where the potential for nutrient limitation was not activated in the model runs (Table 5).

Table 5
Simulated Maximum Tuber Number for *V. americana* (Va) and *P. pectinatus* (Pp) in Relation to Plant Density at Sites Differing in Latitude (Temperate Versus More Southern) and Water Transparency (Clear Versus Turbid) Under Various Nutrient Limitations. Cases of Coexistence Between Va and Pp are Bold and Underlined

Tissue N:P ratio	Plant Density Ratio $N_{Va}:N_{Pp}$	Maximum Tuber No (N m^{-2})							
		Temperate Climate				More Southern Climate			
		Clear		Turbid		Clear		Turbid	
		Va	Pp	Va	Pp	Va	Pp	Va	Pp
No nutrient limitation	28 : 2	**347**	**40**	**299**	**33**	**424**	**21**	**355**	**19**
	27 : 3	**334**	**41**	**293**	**38**	**409**	**25**	**351**	**25**
	26 : 4	26	167	**283**	**43**	26	179	**353**	**32**
	25 : 5	25	167	25	159	25	214	25	173
2.7	28 : 2	28	2	28	2	28	2	28	2
	27 : 3	27	3	27	3	27	3	27	3
	26 : 4	26	4	26	4	26	4	26	4
	25 : 5	25	5	25	5	25	5	25	5
5.4	28 : 2	28	16	28	16	28	16	28	16
	27 : 3	27	24	27	24	27	24	27	24
	26 : 4	26	32	26	32	26	34	26	32
	25 : 5	25	40	25	40	25	42	25	40
10.0	28 : 2	28	152	28	139	28	137	28	137
	27 : 3	27	162	27	147	27	183	27	146
	26 : 4	26	168	26	159	26	173	26	164
	25 : 5	25	167	25	150	25	205	25	166
25.0	28 : 2	347	2	299	2	424	2	355	2
	27 : 3	334	3	293	3	409	3	351	3
	26 : 4	322	4	283	4	408	4	353	4
	25 : 5	310	5	279	5	395	5	342	5
30.0	28 : 2	298	2	253	2	383	2	317	2
	27 : 3	288	3	244	3	375	3	308	3
	26 : 4	279	4	237	4	365	4	308	4
	25 : 5	270	5	229	5	365	5	300	5

Finally, simulations were conducted in which the tissue N:P ratios, measured by Spencer and Ksander (2003), in the surrogate plants used for the model calibration were assigned to the model plants. These simulations suggested that growth limitation by nutrient availability prevents coexistence of *V. americana*

and *P. pectinatus*, since coexistence in the simulations was only found when nutrients were not limiting, i.e. in N+P-fertilized conditions and in non-fertilized conditions in a sandy sediment (Table 6). Only one exception was noted, i.e., plants fertilized with N growing at a Va:Pp density ratio of 28:2 in clear water and a more southern climate.

Table 6
Simulated Maximum Tuber Number for *V. americana* (Va) and *P. pectinatus* (Pp) in Relation to Plant Density at Sites Differing in Latitude (Temperate Versus More Southern) and Water Transparency (Clear Versus Turbid) Using Tissue N:P Ratios Measured in Plants Fertilized with P, N, and P+N. Cases of Coexistence Between Va and Pp are Bold and Underlined

Tissue N:P Ratio	Plant Density Ratio N_{Va}:N_{Pp}	Maximum Tuber No (N m^{-2})							
		Temperate Climate				More Southern Climate			
		Clear		Turbid		Clear		Turbid	
		Va	Pp	Va	Pp	Va	Pp	Va	Pp
P-fertilized Va, 22.04 Pp, 2.68	28 : 2	261	2	247	2	366	2	312	2
	27 : 3	252	3	241	3	357	3	304	3
	26 : 4	242	4	232	4	358	4	294	4
	25 : 5	233	5	223	5	347	5	286	5
N-fertilized Va, 36.28 Pp, 14.23	28 : 2	28	64	28	38	**154**	**52**	28	34
	27 : 3	27	119	27	90	27	116	27	38
	26 : 4	26	138	26	117	26	132	26	111
	25 : 5	25	147	25	129	25	139	25	121
N+P-Fertilized Va, 25.50 Pp, 9.10	28 : 2	**350**	**35**	**305**	**28**	**424**	**29**	**358**	**17**
	27 : 3	**338**	**40**	**298**	**36**	**412**	**25**	**353**	**25**
	26 : 4	**328**	**45**	**290**	**32**	**408**	**33**	**353**	**32**
	25 : 5	25	165	**281**	**40**	25	181	**342**	**40**
Non-Fertilized Va, 7.86 Pp, 9.77	28 : 2	28	154	28	133	28	137	28	132
	27 : 3	27	164	27	147	27	178	27	140
	26 : 4	26	166	26	142	26	173	26	159
	25 : 5	25	165	25	150	25	214	25	173

5 Conclusions and Recommendations

A simulation model was developed that focuses on the ability of two competing submersed macrophytes, meadow-forming and canopy-forming, to maintain their biomass under differing environmental conditions. *Vallisneria americana* (American wildcelery) serves as the example for meadow-forming plants, and *Stuckenia pectinata* (until recently known as *Potamogeton pectinatus* or sago pondweed) for canopy-forming plants. The model can be used to predict changes in species composition of submersed vegetation as a result of changes in the availability of light and nutrient availability in shallow freshwaters.

In the model, the two plant species compete for light and exhibit differing species-specific relations between plant tissue N:P ratio and plant biomass production. For calibration of the model, the species-specific relationships between plant tissue N:P ratio and plant biomass production of *Zannichellia palustris* and *Elodea canadensis* were used. This was done because these species have habitat preferences and nutrient economies presumed to be similar to those of *V. americana* and *P. pectinatus* (the latter being unknown).

Competition for light proved to be a far more important determinant of species composition than the availabilities of N and P in the sediment.

Intraspecific competition for light occurred in *V. americana* stands at higher plant densities than in *P. pectinatus* stands.

Coexistence of the species in mixed stands occurred only at a narrow *V. americana*:*P. pectinatus* plant density ratio, ranging from 28:2 to 26:4 under non-fertilized conditions. At density ratios higher than 28:2, *V. americana* won, and at density ratios lower than 26:4, *P. pectinatus* won. Under N limiting conditions for both species, *P. pectinatus* won the competition, but under P limiting conditions for *P. pectinatus, V. americana* won. The range of ratios that allowed coexistence was expanded by fertilization with both N and P.

These results 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 raised N and P availabilities enhance the potential for coexistence of the species. This may provide a basis for managing these submersed macrophytes.

It is recommended to (a) verify/determine the species-specific relationships between plant tissue N:P ratio and reduction in plant biomass production of *V. americana* and *P. pectinatus*, since data pertaining to other species were used for the model calibration; and (b) validate the model coexistence results by comparison with outcomes of plant competition experiments.

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Appendix A
Plant Growth Model Calibration Tables

Table A1
Parameter Values Used in VALLA

Parameter	Abbreviation	Value	Reference
Morphology, phenological cycle, and development			
First Julian day number	DAYEM	1	
Base temperature for juvenile plant growth	TBASE	3° C	Calibrated
Development rate as function of temperature	DVRVT* DVRRT	0.015 0.040	Calibrated
Fraction of total dry matter increase allocated to leaves	FLVT	0.718	1, 2
Fraction of total dry matter increase allocated to stems	FSTT	0.159	1, 2
Fraction of total dry matter increase allocated to roots	FRTT	0.123	1, 2
Maximum Biomass and Plant density			
Maximum biomass		496 g DW m^{-1}	2
Plant density	NPL	30 m^{-2}	1
Wintering and sprouting of tuber bank			
(Dormant) tuber density	NDTUB	233 m^{-2}	1
Initial weight per tuber	INTUB	0.090 g DW. $tuber^{-1}$	3, 4
Relative tuber death rate (on number basis)	RDTU	0.018 d^{-1}	1
Initial growth of sprouts			
Relative conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g DW^{-1} d^{-1}	5
Relation coefficient tuber weight-stem length	RCSHST	12 m. g DW^{-1}	5, 6
Critical shoot weight per depth layer	CRIFAC	0.0091g DW. 0.1 m $plant\ layer^{-1}$	3, 4
Survival period for sprouts without net photosynthesis	SURPER	23 d	7,8

(Continued)

Table A1 (Concluded)

Parameter	Abbreviation	Value	Reference
Light, photosynthesis, maintenance, growth, and assimilate partitioning			
Water type specific light extinction coefficient	L	0.43-0.80 m^{-1}	1
Plant species specific light extinction coefficient	K	0.0235m^2 g DW^{-1}	9
Potential CO_2 assimilation rate at light saturation for shoots	AMX	0.0165 g CO_2. g DW^{-1} h^{-1}	9
Initial light use efficiency for shoots	EE	0.000011 g CO_2 J^{-1}	10
Reduction factor for AMX to account for senescence plant parts	REDF	1.0	User def.
Daytime temperature effect on AMX as function of DVS	AMTMPT*	0 - 1	
Reduction factor to relate AMX to water pH	REDAM	1.0	
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	10
Dry matter allocation to each plant layer	DMPC*	0-1	9
Thickness per plant layer	TL	0.1 m	11
Water depth	DEPTH	1.4 m	User def.
Daily water temperature (field site)	WTMPT	-, °C	User def.
Total live dry weight measured (field site)	TGWMT	-, g DM m^{-2}	User def.
Induction and formation of new tubers			
Translocation (part of net photosynthetic rate)	RTR	0.247	4, 12,13
Tuber number concurrently initiated per plant	NINTUB	5.5 $plant^{-1}$	13
Critical tuber weight	TWCTUB	14.85 g DW m^{-2}	1, 3,13
Tuber density measured (field site)	NTMT	233 m^{-2}	1
Flowering and Senescence			
Relative death rate of leaves (on DW basis; Q10 = 2)	RDRT	0.021 d^{-1}	1
Relative death rate of stems and roots (on DW basis; Q10=2)	RDST	0.021 d^{-1}	1
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	User def.

Notes: 1. Titus and Stephens 1983; 2. Haller 1974; 3. Korschgen and Green 1988; 4. Korschgen et al. 1997; 5. Bowes et al. 1979; 6. Best and Boyd 1996; 7. Titus and Adams 1979b; 8. Best et al. 1987; 9. Titus and Adams 1979a; 10. Penning de Vries and Van Laar 1982; 11. Titus et al. 1975; 12. Donnermeyer 1982; 13. Donnermeyer and Smart 1985
* Calibration function.

Table A2
Parameter Values Used in POTAM

Parameter	Abbreviation	Value	Reference
Morphology, phenological cycle, and development			
First Julian day number	DAYEM	1	
Base temperature for juvenile plant growth	TBASE	3 ^{o}C	calibrated
Development rate as function of temperature DVR prior to flowering (DVRVT), DVR subsequently (DVRRT)	DVRVT* DVRRT	0.015 0.040	calibrated
Fraction of total dry matter increase allocated to leaves	FLVT	0.731	1,2
Fraction of total dry matter increase allocated to stems	FSTT	0.183	1,2
Fraction of total dry matter increase allocated to roots	FRTT	0.086	1
Maximum Biomass and Plant density			
Maximum biomass		1,952 g DW m^{-2}	3
Plant density	NPL	30 m^{-2}	1,4
Wintering and sprouting of tuber bank			
(Dormant) tuber density	NDTUB	240 m^{-2}	1
Initial dry weight per tuber	INTUB	0.083 g DW. $Tuber^{-1}$	1
Relative tuber death rate (on number basis)	RDTU	0.026 d^{-1}	5
Initial growth of sprouts			
Relative conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g DW^{-1} d^{-1}	6
Relation coefficient tuber weight-stem length	RCSHST	12 m. g DW^{-1}	6,7,8
Critical shoot weight per depth layer	CRIFAC	0.0076 g DW. 0.1 m $plant\ layer^{-1}$	7,8
Survival period for sprouts without net photosynthesis	SURPER	27 d	1
Light, photosynthesis, maintenance, growth, and assimilate partitioning			
Water type specific light extinction coefficient	L	1.07 m^{-1}	1
Plant species specific light extinction coefficient	K	0.095m^2 g DW^{-1}	1
Potential CO_2 assimilation rate at light saturation for shoot tips	AMX	0.019 g CO_2. g DW^{-1} h^{-1}	9
Initial light use efficiency for shoot tips	EE	0.000011 g CO_2 J^{-1}	10
Reduction factor for AMX to account for senescence plant parts over vertical vegetation axis	REDF	1.0	user def.
Daytime temperature effect on AMX as function of DVS	AMTMPT*	0-1	1
Reduction factor to relate AMX to water pH	REDAM	1	1
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	10
Dry matter allocation to each plant layer	DMPC*	0-1	1
Thickness per plant layer	TL	0.1 m	11
Water depth	DEPTH	1.3 m	user def.
Daily water temperature (field site)	WTMPT	-, ^{o}C	user def.
Total live dry weight measured (field site)	TGWMT	-, g DM m^{-2}	user def.
Induction and formation of new tubers			
Translocation (part of net photosynthetic rate)	RTR	0.19	1, 12
Tuber number concurrently initiated per plant	NINTUB	8 $plant^{-1}$	1,8
Critical tuber weight	TWCTUB	19.92 g DW m^{-2}	1,4
Tuber density measured (field site)	NTMT	440 m^{-2}	4
Flowering and Senescence			
Relative death rate of leaves (on DW basis; Q10 =2)	RDRT	0.047 d^{-1}	1
Relative death rate of stems and roots (on DW basis; Q10=2)	RDST	0.047 d^{-1}	1

(Continued)

Table A2 (Concluded)

Parameter	Abbreviation	Value	Reference
Harvesting			
Harvesting	HAR	0 or 1	user def.
Harvesting day number	HARDAY	1-365	user def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	user def.

1. Best et al. 1987; 2. Sher Kaul et al. 1995; 3. Howard-Williams 1978; 4. Van Wijk 1989; 5. Van Wijk 1989; 6. Best and Boyd 1996; 7. Spencer 1987; 8. Spencer and Anderson 1987; 9. Van der Bijl et al. 1989; 10. Penning de Vries and Van Laar 1982; 11. Titus et al. 1975; 12. Van Wijk et al. 1988
* Calibration function

Table A3
Relationship Between DVS of *V. americana*, Day of Year and 3° C Day-Degree Sum in a Temperate Climate (DVR prior to flowering period, DVRVT= 0.015; DVR from flowering period onwards, DVRRT= 0.040)

Developmental Phase		Day Number	3° C Day-Degree Sum
Description	**DVS Value**		
First Julian day number → tuber sprouting and initiation elongation	0 -> 0.291	0 -> 105	1 -> 270
Tuber sprouting and initial elongation → Leaf expansion	0.292 -> 0.875	106 -> 180	271 ->1215
Leaf expansion → floral initiation and anthesis	0.876 - >1.000	181 - >191	1216 -> 1415
Floral initiation and anthesis -> induction of tuber formation, tuber formation and senescence	1.001 -> 2.000	192 -> 227	1416-> 2072
Tuber formation and senescence → senesced	2.001 -> 4.008	228 -> 365	2073 -> 3167
Senesced	4.008	365	3167

Note: Calibration was 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, 1978.

Table A4
Relationship between DVS of *P. pectinatus*, Day of Year and 3° C Day-Degree Sum in a Temperate Climate (DVR prior to flowering period, DVRVT= 0.015; DVR from flowering period onwards, DVRRT= 0.040)

Developmental phase		Day Number	3 °C Day-Degree Sum
Description	**DVS value**		
First Julian day number → tuber sprouting and initiation elongation	0 -> 0.210	0 -> 77	1 -> 193
Tuber sprouting and initial elongation →Leaf expansion	0.211 -> 0.929	78 -> 187	194 -> 1301
Leaf expansion → floral initiation and anthesis	0.930 - >1.000	188 - >195	1302 -> 1434
Floral initiation and anthesis--> induction of tuber formation, tuber formation and senescence	1.001 -> 2.000	196 -> 233	1435 -> 2077
Tuber formation and senescence → senesced	2.001 -> 4.033	234 -> 365	2078 -> 3193
Senesced	4.033	365	3193

Note: Calibration was on field data on biomass and water transparency from the Western Canal near Zandvoort, The Netherlands, 1987 (Best et al. 1987; Appendix C) and climatological data from De Bilt, The Netherlands, 1987.

Appendix B
Variable Listing and Output Parameters Plant Growth Models Available

Variable Listing. Output Parameters Marked with an *

Abbreviation	Explanation	Dimension
AH(i)	Absolute height of vegetation on top of stratum I, measured from the plant top	m
AMAX	Actual CO_2 assimilation rate at light saturation for individual shoots	g CO_2·g DW^{-1}·h^{-1}
AMTMP	Daytime temperature effect on AMX (relative)	--
AMTMPT	Table of AMX as function of DVS	-, -
AMX	Potential CO_2 assimilation rate at light saturation for shoot tips	g CO_2·g DW^{-1}·h^{-1}
ASRQ	Assimilate requirement for plant dry matter production	g CH_2O·g DW^{-1}
ATMTR	Atmospheric transmission coefficient	--
COSLD	Intermediate variable in calculating solar height	--
CRIFAC	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}·$plnt^{-1}$
CRIGWT	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}·m^{-1}
CVT	Conversion factor of translocated dry matter into CH_2O	--
DAVTMP*	Daily average temperature	ºC
DAY	Day number (January 1 = 1)	d
DAYEM	First Julian day number	d
DAYL*	Day length	h
DDELAY	Integer value of DELAY	--
DDTMP*	Daily average daytime temperature	ºC
DEC	Declination of the sun	radians
DELAY	Lag period chosen to relate water temperature to air temp., in cases where water temp. has not been measured	d
DEPTH	Water depth	m
DLV	Death rate of leaves	g DW·m^{-2}·d^{-1}
DMPC(i)	Dry matter allocation to each plant layer (relative)	--
DMPCT	Table to read DMPC(i) as function of depth layer (relative)	--
DPTT*	Table to read water depth as a function of day no	m, d
DRT	Death rate of roots	g DW·m^{-2}·d^{-1}

Abbreviation	Explanation	Dimension
DSINB	Integral of SINB over the day	$s \cdot d^{-1}$
DSINBE	Daily total of effective solar height	$s \cdot d^{-1}$
DSO	Daily extra-terrestrial radiation	$J \cdot m^{-2} \cdot d^{-1}$
DST	Death rate of stems	g $DW \cdot m^{-2} \cdot d^{-1}$
DTEFF*	Daily effective temperature	ºC
DTGA*	Daily total gross CO_2 assimilation of the vegetation	g $CO_2 \cdot m^{-2} \cdot d^{-1}$
DTR	Measured daily total global radiation	$J \cdot m^{-2} \cdot d^{-1}$
DVR	Development rate as function of temperature sum	d^{-1}
DVRRT	Table of post-anthesis development rate as function of temperature sum	d^{-1}, ºC
DVRVT	Table of pre-anthesis development rate as function of temperature sum	d^{-1}, ºC
DVRVT	Development rate pre-anthesis	d^{-1}
DVS*	Development phase of the plant	--
EE	Initial light use efficiency for shoots	g $CO_2 \cdot J^{-1}$
EPHSWT	On/off switch effect epiphyte shading on photosynthesis	--
EPISHD	Epiphyte shading effect on light interception on light interception by the plant as function of DVS	-, -
EPHY	Epiphyte shading effect on light interception by the plant as function of DVS	-, -
ERDC	U.S. Army Engineer Research and Development Center	
FGROS*	Instantaneous CO_2 assimilation rate of the vegetation	g $CO_2 \cdot m^{-2} \cdot h^{-1}$
FGL	Instantaneous CO_2 assimilation rate per vegetation layer	g $CO_2 \cdot m^{-2} \cdot h^{-1}$
FL	Leaf dry matter allocation to each layer of shoot (relative)	--
FLT	Table to read FL as function of DVS	-, -
FLV	Fraction of total dry matter increase allocated to leaves	--
FLVT	Table to read FLV as function of DVS	--
FRDIF	Diffuse radiation as a fraction of total solar radiation	--
FRT	Fraction of total dry matter increase allocated to roots	--
FRTT	Table to read FRT as function of DVS	-, -
FST	Fraction of total dry matter increase allocated to stems	--
FSTT	Table to read FST as function of DVS	-, -
GLV	Dry matter growth rate of leaves	g $DW \cdot m^{-2} \cdot d^{-1}$
GPHOT*	Daily total gross assimilation rate of the vegetation	g $CH_2O \cdot m^{-2} \cdot d^{-1}$
GRT	Dry matter growth rate of roots	g $DW \cdot m^{-2} \cdot d^{-1}$
GST	Dry matter growth rate of stems	g $DW \cdot m^{-2} \cdot d^{-1}$
GTW	Dry matter growth rate of the vegetation (plant excluding tubers)	g $DW \cdot m^{-2} \cdot d^{-1}$
HAR	Harvesting (0 = no harvesting, 1 = harvesting)	--
HARDAY	Harvesting day number	d
HARDEP	Harvesting depth (measured from water surface)	m
HIG(i)	Height on top of stratum I (measured from water surface)	m
HOUR	Selected hour during the day	h
I	Counter in DO LOOP	--
IABS(i)	Total irradiance absorbed per depth layer	$J \cdot m^{-2} \cdot s^{-1}$
IABSL(i)	Total irradiance absorbed per depth layer	$J \cdot m^{-2} \cdot s^{-1}$
IDAY	Integer equivalent of variable DAY	D
INTUB	Initial dry weight of a tuber	g $DW \cdot tuber^{-1}$
IREMOB	Initial value remobilization	g $CH_2O \cdot m^{-2}$
IRS*	Total irradiance just under the water surface	$J \cdot m^{-2} \cdot s^{-1}$
IRZ(i)	Total irradiance on top of depth layer I	$J \cdot m^{-2} \cdot s^{-1}$
IWLVD	Initial dry matter of dead leaves	g $DW \cdot m^{-2}$
IWLVG	Initial dry matter of green (live) leaves	g $DW \cdot m^{-2}$

Abbreviation	Explanation	Dimension
IWRTD	Initial dry matter of dead roots	g DW·m^{-2}
IWRTG	Initial dry matter of green (live) roots	g DW·m^{-2}
IWSTD	Initial dry matter of dead stems	g DW·m^{-2}
IWSTG	Initial dry matter of green (live) stems	g DW·m^{-2}
K	Plant species specific light extinction coefficient	m^{2}·g DW^{-1}, -
KCOUNT	Counter used to calculate number of consecutive days in which seedlings have anegative net photosynthesis	--
KT	Table to read K as function of DVS	--
L	Water type specific light extinction coefficient	m^{-1}
LAT	Latitude of the site	degrees
LT	Table to read L as function of day number	D, m^{-1}
MAINT*	Maintenance respiration rate of the vegetation	g CH_2O·m^{-2}·d^{-1}
MAINTS	Maintenance respiration rate of the vegetation at reference temperature	g CH_2O·m^{-2}·d^{-1}
NDTUB*	Dormant tuber number	dormant tubers·m^{-2}
NGLV	Net growth rate of leaves	g DW·m^{-2}·d^{-1}
NGRT	Net growth rate of roots	g DW·m^{-2}·d^{-1}
NGST	Net growth rate of stems	g DW·m^{-2}·d^{-1}
NGTUB*	Sprouting tuber number	spr·tubers·m^{-2}
NINTUB	Tuber number concurrently initiated per plant	conc·in·tubers·plnt^{-1}
NNTUB*	New tuber number	new tubers ·m^{-2}
NPL	Plant density	plants·m^{-2}
NPREDF	Plant tissue N:P dependent reduction factor	--
NTM*	Tuber density measured (field site)	tubers·m^{-2}
NTMT	Table to read NTM as function of day number	tubers·m^{-2}, d
NTUBD*	Dead tuber number	dead tubers·m^{-2}
NUL	Zero (0)	--
NTUBPD	Dead tuber number previous day	dead p d tubers m^{-2}
PAR	Instantaneous flux of photosynthetically active radiation	J m^{-2} s^{-1}
PARDIF	Instantaneous flux of diffuse PAR	J m^{-2} s^{-1}
PARDIR	Instantaneous flux of direct PAR	J m^{-2} s^{-1}
PI	Ratio of circumference to diameter of circle	--
RAD	Factor to convert degrees to radians	radians degree^{-1}
RC	Reflection coefficient of irradiance at water surface (relative)	--
RCSHST	Relation coefficient tuber weight-stem length	m g DW^{-1}
RDR	Relative death rate of leaves (on DW basis)	d^{-1}
RDRT	Table to read RDR as function of DAVTMP	d^{-1}, ºC
RDS	Relative death rate of stems and roots (on DW basis)	d^{-1}
RDST	Table to read RDS as function of DAVTMP	d^{-1}, ºC
RDTU	Relative death rate of tubers (on number basis)	d^{-1}
REDAM	Reduction factor to relate AMX to pH and oxygen levels of the water (relative)	--
REDAM1	Reduction factor for AMAX to account for effects of current velocity (relative)	-, cm s^{-1}
REDAM2	Reduction factor for AMAX to account for effects of current velocity, table (relative)	-, cm s^{-1}
REDF(i)	Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative)	--
REMOB*	Remobilization rate of carbohydrates	g DW m^{-2} d^{-1}
ROC	Relative conversion rate of tuber into plant material	g CH_2O g DW^{-1} d^{-1}
RTR	Maximum relative tuber growth rate at 20ºC	g DW·tuber^{-1}·d^{-1}
RTRL	Relative tuber growth rate at ambient temperature	g DW·tuber^{-1}·d^{-1}
SC	Solar constant corrected for varying distance sun-earth	J·m^{-2}·s^{-1}

Abbreviation	Explanation	Dimension
SC(i)	Shoot dry matter in depth layer i	g DW·m^{-2}·layer^{-1}
SHTBIO	Shoot biomass; one term for sum WLV + WST	g DW·m^{-2}
SINB	Sine of solar elevation	--
SINLD	Intermediate variable in calculating solar declination	--
STEMLE	Stem length	m
SURFAC	Expression of warning that plant canopy is not at water and tuber class has died	-
SSURPR	Integer value of SURPER	-
SURPER	Survival period sprouting tubers	d
TBASE	Base temperature for juvenile plant growth	ºC
TEFF*	Factor accounting for effect of temperature on maintenance respiration, remobilization, relative tuber growth and death rates	-
TEFFT	Table to read TEFF as function of temperature (Q10 of 2, up to 45ºC)	-, ºC
TGW*	Total live plant dry weight (excluding tubers)	g DW·m^{-2}
TGWM*	Total live plant dry weight measured (field site)	g DW·m^{-2}
TGWMT	Table to read TGWM as function of day number	g DW·m^{-2}, d
TL	Thickness per depth layer	m
TMAX	Daily maximum temperature	ºC
TMIN	Daily minimum temperature	ºC
TMPSUM*	Temperature sum after 1 January	ºC
TRANS*	Translocation rate of carbohydrates	g CH_2O m^{-2} d^{-1}
TREMOB*	Total remobilization	g DW m^{-2}
TW*	Total live + dead plant dry weight (excluding tubers)	g DW m^{-2}
TWCTUB	Total critical dry weight of new tubers	g DW m^{-2}
TWGTUB*	Total dry weight of sprouting tubers	g DW m^{-2}
TWLVD*	Total dry weight of dead leaves	g DW m^{-2}
TWLVG*	Total dry weight of live leaves	g DW m^{-2}
TWNTUB*	Total dry weight of new tubers	g DW m^{-2}
TWRTD*	Total dry weight of dead roots	g DW m^{-2}
TWRTG*	Total dry weight of live roots	g DW m^{-2}
TWSTD*	Total dry weight of dead stems	g DW m^{-2}
TWSTG*	Total dry weight of live stems	g DW m^{-2}
TWTUB*	Total dry weight of tubers	g DW m^{-2}
TWTUBD	Total dry weight of dead tubers	g DW m^{-2}
VEL	Current velocity as function of day number	cm s^{-1}, d
VELSWT	On/off switch for effect current velocity on photosynthesis	-
WLV	Dry weight of leaves (live + dead)	g DW m^{-2}
WRT	Dry weight of roots (live + dead)	g DW m^{-2}
WST	Dry weight of stems (live + dead)	g DW m^{-2}
WTMP*	Daily water temperature	ºC
WTMPT	Table to read WTMP as function of day number	ºC, d
WVEL	Current velocity as function of day number	cm s^{-1}
YRNUM	Year number simulation (1-5)	y

Appendix C
Input Files VALLA v2.0 and POTAM v2.0

MODEL.DAT File Used as Input for VALLA V2.0

```
*-----------------------------------------------------------------------------------------*
* Model data file generated by FST translator version 1.15 TEST ..........*
* - Initial constants as far as specified with INCON statements, ..........*
* - Model parameters,..........*
* - AFGEN functions, ..........*
* - A SCALE array in case of a general translation ..........*
*     ..........*
* File name: MOD_P08_M686_6J_2.DAT; input MODEL.DAT file for run .....*
* of VALLA for Upper Mississippi River Pool 8, 2001 conditions, ..........*
* with velocity-corrected photosynthesis, for SITE_ID M686.6J ..........*
* using La Crosse weather data usa4.001, measured daily values ..........*
* used for wdepth (0.5 m), velocity, and LT (either 0.43, clear,..........*
* 2.00, turbid)..........*
* Date: 5 Sept. 2003 ..........*
* Time: 08:45:00 ..........*
*-----------------------------------------------------------------------------------------*

* Initial constants
* ----------------------
INTUB     = 0.09    ! Initial dry weight of a tuber (g DW. tuber-1)
IREMOB    = 0.      ! Initial value remobilization (g CH2O.m-2)
IWLVD     = 0.      ! Initial dry matter of dead leaves (g DW. m-2)
IWLVG     = 0.      ! Initial dry weight of live leaves (g DW. m-2)
IWRTD     = 0.      ! Initial dry weight of dead roots (g DW. m-2)
IWRTG     = 0.      ! Initial dry weight of live roots (g DW. m-2)
IWSTD     = 0.      ! Initial dry weight of dead stems (g DW. m-2)
IWSTG     = 0.      ! Initial dry weight of live stems (g DW. m-2)
NUL       = 0.      ! Zero (0)
REMOB     = 0.0     ! Remobilization rate of carbohydrates (g
                    CH2O.m-2)
```

* Model parameters
* ------------------------

YRNUM	= 1.	! Year number simulation (1-5) (y)
AMX	= 0.0165	! Potential CO_2 assimilation rate at light saturation for shoot tips (g CO_2. g $DW^{-1}.h^{-1}$)
CRIFAC	= 0.0091	! Critical weight per 0.1 m vegetation layer (g DW per 0.1 m plnt ht^{-1}. m^{-2})
CVT	= 1.05	! Conversion factor of translocated dry matter into CH_2O (-)
DAYEM	= 1.	! First Julian day number (d)
DELAY	= 1.	! Lag period chosen to relate water temperature to air temperature, in cases where water temp. has not been measured (d)
EE	= 0.000011	!Initial light use efficiency for shoots (g CO_2. J^{-1})
HAR	= 0.	! Harvesting (0 = no harvesting, 1 = harvesting)
HARDAY	= 304.	! Harvesting day number (d)
HARDEP	= 0.8	! Harvesting depth (measured from water surface; m)
NDTUB	= 30.	! Dormant tuber number (dormant tubers.m^{-2})
NINTUB	= 5.5	! Tuber number concurrently initiated per plant (conc.in.tubers.$plnt^{-1}$
NPL	= 30.	! Plant density (plants.m^{-2})
RC	= 0.06	! Reflection coefficient of irradiance at water surface (relative; -)
RCSHST	= 12.0	! Relation coefficient tuber weight- stem length (m g DW^{-1})
RDTU	= 0.018	! Relative death rate of tubers (on number basis; d^{-1})
REDAM	= 1.	! Reduction factor to relate AMX to pH and oxygen levels of the water (relative; -)
ROC	= 0.0576	! Relative conversion rate of tuber into plant material (g CH_2O g $DW^{-1}.d^{-1}$)
RTR	= .247	! Maximum relative tuber growth rate at 20ºC (g $DW.tuber^{-1}.d^{-1}$)
SURPER	= 23.	! Survival period sprouting tubers (d)
TBASE	= 3.	! Base temperature for juvenile plant growth (ºC)
TL	= 0.1	! Thickness per depth layer (m)
TWCTUB	= 14.85	! Total critical dry weight of new tubers (g DW. m^{-2})
EPHSWT	= 0.	! On/off switch effect epiphyte shading on photosynthesis
NPRSWT	= 0.	! On/off switch for effect tissue N:P ratio on photosynthesis
VELSWT	= 0.	! On/off switch for effect current velocity on photosynthesis

* AFGEN functions
* ------------------------

! Daytime temperature effect on AMX as function of DVS (-,-)
AMTMPT = -30., 0.00001, 0., 0.00001, 5., 0.12, 15., 0.424, 20., 0.568, 25., 0.735, 30., 0.879, 35., 1.0, 50., 0.00001

! Dry matter allocation to each plant layer (relative; - , layer number)
DMPCT = 1.0, .184, 2.0, .184, 3.0, .184, 4.0, .114, 5.0, .114

! Water depth as function of day number (m, d)
DPTT = 1., 0.5, 365., 0.5

! Development rate prior to flowering period as function of temperature (-,^{o}C)
DVRVT = -15., 0., 0., 0., 30., 0.015

! Development rate from flowering period onwards as function of temperature (-, ^{o}C)
DVRRT = -15., 0., 0., 0., 30., 0.040

! Epiphyte shading effect on light interception by the plant as function of DVS (-, -)
EPHY = 0., 0.0, 2.0, 0.43, 20., 0.0

! Leaf dry matter allocation to each layer of the plant as function of DVS (-,-)
FLT = 0., 0.82, 3.5, 0.82, 20.0, 0.82

! Fraction of total dry matter increase allocated to leaves as function of DVS (-,-)
FLVT = 0., 0.718, 3.5, 0.718, 20.0, 0.718

! Fraction of total dry matter increase allocated to roots as function of DVS (-,-)
FRTT = 0., 0.123, 3.5, 0.123, 20.0, 0.123

! Fraction of total dry matter increase allocated to stems as function of DVS (-,-)
FSTT = 0., 0.159, 3.5, 0.159, 20.0, 0.159

! Plant species specific light extinction coefficient as function of DVS (m^2.g DW^{-1}, -)
KT = 0., 0.0235, 3.5, 0.0235, 20.0, 0.0235

! Water type specific light extinction coefficient as function of day number (m^{-1}, d)
LT = 1., 0.43, 365., 0.43

! Plant tissue N:P ratio as function of day number (-, d)
NPRAT = 1., 24.65, 261., 24.65, 365., 24.65

! Relative death rate of roots as function of daily average temperature (g DW. g $DW.d^{-1}$, ^{o}C)
RDRT = 0., 0.021, 19., 0.021, 30., 0.042, 40., 0.084, 50., 1.

! Relative death rate of shoots as function of daily average temperature (g DW. g $DW.d^{-1}$, ^{o}C)
RDST = 0., 0.021, 19., 0.021, 30., 0.042, 40., 0.084, 50., 1.

! Reduction factor for AMAX to account for effects of current velocity, read from input file (-, cm s^{-1})
REDAM1 = 0., 1.0, 3.82, 1.0, 7.636, 0.989734, 81., 0.0, 120., 0.0

! Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative; -,-)
REDFT = 0.0, 1.0, 1.0, 1.0, 20.0, 1.0

! Factor accounting for effect of temperature on maintenance respiration, remobilization, and relative tuber growth rate (relative; -, ^{o}C)
TEFFT = 0.0, 0.0001, 10., 0.5, 20., 1., 30., 2., 40., 4., 45., 6., 50., 0.0001

! Daily water temperature as function of day number (^{o}C, day)
WTMPT = 1., 0., 365., 0.

! Current velocity as function of day number (cm s^{-1}, d)
WVEL = 1., 36.00, 151., 36.00, 164., 11.00, 178., 37.00, 192., 29.00, 205., 6.00, 221., 25.00, 235., 3.00, 365., 3.00

! Tuber density measured (field site) as function of day number (tubers.m^{-2}, d)
NTMT = 1., 233., 98., 233., 134., 233., 162., 233., 190., 233., 233., 233., 260., 233., 289., 233., 365., 233.

! Total live dry weight measured (field site) as function of day number
(g DW.m^{-2}, d)
TGWMT = 1., 0., 153., 2.4, 166., 3.8, 178., 7.1, 199., 17.3, 220., 50.1, 243., 41.0, 266., 25.3, 365., 0.

MODEL.DAT File Used as Input for POTAM V2.0

----
* Model data file generated by FST translator version 1.15 TEST .....*
* - Initial constants as far as specified with INCON statements, ...*
* - Model parameters,.....*
* - AFGEN functions, ...*
* - A SCALE array in case of a general translation .....*
* .....*
* File name: MOD_P08_POT_M696_5D_1.DAT;input MODEL.DAT file for...*
* run of POTAM for Upper Mississippi River Pool8,2001 conditions,.....*
* without velocity-corrected photosynthesis, for Site_ID M696.5D .....*
* using La Crosse weather data usa4.001, measured daily values .....*
* used for wdepth (o.5 m), velocity, and LT (either 0.43, clear, ...*
* or 2.00, turbid).....*
* Date: 25 April 2001.....*
* Time: 14:00:00 .....*
----

* Initial constants
* ----------

INTUB	= 0.083	! Initial dry weight of a tuber (g DW. $tuber^{-1}$)
IREMOB	= 0.	! Initial value remobilization (g $CH_2O.m^{-2}$)
IWLVD	= 0.	! Initial dry matter of dead leaves (g DW. m^{-2})
IWLVG	= 0.	! Initial dry weight of live leaves (g DW. m^{-2})
IWRTD	= 0.	! Initial dry weight of dead roots (g DW. m^{-2})
IWRTG	= 0.	! Initial dry weight of live roots (g DW. m^{-2})
IWSTD	= 0.	! Initial dry weight of dead stems (g DW. m^{-2})
IWSTG	= 0.	! Initial dry weight of live stems (g DW. m^{-2})
NUL	= 0.	! Zero (0)
REMOB	= 0.0	! Remobilization rate of carbohydrates (g $CH_2O.m^{-2}$)

* Model parameters
* ----------

YRNUM	= 1.	! Year number simulation (1-5) (y)
AMX	= 0.019	! Potential CO2 assimilation rate at light saturation for shoot tips (g CO_2. g DW^{-1}.h^{-}
CRIFAC	= 0.0076	! Critical weight per 0.1 m vegetation layer (g DW per 0.1 m plnt ht^{-1}. m^{-2})
CVT	= 1.05	! Conversion factor of translocated dry matter into CH_2O (-)
DAYEM	= 1.	! First Julian day number (d)
DELAY	= 7.	! Lag period chosen to relate water temperature to air temperature, in cases where water temp. has not been measured (d)
EE	= 0.000011	! Initial light use efficiency for shoots (g CO_2. J^{-1})
HAR	= 0.	! Harvesting (0 = no harvesting, 1 = harvesting
HARDAY	= 304.	! Harvesting day number (d)
HARDEP	= 0.8	! Harvesting depth (measured from water surface; m)
NDTUB	= 30.	! Dormant tuber number (dormant tubers.m^{-2})
NINTUB	= 8.	! Tuber number concurrently initiated per plant (conc.in.tubers.$plnt^{-1}$)
NPL	= 30.	! Plant density (plants.m^{-2})
RC	= 0.06	! Reflection coefficient of irradiance at water surface (relative; -)
RCSHST	= 12.0	! Relation coefficient tuber weight- stem length (m g DW^{-1})
RDTU	= 0.026	! Relative death rate of tubers (on number basis; d^{-1})
REDAM	= 1.	! Reduction factor to relate AMX to pH and oxygen levels of the water (relative; -)
ROC	= 0.0576	! Relative conversion rate of tuber into plant material (g CH_2O g DW^{-1}.d^{-1})
RTR	= .19	! Maximum relative tuber growth rate at 20ºC (g DW.$tuber^{-1}$.d^{-1})
SURPER	= 27.	! Survival period sprouting tubers (d)
TBASE	= 3.	! Base temperature for juvenile plant growth (ºC)
TL	= 0.1	! Thickness per depth layer (m)
TWCTUB	= 19.92	! Total critical dry weight of new tubers (g DW. m^{-2})
EPHSWT	= 0.	! On/off switch effect epiphyte shading on photosynthesis
NPRSWT	= 0.	! On/off switch effect tissue N:P ratio on photosynthesis
VELSWT	= 0.	! On/off switch for effect current velocity on photosynthesis

* AFGEN functions
* ----------

! Daytime temperature effect on AMX as function of DVS (-,-)
AMTMPT = -30., 0.00001, 0., 0.00001, 10., 0.027, 18., 0.51, 20., 0.53, 23., 0.71, 28., 0.91, 30., 1.0, 50., 0.00001

! Dry matter allocation to each plant layer (relative; - , layer number)
DMPCT = 1.0, .043, 2.0, .043, 3.0, .231, 4.0, .254, 5.0, .213

! Water depth as function of day number (m, d)
DPTT = 1., 0.5, 365., 0.5

! Development rate prior to flowering period as function of temperature (-,^{o}C)
DVRVT = -15., 0., 0., 0., 30., 0.015

! Development rate from flowering period onwards as function of temperature (-, ^{o}C)
DVRRT = -15., 0., 0., 0., 30., 0.040

! Epiphyte shading effect on light interception by the plant as function of DVS (-, -)
EPHY = 0., 0.0, 2.0, 1.0, 20., 0.0

! Leaf dry matter allocation to each layer of the plant as function of DVS (-,-)
FLT = 0., 0.8, 3.5, 0.8, 20.0, 0.8

! Fraction of total dry matter increase allocated to leaves as function of DVS (-,-)
FLVT = 0., 0.731, 3.5, 0.731, 20.0, 0.731

! Fraction of total dry matter increase allocated to roots as function of DVS (-,-)
FRTT = 0., 0.086, 3.5, 0.086, 20.0, 0.086

! Fraction of total dry matter increase allocated to stems as function of DVS (-,-)
FSTT = 0., 0.183, 3.5, 0.183, 20.0, 0.183

! Plant species specific light extinction coefficient as function of DVS (m^2.g DW^{-1}, -)
KT = 0., 0.095, 3.5, 0.095, 20.0, 0.095

! Water type specific light extinction coefficient as function of day number (m^{-1}, d)
LT = 1., 0.43, 365., 0.43

! Relative death rate of roots as function of daily average temperature (g DW. g DW.d^{-1}, ^{o}C)
RDRT = 0., 0.047, 19., 0.047, 30., 0.094, 40., 0.188, 50., 1.

! Relative death rate of shoots as function of daily average temperature (g DW. g DW.d^{-1}, ^{o}C)
RDST = 0., 0.047, 19., 0.047, 30., 0.094, 40., 0.188, 50., 1.

! Reduction factor for AMAX to account for effects of current velocity, resd from input file (-, cm s^{-1})
REDAM1 = 0., 0.98469, 3.82, 1., 7.6, 1., 93.33, 0.0, 120., 0.0

! Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative; -,-)
REDFT = 0.0, 1.0, 1.0, 1.0, 5.0, 1.0

! Factor accounting for effect of temperature on maintenance respiration, remobilization, and relative tuber growth rate (relative; -, ^{o}C)
TEFFT = 0.0, 0.0001, 10., 0.5, 20., 1., 30., 2., 40., 4., 45., 6., 50., 0.0001

! Daily water temperature as function of day number (^{o}C, day)
WTMPT = 1., 0., 365., 0.

! Current velocity as function of day number (cm s^{-1}, d)
WVEL = 1., 0.0, 11., 0.0, 23., 0.0, 37., 0.0, 53., 2.0, 67., 0.0, 79., 0.0, 95., 2.0, 108., 7.0123., 10.0, 136., 2.0, 151., 0.0, 164., 0.0, 178., 0.0, 192., 0.0, 205., 1.0, 221., 0.0, 235., 0.0, 247., 0.0, 365., 0.0

! Tuber density measured (field site) as function of day number (tubers.m^{-2}, d)
NTMT = 1., 400., 98., 400., 134., 400., 190., 400., 233., 400., 260., 400., 289., 400., 365., 400.

! Total live dry weight measured (field site) as function of day number (g DW.m^{-2}, d)
TGWMT = 1., 0., 98., 0.64, 134., 8., 190., 50.0, 233., 78.5, 260., 52.0, 289., 29.5, 365., 0.

Appendix D
Example Illustrating Calculations Needed for Runs with Changed Default Values

Details on changing input streams for model runs, handling, and rapid visualizing output are presented in Best and Boyd, 2001a, and Best and Boyd, 2003a. In all examples, almost identical MODEL.DAT files are used for the nominal runs of VALLA V2.0 and POTAM V2.0, and only small changes have to be made. Such changes are illustrated for examples regarding POTAM below. It is recommended to save the default MODEL.DAT file in its original form under a different name on a safe place on your PC to avoid the occurrence of unintended changes in the default MODEL.DAT file. Before reuse of the default MODEL.DAT file, the latter files have to be saved again as MODEL.DAT, to be recognized by the (executable of the) source code.

Example 1: Changes in Tuber Bank Density, Individual Tuber Weight, Tuber Number Concurrently Initiated, of *P. pectinatus*

This run is started from tubers alone, i.e. no green plant weight, a low tuber bank density (i.e. 10 tubers m^{-2}), and a smaller tuber size (of 0.070 g DW $tuber^{-1}$) than in the nominal run on day 1 of the simulation.

Wintering in the form of tubers alone, without remaining plant biomass, is typical under temperate climatological conditions.

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0:
Under the 'Initial constants' section:
IWLVD = 0.
IWLVG = 0.
IWRTD = 0.
IWRTG = 0.

IWSTD = 0.
IWSTG = 0.

Low tuber bank densities typically occur under a high grazing pressure by waterfowl.

Tuber bank density ≥ than the typical plant density of 30 plants m^{-2}

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the 'Model parameters' section:
NDTUB = 30. (or higher)

Tuber bank density < than the typical plant density of 30 plants m^{-2}

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the 'Model parameters' section:
NDTUB = 10. (or lower)
NPL = 10. (same number as NDTUB)
TWCTUB = 6.64 (0.083 (INTUB) x 8. (NINTUB) x 10 (NPL))

A smaller than nominal tuber size may occur in shallow water bodies in relatively warm, temperate climates. Individual tuber weight and tuber number concurrently initiated formed by each plant depend on the light level at which the plant grows. Both tuber weight and number decrease with light level according to the relationship shown in Figure 4 of this report. The tuber weight used in the nominal run is representative for the light level in the calibration situation. However, light levels experienced by *P. pectinatus* vegetation at other sites can be higher or lower, and consequently tuber behavior has to be modified to apply to those situations.

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the 'Initial constants' section:
INTUB = 0.070

Under the 'Model parameters' section:
NINTUB = 6.
SURPER = 22.8 (0.07 (INTUB) x 6 (NINTUB) x 27 (nominal SURPER-value)
TWCTUB = 12.6 (0.07 (INTUB) x 6 (NINTUB) x 30 (NPL, nominal value)

A smaller than nominal tuber number concurrently initiated. In several cases, plant density and tuber number concurrently formed by *P. pectinatus* population is known, but tuber size is not. If tuber number concurrently formed is 10, then according to Figure 4, tuber size would be 0.12 g DW $tuber^{-1}$.

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the 'Initial constants' section:
INTUB = 0.12

Under the 'Model parameters' section:
NINTUB = 10.
SURPER = 32.4 (0.12 (INTUB) x 10 (NINTUB) x 27 (nominal SURPER-value)
TWCTUB = 36. (0.12 (INTUB) x 10 (NINTUB) x 30 (NPL, nominal value)

Example 2: Changes in Anchorage Depth of *P. pectinatus* Populations

P. pectinatus populations occur in a wide variety of water bodies and anchorage depths. Moreover, water levels in these waters may change annually, seasonally, or daily, considerably changing the available space and physical (light and current velocity) and chemical (carbon) environment for the plants. The versions 2.0 of POTAM and VALLA accommodate daily changes in water level.

This run is started from tubers alone, i.e. no green plant weight, a default tuber bank density (i.e. 240 tubers m^{-2}), a default tuber size (of 0.083 g DW $tuber^{-1}$), but the values for measured water depths (DPTT) under the section 'AFGEN functions' have to be changed (1.3 m is default).

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the 'AFGEN functions' section:
A. In a water body with an annually changing water depth of 0.2 m
DPTT = 1., 0.2, 365., 0.2
B. In a water body with a seasonally changing water depth (important for reservoirs and flood-prone, riverine, environments).
DPTT = 1., 0.2, 3., 0.5, 10., 1.0, 365., 0.2

Data pairs have to be entered, by giving first the Julian day number followed by '.,' and subsequently the value of the water depth at that day followed by ','.

Example 3: Changes in Water Transparency Within *P. pectinatus* Populations

P. pectinatus populations occur in a wide variety of water bodies with their typical water transparency patterns. Water transparency in these waters may change considerably annually, seasonally, or daily, changing the available light for the plants. The versions 2.0 of POTAM and VALLA accommodate daily changes in water transparency.

This run is started from tubers alone, i.e. no green plant weight, a default tuber bank density (i.e. 240 tubers m^{-2}), a default tuber size (of 0.083 g DW $tuber^{-1}$), but the values for measured water transparency expressed as light extinction coefficients (LT) under the section 'AFGEN functions' have to be changed (range 0.77 to 5.00 m^{-1} is default).

This requires the following entries in the MODEL.DAT file used as Input for POTAMv 2.0
Under the ‘AFGEN functions’ section:
LT = 1., 2.0, 10., 2.5, 150., 3.0, 365., 2.0

Data pairs have to be entered, by giving first the Julian day number followed by ‘.,’ and subsequently the value of the water depth at that day followed by ‘,’.

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13. SUPPLEMENTARY NOTES

14. ABSTRACT

A simulation model has been developed that focuses on the ability of two competing submersed macrophytes, meadow-forming and canopy-forming, to maintain their biomass under different environmental conditions. *Vallisneria americana* (American wildcelery) serves as the example for meadow-forming plants and *Stuckenia pectinata* (until recently known as *Potamogeton pectinatus* or sago pondweed) for canopy-forming plants. The model can be used to predict changes in species composition of submersed vegetation as a result of changes in the availability of resources in shallow freshwater bodies.

In the model, the two plant species compete for light and exhibit different species-specific relationships between plant tissue nitrogen (N):phosphorus (P) ratio and plant biomass production. The latter species-specific relationships have not been determined in *V. americana* and *P. pectinatus*, and, therefore, for calibration of the model, the specific relationships between plant tissue N:P ratio and reduction in plant biomass production of *Zannichellia palustris* and *Elodea canadensis* were used. The latter species have habitat preferences similar to those of *V. americana* and *P. pectinatus*.

(Continued)

15. SUBJECT TERMS

Competition model
Light
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14. ABSTRACT (continued)

Competition for light proved to be a far more important determinant of species composition than the availabilities of N and P in the sediment.

Intraspecific competition for light did not occur in *V. americana* in a temperate climate, but it was observed at densities $\geq$ 8-9 plants m^{-2} in a more southern climate. It occurred in *P. pectinatus* at plant densities $\geq$4-5 plants m^{-2}.

Coexistence of both species occurred only at *V. americana*:*P. pectinatus* plant density ratios of 28:2 to 26:4 plants m^{-2} in the absence of N and P limitation of growth, irrespective of climate (temperate and more southern climates tested). At density ratios higher than 28:2, *V. americana* excludes sago pondweed, and at density ratios lower than 26:4, *P. pectinatus* excludes *V. americana*. The density ratio range at which coexistence was possible increased with water turbidity between extinction coefficients of 0.43 and 2.00 m^{-1}. Light interception by epiphytes at a level of 25 percent of observed maxima in the Upper Mississippi River allowed coexistence in clear water but prevented it in turbid water in a more southern climate. Under N limiting conditions for both species, *P. pectinatus* displaced *V. americana*, but under P limiting conditions for *P. pectinatus*, *V. americana* won the competition. Coexistence was expanded by fertilization with both N and P.

These results 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 advantage of *P. pectinatus* relative to that of *V. americana*, while raised N and P availabilities enhance the potential for coexistence of both species. These notions can be used as a basis for management of submersed macrophytes.

It is recommended to verify/determine the species-specific relationships between plant tissue N:P ratio and plant biomass production of *V. americana* and *P. pectinatus* and validate the model coexistence results by comparison with outcomes from plant competition experiments.