A carbon flow-based modelling approach to ecophysiological processes and biomass dynamics of *Vallisneria americana*, with applications to temperate and tropical water bodies

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ABSTRACT

A dynamic simulation modelling approach to submersed plant biomass formation has been developed to provide a tool for water resource managers to evaluate key environmental conditions in which submersed aquatic vegetation (SAV) would persist or produce excessive biomass with ensuing consequences for the systems in which they grow, either or not affected by management measures. The model species is *Vallisneria americana* (American wildcelery) and the model name is VALLA. The model describes major, carbon flow-based ecophysiological processes and biomass dynamics of a common plant species. The model contains unique descriptions of: (1) species-characteristic vertical distribution of shoot biomass in the water column, that enables the calculation of the fraction of irradiance actually available for absorption by the SAV; (2) recalculation procedures of this vertical distribution with daily changes in water level and/or shoot mass removal at various levels within the water column, that enables the evaluation of regrowth potential; (3) species-characteristic effects of current velocity on photosynthesis, that enables the evaluation of the effects of hydraulic water body alterations; and (4) relationships of plant process parameters with site-specific climate, that enables the evaluation of effects of different climates. Generally, a good fit was found between simulated and measured biomass in the field. Sensitivity analysis showed that the model is very sensitive to changes in process parameters influencing carbon flow.

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1. Introduction

Submersed aquatic vegetation (SAV) may play important roles in aquatic ecosystems. Roles attributed to 'desirable' species are: stabilization of sediment, amelioration of transparency and regulation of nutrient availability in the water column, and serving as habitat and food source for invertebrates, fish and waterfowl, and roles attributed to 'nuisance' or 'invasive'

SAV species are: excessive biomass production interfering with human utilization of freshwater resources or displacing desirable indigenous communities. Many SAV communities in freshwater and marine environments have experienced dramatic losses during the past three to five decades. Most commonly declines are attributed to decreases in water transparency due to anthropogenic influences, but often they have been attributed to other factors such as high water levels,

extended draw-downs, changes in current velocity, and epi-phyte shading, or to combinations of factors. However, once the vegetation is lost from a given locale, increased sediment resuspension resulting in unfavorable underwater light con-ditions and current velocity may place significant constraints on plant recolonization of that site.

The degree to which SAV influences the ecosystem is related to plant mass and depends on plant species and physical and chemical factors. Therefore, predictions of the environmental impact of management measures concern-ing the aquatic system in which SAV grows should be based on accurate estimates of plant (1) species, mass, and perti-nent physiological properties; (2) contribution to various food chains (live and dead biomass); (3) contribution to biogeo-chemical cycling (carbon, nitrogen, phosphorus) and oxygen regime; and (4) contribution to habitat availability.

We developed a dynamic simulation modelling approach to submersed plant biomass formation to provide a tool for water resource managers to evaluate key environmental con-ditions in which SAV would persist or produce excessive biomass with ensuing consequences for the systems in which they grow, either or not affected by management measures. Simulation models provide a unique tool to investigate the impact of various management and restoration options on the wax and wane of SAV before actual implementation, thereby reducing the overall impact of human development on existing SAV and facilitating successful restoration of for-mer SAV (Carr et al., 1997; Best et al., 2001). The model is based on carbon flow through a SAV within a 1-m^2 water column with light and temperature as driving variables, and includes descriptions of plant responses to current velocity and human influences such as management measures (changes in tur-bidity, mechanical harvesting, grazing, flooding). A relational diagram of the model is provided in Fig. 1. Chenango Lake in New York, a lake historically known for its abundant *Vallisne-ria americana* meadows, was chosen as the site for the initial calibration of the model. The current description of the model has been formatted after Grimm et al. (2006).

The objectives in developing the model were (1) to review and update the model organization, key equations, and parameters (Best and Boyd, 2001, 2007), (2) present base-run analysis of the model with data from Chenango Lake, (3) manipulate the model to explore the value of wintering plant biomass and tuber size, (4) present analyses of model runs for sites at other latitudes, and (5) conduct a sensitivity analysis of the model.

2.   Model overview and scheduling

The VALLA model pertains to *V. americana* Michx. VALLA fol-lows a mechanistic approach explaining plant growth on the basis of the underlying processes, such as phenology, CO_2 assimilation and respiration, as influenced by environmen-tal conditions. CO_2 availability is assumed to be typical for hard water with an alkalinity between 0 and 300 mg L^{-1} and a circumneutral pH; effects of changes in CO_2 availability are not included. The model simulates the carbon flow mass balance of vegetation within in a 1-m^2 water column. This type of model follows the state-variable approach, in that

it is based on the assumption that the state of each sys-tem can be quantified at any moment and that changes in the state can be described by mathematical equations. In this type of model, state, rate, and driving variables are dis-tinguished. State variables are quantities such as biomass. Driving variables characterize the effect of environment on the system at its boundaries, such as climate and environ-mental conditions. Each state variable is associated with rate variables that characterize its rate of change at a certain instant, as a result of specific processes. These variables rep-resent flows of material between state variables, the values of which are calculated from the state and driving variables according to knowledge of the physical, chemical, and bio-logical processes involved. After calculating the values of all rate variables, an Euler scheme was used to describe the changes in the state variables. The time interval of integra-tion was sufficiently small, i.e., smaller than one-tenth of the 'time coefficient' or 'response time' (Rabbinge and De Wit, 1989).

VALLA is implemented as a FORTRAN77 program. For numerical integration, the Runge–Kutta technique is used, which allows employing a variable time-step. The program integrates the equations once per day in the main subrou-tine (MODEL), once per second in the subroutines calculating day length and instantaneous irradiance (ASTRO) and instan-taneous gross assimilation (ASSIM), and at three times of the day in the subroutine calculating daily total gross assimilation (TOTASS; Gaussian integration). Instantaneous gross assimi-lation is calculated per second and converted to hourly rates within ASSIM. The model runs within a FORTRAN SIMULA-TION ENVIRONMENT (FSE) shell, Version 2.1, to enable easy handling of input and output files and rapid visualization of the simulation results (Leffelaar et al., 1993). The model is compatible with other FORTRAN coded models. The organi-zation of the model and its subroutines in combination with the FSE shell is illustrated in Fig. 2.

A similar modelling approach was followed to model *Potamogeton pectinatus* L. (current taxonomic name *Stukenia pectinata* L.), *Hydrilla verticillata* (L.F.) Royle and *Myriophyllum spicatum* L., all plants being similar in growth strategy but significantly different in morphology and physiology. These three models are detailed elsewhere (Best and Boyd, 2007). Of these species *V. americana* and *P. pectinatus* are considered as 'desirable', and *H. verticillata* and *M. spicatum* as 'invasive' species in parts of the U.S.A. *V. americana* is a meadow-forming plant species that used to be common in shallow clear freshwater systems, where its tubers form an impor-tant food source for over-wintering waterfowl (Korschgen and Green, 1988; Spink and Rogers, 1996). Important physiological differences are that *V. americana* has a lower potential photo-synthetic rate at light saturation than the other plants, a lower species-characteristic light extinction coefficient and a higher relative tuber growth rate than *P. pectinatus* with which it often competes for space and sometimes coexist. These are charac-teristics which, besides having most of its biomass close to the sediment surface, make *V. americana* a species that thrives in clear water and grows less in turbid water, whereas the other species grow well in both clear and turbid water. In addition, *V. americana* tubers exhibit innate dormancy whereas *P. pecti-natus* and *H. verticillata* tubers sprout as soon as temperature
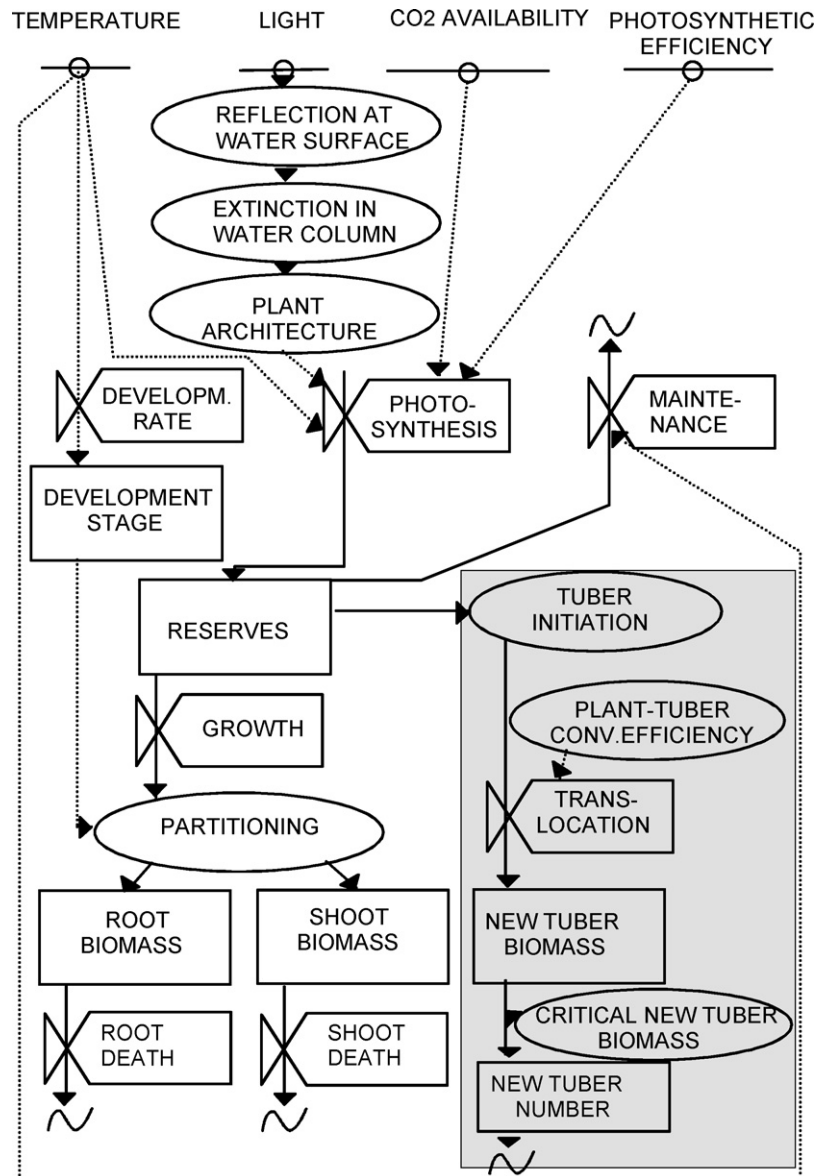
Fig. 1 – Relational diagram illustrating the following model processes in VALLA: (1) phenological cycle and development; (2) photosynthesis, respiration, and biomass formation; and (3) flowering, translocation, senescence, and formation of wintering organs (the latter process on a grey background). Rectangles represent quantities (state variables); valve symbols, flows (rate variables); circles, auxiliary variables; underlined variables, driving and other external variables; full lines, flows of material; dashed lines, information flow (symbols according to Forrester, 1961).

permits, and *M. spicatum* over-winters largely as rhizomes with or without root crowns. Because all these plant species over-winter predominantly vegetatively through plant organs in the sediment, that are depleted and disintegrate in the summer following the season in which they were formed (*V. americana*, *P. pectinatus*, *M. spicatum*) or that persist even longer (*H. verticillata*), their populations are expected to respond to annual changes in environmental conditions.

Our modelling approach is mathematical similar to approaches used in other SAV models, such as developed for Eurasian milfoil (Titus et al., 1975; Collins and Wlosinski, 1985), sago pondweed (SAGA; Hootsmans, 1994), seagrasses (Wetzel and Neckles, 1996; Behm et al., 2004) and generic (MEGA-PLANT; Scheffer et al., 1993; Herb and Stefan, 2003), in that

it describes plant morphology, biomass formation, and vegetative reproduction in relative detail, but it differs in that it relates ecophysiological processes to developmental cycle enabling to use the model for simulations of plant communities in different climates.

3. Model processes

The model simulates the carbon flow mass balance of a *V. americana* vegetation within in a 1-m^2 water column. Key model equations are provided in Appendix A and parameters, variables, and constants are provided in Table 1. A listing of the program is presented in Best and Boyd (2001) and an exe-
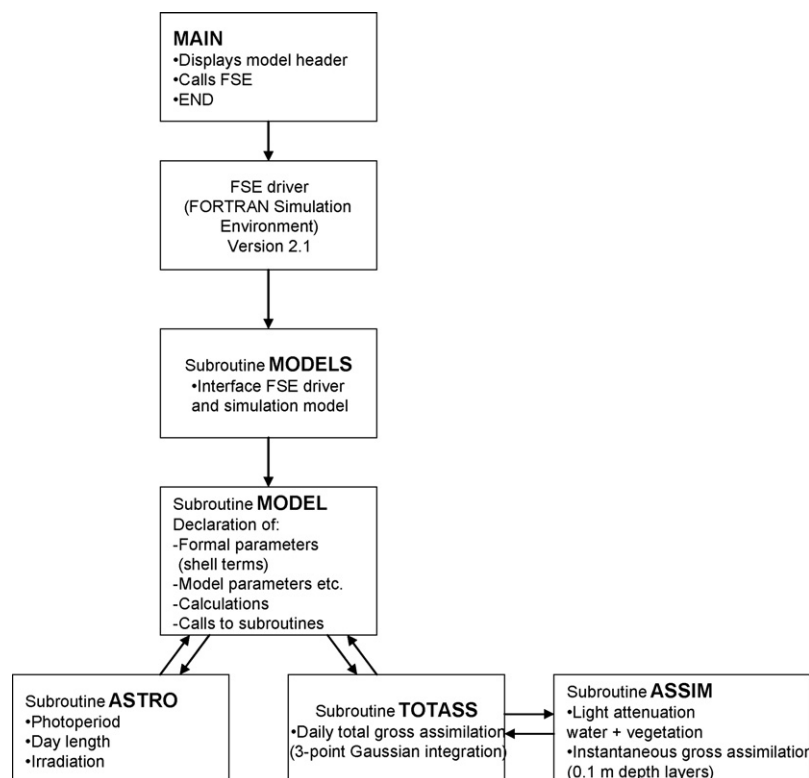
MAIN
•Displays model header
•Calls FSE
•END

FSE driver
(FORTRAN Simulation
Environment)
Version 2.1

Subroutine **MODELS**
•Interface FSE driver
and simulation model

Subroutine **MODEL**
Declaration of:
-Formal parameters
 (shell terms)
-Model parameters etc.
-Calculations
-Calls to subroutines

Subroutine **ASTRO**
•Photoperiod
•Day length
•Irradiation

Subroutine **TOTASS**
•Daily total gross assimilation
(3-point Gaussian integration)

Subroutine **ASSIM**
•Light attenuation
water + vegetation
•Instantaneous gross assimilation
(0.1 m depth layers)

Fig. 2 – Relational diagram illustrating the organization of each model and its subroutines in combination with the FSE shell.

cutable version of the model is available at http://www.el.erdc.usace.army.mil/products.cfm?Topic=model&Type=aquatic.

3.1. Phenological cycle and development

The phenology of a plant community, for which development phase can be used as a measure, quantifies physiological age and is related to its morphological appearance.

Development phase cannot be expressed simply as chronological age because several environmental factors such as temperature and stress (e.g., nutrients, grazing) can speed up or reduce the rate of phenological development. The rate of plant growth per se has no effect on phenological development, as long as the growth rate is not very low (Penning de Vries et al., 1989a). The concept of development phase is used to characterize the whole plant community; it is not appropriate for individual organs. The response of developmental rate to temperature in this model is in accordance with the degree-day hypothesis (Thornley and Johnson, 1990).

In the model, the phenological cycle is described based on published field data collected in a temperate climate, and development rates have been generated by scaling the development phase to the pertinent climatological day-degree sum. In cases where climatological data were lacking for the year when the field data were collected, climatological data for the same or a nearby site of a different year were used, after verifying climatological conditions did not deviate from the usual at that site.

V. americana plants are rooted into the sediment. In summer the plant has a short stem axis, bearing a variable number of stolons. The plant forms a rosette on top of the sediment with up to 1.2 m long, linear strap- to tape-shaped leaves, submersed or floating at the water surface (Korschgen and Green, 1988). The most important means of propagation in the temperate climate of North America is vegetatively by tubers with or without shoots present. Tubers are relatively small, dormant organs that develop on most stolons under special day length and temperature conditions in autumn, and that grow down into the sediment. Tubers are composed of a small amount of dividing tissue surrounded by several fleshy leaves. At the end of the growth season the parent plants senesce and disintegrate and only the tubers hibernate within the sediment until their emergence the following spring, which completes the annual growth cycle. Tubers are depleted and disintegrate during the summer following the season in which they were formed. Flowering occurs once a year, from late-June to August in the northern hemisphere (Donnermeyer, 1982; Titus and Stephens, 1983; Donnermeyer and Smart, 1985). Flowering usually coincides with peak biomass and is followed by sloughing. Seed formation is possible, but not important for short-term persistence.

In the model, development phase is a state variable. The development phase is dimensionless, and its value gradually increases within a growing season. The development rate has the dimension day^{-1}. The multiple of rate and time period (number of days) yields an increment in phase. In the model, the temperature affecting plant development can be chosen as equal to the daily average air temperature at the height of the growing point of the shoots, with a user-defined lag-period to correct for deviations in temperature of the water body in which the aquatic community grows compared with air temperatures. It is more accurate to use water tempera-

Table 1 – Parameters, variables and constants, grouped according to model processes

Var/constant	c/v[a]	Value	Unit	Description	Source
Phenological cycle and development					
FLV(T)	v(tab)	0.718	Unitless	Fraction of total dry matter increase allocated to leaves as function of DVS	1, 2
FST(T)	v(tab)	0.159	Unitless	Fraction of total dry matter increase allocated to stems as function of DVS	1, 2
FRT(T)	v(tab)	0.123	Unitless	Fraction of total dry matter increase allocated to roots as function of DVS	1, 2
DDTMP	v		°C	Daily average temperature (field site)	
DVRV(T)	v(tab)	0.015	day^{-1}	Development rate after flowering as function of temperature	Calibration
DVRR(T)	v(tab)	0.040	day^{-1}	DVR prior to flowering as function of temperature	Calibration
DVS	v		Unitless	Development phase	Calibration
Wintering, sprouting, and growth of sprouts to water surface					
NPL	c	30	m^{-2}	Plant density	1
NDTUB	v	233	m^{-2}	Dormant tuber density	3
INTUB	c	0.090	g DW tuber^{-1}	Tuber size	3, 4
RDTU	c	0.018	day^{-1}	Relative tuber death rate (on number basis)	1
NTUBD	v		N m^{-2}	Dead tuber number	
NTUBPD	v		N m^{-2}	Dead tuber number previous day	
NGTUB	v		N m^{-2}	Sprouting tuber number	
REMOB	v		g CH$_2$O m^{-2} d^{-1}	Remobilization rate of carbohydrates	
ROC		0.0576	g CH$_2$O g^{-1} DW d^{-1}	Relative conversion rate of tuber into plant material	5
RCSHST	c	12	m g^{-1} DW	Relation coefficient tuber weight-stem length	5, 6
CRIFAC	c	0.0091	g DW layer^{-1} plant^{-1}	Critical shoot weight per 0.1-m depth layer	3, 4
SURPER	c	23	day	Survival period for sprouts without net photosynthesis	6, 7
TWGTUB	v		g DW m^{-2}	Total dry weight of sprouting tubers	
Photosynthesis, maintenance, growth, and assimilate partitioning					
SC	c		J m^{-2} s^{-1}	Solar constant corrected for varying distance sun-earth	10
TL	c	0.1	m	Thickness depth layer	
IABS(i)	v		J m^{-2} s^{-1}	Total irradiance absorbed by depth layer I	
IABSL(i)	v		J m^{-2} s^{-1}	Total irradiance absorbed by shoots in depth layer I	
IRZ(i)	v		J m^{-2} s^{-1}	Total photosynthetically active part of irradiance on top of depth layer I	
SC(i)	v		g DW m^{-2}	Shoot dry matter in depth layer I	
K(T)	v(tab)	0.0235	m^2 g^{-1} DW	Plant species specific light extinction coefficient as function of DVS	8
EPISHD	tab	0–0.43	Unitless	Fraction of irradiation shaded by epiphytes	9
AMX	c	0.0165	g CO$_2$ g^{-1} DW h^{-1}	Potential CO$_2$ assimilation rate at light saturation for shoots	8
AMAX	v		g CO$_2$ g^{-1} DW h^{-1}	Actual CO$_2$ assimilation rate at light saturation for shoots	
EE	c	0.000011	g CO$_2$ J^{-1}	Initial light use efficiency for shoots	10
REDF(T)	v(tab)	1		Relative reduction factor for AMX to account for senescence plant parts	User defined
REDAM	c	1	Unitless	Relative reduction factor to relate AMX to water pH and oxygen level	User defined
REDAM1	v(tab)	0–1	Unitless	Relative reduction factor to relate AMX to water current velocity	9
AMTMP(T)	v(tab)	0–1	Unitless	Daytime temperature effect on AMX as function of DVS	11
FGL	v		g CO$_2$ m^{-2} h^{-1}	Instantaneous CO$_2$ assimilation rate per vegetation layer	
GPHOT	v		g CH$_2$O m^{-2} day^{-1}	Daily total gross assimilation rate of the vegetation	
DMPC(T)	v(tab)	0–1	Unitless	Dry matter allocation to each plant layer	8
ASRQ	v		g CH$_2$O g^{-1} DW day^{-1}	Assimilate requirement for plant dry matter production	
FL(T)	v(tab)	0–1	Unitless	Leaf dry matter allocation to each layer of shoot as function of DVS	1, 2
GLV	v		g DW m^{-2} day^{-1}	Dry matter growth rate of leaves	
GST	v		g DW m^{-2} day^{-1}	Dry matter growth rate of stems	

Table 1 (*Continued*)

Var/constant	c/v[a]	Value	Unit	Description	Source
GRT	v		$g\,DW\,m^{-2}\,day^{-1}$	Dry matter growth rate of roots	
GTW	v		$g\,DW\,m^{-2}\,day^{-1}$	Dry matter growth rate of the vegetation (excl. tubers, rhizomes)	
TWLVG	v		$g\,DW\,m^{-2}$	Total dry weight live leaves	
TWSTG	v		$g\,DW\,m^{-2}$	Total dry weight live stems	
TWRTG	v		$g\,DW\,m^{-2}$	Total dry weight live roots	
TGW	v		$g\,DW\,m^{-2}$	Total live plant dry weight (excl. tubers, rhizomes)	
MAINT	v		$g\,CH_2O\,m^{-2}\,day^{-1}$	Maintenance respiration rate vegetation	
MAINTS	v		$g\,CH_2O\,m^{-2}\,day^{-1}$	Maintenance respiration rate vegetation at reference temperature	
Upper biomass limit	c	496	$g\,DW\,m^{-2}$	Maximum plant biomass	2
Flowering, translocation, senescence, and formation of wintering organs					
RTR	c	0.247	$g\,DW\,tuber^{-1}\,day^{-1}$	Maximum relative tuber growth rate at 20 °C	4, 11,12
RTRL	v		$g\,DW\,tuber^{-1}\,day^{-1}$	Relative tuber growth rate at ambient temperature	
CVT	c	1.05	Unitless	Conversion factor for translocated dry matter into CH_2O	10
NINTUB	c	5.5	$N\,plant^{-1}$	Tuber number concurrently initiated per plant	12
TWCTUB	c	14.85	$g\,DW\,m^{-2}$	Total critical dry weight of new tubers	1, 3, 12
NNTUB	v		$N\,m^{-2}$	New tuber number	
RDR(T)	v(tab)	0.021	day^{-1}	Relative death rate of leaves as function of DAVTMP (on DW basis)	1
RDS(T)	v(tab)	0.021	day^{-1}	Relative death rate of stems and roots as function of DAVTMP (on DW basis)	1
TEFF(T)	v(tab)		Unitless	Relative effective temperature function accounting for temperature effect on maintenance respiration, remobilization, maximum tuber growth and death rates as function of temperature	Calibration
TRANS	v		$g\,CH_2O\,m^{-2}\,day^{-1}$	Translocation rate of carbohydrates	

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 (2007); 7: Titus and Adams (1979b); 8: Titus and Adams (1979a); 9: Best et al. (2005); 10: Penning de Vries and Van Laar (1982); 11: Donnermeyer (1982); 12: Donnermeyer and Smart (1985).

[a] A *c* indicates that the parameter is a constant. A *v* indicates that a variable and tab indicates that the parameter is implemented in the model as a Table.

Table 2 – Relationship between development phase (DVS) of *V. americana*, day of year, at a reference temperature of 30 and 3 °C day-degree sum in a temperate climate[a] (DVRVT = 0.015; 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

[a] Calibration was on field data on biomass and water transparency from Chenango Lake, NY, 1978 (Titus and Stephens, 1983) and climatological data from Binghamton (air temperatures) and Ithaca (irradiance), NY, 1978.

tures for this purpose, but since water temperatures are not always available for the site for which the user conducts the simulation, the model can be run using either one. The rate of phenological development can be affected by temperature differently in the vegetative phase and in the reproductive phase, and, therefore, the physiological process of development may not be the same before and after anthesis. The plant development rate was derived from field data, typical for temperate regions, i.e., pertaining to Chenango Lake, New York, USA (Titus and Stephens, 1983; Tables 1–3). Plants in tropical regions behave similar in terms of development phase to those in temperate regions, except that tropical plants require on average a 1.6× higher 3° day-degree sum to complete their individual life cycle than temperate cohorts. The factor 1.6 was found by an extra calibration round of the model version developed for *Hydrilla verticillata* to biomass data from the tropics (Best and Boyd, 2007). Since no published data on *V. americana* biomass from the tropics were available, the calibration factor pertaining to *H. verticillata*, another tuber-forming plant, was used.

3.2. Wintering, sprouting, and growth of sprouts to water surface

Tubers in the tuber bank are the main storage organs for carbohydrates during wintering in a temperate climate. Tuber bank weight is calculated by multiplication of tuber bank density and typical tuber weight (Eq. (A.1)). Tuber bank density may decrease by tuber death with a typical tuber death rate (Eq. (A.1.a); Eq. (A.1.a.1)), and through grazing by waterfowl and other animals. Tuber bank weight may decrease by maintenance, tuber death and by the sprouting of tubers, which transform into plants (Eq. (A.1.1)). Both tuber bank weight and density may increase by the formation of new tubers (Eq. (A.3), (A.3.1), (A.3.2), (A.3.3)). Tubers lie dormant if not disturbed (Van and Steward, 1990), and it is, therefore, to be expected that maintenance processes proceed at a very low level of activity. Tuber death rate, maintenance and growth increase with increasing temperature through a relative, effective temperature function (Q_{10} of 2 with a 20 °C reference temperature).

A certain minimum weight is required for a tuber to sprout. The number of sprouting tubers in the tuber bank is truncated to the typical plant density. At lower tuber bank densities the number of sprouting tubers equals the actual tuber bank density. If wintering plants are present, plant biomass is redistributed over the plants instead of the tubers.

Sprouting of tubers is a function of development phase (Table 2). Plantlets remobilize the tuber carbohydrate reserves by conversion into plant material, and elongate. The plant material is allocated to leaves, stems and roots, following a fixed biomass partitioning pattern.

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

Var/constant	c/v[a]	Value	Unit	Description	Source
Field site characteristics					
DPT(T)	v(tab)	1.4	m	Water depth (field site)	1, User defined
WTMP(T)	v(tab)		°C	Daily water temperature as function of day no (field site)	1, User defined
L(T)	v(tab)	0.43–0.80	m^{-1}	Water type specific light extinction coefficient as function of day no (field site)	1, User defined
WVEL	v(tab)	0–100	$cm\,s^{-1}$	Water type specific current velocity as function of day no (field site)	2, User defined
TGWM(T)	v(tab)		$g\,DW\,m^{-2}$	Total live dry weight measured as function of day no (field site)	1, User defined
NTM(T)	v(tab)	233	$N\,m^{-2}$	Tuber density measured as function of day no (field site)	1, User defined
Management (harvesting)					
HAR	c	0 or 1		Harvesting switch (0 = off, 1 = on)	User defined
HARDAY	c	1–365	day	Harvesting day number	User defined
HARDEP	c	0.1	m	Harvesting depth (measured from water surface)	User defined

1: Titus and Stephens (1983); 2: Best et al. (2005).

[a] A *c* indicates that the parameter is a constant. A *v* indicates that a variable and tab indicates that the parameter is implemented in the model as a Table.

These plantlets may survive at the plant height they can maximally reach, provided the balance of the carbohydrate influx from tuber carbohydrate reserves, efflux from tuber growth respiration, and influx from plantlet photosynthesis is positive. Sprouts/plantlets die if they have a negative net assimilation rate over a user-defined number of days, and the program stops with a warning. Tubers with a nominal size of 0.09 g DW are expected to survive 23 days, based on measured tuber respiration rates (Best and Boyd, 2007). Larger tubers have longer and smaller tubers shorter survival periods. After the death of one tuber class, the next tuber class may sprout, provided more tubers are available in the tuber bank and the development phase is less than required for flowering (Table 3). Up to three tuber classes may sprout annually. The program can resume running for the same year provided the proper conditions are met.

3.3. Photosynthesis, maintenance, growth, and assimilate partitioning

Light availability is an important factor controlling the distribution and abundance of SAV. In aquatic systems a small part of the irradiance can be reflected by the water surface, and further attenuation occurs by water and its suspended solids and by SAV itself, either or not covered by epiphytes. Measured daily total irradiance (wavelength 300–3000 nm) is used as input in the model. Only half of the irradiance reaching the water surface is considered to be photosynthetically active and is, therefore, used as a base for the calculation of CO_2 assimilation. Part of the irradiance (6%) is reflected by the water surface (Golterman, 1975). The subsurface irradiance is attenuated by dissolved substances and particles within the water column resulting in a site- and season-specific water extinction coefficient (Eq. (A.2)). The remaining radiation may be further reduced by epiphyte shading (Eq. (A.2.1)). The vertical profiles of the radiation within the SAV layers are characterized also. The absorbed irradiance for each horizontal SAV layer is derived from these profiles (Eq. (A.2.2)). The SAV light extinction coefficient, K, is plant species-characteristic and assumed to be constant throughout the year. The incoming irradiance is attenuated by the shoots, part of which is absorbed by the photosynthetic plant organs, i.e., the leaves.

Instantaneous rates of gross assimilation are calculated from the absorbed light energy and the photosynthesis-light response of individual shoots, here used synonymously to leaves. The photosynthesis-light response of leaves is described by Eq. (A.2.3). In the photosynthesis-light response equation, the value of potential photosynthetic activity at light saturation (AMX) is species-characteristic and the initial light-use efficiency (EE) typical for C_3 plants. AMX is affected by temperature via a fitted, relative function, AMTMPT, accounting for the measured effect of daytime temperature, and enabling the calculation of the actual photosynthesis rate (AMAX). AMAX is also affected by current velocity via a fitted, relative, function, REDAM1, accounting for the measured effect of current velocity on AMX. Senescence and daily changes in pH and oxygen concentrations may affect AMX. Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer. The instantaneous rate of gross assimila-

tion over the height of the vegetation is calculated by relating the assimilation rate per layer to the species-characteristic biomass distribution and by subsequent integration of all vegetation layers. The daily gross assimilation rate is calculated by using the Gaussian integration method. This method specifies the discrete points at which the value of the function to be integrated has to be calculated, and the weighting factors that must be applied to these values to attain minimum deviation from the analytical solution. A three-point method performs well for calculating daily total assimilation (Goudriaan, 1986; Spitters, 1986).

A portion of the carbohydrates formed is respired to provide energy for maintaining the existing plant components. The maintenance costs increase with increasing metabolic activity, probably because of higher enzyme turnover and higher transport costs (Penning de Vries et al., 1989b). The maintenance cost can be estimated from the chemical composition of the plant. Typical maintenance coefficients for various plant organs have been derived, based on numerous chemical determinations in agricultural crops. They typically range from 0.010 to 0.016 g CH_2O g $AFDW^{-1}$ day^{-1} (Penning de Vries and Van Laar, 1982). These coefficients have also been used in the current model, since plant organ composition was usually in the same range as that of crops. Maintenance respiration increases with increasing temperature through a relative effective temperature function. The Eqs. (A.2.4) and (A.2.4.a) describe the maintenance costs.

The remainder of the carbohydrates is available for conversion into structural plant material, resulting in growth (Eq. (A.2.5)). In this conversion process of the glucose molecule, CO_2 and water are released. The assimilate requirement to produce one unit weight of any particular plant organ is calculated from its chemical composition and the assimilate requirements of the various chemical components. 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; confirmed by Griffin, 1994). The recently determined construction costs for several submersed plant species using a different method (Williams et al., 1987) are generally lower and range 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 factors which may have contributed to the lower cost found. In the model the construction costs typical for agricultural crops have been used, since construction costs calculated for *M. spicatum* leaves with an average chemical composition were similar to those in agricultural plants, i.e. 1.465 g CH_2O g DW^{-1}, and those of stems and roots were presumed to be similar also.

Assimilate partitioning is the process by which assimilates available for growth are partitioned over leaves, stems, roots, and/or storage organs. It depends on physiological age. Assimilate partitioning patterns in most SAV species are unknown. However, partitioning of the biomass resulting from this process in full-grown plants has been published, and these values have been used for calibration in the model (Eqs. (A.2.6)–(A.2.8)). The species-characteristic distribution of shoot biomass is allocated over the vertical axis via a dry matter allocation function (DMPC), which allows changes in shoot biomass distribution with changes in water depth. Seasonal plant biomass maxima may vary considerably over

time and space. In the model, plant biomass may increase up to the greatest published value of 496 g DW m^{-2} (Haller, 1974). Greater biomass values are considered as unrealistic and attributed to selective sampling or to biomass values which were measured on small surface areas and erroneously extrapolated to a m^2 area.

3.4. Flowering, translocation, senescence, and formation of wintering organs

The rate of phenological development can be affected by temperature differently in the vegetative phase and in the reproductive phase. The timing of flowering is, therefore, important for physiological activity and biomass formation, while the actual investment of dry matter in flowers and seeds is minor. In the model, a considerable part of net production is translocated downwards after flowering in the form of carbohydrates considered as equivalent to starch (Penning de Vries et al., 1989b). In this tuber-forming plant the translocation products are largely transported to the tubers, and the remainder of net production is allocated according to the species-characteristic biomass allocation pattern (Eqs. (A.3) and (A.3.1)). Senescence sets in resulting in loss of particulate plant material via a species-characteristic relative death rate, which increases with an increase in temperature through the relative, effective temperature function.

Tubers are induced after flowering (Table 2), formed under short day conditions and within a certain temperature range. The combination of tuber size and concurrently initiated tuber number is species-characteristic (Eq. (A.3.1)). Korschgen et al. (1997) found that individual tuber weight decreased almost linearly with decreasing light level, and parabolically with concurrently formed tuber number per plant. The latter phenomenon forms the basis of our hypothesis that *V. americana* follows an optimization strategy aimed at producing the largest tubers for the light level experienced, because large tubers have a greater survival value than smaller ones. Thus, an established vegetation experiencing a given light level will aim at producing one tuber size class only, i.e., with a size that allows new plants to survive at that site. Consequently, the differences in tuber size in tuber banks may be attributed to differences in environmental conditions and differences in age between tuber size classes (with tubers in the last-completed class being full-size, tubers in the oldest class weighing less because of remobilization processes, and tubers in the youngest class weighing less because incomplete). The combination of 5.5 concurrently initiated tubers and tuber size of 0.090 g DW tuber^{-1} was selected as nominal. The typical relationship between tuber size and concurrently formed tuber number per plant is used to calculate the proper initial values for simulations started from a different tuber size than nominal (Table 4).

Once initiated, a tuber class grows with a typical relative tuber growth rate (RTRL) from translocated material until a preselected critical weight of the new tuber class (TWCTUB) is reached (Eq. (A.3.2)). Temperature influences the maximum relative growth rate (RTR) of tubers through the relative effective temperature function. Once finished, a tuber class is added to the dormant tuber bank, and the plant starts forming a new tuber class (Eq. (A.3.3)). Tuber initiation continues

Table 4 – The relationship between tuber size and concurrently initiated tuber number in *V. americana* (after Korschgen et al., 1997)	
Tuber size (g DW tuber^{-1})	Concurrently initiated tuber number (N plant^{-1})
0.015	0.6
0.035	2.0
0.050	3.0
0.070	4.0
0.086	5.0
0.090	5.5
0.120	5.8

as long as environmental conditions permit, and tubers are formed as long as plants provide assimilates to fill them.

4. Simulations

4.1. Base run analysis of the model with data from Chenango Lake, New York

VALLA was run using the nominal parameter values (Table 1), field site variables (Table 3) and weather data (irradiance and air temperature) as inputs for a 1-year period.

The simulated biomass of plants and tubers are shown in Fig. 3. Simulated plant biomass compared well with measured biomass. Plant biomass reached its maximum at the same time, and peak biomass was somewhat greater in the simulated than in the measured SAV, notably 56.1 versus 50.1 g DW m^{-2}. The latter may be due to the relatively large tuber size/concurrently initiated tuber number combination (0.09 g DW tuber^{-1}, 5.5 tubers plant^{-1}) used to initiate this nominal run. A considerable tuber number remained at the end of the year enabling the plant population to persist the following year. Model explorations indicated, that under the same environmental conditions even a population starting from 1 tuber m^{-2} would reach a similar tuber bank density as nominal within 3 years.

Simulated transport of carbohydrates was substantial in the beginning of the growth season when upward carbohydrate remobilization from the tubers supports initial sprouting, but far greater after flowering when downward carbohydrate translocation from plant organs supports the filling of the tubers. Carbohydrate transport could be in the same range as net assimilation at the beginning and end of the growth season. Maintenance respiration was usually considerably less than assimilation but could be in the same range of translocation just after flowering (data not shown).

Running VALLA with (24-h average) air temperatures with a lag-period of 1 day instead of with measured water temperatures as forcing variables yielded higher assimilation and plant biomass values (data not shown) than found in the nominal case. This difference was attributed to the fact that water temperatures in the lake were relatively low compared to air temperatures, because of the large inflow of groundwater (Titus and Stephens, 1983). In our experience, a lag period of 7 days between model daily air and measured temperatures usually describes this relationship well for shallow, up
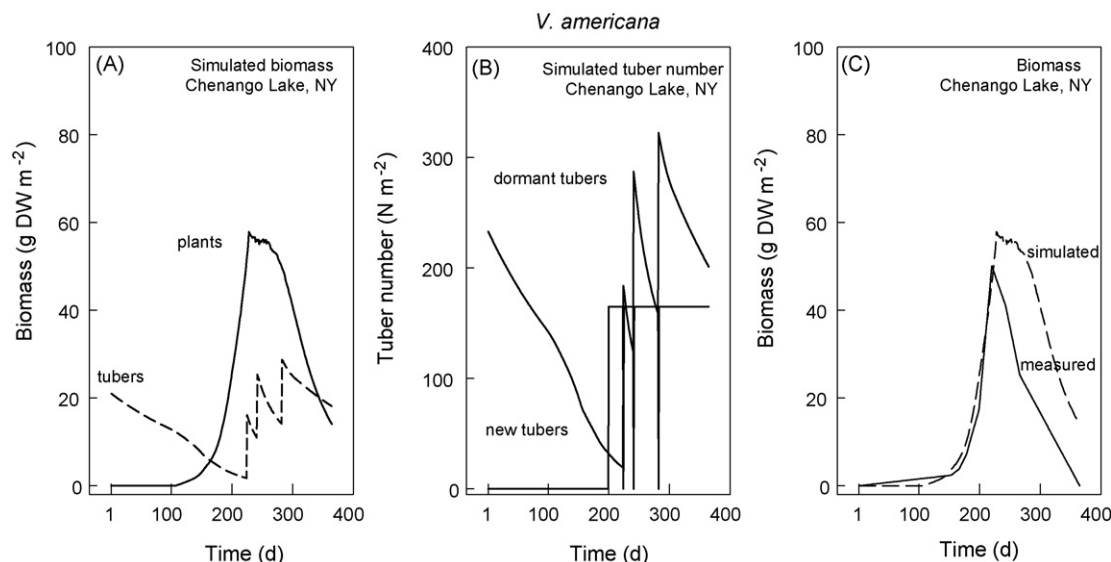
Fig. 3 – Simulated biomass of plants (A), dormant and new tuber numbers (B), and measured plant biomass (C) of *V. americana* in Chenango Lake, NY. Nominal run. Field data 1987 from Titus and Stephens (1983); climatological data 1987, Binghamton, NY (lat 42° 15′N, long 75° 50′W); water depth 1.4 m; light extinction coefficient 0.43 m^{-1}.

to 5–6 m deep, water bodies with a relatively small inflow of groundwater.

4.2. Model manipulation to explore the value of wintering plant biomass and tuber size

Running VALLA for the same lake and year, but with both plants and tubers initially present, showed that simulated peak plant biomass was then far higher and more tuber classes were finished (4 instead of 3 in the nominal case; Fig. 4B). This large difference in peak biomass is due to the ability of the plant community to fully capture the high spring irra-

diance at this latitude of 43° N, which they cannot without wintering shoots. Thus, wintering shoots may provide a distinct advantage for this plant species because more tubers would remain at the end of the year of a relatively large size.

Measured tuber size was smaller than nominal, i.e., 0.055 g DW tuber^{-1}, and another model run starting from the measured tuber size/chosen concurrently initiated tuber number yielded a simulated peak plant biomass that was almost equal to nominal of 48 g DW m^{-2} (Fig. 4C), and the simulated tuber numbers were within the range found in a *V. americana* community in the same lake (Titus and Stephens,
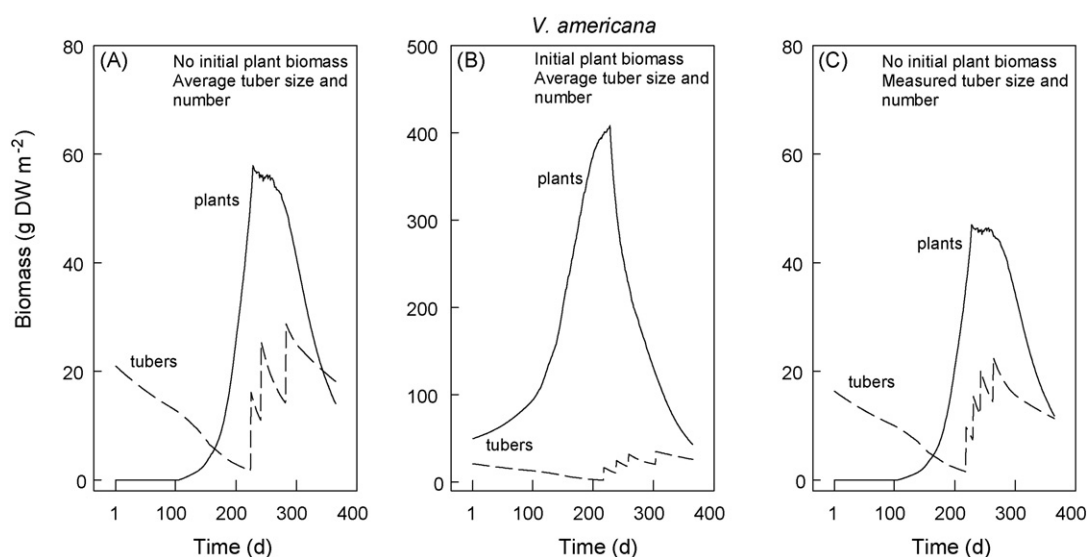

Fig. 4 – Simulated biomass of plants and tubers of *V. americana* in Chenango Lake, NY, started from different initial biomass, but run in the same environmental and climatological, nominal, conditions. (A) Plant biomass 0; tuber size 0.09 g DW; tuber bank 233 m^{-2}; (B) plant biomass 50 g DW m^{-2}; tuber size 0.09 g DW; tuber bank density 233 m^{-2}; (C) plant biomass 0; tuber size 0.055 g DW; tuber bank density 233 m^{-2}.
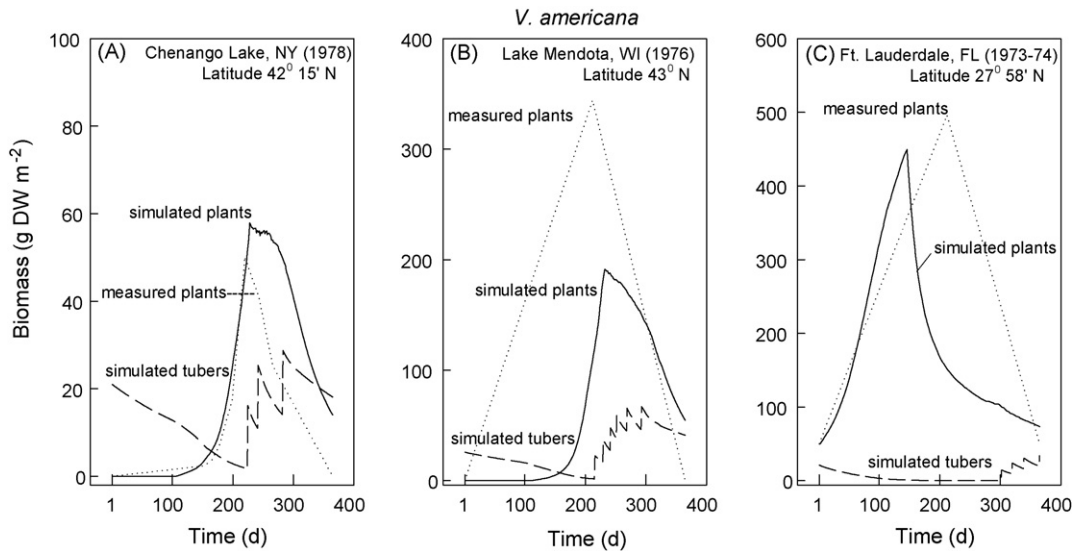
Fig. 5 – Simulated biomass of plants and tubers of *V. americana* at sites differing in latitude. (A) Chenango Lake, NY (lat 42° 15′N, long 75° 50′W; tuber size 0.09 g DW, tuber bank density 233 m^{-2}; water depth 1.4 m; light extinction coefficient 0.43 m^{-1}; climatological data 1987; measured data 1978, Titus and Stephens (1983). (B) Lake Mendota, WI (lat 43° 08′N, long 89° 20′W; tuber size 0.11 g DW, tuber bank density 233 m^{-2}; water depth 0.2 m; light extinction coefficient 0.4 m^{-1}; climatological data 1971–75; measured data 1976, Titus and Adams (1979a). (C) Fort Lauderdale ponds, FL (lat 27° 58′N, long 82° 32′W; plant biomass 50 g DW m^{-2}; tuber size 0.09 g DW, tuber bank density 233 m^{-2}; K-value 0.019 m^2 g^{-1} DW; water depth 1.5 m; light extinction coefficient 0.4 m^{-1}; climatological data 1975–1984; measured data 1973–1974, Haller (1974).

1983). This result illustrates that VALLA generates realistic results for the calibration site.

4.3. Analysis of model runs with data from other latitudes

To investigate whether VALLA could be used to simulate behavior of a *V. americana* community at other sites besides the nominal one (lat 42° 15′ N, long 75° 50′ W), runs were made for one more western site, Lake Mendota, Wisconsin (lat 43° 08′ N, long 89° 20′ W), and another more southern, tropical, site at Fort Lauderdale, Florida (lat 27° 58′ N, long 82° 32′ W).

In the run pertaining to Lake Mendota, the simulation was started from site-specific community, water depth, -transparency, and climatological data.

- Plant community-specific data included: initial plant biomass absent, tuber size 0.03 g DW, concurrently initiated tuber number 1.5 plant^{-1}, and tuber bank density 233 m^{-2}.
- Site-specific environmental data included: water depth 1.2 m and light extinction coefficient 0.7 m^{-1}.

In these conditions simulated plant biomass remained low, maximally 25 g DW m^{-2}, and no tuber classes were finished. Because the simulated maximum plant biomass was far lower than published (average peak biomass 344 and minimum 266 g DW m^{-2}; Titus and Adams, 1979a), and *V. americana* populations in Lake Mendota have been described as stable, several other simulations were done to explore community- and site-specific characteristics favoring such a sustainable population. Increasing the tuber size from 0.03 to 0.09 g DW increased peak biomass from 25 to 105 g DW m^{-2} and the number of finished tuber classes to 5. Increasing water trans-

parency by decreasing the light extinction coefficient from 0.7 to 0.4 m^{-1} increased peak biomass from 25 to 130 g DW m^{-2} and the number of finished tuber classes to 7. Introduction of the largest tuber size published, of 0.11 g DW, again increased peak biomass to 150 g DW m^{-2}, but allowed only 5 tuber classes to be finished. Even in very clear water (extinction coefficient 0.4 m^{-1}), a very shallow, 0.2 m, water depth, and with the most profitable tuber size, the SAV would only be able to produce maximally 195 g DW m^{-2} in Lake Mendota (Fig. 5B). The latter result led us to believe that the high plant biomass range of 266–344 g DW m^{-2} published (Titus and Adams, 1979a) is either an overestimate, or that spring growth starts partly from wintering shoots which was not reported. However, the latter phenomenon has been observed in other Wisconsin lakes (W.F. James, USACE Eau Galle Laboratory, Spring Valley, Wisconsin, USA).

In the run pertaining to Fort Lauderdale, Florida, the simulation was also started from site-specific community, water depth, -transparency, and climatological data.

- Plant community-specific data included: initial plant biomass 50 g DW m^{-2}, tuber size 0.09 g DW, concurrently initiated tuber number 5.5 plant^{-1}, tuber bank density 233 m^{-2}.
- Site-specific environmental data included: water depth 1.5 m and light extinction coefficient 0.4 m^{-1}.

In these conditions simulated plant biomass was high, maximally 403 g DW m^{-2}, and 3 tuber classes were finished late in the year. Tuber sizes and numbers of the Fort Lauderdale community were not published, so comparison between simulated and measured tuber data is not possible. However, simulated maximum plant biomass in this case was

within the measured peak biomass range of 298–496 g DW m^{-2} (Fig. 5C).

Since lower K-values have been reported for other *Vallisneria* species in warmer climates, i.e., of 0.019 m^2 g^{-1} DW in Japan (Ikusima, 1970) and of 0.0051 m^2 g^{-1} DW in Australia (Blanch et al., 1998), new simulations were conducted using these values. Simulation results indicated that simulated peak plant biomass was enhanced to 450 g DW m^{-2} by decreasing the K-value from 0.0235 to 0.019 m^2 g DW^{-1}, and even surpassed the maximum measured value by decreasing the K-value further to 0.0051 m^2 g DW^{-1}.

Comparison of the biomass simulated in the various climatological conditions, indicates that in a temperate climate generally less SAV biomass is produced and investment in vegetative tuber reproduction is relatively higher than in a tropical climate, which agrees with the scarce literature that exists on this topic (Sahai and Sinha, 1973).

4.4. Sensitivity analysis of the model

Sensitivity analysis of a simulation model is required to assess the parameters likely to strongly affect model behavior. The current analysis is based on the effect of a change in one parameter when all other parameters are kept the same. The parameter under study was changed and 1-year simulations were conducted under nominal environmental conditions. As reference level, the nominal parameter values were chosen as presented in Table 1. The results were compared with those of a nominal run. Each parameter was once increased by 20% and once decreased by 20%. 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 nine parameters on two state variables, representing different plant biomass compartments, were tested. A model variable is considered sensitive to a change in the value of a parameter at RS > 0.5 and < −0.5.

$$\text{RS} = \frac{(\text{yield}_i - \text{yield}_r)/\text{yield}_r}{(\text{param}_i - \text{param}_r)/\text{param}_r}$$

where yield$_i$ is the value at parameter value i; yield$_r$ is the value at reference parameter value r; param$_i$ and param$_r$ as above

VALLA was very sensitive to parameter changes (Table 5). Maximum plant biomass was generally more sensitive to changes in the tested parameter values than end-of-year tuber number (Table 5). Maximum plant biomass was sensitive to changes in all parameters in VALLA. End-of-year tuber number/rhizome biomass was sensitive to changes in almost all parameters, except increased plant density (NPL) and relative conversion rate into plant material (ROC), and decreased tuber size (INTUB).

The sensitivity of maximum plant biomass and end-of-year tuber number/rhizome biomass to changes in environmental factors was assessed following the same approach as for sensitivity analysis of the model parameters. For this purpose, parameter changes were based on value ranges taken from literature, which sometimes differed more than 20% from the nominal parameter values presented in Table 3. Also in this analysis, VALLA proved to be very sensitive (Table 6). Maximum plant biomass was generally more sensitive to changes

Table 5 – Relative sensitivity of two state variables to deviations in parameter values from their nominal values as presented in Table 1

Parameter name	Relative sensitivity			
	Maximum plant biomass		EOY[a] tuber no	
	+20%	-20%	+20%	-20%
DVRVT	0.56	-6.04	-2.5	-1.39
DVRRT	0.98	-2.19	-2.47	0.24
NPL	3.39	-0.82	-0.01	2.71
INTUB	3.25	-0.92	-1.79	-0.03
ROC	2.65	-1.37	-0.43	2.33
AMX	5.00	3.02	4.46	2.04
EE	0.50	0.56	-0.73	1.44
RTR	1.76	-2.62	-0.77	2.19
RDR	2.25	-3.03	0.71	0.22

Results were obtained in 1-year simulations under nominal conditions. Sensitive values shaded.
[a]EOY: end of year.

in the tested parameter values than end-of-year tuber number. Changes in light reflection coefficient at the water surface (RC) had no significant effect, while the effects of changes in the other tested parameter values decreased in the order of water type specific light extinction coefficient (LT) greater than water depth (DPTT).

5. Discussion

VALLA can be used to simulate the seasonal changes in daily time-steps of carbon flow-based plant processes and biomass under various site-specific conditions and management scenarios over a 1–5-year period of a desirable SAV species, in climates varying from temperate to tropical. VALLA can be run with default or user-specified input values on plant biomass, tuber size/concurrently initiated tuber number, and tuber bank density. For all runs, climate- and site-specific environmental data can be entered by the user, and scenarios of interest can be explored.

Table 6 – Environmental factor analysis, expressed as relative sensitivity of two state variables to deviations in parameter values from their nominal values as presented in Table 3

Parameter name	Relative sensitivity			
	Maximum plant biomass		EOY[c] tuber no	
	+20%	-20%	+20%	-20%
Climate[a]	-	-0.49	-	-0.87
RC[b]	-0.06	-0.43	-0.06	-0.05
DPT(T)	1.47	-2.43	-2.16	0.48
L(T)	2.09	-2.79	0.04	0.66

Results were obtained in 1-year simulations under nominal conditions. Sensitive values shaded.
[a]Climates at Chenango Lake, NY (lat 42° N), Ft. Lauderdale, FL (lat 27° N).
[b]Light reflection coefficient at water surface; to enable calculation of the relative sensitivity, a very low value of 0.000001 was used.
[c]EOY: end of year.

In the model, phenology is tied to day-degree sum. This enables simulations for different sites and climates facilitating model operation by users who do not possess a full data set on plant characteristics and environmental variables for the water body for which they desire to conduct the simulations. The effect of flowering date can be tested with the model by varying the development rate of the vegetation. Slower rates represent later and faster rates earlier biotypes. A 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. Intuitive prediction of biotype behavior under such highly variable climatic conditions is, therefore, 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. Because only vegetative reproduction is included in the life cycle formulation, the tentative importance of sexual reproduction in different climates and of seeds for long-term survival (>5-year) cannot be explored with the current model versions.

The model is based on the carbon flow through a particular plant community, without limitation by nitrogen and phosphorus of macrophytic growth. Calibration has been done on field data pertaining to hard-water lakes with a circumneutral pH, leaving light as major limiting factor, followed by DIC availability. The results of the sensitivity analysis showed that the model is very sensitive to changes in process parameters influencing carbon flow. The high sensitivity of VALLA may be a consequence of the 'meadow-type' vertical biomass distribution over the water column that would make it greatly susceptible to plant-process and environment-related changes in light absorption in the overlying water layers. Plant species with 'canopy-type' vertical biomass distribution close to or at the water surface, are expected to be less sensitive (Best and Boyd, 2007).

VALLA has been developed as a stand-alone version, but is compatible with other models programmed in FORTRAN. The model can be run using air or water temperatures as inputs. The relationship between air and water temperature may differ from the model calibration, since temperatures within each water body are influenced by catchment morphometry, wind speed, fetch, mixing processes, and upward seepage. An example application of the model to Upper Mississippi River Pool 8 (Best and Boyd, 2007) has illustrated how relatively low and high frequency fluctuations in water levels, current velocity, and epiphyte cover might affect submersed plant populations, and simulation results guide planned changes in water level management. In another application, VALLA was linked to a decision support system used for ecological risk assessment of increased navigation on the Upper Mississippi River (Bartell et al., 2000). VALLA was also linked via a Geographical Information System through an appropriate interface to hydrodynamic and sediment transport models, and this model combination was used to explore habitat suitability in Peoria Lake, Illinois, for *V. americana* (Best et al., 2008).

6. Conclusions

A dynamic simulation modelling approach to biomass formation of a freshwater submersed plant species has been developed, with light and temperature as driving variables, and including descriptions of plant responses to changes in current velocity and human influences such as management measures. The model describes major, carbon flow-based ecophysiological processes and biomass dynamics of one common plant species. The model contains unique descriptions of: (1) species-characteristic vertical distribution of shoot biomass in the water column, that enables the calculation of the fraction of irradiance actually available for absorption by the SAV; (2) recalculation procedures of this vertical distribution with daily changes in water level and/or shoot mass removal at various levels within the water column, that enables the evaluation of regrowth potential; (3) species-characteristic effects of current velocity on photosynthesis, that enables the evaluation of the effects of alterations in hydraulics of the water body; and (4) relationships of plant process parameters with site-specific climate, that enables the evaluation of effects of different climates.

Base run analysis indicated a good fit between simulated and measured plant biomass in temperate and tropical climates, and between simulated and measured tuber bank density in a temperate climate. Validation for tropical climates was limited greatly by the scarcity in available data pertaining to tropical areas. Sensitivity analysis showed that the model is very sensitive to changes in process parameters influencing carbon flow.

Acknowledgements

Appendix A

Eq. (A.1)

$$TWGTUB = NPL \times INTUB \tag{A.1}$$

$$NDTUB = NDTUB - (NTUBD - NTUBPD) \tag{A.1.a}$$

$$NTUBD = RDTU \times NDTUB \times TEFF \tag{A.1.a.1}$$

$$IF (DVS.GE.0.291.AND.DVS.LT.1.) \ THEN$$
$$IF(TWGTUB.LE. (0.01 \times NPL \times INTUB)) \ NGTUB = 0.0 \tag{A.1.1}$$
$$NGTUB = NPL$$

$$TWGTUB = INTGRL(TWGTUB, \ - REMOB, DELT) \tag{A.1.2}$$

$$REMOB = TWGTUB \times ROC \times TEFF \tag{A.1.3}$$

Eq. (A.2)

$$IRZ_{i+1} \quad = IRZ_i \times e \quad (-TL \times L - K \times SC_i) \tag{A.2}$$

$$IABS_i = \frac{(IRZ_i - IRZ_{i+1}) \times SC_i \times K}{(K \times SC_i + TL \times L)} \times (1.0 - EPISHD) \tag{A.2.1}$$

$$IABSL_i = IABS_i \times FL \tag{A.2.2}$$

$$FGL = SC_i \times AMAX \times \left(1 - \exp\left[\frac{-EE \times IABS_i \times 3600}{AMAX \times SC_i}\right]\right) \tag{A.2.3}$$

$$MAINTS = 0.016 \times TWLG + 0.010 \times TWSG$$
$$+ 0.015 \times TWRG \tag{A.2.4}$$

$$MAINT = MAINTS \times TEFF \tag{A.2.4.a}$$

$$GTW = \frac{((REMOB \times CVT) + GPHOT - TRANS - MAINT)}{ASRQ} \tag{A.2.5}$$

$$GLV = FLV \times GTW \tag{A.2.6}$$

$$GRT = FRT \times GTW \tag{A.2.7}$$

$$GST = FST \times GTW \tag{A.2.8}$$

Eq. (A.3)

IF (REMOB. EQ. 0.0) THEN

    IF (DVS. GT. 1.0. AND. DAYL. LT. 14.7)THEN

        IF (DDTMP .GT. 5.0 .AND. DDTMP .LT. 25.0)THEN

            IF (TGW .GT .0.1) THEN

$$TRANS = AMAX1 (0., (RTRL \times 1./CVT) \times (GPHOT - MAINT))) \tag{A.3}$$

$$NNTUB = NPL \times NINTUB \tag{A.3.1}$$

$$TWNTUB = INTGRL(TWNTUB, TRANS, DELT) \tag{A.3.2}$$

IF (TWNTUB .GE. TWCTUB) THEN
$$NDTUB = NDTUB + (NPL \times NINTUB) \tag{A.3.3}$$

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