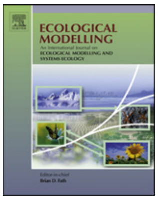
Ecological Modelling 243 (2012) 63–72

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Modeling growth dynamics of *Typha domingensis* (Pers.) Poir. ex Steud. in Lake Burullus, Egypt

Ebrahem M. Eid[a,*], Kamal H. Shaltout[b], Takashi Asaeda[c]

[a] Botany Department, Faculty of Science, Kafr El-Sheikh University, 33516 Kafr El-Sheikh, Egypt
[b] Botany Department, Faculty of Science, Tanta University, 31527 Tanta, Egypt
[c] Institute for Environmental Science and Technology (IEST), Saitama University, 255 Shimo-Okubo, Sakura-ku, Saitama shi 338-8750, Japan

ARTICLE INFO

Article history:
Received 18 February 2011
Received in revised form
27 December 2011
Accepted 14 May 2012
Available online 6 July 2012

Keywords:
Lake Burullus
Partitioned growth model
Seasonal biomass
Southern Cattail

ABSTRACT

Southern Cattail (*Typha domingensis*) occurs everywhere in ditches and marshy places in Egypt and is one of the major components of vegetation stands along the shores of Lake Burullus close to the Deltaic Mediterranean coast. In our study, we applied a published *Typha* model to describe the growth production among the various organs of Southern Cattail in Lake Burullus, one of the Mediterranean eutrophic lakes, in order to answer the following questions: (1) Is the *Typha* model, originally designed for *T. angustifolia* and *T. latifolia*, suited to simulate the growth of Southern Cattail in the south Mediterranean region? and (2) How is biomass production of Southern Cattail distributed among the various plant organs? Above- and below-ground biomass of Southern Cattail was sampled monthly from February 2010 to October 2010 at three sites of Lake Burullus using three randomly distributed quadrats (each of 0.5 m × 0.5 m) at each sampling site. Shoots started to grow in February, reached the maximum biomass of 6327 ± 441 g DW m^{-2} in July, and then rapidly decreased in the fall when they went to senescence stage, thereafter their growth ceased before fully dying off in the winter. The total below-ground biomass reduced to 941 ± 152 g DW m^{-2} in March due to the upward translocation for the initial growth of shoots, gradually increased to a maximum biomass of 2184 ± 366 g DW m^{-2} in July by downward translocation from shoots, then decreased afterwards in the winter to reach 1193 ± 64 g DW m^{-2} in October. Southern Cattail allocated approximately 52% of its total biomass to non-flowering shoots, 19% to flowering shoots, 22.5% to rhizomes and 6.5% to roots. The total above-ground biomass was 2.6 times that of the total below-ground biomass. General trends for above-ground biomass, such as the slow initial growth rate followed by a high growth rate, the timing of peak biomass, and the decline of biomass due to senescence, were successfully reproduced by the model. Many characteristics typical for the below-ground biomass, such as the reduction of rhizome biomass during the early growing season, and the increase in the rhizome biomass during the later period of the season, because of the translocation of materials from current photosynthesis and shoot dry matter, were also reproduced. In general, there was good agreement between the calculated results and field data although simulated results were slightly different from observations for below-ground biomass. Respiration of the above- and below-ground organs consumes a considerable amount of net photosynthetic materials 39% and 7%, respectively. The upward translocation of rhizome resources to form new shoots in February showed 8% to the gross production and the downward translocation afterwards showed a 22% to the gross production. In conclusion, *Typha* model is well-suited to simulate the growth of Southern Cattail stands in the south Mediterranean region and could be used in wetland management activities to predict the potential growth of Southern Cattail in Egyptian wetlands.

1. Introduction

Typha species (cattails) are a rhizomatous perennial that forms dense, nearly monospecific stands through vigorous vegetative growth; a tightly-packed advancing front of ramets excludes other plants (phalanx strategy, *sensu* Lovett-Doust, 1981). Vegetative growth is through under-ground lateral rhizomes which apices grow upward to form the aerial shoot. The unit of vegetative growth is the ramet. In *Typha* species, the ramet consists of the submerged rhizomes, associated roots and shoot. The shoot can exceed 2 m in height and may or may not develop an apical flowering spike (Dickerman and Wetzel, 1985). Although sometimes considered an invasive weed (Newman et al., 1996; Woo and Zedler, 2002), *Typha* species are now attracting attention for their usefulness in various

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* Corresponding author. Tel.: +20 1022648840; fax: +20 47 321 5175.
E-mail address: ebrahem.eid@sci.kfs.edu.eg (E.M. Eid).

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http://dx.doi.org/10.1016/j.ecolmodel.2012.05.028

ecological fields such as purification of polluted water (Coveney et al., 2002; Schroder et al., 2003; Dordio et al., 2009; Hegazy et al., 2011), bank protection against boat wash (Bonham, 1983), wetlands diversity restoration (Newman et al., 1996; Boers et al., 2007), mitigation strategies (Dobberteen and Nickerson, 1991) and the influence of the vegetation on greenhouse gas emissions from wetlands (Chanton et al., 1993; Gross et al., 1993).

During the past few decades, considerable work has been done on the productivity (Mason and Bryant, 1975; Hill, 1987), phenology (Fiala, 1978; Dickerman and Wetzel, 1985), competition (Weihe and Neely, 1997; Grace and Wetzel, 1998; Bellavance and Brisson, 2010), nutrient cycling (Garver et al., 1988; Smith et al., 1988; Sharma et al., 2006) and other related aspects of *Typha* species (Khedr, 1996; Khedr and El-Demerdash, 1997). Most studies, however, depended mainly on empirical relations, and thus the scope for further understanding of the dynamics of growth was limited. In contrast, a mathematical growth model can synthesize quantitative information about physiological processes and thus provide estimates of ecological, physiological or morphological responses that may otherwise be hard to measure (Asaeda and Karunaratne, 2000; Best et al., 2001; Eid et al., 2010). Therefore, there are a variety of fields where a growth model can be effectively used to understand growth responses, and it is especially useful when various kinds of quantities or hard-to-measure data sets are required, or when estimates of material budgets are needed (Asaeda et al., 2005). Although many experiments have analyzed the growth dynamics of *Typha* species, few researchers have attempted to analyze growth dynamics using numerical simulation models. Asaeda et al. (2005) formulated a mathematical model to simulate the growth production (both above- and below-ground) of a well-established, monospecific stand of *Typha angustifolia* and *Typha latifolia* by considering the photosynthesis, respiration, mortality and translocation of material between plant organs using first order differential equations.

Lake Burullus along the deltaic Mediterranean coast of Egypt is one of the RAMSAR sites and was declared as a natural protectorate in 1998 (Shaltout and Al-Sodany, 2008). Southern Cattail (*Typha domingensis* (Pers.) Poir. ex Steud.), warm-temperate and tropical regions plant, occurs everywhere in ditches and marshy places in Egypt (Täckholm, 1974; Boulos, 2005) and is one of the major component of vegetation stands along the shores of Lake Burullus close to the Deltaic Mediterranean coast (Shaltout and Al-Sodany, 2008). Southern Cattail has life-history characteristics indicative of opportunistic species such as high rates of growth, reproduction and biomass turnover, and a greater capacity for phosphorus uptake (Newman et al., 1996; Lorenzen et al., 2001; Miao, 2004).

Plants play an important role in nutrients cycling in the wetlands due to uptake, storage, and release processes. Specifically, plants with potentially high annual primary production can extract large amounts of nutrients from their environment and store these nutrients in biomass and litter (Eid et al., 2010). In addition, macrophytes provide an important structural element in shallow waters for other organisms (e.g., periphytic algae, microbial growth), which in turn might be important for nutrients transformation in wetlands (Brix, 1997). For these reasons, the differences of biomass production over time, its distribution among the various Southern Cattail organs and the effects of water characteristics on its biomass in Lake Burullus is important to understand its interaction with the aquatic ecosystem.

In our study, we applied the *Typha* species model of Asaeda et al. (2005) to describe the growth production among the various organs of Southern Cattail in Lake Burullus one of the Mediterranean eutrophic lakes. A very brief description of the model, the functions allocated to each of its subroutines, and input and output data are also described. A detailed explanation of the model formulation is found in Asaeda et al. (2005). An appendix lists the main equations and parameters used in the model and gives a brief explanation of them. The biomass data of Southern Cattail collected monthly from February 2010 to October 2010 from three sites in Lake Burullus were used to run, calibrate, and validate the model in order to answer the following questions: (1) Is the *Typha* model, originally designed for *T. angustifolia* and *T. latifolia*, suited to simulate Southern Cattail growth in the south Mediterranean region? and (2) How is biomass production of Southern Cattail distributed among the various plant organs?.

2. Materials and methods

2.1. Study area

Lake Burullus is located along the Deltaic Mediterranean coast of Egypt (Long. 31°22′–31°35′N, Lat. 30°31′–31°08′E) with an arid climate characterized by warm summers (20–30 °C) and mild winters (10–20 °C). It has been registered as a site of the RAMSAR Convention (Kassas, 2002) because of its importance for wintering, foraging, refuge and breeding of the migrant birds; and as a suitable habitat for fish particularly the fry and juveniles (Khalil and El-Dawy, 2002). It is located in the northernmost part of the Nile Delta and connects with the Mediterranean Sea through a natural outlet. The lake has an area of 410 km^2, an oblong shape and bordered by the agricultural lands in the south, while a sand bar separates it from the Mediterranean Sea in the north.

2.2. Plant sampling, morphological features and biomass

Sampling was carried out at three sites of Lake Burullus. These sites were best and pure or nearly pure Southern Cattail stands with other species like *Echinochloa stagnina* (Retz.) P. Beauv., *Phragmites australis* (Cav.) Trin. ex Steud. and *Vossia cuspidata* (Roxb.) Griff., forming <5% of the total standing biomass. At each sampling site, above- and below-ground biomass of Southern Cattail was sampled monthly from February 2010 to October 2010 using three randomly distributed quadrats (each of 0.5 m × 0.5 m). Within a quadrat, all Southern Cattail shoots were cut off at ground level, counted, and separated into flowering shoots (leaves and inflorescences) and non-flowering shoots (leaves and non-flowering secondary shoots). Below-ground organs were dug-down in the same three quadrats to 50 cm depth (90–100% of all roots and rhizomes located between 0 and 20 cm depth; Miao and Sklar, 1998) and washed with lake water till free from sediment. Below-ground parts were sorted into rhizomes and roots, while rhizomes were further classified by colors into new and old segments. In the laboratory, samples were carefully washed with tap water over a 4 mm mesh sieve to minimize the material loss. For above- and below-ground biomass estimation, the plant material was oven dried at 85 °C to constant weight. Proportional biomass allocation was calculated as the biomass of a specific tissue divided by the total biomass. The morphological and biomass data were subjected to a repeated measurement ANOVAs to test the differences over time using STATISTICA (Statsoft, 2007).

2.3. Water sampling

At each sampling site, three water samples were collected monthly close to sampling quadrats. The water samples were taken as integrated composite samples from the top of the water surface down to 50 cm. The samples were collected in plastic bottles and brought to the laboratory shortly after collection. Water level and transparency were measured in the field using a leveling rod and Secchi disc of 25 cm in diameter, respectively. Some water parameters were measured directly after collection (pH, electric conductivity (EC), total N and total P). After measuring these, samples were deep-frozen for further analysis of Na, K, Ca and Mg. EC and pH were measured using conductivity and pH-meters (Model DA-1 and ICM 41150, respectively). Atomic absorption (Shimadzu AA-6300) was used for the determination of Na, K, Ca and Mg. Molybdenum blue and indo-phenol blue methods were applied for the determination of total P and total N, respectively, using a spectrophotometer (CECIL CE 1021). All these procedures are outlined in APHA/AWWA/WPCF (1985). The significance of variation in water quality parameters was assessed using one-way analysis of variance (ANOVA-1; SPSS, 2006). To assess the effects of water characteristics on biomass of Southern Cattail, stepwise multiple regressions were calculated using non-correlated water characteristics (TN, TP, Ca, Na and transparency).

2.4. Outline of the *Typha* species growth model

The biomass of *Typha* species (g DW m^{-2}) was divided into above-ground organs (flowering shoots: leaves and inflorescences; non-flowering shoots: leaves and non-flowering secondary shoots) and below-ground organs (roots, new and old rhizomes). The biomass of each organ was formulated to incorporate the net growth of the plant as a function of photosynthesis, respiration and mortality; and to assimilate translocation between shoots and below-ground organs. Process descriptions and associated parameters are listed in Fig. 1 and Appendix A. The phenological cycle of *Typha* species has an important role in the growth model. The plant phenology was interpreted in terms of simple mathematical relationships by regression analysis of published experimental data and these equations were incorporated in the growth equations to trigger the phenological cycle in the growth model. Days of phenological events are estimated from starting time of shoot growth.

2.4.1. Input data

For the simulation, the input data were average climate (daily solar radiation and air temperature) and the initial rhizome and root biomasses. Daily mean air temperature and daily solar radiation (throughout the growing season) are in °C and W m^{-2}, respectively, while rhizomes and roots biomass are in g DW m^{-2}. Daily means of air temperature and solar radiation were obtained for Baltim Weather Station, lies at about 1 km from the natural outlet of Lake Burullus (Lat. 31°33′N, Long. 31°05′E). Daily solar radiation was converted into photosynthetically active radiation using meteorology subroutine. The mean daily air temperature of 2010 was 13.5 °C for February and 27.0 °C for August, while the mean daily total global radiation was 80.5 W m^{-2} for December and 253.7 W m^{-2} for June. The date of shoot emergence was considered as a forcing function and hence it was estimated using field observation.

2.4.2. Below-ground parts subroutine

The rhizome subroutine calculates the daily change in rhizome biomass that includes processes such as remobilization of stored matter from rhizomes to shoots at the beginning of the growing season and translocation of photosynthesized materials and shoots dry matter to rhizomes at the end of the growing season. Root subroutine calculates the daily change in root biomass and the interactions with rhizomes and shoots: first, root growth was simulated by rhizome reserves and later the shoots also contributed to the growth of roots. New rhizome subroutine calculates the biomass of the rhizome, which grows in the current growing season; the main source supporting its growth was considered as shoot translocations.

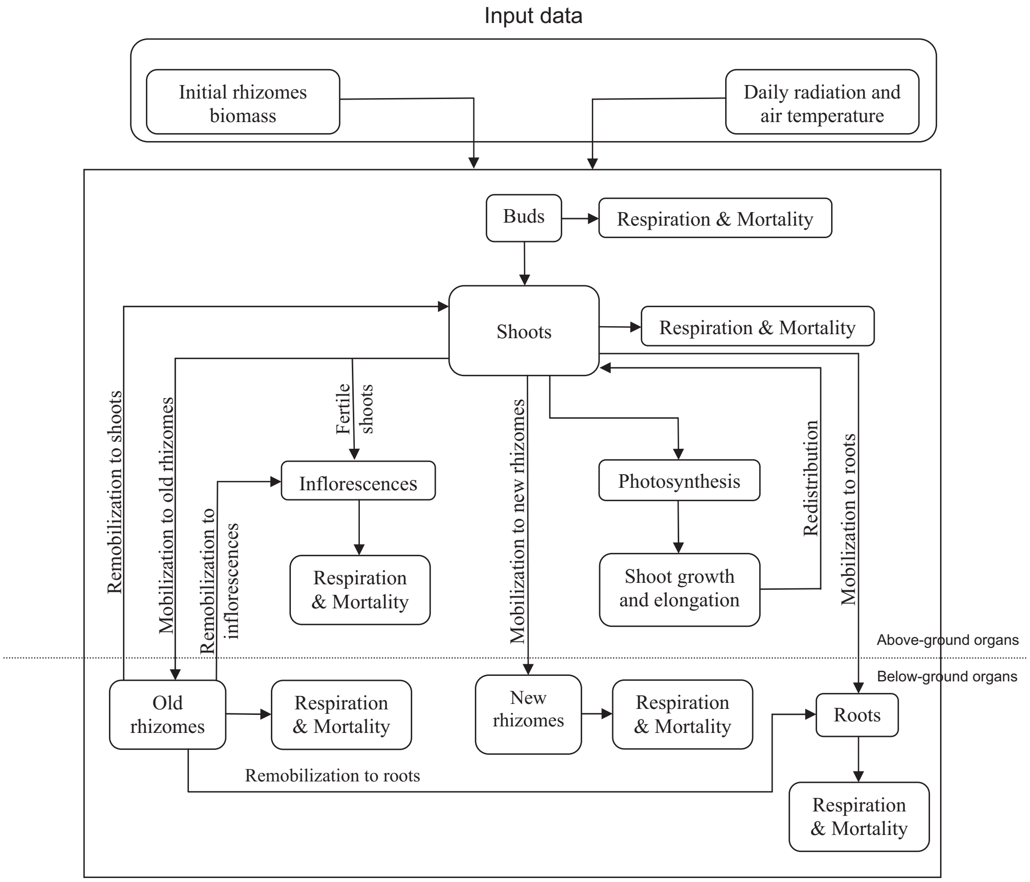

Fig. 1. Flow diagram for the *Typha* species model (Asaeda et al., 2005).

2.4.3. *Shoot subroutine*

This subroutine deals with the daily change in total above-ground biomass. The above-ground biomass of Southern Cattail stand was stratified into 1 cm-thick horizontal layers in which the dry matter budget was calculated. For each layer, growth equations were solved simultaneously using the forth-order Runge–Kutta method (Kloeden and Platen, 1995; Butcher, 2008). The time scale was in Julian days. Plant elongation was considered as the following: the biomass increment for each time step of each layer was calculated and if the growth was positive, a portion of the increased biomass was allocated for elongation, while the rest was allocated for the growth of the same layer. Inflorescences biomass was also calculated in this subroutine. The shoot photosynthesis and dry matter translocation were considered as the major sources of inflorescences production.

2.4.4. *Model execution*

The parameters used in the *Typha* model to simulate growth in a Southern Cattail population in Lake Burullus are listed in Appendix A. All parameters other than the constant of the availability of nutrients, K_{NP}, were fixed during simulation process, and the biomass variation patterns, such as increasing trend, peak time and decreasing trend were compared with the observed data. The value of K_{NP} was calibrated to match the observed biomass in simulation. Growth equations for each layer and organ were solved simultaneously using the fourth order Runge–Kutta method (Kloeden and Platen, 1995; Butcher, 2008). The model was implemented in FORTRAN. The model simulated the seasonal variation of the above-ground biomass (flowering and non-flowering shoots), below-ground biomass (roots and rhizomes) and variations of total production and respiration. One-day time steps were used in the computation.

2.4.5. *Sensitivities of coefficients*

Sensitivity analysis was carried out to investigate the influence of the model parameters on the above- and below-ground biomasses by changing them ±30% of their original values (Asaeda et al., 2005).

2.4.6. *Validation of the model*

The model was validated using the biomass data of Southern Cattail collected monthly from February 2010 to October 2010 from three sites in Lake Burullus. The deviations of simulated results from observed field data were assessed in three ways: the standard deviation as a percent, correlation coefficients and paired *t*-test (SPSS, 2006).

3. Results

Shoots started to grow in February, reached the maximum biomass of 6327 ± 441 g DW m^{-2} in July, and then rapidly decreased in the fall when they went to senescence stage, thereafter their growth ceased before fully dying off in the winter (Fig. 2). The total below-ground biomass reduced to 941 ± 152 g DW m^{-2} in March due to the upward translocation for the initial growth of shoots, gradually increased to a maximum biomass of 2184 ± 366 g DW m^{-2} in July by downward translocation from shoots, then decreased afterwards in the winter to reach 1193 ± 64 g DW m^{-2} in October.

Lake Burullus is characterized as an alkaline, shallow, brackish and polluted lake (Table 1). Significant differences over time were found for individual shoot dry weight, mean biomass of roots, inflorescences, non-flowering and flowering shoots (ANOVA, $P < 0.05$, Table 2). The explained variation of the stepwise multiple regressions ranged between 88.6 and 93.7% for rhizome and shoot biomasses (Table 3). Both shoot and rhizome biomasses were found to be significantly correlated with water Na, whereas root biomass was significantly correlated with water TP. Proportional biomass allocation among the three sites indicates that overall Southern Cattail allocated approximately 52% of its total biomass to non-flowering shoots, 19% to flowering shoots, 22.5% to rhizomes

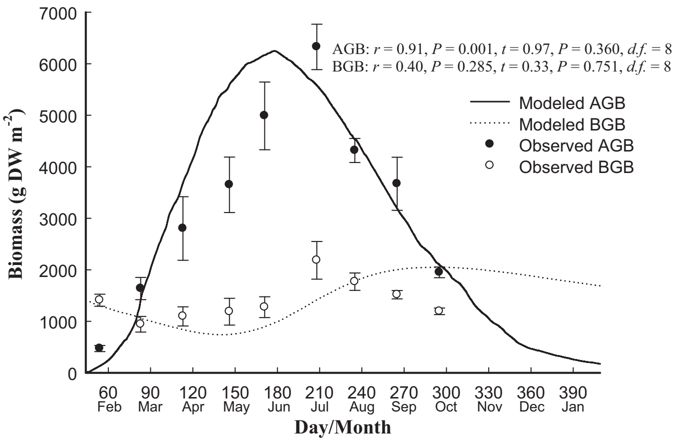

Fig. 2. Observed (symbols) and modeled (lines) quantities of the above (AGB) and below-ground (BGB) biomass of Southern Cattail in Lake Burullus. Vertical bars indicate the standard errors ($N = 9$).

Table 1
Temporal variation in water characters (annual mean ± standard error: SE) supporting Southern Cattail stands in Lake Burullus. Water characteristics were measured monthly between February and October 2010. *F*-values represent the one-way ANOVA, degree of freedom (*df*) = 8.

Characters	Range	Mean ± SE	*F*-value	*P*
Water level (cm)	26.0–98.0	63.4 ± 3.8	0.6	0.768
Transparency (cm)	0.0–80.0	29.6 ± 5.1	0.4	0.900
pH	8.0–9.2	8.6 ± 0.1	1.5	0.236
EC (mS cm^{-1})	5.6–30.0	12.2 ± 1.0	2.2	0.078
TN (mg l^{-1})	8.7–87.1	33.5 ± 3.2	0.3	0.967
TP (mg l^{-1})	0.1–7.3	4.8 ± 2.7	1.0	0.475
Ca (mg l^{-1})	39.4–78.5	50.3 ± 1.9	1.1	0.419
Mg (mg l^{-1})	1.7–43.0	20.3 ± 2.0	2.1	0.086
Na (mg l^{-1})	72.5–345.0	147.1 ± 11.7	3.8	0.009
K (mg l^{-1})	1.2–10.2	3.6 ± 0.4	3.9	0.008

Table 2
Temporal variation in morphological and biomass characteristics (annual mean ± standard error: SE) of Southern Cattail in Lake Burullus. Parameters were measured monthly between February and October 2010. *F*-values represent the repeated measurement ANOVA, degree of freedom (*df*) = 8. AGB: above-ground biomass; BGB: below-ground biomass.

Characteristics	Range	Mean ± SE	*F*-value	*P*
Shoot density (m^{-2})	28–128	61 ± 3	1.8	0.131
Shoot dry weight (g shoot^{-1})	7–162	60 ± 4	7.2	0.000
Number of inflorescences (m^{-2})	0–44	9 ± 1	7.2	0.000
Flowering (%)	0–85	16 ± 3	9.6	0.000
Roots biomass (g DW m^{-2})	91–847	325 ± 18	3.3	0.010
Rhizomes biomass (g DW m^{-2})	343–3194	1131 ± 60	1.9	0.113
Inflorescences biomass (g DW m^{-2})	0–1271	159 ± 34	13.1	0.000
Non flowering shoots biomass (g DW m^{-2})	340–6822	2622 ± 150	3.4	0.008
Flowering shoots biomass (g DW m^{-2})	0–7172	956 ± 177	8.5	0.000
Total above-ground biomass (g DW m^{-2})	340–8211	3578 ± 214	5.9	0.000
Total below-ground biomass (g DW m^{-2})	434–4041	1457 ± 77	2.0	0.096
AGB/BGB ratio	0.2–4.4	2.6 ± 0.1	5.5	0.000

Table 3
Results of stepwise multiple regressions (R^2) between the water characteristics and above- and below-ground biomasses of Southern Cattail in Lake Burullus.

Variable	Simple *r*	Level of entry	Partial R^2	Model R^2
Shoot biomass				
Na	0.79^{*}	1	0.623	0.623
TP	0.57	2	0.124	0.747
Ca	−0.38	3	0.077	0.824
TN	0.61	4	0.076	0.900
Transparency	0.18	5	0.037	0.937
Root biomass				
TP	0.913^{**}	1	0.833	0.833
Ca	−0.094	2	0.061	0.894
Rhizome biomass				
Na	0.869^{**}	1	0.755	0.755
TP	0.819^{**}	2	0.108	0.863
TN	0.394	3	0.023	0.886

* $P < 0.05$.
** $P < 0.01$.

and 6.5% to roots (Fig. 3) and total above-ground biomass was 2.6 times that of the total below-ground biomass. The annual mean of shoot density was 61 ± 3 m^{-2} and only 16% of the shoots flowered (Table 2).

Three emergence pulses of Southern Cattail were observed during the growing season (Fig. 4). The first pulse grows from buds formed during the previous autumn and starts to grow in spring, the second pulse grows 63 days after the first one and the third pulse emerges 119 days after the second. The mean weight of individual shoots of Southern Cattail was 60 ± 4 g DW, reached a peak weight of 113 ± 13 g DW in July, then a sharp fall in shoot weight occurred at senescence and the weight by October was only 29.3% that of the peak weight (Fig. 4). In addition, the mean weight of shoots was negatively related to shoot density ($r = -0.319$, $P = 0.051$).

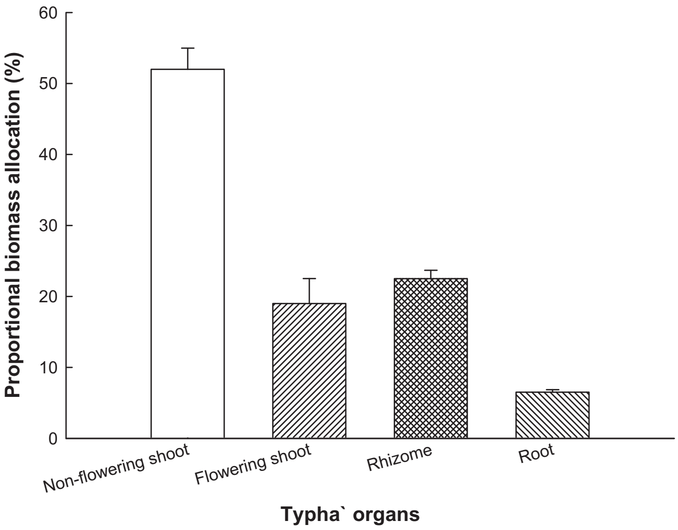

Fig. 3. Proportional biomass allocation of Southern Cattail in Lake Burullus.

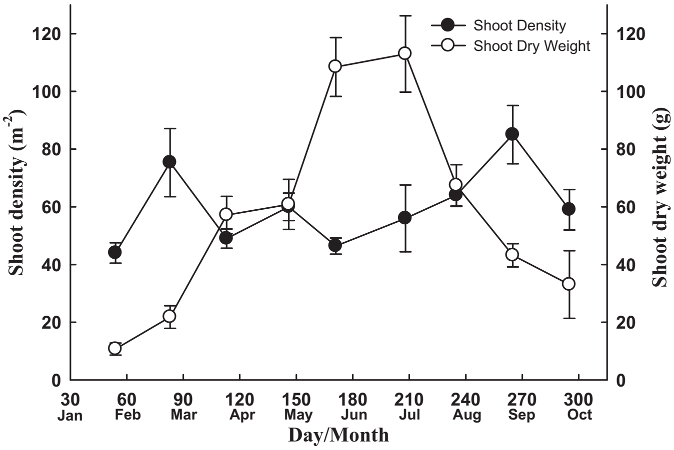

Fig. 4. Shoot dry weight and density of Southern Cattail in Lake Burullus. Vertical bars indicate the standard errors ($N = 9$).

General trends for above-ground biomass, such as the slow initial growth rate followed by a high growth rate, the timing of peak biomass, and the decline of biomass due to senescence, were successfully reproduced by the model (Fig. 2). Many characteristics typical for the below-ground biomass, such as the reduction of rhizome biomass during the early growing season, and the increase in the rhizome biomass during the later period of the season, because of the translocation of materials from current photosynthesis and shoot dry matter, were also reproduced. The level of agreement between the calculated and the actual results, as given by the standard deviation percent, correlation coefficient (*r*) and paired *t*-test, indicated that although simulated results were slightly different from the observations for under-ground biomass, the model is capable for simulating the above-ground biomass (AGB: $SD = 13.5\%$, $r = 0.91$, $P = 0.001$, $t = 0.97$, $P = 0.360$, degrees of freedom (df) = 8; BGB: $SD = 20.8\%$, $r = 0.40$, $P = 0.285$, $t = 0.33$, $P = 0.751$, degrees of freedom (df) = 8).

The sensitivity analysis showed that of all the parameters used, the model was most sensitive to the coefficients related to the gross production (maximum photosynthesis rate P_m, half saturation constant of K_{PAR}), the respiration and mortality losses of leaves and rhizomes and the translocation from leaves to rhizomes ε_{leaf} (Table 4). For example, a 30% increase in the maximum photosynthetic rate increased the above- and below-ground biomasses by 16 and 8%, respectively, while a 30% increase of half-saturation constant of PAR reduced the above- and below-ground biomasses by 5 and 4%, respectively.

The total losses were higher during June and July (Fig. 5) and the net production (the surplus of gross production over losses due to respiration and mortality) peaked in April earlier than the gross production in May and then decreased rapidly, became negative at

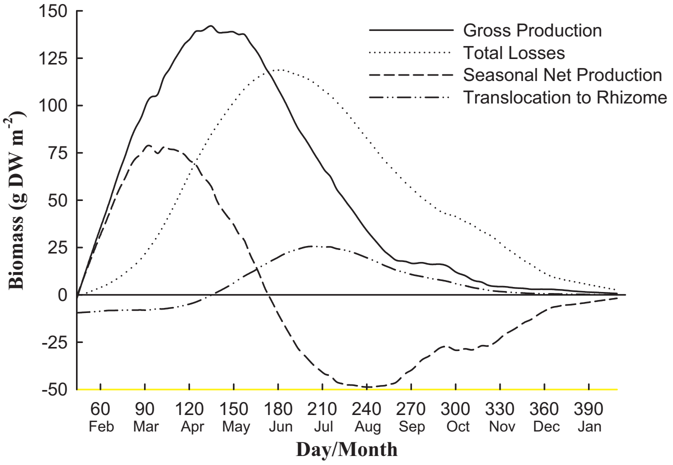

Fig. 5. Seasonal cycle of gross production, total losses due to respiration and mortality, translocation to rhizome and net production (g m^{-2} day^{-1}) of Southern Cattail in Lake Burullus.

Table 4
Sensitivity of *Typha* model output at Lake Burullus with respect to parameters. AGB: above-ground biomass; BGB: below-ground biomass.

Parameter	Symbol	AGB (%) Variation (%)		BGB (%) Variation (%)	
		+30%	−30%	+30%	−30%
Maximum photosynthesis rate	P_m	+16	−25	+8	−17
Dark respiration rate of leaves	β_{leaf}	−7	+9	−7	+8
Dark respiration rate of old rhizomes	$\beta_{rhi\,1,2}$	−0.1	−1	−2	+2
Dark respiration rate of new rhizomes	$\beta_{rhi\,0}$	0	0	−6	+8
Mortality rate of leaves	γ_{leaf}	−4	+11	−4	+8
Mortality rate of old rhizomes	$\gamma_{rhi\,1,2}$	−0.3	+12	−0.5	−2
Mortality rate of new rhizomes	$\gamma_{rhi\,0}$	0	0	−1	+1
Half-saturation constant of age	K_{age}	+4	−9	+4	−7
Half-saturation constant of PAR	K_{PAR}	−5	+12	−4	+8
Fraction of leaf transferred to rhizome	ε_{leaf}	+2	+7	+20	−18

the end of June and reached the lowest value in early of September. The translocation of resources to rhizomes started after the shoots were sufficiently developed in May and ended with all shoots dying off in January.

The production and seasonal fluxes of dry matter of Southern Cattail in Lake Burullus was estimated using the modeled quantities (Fig. 6). The annual gross production, respiration, mortality, translocation to rhizome was 25,076 g DW m^{-2}, 9740 g DW m^{-2}, 9544 g DW m^{-2} and 5415 g DW m^{-2}, respectively. The respiration of the above- and below-organs consumes a considerable amount of net photosynthetic materials 39% and 7%, respectively. The upward translocation of rhizome resources to form new shoots in spring showed 8% to the gross production and the downward translocation afterwards showed a 22% to the gross production.

4. Discussion

The present study shows that Southern Cattail has three emergence pulses during the growing season. The first pulse, subject to increasing solar radiation and rising temperature in spring, grows rapidly from over wintering buds then photosynthesizes throughout the summer, translocating enough photosynthates downwards to grow rhizomes after compensating for the expense of the initial growing stage. In contrast, later pulse (in autumn) experience lower and decreasing radiation levels and lower temperatures, and are unable to compensate for the expense of the initial shoot growth, which leads to a reduction in rhizome biomass. This three emergence pulses during the growing season are comparable to that reported by Asaeda et al. (2005).

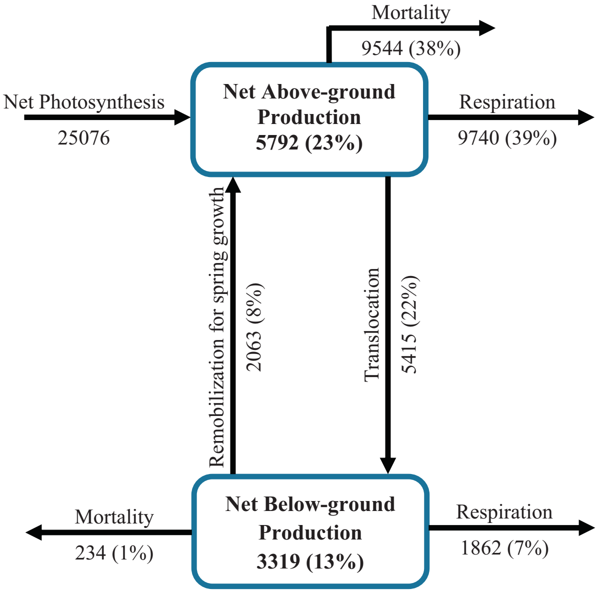

Fig. 6. Production and seasonal fluxes of dry matter of Southern Cattail in Lake Burullus constructed using modeled quantities. Production is expressed as g DW m^{-2} and fluxes expressed as g DW m^{-2} per growing season.

All growing processes in the natural stands of Southern Cattail in Lake Burullus were similar to other growth studies of *T. angustifolia* in Texas, USA (Hill, 1987) and in Minnesota, USA (Garver et al., 1988) and *T. latifolia* in Wisconsin, USA (Smith et al., 1988), in Minnesota, USA (Garver et al., 1988) and in Michigan, USA (Dickerman and Wetzel, 1985; Ulrich and Burton, 1985). The differences in the specific time of growing stage between

Table 5
Examples of maximum above-ground biomass (AGB) of *Typha* species (t DW ha^{-1}) in natural stands all-over the world.

Species	Site	AGB	Reference
T. domingensis	Lake Burullus, Egypt	63	Present study
	San Juan River, Cuba	14–24	Fraga and Kvet (1993)
	Florida, USA	11–12	Miao and Sklar (1998)
	Rio de Janeiro, Brazil	19–25	dos Santos et al. (2006)
	Florida, USA	20	Tian et al. (2010)
T. angustifolia	Norfolk, England	11	Mason and Bryant (1975)
	Texas, USA	29	Hill (1987)
	Minnesota, USA	12–21	Dubbe et al. (1988)
	Connecticut, USA	8–21	Farnsworth and Meyerson (2003)
	Tokyo, Japan	23–27	Sharma et al. (2006)
T. latifolia	Central of USA	4–13	McNaughton (1966)
	New Jersey, USA	19	Jervis (1969)
	Southeastern of USA	23	Boyd and Hess (1970)
	Michigan, USA	13	Dickerman and Wetzel (1985)
	Minnesota, USA	4–15	Dubbe et al. (1988)
T. glauca	Iowa, USA	21	Van der Valk and Davis (1978)
	New York, USA	15	Bernard and Fitz (1979)
	Iowa, USA	12–20	Davis and Van der Valk (1983)
	Minnesota, USA	7–8	Dubbe et al. (1988)
T. orientalis	Inland of Australia	23	Robert and Ganf (1986)
T. subulata	The Valle inferior del Rio Colorado, Argentina	11–19	Sobrero et al. (1997)

these studies may be due to effects of local environmental factors such as climate, water depth and nutrient condition. The maximum above-ground biomass of Southern Cattail was approximately 63 t DW ha^{-1} in Lake Burullus, which is higher than the previous estimates for Southern Cattail (11–25 t DW ha^{-1}; Table 5), *T. angustifolia* (8–29 t DW ha^{-1}), *T. latifolia* (4–23 t DW ha^{-1}), *Typha glauca* (7–21 t DW ha^{-1}), *Typha orientalis* (23 t DW ha^{-1}) and *Typha subulata* (11–19 t DW ha^{-1}). This can be partly attributed to latitudinal differences in photosynthetic rates (Knapp and Yavitt, 1995) and/or to climatic differences in resource translocation to below-ground organs (McNaughton, 1966). This is suggesting that specific conditions in Lake Burullus with high water nutrient concentrations are favorable for the growth of Southern Cattail (Grace, 1988). What we reported in the present study is lower than the data reported for *P. australis* (70 t DW ha^{-1}) in the same study area (Eid et al., 2010).

In the present study, the ratio of maximum below-ground to maximum above-ground biomass (0.4) is much lower than the reported values at high latitudes (1.2 at 40°, 1.6 at 50°, Asaeda et al., 2005; 1.0 at 33°, Hill, 1987; 1.4 at 47°, Garver et al., 1988; 1.5–1.8 at 49°, Dykyjova, 1971). This ratio is comparable to that reported for *P. australis* (0.3) in the same study area (Eid et al., 2010). This may indicate smaller dependence on resource translocation rather than in higher latitude populations. This pattern may be a strategy of Southern Cattail to store more assimilates in below-ground rhizomes in the temperate zone compared with the south Mediterranean zone, where photosynthesis is not a limiting factor for biomass production due to high radiation and a longer growth period. This implication also agrees with the data showing that rhizome proliferation is stimulated by the cool temperature at high latitudes (McNaughton, 1966).

To study the interaction between the above- and below-ground components, understanding the mechanisms related to material allocation to each organ is essential, for which mechanistic modeling approach is essentially effective. In this study *Typha*'s mechanistic growth model was used and the computed results matched the observed data to a satisfactory level. Above-ground biomass in the present study is increased by the surplus of the sum of the initial upward translocation of rhizome reserves and the later photosynthetic gross production over the respiration and mortality losses. Gross production was controlled to the period of growing season, when the above-ground biomass existed, while losses due to the respiration and mortality continued during the whole year. The respiration loss was higher during summer associated with the high above-ground biomass and high air temperature. On the other hand, the mortality loss became higher in late autumn due to the senescence of shoots. The results of these dynamics, the net production peaked earlier than the gross production and then decreased rapidly during late spring, became negative in mid of summer and reached the lowest value in early autumn.

In the present study with longer growing season, higher solar radiation and temperature; the annual gross production (25,076 g DW m^{-2}) was larger than the reported values at higher latitudes (7360 g DW m^{-2} at 40° in New Jersey, USA and 3730 g DW m^{-2} at 50° in Moravia, Czech, Asaeda et al., 2005). In the same time, higher temperature in the present study also resulted in larger respiration and mortality losses which not balanced the annual gross production in the equivalent stage. Therefore, the magnitude of the seasonal cycle of the whole plant net production was larger than that in higher latitudes.

The starting time of translocation of resources to rhizomes was almost two weeks earlier in the present study (31°) than in Moravia, Czech (50°) (Asaeda et al., 2005). In addition, the ending time was two months later at 31° than at 50°. Therefore, the period of the downward translocation was two and half months longer at 31° than at 50°. With the larger net production and the longer period of downward translocation, the annual translocation of resources to rhizomes (5415 g DW m^{-2}) was larger in present study than at higher latitudes (2800 g DW m^{-2} at New Jersey, USA, 40° and 1850 g DW m^{-2} at Moravia, Czech, 50°, Asaeda et al., 2005). In addition, the biomass of under-ground organs increased from 941 to 2184 g DW m^{-2}, which mean that respiration and mortality losses of rhizomes during the translocation period for about 77% of the total translocate and this was much higher than the reported value (30%) at 50° (Asaeda et al., 2005). We found that, in the above-ground production, the contribution of resource translocation from rhizomes (8%) was lower than the contribution at higher latitudes (11% at 40° and 21% at 50°, Asaeda et al., 2005) because of the higher gross production in the growing season and the relatively small rhizome biomass, indicating lower dependence on resource translocation rather than the later net production. These results suggest that Southern Cattail in Lake Burullus may be more resilient than at higher latitudes.

5. Conclusion

In conclusion, we applied a published *Typha* model to describe the growth production among the various organs of Southern Cattail in Lake Burullus, one of the Mediterranean eutrophic lakes. The model was able to simulate with some degree of acceptance the biomass of this plant in the south Mediterranean region. Based on our results, we recommend the following. First, if Southern Cattail is used to remove nutrients, *Typha* stands should be harvested at peak above-ground biomass. In Egypt, this means that harvests should be in July. Harvested plant material could be used as roof or fencing materials. However, over the long term, annual harvesting may lead to the deterioration of Southern Cattail primary production. Thus for the sustainability of individual *Typha* stands, harvests should not be conducted annually; perhaps a certain harvest rotation could be used (similar to crop rotation in farming). To determine appropriate harvest rotations, further study is needed. Second, the model output could be used to derive management recommendations for Southern Cattail control in regions where the species is considered invasive. If the main purpose of Southern Cattail management is to suppress or eradicate the species from a site, then the harvest of the above-ground parts when the rhizome reserves are lowest would be more effective in reducing and impeding the growth. These recommendations are comparable to that reported for *P. australis* in the same study area (Eid et al., 2010).

Acknowledgements

We thank Dr. Hans Luthardt, Max-Planck Institute for Meteorology, Hamburg, Germany for providing us with the solar radiation data and Mr. Mahendra Baniya, Saitama University, for his help during the data analysis. The Graduate Program for Regional Environmental Conservation Experts provided the senior author with funding for a two-week visit at Saitama University (Saitama, Japan), where part of this work was conducted.

Appendix A.

List of (A) equations and (B) parameters used in the *Typha* model to simulate the growth of Southern Cattail population in Lake Burullus, Egypt.

(A).

Governing equations for biomass
For n-year old rhizomes:

$$\frac{\partial B_{rhi}(n)}{\partial t} = -R_{rhi} - D_{rhi} - Rhif \cdot m(n) + k(n)\left[\sum_{l=1}^{l\max} \varepsilon_{fl\cdot nf\cdot se} b_{fl\cdot nf\cdot se}(l) + \sum_{l=1}^{l\max} \varepsilon_{ph} G_{fl\cdot nf\cdot se}(l)\right] \qquad \text{(A1)}$$

For roots:

$$\frac{\partial B_{root}}{\partial t} = -R_{root} - D_{root} + Rhif \cdot F_{root} \qquad \text{(A2)}$$

For leaves of flowering, non-flowering and secondary shoots at the lth layer:

$$\frac{\partial b_{fl,nf,se}(l)}{\partial t} = G_{fl,nf,se}(l) - R_{fl,nf,se}(l) - D_{fl,nf,se}(l) + Rhif \cdot f_{fl,nf,se}(l) - \varepsilon_{fl,nf,se} b_{fl,nf,se}(l) - \varepsilon_{ph} G_{fl,nf,se}(l) \qquad \text{(A3)}$$

For inflorescences at the lth layer (only for flowering ramets):

$$\frac{\partial b_{flo}(l)}{\partial t} = -R_{flo}(l) - D_{flo}(l) + Rhif \cdot f_{flo}(l) \qquad \text{(A4)}$$

The subscripts *rhi*, *fl*, *nf*, *se*, *root* and *flo* indicate rhizomes, leaves of flowering shoots, first cohort non-flowering shoots, shoots from the second cohort, roots and inflorescences, respectively. $b_a(l)$ denotes the biomass of the lth layer of each plant organ and $B_a \left(= \sum_{l=1}^{l=\max} b_a(l)\right)$ is the total biomass. *Rhif* is the daily upward translocation from rhizomes to the above-ground organs. F_a is the fraction of rhizome reserves allocated to above-ground organs and roots, satisfying $F_{fl} + F_{nf} + F_{flo} + F_{root} + F_{se} = 1$. The allocation to the lth layer of the above-ground organs is proportional to the existing biomass in that layer $(f_{fl,\,nf,\,flo,\,se}(l)) = F_{fl,\,nf,\,flo,\,se} b_{fl,\,nf,\,flo,\,se}(l)/B_{fl,\,nf,\,flo,\,se})$; ε_a is the allocation rate to rhizome from organs a, and ε_{ph} is the photosynthesis assimilates assigned to the rhizome system. Second and third cohort shoots normally do not form inflorescences in the year (Fiala, 1978); therefore, the total leaf biomass for non-flowering shoots is the sum of non-flowering shoots of the first cohort plus second and third cohort shoots. $k(n)$ and $m(n)$ are fractions of the biomass translocate to and from n-year-old rhizome $\left(\sum_{n=1}^{n=n\max} k(n) = 1 \text{ and } \sum_{n=1}^{n=n\max} m(n) = 1.\right)$
The daily respiration, mortality and upward translocation rate from rhizome system are proportional to biomass and mean daily temperature:

$$R_a = \beta_a \theta^{T-20} B_a \qquad \text{(A5)}$$

$$D_a = \gamma_a \theta^{T-20} B_a \qquad \text{(A6)}$$

$$Rhif = \alpha_{rhi} \theta^{T-20} B_{rhi} \qquad \text{(A7)}$$

where β_a and γ_a are specific rates of respiration and mortality at 20 °C, respectively, α_{rhi} is the specific rate of upward translocation from rhizomes, T is the mean daily temperature and subscript a represents the plant organ, such as rhizomes, leaves and inflorescences.
The gross photosynthetic rate in lth layer is given by a form of the Michaelis–Menten equation (Savageau, 1995; Lopez et al., 2000):

$$Ga(l) = k_{co} P_m K_{NP} \frac{PAR(l)}{K_{PAR} + PAR(l)} \times \frac{K_{age}}{K_{age} + Age} \theta^{-|T-20|} b_a(l) \qquad \text{(A8)}$$

where P_m is the maximum photosynthesis rate (g CO_2 g^{-1} day^{-1}) of the plant at 20 °C in the absence of light and nutrient limitations, k_{co} is the conversion constant of carbon dioxide to ash-free dry weight (g g^{-1} CO_2), $PAR(l)$ is the daily photosynthetically active radiation in lth layer (μmol m^{-2} day^{-1}), *Age* is the age of shoots from the start of growth (days), K_{PAR} and K_{age} are the half saturation constants of *PAR* (μmol m^{-2} day^{-1}) and the effect of *age* (days) on the rate of photosynthesis, respectively, θ is the temperature constant, K_{NP} is the constant of the availability of nutrients, T is the mean daily temperature, $b_a(l)$ is the leaf biomass of the lth layer.
The critical layer biomass for buds, B_{cri} (g m^{-2} layer^{-1}) seems reasonably related to the existing fresh rhizome biomass as well as mean daily temperature (Asaeda and Karunaratne, 2000):

$$B_{cri} = \alpha_{kz} \theta^{(T-20)} B_{rhi}^{2/3} \qquad \text{(A9)}$$

Most of buds are formed from the terminals of the fresh rhizomes (Linde et al., 1976) at the expense of their resources. When the amount of material mobilized from the fresh rhizomes exceeds the critical biomass of the layer, the buds will emerge from the first layer, extending into the next layer and subject to further elongation processes. The parameter a_{kz} (=0.0049) is account for the bud formation (Asaeda et al., 2005).

(B).

Parameter	Symbol	Value	Unit	Reference
Initial rhizomes biomass		1114	g m^{-2}	Measured
Initial roots biomass		295	g m^{-2}	Measured
Date of shoot emergence		44	days	Estimated
Maximum photosynthesis rate	P_m	0.30	g CO_2 g^{-1} day^{-1}	Gartner (1976)
Dark respiration rate of leaves	β_{leaf}	0.006	g g^{-1} day^{-1}	Gustafson (1976)
Dark respiration rate of roots	β_{root}	0.003	g g^{-1} day^{-1}	Calibrated
Dark respiration rate of old rhizomes	$\beta_{rhi\,1,\,2}$	0.002	g g^{-1} day^{-1}	Gustafson (1976)
Dark respiration rate of new rhizomes	$\beta_{rhi\,0}$	0.0035	g g^{-1} day^{-1}	Gustafson (1976)
Mortality rate of leaves	γ_{leaf}	0.004	g g^{-1} day^{-1}	Calibrated
Mortality rate of roots	γ_{root}	0.0003	g g^{-1} day^{-1}	Calibrated
Mortality rate of old rhizomes	$\gamma_{rhi\,1,\,2}$	0.0004	g g^{-1} day^{-1}	Calibrated
Mortality rate of new rhizomes	$\gamma_{rhi\,0}$	0.0003	g g^{-1} day^{-1}	Calibrated
Half-saturation constant of PAR	K_{PAR}	13.0×10^6	μmol m^{-2} day^{-1}	Sale and Orr (1986)
Extinction coefficient of plant	ak	0.25	–	Dykyjova (1971)
Half-saturation constant of age	K_{age}	125	days	Sale and Orr (1986)
Fraction of rhizome transferred to AGB	α_{rhi}	0.012	–	Asaeda et al. (2005)
Fraction of leaf transferred to rhizome	ε_{leaf}	0.026	–	Asaeda et al. (2005)
Temperature constant	θ	1.09	–	Asaeda and Bon (1997)
Constant for calculation of LAI	A_{lai}	0.0231	–	Cary and Weerts (1984)

Parameter	Symbol	Value	Unit	Reference
Constant for calculation of LAI	B_{lai}	0.8588	–	Cary and Weerts (1984)
Elongation rate of leaf	A_{ke}	0.4	–	Calibrated
Conversion constant of CO_2 to ash-free dry weight	k_{co}	0.65	$g\,g^{-1}\,CO_2$	Ondok (1978)
Bud formation	a_{kz}	0.0049	–	Asaeda and Karunaratne (2000)

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