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Verification of a numerical growth model of *Pistia stratiotes* L. using field data from tropical and subtropical sites

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ABSTRACT

The growth model of *Pistia stratiotes* L. (*Pistia*-model) was verified using two independent sets of published field data (07° 26' N, 03° 53' E Nigeria; 27° 30' N, 80° 30' W USA) to answer the following question: Is the *Pistia*-model, originally designed for *P. stratiotes* under natural conditions in Egypt, suitable to simulate the growth of *P. stratiotes* in tropical and subtropical regions? The *Pistia*-model simulates the growth dynamics and biomass production of well-established, monospecific stands of *P. stratiotes* based on fixed carbon gain and loss using first-order differential equations. General trends for shoots biomass, such as the slow initial growth rate followed by a high growth rate, the peak biomass, and the decline of biomass due to senescence, were successfully reproduced by the *Pistia*-model. Many characteristics typical for the roots biomass, such as the increase in the roots biomass during the early growing season because of the translocation of materials from shoots, and the reduction of roots biomass during the later period of the season, were also reproduced. The level of agreement between the simulated values and actual field data indicated that the *Pistia*-model can simulate the biomass of *P. stratiotes* over a wide range of latitudes.

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Shoots biomass; roots biomass; fluxes of dry matter; free-floating macrophytes; latitudinal effect; *Pistia*-model; water lettuce

1. Introduction

Water lettuce (*Pistia stratiotes* L.) is a perennial free-floating aquatic macrophyte of the family Araceae (Eid et al. 2016). It has a worldwide distribution in tropical and sub-tropical waters, and is absent only in Antarctica (Parsons & Cuthbertson 2001). Holm et al. (1977) described this plant 'as one of the most widely distributed of all the hydrophytes' occurring in most of the warmer regions of the world. *P. stratiotes* is one among the world's worst weeds (Holm et al. 1977) and it was considered as invasive species (Yang et al. 2014). *P. stratiotes* has adverse effects on biodiversity and the environment, due to the ability of developing dense mats, impeding fishing and boat transport, as well as constituting a health hazard by sheltering disease carrying insects and snails (Abbasi et al. 1991; Mbatia & Neuenschwander 2005; Yang et al. 2014). On the other hand, *P. stratiotes* has been shown to have great potential for the management of water quality, due to its capacity for the accumulation of heavy metals from wastewater (Srivastava et al. 2008; Galal & Farahat 2015).

A simulation model for growth dynamics and biomass productions of *P. stratiotes* has been developed and called *Pistia*-model (Eid et al. 2016). This model is based on fixed carbon gain and loss (photosynthesis, respiration, mortality, and translocation of materials from shoots to roots) using first-order differential equations. *Pistia*-model distinguishes two state variables, shoots and

roots, and it is driven by solar radiation and air temperature and depends on initial shoots and roots biomass and the nutrient (TN, total nitrogen and TP, total phosphorus) status of the growing medium. In the present study, the growth model of *P. stratiotes* (*Pistia*-model) was verified using two independent sets of published field data (07° 26' N, 03° 53' E Nigeria; 27° 30' N, 80° 30' W USA) to answer the following question: Is the *Pistia*-model, originally designed for *P. stratiotes* under natural conditions in Egypt, suitable to simulate the growth of *P. stratiotes* in tropical and subtropical regions?

2. Materials and methods

2.1. Outline of the *Pistia*-model

The *Pistia*-model is a dynamic numerical model developed by Eid et al. (2016) to simulate the growth dynamics and biomass production of *P. stratiotes* under natural conditions in Egypt based on fixed carbon gain and loss using first-order differential equations. The biomass of *P. stratiotes* (g DM m⁻²) was divided into two fractions (shoots and roots) which were considered as the state variables. The biomass of each fraction was reproduced by the *Pistia*-model by integrating over time the net growth of the plant as a function of photosynthesis, respiration, mortality, and translocation. Equations, process descriptions, and associated parameters are listed in Appendices 1 and 2. The *Pistia*-model simulates the seasonal variation of the shoot and root biomasses (g DM m⁻²) and calculates the gross production, total losses (total metabolic losses due to respiration and mortality), translocation to the roots (translocation of photosynthetic assimilates from shoots to the roots), and net production (difference between gross production and total losses). In the *Pistia*-model, solar radiation, air temperature, TN, TP, and the initial biomass of the shoots and roots were considered forcing functions. The *Pistia*-model is written in FORTRAN and consists of a main program and three subroutines with one-day time steps used in computation.

2.2. Input data subroutine

This subroutine allows the user to interact with the *Pistia*-model to establish the simulation conditions. For the simulation, the input data were the daily solar radiation (MJ m⁻² day⁻¹) (Figure 1), the daily averaged air temperature (°C) (Figure 1), the initial biomass of shoots and roots (g DM m⁻²), and the TN (mg L⁻¹) and TP (mg L⁻¹) of water supporting *P. stratiotes* populations (Table 1). This subroutine converts daily solar radiation to photosynthetic active radiation (PAR) using a conversion factor of 0.45 (Asaeda & Karunaratne 2000). In the *Pistia*-model, air temperature influenced the rates of many processes, but PAR only drove photosynthesis (Eid et al. 2016).

2.3. Shoots subroutine

This subroutine addresses the daily change in shoots biomass and the interactions with the roots. Photosynthesis is the source supporting shoots growth.

2.4. Roots subroutine

This subroutine calculates the daily change in roots biomass. The translocation of photosynthesized materials is the source supporting roots growth.

2.5. Model implementation

The main program first calls the input data subroutine to establish the initial conditions of the simulation run. Once the model is initialized, the program, on each simulation day, reads the input data

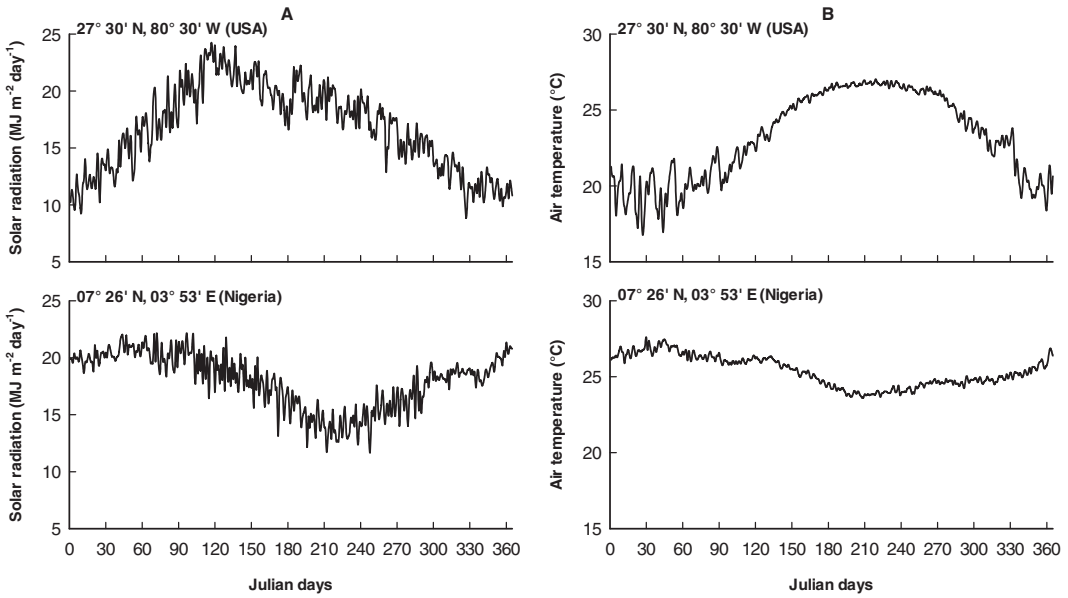


Figure 1. Meteorological characteristics (NASA-POWER 2016) driving the simulations at different latitudes: 07° 26' N, 03° 53' E (Nigeria) and 27° 30' N, 80° 30' W (USA). (A) Daily solar radiation ($\text{MJ m}^{-2} \text{day}^{-1}$), (B) daily average air temperature ($^{\circ}\text{C}$).

Table 1. Characteristics of sampling sites supporting *Pistia stratiotes* populations at different latitudes.

| Parameter | Awba Lake ^a | South Florida ^b |
|---|------------------------|----------------------------|
| Country | Nigeria | USA |
| Latitude | 07° 26' N | 27° 30' N |
| Longitude | 03° 53' E | 80° 30' W |
| Climate | Tropical | Subtropical |
| Mean daily air temperature ($^{\circ}\text{C}$) | 23.9–26.9 | 19.4–26.7 |
| Mean daily solar radiation (MJ m^{-2}) | 14.0–20.7 | 11.5–21.6 |
| Study period | February–May 1979 | November 1985–April 1987 |
| Initial shoots biomass (g DM m^{-2}) | 49.5 | 23.5 |
| Initial roots biomass (g DM m^{-2}) | 7.1 | 6.3 |
| Area (m^2) | 94,500 | 170 |
| Depth (m) | 5.5 | 1.0 |
| Water characteristics | | |
| Type | Eutrophic | Eutrophic |
| pH | 6.6–8.4 | 6.7–7.0 |
| Total solids (mg L^{-1}) | 66–838 | |
| Dissolved oxygen (mg L^{-1}) | 0.9–7.9 | 1.2–2.1 |
| NH_4 (mg L^{-1}) | 0.44–1.16 | 1.23–1.54 |
| P (mg L^{-1}) | 0.04–0.18 ^c | 0.51–20.88 ^d |

^aSharma and Sridhar (1981).

^bDeWald and Lounibos (1990).

^cWater soluble P.

^dTotal P.

and calls the shoots subroutine and roots subroutine to simulate *P. stratiotes* growth. The growth equations for shoots and roots were solved simultaneously using the fourth-order Runge–Kutta method (Butcher 2008). The time scale was in Julian days and at the end of each simulation day, the program outputs the daily results.

2.6. Description of the two field studies

2.6.1. Awba Lake, Nigeria (07° 26' N, 03° 53' E)

The study was conducted in the period from February 1979 to May 1979 at the eastern, center and western tip of Awba Lake, Nigeria (Sharma & Sridhar 1981). It is a man-made lake and has a volume of 227 million L of water. The whole lake was covered with a carpet of *P. stratiotes* which in the shallow areas, especially near the banks, occurs in association with *Nymphaea* species. The plant samples were collected from three different points in the lake at weekly intervals over a period of four months, covering two seasons peculiar to Nigeria, one the dry season and the other the wet season. The individual plant method of Newbould (1967) was used to estimate the biomass and productivity of *P. stratiotes*. The collected plant samples were counted and dried at 105 °C for 24 h and the dry weights were determined. Because meteorological data for the year 1979 were not available, 10-year data from 1984 to 1993 (NASA-POWER 2016) for daily solar radiation and daily air temperature were averaged to estimate the appropriate values for 1979.

2.6.2. Florida, USA (27° 30' N, 80° 30' W)

The field study was carried out in the period from November 1985 to April 1987 at an unused aquaculture pond and a road side drainage ditch in Florida, (USA) by DeWald and Lounibos (1990) to examine the seasonal trends in leaf area, leaf and plant densities, leaf and root biomasses, and flowering. The methods used for the plant sampling were modifications of those described by Hall and Okali (1974) for *P. stratiotes* in Lake Volta (Ghana). At 30 days intervals, five random quadrats were collected from each site using a stainless steel sampling tool 30 × 30 × 70 cm, with serrated teeth around the perimeter of the bottom to penetrate the *P. stratiotes* mat. The number of plants was counted as well as the number of leaves and flowers. The surface area of leaves in each sample was measured using a Licor leaf area-meter. Dry weights of shoots and roots were measured after oven drying at 80 °C for 48 h. The daily means of air temperature and solar radiation for Florida sites were obtained from the website of NASA-POWER (2016).

2.7. Verification of the Pistia-model

The *Pistia*-model was verified using two independent sets of published field data: 07° 26' N, 03° 53' E (Nigeria) and 27° 30' N, 80° 30' W (USA), for which field data were available. In the present study, the biomass and leaf area index (LAI) data collected from the two sites in Florida (aquaculture pond and a road side drainage ditch) were averaged and the means were used in the verification. The daily means of air temperature and solar radiation were obtained for these two latitudes from the website of NASA-POWER (2016) (Figure 1), and TN and TP were obtained from literature (Table 1). Because no initial shoots or roots biomass was reported, a series of simulations were conducted using different initial shoots and roots biomass values, and the value that provided the best fit of the simulated biomass to the actual biomass (from the two published field studies) was then used (Table 1). The deviations of the simulated results from the observed field data were assessed in three ways: standard deviation as a percent, regression of observed (*y*-axis) vs. simulated data (*x*-axis) and Wilcoxon signed-rank test (Pineiro et al. 2008; Eid et al. 2012). All the statistical analyses were carried out using Statistica 7.1 (Statsoft 2007).

3. The simulation results

In Awba Lake, the shoots started to grow at the beginning of February (142.6 g DM m⁻²), reached its maximum biomass of 371.8 g DM m⁻² in mid of March, and then decreased and reached the lowest value at the end of May (195.6 g DM m⁻²) when the plants moved into the senescence stage (Figure 2). The roots biomass increased from 26.4 g DM m⁻² at the beginning of February to 67.0 g DM m⁻² in mid-March and decreased to a minimum of 14.1 g DM m⁻² in early May. In Florida,

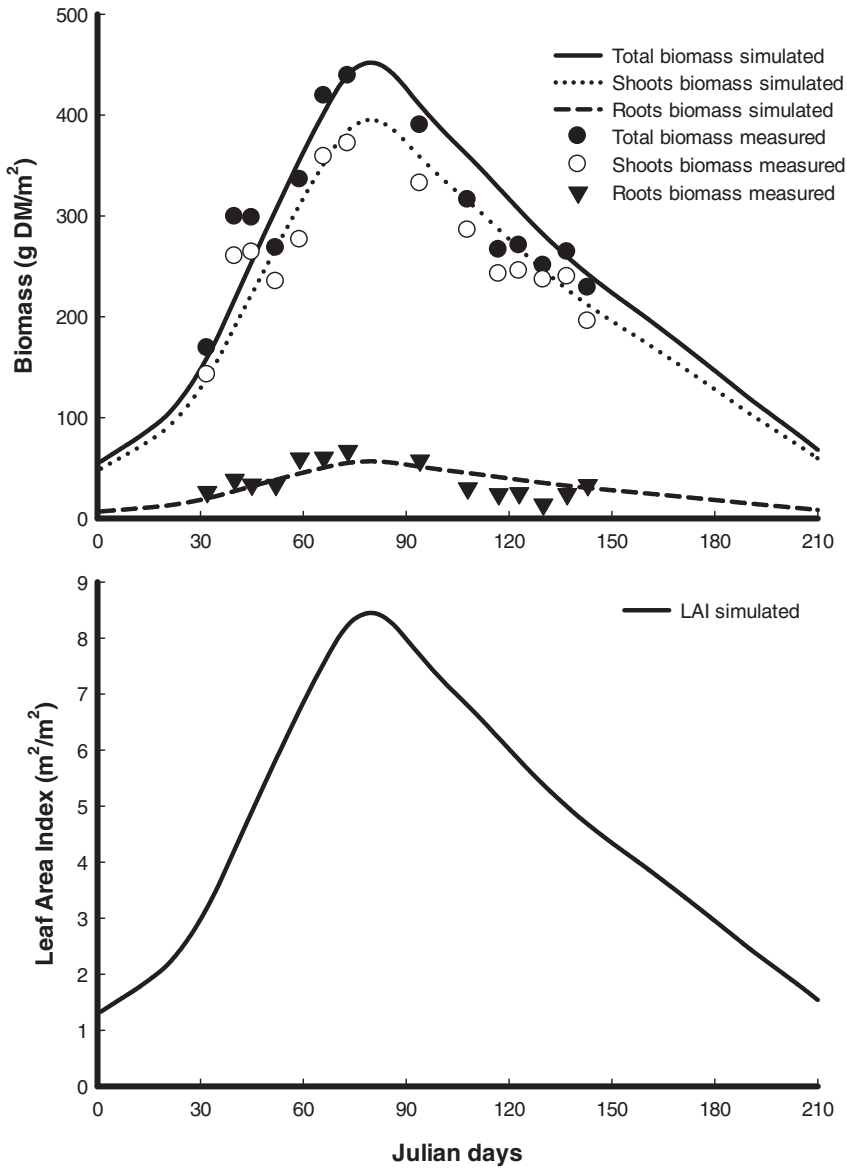


Figure 2. Simulated results (lines) and measured data (symbols; data from Sharma & Sridhar 1981) of the biomass and leaf area index (LAI) of *Pistia stratiotes* populations at 07° 26' N, 03° 53' E. Total biomass = shoots biomass + roots biomass.

the shoots started to grow at the beginning of March (19.9 g DM m⁻²), reached its maximum biomass of 335.9 g DM m⁻² at the beginning of October, and then decreased and reached the lowest value in next February (200.4 g DM m⁻²) when the plants moved into the senescence stage (Figure 3). The roots biomass increased from 33.1 g DM m⁻² at the beginning of March to 62.0 g DM m⁻² at the beginning of September and decreased to a minimum of 39.5 g DM m⁻² in next February. The maximum shoots biomass was 10.7% higher in Awba Lake compared to Florida site, while maximal biomass of roots was 1.1 times in Awba Lake that in Florida.

The capability of the *Pistia*-model to predict the seasonal variation of shoots and roots biomass as well as LAI of *P. stratiotes* was verified using published field data from two different populations of *P. stratiotes* growing in Awba Lake (Nigeria) and Florida (USA). General trends for the shoots

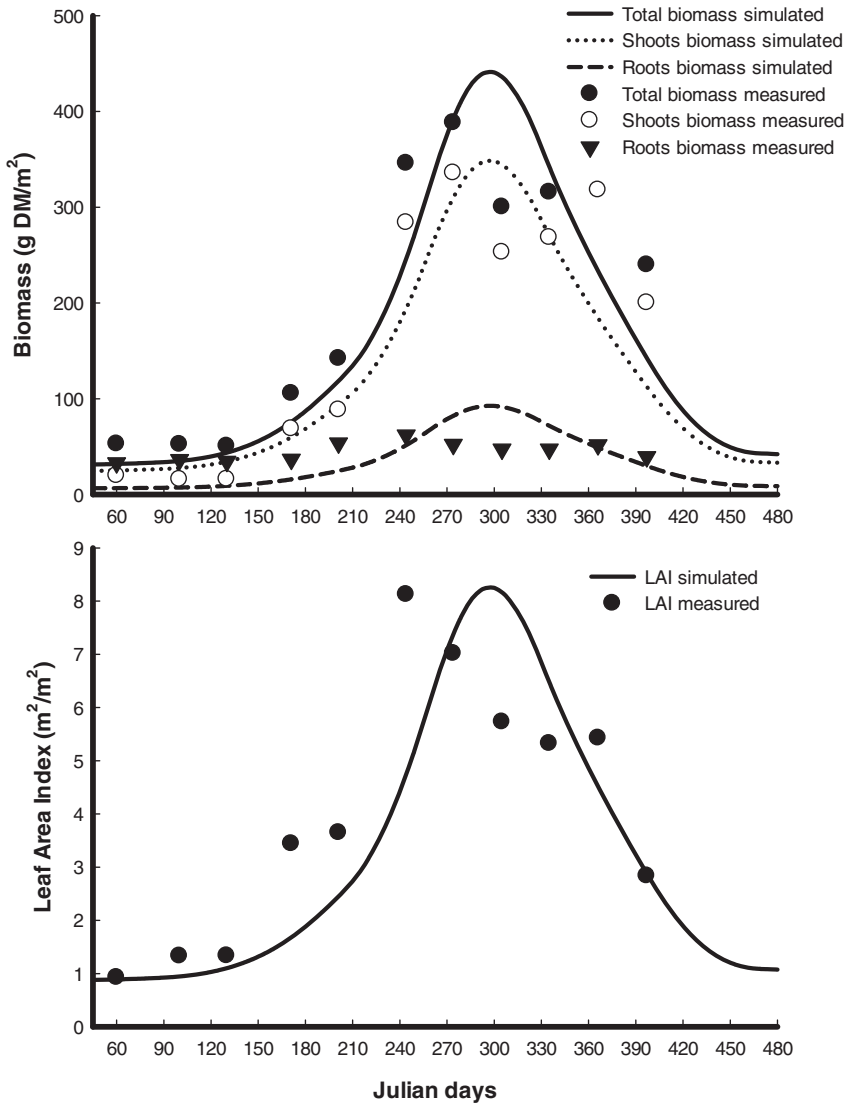


Figure 3. Simulated results (lines) and measured data (symbols; data from DeWald & Lounibos 1990) of the biomass and leaf area index (LAI) of *Pistia stratiotes* populations at 27° 30' N, 80° 30' W. Total biomass = shoots biomass + roots biomass.

biomass and LAI, including a slow initial absolute growth rate followed by a high absolute growth rate, peak of biomass and LAI, end of growth, and decline of biomass and LAI, were successfully reproduced by the *Pistia*-model (Figures 2 and 3). Many characteristics typical to the roots biomass, such as the increase in the biomass during the early growing season due to the translocation of materials from the shoots and the reduction of biomass during the later period of the season, were also reproduced. The level of agreement between the simulated values and the actual field data indicated that although the simulated results were a little different from the observations, the *Pistia*-model is capable of simulating seasonal changes in biomass of shoots and roots and LAI for *P. stratiotes* populations in tropical (Awba Lake) and subtropical (Florida) regions (Figures 2 and 3). The results of the Wilcoxon signed-rank test indicated that there was no significant difference between the estimated and actual means of the biomass and LAI (no field data for comparison existed for Awba Lake) (Table 2).

Table 2. The deviations of simulated results reproduced by *Pistia*-model from observed field data at different latitudes.

| Latitude | Longitude | Country | Parameter | Standard deviation (%) | Regression analysis | | | | Wilcoxon signed-rank test | |
|-----------|-----------|---------|---|------------------------|---------------------|-------|----|-------|---------------------------|-------|
| | | | | | r | P | df | slope | z-value | P |
| 07° 26' N | 03° 53' E | Nigeria | Total biomass (g DM m ⁻²) | 6.8 | 0.889 | 0.000 | 13 | 0.939 | -1.350 | 0.177 |
| | | | Shoots biomass (g DM m ⁻²) | 6.9 | 0.894 | 0.000 | 13 | 1.008 | -1.412 | 0.158 |
| | | | Roots biomass (g DM m ⁻²) | 18.9 | 0.710 | 0.004 | 13 | 0.422 | -0.408 | 0.683 |
| 27° 30' N | 80° 30' W | USA | Total biomass (g DM m ⁻²) | 16.5 | 0.884 | 0.000 | 10 | 0.943 | -1.511 | 0.131 |
| | | | Shoots biomass (g DM m ⁻²) | 17.7 | 0.885 | 0.000 | 10 | 0.788 | -0.445 | 0.657 |
| | | | Roots biomass (g DM m ⁻²) | 33.9 | 0.668 | 0.025 | 10 | 2.155 | -0.800 | 0.424 |
| | | | Leaf area index (m ² m ⁻²) | 17.1 | 0.850 | 0.001 | 10 | 0.923 | -0.978 | 0.328 |

The production and seasonal fluxes of dry matter of *P. stratiotes* in Awba Lake were estimated using the modeled quantities (Figure 4). The annual gross production and net shoots production was 1699.4 and 798.5 g DM m⁻², respectively. The supply of photosynthesized materials for roots growth showed 11.0% to the gross production. The respiration of the shoots and roots consumes a considerable amount of net photosynthetic materials 28.9% and 2.4%, respectively. The mortality of the shoots and roots consumes a considerable amount of net photosynthetic materials 2.1% and 0.3%, respectively. The production and seasonal fluxes of dry matter of *P. stratiotes* in Florida were estimated using the modeled quantities (Figure 5). The annual gross production and net shoots production were 1241.0 and 577.1 g DM m⁻², respectively. The supply of photosynthesized materials for roots growth showed 12.7% to the gross production. The respiration of the shoots and roots consumes a considerable amount of net photosynthetic materials 26.0% and 0.6%, respectively. The mortality of the shoots and roots consumes a considerable amount of net photosynthetic materials 2.1% and 0.3%, respectively.

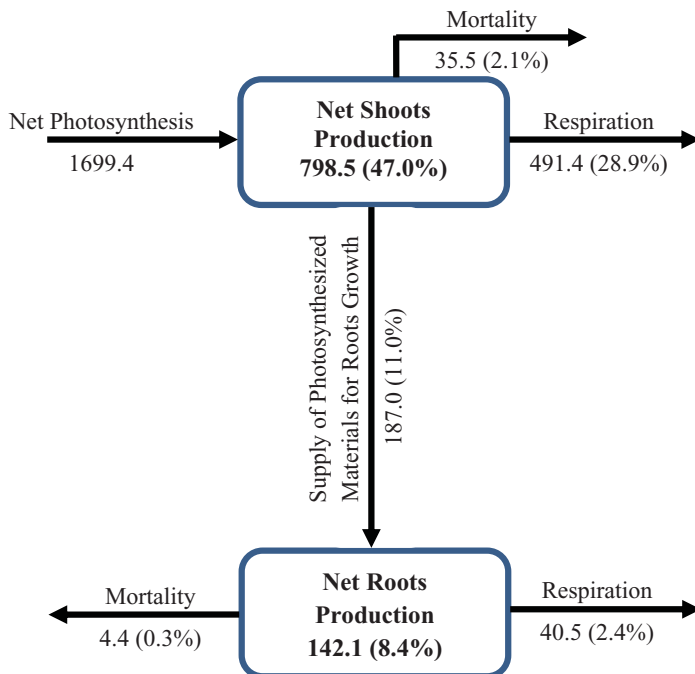


Figure 4. Production and seasonal fluxes of dry matter of *Pistia stratiotes* populations at 07° 26' N, 03° 53' E (Nigeria) constructed using simulated quantities. Production is expressed as g DM m⁻² and fluxes expressed as g DM m⁻² per year.

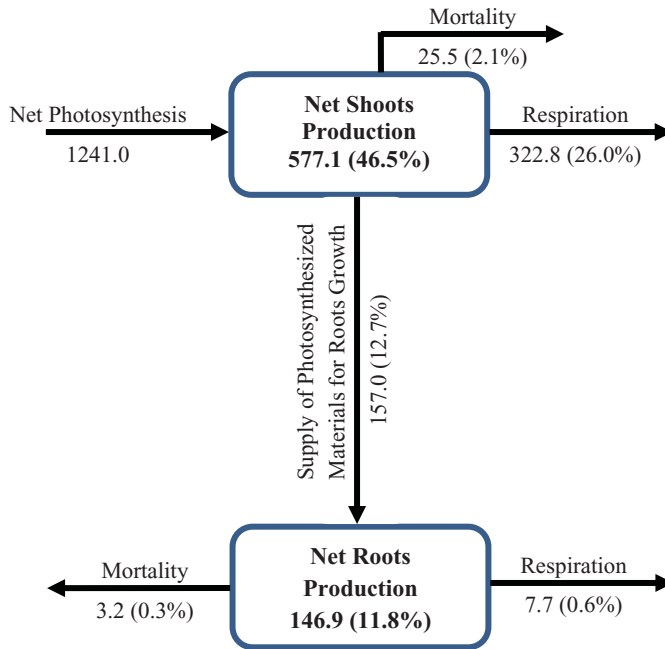


Figure 5. Production and seasonal fluxes of dry matter of *Pistia stratiotes* populations at 27° 30' N, 80° 30' W (USA) constructed using simulated quantities. Production is expressed as g DM m⁻² and fluxes expressed as g DM m⁻² per year.

4. Discussion

The objective of the present study was to verify the *Pistia*-model (a mathematical model developed to simulate the growth pattern of a well-established, monospecific stand of *P. stratiotes* under natural conditions) using two independent sets of published field data. The difficulty in finding good quality, suitable data-sets (which present the seasonal growth pattern of both shoots and roots biomass of *P. stratiotes*) poses a considerable impediment in such verifications. Perdomo et al. (2008) have tried using a cyclic function and double monod equations to determine the growth dynamics of *P. stratiotes* under natural conditions in temperate climate, where this study depended mainly on empirical relations, and thus its scope for further understanding of the dynamics of growth was limited. According to the authors' knowledge, the study of Eid et al. (2016) is the first study that have been carried out to analyze the growth dynamics of *P. stratiotes* using numerical simulation models. A special feature of the *Pistia*-model verified in the present study is its ability to predict the growth pattern of monospecific stands of *P. stratiotes* from varying locations. Predicting the growth and production of *P. stratiotes* is necessary in aquatic habitat management and making such tools commercially available for such purposes is long delayed (Eid et al. 2016). Generally, the quantitative estimation of parameters related to plant growth such as translocation of photosynthesized materials between plant organs, respiration, and mortality of plant organs, is difficult by direct measurement. In contrast, the *Pistia*-model which was tested in this paper can synthesize quantitative information about the physiological processes and thus deliver estimates of ecological and physiological responses that may be hard to measure directly.

Daily average air temperature- and daily solar radiation-sum values in Awba Lake were about 9.2% and 7.3%, respectively, higher than the Florida site (Figure 6). *P. stratiotes* in Awba Lake experiences higher temperature and more daily solar radiation throughout the growing season than it does in Florida site. Photosynthetic production and net production were higher in Awba Lake (1699.4 and 940.6 g DM m⁻² yr⁻¹, respectively) than in the populations in Florida (1241.0 and

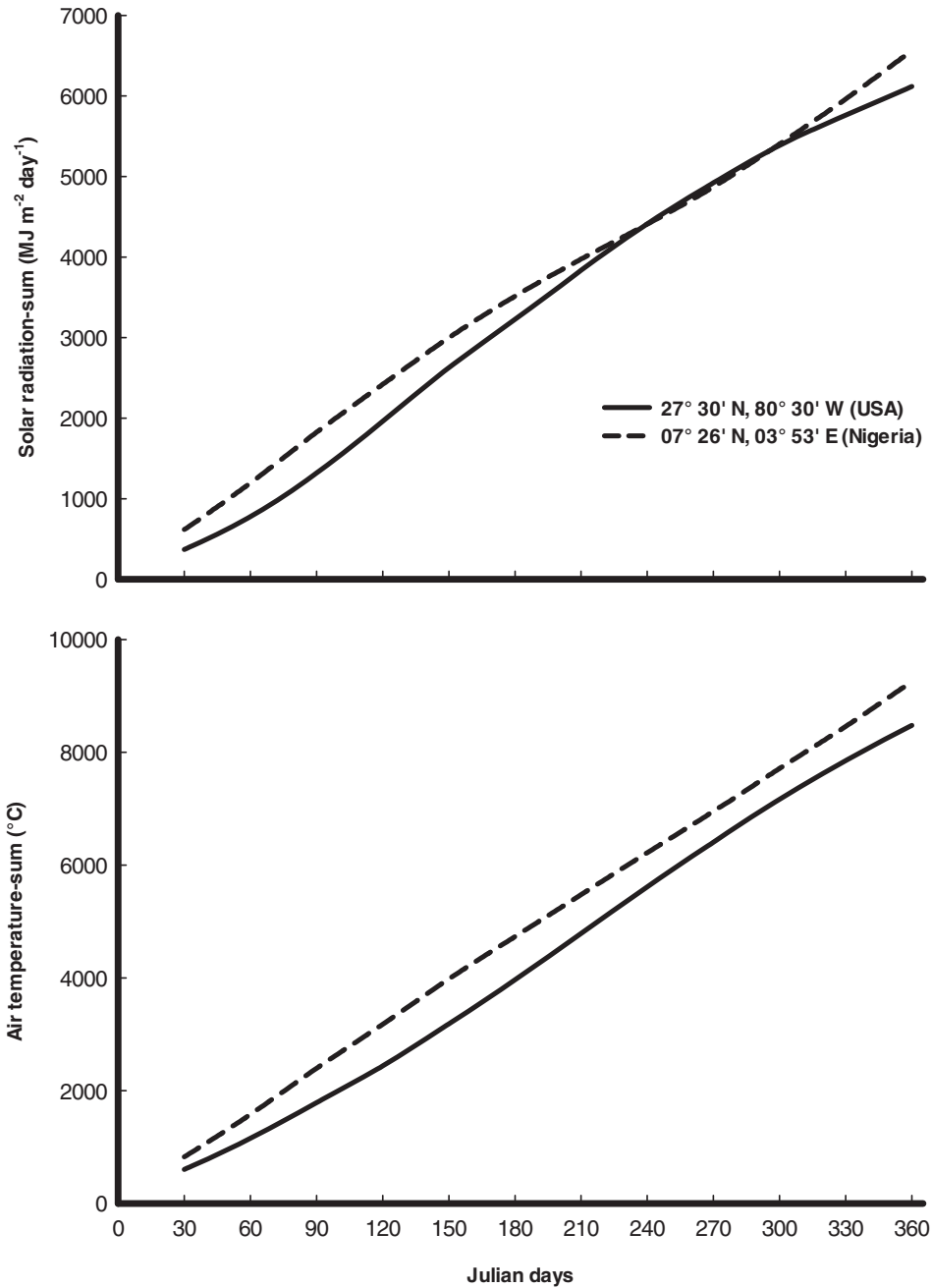


Figure 6. Daily solar radiation (MJ m⁻² day⁻¹) and daily average air temperature (°C) sums at 07° 26' N, 03° 53' E (Nigeria) and 27° 30' N, 80° 30' W (USA).

724.0 g DM m⁻² yr⁻¹, respectively). The more productive nature of *P. stratiotes* in Awba Lake seems to be mainly due to greater solar radiation as well as warmer temperatures. Moreover, Awba Lake receives considerable amounts of organic pollution, which promote the growth of *P. stratiotes* (Sharma & Sridhar 1981). However, in Awba Lake, the larger biomass and higher temperature resulted in larger respiration and mortality losses where the respiration and mortality were 60.9%

and 39.0% higher for *P. stratiotes* populations in Awba Lake compared to Florida site. In the present study, shoots respiration consumes a considerable amount of photosynthetic production (26.0%–28.9%). Therefore, respiration of shoots is an unavoidable component when constructing the carbon budget of *P. stratiotes*. Irrespective of the variation in the climatic conditions, the percentage of annual fluxes remained more or less equal, illustrating the adaptation of this species to different climatic conditions.

The growth trends of *P. stratiotes* in Awba Lake and Florida were like that of our previous study on the same species in Egypt (Eid et al. 2016). The differences in the specific time of the growing stages between these studies were related to the effects of local environmental factors, such as climate and nutrient conditions. The maximum total biomass of *P. stratiotes* in Awba Lake (43.9 t DM ha⁻¹) and Florida (38.8 t DM ha⁻¹) is higher than the maximum total biomass recorded in Mediterranean region (35.8 t DM ha⁻¹; Eid et al. 2016). This finding is supported by our previous study on *Eichhornia crassipes* (Eid & Shaltout 2017), which indicated that the gross and net production of *E. crassipes* populations were higher in the tropical and sub-tropical regions than in the Nile Delta (Mediterranean region). Since biomass is often largely determined by specific habitat conditions (Luther 1983), the high biomass in the tropical and sub-tropical regions could be due to environmental factors that vary with latitude such as temperature, day length, solar irradiance, and length of growing season (Sand-Jensen 1989; Eid et al. 2010, 2013). Variation may also be partly attributed to biotic factors such as mutualists/facilitators or predators/pathogens. The growth and maximum photosynthesis of *P. stratiotes* are driven by air temperature and solar radiation (Eid et al. 2016) and depend on the nutrient status of the growing medium (Hall & Okali 1974). This finding means that the growth and total biomass of *P. stratiotes* correlate with latitudinal changes in air temperature and solar radiation. A similar finding was reported by Asaeda et al. (2005) and Hai et al. (2006) for the emergent macrophytes *Typha angustifolia* and *Typha latifolia* and Eid and Shaltout (2017) for *E. crassipes*.

5. Conclusion

In conclusion, the *Pistia*-model was applied to Awba Lake (Nigeria) and Florida (USA). Generally, a good fit was found between simulated and measured biomass and LAI. *Pistia*-model can be used to assess growth of *P. stratiotes* under various site specific and climatological conditions and thus used as a predictive tool for assessing the potential growth of *P. stratiotes* over a wide range of latitudes. It might be useful for practical applications, such as the management of irrigation and drainage canals, and to derive management recommendations for *P. stratiotes* control in regions where the species is considered invasive by assessing the critical growth stages of this plant.

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Appendices

Appendix 1. List of equations used in *Pistia*-model to simulate the growth of *Pistia stratiotes* populations at different latitudes

Rates of change (g DM m⁻² day⁻¹) of the state variables (g DM m⁻²)

$$\frac{\partial \text{Shoots}}{\partial t} = \text{Shoots Growth} - \text{Shoots Respiration} - \text{Shoots Mortality} - \text{Supply of photosynthesized materials for Roots Growth}$$

$$\frac{\partial \text{Roots}}{\partial t} = \text{Supply of photosynthesized materials for Roots Growth} - \text{Roots Respiration} - \text{Roots Mortality}$$

Main processes (g DM m⁻² day⁻¹)^a

$$\text{Shoots Growth} = \text{Gross Photosynthesis rate}_{20} \cdot \text{Organ}_{\text{sh}} \cdot f(T)$$

$$\text{Shoots Respiration} = \text{Shoots Respiration rate}_{20} \cdot \text{Organ}_{\text{sh}} \cdot f(T)$$

$$\text{Shoots Mortality} = \text{Shoots Mortality rate}_{20} \cdot \text{Organ}_{\text{sh}} \cdot f(T)$$

Supply of photosynthesized materials for Roots Growth (Gamage & Asaeda 2004)

$$= G_{\text{rt}} \cdot \frac{K_{\text{rt}}}{K_{\text{rt}} + \text{Age}_{\text{rt}}} \cdot \text{Organ}_{\text{rt}} \cdot f(T)$$

$$\text{Roots Respiration} = \text{Roots Respiration rate}_{20} \cdot \text{Organ}_{\text{rt}} \cdot f(T)$$

$$\text{Roots Mortality} = \text{Roots Mortality rate}_{20} \cdot \text{Organ}_{\text{rt}} \cdot f(T)$$

Functions^b

$$f(T) = \theta^{(T - 20)}$$

The gross photosynthesis rate of macrophytes is described by a form of the Michaelis–Menten equation (Jørgensen et al. 1981) as

$$\text{Gross Photosynthesis rate}_{20} \text{ (g gross photosynthesis g}^{-1} \text{ shoots biomass day}^{-1}) = K_{\text{co}} \cdot P_{\text{max}} \cdot \frac{N}{N + K_N} \cdot \frac{P}{P + K_P} \cdot \frac{\text{PAR} \cdot e^{-K_{\text{le}} \cdot \text{LAI}}}{K_{\text{PAR}} + \text{PAR} \cdot e^{-K_{\text{le}} \cdot \text{LAI}}}$$

The relationship of shoots biomass (g DM m⁻²) and leaf area index (LAI) was developed by Eid et al. (2016) ($r = 0.969$, $P < 0.001$) using the measured data: $\text{LAI} = 0.314 + 0.018 \times \text{Shoots biomass}$.

^aOrgan_{sh} is shoots biomass (g DM m⁻²); Organ_{rt} is roots biomass (g DM m⁻²); Rate₂₀ is the rate (day⁻¹) at 20 °C; $f(T)$ is the temperature function correcting the rates for the daily averaged air temperature (T , °C).

^b θ is the Arrhenius constant; K_{co} is the conversion constant of CO₂ to dry matter (g g⁻¹ CO₂); P_{max} is the maximum photosynthetic growth rate (g CO₂ g⁻¹ day⁻¹); PAR is the photosynthetic active radiation (MJ m⁻² day⁻¹); K_{PAR} is the half saturation constant for the photosynthetic active radiation (MJ m⁻² day⁻¹); K_{le} is the light extinction coefficient within the canopy (m² (ground) m⁻² (leaf)); LAI is the leaf area index of the stand (m² (leaf) m⁻² (ground)); N is the concentration of total nitrogen in water (mg N L⁻¹); K_N is the half saturation constant for nitrogen uptake (mg N L⁻¹); P is the concentration of total phosphorus in water (mg P L⁻¹); K_P is the half saturation constant for phosphorus uptake (mg P L⁻¹); G_{rt} is the maximum roots growth rate (g g⁻¹ day⁻¹); Age_{rt} is the age of roots from the start of growth (days); K_{rt} is the half saturation constant of the effect of age (days) on the roots growth rate.

Appendix 2. List of parameters used in *Pistia*-model to simulate the growth of *Pistia stratiotes* populations at different latitudes

| Parameter | Symbol | Value | Unit | Reference |
|--|-----------------------|-------|---|------------------------|
| Shoots respiration rate | β_{sht} | 0.01 | $\text{g g}^{-1} \text{day}^{-1}$ | Lorber et al. (1984) |
| Roots respiration rate | β_{rt} | 0.01 | $\text{g g}^{-1} \text{day}^{-1}$ | Lorber et al. (1984) |
| Shoots mortality rate | γ_{sht} | 0.001 | $\text{g g}^{-1} \text{day}^{-1}$ | Eid et al. (2016) |
| Roots mortality rate | γ_{rt} | 0.001 | $\text{g g}^{-1} \text{day}^{-1}$ | Eid et al. (2016) |
| Arrhenius constant | θ | 1.07 | | Soetaert et al. (2004) |
| Conversion constant of CO ₂ to dry matter | K_{co} | 0.83 | $\text{g g}^{-1} \text{CO}_2$ | Perdomo et al. (2008) |
| Maximum photosynthetic growth rate | P_{max} | 0.283 | $\text{g CO}_2 \text{g}^{-1} \text{day}^{-1}$ | Eid et al. (2016) |
| Half saturation constant for the photosynthetic active radiation | K_{PAR} | 11.1 | $\text{MJ m}^{-2} \text{day}^{-1}$ | Sale et al. (1985) |
| Light extinction coefficient within the canopy | K_{le} | 0.019 | $\text{m}^2 \text{m}^{-2}$ | Eid et al. (2016) |
| Half saturation constant for nitrogen uptake | K_{N} | 0.15 | mg N L^{-1} | Hu et al. (1998) |
| Half saturation constant for phosphorus uptake | K_{P} | 0.01 | mg P L^{-1} | Hu et al. (1998) |
| Maximum roots growth rate | G_{rt} | 0.15 | $\text{g g}^{-1} \text{day}^{-1}$ | Tucker (1983) |
| Half saturation constant of the effect of age on the roots growth rate | K_{rt} | 12.0 | Days | Eid et al. (2016) |