



ELSEVIER

Aquatic Botany 81 (2005) 300–314

**Aquatic  
botany**

www.elsevier.com/locate/aquabot

# Water hyacinth in Lake Victoria: Why did it vanish so quickly and will it return?

Adrian E. Williams\*, Hamish C. Duthie,  
Robert E. Hecky

*Biology Department, University of Waterloo, 200 University Avenue West,  
Waterloo, Ont., Canada N2L 3G1*

Received 29 January 2003; received in revised form 31 December 2004; accepted 3 January 2005

## Abstract

Water hyacinth has been a cause of great concern in terms of environmental and socio-economic impacts within Lake Victoria. In the late 1990s however it rapidly disappeared but since the causes are unknown its possible return cannot be predicted. Growth chamber and laboratory experiments investigating CO<sub>2</sub> assimilation and growth rate found that different phenotypic, density-acclimated, growth forms of water hyacinth behaved differently. PI-curves and changes in biomass revealed that short bulbous (SB) growth forms took up CO<sub>2</sub> more rapidly and increased in biomass quicker than tall non-bulbous (TN) growth forms. This allows the two growth forms to flourish within two different niches. One, the SB form, as a colonising opportunist and the other as a taller plant that attempts to avoid self-shading in dense mats. Light is an important limiting factor to water hyacinth growth. Light becomes non-limiting to CO<sub>2</sub> uptake at a PAR of  $\approx 2000 \mu\text{E m}^{-2} \text{s}^{-1}$ . In Lake Victoria this light level occurs for about 6 h around midday. Plant growth is thus light limited for most of the day and can be limited even at midday during cloudy weather. Although weevils likely played a role in the rapid disappearance of water hyacinth, its demise was too rapid and synchronous in this large lake for weevils to be solely responsible. The cloudy, wet El Nino weather of 1997/1998 was probably a major contributory factor to poor growth that led to the reduction in water hyacinth biomass lake-wide. Currently within Lake Victoria an improved light climate, an ever increasing

\* Corresponding author. Present address: APEM Ltd., Enterprise House, Manchester Science Park, Lloyd Street North, Manchester M15 6SE, UK.

*E-mail address:* ae.williams@virgin.net (A.E. Williams).

supply of nutrients and a potentially unstable weevil population will likely allow the resurgence of this aggressive weed.

© 2005 Elsevier B.V. All rights reserved.

*Keywords:* *Eichhornia crassipes*; El Nino; Lake Victoria; Light limitation;  $P_{\max}$ ; PI-curve; Water hyacinth; Weevils

---

## 1. Introduction

Water hyacinth (*Eichhornia crassipes* (Martius) Solms-Laubach), is found in a number of differing morphological growth forms and the morphology and architecture of leaves, petioles and clonal groups can be highly plastic (Pieterse, 1978; Center and Spencer, 1981; Watson et al., 1982). However two forms dominate (Wright and Purcell, 1995; Julien et al., 1999). One, typically found in open water or at the edges of plant mats, is characterised by short bulbous (SB) and buoyant petioles whilst another form occurs in crowded areas, with slender, tall, non-bulbous (TN) petioles. As the forms are phenotype adaptations the SB form can develop into the TN form if crowding occurs and sufficient nutrients are available (Pieterse, 1978).

Water hyacinth has been in Africa, namely the River Nile, since the 1870s but was not reported in Lake Victoria until 1989 although it is believed to have been present since at least the early 1980s (Twongo and Balirwa, 1995). The problems associated with water hyacinth however did not become apparent in Lake Victoria until the early 1990s. By 1995 80% of the Ugandan coastline was inundated with the plant (Matagi, 2002). The weed typically formed a fringe that extended out from the shore for 15 m although in sheltered bays, such as Inner Murchison Bay, this fringe extended out beyond 50 m. Moreover, dense floating mats reaching 300 ha in size formed within the sheltered bays surrounding Lake Victoria.

Lake Victoria is boarded by Kenya, Tanzania and Uganda and it is the second largest lake in the world with approximately 20 million people living within its catchment. Water hyacinth has impacted these communities by reducing the supply of clean potable water and causing difficulties in water extraction, blocking irrigation canals, increasing transportation costs, reducing fish catches and decreasing available landing sites (Twongo et al., 1995; Lindsey and Hirt, 1999). Reportedly it has also increased disputes between local communities, caused an increase in vector borne diseases, reduced tourism and overall been responsible for the translocation of communities away from Lake Victoria (LVEMP, 2000). Furthermore local communities have reported a decrease in biodiversity. Accumulations of water hyacinth at Owen Falls Dam, at the Nile outlet, have led to the intermittent closure of the hydroelectric plant at Jinja disrupting electrical service to the capital of Kampala (Twongo and Balirwa, 1995).

Despite water hyacinth's invasive nature and dominance in Lake Victoria in the 1990s, water hyacinth had largely disappeared from Lake Victoria by the end of 1998. Although patches were present and growing, especially in areas rich in nutrients such as near river mouths and Inner Murchison Bay, which receives much of the municipal sewerage from Kampala, water hyacinth populations were low (LVEMP, 2001). What were the reasons for

this rapid reduction? Several possibilities for the speedy demise of water hyacinth in Lake Victoria have been forwarded.

The impact of South American *Neochetina* spp. weevils on water hyacinth is widely published. Whilst on occasion their success has been limited if not non-existent (Salmah et al., 1991; Julien et al., 2001) they have been used successfully throughout the world in countries such as Australia, USA, Sudan, India and Papua New Guinea (Julien et al., 1999). Weevils were first introduced on a large scale into Lake Victoria in December 1996 (Ochiel et al., 1999; LVEMP, 2000). However the rapid decrease in water hyacinth abundance from December 1996 to 1998 (2 years) was extraordinarily fast. Although there is no set time lag between the introduction of weevils and an impact on water hyacinth it is usual that weed control is achieved between 3 and 5 years after the initial introduction as the weevils need to increase their population size dramatically from the relatively few that are introduced (Julien et al., 1999). This however assumes that an integrated approach to control is in place that involves mechanical, biological and possibly chemical aspects of control (De Groot, 1993; Julien et al., 1999). Weevils alone were therefore probably not responsible for the rapid reduction in weed biomass.

Lake Victoria is becoming more eutrophic (Bootsma and Hecky, 1993; Hecky, 1993) and eutrophication may have been a factor in the successful invasion of water hyacinth as it has a high nutrient requirement. If physico-chemical and nutrient regimes changed within Lake Victoria during the reduction in the weed's population then nutrient limitation might have been responsible. However little evidence for this is seen from a long-term data set (Fisheries Resources Research Institute of Uganda (FIRRI), unpublished data).

Other possible factors include the illegal use of herbicides. However due to the size of the lake there would have to have been a highly regimented application programme costing millions if not billions of dollars. Therefore herbicide use was not responsible for the decline.

Alternatively weather may have been important. The effects of El Nino in 1997/1998 and a reduced light climate or rising water levels that can dislodge large grounded mats and transport them offshore where wave action increases plant mortality (Ogwang and Molo, 1999) could have been significant.

Clearly there is uncertainty as to the factors leading to the weeds reduction. As a consequence there is also uncertainty as to what conditions might cause a resurgence of water hyacinth. Indeed it appears that very few measurements were taken concerning the growth or decline of water hyacinth and environmental variables associated with these growth patterns in Lake Victoria. To date the main focus of work has centred on the removal of the weed (Mitchell, 1985; De Groot, 1993; Twongo and Balirwa, 1995), the impacts and interactions that the weed has on the system (Willoughby et al., 1993; Masifwa et al., 2001) or the spread and distribution of the weed (Twongo et al., 1995) but not simply understanding its basic biology within Lake Victoria. It was therefore imperative to understand the growth of water hyacinth, what encourages it and what causes its cessation.

The objectives of the research were therefore to understand the reasons behind the decline in water hyacinth biomass within Lake Victoria and consider its potential for resurgence. These objectives were pursued through the use of growth chamber and

laboratory experiments investigating CO<sub>2</sub> assimilation and growth rate of water hyacinth plants. This was undertaken as a collaborative project between the University of Waterloo, Canada and FIRRI, Uganda.

## 2. Methodology

### 2.1. Apparatus and measurement of CO<sub>2</sub> assimilation

A quick and relatively easy method was required to identify the potential for water hyacinth resurgence in bays around Lake Victoria. CO<sub>2</sub> assimilation was deemed a suitable measure of potential plant growth and therefore resurgence. Following the successful testing of a small Perspex growth chamber in greenhouses at the University of Waterloo a larger growth chamber was fabricated and transported ready for assembly to Uganda in July 2001. The box, measuring 300 mm × 300 mm × 600 mm, was made from 6 mm Perspex sheet (Fig. 1). Edges were step cut to increase stability and glued using Methylene Chloride. All joints were made airtight with silicon. An electrical cable was passed through one wall so as to power a small aquarium pump that sat inside the chamber and circulated air within the system. The cable hole was sealed with a rubber O-ring and silicon. A small electronic barometer was also placed inside the chamber (Fig. 1). The chamber opening was circular and, to allow easy access, 254 mm in diameter. A Perspex lid bolted onto five 3 mm shanks embedded into a 13 mm Perspex rim mounted around the opening. A seal was maintained between box and lid using a rubber O-ring and groove cut into the lid inside the outer ring of bolt-holes. Inlet and outlet air joints were fitted into the lid so as to allow air to be pumped from the chamber and into a Li-Cor LI-6252 CO<sub>2</sub> Infra Red Gas Absorption

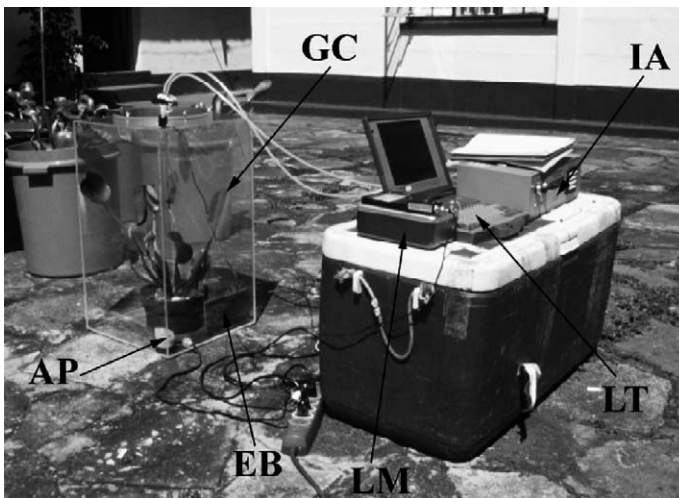


Fig. 1. Experimental apparatus showing (clockwise) growth chamber (GC), CO<sub>2</sub> IRGA analyser (IA), laptop (LT), light meter (LM), electronic barometer (EB) and aquarium pump (AP).

analyser where CO<sub>2</sub> concentrations were determined before the air returned to the chamber (Fig. 1). The system as a whole was therefore closed and allowed a continuous flow of air to be circulated and monitored.

Individual plants were drip dried for 5 min, weighed and the roots sealed in a plastic bag so as to avoid CO<sub>2</sub> being released from water around the roots. Plants were placed into the chamber and the lid sealed. Air immediately began to circulate through the closed system and the gas analyser measured CO<sub>2</sub> concentration and temperature. A measurement of CO<sub>2</sub> concentration, temperature and atmospheric pressure was taken exactly 1 min after the lid was placed onto the bolt shanks and the system became closed. This allowed the nuts to be put in place and a small amount of time for stabilisation within the closed system. Exactly 3 min after these initial readings the measurements were retaken. The lack of available technology meant that the temperature inside the chamber increased by approximately 1 °C over the 3 min. It was not believed that the reduction in CO<sub>2</sub> within the chamber over the 3-min period (mean reduction = 10.5 and 11.4% for SB and TN forms, respectively) was sufficient to influence photosynthetic rate. All data were logged automatically using a laptop linked to the CO<sub>2</sub> analyser. Assimilation of CO<sub>2</sub> was calculated using Eq. (1) (after Hall et al., 1993).

$$A = \frac{(C_1(P_1/T_1) - C_2(P_2/T_2))V}{(t_2 - t_1)SR} \quad (1)$$

where *A*: CO<sub>2</sub> assimilation μmol g<sup>-1</sup> min<sup>-1</sup>; *C*<sub>1</sub>: CO<sub>2</sub> fraction μmol mol<sup>-1</sup> (PPM) at time 1; *P*<sub>1</sub>: pressure kPa at time 1; *T*<sub>1</sub>: temperature (K) at time 1; *C*<sub>2</sub>: CO<sub>2</sub> fraction μmol mol<sup>-1</sup> (PPM) at time 2; *P*<sub>2</sub>: pressure kPa at time 2; *T*<sub>2</sub>: temperature (K) at time 2; *V*: volume in litres; *t*<sub>1</sub>: time at start in minutes; *t*<sub>2</sub>: time at end in minutes; *S*: plant weight in grams; *R*: universal gas constant (8.3147295 l kPa K<sup>-1</sup> mol<sup>-1</sup>).

Light intensity, measured as photosynthetic active radiation (PAR), was monitored throughout the experiments using a Li-Cor LI-250A light meter and a LI-190SA quantum sensor.

## 2.2. Experiment 1—Measuring *P*<sub>max</sub> and defining *PI*-curves

Four individuals of both growth forms were collected from Napoleon Bay near FIRRI in July 2001 and placed individually into large buckets measuring 40 cm in diameter and 41 cm deep. The buckets were placed in the courtyard at FIRRI and 50 l of tap water added and amended with nutrient salts to match concentrations found within Inner Murchison Bay. This bay receives sewage and runoff from the city of Kampala and thus has concentrations of Total Phosphorus (TP) approximately 10 times that of the open lake water. The addition of these nutrient salts also reflected an ideal growth medium as suggested in the literature (Haller et al., 1970; Knipling et al., 1970; Desougi, 1984; Debusk and Dierberg, 1989; Reddy et al., 1990). The final growth medium contained 10 mg N l<sup>-1</sup>, 10 mg P l<sup>-1</sup>, 1.5 mg Fe l<sup>-1</sup> and 15 mg Ca l<sup>-1</sup>. Over a period of 3 days plants were removed and placed in the growth chamber and measurements taken as described above. Between measurements plants were removed from the chamber, allowed to recover for an hour and the procedure repeated with differing PAR levels as provided by the natural change in the day. In addition various shading devices such as cloth and plastic sleeves that

were cut and made to measure the chamber were also used. In all cases the plants were sealed inside the chamber for only 4 min. That is 1 min preparation and stabilisation and 3 min for the actual data collection.

With the photosynthetic rate normalised for plant wet weight using Eq. (1), PI-curves for individual plants of the two growth forms were fitted iteratively to the rectangular (Michaelis–Menten) hyperbola equation with a function for the rate of respiration in darkness included (Eq. (2), after Lederman and Tett, 1981) to get statistically correct estimates of the equation parameters.

$$y = \left( \frac{P_{\max}x}{K_m + x} \right) - R_d \quad (2)$$

where  $P_{\max}$  is the light saturated photosynthetic rate,  $R_d$  is the rate of respiration in darkness defined as the intercept on the ordinate and  $K_m$  is the half-light saturated photosynthetic rate.

The predicted PI-curves for the two growth forms (plants combined) were plotted along with the observed data and the proportion of the total variation explained by each model calculated to obtain the  $r^2$  value. The significance of these values were tested using an  $F$ -statistic which compared the model sum of squares (SS) with the residual sum of squares (RSS), adjusted for the difference in the number of degrees of freedom (df). Simultaneous comparisons of the two curves were then undertaken to determine whether the two graphs were actually different or whether one curve (the combined curve) could describe both data sets equally well. This was undertaken by again using an  $F$ -statistic (Eq. (3), after Zar, 1984) to determine whether the difference in the RSS between the two models (adjusted for their difference in df) was small relative to the  $RSS_{\text{comb}}$  of the combined model (also adjusted for its  $df_{\text{comb}}$ ).

$$F = \left( \frac{RSS_{\text{comb}} - (RSS_1 + RSS_2)}{df_{\text{comb}}(df_1 + df_2)} \right) \left( \frac{df_1 + df_2}{RSS_1 + RSS_2} \right) \quad (3)$$

With the data being described significantly well by the models ( $P < 0.001$ ) and the two models being significantly different from one another ( $P < 0.001$ ) it was then necessary to determine where the differences between the models lay. The best-fit values of each parameter ( $P_{\max}$ ,  $K_m$ , and  $R_d$ ) for the two models (TN and SB) were compared with one another using an  $F$ -statistic. All curve fitting and analysis was undertaken using GraphPad Prism version 4.00 for Windows.

### 2.3. Experiment 2—Rate of plant growth and total biomass increase

Eight plants each of the two growth forms were taken from Napoleon Bay in July 2001, drip dried for 5 min, and their wet weights determined. Measurements were taken of petiole length (from the crown to the narrow isthmus), petiole number, leaf width, leaf length (from the narrow isthmus to the distal apex), leaf lamina area (area = length  $\times$  width  $\times$  0.85; Methy and Roy, 1993) and the number of stolons/ramets budding from the main plant. The plants were then placed individually in separate buckets containing water rich in nutrients as might be found in Murchison Bay and described above. The plants were left for 1 week and total wet weight (original plant

and new growth) measured. Due to the availability of resources nutrient concentrations were not measured at the end of the experiment. However due to the initial high concentrations it was not considered likely that nutrient limitation occurred during the experimental period. The original plants also had their morphological parameters re-measured. Biomass increase as  $\text{g day}^{-1}$  and relative growth rate (RGR) were calculated for each plant (Eq. (4), Causton and Venus, 1981) and *t*-tests performed to see if growth rate varied between the two forms.

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad (4)$$

where  $W_1$  and  $W_2$  are initial and final plant wet weight and *t* is the incubation period in days. Differences were also determined using *t*-tests for the morphological variables measured.

#### 2.4. Experiment 3—Using $\text{CO}_2$ assimilation to predict future biomass

During August 2001 eight plants of each growth form were grown separately in buckets for 18 days. The water in all buckets started as in previous experiments with a good supply of nutrients. Halfway through the experiment half of the buckets were emptied and refilled with fresh nutrient rich medium whilst the other half were not. As a result there were plants of both growth forms varying in health by the end of the experiment. Throughout the course of the experiment  $\text{CO}_2$  assimilation was measured every 3 days for each plant using the technique described previously. However  $\text{CO}_2$  assimilation was only measured whilst PAR was above  $2000 \mu\text{E m}^{-2} \text{s}^{-1}$  and as such light was approximately saturating ( $P_{\text{max}}$  was approached; see Experiment 1 results below). In addition wet weight was measured and daily biomass percentage increase calculated for each plant over each 3-day period. At the end of the experiment  $\text{CO}_2$  assimilation measurements were plotted against the preceding 3-day percentage biomass increase and a linear regression performed to see how closely  $\text{CO}_2$  assimilation could predict future biomass increase and thus future resurgence.

#### 2.5. Measurements of daily and annual PAR cycles

For 17 days from 13/8/01 to 29/8/01 measurements of PAR were taken at hourly intervals from 9 a.m. to 6 p.m. Hourly means were plotted to ascertain how PAR varied over a typical August day. Ideally the weather station at FIRRI would have supplied daily irradiance data for a number of years so that long-term patterns could have been assessed but unfortunately the weather station had been broken for a number of years and such data were not available. As 17 days is a relatively short period to assess and understand ‘usual’ patterns, these data were compared to data modelled by the NOAA-CIRES Climate Diagnostics Center’s NCEP-DOE Reanalysis 2 project. This project has modelled irradiance data as “downward solar flux at surface”. The data are available as predicted/extrapolated midday measurements i.e. near daily peak measurements, in  $\text{W m}^{-2}$  and so these data were converted to PAR as  $\mu\text{E m}^{-2} \text{s}^{-1}$  by a multiplication of 4.57 (Langhans and Tibbitts, 1997) and plotted for 1996–2001.

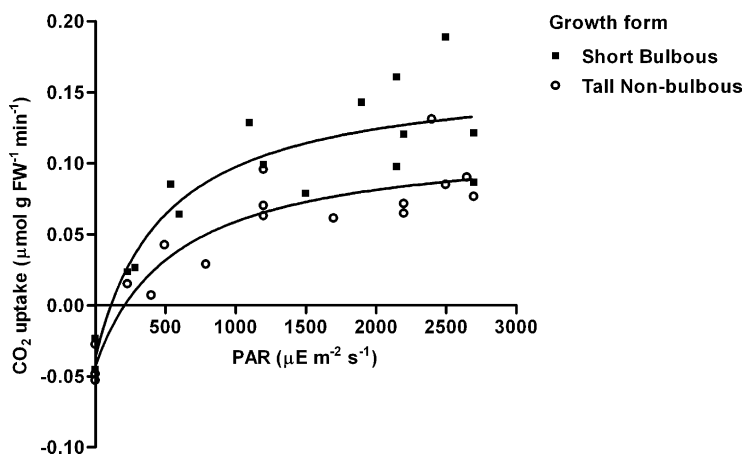


Fig. 2. Photosynthesis–irradiance curves of the short bulbous (SB) and tall non-bulbous (TN) growth forms of *E. crassipes*. Iteratively fitted tangent hyperbolae were significant and different ( $r^2 = 0.82$  for SB;  $r^2 = 0.87$  for TN;  $P < 0.001$  and  $n = 4$  in both cases). Parameter estimates are given in Table 1.

### 3. Results

#### 3.1. PI-curves

The fitted PI-curves for SB and TN water hyacinth growth forms correlated well with the observed data with  $r^2$  values of 0.82 and 0.88, respectively and  $P < 0.001$  in both cases (Fig. 2). Simultaneous comparison found the curves to be significantly different ( $P < 0.001$ ).  $P_{\max}$  and  $K_m$  were significantly higher ( $P < 0.001$  for both) for SB forms than TN forms. Photosynthesis for both forms approached light saturation at approximately PAR  $2000 \mu\text{E m}^{-2} \text{s}^{-1}$  but photoinhibition was not apparent even when PAR reached  $2800 \mu\text{E m}^{-2} \text{s}^{-1}$  (Fig. 2). Whilst observed  $R_d$  values were very similar for both growth forms the initial slopes of the observed data ( $\alpha$ ) were different ( $P < 0.05$ ) with the SB form having a steeper  $\alpha$  than the TN growth form.

#### 3.2. Total biomass

Total wet weight biomass increased over the course of the week and the SB forms were lighter than the TN forms ( $P < 0.001$ , Table 1). The RGR was significantly higher in the SB forms than in the TN forms ( $P < 0.005$ , Table 1).

#### 3.3. Petiole number and length and leaf size

The number of petioles did not differ significantly between the two growth forms with both forms having around 7 at the start of the week and 10 by the end (Table 1). The TN forms had significantly longer petioles and longer and wider leaves than the SB forms ( $P < 0.001$  in all cases). Over the course of the week biomass increased, however in the TN

Table 1

Comparison of traits of the short bulbous (SB) and tall non-bulbous (TN) growth forms of *E. crassipes*

Trait	Aspect	Short bulbous		Tall non-bulbous		Significance		
		Mean	S.E.	Mean	S.E.	SB between dates	TN between dates	SB vs. TN
PI-curve	$P_{\max}$	0.200	0.0286	0.159	0.0200			***
	$K_m$	499	276	568	262			***
	$R_d$	-0.0362	0.0201	-0.0425	0.0110			NS
	$\alpha$	0.0133	0.00226	0.00882	0.00116			*
Biomass	Start	120	13.5	236	10.4			***
	End	263	66.0	412	29.5	***	***	***
	Daily increase	20.3	1.90	25.1	3.30			NS
	RGR	0.114	0.00804	0.0781	0.00669			**
Petiole length	Start	11.9	0.485	31.6	1.20			***
	End	13.8	0.420	32.0	1.17	***	NS	***
Petiole number	Start	6.50	0.423	7.38	0.460			NS
	End	9.50	0.423	10.5	0.707	NS	NS	NS
Leaf width	Start	9.58	0.346	12.4	0.342			***
	End	9.55	0.228	13.1	0.207	NS	NS	***
Leaf length	Start	7.65	0.225	12.0	0.311			***
	End	7.94	0.203	12.4	0.234	NS	NS	***
Leaf lamina area	Start	64.7	3.45	130	5.71			***
	End	66.2	2.81	138	4.93	NS	NS	***
Stolon number	Start	0		0				
	End	4.63	0.375	3.12	0.398			*
	Daily increase	0.661	0.0536	0.446	0.0569			*

Units:  $P_{\max}$ ,  $R_d$  and  $K_m$  ( $\mu\text{mol CO}_2 \text{ g FW}^{-1} \text{ min}^{-1}$ );  $\alpha$  ( $\mu\text{mol CO}_2 \text{ g FW}^{-1} \text{ s}^{-1}/\mu\text{mol light m}^{-2} \text{ s}^{-1}$ ); biomass (g FW); relative growth rate ( $\text{day}^{-1}$ ); petiole length, leaf width and leaf length (cm); LLA ( $\text{cm}^2$ ). NS: not significant; blank: not applicable);  $n = 8$  for all 'traits' and growth forms except 'PI-curve' where  $n = 4$ ; all data to 3S.F.

\* Significance  $P < 0.05$ .

\*\* Significance  $P < 0.01$ .

\*\*\* Significance  $P < 0.001$ .

form this was seen only in terms of new growth as the morphology of the plants remained the same. Mean TN petiole length, leaf length, leaf width and leaf lamina area remained relatively constant throughout. The SB forms showed a slightly different response with the petiole length increasing significantly from 11.9 to 13.8 cm ( $P < 0.001$ , Table 1).

### 3.4. Stolon density

No stolons were present at the start of the experiment but they developed as the experiment progressed. Growth form had a significant effect on the number of stolons ( $P < 0.05$ , Table 1). SB plants produced more stolons than TN individuals with average stolon production being 0.66 and 0.45  $\text{plant}^{-1} \text{ day}^{-1}$ , respectively.

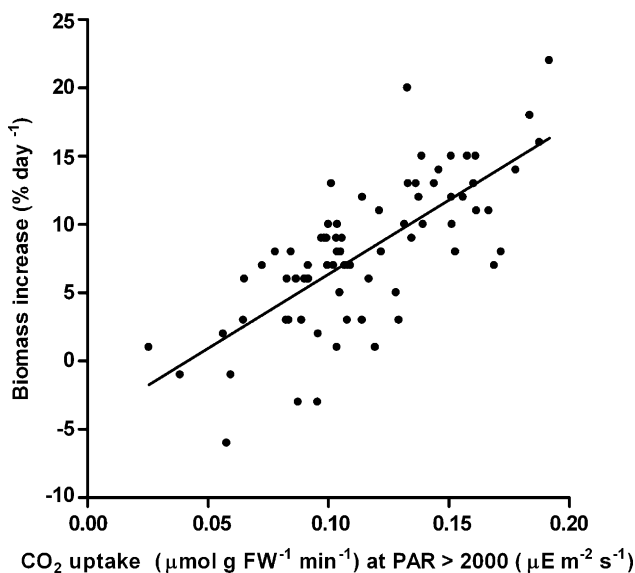


Fig. 3. Linear regression of daily biomass increase (% day<sup>-1</sup>) for two growth forms of water hyacinth grown over 18 days in various conditions against CO<sub>2</sub> assimilation at PAR >2000 μE m<sup>-2</sup> s<sup>-1</sup>.

### 3.5. CO<sub>2</sub> assimilation to predict future biomass

When data relating to CO<sub>2</sub> assimilation at PAR >2000 μE m<sup>-2</sup> s<sup>-1</sup> for individual plants ranging in growth form and condition were plotted against that plant's subsequent 3-day biomass increase (% day<sup>-1</sup>) a linear regression revealed a positive and significant trend ( $r^2 = 0.54$ ,  $P < 0.001$ , Fig. 3).

### 3.6. Measurements of daily and annual PAR cycles

Daily PAR reached its maximum of just under 3000 μE s<sup>-1</sup> m<sup>-2</sup> at 1 p.m. local standard time (LST). Either side of this zenith there was a sharp and steady reduction in PAR to around 1000 μE m<sup>-2</sup> s<sup>-1</sup> at 9 a.m. and 5 p.m. On average the light saturation required to achieve  $P_{\max}$  for both growth forms was approached at 2000 μE s<sup>-1</sup> m<sup>-2</sup>. This light level was typically available for 4 h a day between 11 a.m. and 3 p.m. LST. When the NCEP-DOE Reanalysis 2 project's modelled data were compared to the actual measurements for the same period, it was found that the average midday PAR measurement for the modelled data was  $2694 \pm 165$  μE m<sup>-2</sup> s<sup>-1</sup> whilst the measured midday average was  $2400 \pm 184$  μE m<sup>-2</sup> s<sup>-1</sup>. A  $t$ -test confirmed that the data were not significantly different ( $P > 0.05$ ). When the modelled data for the whole period from 1996 to 2001 were compared between years (Fig. 4) it was seen that 1997 had a significantly lower midday PAR than 1996, 1999 and 2000 ( $t$ -test  $P < 0.05$ ). During 1998 and 2001 midday PAR levels were not significantly different from one another or 1997 although 2001 had, on average, lower midday PAR levels than 2000 ( $t$ -test,  $P < 0.05$ ).

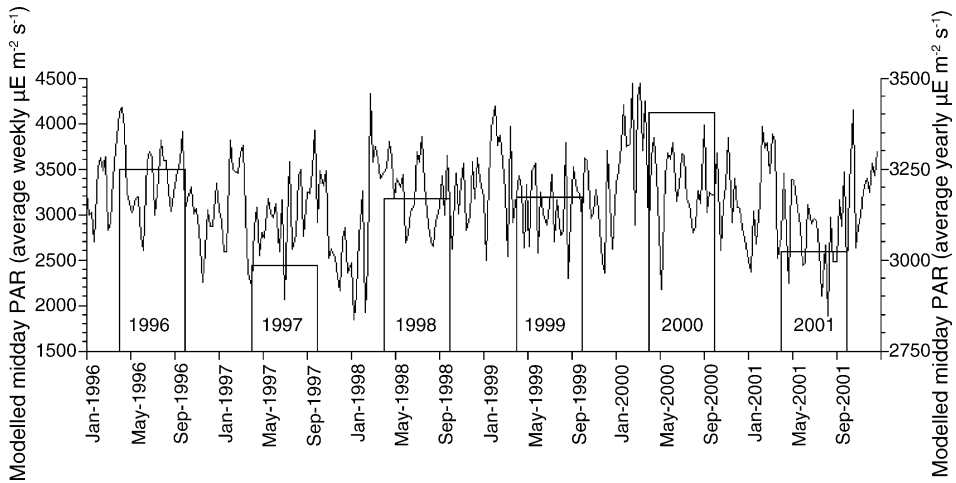


Fig. 4. Average weekly and yearly modelled midday PAR for Jinja, Uganda from 1996 to 2001.

As Jinja is close to the equator and thus the sunset and sunrise times fairly constant throughout the year, then irrespective of the peak PAR of a 'typical' day, the slope of the decline either side of the zenith to  $1000 \mu\text{E m}^{-2} \text{s}^{-1}$  is steep. It is therefore probable that a PAR of  $>2000 \mu\text{E m}^{-2} \text{s}^{-1}$  is typically experienced for, on average, 6 h a day.

#### 4. Discussion

The PI-curves differed significantly between the two forms. The SB form took up  $\text{CO}_2$  at a significantly faster rate than the TN form ( $P < 0.05$ ). The ascending slope ( $\alpha$ ) at light-limiting PAR is a function of both light-harvesting efficiency and photosynthetic energy conversion efficiency (Henley, 1993). However unfortunately photosynthetic rate was normalised for wet weight and not chlorophyll and as such differences between the growth forms could not be attributed to light harvesting versus photosynthetic energy conversion efficiencies. Nonetheless as  $\alpha$  was steeper in the SB forms these probably did use more light energy in electron transfer than the TN forms (Henley, 1993). Moreover,  $P_{\text{max}}$  was higher in the SB form than in the TN form ( $P < 0.05$ ). As such, SB forms apparently assimilated more carbon than the TN forms.

SB forms had a faster rate of clonal branching ( $P < 0.05$ ) than TN forms. Moreover, RGRs indicated that the SB forms increased their wet weight biomass more rapidly than TN forms ( $0.11 \text{ day}^{-1}$  as opposed to  $0.08 \text{ day}^{-1}$ ,  $P < 0.005$ ). In comparison to other aquatic plants neither form grew as fast as *Lemna gibba* which can have a RGR of around  $0.25 \text{ day}^{-1}$  (Körner et al., 2001) although both forms grew faster than *Elodea canadensis* whose RGR is approximately  $0.05 \text{ day}^{-1}$  in nutrient rich conditions (Madsen and Cedergreen, 2002). In absolute terms both mature SB and TN forms gained biomass at about the same rate ( $20\text{--}25 \text{ g day}^{-1}$ ). These results must have occurred because the ramets and/or stolons of the TN forms were larger/longer than those of the SB forms. Indeed whilst

the SB forms produced more stolons and ramets and increased their petiole length, TN forms produced fewer daughter plants and did not change morphologically. Elongation of the stolon is a common response to low light conditions as plants try to increase their potential to intercept light (Methy et al., 1990; Larcher, 1995). Therefore TN forms place more effort into producing support structures i.e. petioles which are extremely important structurally in dense stands (Pieterse, 1978; Methy and Roy, 1993). This agrees with work by Center and Spencer (1981) who suggested that water hyacinth plant form was related to the energy budget of the plant in terms of the relationship between energy assimilation and the metabolic cost of producing and maintaining increased structure.

Overall, our experiments suggest that the two dominant growth forms are plastic phenotypes that fill different ecological niches. The short, bulbous (SB) form is structurally more adept at floating, grows quickly and branches more rapidly, enhancing its capacity to colonise free habitat. The second, taller form, responds to self-shading and most likely expends more energy on structural vertical development, nutrient sequestering and sexual reproduction rather than horizontal expansion. The forms are however plastic (Table 1).

As a measure of potential growth and thus resurgence, instantaneous  $\text{CO}_2$  assimilation measurements were found to be both quick and relatively accurate with linear regression between  $\text{CO}_2$  assimilation and future wet weight biomass increase obtaining an  $r^2$  of 0.54 ( $P < 0.001$ ). However the actual light history of the incubated samples is not known and only  $P_{\text{max}}$  was measured rather than daily integral production. Therefore although a plant may have a high potential for photosynthetic activity the actual activity will be lower since it is restricted to the part of the day in which solar radiation is adequate.

As explained in the introduction the rapid disappearance of water hyacinth from Lake Victoria was unlikely to have been as a result of a reduction in nutrient availability. Moreover, the introduction of weevils occurred only 2 years prior to the massive reduction in plant biomass and alone were probably not responsible either. In another of Uganda's lakes, Lake Kyoga, weevils were introduced in 1993. Five years later in 1998 control of water hyacinth had been achieved. Of particular interest however is that the largest reduction in plant density was seen during the El Nino years of 1997/1998 (Ogwang and Molo, 1999). The effects of El Nino were given some credit for the plants demise but much of the credit was directed towards the washing out of water hyacinth from the system. Although this no doubt occurred and had an effect the increase in cloud cover and resulting decrease in light may also have had a significant role. Washout of hyacinth from Lake Victoria would not have been as effective because of the long water residence time in this lake.

Light on the other hand can limit maximum growth throughout the entire lake. The intensity of light required to reach  $P_{\text{max}}$  was approached at  $2000 \mu\text{E m}^{-2} \text{s}^{-1}$ . This is similar to that recorded by Larigauderie et al. (1986). In 2001 this level of light was typically available at Jinja for around 6 h a day. This window is however reduced during the two wet seasons when PAR may not rise above  $400 \mu\text{E m}^{-2} \text{s}^{-1}$  for several days (G. Silsbe, pers. comm.). Although this is not apparent from the modelled NCEP-DOE Reanalysis 2 project's data such a situation was recorded during October 2001 (G. Silsbe, pers. comm.). According to the predicted PI-curves these low levels of light will result in a  $\text{CO}_2$  assimilation of between 0.05 and  $0.02 \mu\text{mol g FW}^{-1} \text{min}^{-1}$  depending on the growth form (SB and TN, respectively). Such levels of  $\text{CO}_2$  assimilation will eventually lead to a decrease in plant biomass (Fig. 3).

A 5-year study of cloud cover over Lake Victoria found that, in the north east quadrant of Lake Victoria, the yearly average day time cloud cover was 59%. However during the two wet seasons (March–May and October–December, respectively) daytime cloud cover reaches 72% with an average of around 65%. The dry seasons have a cloud cover as low as 45% and an average of around 50% (Yin et al., 2000). During a typical El Nino event rainfall is expected to increase by about 15–25% over Lake Victoria. However during the 1997/1998 El Nino event unusual warming of the western equatorial Indian Ocean during 1997 resulted in a rainfall increase of 20–160% over Lake Victoria with highs being reached during the short rainy season (Birkett et al., 1999). These exceptional levels of rain and presumably higher level of cloud cover over Lake Victoria, will ultimately have reduced the level of PAR reaching the water surface, as seen from the modelled midday PAR levels (Fig. 4). Indeed between 1996 and 2001 the number of days where the modelled PAR levels do not rise above  $2000 \mu\text{E m}^{-2} \text{s}^{-1}$  is on average 27 for 1996, 1999 and 2000 however this almost doubles to an average of 45 days during 1997 and 1998. The cloudy dark weather caused by the 1997/1998 El Nino event will thus have had a large impact on the growth of water hyacinth.

The introduction of weevils into Lake Victoria has had an impact on water hyacinth populations but the wet and cloudy weather of 1997/1998 almost certainly played a major part by accelerating the decline through direct effects of reduced light on hyacinth growth throughout the lake basin. The return of water hyacinth will depend on the availability of light and nutrients and the abundance and stability of weevil populations. The light climate has improved since 1997/1998, the availability of nutrients is guaranteed especially in nutrient rich bays such as Inner Murchison Bay and weevil populations although present are likely unstable. The return of water hyacinth proliferation within Lake Victoria may therefore be just a matter of time. Indeed whilst the weed has remained sparse since the late 1990s, there are indications that a resurgence may be starting (IMPECCA, 2001; TNV, 2002).

## Acknowledgements

The authors would like to thank NSERC for funding as well as all at FIRRI, Uganda, for inviting us to stay and for providing us with much needed infrastructure and logistical support as well as allowing us access to historic data. In particular we would like to thank Dr. Richard Ogutu Ohwayo, Dr. Tim Twongo, Dr. John Balirwa, Dr. Rose Mugidde, Mr Hannington Ogutu, Musana, Linda and Emily. We also thank Mr. Scott Higgins for carrying out a very useful literature review concerning nutrient requirements of water hyacinth. Finally, the primary author would like to thank all his new found friends in Canada and Uganda for making his stays there so memorable.

## References

- Birkett, C., Murtugudde, R., Allan, T., 1999. Indian Ocean climate event brings floods to East Africa's lakes and Sudd marsh. *Geophys. Res. Lett.* 26, 1031–1034.

- Bootsma, H.A., Hecky, R.E., 1993. Conservation of the African great lakes: a limnological perspective. *Conserv. Biol.* 7, 644–656.
- Causton, D.R., Venus, J.C., 1981. *The Biometry of Plant Growth*. Edward Arnold Publishers Ltd., London.
- Center, T.D., Spencer, N.R., 1981. The phenology and growth of water hyacinth (*Eichhornia crassipes* (Mart.) Solms) in a eutrophic north-central Florida lake. *Aquat. Bot.* 10, 1–32.
- De Groot, P.J., 1993. Introduction and summary. In: Greathead, A., De Groot, P.J. (Eds.), *Control of Africa's Floating Water Weeds*. Commonwealth Science Council, Series no. CSC (93) AGR-18, Proceedings 295, pp. 1–9.
- Debusk, T.A., Dierberg, F.E., 1989. Effects of nutrient availability on water hyacinth standing crop and detritus deposition. *Hydrobiologia* 174, 151–159.
- Desougi, L.A., 1984. Mineral nutrient demands of the water hyacinth (*Eichhornia crassipes* (Mart.) Solms) in the White Nile. *Hydrobiologia* 110, 99–108.
- Hall, D.O., Scurlock, J.M.O., Bolhar-Nordenkamp, H.R., Leegood, R.C., Long, S.P., 1993. *Photosynthesis and Production in a Changing Environment: A Field and Laboratory Manual*. Chapman and Hall, London.
- Haller, W.T., Knipling, E.B., West, S.H., 1970. Phosphorus absorption by and distribution in water hyacinths. *Proc. Soil Sci. Soc. Florida* 30, 64–68.
- Hecky, R.E., 1993. Peter Kilham memorial lecture: the eutrophication of Lake Victoria. *Verh. Int. Ver. Theor. Ang. Limnol.* 25, 39–48.
- Henley, W.J., 1993. Measurement and interpretation of photosynthetic light response curves in algae in the context of photoinhibition and diel changes. *J. Phycol.* 29, 729–739.
- IMPECCA, 2001. Biological and integrated control of *Eichhornia crassipes*. *Water hyacinth news*, vol. 4. The IMPECCA Programme, CABI Bioscience, UK.
- Julien, M.H., Griffiths, M.W., Stanley, J.N., 2001. Biological control of water hyacinth 2. The moths *Niphograpta albiguttalis* and *Xubida infusellus*: biologies host ranges and rearing, releasing and monitoring techniques for biological control of *Eichhornia crassipes*. *ACIAR Monograph No. 79*.
- Julien, M.H., Griffiths, M.W., Wright, A.D., 1999. Biological control of water hyacinth. The weevils *Neochetina bruchi* and *N. eichhorniae*: biologies, host ranges and rearing, releasing and monitoring techniques for biological control of *Eichhornia crassipes*. *ACIAR Monograph No. 60*.
- Knipling, E.B., West, S.H., Haller, W.T., 1970. Growth characteristics, yield potential and nutritive content of water hyacinths. *Proc. Soil Sci. Soc. Florida* 30, 51–63.
- Körner, S., Das, S.K., Vermaat, J.E., Veenstra, S., 2001. The effect of pH variation at the ammonium/ammonia equilibrium in wastewater and its toxicity to *Lemna gibba*. *Aquat. Bot.* 71, 71–78.
- Langhans, R.W., Tibbitts, T.W., 1997. *Plant growth chamber handbook*. Iowa Agriculture and Home Economics Experiment Station Special Report No. 99, Agriculture Information Services, Iowa State University, Iowa.
- Larcher, W., 1995. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, third ed. Springer Verlag, New York.
- Larigauderie, A., Roy, J., Berger, A., 1986. Long term effects of high CO<sub>2</sub> concentration on photosynthesis of water hyacinth (*Eichhornia crassipes* (Mart.) Solms). *J. Exp. Bot.* 37, 1303–1312.
- Lederman, T.C., Tett, P., 1981. Problems in modelling the photosynthesis—light relationship for phytoplankton. *Bot. Mar.* 24, 125–134.
- Lindsey, K., Hirt, H.M., 1999. *Use Water Hyacinth—A Practical Handbook of Uses for the Water Hyacinth from Across the World*. Marianum Press, Kisubi, Uganda.
- LVEMP, 2000. Water hyacinth and other invasive weeds in Lake Victoria: A status report. Lake Victoria Environmental Management Project, Fisheries Resources and Research Institute, Jinja, Uganda.
- LVEMP, 2001. Water hyacinth control component. In: *First Lake Victoria Environmental Management Programme (LVEMP) Regional Scientific Conference*. Kisumu, Kenya.
- Madsen, T.V., Cedergreen, N., 2002. Sources of nutrients to rooted submerged macrophytes growing in a nutrient-rich stream. *Freshwater Biol.* 74, 283–291.
- Masifwa, F.W., Twongo, T., Denny, P., 2001. The impact of water hyacinth, *Eichhornia crassipes* (Mart.) Solms on the abundance and diversity of aquatic macroinvertebrates along the shores of northern Lake Victoria Uganda. *Hydrobiologia* 452, 79–88.
- Matagi, S.V., 2002. Some issues of environmental concern in Kampala, the capital city of Uganda. *Environ. Monit. Assess.* 77, 121–138.

- Methy, M., Roy, J., 1993. Morphogenetic changes induced by a low red: far-red ratio and their growth consequences in water hyacinth (*Eichhornia crassipes*). J. Exp. Bot. 44, 1275–1280.
- Methy, M., Alpert, P., Roy, J., 1990. Effects of light quality and quantity on growth of the clonal plant *Eichhornia crassipes*. Oecologia 84, 265–271.
- Mitchell, D.S., 1985. African aquatic weeds and their management. In: Denny, P. (Ed.), The Ecology and Management of African Wetland Vegetation. Dr. W. Junk Publishers, pp. 177–202.
- Ochiel, G.R.S., Mailu, A.M., Gitonga, W., Njoka, S.W., 1999. Biological control of water hyacinth on Lake Victoria Kenya. In: Hill, M.P., Julien, M.H., Center, T.D. (Eds.), Proceedings of the First IOBC Global Working Group Meeting for the Biological and Integrated Control of Water Hyacinth, Weeds Research Division, ARC, South Africa, pp. 115–118.
- Ogwang, J.A., Molo, R., 1999. Impact studies on *Neochetina bruchi* and *Neochetina eichhorniae* in Lake Kyoga Uganda. In: Hill, M.P., Julien, M.H., Center, T.D. (Eds.), Proceedings of the First IOBC Global Working Group Meeting for the Biological and Integrated Control of Water Hyacinth, Weeds Research Division, ARC, South Africa, pp. 10–13.
- Pieterse, A.H., 1978. The water hyacinth (*Eichhornia crassipes*)—a review. Abst. Trop. Agric. 4, 9–42.
- Reddy, K.R., Agami, M., Tucker, J.C., 1990. Influence of phosphorus on growth and nutrient storage by water hyacinth (*Eichhornia crassipes* (Mart.) Solms) plants. Aquat. Bot. 37, 355–365.
- Salmah, M.R., Mansor, M., Ahmad, A.B., 1991. A preliminary study of the distribution of *Neochetina eichhorniae*—a possible biological agent for water hyacinth in Kerian District Perak. In: Bidin, A.A. (Ed.), Proceeding Asas dan Gunaan dalam Biologi, UKM, Malaysia, pp. 24–28.
- TNV, 2002. Hyacinth back with vengeance. The New Vision, October 8th, 2002. Uganda.
- Twongo, T., Balirwa, J.S., 1995. The water hyacinth problem and the biological control option in the highland lake region of the upper Nile basin—Uganda's experience. The Nile 2002 conference: Comprehensive water resources development of the Nile basin—Taking Off. Arusha, Tanzania Arusha, Tanzania.
- Twongo, T., Bugenyi, F.W.B., Wanda, F., 1995. The potential for further proliferation of water hyacinth in Lakes Victoria Kyoga and Kwania and some urgent aspects for research Afr. J. Trop. Hydrobiol. Fish. 6, 1–10.
- Watson, M.A., Carrier, J.C., Cook, G.S., 1982. Effect of exogenously supplied gibberelic acid (GA<sub>3</sub>) on pattern of water hyacinth development. Aquat. Bot. 13, 57–68.
- Willoughby, N.G., Watson, I.G., Lauer, S., Grant, I.F., 1993. An investigation into the effects of water hyacinth on the biodiversity and abundance of fish and invertebrates in Lake Victoria, Uganda. NRI Project no. 10066/A0328.
- Wright, A.D., Purcell, M.F., 1995. *Eichhornia crassipes* (Mart.) Solms-Laubach. In: Groves, R.H., Shepherd, R.C.H., Richardson, R.G. (Eds.), The Biology of Australian Weeds, vol. 1. R.G and F.J. Richardson Publications, Melbourne, pp. 111–122.
- Yin, X., Nicholson, S.E., Ba, M.B., 2000. On the diurnal cycle of cloudiness over Lake Victoria and its influence on evaporation from the lake. Hydrol. Sci. 45, 407–424.
- Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall International Inc., New Jersey.