

Full Length Research Paper

Impact of interspecific competition by compatriot aquatic weeds on water hyacinth *Eichhornia crassipes* (Martius) Solms growth and development in the Kagera River

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Accepted 17 March, 2011

The phenotype of a plant is strongly influenced by the presence of neighbouring plants often resulting into change in growth and development. We have demonstrated to our knowledge for the first time, the influence of three aquatic weed species (*Commelina* sp., *Justicia* sp. and *Vossia cuspidata*) on growth and development of water hyacinth (*Eichhornia crassipes*). We found that *Commelina* sp., *Justicia* sp. and *V. cuspidata* significantly ($P < 0.001$) suppressed water hyacinth total fresh weight when growing together both in the Kagera River and greenhouse. *Justicia* sp. gave the highest (51%) water hyacinth fresh weight reduction when compared to fresh weight in pure stand probably due to competition effect. In the Kagera River but not greenhouse, water hyacinth plants were significantly taller ($F_{(4,1371)} = 150.53$, $P < 0.001$) in pure stands than when growing in mixtures. *V. cuspidata* strongly suppressed water hyacinth plant height although water hyacinth compensated by producing elevated number of ramets (daughter plants). In greenhouse environment, the number of ramets per plant was higher in mixtures than in pure water hyacinth treatment. Correlation analysis revealed a strong significant negative relationship between plant height and number of ramets. Competition for space and resources was suggested to be the major influential factor as water hyacinth in pure stands tended to have higher density and total biomass per unit area than when grown in mixtures. Analysis of water hyacinth ratios to other aquatic weeds showed a significant effect on water hyacinth growth and development in terms of fresh weight, plant height, leaves per plant and ramets. These data show that neighbouring aquatic weeds are important component in the regulation of water hyacinth growth and development in the aquatic ecosystem.

Key words: *Commelina* sp., *Justicia* sp., Kagera river, water hyacinth.

INTRODUCTION

Eichhornia crassipes (Martius) Solms is often regarded as the most troublesome aquatic weed in the world (Holm et al., 1991; Lu et al., 2007). *E. crassipes* possesses specialized growth habits, physiological characteristics, and reproductive strategies that allow for rapid growth and expansion in freshwater environments and has spread rapidly throughout the tropics and subtropics

(Pushpa and John, 2010). It has become a serious weed in freshwater habitats in rivers, lakes and reservoirs in tropical and warm temperate areas worldwide, where it displaces native aquatic plant and animal communities (Navarro and Phiri, 2001). *E. crassipes* forms large, free-floating, monospecific mats that compete with other aquatic species for light, nutrients and oxygen (Pushpa and John, 2010). Water hyacinth floating mats reduce dissolved oxygen levels and light and significantly alter invertebrate and vertebrate communities. As biomass from mats decomposes, organic input to sediments

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increases dramatically (Gopal, 1987; Jafari, 2010). *E. crassipes* grows in shallow temporary ponds, wetlands and marshes, sluggish flowing waters and large lakes, reservoirs, and rivers (Center et al., 2005). Plants can tolerate extremes of water level fluctuation and seasonal variations in flow velocity, and extremes of nutrient availability, pH, temperature and toxic substances (Gopal, 1987; Pushpa and John 2010). *E. crassipes* forms dense, monospecific, free-floating mats in still to slow moving waters. Winds or currents may disperse these mats. During mat development, plants allocate most production to root biomass with little increase in average plant size. As plants mature, they increase in average biomass and production of daughter plants with reduced allocation to roots (Center et al., 2005). At peak density, daughter-plant production is reduced but average plant size continues to increase, resulting in plant mortality (Madsen, 1993; Center et al., 2005). Young plants in low-density mats form a great deal of float tissue. In higher density mats, the proportion of float tissue decreases as surrounding plants support each other (Sculthorpe, 1985; Center et al., 2005). In existing mats, plants reallocate biomass to the emergent shoots following winter. In early spring, ramet production increase, resulting in high leaf densities and high foliar height diversity (Center et al., 2005). Some smaller plants are lost, resulting in lower absolute density (Center and Spencer 1981; Center et al., 2005).

The spatial arrangements of the plants in herbaceous communities are seldom random on the scales at which competitive interactions are likely to occur (Cain et al., 1995; Keddy, 2001). Neighbourhood models relate the performance of individual plants to the competitors surrounding them, by relating the growth, seed-production, or survival of target plant to the number, proximity, and sometimes size, of competitors (Mack and Harper, 1977; Weiner, 1984; Center et al., 2005). Kagera River, which originates in the highlands of northern Rwanda and discharge into the Lake Victoria in Northwestern Tanzania, is densely colonized by aquatic water hyacinth. Water hyacinth may be found in association with a variety of other deep water or free-floating aquatic plants. In the this river, water hyacinth is commonly found growing with macrophytes, especially hippograss *Vossia cupsidata*, *Justicia* sp., *Commelina* sp. and papyrus, *Cyperus papyrus* (Ndunguru et al., 2000). This study was initiated with an objective of finding out if at all there was an influence of the neighbouring aquatic plants on the growth and development of water hyacinth in the Kagera River.

MATERIALS AND METHODS

The effect of compatriot aquatic weed species, their ratios and their interaction on the growth performance of water hyacinth was conducted in the Kagera River (natural habitat) and in the greenhouse (at Kyaka station) in Tanzania between 2005 and 2006.

Study species

Three aquatic weed species commonly growing and fringing the open water of the Kagera River in mixture with water hyacinth (*E. crassipes*) was chosen for this study. Hippograss, *V. cupsidata* (Roxb.) Griff. is a characteristic grass of the stump areas African flood plains and forms dense, semi floating, beds and established mats persist for an indefinite period under less than optimum period (Naror and Phiri, 2001). Plants usually grow in water up to 1 m deep at the margins of water bodies and fringes the open waters, develop large number of roots and rootless from the nodes of the spongy stem (Bor, 1960; Pushpa and John, 2010). *Justicia* sp. grows in shallow waters, margins and beds of streams, marshy shores and ponds, lakes and ditches. It can grow to a depth of 1.3 m (Carter and Grace, 1986). Once established, plants spread by rhizomes and often form large colonies and form roots at the nodes and plants can ascend above to about 1 m tall (Penfound, 1940; Carter and Grace, 1986).

Description of study site

Kagera River that originates from the highlands of Burundi and Rwanda flows into the Lake Victoria on the northwestern side of Tanzania. The average width of Kagera River is between 40 and 70 m with a total depth of 3 to 6 m on average. Water temperature is between 20 to 22°C (Rutagemwa, 2001). Large part of Kagera River consists of scattered clumps of papyrus and *Vossia* fringing both banks of the river. Water hyacinth infestation in the Kagera River is heavy usually interspersed with clumps of waterweeds such as *Vossia* sp., *Commelina* sp., *Justicia* sp., papyrus and others fringing the river banks. Occasionally, pure water hyacinth 2 to 5 m wide fringes several other locations of the river and there is active flow of water hyacinth down the river. Water hyacinth in the Kagera River was reported for the first time in the 1980s probably originating in the upper reaches of the river probably in Rwanda (Labrada, 1996). Despite introduction of *Neochetina* weevil for water hyacinth control in the Kagera River, several impact assessment surveys revealed virtually no weevil establishment. It was hypothesized that the only stress-induced on fringing water hyacinth is that resulting from competition by other neighbouring aquatic weed species for resources like food, light, water, space for growth and reproduction.

Field site sampling

Wooden frame measuring (1 × 1 m) was used for sampling by placing it on the weed mats. To avoid confounding edge effects, sampling was done by throwing the frame into weed mats at the centre to define 1 m² sampling units in July 2005. Only a weed mixture containing at least 20% of the competing species (*V. cupsidata*, *Justicia* sp. and *Commelina* sp) was chosen for sampling. The weed mixtures sampled were: (1) Water hyacinth + *Vossia cupsidata*; (2) Water hyacinth + *Justicia* sp.; (3) Water hyacinth + *Commelina* sp., (4) Water hyacinth + *V. cupsidata* + *Justicia* sp. + *Commelina* sp., and (v) Water hyacinth alone (Figure 1). For each weed mixture, a total number of water hyacinth plants and the other species in the frame were counted. Then 10 water hyacinth plants were randomly removed from each frame and individual plants weighed after draining the water briefly to obtained total plant fresh weight using a spring balance. Plant height of water hyacinth was measured using a special calibrated ruler from the base of the plant to the apical tip of the tallest leaf. In addition, number of leaves and ramets (stoloniferous daughter plant) per plant was counted and recorded. For each weed mixture, a total of 32 sampling points (320 plants) selected randomly on both sides of the Kagera River were sampled using a motorized 15' fibre glass

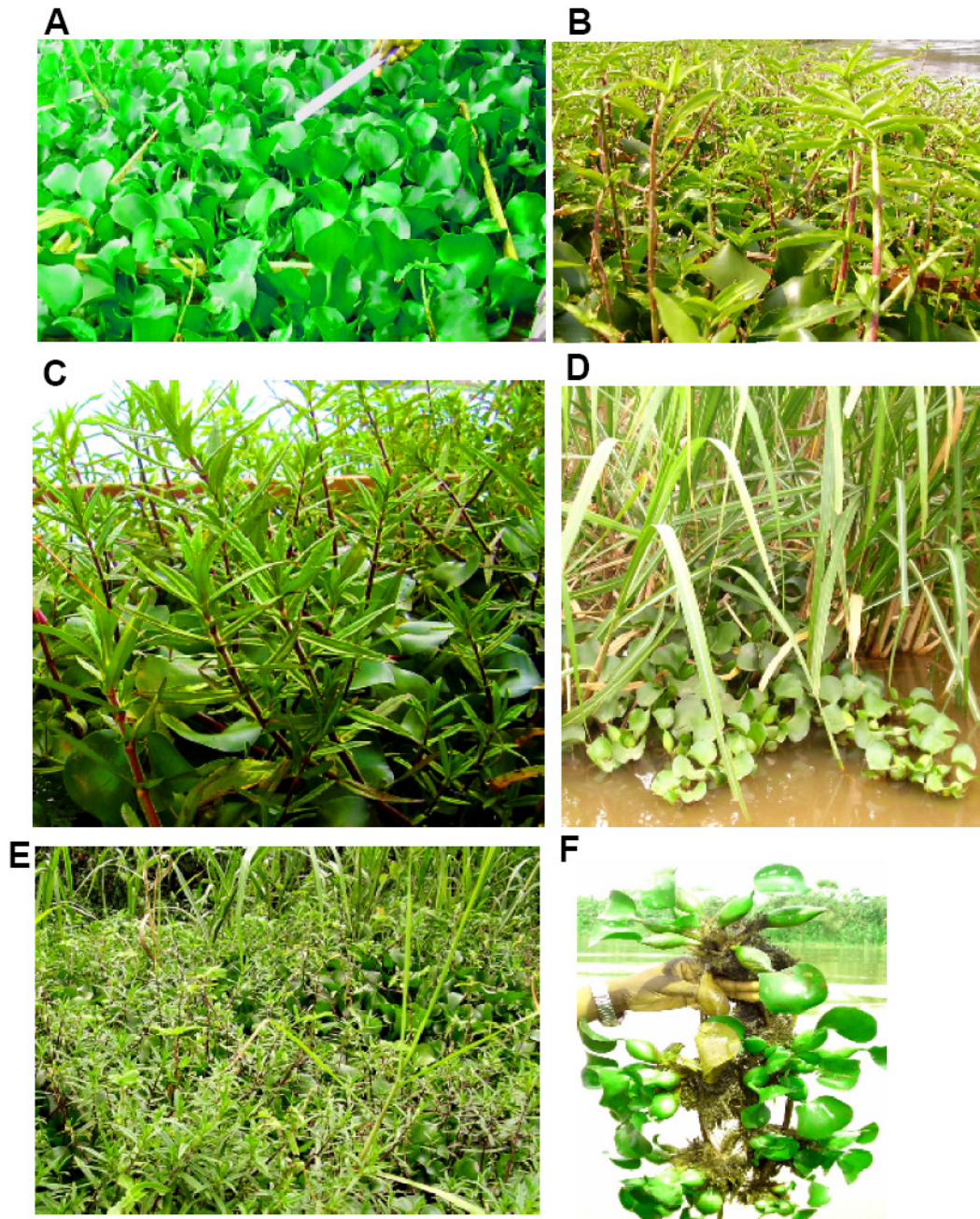


Figure 1. Different water hyacinth/aquatic weed mixtures sampled in the Kagera River (A to E): (A) Pure water hyacinth stand; (B) Water hyacinth + *Commelina* sp.; (C) Water hyacinth + *Justicia* sp.; (D) Water hyacinth + *V. cuspudata*; (E) Water hyacinth + *Commelina* sp. + *Justicia* sp. + *V. cuspudata*, and (F) Elevated number of water hyacinth ramets in response to light competition with *V. cuspudata*.

boat following a zigzag pattern. Distance between sampling point was between 100 to 150 m. A similar sampling was conducted in 32 points comprising of pure water hyacinth stand to serve as control treatment.

Greenhouse experiment

Young water hyacinth (c. 15 cm long) collected from the Kagera River were planted in plastic containers (53 cm diameter) filled with

water 50 L from the same Kagera River. Water hyacinth was grown in monoculture, and in combination (i) Water hyacinth + *V. cuspudata*, (ii) Water hyacinth + *Justicia* sp. (iii) Water hyacinth + *Commelina* sp. and (iv) Water hyacinth + *V. cuspudata* + *Justicia* sp. + *Commelina* sp. Both *Commelina* and *Justicia* sp. plants used for this experiment were young with at least 5 nodes long. The size of *V. cuspudata* ranged from 15 to 20 cm long. To avoid intra species competition for water hyacinth, only a single plant was placed in each container. The number of other weed species introduced per container was five and there were four replicates for each

Table 1. Water hyacinth growth characteristics sampled when growing with different aquatic weed combinations in the Kagera River.

Weed combination	Fresh weight (g)	Plant height(cm)	Leaves/plant	Plant density/m ²	Total biomass/ m ²	Ramets/plant
Water hyacinth	652.7 ± 56.9 ^c	38.4 ± 0.6 ^e	9.3 ± 7 ^b	51.7 ± 3.4 ^c	30.98 ± 4.21 ^c	1.3 ± 6 ^b
Water hyacinth + <i>Commelina</i> sp	452.2 ± 12.7 ^b	33.7 ± 0.6 ^d	9 ± 7 ^{ab}	38.9 ± 2.7 ^b	16.09 ± 1.27 ^b	0.8 ± 5 ^a
Water hyacinth + <i>Justicia</i> sp	320.2 ± 9.6 ^a	26.5 ± 0.9 ^b	8.6 ± 0.27 ^a	37.9 ± 2.3 ^b	12.3 ± 1.01 ^a	0.8 ± 5.5 ^a
Water hyacinth + Hippogloss	332.7 ± 27 ^a	21.8 ± 0.5 ^a	8.6 ± 7 ^a	26 ± 2.5 ^a	7.77 ± 0.82 ^a	1.2 ± 7.5 ^b
Water hyacinth + <i>Commelina</i> sp + <i>Justicia</i> sp + Hippogloss (<i>Vossia cupsidata</i>)	342 ± 11.7 ^a	29.2 ± 0.6 ^c	9 ± 0.28 ^{ab}	28.3 ± 2.7 ^a	9.50 ± 1.21 ^a	0.73 ± 5.4

^aMeans (± SE) followed by the same letters are not statistically significant different at 0.05.

Table 2. Variations of water hyacinth growth parameters at different aquatic weed combination in controlled on-station experiment (N = 24).

Weed combination	Fresh weight (g)	Plant height(cm)	Leaves/plant	Plants/container	Ramets/plant
Water hyacinth	180.8 ± 8.52 ^c	8.69 ± 0.42 ^a	10.54 ± 0.38 ^a	1.2 ± 8.46 ^a	0.21 ± 8.46 ^a
Water hyacinth + <i>Commelina</i> sp.	129.08 ± 9.26 ^{bc}	8.8 ± 0.6 ^a	10.7 ± 0.46 ^a	1.5 ± 0.15 ^{ab}	0.5 ± 0.15 ^a
Water hyacinth + <i>Justicia</i> sp.	151.66 ± 9.56 ^c	8.88 ± 0.43 ^a	9.9 ± 0.38 ^a	1.87 ± 0.14 ^{bc}	0.87 ± 0.13 ^{bc}
Water hyacinth + Hippogloss	98.19 ± 4.57 ^a	8.24 ± 0.29 ^a	9.75 ± 0.46 ^a	1.37 ± 0.1 ^a	0.37 ± 0.1 ^a

treatment. Plants were left to grow in the pots for a period of 4 months (July to October 2005). The containers were randomly arranged on four lines on the floor in the greenhouse and re-randomized twice three times in the course of the experiment. Water hyacinth growth parameters similar to that collected in a typical natural population (in the Kagera River) were taken in the date of experimental initiation and onward every after 2 weeks for a period of three months. Plants were not fertilized.

Data analysis

Averages taken from all plants examined in each sampling unit were used in all analysis (n = 32 units per weed mixture). Per unit biomass of water hyacinth in the field samples was calculated by multiplying mean fresh weight by its density per unit area. Pearson correlations were used to test for associations between fresh weight and plant height, life leaves per plant, and ramets. The effect of weed mixture on water hyacinth growth and development

and their mixture ratios for field samples were assessed with weed mixture as a fixed effect in analysis of variance (ANOVA) and Duncan mean comparison (P < 0.05) using SPSS 10.0 statistical package. For greenhouse experiment, effect of weed combination, time and its interaction were assessed with weed combination as main factor using a multivariate analysis of variance GLM (SPSS 10.0) and Duncan mean comparisons (P < 0.05). Effect of weed mixtures on per unit area biomass of water hyacinth was assessed using one-way ANOVA.

RESULTS

Total plant fresh weight

Total water hyacinth fresh weight was significantly higher ($F_{(4,1371)} = 23.50$, $P < 0.001$) in water hyacinth growing alone than when growing with other aquatic weeds in the natural habitat of the

Kagera River (Table 1). The lowest fresh weight (320.2 ± 9.6 g (g)) was recorded for water hyacinth growing with *Justicia* sp. *Commelina* sp. had less negative impact on water hyacinth fresh weight than other aquatic weed species (Table 1). As observed in the natural aquatic habitat in the Kagera River, water hyacinth grown alone in green house displayed significantly ($F_{(4,1371)}$, $P < 0.001$) more fresh weight than when grown in mixture (Table 2). Fresh weight was the lowest (98.19 ± 4.57 g) for water hyacinth plants grown with *V.cupsidata* compared to control (water hyacinth grown alone) (Table 2).

Water hyacinth plant height

For the study in the Kagera River, statistical

Table 3. Multivariate analysis of variance describing significance of factors weed combination (WC), and time (T) on water, hyacinth growth parameters.

Source	Dependent variable	df	Mean square	F	Sig.
WC	Fresh weight (g)	4	26510.554	13.899	0.000 S
	Plant height (cm)	4	2.993	0.707	0.591 NS
	Number of leaves per plant	4	4.096	0.8	0.528 NS
	Ramets per plant	4	4.221	8.268	0.000 S
	Number of plants/container	4	4.221	8.268	0.000 S
	Error			115	
	Total			119	
T	Fresh weight (g)	5	3586.212	1.330	0.257 NS
	Plant height (cm)	5	24.774	7.479	0.000 S
	Number of leaves/plant	5	80.073	44.507	0.000 S
	Ramets/plant	5	2.088	3.654	0.004 S
	Number of plants/container	5	2.088	3.654	0.004 S
	Error			114	
	Total			119	
T × WC	Fresh weight (g)	20	743.352	0.359	0.994 NS
	Plant height (cm)	20	4.167	1.328	0.182 NS
	Number of leaves/plant	20	1.888	1.124	0.341 NS
	Ramets/plant	20	0.276	0.581	0.917 NS
	Number of plants/container	20	0.276	0.581	0.917 NS
	Error			90	
	Corrected total			119	

analysis showed that water hyacinth plants growing alone (without competition) were significantly ($F_{(4,1371)} = 150.53$, $P < 0.001$) taller than those growing in association with other aquatic weeds (Table 1). Hippograss (*V. cupsidata*) strongly suppressed growth of water hyacinth as indicated by a reduction in plant height from 39.4 ± 0.6 cm in pure stand to 21.8 ± 0.5 cm in mixture with *V. cupsidata* (Table 1). In controlled environment in the green house experiment, none of the aquatic weed species had a significant competitive effect on the plant height of water hyacinth (Table 3). Similarly, there was no significant effect of other aquatic weeds on water hyacinth number of leaves per plant in both greenhouse and the River Kagera (Table 3).

Impact of neighbouring aquatic weeds on water hyacinth plant density and biomass

In the analysis of the full data set obtained from the Kagera River, water hyacinth plant density was significantly higher ($F_{(4,115)} = 13.32$, $P < 0.001$) when growing alone than in mixture (Table 1). Compared to the control treatment (pure water hyacinth stand), water hyacinth growing together with hippograss (*V. cupsidata*) showed the least plant density (26.03 ± 2.5

plants/m²) about 49.6% reduction (Table 1). For water hyacinth in pure stand, plant density ranged from 25 to 102 plants/m² while those in mixture with *V. cupsidata*, *Justicia* sp. or *Commelina* sp. ranged only from 5 to 75 plants/m². Mean per unit area water hyacinth biomass varied significantly between weed mixtures ($F_{(4,154)} = 18.587$, $P < 0.001$). The highest biomass was recorded for pure water hyacinth (30.98 ± 4.21 Kg/m²) on average and the lowest (7.7 ± 0.82 Kg/m²) for water hyacinth + *Vossia cupsidata* mixture, an almost 75% reduction (Table 1). For greenhouse experiment, number of water hyacinth plants per container significantly changed with weed combination (Table 3). When water hyacinth was grown alone, the number of water hyacinth plants averaged 1.2 ± 8.46 per container. In the overall greenhouse experiment, the highest water hyacinth plant number per container was observed in water hyacinth + *Commelina* sp. + *Justicia* sp. + *V. cupsidata* combination and ranged from one to four (Table 1).

Impact of neighbouring aquatic weeds on water hyacinth ramet production

Water hyacinth reproduces mainly asexually by means of stoloniferous ramets produced. To investigate the

Table 4. Pearson correlation analysis of water hyacinth growth parameters for on-station experiment after growing with other aquatic weeds.

Field study	FW	Ph	Lp	R ^a
FW	1.000			
Ph	0.261**	1.000		
Lp	0.065*	0.101**	1.000	
RM	0.178**	-0.053*	0.059*	1.000
Greenhouse study				
FW	1.000			
Ph	0.161	1.000		
LP	-0.047	-0.120	1.000	
RM	0.191*	-0.229*	0.255**	1.000

** Correlation is significant at the 0.01 level (2-tailed); *Correlation is significant at the 0.05 level (2-tailed); ^aFW = fresh weight (gm); Ph = plant height (cm); LP = Leaves/plant; RM = ramets/plant.

interspecific competition effect of neighbouring aquatic weeds on water hyacinth's ramet production in the Kagera River, the number of ramets for individual water hyacinth plant in each weed combination was counted. The number of water hyacinth ramets was significantly lower ($P < 0.001$) in weed mixtures than in pure stand (Table 3) except in water hyacinth + *V. cuspidata* weed combination. In this treatment, number of ramet was higher (1.2 ± 7.5 ramets/plant) by 37% than in other mixtures. The maximum number of ramets per plant in this weed mixture reached four per plant. The least number of ramets per plant on average was recorded for water hyacinth + *Commelina* sp. + *Justicia* sp. + *V. cuspidata* combination (Table 1). In the greenhouse experiment, number of ramets significantly varied between treatments (Table 3). Number of ramets per plant was significantly higher in mixtures than in water hyacinth monoculture. Water hyacinth + *Commelina* sp. + *Justicia* sp. + *V. cuspidata* combination gave the highest number of ramets (1.25 ± 0.2 ramets/plant) on average followed by water hyacinth + *Justicia* sp. combination (Table 2).

Relationship between water hyacinth growth components

When Pearson correlation analysis was performed on Kagera River sample data, there was a negative significant relationship between plant height and number of ramets (Table 4). A similar relationship was observed for the greenhouse experiment. Plants with high fresh weight tended to have significantly large number of ramets both in the field and greenhouse (Table 4). In addition, they appeared to be taller in the natural habitat than in greenhouse condition. There was no correlation between mean water hyacinth fresh weight and plant height in the greenhouse experiment.

Changes in water hyacinth plant growth parameters over time in the greenhouse

The water hyacinth plant growth parameters (plant height, number of leaves per plant, ramets per plant, and number of plants per container) significantly changed with time ($P < 0.001$) (Table 3). Water hyacinth plant fresh weight did not significantly change with time ($P > 0.05$) and there was no interaction between time and weed combination factors. After a period, water hyacinth plant height significantly decreased from 10.7 ± 0.46 cm at T0 to 8.17 ± 0.46 cm at T5 (Figure 2). However, mean number of water hyacinth plants in the containers significantly increased from one plant at T0 to 1.85 ± 0.19 plants at T5 (Figure 3). Number of water hyacinth plant ramets also significantly increased over time in such that by T5 (3 months), there were 0.85 ± 0.19 ramets/plant on average as compared to zero at T0 (beginning of the experiment).

Effect of ratios of water hyacinth to competitors on water hyacinth growth performance

To avoid genetic influence of different neighbour plant species on the results, the impact of water hyacinth to other aquatic weed ratio on water hyacinth growth and development was examined separately. The ratio was calculated by dividing the total number of water hyacinth plants per square meter by total number of other aquatic weed in the mixture. High value indicates that the number of the other species exceeds that of water hyacinth in the mixture and vice versa when the number is low. For Water hyacinth + *Commelina* sp. weed mixture, all the water hyacinth plant growth parameters examined (fresh weight, plant height, number of leaves and ramets) effect of water hyacinth to *Commelina* sp. ratio on water hyacinth growth and development was significant, $F_{(31, 281)}$

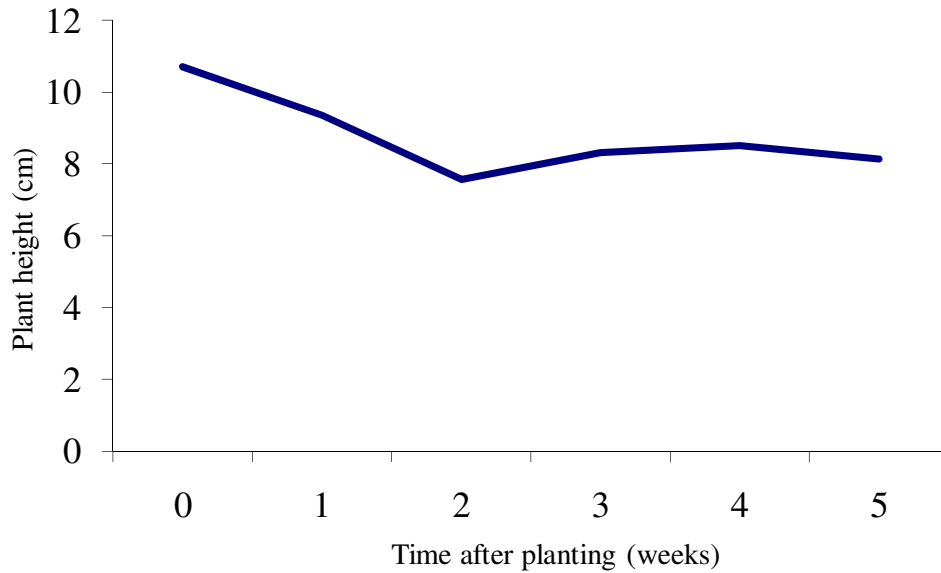


Figure 2. Changes in water hyacinth plant height with time in greenhouse experiment grown with different aquatic weed combination.

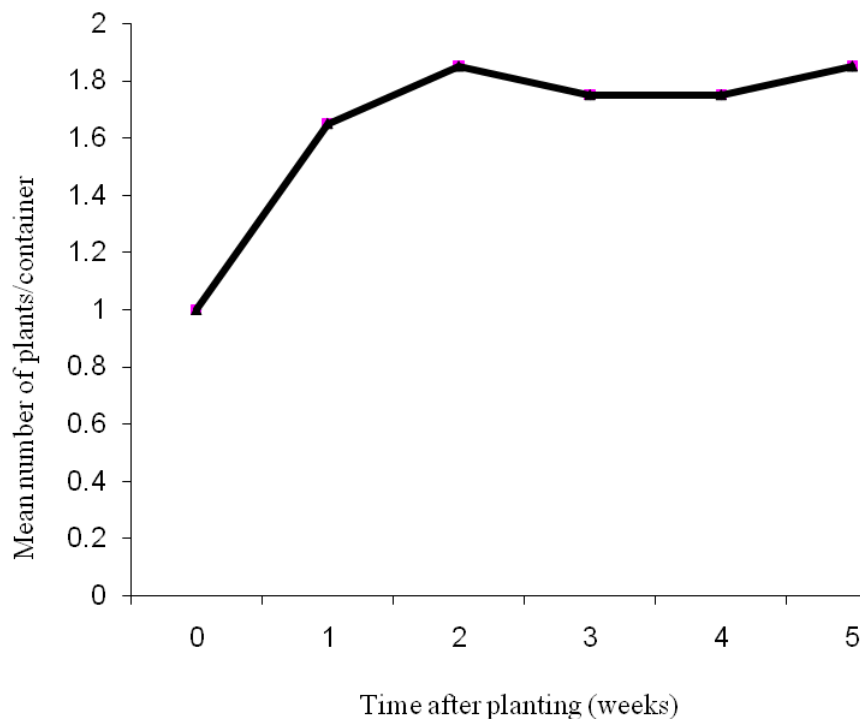


Figure 3. Changes in water hyacinth number of plants per container during the period of the experiment in the greenhouse.

= 4.00, $P < 0.001$ for fresh weight, $F_{(31, 281)} = 12.776$, $P < 0.001$) for plant height, $F_{(31, 281)} = 2.646$, $P < 0.001$ for number of leaves per plant and $F_{(31, 281)} = 3.385$, $P < 0.001$ for number of ramets per plant. Changes in water hyacinth total plant fresh weight in response to water

hyacinth:*Commelina* sp ratio is presented in Figure 4a. With a few exceptions, as expected, low ratio values (when *Commelina* sp. density exceeded that of water hyacinth in the mixture) were associated with declining fresh weight. Similarly, high ratio values (example 1.45)

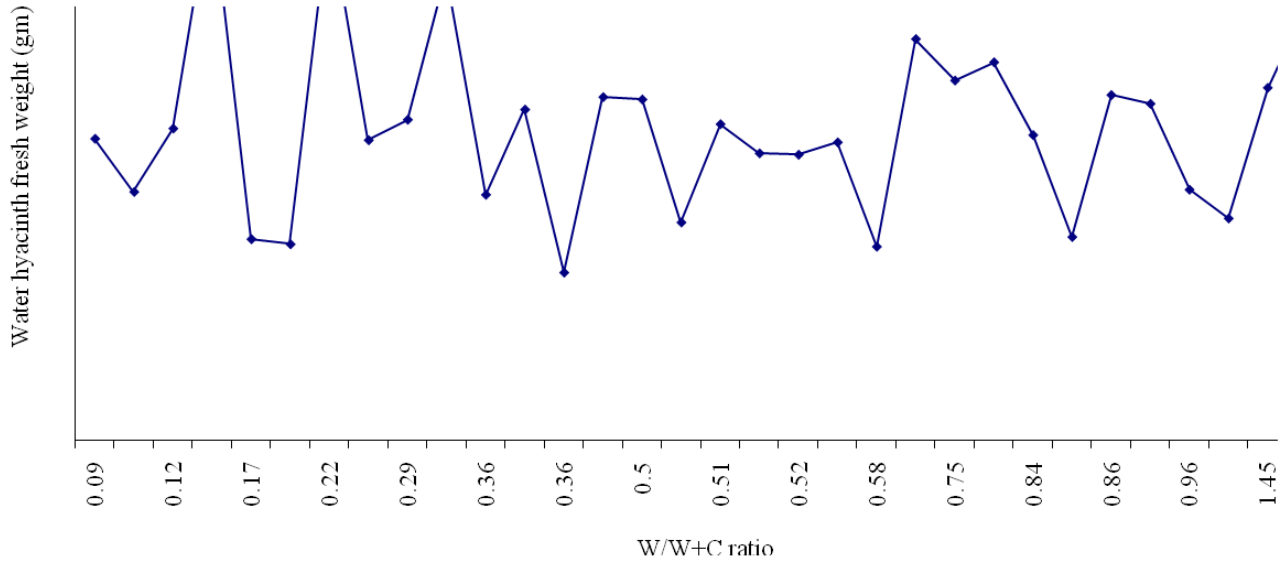


Figure 4a. Changes in water hyacinth fresh weight under water hyacinth (W) and *Commelina* sp. (C) weed mixture at different w/c ratios.

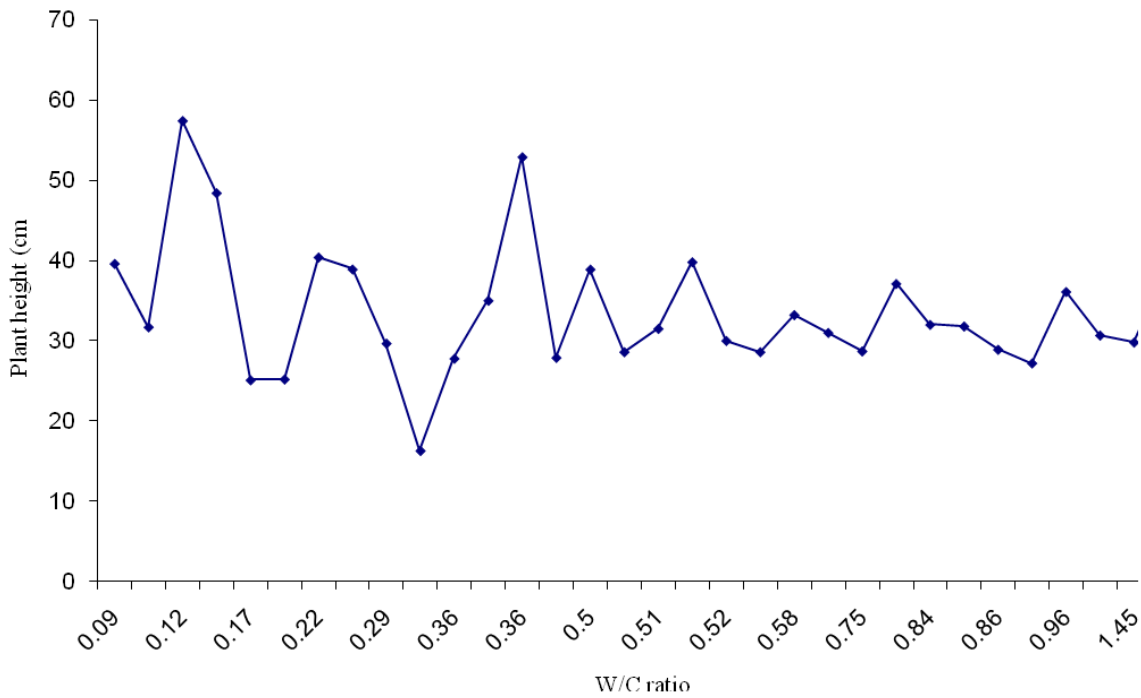


Figure 4b. Changes in water hyacinth plant height under water hyacinth (W) and *Commelina* sp. (C) weed mixture at different W/C ratio.

were associated with high fresh weight because of decreased density of *Commelina* sp. in the mixture, which imparted minimum competition effect on water hyacinth fresh weight (Figure 4a). In terms of water hyacinth plant height (Figure 4b) at low ratios (0.09 to 0.5), there was high water hyacinth mean plant height

while at higher ratios (0.51 to 1.45), there was a relatively low water hyacinth plant height uniformly.

For water hyacinth + *Justicia* sp mixture, the ratio of water hyacinth (W) to *Justicia* sp. (J) had a significant effect on water hyacinth growth performance. Water hyacinth fresh weight significantly ($F_{(31, 277)} = 4.258, P <$

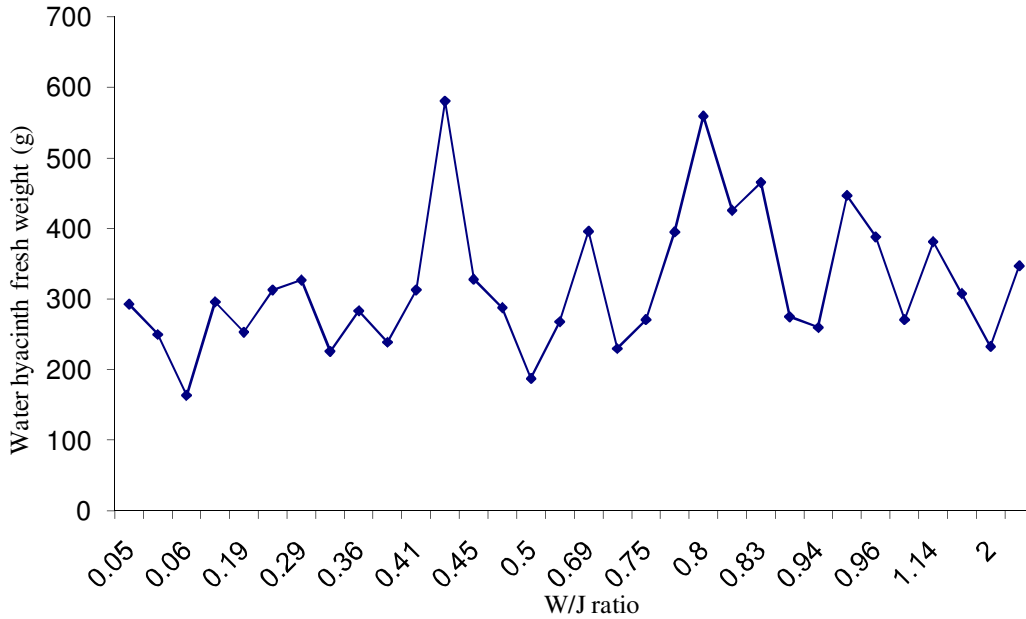


Figure 5a. Changes in water hyacinth fresh weight under water hyacinth (W) and *Justicia* sp. (J) weed mixture at different W/J ratios in the Kagera River.

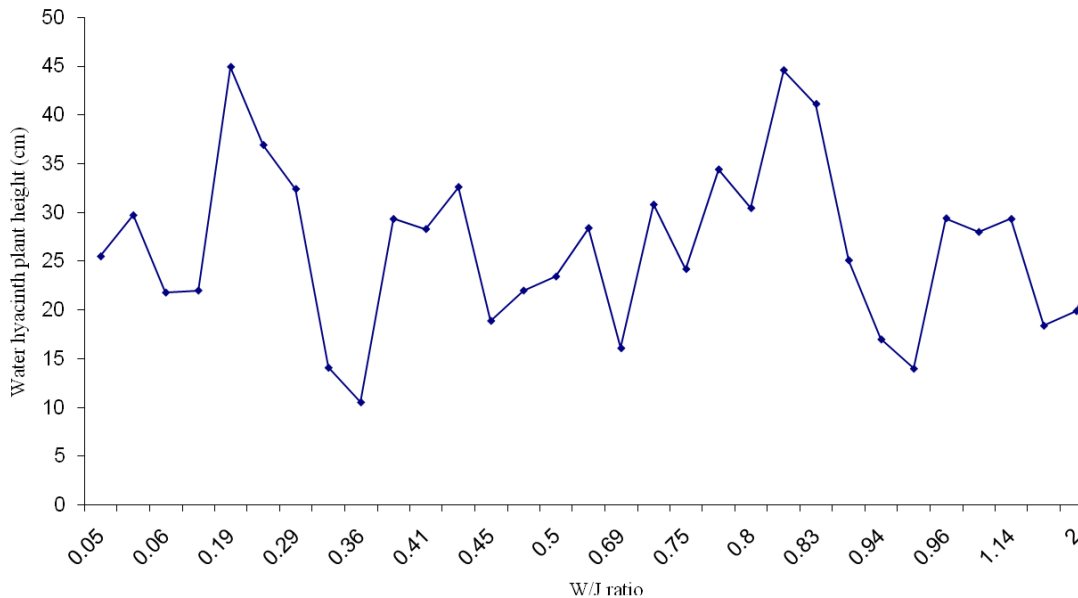


Figure 5b. Changes in water hyacinth plant height under water hyacinth (W) and *Justicia* sp. (J) weed mixture at different W/J ratios in the Kagera River.

0.001) changed with ratio. This pattern was also shown for water hyacinth plant height, mean number of leaves and ramets per plant. The W/J ratio ranged from 0.05 to 2.0. Figure 5 presents changes in water hyacinth fresh weight in response to W/J ratio. At low values (0.05 to 0.41) fresh weight was significantly low (Figure 5a) probably because of increased competition effect of *Justicia* as a result of elevated density in the weed

mixture. At higher ratios, there was a significantly high fresh weight resulting from decreased competition effect from *Justicia* due to low density in the mixture. However, the trend was different for water hyacinth plant height (Figure 5b).

There was no significant effect of water hyacinth (W) to *V. cupsidata* (V) ratio on water hyacinth plant fresh weight ($P = 0.291$) and mean number of leaves per plant

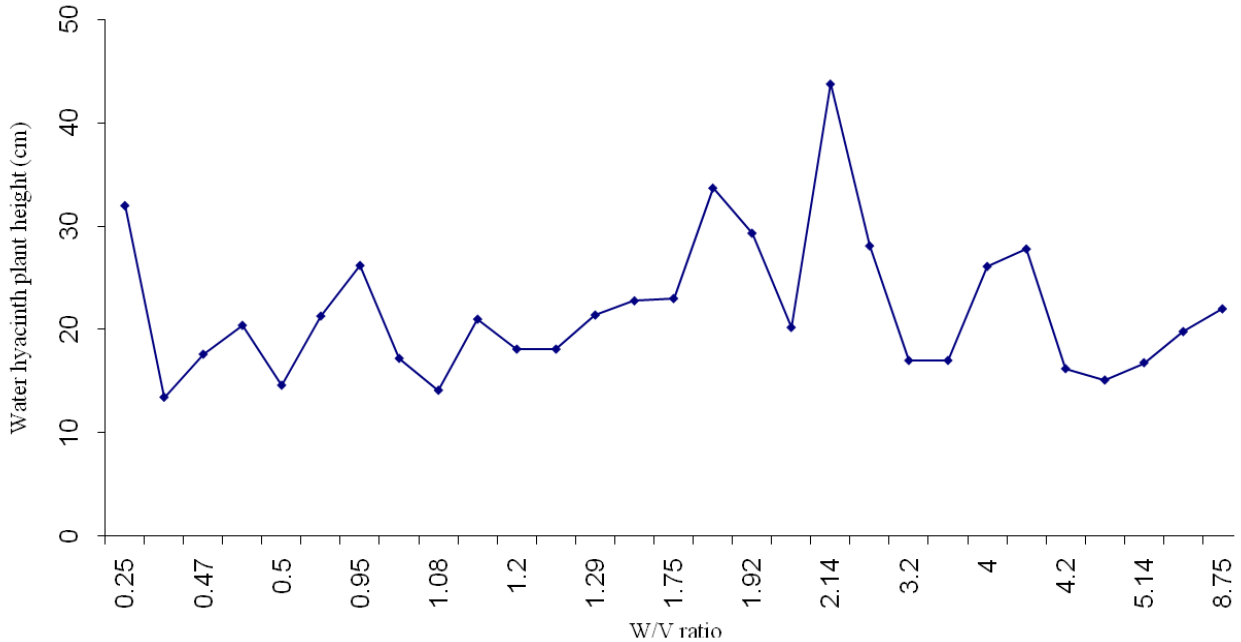


Figure 6a. Changes in water hyacinth plant height under water hyacinth (W) and *V. cupsidata* (V) weed mixture at different W/V ratios in the Kagera River.

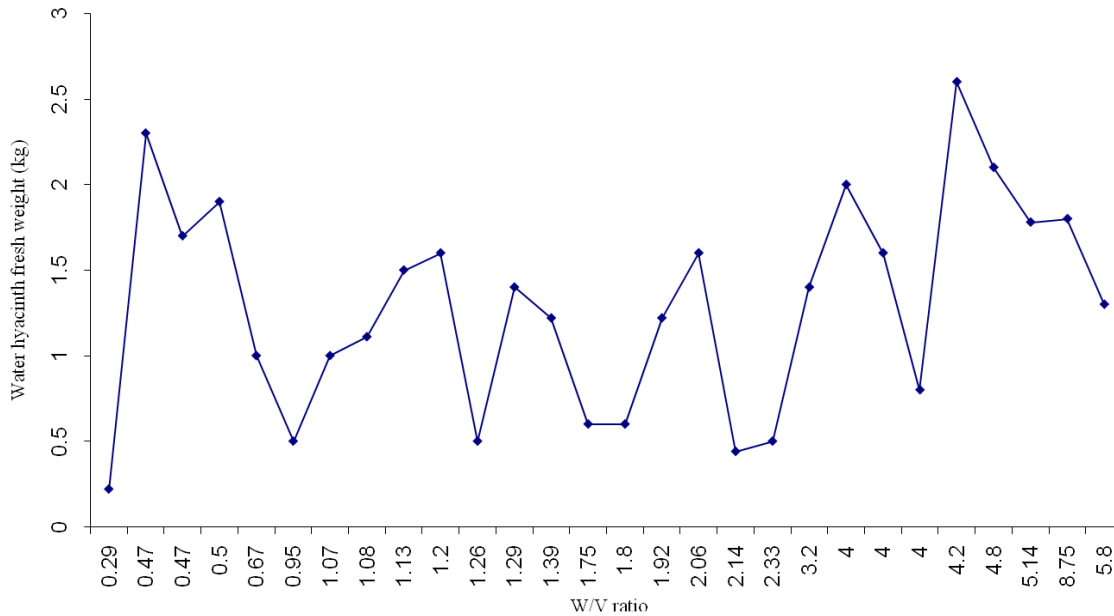


Figure 6b. Changes in water hyacinth fresh weight under water hyacinth (W) and *V. cupsidata* (V) weed mixture at different W/V ratios in the Kagera River.

($P = 0.094$). However, W/V ratio significantly influenced water hyacinth plant height ($F_{(28, 254)} = 11.298, P < 0.001$) and mean number of ramets per plant ($F_{(28, 254)} = 2.754, P < 0.001$). At low W/V ratios (Figure 6a and 6b), there was a reduced water hyacinth plant height as compared to that observed in high ratios. The effect of W/C+J+V ratio

had significant effect on water hyacinth fresh weight, plant height as well as mean ramets per plant ($P < 0.001$). However, the ratio had no significant impact on number of life leaves per plant ($P = 0.399$). At elevated density of C+J+V in the mixture (low ratios), fresh weight was significantly reduced than in high ratios (0.56 to 1.19)

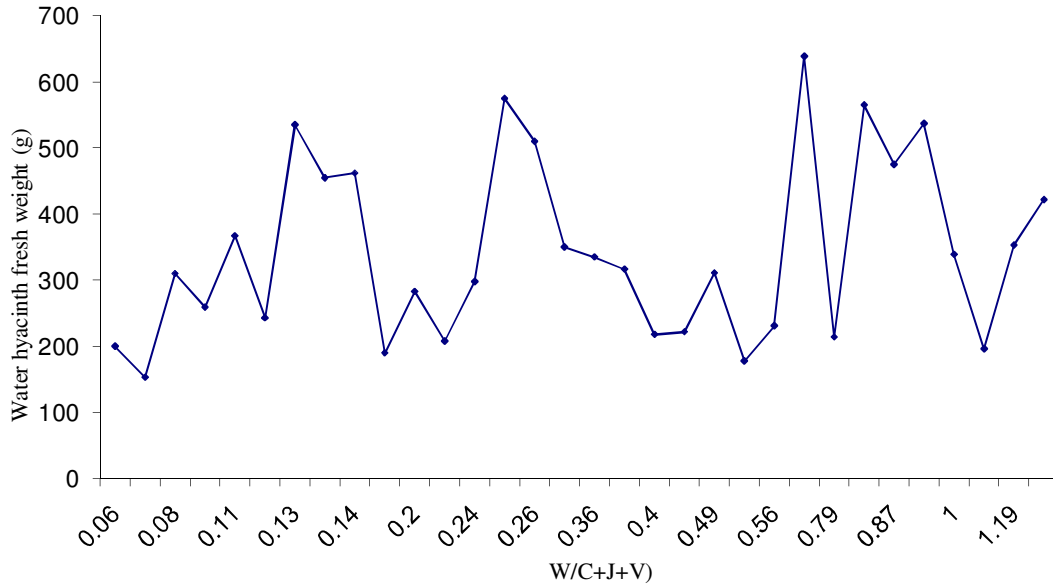


Figure 7a. Changes in water hyacinth fresh weight under water hyacinth (W+C+J+W) weed mixture at different W/C+J+V ratios in the Kagera River

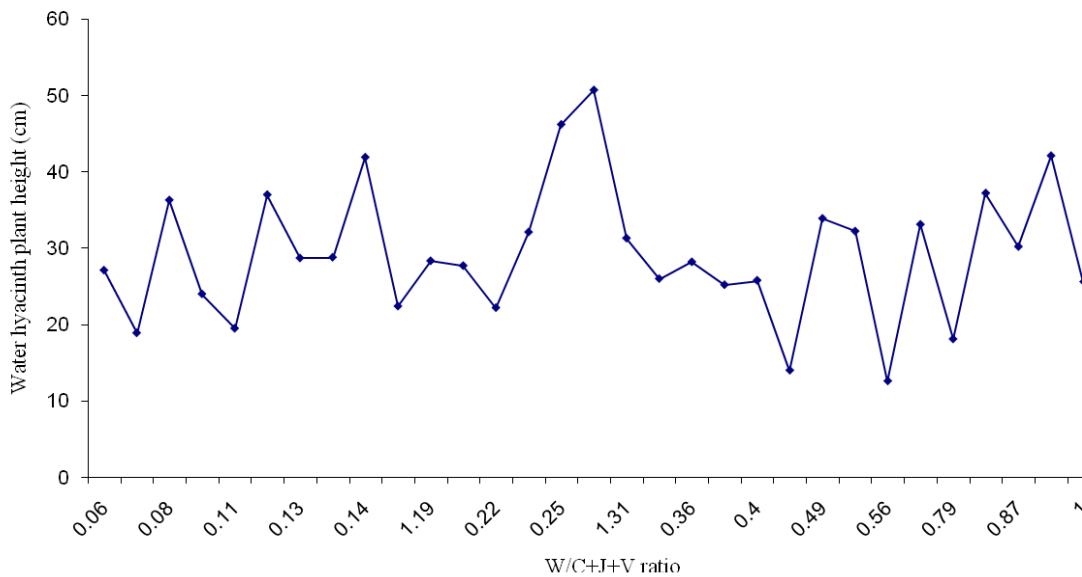


Figure 7b. Changes in water hyacinth plant height under water hyacinth (W+C+J+W) weed mixture at different W/C+J+V ratios in the Kagera River.

(Figure 7a). The pattern was not consistent probably because of inter species competition ability differences. The relationship between the ratios to water hyacinth plant height was therefore not clear (Figure 7b).

The interaction between weed mixtures and water hyacinth/other aquatic weed ratios on growth and development of water hyacinth was significant in terms of all parameters measured (Table 5). Similarly water hyacinth to other aquatic weed ratios produced no

significant effect on water hyacinth density across all the sampling units (Table 5).

DISCUSSION

The phenotype of a plant is strongly influenced by the presence of neighbouring plants. The present study demonstrated significant impact of neighbour plants on

Table 5. Summary of analysis of variance performed on the effect of weed mixtures, their combination ratios and interactions on water hyacinth growth performance in the Kagera River.

Factor	df	Fresh weight		Plant height		Ramets		Plant density	
		F ratio	P	F ratio	P	F ratio	P	F ratio	P
Weed combination (A)	4	23.506	<0.001	150.537	<0.001	25.964	<0.001	13.324	<0.001
Water hyacinth/other aquatic weed ratio (B)	31	1.729	<0.01	8.543	<0.001	2.506	<0.01	0.599	0.947
A × B	121	1.903	<0.001	8.401	<0.001	3.264	<0.001	ND	ND

growth and development of water hyacinth growing in mixture with other aquatic weed species. There was a strong suppression of hyacinth growth in terms of fresh weight, plant height, ramets and plant density probably due, to interspecific competition. In some occasions, however, water hyacinth plants responded to the competitive stress by feedback mechanisms, which involved production of elevated number of ramets, as was the case of water hyacinth growing in mixture with hippograss (*V. cupsidata*) in the Kagera River. This observation could be interpreted as shade avoidance reaction when growing with *V. cupsidata* which compete for light and water hyacinth plants could attempt to allocate functional leaves and roots in the resource (light) rich zones of their surrounding environment as this response increase the amount of light that can be captured, leading to increased plant fitness in crowded condition. This phenomenon has been recently demonstrated in other plant species by Pierik et al. (2004). Of the three aquatic weed species used in the present study, *Justicia* sp. when growing in high proportion with water hyacinth displayed a strong negative impact on water hyacinth fresh weight in the Kagera River suggesting that it exerted a high competitive stress on water hyacinth. This could be so because *Justicia* sp. produces a massive root system to help in competing for water resources, particularly nutrient. In the greenhouse experiment however, the highest reduction in water hyacinth fresh weight occurred in plants grown with *V. cupsidata*.

Observation from the study shows that water hyacinth plants growing under competition-free conditions (pure stand) had significantly higher fresh weight than when growing with other aquatic weeds both in the field and greenhouse. This is likely due to negative competition effect from other aquatic weeds in the mixtures for resources in the crowding environment resulting to reduction in fresh weight. Since the magnitude and extend of the reduction differed between plant species involved in the mixture clearly suggest that competition intensity also differed between individual plant species as demonstrated earlier (Grace, 1995; Center et al., 2005). Spencer and Ksander (2000) found a reduction in individual plant weights of hydrilla aquatic weed as a result of increased density of American pondweed in a mixture. Water hyacinth total biomass per unit area was also reduced in the presence of other aquatic species

with *V. cupsidata* giving the highest reduction of 75% suggesting that it imparted a strong negative competition effect in the mixture, an indication of its dominance.

Interference between individual plant species in an ecological niche can affect individual plant survival, growth, and reproduction (Grace and Tilman, 1990; Keddy, 1989, Lu et al., 2007). Water hyacinth plant height in the Kagera River was affected by the presence of other aquatic weeds in the mixture. There was a reduction in plant height by other aquatic weeds with the highest reduction recorded when it was growing with *V. cupsidata*. The large size nature of *V. cupsidata* could have caused light shading effect probably by altering amount of light available to water hyacinth, which is a creeping plant and poor at invading tall grass. Spencer and Ksander (2000) using light measurement experiment reported that taller American pondweed plants clearly altered suppressed height of hydrilla in the mixtures by reducing amount of light that could be captured by it. Reduction in water hyacinth plant height by other aquatic weeds was not reproduced in greenhouse because three months was not long enough to allow for effective weed density of the competitor weed to build up large enough to bring about light reduction effect on water hyacinth. This observation is supported by a decrease in plant height with time in the greenhouse experiment. Rees (1995) large-seeded annual plants have greater competitive ability and that a competition-colonization trade off promotes co-existences, in which the smaller-seeded annuals are weak competitors that co-exist with more competitive species by virtue of their greater seed production. In the present study, the small sized water hyacinth plants survive by producing large number of ramets.

In the Kagera River, it was apparently that *V. cupsidata* significantly suppressed water hyacinth plant density and total biomass per unit area. This result may be a consequence of high interspecific competition for space and resources by *V. cupsidata* leading to a reduced biomass production and density particularly under elevated densities of *V. Cupsidata*. Decreased growth of individual submerged aquatic plant because of increasing plant density of neighbours has been reported for *Eleocharis acicularis* and *Juncus pelocarpus* forma submerses (MacGreary and Carpenter, 1987, Ndunguru et al., 2001). Correlation analysis revealed a significant negative relationship between plant height and ramets

both in the field and greenhouse suggesting that decreased plant height was associated with elevated number of ramets per plant. This was observed when water hyacinth was growing with *V. cupsidata* and could be attributed to compensation effect as a light shade avoidance response. Center et al. (2005) observed nutrient availability as a factor that can influence interspecific weed competition. The influence of nutrients on water hyacinth competition outcomes observed in the present study cannot be totally excluded.

Across all treatments in the Kagera River, water hyacinth growth parameters varied significantly with water hyacinth, other aquatic weed ratios such that at elevated density of the competitor (low ratios) resulted to a significant suppression plant height, and fresh weight reduction except for water hyacinth + *V. cupdiata* where effect of ratios were not significant. Water hyacinth plant density was not significantly affected by ratios. The effect of W/C+J+V ratio on water hyacinth fresh weight was significant but the pattern was not consistent probably because three different species with different competing abilities were involved in the crowding environment.

Although it had been shown that density-dependence only weakly regulates plant population sizes; this investigation in contrast, highlights the fact that high density of competing neighbour species in the mixture resulted to suppressed growth of water hyacinth at least in the Kagera River. The fact that some positive effect of competition from neighbourhood species was observed in the Kagera River suggests that other aquatic weed have both positive and negative effect on water hyacinth proliferation in the river. Interaction between water hyacinth and other aquatic weeds suggest that efforts to manage the weed should not only be focused on water hyacinth but rather on other aquatic weeds growing with it (ecosystem approach of weed management). Inability to reproduce the field data in the greenhouse needs further investigation. However, the competitive ability of a species depends on the environment. There is no 'super species' that are competitively superior in all environments; rather, there are some trade offs among the traits that are beneficial in some environments, but which cause plants to be poor competitors in other environments. For a plant to compete successfully in particular environment, it must have specific eco-physiological traits that allow effective growth in that environment. It would be unrealistic to expect parameters measured in the field to produce the same data in greenhouse, but the greenhouse allowed us to remove the variability of the real world, thus allowing the impact of some factors to be measured in isolation, and then use the results to generate hypothesis than can be further tested in the field.

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