J. Aquat. Plant Manage. 49:19-27

Distribution, interspecific associations and abundance of aquatic plants in Lake Bisina, Uganda

BRIAN GIDUDU, R. S. COPELAND, F. WANDA, H. OCHAYA, J. P. CUDA, AND W. A. OVERHOLT*

ABSTRACT

A survey of floating-leafed and submersed aquatic plants was conducted in Lake Bisina, Uganda. Seven of the species collected were not previously reported from Lake Bisina, including *Stuckenia pectinata* (L.) Börner, *Utricularia reflexa* Oliv., *Utricularia foliosa* L., *Caldesia parnassifolia* (L.) Parl., *Wiesneria filifolia* Hook. f., *Brasenia schreberi* J. F. Gmel., and a multicelluar algae, *Chara* sp. Examination of pairwise associations between plant species revealed that the *Chara* sp. was negatively associated with *Najas horrida* ex Magn., *Nymphaea caerulea* Savigny, and *Utricularia reflexa* Oliv., which was likely due to differences in habitat requirements. A strong, positive association between *N. caerulea* and *U. reflexa* may have been due to niche similarities, but may also indicate a commensal relationship with *U. reflexa* performing well under shaded conditions provided by *N. caerula*. *Hydrilla verticillata* was the only species associated with water clarity, with abundance increasing as turbidity increased. This study provides new baseline information on the diversity, distribution, and interspecific associations of floating-leafed and submersed aquatic plants in Lake Bisina, Uganda, that will be useful for comparison with future biological studies.

Key words: aquatic plants, hydrilla, macrophytes, shallow lake.

*First author: Crop Science Department, Makerere University, Kampala, Uganda; second author: International Centre of Insect Physiology and Ecology, Nairobi, Kenya; third author: National Fisheries Resources Research Institute, Jinja, Uganda; fourth author: University of Florida, Gainesville, FL, USA; fifth author: University of Florida, Fort Pierce, FL, USA. Corresponding author's E-mail: billover@ufl.edu. Received for publication July 28, 2010 and in revised form October 30, 2010.

INTRODUCTION

Aquatic plants are central members of wetland communities that provide food and shelter, directly or indirectly, for many organisms; erosion control; oxygen enrichment of water through photosynthesis; nutrient cycling; absorption of pollutants (Cook 1974, Halls 1997); reduction of sediment suspension; refuges for zooplankton from fish grazing; and suppression of algal growth by competing for nutrients and light and the release of allelopathic substances (Takamura et al. 2003). Aquatic plant distribution, abundance, and vigor are influenced by abiotic factors including water temperature, pH, dissolved oxygen, nutrient levels, turbidity (Squires et al. 2002), sediment type, water and wind currents, depth, and changes in water levels (Wetzel 1983). Biotic components of a given water body, such as the presence and density of herbivorous fish (Hanson and Butler 1994), insects, mollusks, diseases (fungi, nematodes), plant-to-plant interactions, and movement of vegetative portions of aquatic plants by man (e.g., plant parts entangled in fish nets) also influence the distribution and abundance of aquatic plants.

Lake Bisina (N 2.649, E 33.970) is part of the Kyoga lakes system in central Uganda. The Kyoga system receives inflow from Lake Victoria through the Nile River and from streams arising on the slopes of Mount Elgon to the east. The system includes several lakes connected by large areas of papyrus swamp (Green 2009). Lake Bisina is east and upstream of the larger Lake Kyoga, through which the Nile flows. Bisina receives its fluvial input from streams originating on Mount Elgon to the east and the Apendura River to the north. Slightly higher (1041 m a.s.l.) than Lake Kyoga (1026 m), it outflows gently through its western, swampy margins toward Kyoga. As such, Bisina is not directly influenced by either the Nile or the downstream Kyoga-system lakes. Lake Bisina grows and shrinks depending on rainfall, but in a typical year covers about 150 km^2 with a mean depth of 3 m (Vanden Bossche and Bernacsek 1990). It is a designated wetland of international importance (RAMSAR site) because of its unique biodiversity and support of rare and endangered species (Byaruhanga and Kigoolo 2005). The lake can be divided into 3 zones based on the aquatic macrophyte flora: the submersed aquatic plant zone, the Nymphaea zone, and the emergent plant zone.

Katende (2004) examined the species diversity of aquatic macrophytes in Lake Bisina but provided no information on the distributions or interspecific associations of plants in the lake. As part of a project to search for insect herbivores of *Hydrilla verticillata* (Overholt and Wheeler 2006), the aquatic plant communities of several water bodies in Uganda, Kenya, and Burundi were surveyed, including Lake Bisina. Observations during sampling expeditions indicated that the aquatic plant species in Lake Bisina exhibited clear and consistent spatial patterns. The objective of this study was to describe and examine those patterns and attempt to explain the patterns based on water depth, physico-chemical water conditions, and inter-relationships between plants.

MATERIALS AND METHODS

Plant samples

Sampling was conducted in Lake Bisina on 7 occasions between February 2008 and August 2009. Locations for sampling were selected by traversing the lake along several transects and stopping at approximately 1 km intervals to collect samples. On three occasions (April 2008, January 2009, and April 2009) an effort was made to sample as much of the lake as possible by following 5 to 7 transects and revisiting many of the same sites. However, due to a lack of specific landmarks, drift of the boat during sampling, and inherent inaccuracy of the GPS units (30 m), it proved impossible to sample the exact same sites repeatedly. On the other four occasions, sampling was targeted to cover isolated bays and the extreme eastern and western portions of the lake. In total, 199 locations were sampled with 11 to 46 locations visited on each sampling occasion. At each sampling location, vegetation was collected from a boat by throwing a grappling hook attached to a rope and then dragging the hook along the bottom until it was located below the boat. The hook was then slowly lifted to the surface and the collected vegetation was placed on the bottom of the boat. At each location, the grappling hook was thrown three times, each time in a different direction. Plant species were recorded when known, or a voucher sample was collected and pressed for later identification. Water depth was measured at each location using a weighted rope, and water clarity was measured on three of the sampling dates (June 2008, January 2009, and April 2009) with a Secchi disk. The relative abundance of each plant species in each sample of three grappling-hook throws was estimated using a DAFOR scale (Hurford 2006) with scoring modified as follows: 5 (dominant) ≥76% of the estimated biomass of a sample, 4 (abundant) = 51-75%, 3 (frequent) = 26-50%, 2 (occasional) = 5-25%, 1 (rare) = >0 and <5%, and 0 = absent.

Water samples

Water samples were taken from each sampled location on two occasions, January and April 2009, representing the dry and rainy seasons, respectively. Samples were collected in 2L PVC Van Dorn Bottles at approximately 30 cm depth and then transferred to clean plastic 2 L bottles sealed with a lid. The samples were maintained in a cooler on ice for less than 48 h prior to analyses. Chemical analyses for orthophosphates, nitrates, and chlorophyll *a* were based on methods described by Stainton et al. (1977). Dissolved oxygen, pH, and temperature were measured using a portable water quality meter (Fisher Scientific Accumet®).

Data analyses

The frequency of occurrence (incidence) of each plant species was determined by dividing the number of locations where the plant was found by the total number of locations sampled on each sampling occasion. Average incidence was the mean value of incidence of the seven sampling occasions. The abundance of each plant was derived in a similar manner by summing the abundance of each plant on each sampling occasion and dividing by the number of locations sampled. Confidence intervals (95%) were constructed around the mean of incidence and abundance of each species (mean ± SE × 0.994; Payton et al. 2003). An index of prevalence (*Ip*) was calculated for each plant species as the product of each plant's incidence and abundance (Zhou et al. 2003) as follows:

$$Ip = \left[\frac{Fo}{N}\right]\left[\frac{S}{N}\right]$$

where *Fo* = the number of locations a species was found, *N* = the number of locations sampled, and *S* = the sum of the abundance values (DAFOR scores) for a species. Because *Ip* is the product of two terms, a 95% confidence interval for the mean *Ip* could be calculated using a statistical inference method provided by Buonaccorsi and Liebold (1988). Incidence, abundance, and prevalence were compared between species by examining overlap between 95% confidence intervals (Payton et al. 2003).

The relationships of water depth and water clarity (Secchi reading) to abundance of each species were examined with linear regression. The frequency distributions of the eight most prevalent plants in 0.5 m wide depth classes were plotted to illustrate vertical distributional differences in relation to water depth.

Presence-absence data at all sampling locations for all pairwise combinations of the 10 most abundant plant species were analyzed using a chi-square test with Yate's continuity correction to determine whether certain species tended to occur together or apart more often than expected by random chance (Turner et al. 2004). Chi-square probabilities were adjusted for the number of chi-square tests using the Dunn-Sidak equation, as follows:

$$\propto = 1-(1-\propto')^k$$

where α = adjusted P-value, $\propto'$ = calculated P-value, and k = number of chi-square tests (Sokal and Rohlf 1995). Yule's V was used to examine the strength and direction of the association of pairs of species with statistically significant (adjusted $P < 0.05$) chi-square values. Yule's V ranges from +1 for absolute positive association (two plants only occur together) to -1 (two plants never occur together; Turner et al. 2004).

To determine whether plant distribution data could be pooled over sampling dates, it was necessary to examine whether plant distributions changed over time. Interpolated density surfaces were generated for the five most prevalent plant species (*N. careula*, *H. verticillata*, *P. schweinfurthii*s *N. horida*, and *C. demersum*) for three sampling dates (April 2008, January 2009, and April 2009) using the Inverse Density Weighted (IDW) method in the Geospatial Analyst of ArcMap 9.2 (ESRI; Redlands, CA). The IDW method makes predictions at locations not sampled from weighted averages of nearby known values, giving closer values more influence on the predicted value than those that are farther away. The three dates used for comparisons were selected because samples on those dates were spread more or less evenly throughout the lake. On other dates, sampling was in more limited areas of the lake, and thus interpolated surfaces would not have been representative. Matrices (each cell = 34.1 m × 34.1 m) of the interpolated surfaces were exported from ArcMap 9.2 and compared between sampling dates (within plant species) using Mantel tests (Sokal and Rohlf 1995) with 100 permutations in R statistical software (R Development Core Team 2004). In total, 15 Mantel tests were conducted; three (April 2008 vs. January 2009, April 2008 vs. April 2009, and January 2009 vs, April 2009) for each of the five plant species. Interpolated abundance surfaces of the five most prevalent plants were generated from data pooled over all sampling dates once it was determined that distributions were highly correlated between sampling dates (see results).

Physico-chemical parameters (temperature, pH, conductivity, phosphates, nitrates, and chlorophyll *a*) were compared between the two sampling occasions using a t-test.

RESULTS AND DISCUSSION

The depth of Lake Bisina at sampling locations ranged from 0.6 to 5.0 m with an average depth of 2.89 m (±0.6 SE; Figure 1). Of the 199 locations sampled, at only four were no plants found, three of which were in the deepest part of the lake (4.9 to 5.0 m), and the fourth had a rocky bottom. A total of 15 vascular plants and one multicellular green algae, *Chara* spp., were collected. The majority of species (11) were submersed, and the other five were floating-leafed plants (Table 1). The index of prevalence, which combines incidence and abundance, indicated that *N. caerulea* was by far the most prevalent floating-leaf plant (Figure 2). The other four floating-leaf plants, *Nuphar* spp., *N. lotus*, *C. parnassifolia*, and *B. schreberi*, had very low indices of prevalence and could be considered rare. *Najas horrida* was the most prevalent submersed plant, followed by *C. demersum* and *P. schweinfurthii. Hydrilla verticillata* was less prevalent than *C. demersum*, but not different from *P. schweinfurthii. Utricularia reflexa, O. ulvifolia*, and *Chara* sp. were of lesser prevalence, and the remaining species had very low prevalence.

The abundances of six of the plants were significantly related to water depth (Table 2), although the coefficients of determination for all relationships were low, indicating that the relationships may not have been linear and/or factors other than depth also influenced the abundance of these plants. *Chara* sp. was positively associated with water depth, whereas the abundances of the other five species (*C. demersum*, *H. verticillata*, *O. ulvifolia*, *N. caeruleai*, and *U. reflexa*) were negatively related to depth. Based on the coefficient of determination (R^2), the abundance of the floating-leafed plant *N. caerulea* was most strongly related to depth, with abundance decreasing 0.95 on the DAFOR scale for each meter increase in depth. The frequency distributions at different depth classes of the eight most commonly collected plants (Figure 3) show that *Najas horrida*, *C. demersum*, *P. schweinfurthii*, and *H. verticillata* occurred at a similar range of depths from about 0.9 to 4.5 m, with the highest incidence from 3 to 3.5 m. *Ottelia ulvifolia*, *N. caerulea*, and *U. reflexa* tended to occur in shallow water, and *Chara* sp. only occurred in deeper areas of the lake from 3.15 to 4.34 m (Figure 3).

Hydrilla verticillata was the only species in which abundance was related to water clarity (Secchi reading). Abundance of *H. verticillata* decreased as water clarity increased ($F_{1,83} = 12.57$, $P = 0.0006$, $R^2 = 0.11$). Mean water clarity was higher in January (2.09 m) and April 2009 (1.92 m) than in June 2008 (1.63; $F_{2,82} = 5.75$, $P = 0.004$).

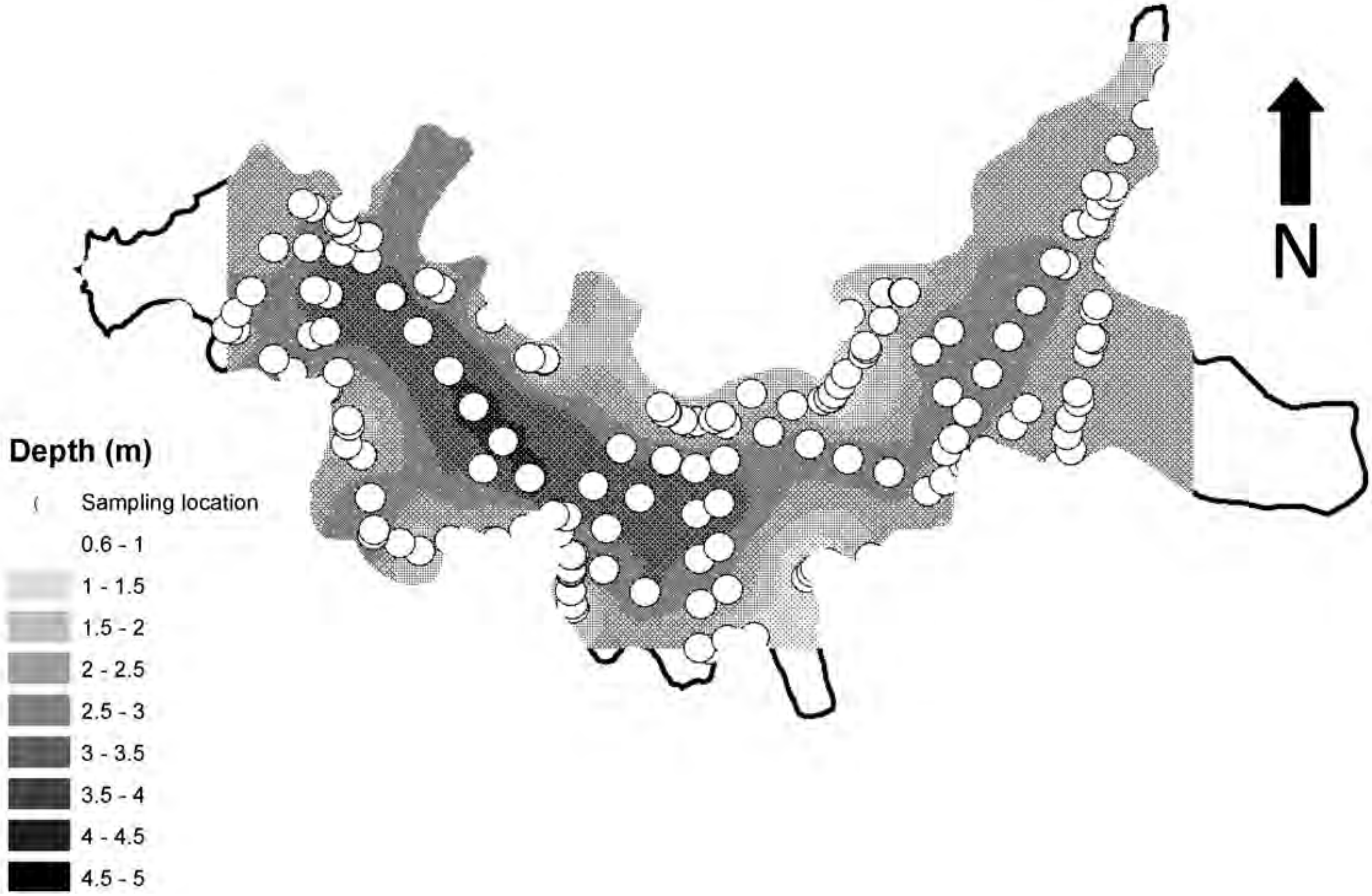

Figure 1. Sampling locations and interpolated water depth in Lake Bisina, Uganda.

Examination of associations of all possible pairwise combinations (36) of plant species that were encountered more than three times revealed that seven pairs of plants were either found to co-occur more often than expected by random chance or were found to occur separately more often than expected (Table 3). The strongest positive association was between *N. caerulea* and *U. reflexa*, and the strongest negative association was between *N. horrida* and *Chara* sp.

The Mantel tests to examine whether plant distributions of the five most prevalent plants were correlated between sampling dates were all highly significant (Mantel r ranging from 0.602 to 0.903, $P < 0.01$ in all cases), indicative that distributions did not change over time. Therefore, data from all sampling occasions were pooled to create plant abundance surfaces (Figure 4). *Najas horrida* was most abundant in the far western part of the lake but also occurred throughout the lake except in the deepest parts. *Ceratophyllum demersum* was found in protected bays and was most abundant along the northwestern shore. *Nymphaea caerulea* also tended to be most abundant in bays. *Hydrilla verticillata* density was highest at one location along the eastern-central part of the north shore of the lake and, to a lesser extent, along the central southern shore. *Potamogeton schweinfurthii* was most abundant in the western part of the lake, but not near shore, and also along a southwest to northeast axis on the eastern side of the lake.

Water temperature was about one degree higher in April 2008 than in January 2009, and conductivity was lower in the April than in the January sample (Table 4). Phosphates, pH, nitrates, and chlorophyll *a* were not different between the two sampling occasions. Total dissolved solids (TDS) were only measured in January 2009, and dissolved oxygen (DO) and redox were only measured in April 2008, and thus no comparisons were made. All measurements are included here to provide data for comparison with other East African lakes and for future studies on Lake Bisina.

The majority of plants found in the survey were previously reported to occur in Lake Bisina (Katende 2004), and two of the plants were probably reported by Katende but under different names (*P. schweinfurthii* as *P. schweintanithi* and *N. caerulea* as *N. noudian*). However, several of the plants recovered were not previously reported from Lake Bisina, including *S. pectinata*, *U. reflexa*, *U. foliosa*, *W. filifolia*, *C. parnassifolia*, *B. schreberi*, and the *Chara* sp. The intensity of sampling in Katende's (2004) study is not entirely clear, but it appears that plants were collected on one occasion at an unreported number of sites, as opposed to the 199 locations sampled over 18 months in our study. Additionally, it is evident from the diversity of species reported by Katende (2004) that many of his samples were collected in emergent vegetation in swampy areas bordering the lake, whereas all our samples

TABLE 1. GROWTH HABITS AND GEOGRAPHIC DISTRIBUTIONS OF PLANT SPECIES COLLECTED IN LAKE BISINA, UGANDA, FEBRUARY 2008 TO AUGUST 2009.

Plant species	Family	Growth habit	Native range	Reported from Uganda	Reported from Lake Bisina
Najas horrida Magn.	Hydrocharitaceae	submersed	Africa to Sinai[1]	Triest 1989	Katende 2004
Hydrilla verticillata (L.f.) Royale	Hydrocharitaceae	submersed	Eastern Europe to Asia, Uganda to North Zambia[1]	Simpson 1989	Katende 2004
Ottelia ulvifolia (Planch.) Walp.	Hydrocharitaceae	submersed	Tropical and South Africa, Madagascar[1]	Simpson 1989	Katende 2004
Potamogeton schweinfurthii A. Benn	Potamogetonaceae	submersed	Africa, Mediterranean Islands, Arabian Peninsula[1]	Symoens 2006	Katende 2004[7]
Stuckenia pectinata (L.) Börner	Potamogetonaceae	submersed	Cosmopolitan[1]	Symoens 2006[4]	no
Potamogeton richardii Solms	Potamogetonaceae	submersed	Cameroon, Eritrea to South Africa, Madagascar[1]	Symoens 2006	Katende 2004
Ceratophyllum demersum L.	Ceratophyllaceae	submersed	Cosmopolitan[1]	Wilmot-Dear 1985	Katende 2004
Nymphaea caerulea Savigny	Nymphaeaceae	floating-leafed	Africa, Arabian Peninsula[2]	Verdcourt 1989[5]	Katende 2004[8]
Nymphaea lotus L.	Nymphaeceae	floating-leafed	Africa, Southeastern Europe[2]	Verdcourt 1989	Katende 2004
Nuphar spp.	Nymphaeceae	floating-leafed	—	—	—
Utricularia reflexa Oliv.	Lentibulariaceae	submersed	Africa[3]	Taylor 1973	No
Utricularia foliosa L.	Lentibulariaceae	submersed	Africa, America[3]	Taylor 1973	No
Wiesneria filifolia Hook.f.	Alismataceae	submersed	Uganda to North Botswana, Madagasca[1]	WCSPF[1]	No
Caldesia parnassifolia (L.) Parl.	Alismataceae	floating-leafed	Europe, East Africa, Madagascar, China to Queensland[1]	Carter 1960[6]	No
Brasenia schreberi J.F. Gmel.	Cabombaceae	floating-leafed	Africa, Temperate and Tropical Asia, Eastern Australia, America[1]	Verdcourt 1971	No
Chara sp.	Characeae	submersed	—	—	No

[1]World Checklist of Selected Plant Families 2010
[2]Global Biodiversity Information Facility 2010
[3]Taylor 1989
[4]as Potamogeton pectinatus
[5]as *Nymphaea nouchali* var. *caerulea*
[6]as *Caldesia reniformis*
[7]likely included in Katende 2004 as *Potamogeton schweintanithi*
[8]likely included in Katende 2004 as *Nymphaea noudian*.

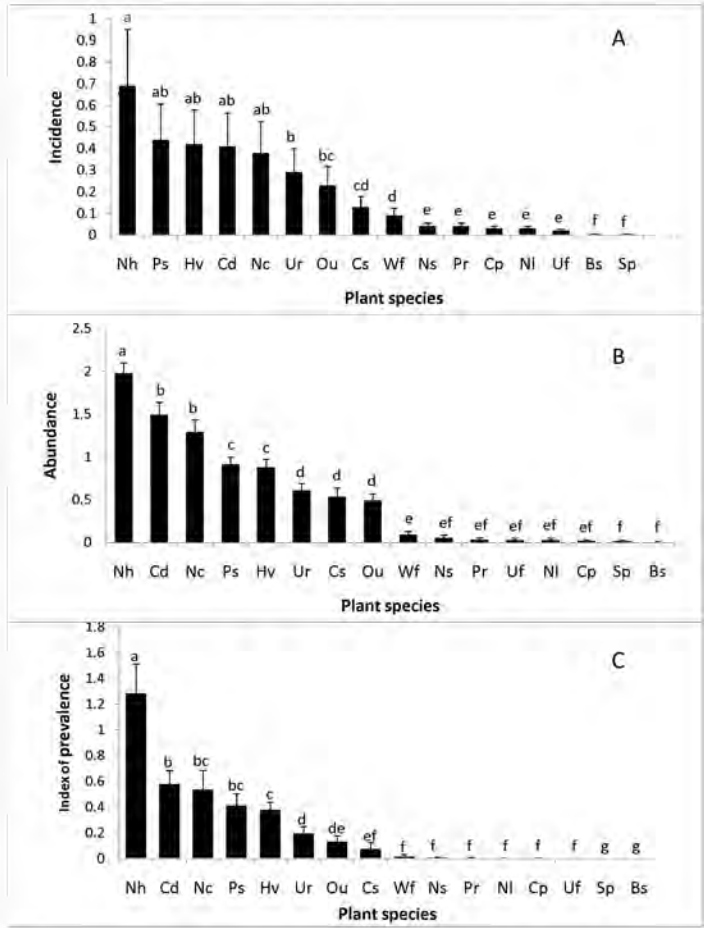

Figure 2. Incidence (A), abundance (B) and prevalence (C) of plants collected in Lake Bisina, Uganda, February 2008 to August, 2009. Bars capped by the same letter are not statistically different (P > 0.05). Nh = *Najas horrida*, Cd = *Ceratophyllum demersum*, Nc = *Nymphaea caerulea*, Ps = *Potamogeton schweinfurthii*, Hv = *Hydrilla verticillata*, Ur = *Utricularia reflexa*, Ou = *Ottelia ulvifolia*, Cs = *Chara* sp., Wf = *Wiesnera filifolia*, Ns = *Nuphar* sp., Pr = *Potamogeton richardii*, Nl = *Nymphaea lotus*, Cp = *Caldesia parnassifolia*, Uf = *Utricularia foliosa*, Sp = *Skuckenia pectinata*, Bs = *Brasenia schreberi.*

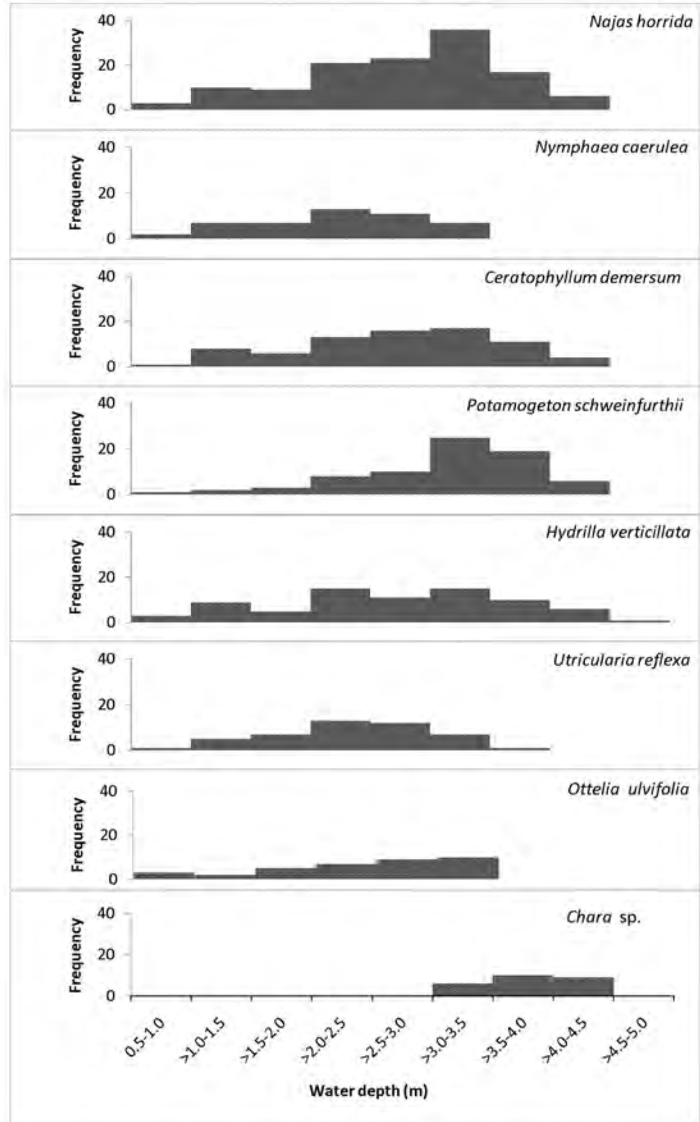

Figure 3. Frequency distributions at different depth classes of the eight most prevalent aquatic plants in Lake Bisina, Uganda.

were collected from the lake proper. Katende (2004) did not report any *Chara* spp. from Lake Bisina or any of the other nine lakes included in his study, although he may have ignored the algae because his study focused on vascular plants. The only reports of *Chara* spp. in Uganda lakes are from Lake Bunyonyi in southwestern part of the country (Denny 1971, 1973). Thus, with the greater intensity and focus of our sampling, it is not surprising that several of the less common submersed and floating-leafed aquatic species in Lake Bisina were found in the present study.

Table 2. Linear regressions of plant abundance on water depth of six species of aquatic plants in Lake Bisina, Uganda.

Plant species	Slope	F	P-value	Adj R^2
Ceratophyllum demersum	0.54	10.51	0.0014	0.05
Hydrilla verticillata	0.55	26.95	<0.0001	0.13
Otellia ulvifolia	0.39	18.73	<0.0001	0.09
Nymphaea caerulea	0.95	46.41	<0.0001	0.22
Utricularia reflexa	-0.45	24.22	<0.0001	0.12
Chara spp.	0.06	30.50	<0.0001	0.15

Positive or negative associations between plants can occur due to similarities or differences in habitat requirements, or to direct interactions between species (e.g., mutualism, commensalism, competition, and predation; Roxburgh and Chesson 1998). The *Chara* sp. was negatively associated with *N. horrida*, *N. caerulea*, and *U. reflexa*, and all of these associations may be due to differences in habitat requirements. *Nymphaea caerulea* and *U. reflexa* were negatively related to water depth, while *Chara* sp. was positively associated with depth. *Chara* spp. are known to often occur in deeper water than vascular macrophytes due to high shade tolerance, and may be competitively excluded in shallow water by vascular macrophytes (Kufel and Kufel 2002). The negative relation-

TABLE 3. PAIRWISE ASSOCIATIONS BETWEEN PLANT SPECIES FOUND IN LAKE BISINA, UGANDA.

Species 1	Species 2	Species 1 present/ Species 2 present	Species 1 absent/ Species 2 present	Species 1 present/ Species 2 absent	Species 1 absent/ Species 2 absent	Chi-square	P-value[1]	Yule's V
Ceratophyllum demersum	*Potamogeton schweinfurthii*	21	68	65	45	25.26	<0.0001	-0.356
Najas horrida	*Hydrilla verticillata*	73	13	71	42	11.87	0.02137	0.237
Najas horrida	*Utricularia reflexa*	49	5	95	50	12.52	0.0143	0.251
Najas horrida	*Chara sp.*	6	20	138	35	36.32	<0.0001	-0.427
Nymphaea caerulea	*Utricularia reflexa*	40	14	25	120	57.78	<0.0001	0.539
Nymphaea nouchali	*Chara* sp.	0	26	65	108	14.51	<0.0001	-0.270
Utricularia reflexa	*Chara* sp.	0	26	54	119	11.14	0.0284	-0.237

[1]P-values adjusted using the Dunn-Sidak correction. Yule's V indicates the direction (positive or negative) and strength of associations between species.

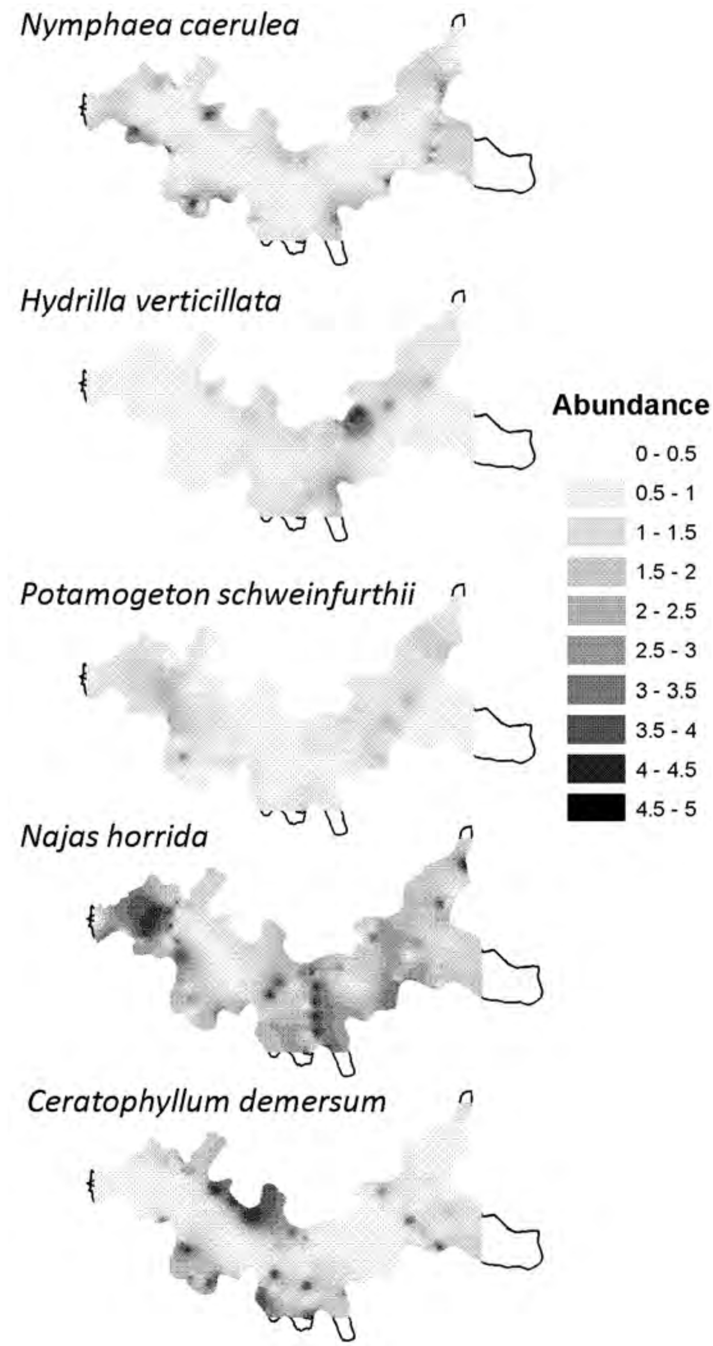

Figure 4. Interpolated surfaces of abundance of *Nymphaea caerulea*, *Hydrilla verticillata*, *Potamogeton schweinfurthii*, *Najas horrida*, and *Ceratophyllum demersum*. Abundance estimated on a scale of 0-5 (see modified DAFOR scale scoring in text).

ship between the *Chara* sp. and *N. horrida* was also probably due to partitioning of the lake by water depth, although the relationship of *N. horrida* with water depth was not statistically significant. The negative association between *C. demersum* and *P. schweinfurthii* is interesting because they both occur at similar water depths (Figure 3) but in different locations of the lake (Figure 4). *Ceratophyllum demersum* tended to be most abundant in sheltered bays, whereas *P. schweinfurthii*

TABLE 4. PHYSICO-CHEMICAL PARAMETERS OF WATER IN LAKE BISINA IN APRIL 2008 AND JANUARY 2009.

Month /year	N	Temperature	DO mg/L	pH	TDS mg/L	Conductivity	PO_4-P (ug/L)	NO_3-N (ug/L)	Chl-*a* (ug/L)
Jan 09	38	26.5 ± 0.14 b	—	7.9 ± 0.13 a	138.5 ± 0.7	276.9 ± 1.5 a	16.1 ± 2.2 a	21.2 ± 3.1 a	5.0 ± 1.2 a
Apr 09	37	27.7 ± 0.14 a	6.8 ± 0.1	8.1 ± 0.07 a	—	254.4 ± 6.1 b	12.0 ± 1.5 a	26.3 ± 1.4 a	3.8 ± 0.3 a

was abundant in more open areas of the lake. The former species lacks true roots but anchors itself to the bottom with modified leaves (rhizoids), which may explain its occurrence in sheltered bays (Best 1980). The strong positive association between *N. caerulea* and *U. reflexa* may have been due to niche similarities but may also suggest a commensal relationship with *U. reflexa* performing well under shaded conditions provided by the floating leaves of *N. caerula*. Alternatively, *Utricularia* spp. are rootless, and thus may simply get caught on the stems of *N. caerulea*. Kateyo (2006) also mentioned a positive association between *N. caerulea* and a *Utricularia* sp. in Lake Nabugabo, Uganda.

The vertical distributions of *N.caerulea* and *H. verticillata* in relation to water depth were similar to those reported for the same plants in Lake Bunyonyi, Uganda, by Denny (1971), although *H. verticillata* was found infrequently between 4.5 and 7 m in Lake Bunyonyi, whereas it was not found deeper than 4.5 m in our study (although the deepest location sampled in the present study was 5 m). However, the vertical distribution of *C. demersum* was wider in Lake Bunyonyi (~0.2 to 7 m, mean ≈ 3.1) than in Lake Bisina (0.6 to 4.3 m, mean = 2.7 m), and the distributions of the *Chara* sp. were very different, with the Lake Bunyonyi *Chara* sp. occurring in shallow water (~0.2 to ~5.2 m, mean depth ≈ 2.1 m), whereas the *Chara* sp. in Lake Bisina was only found in deeper portions of the lake within a very narrow range of depths (3.2 to 4.3 m, mean = 3.8). This could be attributed to the presence of different *Chara* spp. in the lakes and/or environmental differences resulting in dissimilar vertical distributions.

Hydrilla verticillata was the only species associated with water clarity, with abundance increasing as clarity decreased. The area of the lake where *H. verticillata* was most abundant (Figure 4) was just offshore from a small village. During sampling in this area, women were observed washing clothes, and cattle drank by entering the water, which may provide an explanation for the elevated turbidity, either through physical disturbance of the bottom or promotion of phytoplankton and algal growth due to high nutrient levels. Interestingly, the other area where *H. verticillata* was relatively abundant on the south side of the lake was also next to a village. Van et al. (1976) compared the light requirements of three submersed macrophytes, *H. verticillata*, *C. demersum*, and *Myriophyllum spicatum* L., and found that *H. verticillata* required the least amount of light to achieve half its maximum photosynthetic rate. The same authors concluded that *H. verticillata* had a distinct competitive advantage over the other 2 species because of its superior ability to perform under low light. Underscoring its ability to fix carbon at low light levels, *H.verticillata* in Lake Tanganyika was found growing at 8 m depth off Nyanza Lac, Burundi (Copeland unpub. data) and also at 10 m depth off Kigoma, Tanzania (Eggermont et al. 2008). This reasoning may provide a possible explanation for the abundance of *H. verticillata* in turbid areas of the Lake Bisina. *H. verticillata* may out-compete other species in Lake Bisina when light is limited, or in potentially nutrient enriched conditions, but other species have an advantage in clearer or lower nutrient areas of the lake. A similar light-mediated competitive interaction between two *Potamogeton* spp. was recently reported by Spencer and Rejmánek (2010).

Hydrilla verticillata was introduced into the southern United States in the 1950s by the aquarium trade (Schmitz et al. 1991) and rapidly spread to become one of the most serious aquatic invaders in many lakes, rivers, and canals (Balciunas et al. 2002). *Hydrilla verticillata* causes problems because it grows in large, dense monocultures that interfere with water flow, recreational activities, and displace native aquatic plant communities (Langeland 1996), although the impacts of *H. verticillata* on native biodiversity have recently been questioned (Hoyer et al. 2008). This situation differs greatly from that encountered in Lake Bisina, where *H. verticillata* grows in association with several other plants (mean number of other plant species found growing at locations where *H. verticillata* occurred = 2.48 ± 1.1), has a patchy distribution (Figure 4) and is only moderately abundant compared to the other plants in the lake. The reasons for the difference in abundance of *H. verticillata* in Lake Bisina and freshwaters in the southern United States are unknown but could be due to differential pressure from biotic factors and/or differences in water quality. Florida lakes in general are less alkaline than Lake Bisina, and nutrients tend to be much higher in Florida lakes (Hoyer et al. 1996). Additionally, genetic differences may play a role, as several studies have described physiological differences between hydrilla populations (e.g., Steward 2000, Puri et al. 2007, Maki and Calatowitch 2008).

Lake Bisina is designated a RAMSAR site (wetland of international importance; Byaruhanga and Kigoolo 2005), because of its (1) unique macrophyte ecosystem, (2) support of rare and endangered organisms, (3) support of populations of plants and animals important for maintaining biodiversity of the region, (4) support for bird and animal species at a critical stage in their life cycles, (5) support of endemic fishes, and (6) importance as a spawning ground for fish. Our study provides new information on the diversity, distribution, and interrelationships of floating-leafed and submersed aquatic plants in Lake Bisina, Uganda, including several first records of species occurrences in the lake. This information, coupled with the physico-chemical water data, provide a solid baseline for comparison with future biological studies on Lake Bisina and for the design of conservation management strategies.

ACKNOWLEDGEMENTS

We greatly appreciate the assistance provided by Dr. C. D. K. Cook for the identification of the vascular aquatic plants, and Dr. Anders Langangen for guidance on the identification of the *Chara* sp. We also thank Mr. James Colee for his valuable assistance with statistical analyses. The following agencies provided financial support for the study: the Florida Fish and Wildlife Conservation Commission, the South Florida Water Management District, the Saint Johns Water Management District and Osecola County, Florida.

LITERATURE CITED

Balciunas JK, Grodowitz MJ, Cofrancesco AF, Shearer JF. 2002. *Hydrilla*. In: Van Driesche R, Blossey B, Hoddle M, Lyon S, Reardon R, editors. Biological Control of Invasive Plants in the Eastern United States, USDA Forest Service Publication FHTET-2002-04.

Best EPH. 1980. Effects of nitrogen on the growth and nitrogenous compounds of *Ceratophyllum demersum*. Aquat. Bot. 8:197-206.

Buonaccorsi J, Liebold A. 1988. Statistical methods for estimation of ratios and products in ecological research. Environ Entomol. 17:572-580.

Byaruhanga A, Kigoolo S. 2005. Lake Bisina Wetland System Ramsar Information Sheet. The Ramsar Convention on Wetlands. [cited Mar 2010]. Available at: http://ramsar.wetlands.org/Database/Searchforsites/tabid/765/Default.aspx.

Carter S. 1960. Flora of tropical East Africa: Alismataceae. Crown Agents, London. 16 p.

Cook CDK. 1974. Water plants of the world. Hague (Netherlands): Dr. W. Junk Publishers. 561 p.

Denny P. 1971. Zonation of aquatic macrophytes around Habukara Island, Lake Bunyonyi, S. W. Uganda. Hidrobiologia. 12:249-257.

Denny P. 1973. Lakes of south-western Uganda: II. Vegetation studies on Lake Bunyonyi. Freshwater Biol. 3:123-135.

Eggermont H, Kennedy D, Hasiotis ST, Verschuren D, Cohen A. 2008. Distribution of living larval Chironomidae (Insecta: Diptera) along a depth transect at Kigoma Bay, Lake Tanganyika: implications for palaeoenvironmental reconstruction. Afr Entomol. 16:162-184.

Global Biodiversity Information Facility. 2010. [cited Mar 2010]. Available from http://www.gbif.org/index.php?id=269.

Green J. 2009. The Kyoga catchment. In The Nile: Origin, Environments, Limnology and Human Use. In: Dumont HJ, editor. Monog Biol. 89: 205-214. (Netherlands): Springer. 214 p.

Halls AJ, editor. 1997. Wetlands, biodiversity and the Ramsar Convention: The role of the convention on wetlands in the conservation and wise use of biodiversity. Ramsar Convention Bureau, Gland, Switzerland. [Mar 2010. Available from http://www.ramsar.org/cda/en/ramsar-pubs-books-wetlands-biodiversity-21181/main/ramsar/1-30-101%5E21181_4000_0__.

Hanson MA, Butler MG. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Can J Fish AquatSci. 51:1180-1188.

Hoyer MV, Canfield DE Jr, Horsburgh CA, Brown K. 1996. Florida freshwater plants: A handbook of common aquatic plants in Florida lakes. Gainsville (FL): University of Florida; Institute of Food and Agricultural Sciences. 260 p.

Hoyer MV, Jackson MW, Allen MS, Canfield DE Jr. 2008. Lack of exotic hydrilla infestation effects on plant, fish and aquatic bird community measures. Lake Reserv Manage. 24:331-338.

Hurford C. 2006. Minimizing observer error. In: Hurford C, Schrieider M, editors. Monitoring nature conservation in cultural habitats: A practical guide and case studies. (Netherlands): Springer. p. 79-82.

Katende AB. 2004. The diversity of macrophytes in some Kyoga basin lakes and their importance as fish habitat. Afr J Ecol. 42:42-45.

Kateyo EM. 2006. Biodiversity of an interface zone of a nutrient-deficient lake (Nabugabo) in Uganda: macrophytes. Afr J Ecol. 45:130-134.

Kufel L, Kufel I. 2002. *Chara* beds acting as nutrient sinks in shallow lakes - a review. Aquat.Bot. 72:249-260.

Langeland KA. 1996. *Hydrilla verticillata* (L. F.) Royale (Hydrocharitaceae), the "perfect aquatic weed." Castanea. 61:293-304.

Maki CK, Calatowitsch SM. 2008. Cold tolerance of the axillary turions of two biotypes of Hydrilla and northern watermilfoil. J Aquat Plant Manage. 46:42-50.

Overholt WA, Wheeler GS. 2006. Renewed efforts to identify Hydrilla biocontrol agents in Asia and Africa. Biocontrol News and Information. 27:53N.

Payton ME, Greenstone MH, Schenker N. 2003. Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? J Insect Sci. 3:34.

Puri A, MacDonald GE, Haller WT, Singh M. 2007. Growth and reproductive physiology of fluridone susceptible and resistant Hydrilla (*Hydrilla verticillata*) biotypes. Weed Sci. 55:441-445.

R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [cited Aug 2010]. Available from http://www.Rproject.org.

Roxburgh SH, Chesson P. 1998. A new method for detecting species associations with spatially autocorrelated data. Ecology. 79:2180-2192.

Spencer DF, Rejmánek M. 2010. Competition between two submersed aquatic macrophytes, *Potamogeton pectinatus* and *Potamogeton gramineus*, across a light gradient. Aquat Bot. 92:239-244.

Schmitz DC, Nelson BV, Nall LE, Schardt JD. 1991. Exotic aquatic plants in Florida: an historical perspective and review of the present aquatic plant regulation program. In: Center TD, Doren RF, Hofstetter RL, Myers RL, Whiteaker LD, editors. Proceedings of a Symposium on Exotic Pest Plants. November 2-4, 1988, Miami, Florida. Washington, (DC): United States Department of the Interior; National Park Service. p. 303-336.

Simpson D. 1989. Flora of tropical East Africa: Hydrocharitaceae. Rotterdam (Netherlands): Balkema. 29 p.

Sokal RR, Rohlf FJ. 1995. Biometry: The principles and practice of statistics in biological research. 3rd edition. New York (NY): Freeman. 881 p.

Squires MM, Lesack LFW, Huebert D. 2002. The influence of water transparency on the distribution and abundance of macrophytes among lakes of the Mackenzie Delta, Western Canadian Arctic. Freshwater Biol. 47:2123-2135.

Stainton MP, Capel MJ, Armstrong FAJ. 1977. The chemical analysis of freshwater. 2nd edition. Canadian Fisheries and Marine Services Miscellaneous Special Publication 25. 180 p.

Steward KK. 2000. Influence of photoperiod on vegetative propagule production in three turion-producing races of Hydrilla verticillata (L. f.) Royle. Hydrobiologia. 432:1-8.

Symoens JJ. 2006. Flora of tropical East Africa: Potamogoneaceae. Kew (UK): Royal Botanic Gardens. 20 p.

Takamura N, Kadona Y, Fukushima M, Nakagawa M, Kim B-H O. 2003. Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. Ecol Res. 18:381-395.

Taylor P. 1973. Flora of tropical East Africa: Lentibulariaceae. London (UK): Crown Agents. 27 p.

Taylor P. 1989. The genus *Utricularia*: a taxonomic monograph. London (UK): Kew Bulletin Additional Series XIV. 736 p.

Triest L. 1989. Flora of Tropical East Africa: Najadaceae. Rotterdam (Netherlands): Balkema. 9 p.

Turner SJ, Johnson AR, Whitford WG. 2004. Pairwise species associations in the perennial vegetation of the northern Chihuahuan desert. Southwest Nat. 49:1-10.

Van TK, Haller WT, Bowes G. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. Plant Physiol. 58:761-768.

Vanden Bossche JP, Bernacsek GM. Source book for the inland fishery resources of Africa: 1. CIFA Technical Paper. No. 18.1. Rome, FAO. 1990. 411 p. [cited Mar 2010]. Available from http://www.fao.org/docrep/005/T0473E/T0473E00.HTM.

Verdcourt B. 1971. Flora of Tropical East Africa: Cabombaceae. London (UK): Crown Agents,. 3 p.

Verdcourt B. 1989. Flora of Tropical East Africa: Nymphaeaceae. Rotterdam (Netherlands): Balkema 16 p.

Wetzel RG. 1983. Limnology. 2nd edition. New York (NY): Saunders College Publishing. 860 p.

Wilmot-Dear CM. 1985. Flora of Tropical East Africa: Ceratophyllaceae. Rotterdam (Netherlands): Balkema 4 p.

[WCFPF] World Checklist of Selected Plant Families. 2010. The Board of Trustees of the Royal Botanic Gardens, Kew. [cited Mar 2010].Available from http://apps.kew.org/wcsp/home.do.

Zhou G, Overholt WA, Kimani-Njogu SW. 2003. Species richness and parasitism in an assemblage of parasitoids attaching maize stem borers in coastal Kenya. Ecol Entomol. 28:109-118.