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Biomass and net aboveground primary productivity of macrophytes in relation to physico-chemical factors in the littoral zone of Lake Ziway, Ethiopia*

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Abstract: Biomass and net aboveground primary productivity of the macrophyte community was assessed at seven sites near the shore of Lake Ziway between August 2010 and July 2011 with the Weigert and Evans method. *Typha latifolia* (813.3 ± 27.8 g DW m^{-2}) and *Cyperus papyrus* (795.1 ± 189 g DW m^{-2}) were dominant in terms of biomass although their distribution was restricted to only a few parts of the lake. The productivity of these macrophytes was also found to be higher (2394 and 2196 g DW m^{-2} yr^{-1}, respectively) than other macrophytes in the lake. Although *Arundo donax* and *Potamogeton schweinfurthii* had higher relative density and frequency than other macrophytes in the lake, their biomass and productivity were found to be low. Redundancy analysis suggested that relatively high concentration of soluble reactive phosphate, nitrate, total phosphorus, and total Kjeldahl nitrogen concentration in the sediment were correlated with high biomass and production of the macrophytes. pH was inversely correlated with most of the macrophytes which suggested that high pH of the lake may negatively influence the productivity and biomass of the macrophytes. Even though macrophytes seem to contribute more production (carbon) to the system than phytoplankton in Lake Ziway, their biomass and productivity is still low compared to other freshwater systems. Low nutrient levels in the lake system may be limiting the productivity and biomass of the macrophytes in the lake.

Resumen: La biomasa y la productividad primaria aérea neta de la comunidad de macrófitasfueron evaluadas en siete sitios cercanos a la orilla del lago Ziway entre agosto de 2010 y julio de 2011con el método de Weigert y Evans. *Typha latifolia* (813.3 ± 27.8 g PS m^{-2}) y *Cyperus papirus* (795.1 ± 189 g PS m^{-2}) fueron dominantes en términos de biomasa, aunque su distribución estuvorestringida a unas pocas partes del lago. También se encontró que la productividad de estas macrófitas fue mayor (2.394 y 2.196 g PS m^{-2} $año^{-1}$, respectivamente) que la de otras macrófitas en el lago. A pesar de que *Arundo donax* y *Potamogeton schweinfurthii* tuvieronvalores mayoresde densidad y frecuencia relativas que otras macrófitas en el lago, sus valoresde biomasa y productividad fueron bajos. Un análisis de redundancia sugirió que las concentraciones relativamente altas de fosfatosolublereactivo, nitrato, fósforo total y la concentración total de nitrógeno Kjeldahl en el sedimento están correlacionadas con una biomasa yuna producción altas de las macrófitas. El pH estuvo correlacionado inversamente con la mayoría de las macrófitas, lo que sugiere que un pH alto del lago puede influir negativamente en la productividad y la biomasa de las macrófitas. A pesar de que las macrófitas parecen contribuir con una producción (carbono) mayor para el sistema que el fitoplancton en el lago Ziway, su biomasa y productividad siguen siendo bajas en comparación con otros sistemas

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dulceacuícolas. Los niveles bajos de nutrimentos en el sistema lacustre pueden estar limitando la productividad y la biomasa de las macrófitas en el lago.

Resumo: A biomassa acima do solo e a produtividade primária líquida da comunidade de macrófitas foram avaliadaspelo o método de Weigert e Evans,em sete locais perto da margem do Lago Ziway, entre agosto de 2010 e julho de 2011. A *Typha latifolia* (813,3 ± 27,8 g DW m^{-2}) e *Cyperus papyrus* (795,1 ± 189 g DW m^{-2}) foram dominantes em termos de biomassa, embora a sua distribuição fosse restrita a apenas algumas partes do lago. A produtividade das macrófitas também foi encontrada ser mais elevada (2394 e 2196 g DW m^{-2} yr^{-1}, respectivamente) do que outros macrófitas no lago. Apesar da *Arundo donax* e *Potamogeton schweinfurthii* terem apresentadomaior densidade relativa e frequência do que outras macrófitas no lago, a sua biomassa e produtividade foi baixa. A análise de redundância sugeriu que a relativamente elevada concentração de fosfato solúvel reativo, nitrato, fósforo total, e a concentração total de azoto Kjeldahl no sedimento estavam correlacionados com a elevada biomassa e produçãodas macrófitas. O pH estava inversamente correlacionado com a maioria das macrófitas,o que sugerira que o alto pH do lago pode influenciar negativamente a produtividade e a biomassa das macrófitas. Apesar disso, as macrófitas parecem contribuir com mais produção (de carbono) para o sistema do que o fitoplâncton no Lago Ziway, mas a sua biomassa e produtividade ainda é baixa em comparação com outros sistemas de água de água doce. Os baixos níveis de nutrientesno sistema lagunar pode estar a limitar a produtividade e a biomassa das macrófitas no lago.

Key words: Biomass, littoral zone, macrophytes, primary productivity, redundancy analysis, ziway.

Introduction

The littoral zone of lake ecosystems is an important region that affects the whole structure and function of the system. It buffers the movement of substances that flows into the lake from catchment runoff or streams thereby affecting the physical and biological processes in lake ecosystems (Peters & Lodge 2009). It is also the most productive area of lakes and is known to be an important contributor of energy to higher trophic levels of the system (Goldsborough *et al.* 2005; Peters & Lodge 2009; Wetzel 1990). Recently, the contribution of the littoral zone of shallow lakes to the ecological integrity and functions of the system has attracted the interest of many researchers. One of the means to describe the functions of the littoral zone of a lake ecosystem is by determining productivity of the zone to provide a quantitative base for further research on the whole lake ecosystem (Cronin *et al.* 2006; Klopateki & Stearns 1978).

For a number of years, most limnological studies on primary productivity of the littoral zones of lakes have focused largely on the photosynthetic bacteria and phytoplankton (e.g. Currie & Kalff 1984; Wetzel 1964) and the contribution of primary production by other photosynthetic organisms was given less attention until recent years. Almost all primary productivity research on fresh waters conducted in Ethiopia has focused on phytoplankton (e.g. Kifle 1985; Kifle & Belay 1990; Tilahun 1988) whereas the contribution of other photosynthetic organisms was overlooked. Since the contribution of macrophytes to the productivity of lakes is sometimes higher than other producers in the system, the productivity of the system would be underestimated if macrophytes are not included in productivity studies in rivers, marshes, ponds and large shallow lakes (Wetzel 1964).

Macrophytes not only serve as a nutrient source or sink (e.g. Carpenter 1980; Carignan & Kalff 1982) and substrate for other organisms in the littoral region of a lake, but also contribute energy and nutrient to the system by their primary production and detritus formation (Peters & Lodge 2009). According to Westlake (1963), the littoral zones of lakes and reservoirs are among the most productive regions of the world in terms of primary production, because of the contribution of macrophytes. Thus, these plants can be an important component in the biogeochemistry process of aquatic ecosystems.

Most of the earlier studies on macrophyte productivity focused on single species. *Typha*, *Scirpus* and *Carex* species have been intensively studied in many temperate aquatic systems (Auclair *et al.* 1976; Kistritz *et al.* 1983; Pegman & Ogden 2005), while *Cyperus papyrus* is the most commonly studied species in many tropical lakes (e.g. Saunders *et al.* 2007). However, attempts to simultaneously measure the primary production of several freshwater macrophyte communities have been few in number (Rich *et al.* 1971).

It is evident that the primary production in aquatic ecosystems can affect other ecosystem functions (Wetzel 2001). Information of autotrophic production can help to understand the functioning of lakes which is fundamental to the sustainable management of the system. Estimating macrophyte productivity and biomass in lakes is not only important for quantifying ecological functions, but it also indicates the trophic status of the lake and contributes to the understanding of carbon dynamics in aquatic systems, which in turn can help to understand the role of macrophytes and their habitat in global climate change (Mitsch & Bouchard 1998). As the productivity of macrophytes and other producers can be highly influenced by the dynamics of many chemical elements and physical parameters, it is important to measure these parameters to explain trends in macrophyte productivity (Wetzel 2001).

The present study attempts to determine the contribution of macrophyte primary productivity to the total photosynthetic carbon fixation or energy budget of Lake Ziway and is part of a larger research effort to describe the role of macrophytes in the function of the lake ecosystem.

Materials and methods

Description of the study area

Lake Ziway is a freshwater lake that lies in the Ethiopian rift valley at 8° 01' N/38° 47' E (Fig.1) and at an altitude of 1636 m above sea level (Von Damm & Edmond 1984). The lake has a surface area of 442 km^2, a maximum depth of 8.9 m and an average depth of 2.5 m (Von Damm & Edmond 1984). Lake Ziway is an open lake which is fed by Ketar and Meki Rivers that drain from the Southeastern and Northwestern highlands, respectively, and drains into Lake Abijata through the Bulbula River in the south (Fig. 1). Climatic condition of Lake Ziway region is a semiarid type. The annual precipitation ranges between 650 and 1200 mm whereas mean annual temperature is between 15 and 25 °C (Legesse *et al.* 2001).

Recently, much research has been done on the ecology and biology of the lake in attempts to conserve the lake resources and come up with better management options. The ecology of phytoplankton (Tilahun 2006), zooplankton (Dagne *et al.* 2008), and fish (Yohannes 2003) were extensively described by these authors and many other studies. Most of earlier researchers who conducted botanical studies around the lake focused on describing the diversity of the vegetation on the islands and the edge of the lake and on how lakeside community make of use of indigenous plants (Giday 2001; Zegeye *et al.* 2006). However, efforts to describe the role of macrophytes in the functioning of the lake are scarce. Since the macrophytes and trees around the shore are being heavily cleared by the lakeside communities for different purposes (e.g., house roofing, making rafts), knowing the status of the plants is crucial for wise use of these resources. Removal of macrophytes is intensified in the sites close to human settlements.

Net aboveground primary productivity

Net aboveground primary productivity (NAPP) of macrophyte species was determined at seven sites within the littoral zone of the lake (Fig. 1). The sites were selected based on their proximity to human settlements and anthropogenic effect and accessibility for the study. Bulbula, ZFR (near to Ziway Fisheries Research Center) and Kontula sites are close to human settlements, local farms, and some industries (e.g., floriculture, particularly at the Bulbula site) whereas the other sites, Kobo, Gelila, Abeye 1, and Abeye 2, are relatively far from such impacts. Relatively, the edges of the first three sites were better covered by riparian vegetation than the other sites. The aim of this category or site selection was to encompass varying environmental conditions in the assessment of biomass and productivity of macrophytes.

NAPP of each macrophyte species was estimated between August 2010 and July 2011 with the method of Weigert & Evans (1964) as described in Cronk & Fennessy (2001), mainly after measuring the dry weight monthly and determining the average decomposition rate of each species. The method sums live and dead material

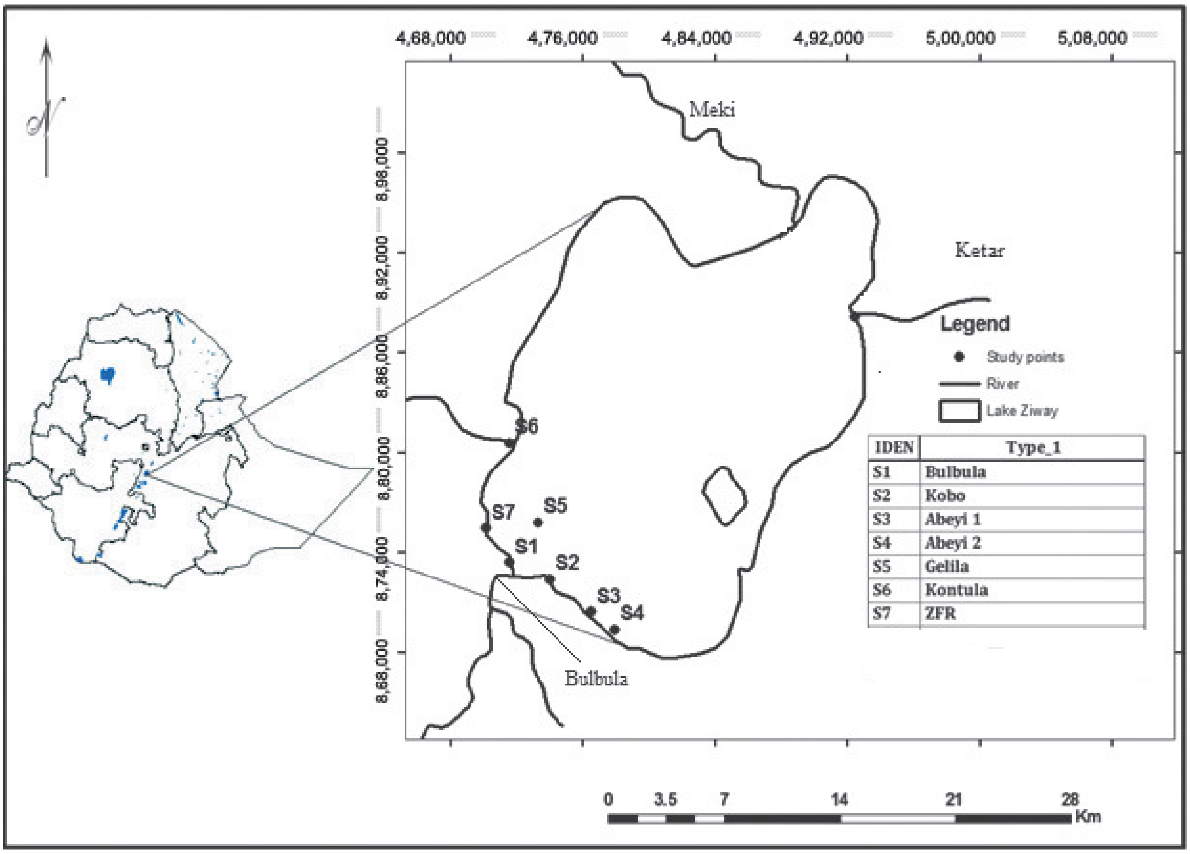

Fig. 1. Map of Ethiopia (Inset) and the study sites in Lake Ziway.

produced during each sampling interval and adds an estimate for the decomposed plant material during the interval (Cronk & Fennessy 2001). According to Santos & Esteves (2004), the methods that incorporate corrections for biomass loss during sampling intervals, such as Weigert & Evans (1964), should be used in net primary productivity studies in tropical aquatic systems. This is because, due to the dynamics of tropical environment, the use of methods that do not correct for biomass losses due to mortality during sampling intervals can greatly underestimate NAPP.

A quadrat with 0.625 m^2 area was used, as in Lee (1990), to harvest the macrophytes along transect that extended from the shore towards the open water of the lake as far as the depth where submerged species were found. At least four quadrats were laid in each site at 25 m interval along the transect following Gaudet & Muthuri (1981) and the quadrat samples were averaged for analysis. As much as possible, all aboveground parts of the plants, dead and live, were harvested. The macrophytes were washed to remove any attached organisms. Samples were segregated by species and placed in plastic containers. Dead and live species were also separated. All aboveground material was placed in plastic bags and taken to the laboratory for determination of dry weight. The aboveground dry weight biomass of each macrophyte species was measured by drying in an oven at 105 °C for 24 h (Wetzel & Likens 1991) and monthly (at the end of each month during the study time).

Net Primary Productivity was calculated using the following formula:

$$Y_i = \Delta b_i + d_i$$

where, Y_i is Net aboveground primary productivity, bi is standing crop of live material after time of i (a month in the case of this study) and d_i is mortality of live material,

d_i =standing crop dead material + decomposed material during the month (which was estimated from 'litterbag' decomposition experiment).

'Litterbag' decomposition experiment

Fresh macrophyte samples of each species were harvested from the littoral sites of the lake, washed to remove debris and other attached material, chopped and weighed. 30 g of culm of each species was used for the study after drying for 3 h in the air. The macrophytes litters were transferred to litter bags made of nylon net (replicated for each species) with standard size of 15 x 20 cm and a mesh size of 1.5 mm after Kufel *et al.* (2004). The bags were incubated *in situ* at 0.5 m below the surface (near the sediment) near the shore by tying with cemented stands following Wetzel & Likens (1991). Two litter bags of each species were retrieved at two week intervals for the determination of change in dry weight over the sampling time.

Nutrient and physico-chemical variable analysis

Physical parameters (pH, temperature, and conductivity) of the lake were measured *in situ* at the end of every month (once in a month) between August 2010 and July 2011. The measurements were taken twice at 1 m depth at each sampling plot of the sites during each visit and the averages were taken for analysis. pH and temperature were measured with a digital pH meter (Hanna 9024) and conductivity was measured using a conductivity meter (Elmetron - model of CC-411). Secchi depth was measured with a secchi disc of 20 cm diameter.

Composite water samples (by merging sample from the surface and 1 m depth) were taken once in a month from each sampling site in duplicates for nutrient analysis. Water chemistry analysis of dissolved inorganic nutrients was conducted monthly spectrophotometrically in the limnology laboratory of Addis Ababa University. Nitrate was analyzed with sodium salicylate method (Roberg & Edwards 1983), ammonium with indo-phenol blue (APHA 1995), and soluble reactive phosphate (SRP) with ascorbic method (APHA 1999). Nitrite concentration was determined by the reaction between sulfanilamide and N-naphthyl-(1)-ethylendiamin-dihydrochloride (APHA 1995). Sediment samples were taken, twice during dry and twice during wet seasons, from each study site, for analysis of total nitrogen and phosphorous concentration in the sediment, using a 40 cm diameter PVC corer after Powel (2008) from approximately 15 cm of the sediment surface. When the depth didn't allow the use of the PVC corer, an Ekman grab was used. Two samples were taken from each site during each visit and the result of the analysis was averaged. Total nitrogen was determined using the Kjeldahl procedure following Bremner & Mulvaney (1982) while total phosphorous was determined using vanadate-molybdate yellow method after ashing and nitric acid digestion following the procedure of Chapman & Pratt (1961).

Data analysis

An Analysis of Variance (ANOVA) was used to test if aboveground biomass of the macrophytes varied between sites followed by a Tukey test to identify which sites were significantly different from the others in terms of biomass. Redundancy analysis (RDA) was performed to observe the relation of species biomass and productivity data to environmental factors using CANOCO 4.5 software. Before selecting RDA for this analysis, DCA (Detrended Correspondence Analysis) was conducted to check the response of the species data (biomass and productivity of the macrophytes) to the environmental variables. The results showed that the species data had linear responses to environmental variables and the range of variation of the environmental variables was narrow, as observed from the length of longest gradient which was less than 3 in both cases (ter Braak 1987). According to ter Braak (1987), and Leps & Smilauer (1999), RDA has to be used if the species data is assumed to show linear response to the environmental variables or if length of longest gradient is less than 3 during DCA analysis. Both data, species (biomass and productivity) and environmental, were log-transformed.

Results

Macrophytes biomass

Mean macrophyte biomass of the lake was estimated to be 1020.2 ± 214.7 g DW m^{-2} and the highest biomass was recorded at Kontula (1996.7 g DW m^{-2}) and the lowest at Kobo site (581.3 g DW m^{-2}). *Typha latifolia* and *Cyperus papyrus* were found to be dominant in terms of aboveground biomass (813.3 ± 27.8 g DW m^{-2} and 795.1 ± 189 g DW m^{-2} respectively) on the sites where they occurred (Fig. 2). *T. latifolia* was found at Kontula and Bulbula site whereas *C. papyrus* at Kontula. On the other hand, in spite of their dominance in relative abundance and frequency and wider occurrence in the lake, the biomass (g DW m^{-2}) of *Arundo donax* (251.7 ± 52.4), *Echinochloa colona* (211.2 ± 36.7), *Cyperus articulatus* (201.9 ± 39.7), *Nymphaea lotus* (139.1 ± 39.4), and *Potamogeton schweinfurthii* (167.8 ± 39.1 g DW m^{-2}) was relatively low. The lowest macrophyte biomass was

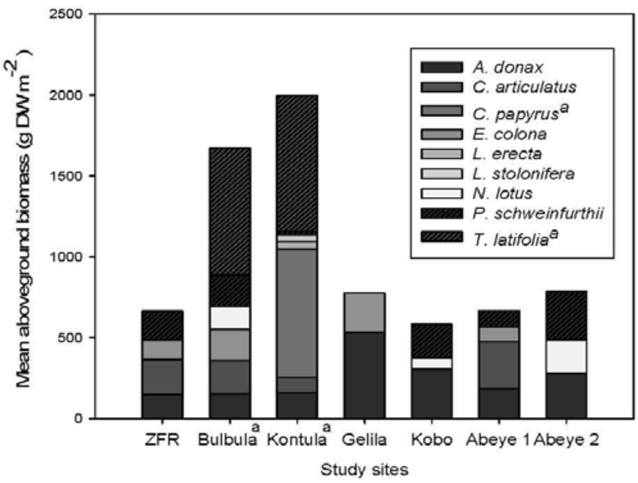

Fig. 2. Mean aboveground biomass of macrophytes at Lake Ziway sites ([a] refers sites and macrophytes that had significantly higher biomass than other groups, Tukey Games-Howell test, $P < 0.05$).

recorded for *Ludwigia erecta* and *Ludwigia stolonifera,* 44.3 and 39.2 g DW m^{-2}, respectively, which occurred only at one site (the same site).

There was statistically significant variation in biomass of the macrophytes among the sites (one-way ANOVA, $F_{6,77} = 17.36, P < 0.05$). Biomass of macrophytes was considerably higher at Kontula and Bulbula sites where *T. latifolia* contributed significantly to the total biomass (Fig. 2). On the other hand, Kobo, ZFR and Abeye 1 had lower macrophyte biomass than the other sites.

The peak biomass attained by the species in the lake varied depending on season and the site. However, most of the species attained peak biomass between March and July. *T. latifolia* attained peak biomass in May at both sites where the species occurred (Fig. 3b and c) and *C. papyrus* in March (Fig. 3c). *A. donax, E. colona, P. schweinfurthii*, and *C. articulatus* attained their peak biomass between January and July in the sites where they occurred (Fig. 3).

Macrophyte aboveground biomass in relation to environmental variables

The first two axes of the RDA explained 70 % of the species-environment variance (Table 1). The RDA ordination of the species-biomass association indicated that secchi depth, SRP, nitrate, ammonium and total nitrogen of the sediment, conductivity, and temperature were positively correlated with the first axis. Except for the last two variables, the others were strongly correlated with the axis (Fig. 4). The biomass of *C. papyrus, L. erecta, L. stolonifera,* and *T. latifolia* was associated with relatively high values of secchi depth, SRP, nitrate, ammonium, and total nitrogen of the sediment. *T. latifolia* biomass was strongly and positively correlated with SRP concentration and it occurred only at Kontula and Bulbula sites where SRP concentration was relatively high. The biomass of *C. articulatus* was more strongly correlated with nitrate than other environmental variables. On the other hand, biomass of *A. donax* was inversely associated with SRP and nitrate concentrations of the water. Nitrite, total phosphorous of the sediment, and pH were negatively correlated with the first axis. The second axis was positively correlated with all environmental variables used in this study except pH, nitrate, and nitrite. Relatively high biomass of *A. donax* was associated with relatively high values of total phosphorous in the sediment. Biomass of *E. colona* had a positive but very weak correlation with conductivity, and pH and a negative association with the other environmental variables.

Net aboveground primary productivity

The mean NAPP of macrophytes at the study sites was found to be 3623.7 g DW m^{-2} yr^{-1}. The highest NAPP was recorded at the Kontula site (7224 g DW m^{-2} yr^{-1}) and the lowest at the Kobo site (2192.6 g DW m^{-2} yr^{-1}) (Fig. 5). *T.latifolia* and *C. papyrus* had the highest NAPP, 2394 and 2196 g DW m^{-2} yr^{-1}, respectively, followed by *A. donax* (864.2 g DW m^{-2} yr^{-1}) and *P. schweinfurthii* (774.2 g DW m^{-2} yr^{-1}).

The RDA analysis indicated that the first two axes explained 69.6 % of the cumulative percentage of variance of NAPP of the macro-phytes versus physico-chemical factors correlation (Table 2). The first axis was positively related with secchi depth, total nitrogen of the sediment, SRP, ammonium, nitrate, conductivity, and temperature. Except temperature and conductivity, the other parameters were strongly correlated with the axis (Table 2). The second axis, which explained 29.7 % of the variance, was positively correlated with secchi depth, total nitrogen of the sediment, SRP, ammonium, total phosphorous of the sediment, and nitrite. Nitrite had a weak association with this axis.

Factors that affected the productivity of the macrophytes were variable for different macrophytes. Productivity of *T. latifolia*, *C. papyrus*, *L. erecta,* and *L. stolonifera* were strongly and positively related to secchi depth, SRP, ammonium, total nitrogen in the sediment, and nitrate. On the other hand, productivity of *A. donax, C. articulatus, P. schweinfurthii*, and *N. lotus* was positively related with conductivity, temperature, and nitrate, though the correlation between conductivity and temperature and the productivity of the macrophytes was weak (Fig. 6). Conductivity and temperature seem also to have little influence in affecting both biomass and productivity of the other macrophytes as their correlations with the macrophytes were low.

Discussion

Aboveground biomass

T. latifolia attained the highest biomass among the macrophytes in Lake Ziway during the present study. Biomass of *T. latifolia* (813.3 ± 27.8 g m^{-2}) observed in this study was in the range estimated for the species by Pratt *et al.* (1984) (4.3-14 t ha^{-1}), but was greater than most biomass estimates of *T. latifolia*, particularly in temperate freshwater marshes (e.g., Atkinson *et al.* 2010; McNaughton 1966). On the other hand, *T. latifolia* biomass in this study was lower compared to the biomass recorded in some fresh water systems (e.g., Boyd & Hess 1970; Kleopatic & Stearns 1978).

The biomass of *T. latifolia* seems to be stunted mainly due to the lower SRP in most sites of Lake Ziway and this agrees with the observation of Atkinson *et al.* (2010). Macek & Rejmankova (2007) hypothesized that phosphorous input into wetlands will result in expansion of *T. latifolia* biomass and can even lead to competitive exclusion of other co-occurring species. Plants can uptake phosphorous only when dissolved in water as ortho-phosphates or poly-phosphates (Shuman 1994).

Mean aboveground biomass of *C. papyrus* (795.1 ± 189 g DW m^{-2}) in Lake Ziway was low compared to biomass of the same plant in many similar African lakes. For example, Jones & Muthuri (1997) reported the total standing biomass of the papyrus in Lake Naivasha to be 7800 g DW m^{-2}. Mnaya *et al.* (2007) reported the average value of above ground biomass of the plant in Lake Victoria to be 5789 g DW m^{-2}. According to Perbangkhem & Polprasert (2010), papyrus can attain aboveground biomass of 2200 to 3100 g DW m^{-2} in tropical climate area with abundant sunlight. This signifies the importance of other factors (mainly nutrients) in limiting the biomass of this species in the lake rather than factors associated with geographical location of the lake (e.g., light and temperature).

RDA analysis suggested that relatively high total nitrogen concentration of the sediment, ammonium, and SRP were important factors which may support the high biomass of *C. papyrus* and *T. latifolia*. These species were absent in sites where the total nitrogen of the sediment, ammonium, and SRP concentrations were low. Similarly, in Lake Naivasha, the concentration of ammonium ions and soluble reactive phosphate were higher in papyrus swamp water than in other regions of the lake (Muthuri & Jones 1997).

Cyperus papyrus biomass was negatively associated with pH and nitrite. El Ghani *et al.* (2010) stated that the plant grows in fresh water with pH varying from 6.6 to 7.5. The presence of relatively high pH in Lake Ziway (7.8 - 8.6) may be negatively affecting the biomass of *C. papyrus* and most of other macrophytes in Lake Ziway. pH affects the rate of nutrient uptake by macrophytes. Titus & Stone (1982) observed that the increase in pH from 7.0 to 9.0 significantly reduced the rate of uptake of inorganic carbon by *Myriophyllum spicatum*. Van *et al.* (1976) also observed negative relationships between increases in pH and decreases in CO_2 availability and the photosynthetic rate for *Hydrilla verticillata*, *Myriophyllum spicatum*, and *Ceratophyllum demersum*. According to Shuman (1994), the rate of uptake of ortho-phosphates or poly-phosphates by plants is highly pH-dependent and optimal uptake occurs at 6.5. Thus, a relatively high pH might have hindered the expansion of macrophytes such as *T. latifolia* which require higher soluble phosphorous. It is highly possible that the relatively high pH in Lake Ziway could be one factor that has limited the biomass of macrophytes. pH and nitrite were not only negatively correlated with *C. papyrus* and *T. latifolia* biomass, but also with most of the macrophytes in this study. The negative correlation between the macrophytes and nitrite might be related to the toxicity of the nutrient to aquatic plants and inability of the plants to assimilate it (Alonso & Camargo 2009).

A. donax biomass in this study (1.495-5.31 t h^{-1}) was much lower than biomass of the species reported in many water bodies, both tropical and temperate (Giessow *et al.* 2011; Sharma *et al.* 1998; Spencer *et al.* 2006). Sharma *et al.* (1998) reported the aboveground biomass of the plant to

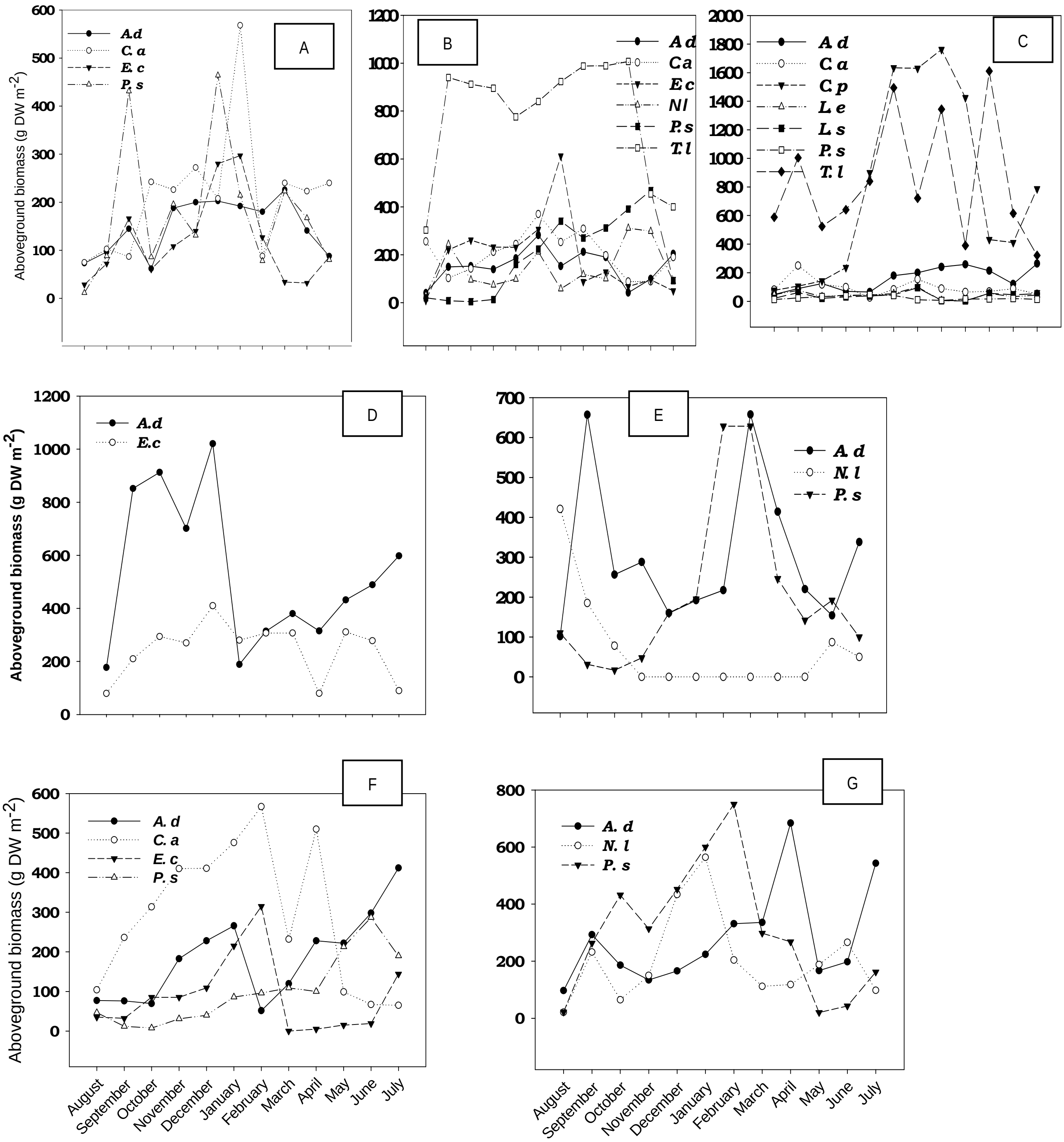

Fig. 3. Seasonal variation of macrophyte biomass in the study sites (A- ZFR, B-Bulbula, C-Kontula, D-Gelila, E-Kobo, F-Abeye 1 and G- Abeye 2; Abbreviations of legends: *A.d- Arundo donax, C.a- Cyperus articulatus, C.p- Cyperus papyrus, E.c- Echinochloa colona, L.e- Ludwigia erecta, L.s- Ludwigia stolonifera, N.l - Nymphaea lotus, P.s - Potamogeton schweinfurthii, T.l – Typha latifolia*).

Table 1. Result of redundancy analysis (RDA) of macrophyte biomass versus physico-chemical variables relationship including eigenvalues and percentage of variance explained by the first two axes.

Variables	Axis 1	Axis 2
Eigenvalues	0.423	0.277
Cumulative percentage variance of biomass-environment relation	42.3	70.0
pH	-0.7245	-0.0050
Conductivity	0.0785	0.3149
Temperature	0.2183	0.1852
Secchi depth	0.9139	0.2304
SRP	0.8338	0.0607
Nitrate	0.8253	-0.2084
Nitrite	-0.5048	-0.0484
Ammonium	0.6290	0.2943
Sed TN	0.8225	0.2929
Sed TP	- 0.6682	0.2968

be 36-167 t hr^{-1} in India, whereas Spencer *et al.* (2006) and Giessow *et al.* (2011) reported the biomass of the species to be 171 and 155 t hr^{-1}, respectively, in different lake sites in the USA. The biomass of *A. donax* was associated with total phosphorous concentration of the sediment. It was recorded that the biomass of perennial plants such as *A. donax* was higher where there were higher nutrients (e.g. Ercoli *et al.* 1999; Maryan 1997). However, recently, Angelini *et al.* (2005) reported that higher biomass of this plant can also be observed where such resources are low.

Net aboveground primary productivity

The aboveground primary productivity of Lake Ziway was much higher than the average estimation of Colinvaux (1993) for lakes (tropical and temperate) (500 g DW m^{-2} yr^{-1}). However, the NAPP of most of the macrophytes investigated in this study was lower than similar species in other water bodies. The productivity of *A. donax* (864 g Dw m^{-2} yr^{-1} or 8.64 t ha^{-1} yr^{-1}) and *C. papyrus* (2196 g DW m^{-2} yr^{-1} or 21.96 t ha^{-1} yr^{-1}) was below the range observed by Westlake (1975) in freshwater systems (12-38 and 30-50 t ha^{-1} yr^{-1} of productivity for both species, respectively). The productivity of *A. donax* (8.65 t ha^{-1} yr^{-1}) was also lower compared to estimates from the Mediterranean Sea where most of the research related to biomass and production of *A. donax* was done. Di Nasso *et al.* (2011) reported an average yield of 30 t ha^{-1} yr^{-1} of *A. donax* in Italy, whereas Angelini *et al.* (2009) stated that it can attain higher productivity (38 t ha^{-1} yr^{-1}) in the same region.

Productivity of *A. donax* was most highly correlated with nitrate in this study. A study on the impact of nutrient enrichment from residential and agricultural land use types on *A. donax* infestation throughout several watersheds in Southern California showed that water systems with enriched soil nitrate supported *A. donax* infestation whereas sites with lower nitrogen levels did not (Coffman 2007). Decruyenaere (2000) reported that the plant invaded more readily in areas where soil nitrogen was high, growing rapidly with elevated nutrients. In this study, such a strong association was not observed between productivity of *A. donax* and nitrogen concentration of the sediment, most probably due to the low nitrogen level of the sediment in most of the study sites, except Kontula. In addition, only Kjeldahl total nitrogen was determined in this study. Sediment nitrate must be measured to characterize the relationship between *A. donax* productivity and total sediment nitrogen. However, nitrogen concentration in the sediment could increase in the lake from catchment erosion as some of the farms are expanding and using inorganic fertilizers which can facilitate the infestation of the reed. But, currently, the productivity of *A. donax* seems to be low in the lake.

The productivity of *T. latifolia* (23.94 t ha^{-1} yr^{-1}) was within the range estimated by Westlake (1975) (11-33 t ha^{-1} yr^{-1}). The high productivity of *T. latifolia* can be explained in a number of ways. The most important reasons are that *T. latifolia* is not limited by the shortage of water in a natural wetland and the canopy arrangement of the leaves appears to increase the efficiency with which directly incident and reflected sunlight can be utilized in photosynthesis (Sheehy & Cooper 1973). Because of the upright leaf angle orientation, a greater proportion of the leaf area is exposed to direct sunlight.

Comparison of macrophyte and phytoplankton primary productivity

Tilahun & Ahlgren (2010) estimated the primary production of phytoplankton in Lake Ziway to be 390 g C m^{-2} yr^{-1} which is equivalent to 780 g DW m^{-2} yr^{-1} following the conversion factor of Strickland (1966) (mg DW of phytoplankton is approximately twice mg C). Phytoplankton productivity was much lower when compared to the mean macrophyte productivity of the lake (3623.7 g DW

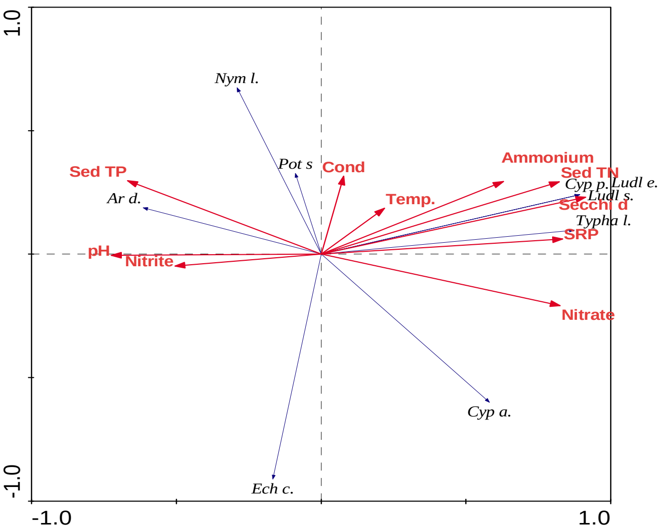

Fig. 4. Biplots of the first two axes of the redundancy analysis showing the association of macrophyte species biomass and environmental variables (Abbrevation: *Ar d - Arundo donax, Cyp a - Cyperus articulatus, Cyp p. - Cyperus papyrus, Ech c - Echinochloa colona, Ech s. - Ludl e. - Ludwigia erecta, Ludl s., - Ludwigia stolonifera, Nym l. - Nymphaea lotus, Pot s. - Potamogeton schweinfurthii, Typha l. - Typha latifolia*, SRP - soluble reactive phosphate, Cond. - conductivity, Temp- Temperature, Sed TP- Sediment total phosphorous and Sed TN- Sediment total nitrogen).

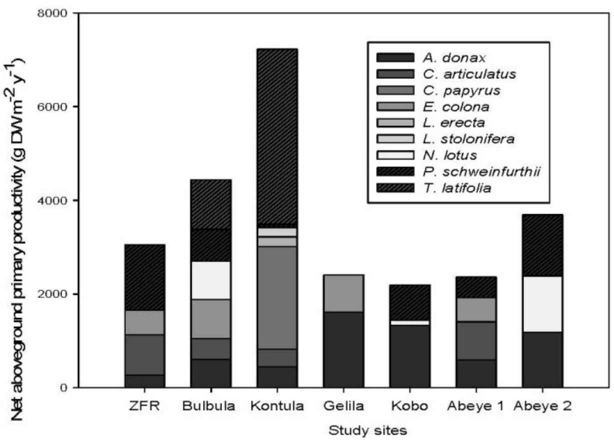

Fig. 5. Net aboveground productivity of macrophytes at Lake Ziway sites.

m^{-2} yr^{-1}). Furthermore, mean NAPP of macrophytes of Lake Ziway was also higher than phytoplankton mean gross integral photosynthesis or gross oxygen production with the concomitant production of carbon dioxide (3978.4 g O_2 m^{-2} yr^{-1}) obtained by Hailu (2011). The value was equivalent to 1193.5 g C m^{-2} yr^{-1} or 2387.04 g DW m^{-2} yr^{-1} following conversion factors of Ryther (1956) and Strickland (1966). These results suggest that macrophytes contribute more primary production to the lake system than phytoplankton. It also supports the supposition that the lower biomass of phytoplankton in Lake Ziway might be due to the competitive dominance of macrophytes over phytoplankton for available resources or through production of repressive chemicals and increased turbidity (Beneberu & Mengistou 2010).

The contribution of epiphytes and macrophytes to the total annual primary production is often significant in shallow lakes with large littoral zones such as Lake Ziway (Davis 1965; Galanti & Romo 1997). A study on the primary production of phytoplankton, submerged macrophytes, and their epiphytes, in two large shallow lakes, Lake Peipsi and Lake Vortsjarv (Estonia), showed that macrophytes accounted for the largest percentage of primary production, 84.2 % in Lake Peipsi and 58 % in Lake Vortsjarv (Noges *et al.* 2009). Similarly, the macrophyte community in Lake Ziway (with its extensive vegetated littoral zone) seems to contribute the highest percentage of primary production than phytoplankton. However, the primary productivity of the macrophytes, especially *T. latifolia*, has to be corroborated by other methods, as the Weigert & Evans (1964) method was criticized by some researchers (e.g., Dickerman *et al.* 1986) to overestimate productivity.

Seasonal variation in biomass dynamics of macrophytes in Lake Ziway

Even though there was no statistically significant seasonal difference in abundance of macrophytes in Lake Ziway during the study period, the biomass of most species peaked between March and July which was the beginning of the rainy season. Several reports have documented wide seasonal variation of biomass of macrophytes in tropical environments (e.g. Camargo & Esteves 1995; Camargo & Esteves 1996). It is evident that seasonal variation of biomass production in tropical regions is usually related to the seasonal variation of rainfall and water level, usually produced by a flood pulse (e.g. Camargo & Esteves 1995; Junk 1986, Junk & Piedade 1993), unlike temperate regions where a seasonal variation of aquatic macrophytes biomass production is a function of temperature and photoperiod (Payne 1986).

Table 2. Result of redundancy analysis (RDA) of NAPP versus physico-chemical relationship including eigenvalues and percentage variance explained by the first two axes.

Variables	Axis 1	Axis 2
Eigenvalues	0.399	0.297
Cumulative percentage variance of productivity-environment relation	39.9	69.6
pH	-0.7308	-0.0902
Conductivity	0.1754	-0.1746
Temperature	0.3112	-0.3926
Secchi depth	0.9191	0.2315
SRP	0.8133	0.2622
Nitrate	0.7818	-0.3084
Nitrite	-0.4762	0.0334
Ammonium	0.6622	0.4127
Sed TN	0.8200	0.4940
Sed TP	0.6619	0.4359

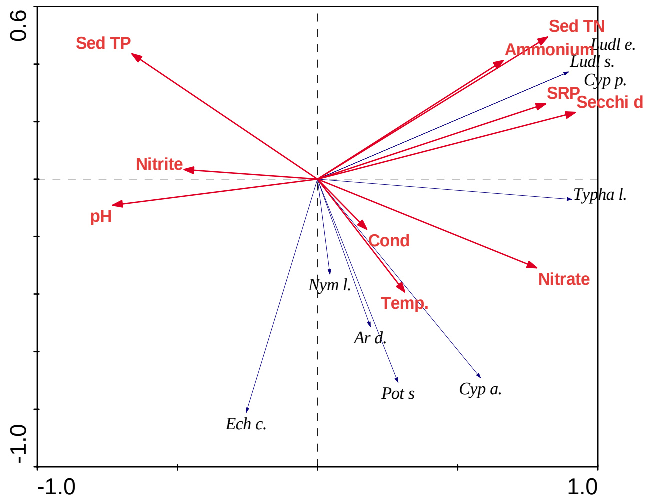

Fig. 6. Biplots of the first two axes of the redundancy analysis showing the association of macrophyte species productivity and environmental variables, For abbreviations, see the legend for Fig. 4.

In conclusion, macrophyte production in Lake Ziway is low, though the macrophyte community may be contributing more carbon to the system than phytoplankton. The low macrophyte productivity is likely due the low availability of nutrients in the lake because aquatic ecosystems that have lower dissolved nutrients in the system generally exhibit low macrophyte primary productivity (Wetzel 1983). RDA analyses suggested that nutrients were relatively more important in affecting productivity and biomass of macrophytes than physical factors such as conductivity and temperature, whereas pH and nitrite status of the lake negatively affected the biomass and production of most macrophyte species. In addition, the current practice around the lake, such as harvesting macrophytes by the lakeside community for different household purposes should be prohibited, since the biomass and production of most of macrophyte species is already low in the lake, even in the sites where the biomass and productivity was considerably higher (Bulbula and Kontula sites) than other studied sites.

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References

Alonso, A. & J. A. Camargo. 2009. Effects of pulse duration and post-exposure period on the nitrite toxicity to a freshwater amphipod. *Ecotoxicology and Environmental Safety* **72**: 2005-2008.

Angelini, L. G., L. Cecarrini & E. Bonari. 2005. Biomass yield and energy balance of giant reed (*Arundo donax* L.) cropped in central Italy as related to different management practices. *European Journal of Agronomy* **22 :** 375-389**.**

Angelini, L. G., L. Ceccarini, N. Di Nasso & E. Bonari. 2009. Comparison of *Arundo donax* L. and Miscanthus x giganteus in a long-term field experiment in Central Italy: analysis of productive characteristics and energy balance. *Biomass Bioenergy* **33**: 635-643.

APHA. 1995. *Standard Methods*. 19th edn., American Public Health Association, Washington**.**

APHA. 1999. *Standard Methods for the Examination of Water and Waste Water*. 20th edn., American Public Health Association, New York.

Atkinson, R. B., J. E. Perry, G. B. Noe, W. L. Daniels & J. Cairns. 2010. Primary productivity in 20-year old created wetlands in southwestern Virginia. *Wetlands* **30**: 200-210.

Auclair, A. N. D., A. Bouchard & J. Pajaczkowskip. 1976. Plant standing crop and productivity relations in a Scirpus-Equisetum wetland. *Ecology* **5**: 941-952.

Beneberu, G. & S. Mengistou. 2010. Oligotrophication trend in Lake Ziway, Ethiopia. *SINET: Ethiopian Journal of Sciences* **32**: 141-148.

Boyd, C. E. & L. W. Hess. 1970. Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. *Ecology* **51**: 296-300.

Bremner, J. M. & C. S. Mulvaney. 1982. Nitrogen-total. pp. 599- 609. *In:* R. H. Miller & D. R. Keeney (eds.) *Methods of Soil Analysis. Part II*: *Chemical and Microbiological Properties*. American Society of Agronomy and Soil Sciences Society of America, Madison, U.S.A.

Camargo, A. F. M. & F. A. Esteves. 1995. Biomass and productivity of aquatic macrophytes in Brazilian lacustrine ecosystems. pp. 137-149. *In:* J. G. Tundisi, C. E. M. Bicudo & T. T. Matsumura (eds.) *Limnology in Brazil*. ABD/SBL, Rio de Janeiro.

Camargo, A. F. M. & F. A. Esteves. 1996. Influence of water level variation on biomass and chemical composition of the aquatic macrophyte *Eichhorrina azurea* (Kunth) in an oxbow lake of the Rio Mogi-Guap (SBo Paulo, Brazil). *Archiv für Hydrobiologie* **135**: 423-432.

Carignan, R. & J. Kalff. 1982. Phosphorus release by submersed macrophytes: Significance to epiphyton and phytoplankyton. *Limnology and Oceanog*raphy **27**: 419-427.

Carpenter, S. R. 1980. Enrichment of Lake Wingra, Wisconsin, by submersed macrophyte decay. *Ecology* **61:** 1145-1155.

Chapman, H. D. & F. P. Pratt. 1961. *Ammonium Vandate-Molybdate Method for Determination of Phosphorus*. 1st edn., California: California University, Agriculture Division, USA.

Coffman, G. C. 2007. *Factors Influencing Invasion of Giant Reed* (Arundo donax) *in Riparian Ecosystems of Mediterranean-type Climate Regions*. Doctoral Thesis, Los Angeles, USA.

Colinvaux, P. 1993. *Ecology*. John Wiley and Sons, New York.

Cronin, G., W. M. Lewis Jr. & M. A. Schiehser. 2006. Influence of freshwater macrophytes on the littoral ecosystem structure and function of a young Colorado reservoir. *Aquatic Botany* **85**:37-43.

Cronk, J. K. & M. S. Fennessy. 2001. *Wetland Plants: Biology and Ecology*. CRC, U.S.A.

Currie, D. J. & J. Kalff. 1984. The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater. *Limnology and Oceanography* **29**: 311-321.

Dagne, A., A. Herzig, C. D. Jersabek & Z. Tadesse. 2008. Abundance, species composition and spatial distribution of Planktonic rotifers and Crustaceans in Lake Ziway (Rift Valley, Ethiopia). *International Review of Hydrobiology* **93**: 210-226.

Davis, G. S. 1965. *The Productivity of the Macrophytes of Marion Lake*. University of British Colombia, U.S.A.

Decruyenaere, J. G. 2000. *Seasonal and Site Eeffects on the Vegetative Reproduction and Demography of* Arundo donax *L. (Poaceae)*. M.Sc. Thesis, University of California, U.S.A.

Dickerman, J. A., A. J. Stewart & R. G. Wetzel. 1986. Estimates of net annual aboveground production: sensitivity to sampling frequency. *Ecology* **67**: 650-659.

Di Nasso, N. N., N. Roncucci, F. Triana, C. Tozzini & E. Bonari. 2011. Seasonal nutrient dynamics and biomass quality of giant reed (*Arundo donax* L.) and Miscanthus (*Miscanthus* X *giganteus* Greef et Deuter) as energy crops. *Italian Journal of Agronomy* doi:10.4081/ija.2011.e24

EL-Ghani, M., A. M. El Fiky, A. Soliman & A. Khattab. 2010. Environmental relationships of aquatic vegetation in the freshwater ecosystem of the Nile Delta, Egypt. *African Journal of Ecology* **49:** 103-118.

Ercoli, L., M. Mariotti, A. Masoni & E. Bonari. 1999. Effect of irrigation and nitrogen fertilisation on biomass yield and efficiency of energy use in crop production of *Miscanthus*. *Field Crops Research* **63**: 3-11.

Galanti, G. & S. Romo. 1997. Epiphyton biomass on the floating leaved water chestnut (*Trapa natans*) and its importance for the carbon balance in the eutrophic Lake Candia (N. Italy). *Memorie dell'Istituto Italiano di Idrobiologia* **56**: 95-111.

Gaudet, J. J. & F. M. Muthuri. 1981. Nutrient relationships in shallow water in an African lake, Lake Naivasha. *Oecologia* **49:** 109-118.

Giday, M. 2001. An ethnobotanical study of medicinal plant used by the Zay people in Ethiopia. *CBM:s Skriftserie* **3:** 81-99.

Giessow, J., J. Casanova, R. Lecler, R. MacArthur & J. Giessow. 2011. Arundo donax *(giant reed): Distribution and Impact Report*. California Invasive Plant Council, California.

Goldsborough, L. G., R. L. McDougal & A. K. North. 2005. Periphyton in freshwater lakes and wetlands. pp. 71-89. *In*: M. E. Azim, M. C. J. Verdegem, A. A. van Dam & M. C. M. Beveridge (eds.) *Periphyton: Ecology, Exploitation and Management*. CABI Publishing, London.

Hailu, M. 2011. *Ecosystem Structure, Trophic Link and Functioning of a Shallow Rift Valley Lake: the Case of Lake Ziway (Ethiopia).* M. Sc. Thesis, Addis Ababa University, Addis Ababa.

Jones, M. B. & F. Muthuri. 1997. Standing biomass and carbon distribution in a papyrus (*Cyperus papyrus* L.) swamp on Lake Naivasha, Kenya. *Journal of*

Tropical Ecology **13**:347-356.

Junk, W. J. & M. T. F. Piedaede. 1993. Biomass and primary production of herbaceous plant communities in the Amazon floodplain. *Hydrobiologia* **263**: 155-162.

Junk, W. J. 1986. Aquatic plants of the Amazon system. pp. 319-337. *In*: B. R. Davies & K. F. Walker (eds.) *The Ecology of River Systems*. Dr. Junk Publishers, Netherlands.

Kifle, D. 1985. *Variation in Phytoplankton Primary Production in Relation to Light and Nutrients in Lake Awassa*. M. Sc. Thesis, Addis Ababa University, Addis Ababa.

Kifle, D. & A. Belay. 1990. Seasonal variation in phytoplankton primary production in relation to light and nutrients in Lake Awassa, Ethiopia. *Hydrobiologia* **196**: 217-227.

Kistritz, R. U., J. K. Hall & I. Yesaki. 1983. Productivity, detritus flux, and nutrient cycling in a *Carex lyngbyei* tidal marsh. *Estuaries* **6**: 227-236.

Kleopateki, J. M. & F. W. Stearns. 1978. Primary productivity of emergent macrophytes in a Wisconsin freshwater marsh ecosystem. *American Midland Naturalist* **100**: 320-332.

Kufel, L., I. Kufel & J. Krolikowska. 2004. The effect of lake water characterstics on decomposition of aquatic macrophytes. *Polish Journal of Ecology* **52:** 261-273.

Lee, S. Y. 1990. Net aerial primary productivity, litter production and decomposition of the reed *Phragmites communis* in a nature reserve in Hong Kong: Management implications. *Marine Ecology Progress Series* **66:** 161-173.

Legesse, D., C. Vallet & F. Gasse. 2001. Precipitation-runoff modelling in the Ziway-Shala Basin, Ethiopian Rift Valley. *http://atlas-conferences.com/c/a/g/c/23.htm*

Leps, J. & P. Smilauer. 1999. *Multivariate Analysis of Ecological Data*. University of South Bohemia, Ceske Budejovice, Czech.

Macek, P. & E. Rejmankova. 2007. Response of emergent macrophytes to experimental nutrient and salinity additions. *Functional Ecology* **21:** 478-488.

Maryan, P. S. 1997. Future prospects for energy crops in the UK. pp. 449-454. *In*: M. J. Bullard, R. G. Ellis, M. C. Heath, J. D. Knight, M. A. Lainsbury & S. R. Parker (eds.) *Biomass and Energy Crops*. AAB, Vol. 49, UK.

McNaughton, S. J. 1966. Ecotype function in the *Typha* community-type. *Ecological Monographs* **36**: 297-325.

Mitsch, W. J. & V. Bouchard. 1998. *Olentangy River Wetland Research Park at The Ohio State University*. Annual Report 1997, School of Natural Resources, The Ohio State University, U.S.A.

Mnaya, B., T. Asaeda, Y. Kiwango & E. Ayubu. 2007. Primary production in papyrus (*Cyperus papyrus* L.) of Rubondo Island, Lake Victoria, Tanzania. *Wetlands Ecology and Management* **15**: 269-275.

Muthuri, F. M. & M. B. Jones. 1997. Nutrient distribution in a papyrus swamp: Lake Naivasha, Kenya. *Aquatic Botany* **56**: 35-50.

Noges, T., H. Luup & T. Feldmann. 2009. Primary production of aquatic macrophytes and their epiphytes in two shallow lakes (Peipsi and Võrtsjärv) in Estonia. *Aquatic Ecology* **44**: 83-92.

Payne, A. I. 1986. *The Ecology of Tropical Lakes and Rivers*. John Wiley Press, New York.

Pegman, A. P. M. & J. Ogden. 2005. Productivity-decomposition dynamics of *Typha orientalis* at Kaitoke Swamp, Great Barrier Island, New Zealand. *New Zealand Journal of Botany* **43**: 779-789.

Perbankhem, T. & C. Polprasert. 2010. Biomass production of papyrus (*Cyperus papyrus*) in constructed wetland treating low-strength domestic wastewater. *Bioresource Technology* **101:** 833-850.

Peters, J. A. & D. M. Lodge. 2009. Littoral zone. pp. 18-27. *In*: G. E. Likens (ed.) *Lake Ecosystem Ecology*. Elsevier, USA.

Powel, K. M. 2008. *Quantifying Soil Organic Carbon (SOC) in Wetlands Impacted by Groundwater Withdrawals in West-Central Florida*. M.Sc. Thesis, University of South Florida, USA.

Pratt, D. C., D. R. Dubbe, E. G. Garver & P. J. Linton. 1984. *Wetland Biomass Production: Emergent Aquatic Management Options and Evaluations*. Technical Report, Virginia, USA.

Rich, P. H., R. G. Wetzel & N. Van Thuy. 1971. Distribution, production and role of aquatic macrophytes in a Southern Michigan marl lake. *Freshwater Biology* **1**: 3-21.

Roberg, W. P. & A. Edwards. 1983. Water and waste water analysis for nitrate via nitration of salicylic acid. *Communications in Soil Science and Plant Analysis* 1207-1215.

Ryther, J. H. 1956. The measurement of primary production. *Limnology and Oceanography* **1**: 72- 84.

Santos, A. D. & E. D. Esteves. 2004. Comparison of calculation procedures of primary productivity by macrophytes in a shallow tropical coastal lagoons. *Acta Limnologica Brasiliensia* **16**: 239-249.

Saunders, M. J., M. B. Jones & F. Kansiime. 2007. Carbon and water cycles in tropical papyrus wetlands. *Wetlands Ecology and Management* **15**: 489-498.

Sharma, K. P., S. P. S. Kushwaha & B. Gopal. 1998. A comparative study of stand structure and standing crops of two wetland species, *Arundo donax* and *Phragmites karka*, and primary production in

Arundo donax with observations on the effect of clipping. *Tropical Ecology* **39**: 3-14.

Sheehy, J. E. & J. P. Cooper. 1973. Light interception, photosynthetic activity, and crop growth rate in canopies of six temperate forage grasses. *The Journal of Applied Ecology* **10:** 239-250.

Shuman, L. M. 1994. Mineral nutrition. pp. 149-182. *In:* R. E. Wilkinson (ed.) *Plant - Environment Interactions*. Marcel Dekker, Inc., New York.

Spencer, D. F., P. Liow, W. K. Chan, G. G. Ksander & K. D. Getsinger. 2006. Estimating *Arundo donax* shoot biomass. *Aquatic Botany* **84**:272-276.

Strickland, J. D. H. 1966. *Measuring the Production of Marine Phytoplankton. Bulletin No. 122.* Fisheries Research Board of Canada, Ottowa, Canada.

ter Braak, C. J. E. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* **69**:69-77.

Tilahun, G. 1988. *A Seasonal Study on Primary Production in Relation to Light and Nutrients in Lake Ziway, Ethiopia*. M.Sc. Thesis, Addis Ababa University, Addis Ababa.

Tilahun, G. 2006. Seasonal variation in species composition, abundance, size fractionated biomass and primary production of phytoplankton in lakes Ziway, Awassa and Chamo. Ph. D. Dissertation, Addis Ababa, Ethiopia.

Tilahun, G. & G. Ahlgren. 2010. Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awassa and Chamo. *Limnologica* **40**:330-342.

Titus, J. E. & W. H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH. *Limnology and Oceanography* **27**:151-160.

Van, T. K., W. T. Haller & G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology* **58**: 761-768.

Von Damm, K. L. & I. M. Edmond. 1984. Reverse weathering in the closed basin lakes of Ethiopian Rift. *SINET: Ethiopian Journal of Sciences* **284**: 835-862.

Westlake, D. F. 1963. Comparisons of plant productivity. *Biological Reviews* **38**:385-425.

Westlake, D. F. 1975. Primary productivity of freshwater macrophytes. pp. 189-206. *In*: J. P. Cooper (ed.) *Photosynthesis and Productivity in Different Environments*. Cambridge Univ. Press, Cambridge.

Wetzel, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large shallow lake. *Internationale Revue Der Gesamten Hydrobiolie* **49**: 1-61.

Wetzel, R. G. 1983. *Limnology*. 2nd edn. Philadelphia: Saunders College Publishing, U.S.A.

Wetzel, R. G. 1990. Land-water interfaces: metabolic and limnological regulators. *Verhandlungen des Internationalen Verein Limnologie* **24**: 6-24.

Wetzel, R. G. & G. E. Likens. 1991. *Limnological Analysis*. Springer Verlag, New York.

Wetzel, R. G. 2001. *Limnology: Lake and River Ecosystems*. Academic Press, U.S.A.

Weigert, R. G. & F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. *Ecology* **45**: 49-63.

Yohannes, F. 2003. Management of Lake Ziway. M.Sc. Thesis, University of Tromiso, Tromiso, Norway.

Zegeye, H., D. Teketay & E. Kelbesa. 2006. Diversity, regeneration status and socio-economic importance of the vegetation in islands of Lake Ziway, southcenteral Ethiopia. *Flora* **201**: 483-498.

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