Nutrient dynamics of two aquatic angiosperms in an alpine lake, Taiwan

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Abstract. Seasonal variations of nutrients in the lakewater, porewater in the lake sediment, and tissues of dominant aquatic angiosperms, *Schoenoplectus mucronatus* (L.) Pall. subsp. *robustus* (Miq.) T. Koyama and *Sparganium fallax* Graebn., in the Yuan-Yang Lake were studied. Nutrients in the lakewater were scarce and did not vary significantly between seasons. The porewater, in general, had higher concentrations of nutrients than the lakewater. The nutrient concentrations of porewaters were varied among sampling sites. Decomposition of organic matters in the lake and geographical characteristics of the watershed are the sources of differences in nutrient contents among sampling sites of porewaters in the lake. Higher contents of dissolved organic carbon and ammonium and potassium ions in the porewater were found in sites of water entrance areas. High contents of Ca and Mg ions in the lakewater and porewater were only found in the northwestern site of the lake. Nitrogen and potassium, which are concentrated in the aboveground tissues, are the major elements in tissues of dominant aquatic angiosperms. Nitrogen and potassium were consumed luxuriously before the growing season, and the contents in tissues gradually decreased during the growing period. However, no obvious seasonal change was found for Na, Ca, and Mg. The yearly budget of uptake and loss of nutrients through *Sparganium fallax* is estimated to be 13.8 g m⁻² N, 1.1 g m⁻² P, and 19.8 g m⁻² K in 1997, and 9.9 g m⁻² N, 0.6 g m⁻² P, and 9.2 g m⁻² K in 1998.

Keywords: Nitrogen; Nutrients; Potassium; Schoenoplectus mucronatus ssp. robustus; Sparganium fallax; Yuan-Yang Lake.

Introduction

This study is a part of the long-term ecological research in the Yuan-Yang Lake ecosystem, Taiwan. We attempted to gather seasonal standing crop and production data of dominant aquatic angiosperms in the lake and to relate these to the population dynamics of these plants and nutrient cycling in the ecosystem.

A previous study (Hwang et al., 1996) pointed out that the dominant aquatic angiosperms in the lake — *Schoenoplectus mucronatus* (L.) Pall. subsp. *robustus* (Miq.) T. Koyama and *Sparganium fallax* Graebn.--showed a luxury uptake of nitrogen and potassium in the young shoots early in the growing season. This phenomenon has been observed in a variety of aquatic angiosperms (Bernard and Solsky, 1977; Boyd, 1969, 1970; Boyd and Vickers, 1971; Gerloff and Krombholz, 1966; Kistritz et al., 1983) and may afford a competitive advantage to aquatic macrophytes if those ions are limited (Boyd, 1969). The purpose of the study reported here was to determine the seasonal changes of mineral nutrients in the water and in tissues of dominant aquatic angiosperms in the lake to gain insights into nutrient cycling in the alpine lake ecosystem.

Materials and Methods

Sampling Sites

Lakewater, porewater beneath the sediment of the aquatic angiosperm communities, and the plant tissues of two dominant aquatic angiosperms: *Schoenoplectus mucronatus* (L.) Pall. subsp. *robustus* (Miq.) T. Koyama and *Sparganium fallax* Graebn. were sampled at four sites in the Yuan-Yang Lake from August 1996 to October 1998 at monthly intervals. One additional site without any aquatic angiosperm growing (Site B, described below) was added in October 1997 to represent a control site for estimating the potential nutrient concentration in the sediment.

The lake, at 1670 m in the Yuan-Yang Lake Nature Preserve, has an east-west oriented spoon-shape, with the narrow part toward the east (Figure 1). The geographical characteristics and the distribution of the aquatic angiosperms in the Yuan-Yang Lake Nature Preserve have been described by Chou et al. (2000) and Hwang et al. (1996). The five sites used in this study were chosen for their hydrological and vegetative characteristics (Figure 1).

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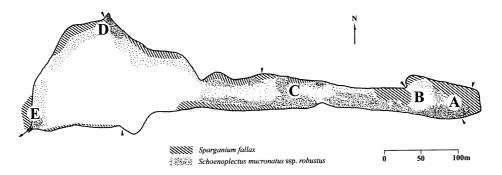


Figure 1. The sampling sites in the Yuan-Yang Lake. Arrows indicate the major water entrance areas. Letter symbols denote the sampling sites.

They include: Site A, one of the major water input areas with both dominant aquatic angiosperms growing; Site B, one of the major water input areas without aquatic angiosperm growing; Site C, with both dominant aquatic angiosperms growing, but no major water input from the surrounding upland; Site D, one of the major water input areas with both dominant aquatic angiosperms growing; and Site E, the lake outlet area with both dominant aquatic angiosperms growing.

Field Procedures

Two blocks were randomly chosen for each plant species in each site. Healthy plants (five individuals of *Schoenoplectus mucronatus* ssp. *robustus* and three individuals of *Sparganium fallax*) were collected from each block. Two lakewater samples (100 ml) were collected with acid-washed polyethylene bottles at 10 cm below the water surface from each block. Porewater was collected using a porous ceramic cup (maximum pore size 2.5 μ m, 655 round bottom tapered neck cups, Soilmoisture Equipment Corp., California) equipped with a PVC pipe and hand-operated Nalgene vacuum pump (Nalge Nunc International, New York). Two samples (100 ml each) were collected from 30 cm beneath the lake sediment from each block. All plant and water samples were stored in an ice-chest in the field.

Laboratory Analysis

Plant materials were washed with tap water and rinsed with distilled water in the lab. All materials were separated into aboveground, rhizome, and root tissues. Sample preparation for total nitrogen, phosphate, and nutrient element (Ca^{2+} , Mg^{2+} , Na^+ , and K^+) determination in plant tissues was the same as in Hwang et al. (1996).

The pH value of water samples was measured at field with a portable pH meter. Lakewater sample was filtered through a glass fiber filter (Type A/E Glass Fiber Filter, Gelman Sciences, Ann Arbor, Michigan, USA) immediately after returning to the lab. Filtered lakewater and porewater samples were analyzed immediately for ammonium concentration by a modified Solorzano method (Liddicoat et al., 1975), and phosphate concentration by the molybdenum blue-ascorbic acid method (Murphy and Riley, 1962). Analyses of the four base cations (Ca^{2+} , Mg^{2+} , Na^+ , and K^+) were the same as in Hwang et al. (1996). Dissolved organic carbon (DOC) in the lakewater and porewater was analyzed by a carbon analyzer (Model 1010 TOC Analyzer, OI Analytical, Texas).

Results

pH Value

The average pH value of the lakewater was between 4 and 6. There was no obvious seasonal variation; however, variation between sampling sites (Figure 2A) existed. The pH value of the lakewater was lower in the eastern part of the lake (Site A) than in the western part (Site D) (Figure 2A). The differences of the average pH values among seasons in lakewater were noticed as affected by the rain. The pH value of the lakewater was lower right after heavy rain and higher during a dry period.

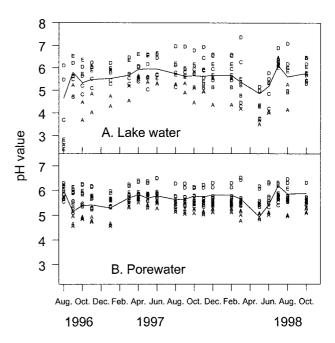


Figure 2. The seasonal changes of pH value in the (A) lakewater and (B) porewater in the community of *Sparganium fallax* and *Schoenoplectus mucronatus* ssp. *robustus*.

The average pH value in the porewater was between 5 and 6 (Figure 2B) and the variation was much less than that in the lakewater (Figure 2A). As with the lakewater, the eastern part of the lake had lower pH values than the western part.

DOC Distribution

The distribution of DOC in the lakewater and porewater was highly variable among sites and between plant species within the same site (Figure 3). In general, a higher concentration of DOC was found in the porewater (Figure 3B) than in the lakewater (Figure 3A), and it was higher in sites of water entrance areas (sites A, B, and D) than the rest of the lake (Figure 3). Furthermore, the sites underneath *Sparganium fallax* communities had a higher concentration of DOC than sites underneath *Schoenoplectus mucronatus* ssp. *robustus* communities (Figure 3B).

Nutrient Ions in the Lakewater

In general, the concentrations of nutrient ions in lakewater remained very low, unaffected by the season or plant species. One exception was found in site D where the lakewater had much higher concentrations of Ca and Mg ions than other sites. The mean and range of the concentrations of nutrient ions in the Yuan-Yang Lake are listed in Table 1.

In contrast to the generally low concentrations of nutrient ions in the lakewater, the porewater expressed higher variability among sites and between plant communities within the same site (Table 2, Figure 4). Porewater taken from the Sparganium fallax community had much higher concentrations of NH_4^+ -N and K⁺ than those from the Schoenoplectus mucronatus ssp. robustus community. Such differences were due to the difference in the growth substrate between these two species. Sparganium fallax grows in the lake and anchors roots in the sediment at the lake floor while Schoenoplectus mucronatus ssp. robustus grows at the edge of the lake and the community forms a floating mat on the lake (Hwang et al., 1996). Therefore, the concentrations of nutrient ions in the porewater taken from the community of Schoenoplectus mucronatus ssp. robustus were very low, except for Ca and Mg ions at Site D (Table 2), and were similar to those in the lakewater (Table 1).

1.76

nd

Maximum

Minimum

The concentrations of nutrient ions in the porewater of *Sparganium fallax* communities were different among sampling sites. At water entrance areas, e.g. site A, B, and D, concentrations of NH_4^+ -N were much higher than at sites C or E (Figure 4). Moreover, the concentrations of NH_4^+ -N and PO_4^{3-} -P in the porewater of Site B (control)

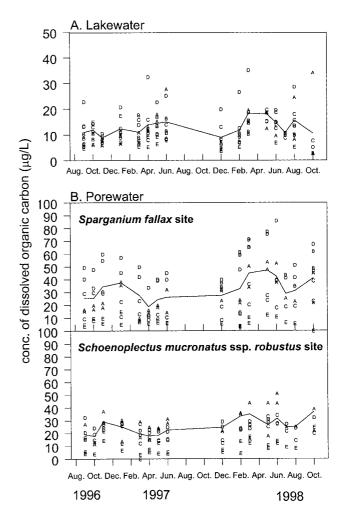


Figure 3. The seasonal changes in the concentration of dissolved organic carbon in the (A) lakewater of the lake and (B) porewater underneath the communities of *Sparganium fallax* and *Schoenoplectus mucronatus* ssp. *robustus*. Letter symbols denote the average concentration of the sampling site.

16.80

0.57

8.99

0.10

13 97

4 35

		PO ₄ ³⁻ -P 5		Na ⁺	Ca ²⁺		Mg ²⁺	
Site ^a	NH ₄ ⁺ -N 5		K+ 5					
					4	D	4	D
Mean (mg/L) (1SD)	0.11 (0.26)	0.017 (0.014)	0.20 (0.16)	0.47 (0.22)	1.20 (1.09)	6.98 (3.69)	1.89 (1.83)	8.84 (3.07)
Range (mg/L)								

Table 1. The contents of nutrient ions of the lakewater in the Yuan-Yang Lake from Aug. 1996 to Oct. 1998. Mean (1SD), n=44.

^a Site represents the number of sites used to calculate the mean and the range of the content. 5 denotes five sites: A, B, C, D, and E. 4 denotes four sites: A, B, C, and E. D denotes site D only.

1.03

0.14

6.06

nd

0.95

0.02

0.070

nd

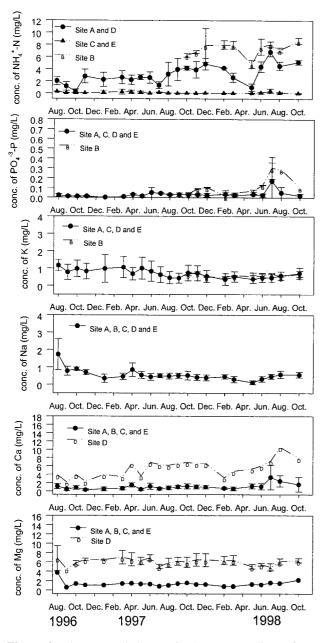


Figure 4. The seasonal changes in the concentrations of nutrient ions in the porewater underneath the community of *Sparganium fallax* in the Yuan-Yang Lake.

were always higher than at other *Sparganium fallax* communities growing sites (Figure 4). As in the lakewater (Table 1), Site D had much higher contents of Ca and Mg ions (Figure 4), due to the geographical characteristics in this area. Other than those ions and specific sites mentioned above, the concentrations of other nutrient ions in the porewater of the lake were low and did not change seasonally (Figure 4).

Nutrient Elements in Tissues of Dominant Aquatic Angiosperms

The concentrations of nutrient elements in tissues of dominant aquatic plants were not affected by the nutrient contents in the water environment. There was no significant difference in the tissue nutrient content among sites. Therefore, the tissue constituent data of the same plant species collected from all sites in each month were pooled together for seasonal comparisons. In general, the aboveground tissue had the highest concentrations of nutrient elements, and the root tissue had the lowest in the two dominant aquatic angiosperms, Sparganium fallax (Figure 5) and Schoenoplectus mucronatus ssp. robustus (Figure 6). Nitrogen and potassium were the two most abundant nutrient elements in tissues of the two dominant aquatic angiosperms (Figures 5 and 6). The concentration of potassium in the aboveground tissues could reach 6% and 4% of tissue dry weight in Sparganium fallax (Figure 5) and Schoenoplectus mucronatus ssp. robustus (Figure 6), respectively, right before the onset of growing season. Then, it decreased gradually to ca 2% and 1% of tissue dry weight in Sparganium fallax (Figure 5) and Schoenoplectus mucronatus ssp. robustus (Figure 6), respectively, as the population biomass reached its maximum in August. The highest concentration of nitrogen could reach 3.5% and 2.5% of tissue dry weight and decrease to ca 1% of tissue dry weight in Sparganium fallax (Figure 5) and Schoenoplectus mucronatus ssp. robustus, respectively (Figure 6). However, the annual lowest concentrations of N, P, and K in the aboveground tissue were higher in 1997 than in 1998 (Figures 5 and 6).

The concentrations of P, Na, Ca, and Mg in plant tissues were all below 0.5% of tissue dry weight (Figures 5

Table 2. The contents of nutrient ions of the porewater underneath the community of *Schoenoplectus mucronatus* ssp. *robustus* in the Yuan-Yang Lake from Aug. 1996 to Oct. 1998. Mean (1SD), n=22.

Siteª	NH4 ⁺ -N 5	PO ₄ ³⁻ -P 5	K+ 5	Na+ 5	Ca ²⁺		Mg^{2+}	
					4	D	4	D
Mean (mg/L) (1SD)	0.12 (0.37)	0.020 (0.015)	0.23 (0.20)	0.49 (0.24)	1.84 (0.58)	10.55 (2.44)	11.48 (1.54)	20.68 (7.86)
Range (mg/L) Maximum Minimum	1.76 nd	0.070 0.025	0.95 0.04	1.03 0.17	3.16 0.71	15.90 6.23	13.20 5.71	34.00 8.00

^a Site represents the number of sites used to calculate the mean and the range of the content. 5 denotes five sites: A, B, C, D, and E. 4 denotes four sites: A, B, C, and E. D denotes site D only.

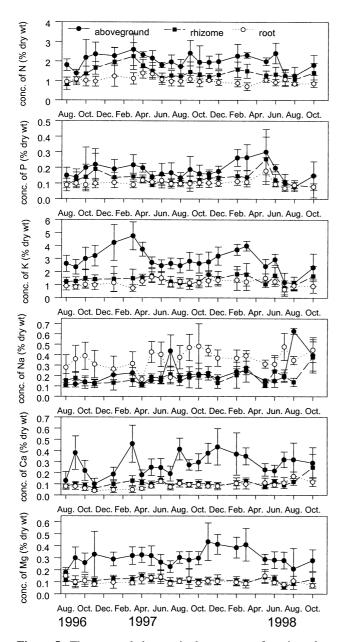


Figure 5. The seasonal changes in the contents of nutrient elements in tissues of *Sparganium fallax*.

and 6). Unlike the seasonal variations of N, P, and K in the aboveground tissues, the concentrations of Na, Ca, and Mg in all plant tissues did not show significant seasonal changes during the year (Figures 5 and 6).

Discussion

Yuan-Yang Lake is a catchment of the Yuan-Yang Lake Nature Preserve and the headwater of the Ta-han River (Liu and Hsu, 1973). Rainwater is the major water source for the lake. The rainwater can easily carry organic debris from the forest floor of the surrounding slope to the lake. During typhoon season, broken branches and falling trees damaged by the strong wind and heavy rain are easily

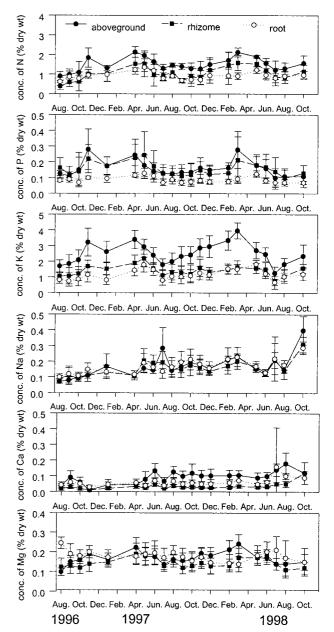


Figure 6. The seasonal changes in the contents of nutrient elements in tissues of *Schoenoplectus mucronatus* ssp. *robustus*.

found to accumulate around the lake. Thick layer of branch and leaf debris on the lake sediment can be found in the water entrance areas around the lake. The results of this study indicate that organic matter decomposition is a major source of nutrients, e.g. N and P, to the lake. The porewater collected from the lake sediment had significantly higher concentrations of NH_4^{+} -N and PO_4^{-3} -P (Figure 4) than the lakewater (Table 1). Moreover, the porewater collected from the major water entrance areas, especially at the control site (B), had significantly higher concentrations of NH_4^{+} -N and PO_4^{-3} -P than the lake's other areas (Figure 4). In conjunction with the lower pH value (Figure 2), except at Site D where the high pH value could be affected by the high concentrations of Ca and Mg in the sediment, and higher DOC (Figure 3) in these major water entrance areas, these results suggest that decomposition of organic matter is a major process supplying essential nutrients for the growth of aquatic plants in the lake. Similar results were suggested by Otsu et al. (1989).

The concentrations of nutrients were generally low and lacked seasonal variation in the lakewater of the Yuan-Yang Lake (Table 1). Three possible effects could have contributed to the oiligotrophication in this lake. Firstly, low nutrient rainwater and nutrient conservative forest have caused low nutrient content in the streams of the watershed. The Yuan-Yang Lake Nature Preserve has been protected intentionally from human disturbance since 1969 (Liu and Hsu, 1973) and could be classified as unpolluted, old-growth temperate forest. According to the "nutrient retention hypothesis" (Vitousek and Reiners, 1975), the concentrations of nutrients in watershed streams would reflect what was in the input from the atmospheric precipitation (Hedin et al., 1995). Studies on the chemical properties of streams around the lake agree with the hypothesis. The concentrations of NH_4^+ -N and PO₄⁻³-P in the streams were about one order magnitude lower than those in the lakewater, and the rainfalls greatly affected the contents of nutrients in these streams (Dr. Jiunn-Tzong Wu, per. comm.). Secondly, diffusion of nutrients in the shallow water area from the sediment to the lakewater could be restricted because of the oxidized condition on the sediment surface (Mortimer, 1941). The oxygen content in the lakewater was high (above 80% of saturated dissolved oxygen)(Hwang's unpublished data) above the sediment during daytime at the eastern part and at the edge of the lake, where most of the organic matter accumulates. A dense population of algae in these areas could have caused high oxygen content in the lakewater. Therefore, according to Mortimer (1941), insoluble ferric complex, formed and deposited on the sediment surface under oxidized conditions in the lake, would probably absorb the base content in the water and create a barrier in the surface of the sediment to the free exchange of ions between sediment and water. Much higher concentrations of $NH_{4}^{+}-N$, $PO_{4}^{-3}-P$, and K^{+} in the porewater of major water entrance areas (Figure 4) than those in the lakewater (Table 1) generally reflected the diffusion barrier phenomenon. Thirdly, the nutrients were depleted by the uptake of aquatic angiosperms and algae in the lake (Otsu et al., 1989). Dense populations of aquatic angiosperms, Sparganium fallax and Schoenoplectus mucronatus ssp. robustus, have occupied the eastern half of the lake and along the edge of the western part of the lake, where the depth of the water was not deeper than 2 meters (Hwang et al., 1996). Stem density reached 450 shoots m⁻² and 3000 shoots m⁻² in the population of Sparganium fallax and Schoenoplectus mucronatus ssp. robustus, respectively (Hwang et al., 1996). In particular, the growth of Schoenoplectus mucronatus ssp. robustus used to form a floating mat on the lake, which took nutrients directly from the lakewater. In addition, dense algal mats, mostly formed by Spirogyra spp. (Dr. Jiunn-Tzong Wu, per. comm.), were growing between and within the populations of aquatic angiosperms. The growth of these highly productive plants and algae could have kept the concentrations of nutrients low in the lakewater.

Both aquatic angiosperms Sparganium fallax and Schoenoplectus mucronatus ssp. robustus showed a "luxury uptake" of nitrogen and potassium in overwintering shoots, and the element content gradually decreased as the growth increased (Figures 5 and 6). This phenomenon has been observed in a variety of aquatic angiosperms (Auclair, 1977; Bernard and Solsky, 1977; Boyd, 1969, 1970; Boyd and Vickers, 1971; Brock and Bregman, 1989; Gerloff and Krombholz, 1966; Kistritz et al., 1983; Mason and Bryant, 1975). Boyd (1969) suggested that the luxury uptake of nutrients early in the growing season afforded a competitive advantage to aquatic macrophytes if nutrients were limited during the growing season. However, such seasonal changes of essential nutrient contents in the aboveground tissues of aquatic angiosperms in the Yuan-Yang Lake could be a reflection of growth difference between the aboveground and belowground tissues affected by the difference of air and water temperature in different seasons. In winter, where the water temperature (ca 10°C) in the lake sediment is much higher than the air temperature, the nutrients absorbed by roots are accumulated in the aboveground tissues while the air temperature is still too low for the aboveground tissues to grow. As the air temperature rose in spring and summer (Hwang et al., 1996), the subsequent decrease in tissue nutrient contents was attributed to the dilution and metabolism of nutrients in the rapidly increasing aboveground biomass (Kistritz et al., 1983).

The growth of aquatic angiosperms in Yuan-Yang Lake was probably not limited by the nutrient availability. Although the nutrient contents in the porewater has revealed significant differences (Figure 4), the tissue nutrient contents of the aquatic angiosperms did not vary significantly between samples collected from different sites. Furthermore, the contents of nitrogen and phosphorus in the aboveground tissues of both aquatic angiosperms were all higher than the critical contents for the growth of aquatic angiosperms, e.g. 1.3% N and 0.13% P suggested by Gerloff and Krombholz (1966). They have indicated a luxurious status of nutrients in the lake for the growth of aquatic angiosperms. The nutritious status of the lake probably accounts for the fact that no apparent downward translocation of nutrients in the tissues of aquatic angiosperms was found at the end of the growing season in this study (Figures 5 and 6). Some aquatic angiosperms exhibited a rapid downward translocation of nutrients at the end of growing season and during the winter (Kistritz et al., 1983).

One of the important functions in the nutrient cycling process for the aquatic angiosperms is the translocation of nutrients from the sediment upward to the lakewater, in which nutrients are either uptaken by other organisms or exported out of the system. Since no apparent downward translocation of nutrients from the aboveground tissues to belowground tissues in *Sparganium fallax* occurred (Figure 5), the translocation of nutrients from the sediment to the lakewater through *Sparganium fallax* can be estimated. Estimation could be done by calculating the average net primary productivity of the aboveground tissue of *Sparganium fallax*, which was ca 800 gdw m⁻² y⁻¹ (Hwang et al., 1996), and the aboveground nutrient contents at the end of the growing season (Figure 5). Therefore, the yearly budget of nutrient uptake into the lakewater is 13. 8 g m⁻² N, 1.1 g m⁻² P, and 19.8 g m⁻² K in 1997, and 9.9 g m⁻² N, 0.6 g m⁻² P, and 9.2 g m⁻² K in 1998. The yearly variation was caused by the difference in the concentrations of nutrients at the end of the growing season between these two years. However, the cause for the yearly difference in nutrient contents is not yet known.

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鴛鴦湖關係兩種優勢水生維管束植物營養鹽季節性變化

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本研究調查鴛鴦湖中營養鹽在湖水中、湖底泥土壤水中和湖中兩種優勢水生維管束植物,水毛花和 東亞黑三稜,組織中的季節性變化。營養鹽含量在湖水中偏低且無顯著的季節性變化。然而在湖底泥上壤 水中則較在湖水中高且则顯受地區性特徵的影響。在主要進水口地區的湖底泥上壤水中含有較高量的可溶 性有機碳、氨態氮和鉀離子。而在湖西北角的主要進水口地區的湖底泥上壤水中則含有非常高量的鈣和鎂 離子。氦和鉀元素是水毛花和東亞黑三稜地上部組織之主要營養元素。此二元素在植物生長季開始前會被 大量吸收並累積在地上部組織中,然後隨著植物生長而逐漸下降。至於其他元素,例如鈉、鈣和鎂則無此 現象。鴛鴦湖中每年經山東亞黑三稜組織吸收後而流失之營養鹽流量,信計在 1997 年約 13.8 gm²N、 1.1 gm²P 和 19.8 gm²K;而在 1998 年約 9.9 gm²N、 0.6 gm²P 和 9.2 gm²K。

關鍵詞:營養鹽;氦;鉀;水毛花;東亞黑三稜;鴛鴦湖;水生維管束植物。