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Primary production and chemical composition of emergent aquatic macrophytes, *Schoenoplectus mucronatus* ssp. *robustus* and *Sparganium fallax*, in Lake Yuan-Yang, Taiwan

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Abstract. The climate in the Yuan-Yang Lake Area is temperate with high humidity due to rainfall and fog and characterized by low solar radiation and low air temperature. The aquatic macrophyte *Schoenoplectus mucronatus* ssp. *robustus* grows at the edge of the lake. For most of the population, only below-ground tissue is in the water. The plants cover an area of about 0.6 ha. During this study the annual production of above-ground tissue ranged from 400 to 900 gdw m^{-2} y^{-1}. The below-ground tissue, which could not be distinguished from dead tissue, showed no significant change. Growth of the plant started in March, and the biomass reached a maximum in July, followed by a decline in above-ground biomass, stem number, and plant height. Starting in July, the soluble carbohydrate content of the below-ground tissues increased significantly relative to that of the above-ground tissues, indicating an allocation of energy to below-ground tissues. Close to *Schoenoplectus mucronatus* ssp. *robustus, Sparganium fallax* was growing in water no deeper than 2m and covered an area of about 1.5 ha. Annual net productivity of *Sparganium fallax* ranged from 600 to 1500 gdw m^{-2} y^{-1} during the study, half of which was below-ground tissue. Growth started in February; the biomass reached a maximum in July and then decreased, along with the plant height. However, the number of seedlings under water increased in August, and the soluble carbohydrate content of above-ground and below-ground tissues did not change significantly. Potassium and nitrogen were the major mineral nutrients in the tissues of both plants, reaching a maximum concentration in the above-ground tissues in March and April; possibly due to the onset of growth. The variation of annual primary productivity of both aquatic macrophytes was correlated with the magnitude of the maximum potassium content in the above-ground tissues of both plants, which indicated that the environment could be potassium limited. However, different patterns of seedling growth and metabolite translocation between these two aquatic macrophytes revealed differences of adaptation strategy in different habitats.

Keywords: Aquatic macrophytes; Biomass; Mineral nutrients; Productivity; *Schoenoplectus mucronatus* ssp. *robustus*; Soluble carbohydrates; *Sparganium fallax*.

Introduction

The Yuan-Yang Lake Area was declared a nature preserve by the Council of Agriculture, Executive Yuan, ROC in 1986 for protection of the integrity of the mountain lake, cypress virgin forest, and *Sparganium fallax* Graebn. in the area. According to Liu and Hsu (1973), the vegetation in this area can be classified into three communities: hydrophytic communities in the lake, hygrophytic communities in the marsh, and mesophytic communities on the slopes. In the lake, the community consists of three dominant species occupying different water depths, *Potamogeton octandra* Poir., *Schoenoplectus mucronatus* (L.) Pall. subsp. *robustus* (Miq.) T. Koyama, and *Sparganium fallax*. In the marsh, the communities are made up of *Miscanthus transmorrisonensis* Hayata and *Schoenoplectus mucronatus* ssp. *robustus*. On the slopes, the dominant species are *Chamaecyparis formosensis* Matsum. and *Chamaecyparis obtusa* Sieb. & Zucc. var. *formosana* (Hayata) Rehder. The growth of hydrophytic communities is mainly supported by the streams which carry nutrients and the organic matter from the slope into the lake (Otsu et al., 1989). The lake was classified as a mesotrophic lake by Otsu et al. (1989), however, a recent study based on algae composition in the lake suggested that was actually oligotrophic (Dr. Jiunn-Tzong Wu, per. comm.).

Previous ecological studies on the preserve area have emphasized general species distribution surveys and resource inventories. However, information on the population abundance and dynamics in this area is still lacking (Liu, 1987). There is an urgent need to gather dynamic ecological information because of rapidly developing of tourism, which will have a great impact on this area. Without knowing the dynamics of population abundance and interactions between biotic and abiotic factors, one may not be able to evaluate or predict the impact on the ecosystem of regional change caused by human activities (Hedin et al., 1995).

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This study, part of the long-term ecological study of the Yuan-Yang lake ecosystem, was to understand the functional roles of emergent aquatic macrophytes in the ecosystem. In this report, we documented the seasonal changes of primary production and chemical compositions of two dominant emergent species, *Schoenoplectus mucronatus* ssp. *robustus* and *Sparganium fallax*, in the lake.

Materials and Methods

Study Site

The Yuan-Yang Lake Nature Preserve is located at the northern part of the Hsueh-Shan Mountain Range of Taiwan at 24° 35' N latitude and 121° 24' E longitude (Figure 1). The whole preserve area, 374 ha, is a watershed and the headwater of the Ta-han River, which drains into the Shihmen Reservoir. The elevation of the area ranges from 1,650 to 2,430 m above sea level. The lake, at 1,670 m, is located at the edge of the preserve area, which forms an east-west oriented spoon-shape, with the narrow part toward the east (Figure 2A). The maximum length of the lake is 650 m, and the maximum width is 150 m. The lake area is 3.3 ha. Its maximum depth is ca. 4.5 m, in the western part, but less than 2 m in the eastern part.

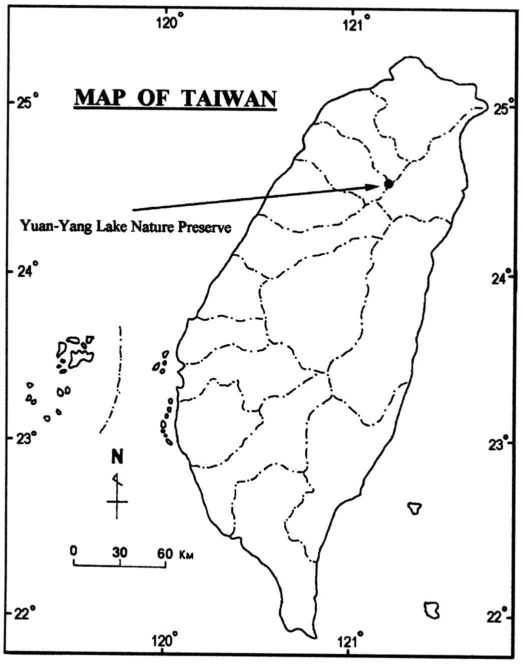

Figure 1. The geographical position of Yuan-Yang Lake Nature Preserve.

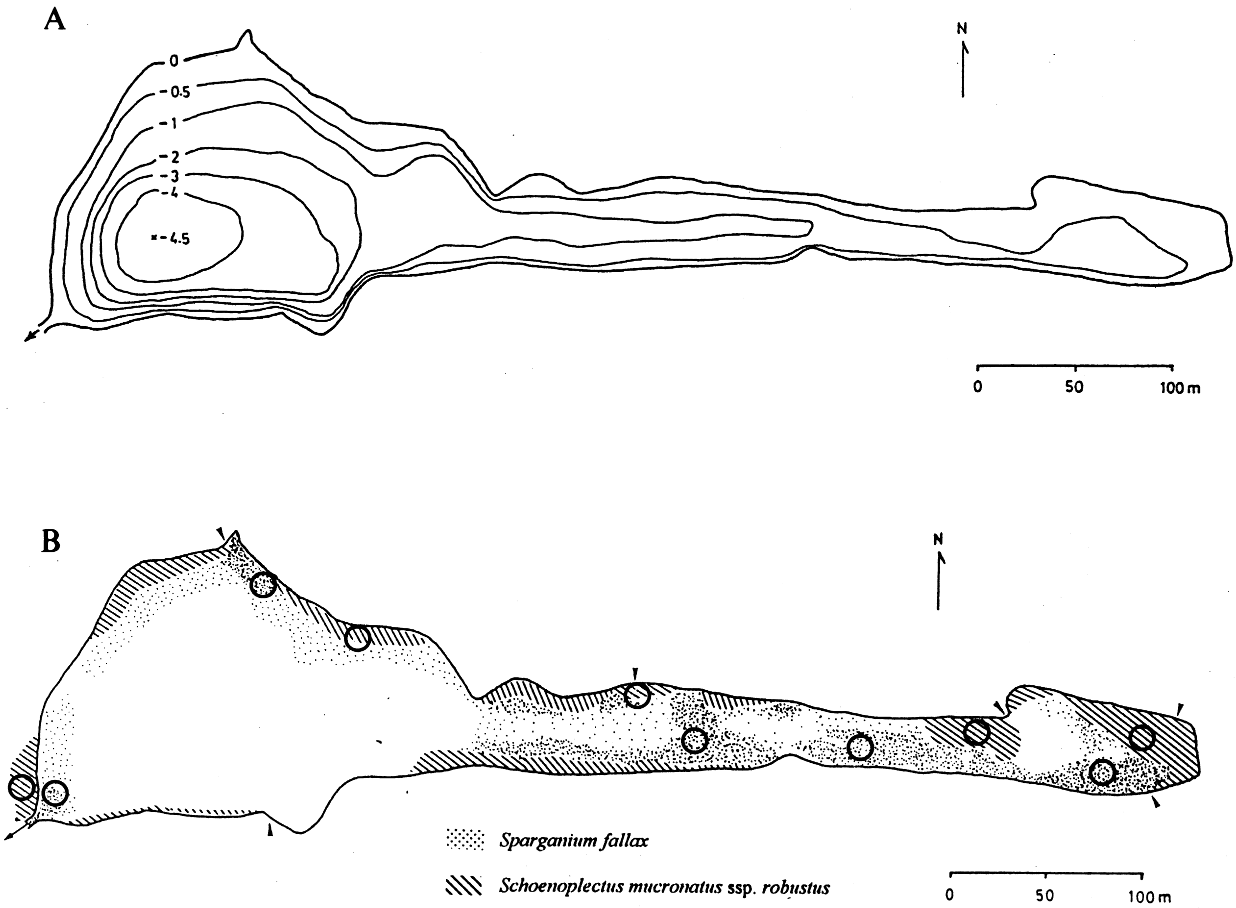

Figure 2. A, Bathymetric map of Lake Yuan-Yang; B, Distribution and permanent sampling blocks (round circle) of *Schoenoplectus mucronatus* ssp. *robustus* and *Sparganium fallax* in the lake. Arrows indicate direction of water flow.

Meteorological Data Collection

A meteorological station was installed in October 1992. A pyranometer sensor (LI-200SA, Li-Cor, NE, USA), an air temperature sensor, and a rain gauge tipping bucket (Model 1000-20, Sierra Misco, CA, USA) were connected to a data logger (Li-1000, Li-Cor, NE, USA; replaced by CR10, Campbell Scientific, Utah, USA in Jan. 1993). Data on solar radiation was recorded as a daily total and air temperature was recorded as an hourly mean value based on readings taken every minute. Precipitation was recorded as a daily total. Meteorological data in the data logger were collected once a month using a portable computer.

Plant Materials

Two dominant emergent aquatic species, *Schoenoplectus mucronatus* ssp. *robustus*, and *Sparganium fallax*, were studied. *Schoenoplectus mucronatus* ssp. *robustus* covered ca. 0.6 ha of the marsh area and the borders of the lake, with only the below-ground tissues in the water for most of the population. *Sparganium fallax* grew in water less than 2 m deep, next to the *Schoenoplectus mucronatus* ssp. *robustus* population, and covered ca. 1.6 ha of the area (Figure 2B).

Biomass Determination

Biomass was determined by harvest. Five permanent blocks around the lake were chosen for each species (Figure 2B). Two 15 × 15 cm^2 quadrats, separated by 10 m, were randomly chosen each month from each block, from which all plant materials were collected and then cleaned of debris in the lab. All materials were separated into above-ground, below-ground, and dead tissues. Shoot number and plant height (vertically from the substrate to the tallest part of the plant) in each quadrat were recorded and then they were oven-dried at 75°C for 7–10 days. Primary productivity was calculated from the difference between minimum and maximum biomass.

Soluble Carbohydrate and Mineral Nutrients Determination

Five individuals of *Schoenoplectus mucronatus* ssp. *robustus* and three individuals for *Sparganium fallax* were collected from each permanent block (Figure 2B) monthly for determination of total soluble carbohydrate and mineral nutrient content. They were washed in the lab and oven-dried at 75°C for a week. The dried tissues were ground to pass a 0.5-mm sieve. Samples for total soluble carbohydrate determination were prepared according to Karsten et al. (1991) and determined by the Anthrone method (Jermyn, 1975). Sample powder was extracted by distilled water (10 mg ml^{-1} extraction volume) at 80°C for 4 h. Following extraction, homogenates were centrifuged at 4,500 g for 10 min. To aliquots (1 ml) of distilled water extracts in a 75 ml test tube were added concentrated HCl (1 ml) and 90% formic acid (0.1 ml) followed by freshly prepared anthrone reagent (8 ml), added slowly to avoid excessive frothing. Anthrone reagent was prepared by dissolving anthrone (20 mg/100 ml) in 80% (v/v) H_2SO_4 at the room temperature. After mixing the contents, the tube was heated in a boiling-water bath for exactly 12 min and immediately plunged into an ice-water bath. Sucrose was used as a standard. Optical density was read at 630 nm after stirring on a Vortex mixer and allowing to stand 5 min to disperse bubbles.

Sample preparation for mineral nutrient determination was according to Kalra and Maynard (1991). The dry ashing method was chosen for Ca, Mg, Na, and P determination. Sample powder (0.5 g) was ashed in a muffle furnace at 470°C for 16 h (overnight). The ash residue was digested further in 3 ml of 6M HCl and 0.25 ml of concentrated HNO_3 on hot plate at 80°C for 2 h, followed by adding 3 ml of 6M HCl and water to bring the mineral elements into solution, after filtering through Whatman 42 filter paper. Total phosphate was determined by the vanado-molybdo-phosphoric yellow color method; potassium and sodium by flame photometry; and calcium and magnesium by atomic absorption spectrophotometry. Total nitrogen in sample powder was determined by a CHN analyzer (NA 1500 series 2, Fisons Instruments, Italy).

Results and Discussion

Climate

The total daily solar radiation (Figure 3) was generally low in the Yuan-Yang Lake Area. Although clear day radiation in June could reach 25 MJ m^{-2} and ca. 15 MJ m^{-2} during the winter (Figure 3), the monthly average daily solar radiation was only ca. one third of the clear day value (Figure 3). Low solar radiation in the area is mainly caused by the high frequency of cloud and fog coverage. The period during which cloud and fog covered the area varied with the season. During summer, cloud and fog only stayed in a short period of time, mainly in the afternoon. However, cloud and fog always covered the whole area accompanied by drizzle or rain lasting several days during winter due to the effect of the northeast monsoon.

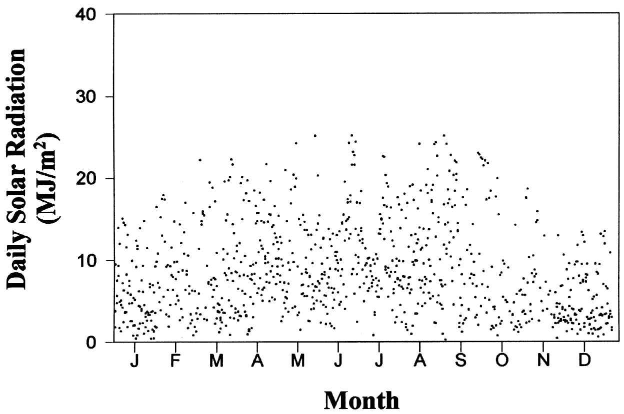

Figure 3. Daily solar radiation (megajoule per meter square, MJ/m^2) at Yuan-Yang Lake during Nov. 1992 to Jul. 1995. Data from different years were pooled together.

The monthly mean, maximum and minimum air temperatures at the Yuan-Yang Lake Area during the study are shown in Figure 4. The mean annual air temperature was ca. 13°C. The highest air temperature was ca. 27°C during the period of June to August, but the lowest air temperature in this period was only around 10°C. During the winter, the lowest air temperature was equal to or lower than zero, but the maximum temperature was above 16°C in this period. The lowest air temperature dropped to -4°C during a two-day snowfall in January 1993. The lowest air temperature started to drop to below 5°C in August and did not rise to above 5°C until March the next year (Figure 4) except for in November 1994. Thus, plants growing in the area experienced 16°C air temperature all the year round, while facing air temperatures below 5°C from August to March the next year, which could be related to the cessation of the growth of the mature aquatic plant population during the period (see below).

The annual rainfall was about 2,600 mm in 1993 and 3,500 mm in 1994. The rainfall data may have been underestimated for this area due to not counting the cloud and fog coverage and some missing data (Figure 5). The frequency of rainfall was very high in this area, ranging from 15 to 27 days per month. In general, the monthly rainfall was ca. 200 mm per month (Figure 5) in the absence of typhoons. The shortage of the annual rainfall in 1993 was due to the lack of typhoons passing Taiwan that year. Although typhoons are a major source of water for this island, no sign of drought was observed at this area in 1993 due to the high frequency of cloud and fog coverage. High frequency of cloud and fog coverage was one of the important factors contributing to the growth of the cypress forest in Taiwan (Liu and Hsu, 1973).

This meteorological data supports the description of the climate of the area as temperate heavy moist (Liu and Hsu, 1973).

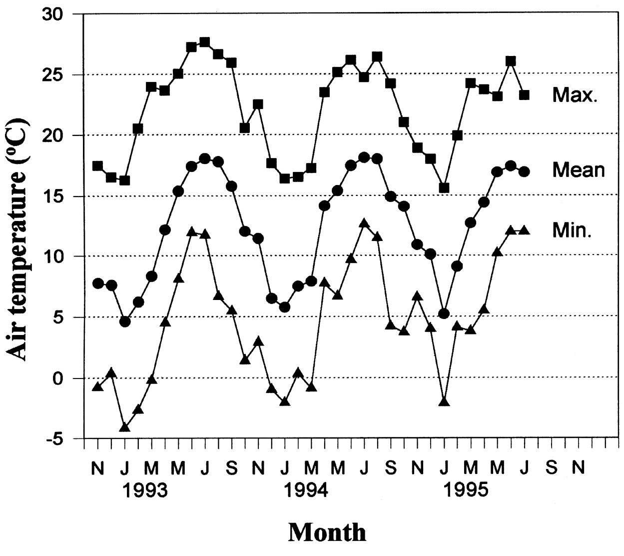

Figure 4. Monthly mean, maximum, and minimum air temperature at Yuan-Yang Lake during Nov. 1992 to Jul. 1995.

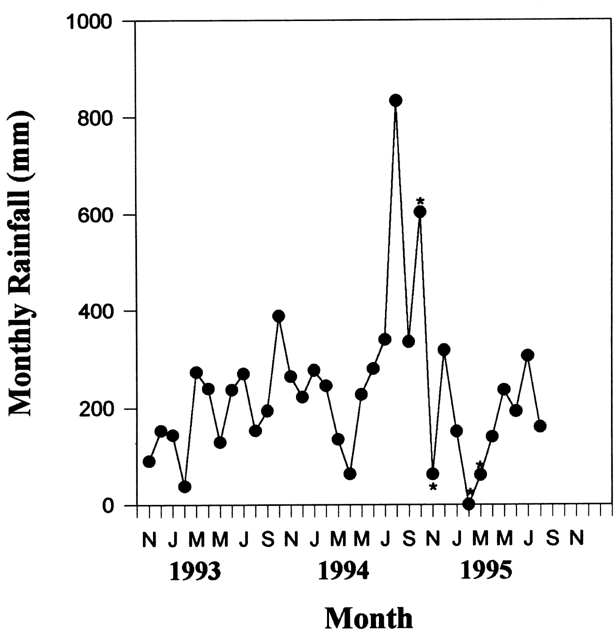

Figure 5. Monthly duration of rainfall at Yuan-Yang Lake. The '*' indicates insufficient data for the month.

Schoenoplectus mucronatus ssp. *robustus*

The *Schoenoplectus mucronatus* ssp. *robustus* population grew in the marsh area and at the borders of the lake where the water was shallow. Most of the time only below-ground tissues; rhizomes and roots, were submerged in water. The growing season (Figure 6) of *Schoenoplectus mucronatus* ssp. *robustus* was in accordance with the rise of air temperature (Figure 4). The growth of the *Schoenoplectus mucronatus* ssp. *robustus* population started in April and reached a maximum in July (Figures 6 and 7), while the lowest air temperature was above 5°C (Figure 4). After the growing peak, the above-ground tissues gradually turned brown while the lowest air temperature decreased to below 5°C (Figure 4). These standing deads formed a thick blanket in which new shoots of *Schoenoplectus mucronatus* ssp. *robustus* were still green and growing (Figure 7), which kept the minimum above-ground biomass at 150 ± 20 gdw m^{-2} (Figure 6A), the shoot number at 1200 ± 500 shoot m^{-2} (Figure 6C), and average plant height at 20 ± 10 cm (Figure 6D). In July 1993 when population growth reached maximum, the above-ground biomass reached 1000 ± 400 gdw m^{-2} (Figure 6A), the shoot number grew to 2900 ± 800 shoot m^{-2} (Figure 6C), and average plant height to 60 ± 10 cm (Figure 6D). The below-ground tissues also increased during the growing season (Figure 6B), but the living roots and deads were not separated in this study because of an identification problem. Thus, the annual above-ground primary productivity of *Schoenoplectus mucronatus* ssp. *robustus* was 850 ± 280 gdw m^{-2} y^{-1} in 1993, but only 600 and 400 gdw m^{-2} y^{-1} in 1994 and 1995, respectively. A similar decrease was observed in the below-ground tissue (Figure 6B) and shoot density (Figure 6C), but not in the average plant height (Figure 6D).

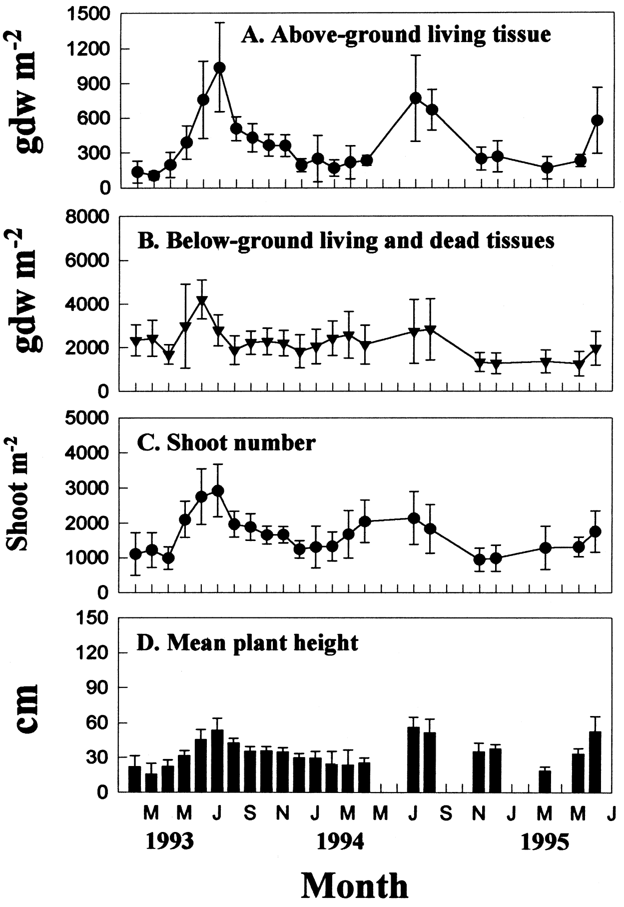

Figure 6. Population parameters of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang Lake: A, above-ground biomass; B, below-ground living and dead biomass; C, shoot density and D, average plant height.

The primary productivity of *Schoenoplectus mucronatus* ssp. *robustus* is much lower than that of plants grown in the freshwater marshes of temperate areas like the United States. Net primary productivity for temperate areas ranges from 900 to 5500 gdw m^{-2} y^{-1} (Mitsch and Gosselink, 1986). The low productivity of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang lake could be caused by its low solar radiation all the year round (Figure 3) and its low nutrient status (Dr. Jiunn-Tzong Wu, per. comm.).

The soluble carbohydrate content in the above-ground tissues of *Schoenoplectus mucronatus* ssp. *robustus* was about 15% of dry weight, based on sucrose, but the content in the below-ground tissues was variable, ranging from 10 to 45%, depending on the seasons (Figure 8). A higher proportion of soluble carbohydrate content was found in below-ground tissues relative to above-ground tissues after July, the peak of the growing season (Figure 8), which suggested an allocation of metabolites from above-ground to below-ground tissues for the growth of new stems in the next season. Such allocation of soluble carbohydrate to below-ground organs is a common phenomenon and is important for the growth and development of perennial grasses in spring and summer in the temperate and arctic areas (Mooney and Billings, 1960; Fonda and Bliss, 1966; Roseff and Bernard, 1978). An unusually high concentration of soluble carbohydrate content in both above-ground and below-ground tissues was found in November, 1994 (Figure 8). This could have been related to the burst of the lowest air temperature at that time (Figure 5), but the truth needs further investigation.

Potassium and nitrogen were the major mineral nutrients in the above-ground tissues of *Schoenoplectus mucronatus* ssp. *robustus* (Figure 9), and they showed a rapid accumulation of concentration in tissues at the onset of the population growth (Figure 9). Nitrogen content in the above-ground tissues was 2.7% immediately before the growing month, twice as much as during the rest of the year. A similar situation was found in potassium and phosphate content: 3.3% vs 2.0% for potassium, and 0.9% vs 0.13% for phosphate (Figure 9). There is no explanation for the unusually high potassium concentration, 6.4%, in the above-ground tissue in March 1993 (Figure 9), but

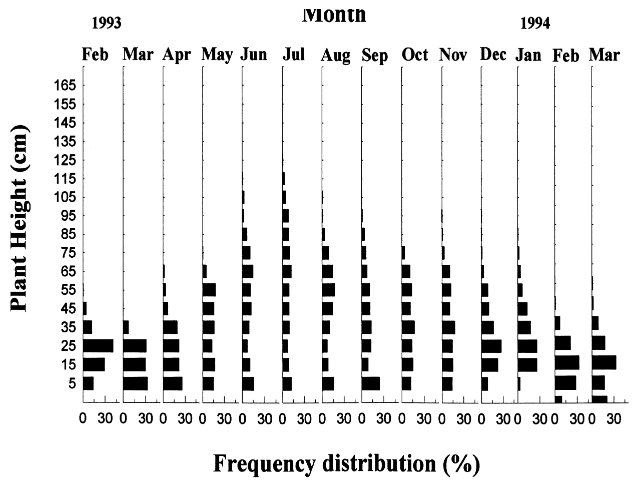

Figure 7. The monthly frequency distribution histograms for plant height of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang Lake.

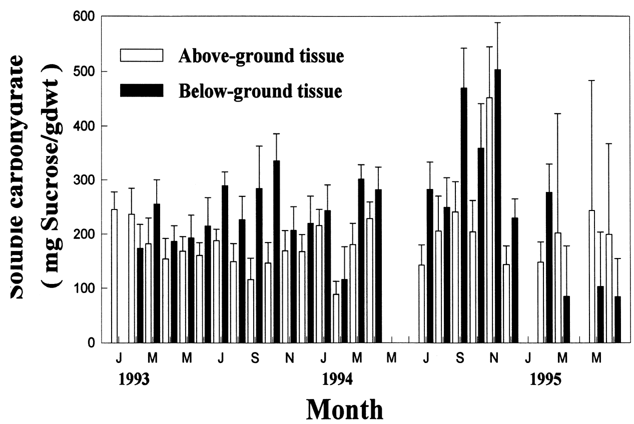

Figure 8. Seasonal changes in soluble carbohydrate content in tissues of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang Lake.

the decrease of the maximum potassium concentration from 1993 to 1995 is similar to the decrease of the annual primary productivity of the plant (Figure 6A). The concentrations of Na, Ca, and Mg were low, compared to K, N, and P, and did not vary significantly with the seasons (data not shown). The concentration range of Ca, Mg, and Na in the above-ground tissue of *Schoenoplectus mucronatus* ssp. *robustus* was 0.07–0.21%, 0.11–0.27%, and 0.07–0.16%, respectively. The trend was similar for ions in the below-ground tissues, but above-ground tissues had a higher nitrogen and potassium content than the below-ground tissues (Figure 10).

Rapid accumulation of nitrogen, phosphate, and potassium contents in tissues before the growing season were found in other aquatic plants; *Scirpus americanus* Pers. and *Typha latifolia* L. (Boyd, 1970), *Carex lacustris* Willd. (Bernard and Solsky, 1976), and *Eleocharis quadrangulata* (Michx.) R. & S. (Boyd and Vickers, 1971). However, whether the increased ion content in tissues of *Schoenoplectus mucronatus* ssp. *robustus* before the growing season is due to the translocation of ions from the dying mother plants (Bernard and Solsky, 1976) or to the increased ion concentration in the streams draining the surrounding forest in spring (Likens et al., 1977) needs further investigation.

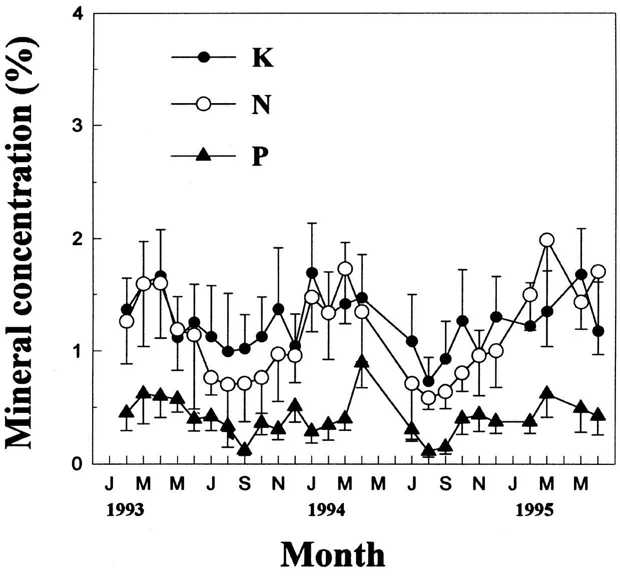

Figure 10. Seasonal changes in major nutrient contents in the below-ground tissues of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang Lake.

Sparganium fallax

Sparganium fallax grew in water where the depth was less than 2 m. Most of the above-ground tissues of *Sparganium fallax* were submerged in water and only a small part of the leaves was exposed to the air.

The growing season of *Sparganium fallax* was also in accordance with the increased air temperature. Population

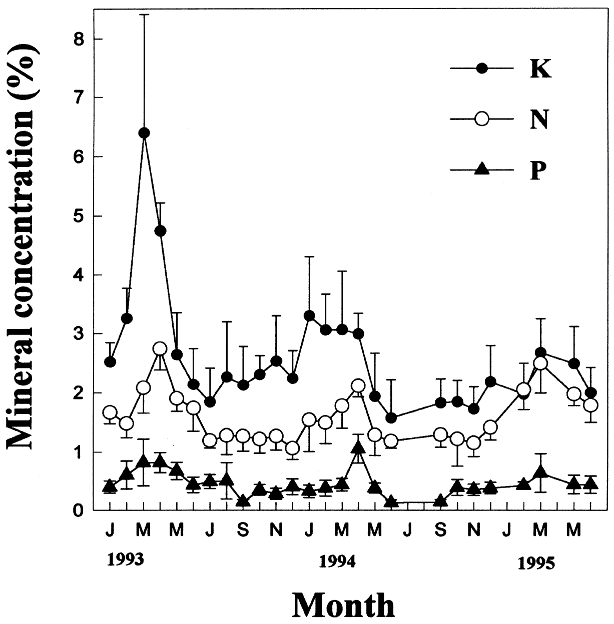

Figure 9. Seasonal changes in major nutrient contents in the above-ground tissues of *Schoenoplectus mucronatus* ssp. *robustus* at Yuan-Yang Lake.

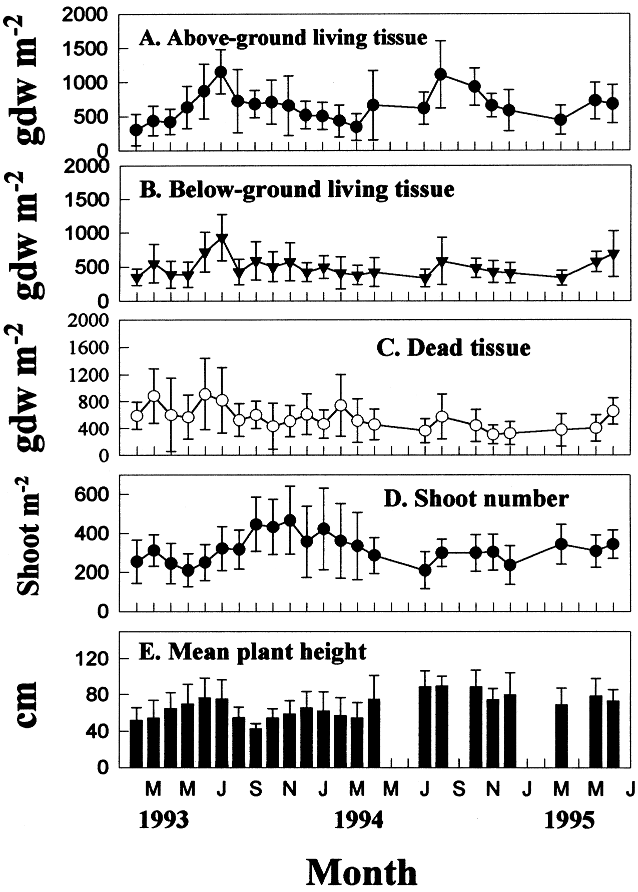

Figure 11. Population parameters of *Sparganium fallax* at Yuan-Yang Lake: A. above-ground biomass, B. below-ground biomass, C. total dead tissue, D. shoot density and E. average plant height.

growth started in March and reached a maximum in July (Figure 11) while the air temperature was rising (Figure 4). In 1993, the biomass of above-ground tissues increased from 300 ± 200 gdw m^{-2} in February to 1150 ± 300 gdw m^{-2} in July (Figure 11A), and from 350 ± 100 gdw m^{-2} in February to 900 ± 350 gdw m^{-2} in July for the below-ground tissues, including rhizomes and roots (Figure 11B). So, the primary productivity of *Sparganium fallax* was 850 ± 250 gdw m^{-2} y^{-1} for the above-ground tissues and 550 ± 250 gdw m^{-2} y^{-1} for the below-ground tissues, and in total 1400 ± 250 gdw m^{-2} y^{-1}, but the total productivity decreased in 1994 and 1995 to 970 and 630 gdw m^{-2} y^{-1}, respectively (Figure 11). This decreasing trend was similar to that of *Schoenoplectus mucronatus* ssp. *robustus* (Figure 6). During growing season, the average plant height increased from 50 cm to ca. 80 cm (Figure 11E), and the shoot density was somewhat constant, ca. 300 shoot m^{-2} (Figure 11D). After the growing season, the biomass of *Sparganium fallax* stabilized at ca. 650 gdw m^{-2} for the above-ground tissues and 500 gdw m^{-2} for the below-ground tissues due to the appearance of small shoots from rhizomes (Figures 11 and 12). However, cold temperatures in winter killed most of the mature plants with leaves above water level. Continuous growth of new plants after the growing season in *Sparganium fallax* was probably due to the constant water temperature in the lake. The water temperature 40 cm below the surface remained at ca. 15°C all year. Thus, lake water provided thermal protection for *Sparganium fallax* against freezing in winter.

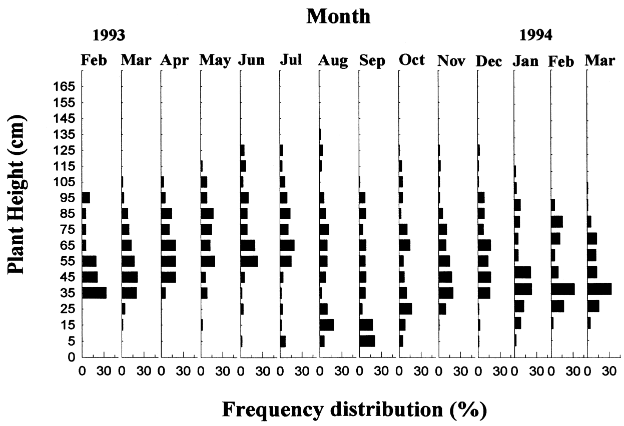

Figure 12. The monthly frequency distribution histograms for plant height of *Sparganium fallax* at Yuan-Yang Lake.

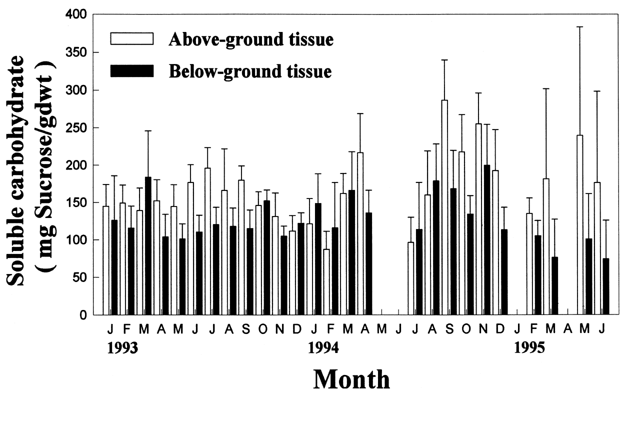

Figure 13. Seasonal changes in soluble carbohydrate content in tissues of *Sparganium fallax* at Yuan-Yang Lake.

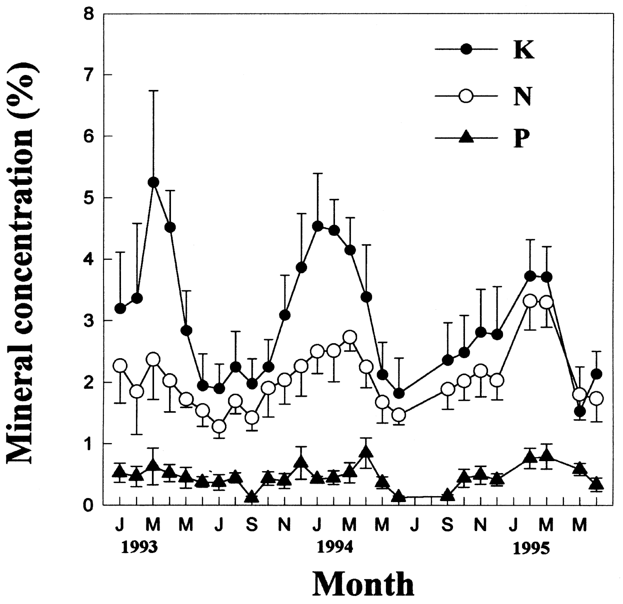

Figure 14. Seasonal changes in major nutrient contents in the above-ground tissues of *Sparganium fallax* at Yuan-Yang Lake.

In general, soluble carbohydrate content, based on sucrose, in the above-ground tissues and below-ground tissues was only ca. 15% and 10% of the dry tissues (Figure 13), respectively. The content increased in the above-ground tissues at the end of the growing season to ca. 18%. In the below-ground tissues, however, the content increased just before the growing season (Figure 13). The soluble carbohydrate content in the below-ground tissues did not increase right after the growing season due to the continuous appearance of new stems from rhizomes (Figure 12). This pattern of metabolite allocation is different from that of *Schoenoplectus mucronatus* ssp. *robustus* (Figure 8), which may reflect the differences in adaptation strategy. *Sparganium fallax* grows in water, which provides thermal protection for the young plants, but a freezing cold front may kill all the above-ground tissues of *Schoenoplectus mucronatus* ssp. *robustus*. A high level of soluble carbohydrates may be necessary to provide an energy source for the winter time growth of *Schoenoplectus mucronatus* ssp. *robustus*.

Potassium and nitrogen were also the major mineral nutrients in the above-ground tissues of *Sparganium fallax* (Figure 14), and they showed a rapid accumulation of concentration in tissues at the onset of the population growth (Figure 14). Nitrogen content in the above-ground tissues was 2.5% immediately before the growing month, twice as much as during the rest of the year. A similar situation

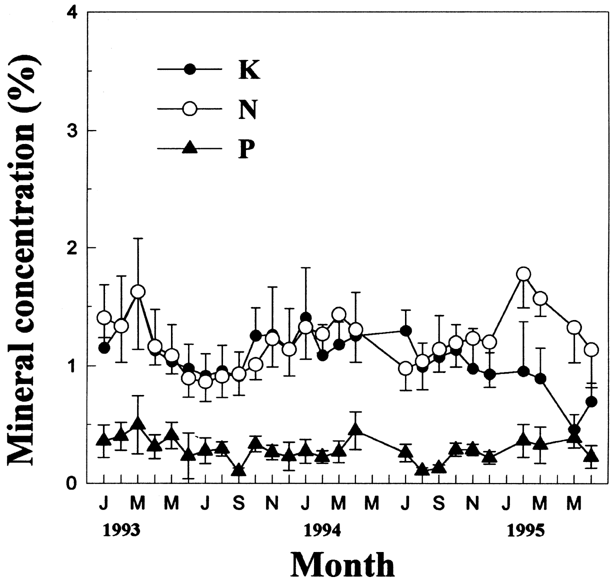

Figure 15. Seasonal changes in major nutrient contents in the below-ground tissues of *Sparganium fallax* at Yuan-Yang Lake.

was found in potassium: 4.5% vs 2.0% (Figure 14). As in *Schoenoplectus mucronatus* ssp. *robustus* (Figures 6A and 9), the decrease of the maximum potassium concentration from 1993 to 1995 (Figure 14) mimics the decrease of primary productivity (Figure 11A) in the population of *Sparganium fallax*. The concentrations for Na, Ca, and Mg were low, compared to K, N, and P, and did not vary significantly with the seasons (data not shown). The concentration range of Ca, Mg, and Na in the above-ground tissue of *Sparganium fallax* was 0.2–0.65%, 0.24–0.46%, and 0.04–0.21%, respectively. The trend was similar for ions in the below-ground tissues, but the above-ground tissues had a higher nitrogen and potassium content than the below-ground tissues (Figure 15).

Conclusions

The climate at Yuan-Yang Lake is temperate heavy moist. A high frequency of cloud and fog coverage kept this area in high humidity while, on the other hand, reducing the incoming solar radiation. The growth of both aquatic macrophytes was in accordance with the seasonal changes of air temperature. Both aquatic plants had a similar pattern of seasonal dynamics of primary production and mineral nutrient content in the above-ground tissues. The correlation between the annual primary production and the maximum potassium content in the above-ground tissues before the growing season in both plants might indicate that the environment of Yuan-Yang lake was potassium limited for the growth of aquatic macrophytes. However, the pattern of seasonal distribution of soluble carbohydrate content in tissues was different, which reflected the difference of adaptation strategy for growing in different habitats.

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