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Foliar Nutrient Dynamics of Five Dominant Plant Species in Yuanyang Lake Nature Preserve, Taiwan

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ABSTRACT: The vegetation composition of Yuanyang Lake (YYL), a subalpine natural preserve in Taiwan, could be divided into two major communities, the coniferous-hardwood and the swamp communities. Nutrient contents of N, P, K and Mg in mature and senescent leaves of *Chamaecyparis obtuse* var. *formosana* and *Rhododendron formosanum*, dominating the coniferous-hardwood community, *Sparganium fallax*, *Schoenoplectus mucronatus* subsp. *robustus*, and *Miscanthus transmorrisonensis*, the swamp community, were measured in April, July and October of 2002 and January of 2003. The objectives of this study were to compare the seasonal changes in nutrient contents of leaves among the five species and to determine the extent of nutrient loss in these species prior to leaf fall. In general, mature leaves of marsh plants had higher N, P and K contents than those of the two terrestrial plants. Among the nutrients measured, only Mg contents showed consistently seasonal trend. Mature and senescent leaves of the five species had consistently higher Mg contents in April than those collected in other seasons. In comparison between mature and senescent leaves, senescent leaves always had significantly lower N, P, and K contents than mature leaves, indicating loss of these nutrients from aging leaves. Potassium was the greatest among the nutrients lost. In comparison between terrestrial and marsh plants, senescent leaves of marsh plants lost significantly more P than those of the two terrestrial plants.

KEY WORDS: Nutrients, Senescent, YYL, *Rhododendron formosanum, Chamaecyparis obtuse, Sparganium fallax, Schoenoplectus mucronatus, Miscanthus transmorrisonensis.*

INTRODUCTION

The Yuanyang Lake (YYL) Nature Preserve is one of the six Taiwan Long-Term Ecological Research (LTER) sites. One of the main objectives of the Taiwan LTER project is to elucidate the mechanisms involved in ecological processes, i.e. energy flow and nutrient cycling. Vegetation is a major component of ecosystem nutrient cycles. In addition, the primary productivity of ecosystems is affected by nutrients availability. Hence an understanding of the nutrient contents of plant community can assist in understanding the functions of ecosystems. The vegetation composition of YYL could be divided into two major communities, a coniferous-hardwood and a swamp communities, the former is dominated by *Chamaecyparis obtusa* var. *formosana* and *Rhododendron formosanum*, and the later by *Miscanthus transmorrisonensis*, *Schoenoplectus mucronatus* subsp. *robustus* and *Sparganium fallax* (Chou *et al*., 2000). Hwang *et al.* (1996) compared the chemical composition of the two aquatic macrophytes, *S. mucronatus* and *S. fallax* but did not measure that of the terrestrial plants in the forest ecosystem. In extension of that study, we analyzed nutrients, N, P, K and Mg in leaves of the five dominant plant species in the ecosystem. Thus, in addition to understand if there is seasonal variation in foliar nutrient contents, we could also compare the nutrient contents between the two communities.

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During leaf senescence, part of the nutrients is resorbed and/or leached from the leaves and the remainder is retained in the leaf litter. Resorption and leaching result in changes in litter composition. This may have direct implications for litter decomposition rates and nutrient release, because decomposition and nutrient release from litter are very often positively related to the N concentrations in litter and negatively related to the C/N ratio (Coulson and Butterfield, 1978; Taylor *et al.*, 1989). At the ecosystem level, nutrient lost from senescing leaves has important implications for element cycling. Most studies on nutrient lost from senescing leaves were performed on evergreen and deciduous trees and few on forbs and graminoids (Aerts, 1996). In contrast, very limited studies were conducted on aquatic plants (Shaver and Melillo, 1984). Hence, the second objective of this study was to determine the extent of nutrients lost prior to leaf fall and to compare that between terrestrial and marsh plants in the YYL ecosystem.

MATERIALS AND METHODS

The Yuanyang Lake Natural Preserve (24º 35' N, 121º 24' E) is located in the northern part of Hsinchu County in Taiwan. The monthly mean air temperature ranged from 5 to 17.5 ºC from 1992 to 1995, and the mean annual rainfall was ca. 3000 mm (Hwang *et al.*, 1996). The climate of the area is classified as temperate heavy moist (Liu and Hsu, 1973). The Yuanyang Lake (YYL), an oligotropic lake at elevation of 1670 m, is at the edge of the Nature Reserve. Five dominant perennial species, including two terrestrial species, *C. obtusa* (an evergreen conifer) and *R. formosanum* (a broad-leaf tree), two emergent aquatic macrophytes, *S. mucronatus* subsp. *robustus* and *S. fallax* and one grass, *M. transmorrisonensis*, were chosen for the study. *S. mucronatus* populations grew in the marsh area and at the borders of the lake covered ca. 0.6 ha, while *S. fallax* in water less than 2 m deep and covered ca. 1.6 ha of the area (Hwang *et al.*, 1996). *M. transmorrisonensis*, an C_4 graminae growing along the lake, together with *S. mucronatus* subsp. *robustus* and *S. fallex* dominated the marsh community (Chou *et al.*, 2000).

Mature and senescent leaves from ten populations of each species were collected in April, July, and October of 2002 and January of 2003. Fully developed, healthy and remaining green leaves were chosen as mature leaves. Senescent leaves were selected as those which were yellow but still attached to the plants. Ten separate leaf samples collected from each species during each season were rinsed with distilled water; then oven dried (70 ºC) to a constant weight and ground to a fine powder with an electric grinder.

Nitrogen contents were determined using an elemental analyzer (NA 1500, Fison, Italy). Potassium and Mg contents of plant material were determined by HCl (6M) extraction (Lambert, 1976), followed by atomic absorption (model 2380, Perkin-Elmer). Total leaf P was determined colorimetrically by the vanadomolybodophosphoric yellow method (Kitson and Mellon, 1944).

The nutrient lost (%) from the senescent leaves during each sampling was estimated as [1 – (nutrient content of senescent leaves/ nutrient content of mature leaves)] * 100. The mean nutrient loss of each element for each species was then calculated as the average of the four samplings.

For individual species, one-way analysis of variance followed by Fisher's least significant difference test (SYSTAT, Statistical Solution Limited, Ireland) were used to test for differences among mature and senescent leaves, taking $P < 0.05$ as significant.

RESULTS

Nutrient contents in mature leaves

In general, mature leaves of marsh plants had higher N, P, and K than the terrestrial species (Figs. 1-3). However, mature leaves of the five plant species contained similar amount of Mg (Fig. 4).

No consistent seasonal pattern was found in leaf N, P, and K contents, but a consistent trend was found in leaf Mg content measured in the five species. In contrast to leaves sampled in July, October, and January, which had similar amount of Mg (Fig. 4), those sampled in April had significantly higher contents of Mg.

Mature vs. senescent leaves

The contents of N, P, and K were significantly reduced in senescent leaves in all samplings (Figs. 1-3). No consistent, seasonal pattern of reduction in these nutrients was found among the species. Among the nutrients lost from the senescent leaves, potassium was the greatest. Most of the K (> 80 %) was lost from senescent leaves (Fig. 3, Table 1).

Surprisingly, no significant difference was found in Mg content between mature and senescent leaves sampled in April, but during other periods of sampling, senescent leaves generally had less Mg contents than mature leaves (Fig. 4). As a result, senescent leaves also showed an annual lost of Mg (Table 1).

In comparison between terrestrial and marsh plants, senescent leaves of marsh plants lost similar K, but significantly more P and Mg than those of the two terrestrial plants (Table 1). No consistent trend was found between terrestrial and marsh plants in the degree of N lost from senescent leaves.

DISCUSSION

N, P, and K contents in mature leaves showed clear differences between the three marsh plants and the two terrestrial plants, with the former having higher N, P and K contents than the later (Figs. 1-3). Grime *et al.* (1997) found high concentrations of foliar N, P, K, Ca and Mg coincided with the capacity for rapid growth in productive conditions. Thus, the results indicate that marsh plants might have higher growth rate than the two terrestrial plants. In addition, as carbon assimilation of a leaf is linearly related to the nitrogen content of that leaf (Field, 1983; Hunt *et al.*, 1985; Evans, 1989), this implies that N concentration in mature leaves has consequence for the carbon gain. Magnesium is one of the major constitutes of chlorophyll, hence the pattern of seasonal changes in Mg content in leaves suggests different photosynthetic activity. The relationship between the pattern of nutrients and the carbon assimilation of the species measured is currently under study.

In comparison between mature and senescent leaves, senescent leaves showed lower N, P, and K contents than mature leaves, indicating loss of these nutrients from aging leaves. The nutrients lost from senescent leaves were resorbed and/or leached from the leaves. The susceptibility to leaching loss is greatest for monovalent cations, less for divalent cations, and least for organically bound nutrients (Tukey, 1970; Chapin and Moilanen, 1991; Aerts and Chapin, 2000). Due to the heavy rainfall in the YYL area, leaching might have caused a great proportion of K lost from senescent leaves, though the possibility of resorption could not be ruled out. Collecting nutrients leached from leaves of the terrestrial plants in the YYL forest

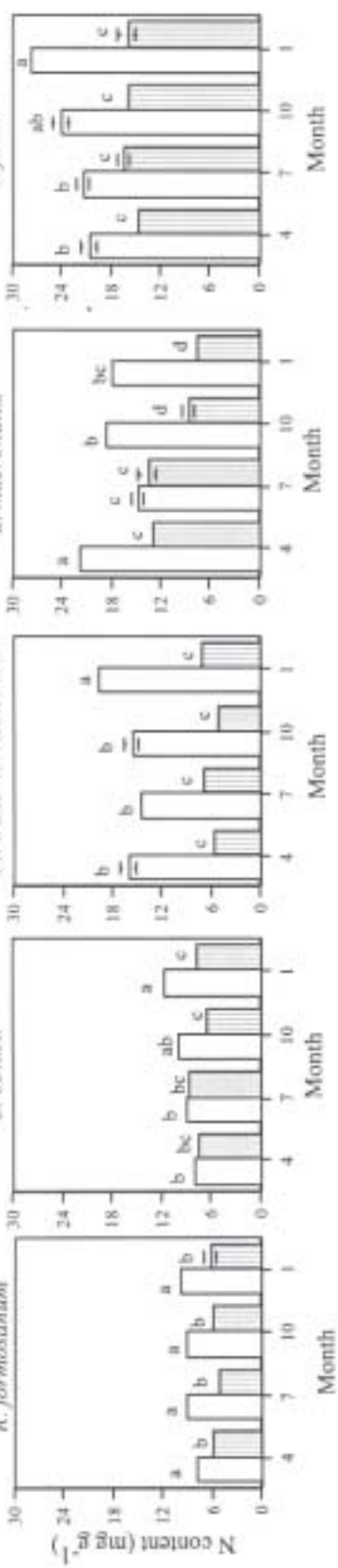

Fig. 1. Nitrogen contents of mature (open bars) and senescent leaves (solid bars), sampled in April, July and Oct. of 2002 and Jan. of 2003, of five dominant plant species of YYL Natural Preserve in Taiwan. Vertical bars represent ± 1 s.e. of treatment means (n = 10). Values with different letters indicate significant difference ($P < 0.05$) of the same species among samplings.

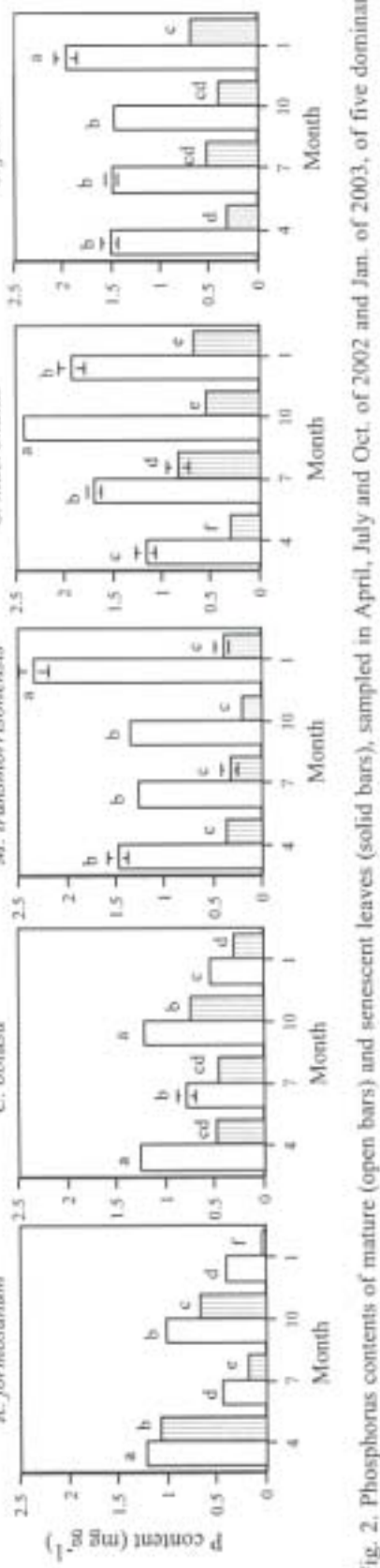

Fig. 2. Phosphorus contents of mature (open bars) and senescent leaves (solid bars), sampled in April, July and Oct. of 2002 and Jan. of 2003, of five dominant plant species of YYL Natural Preserve in Taiwan. Statistical test as in Fig. 1.

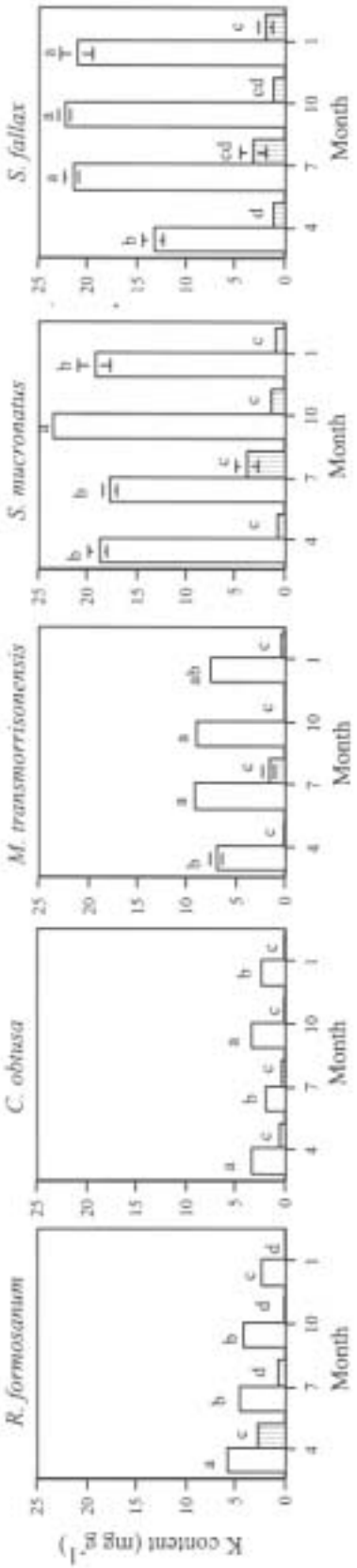

Fig. 3. Potassium contents of mature (open bars) and senescent leaves (solid bars), sampled in April, July and Oct. of 2002 and Jan. of 2003, of five dominant plant species of YYL Natural Preserve in Taiwan. Statistical test as in Fig. 1.

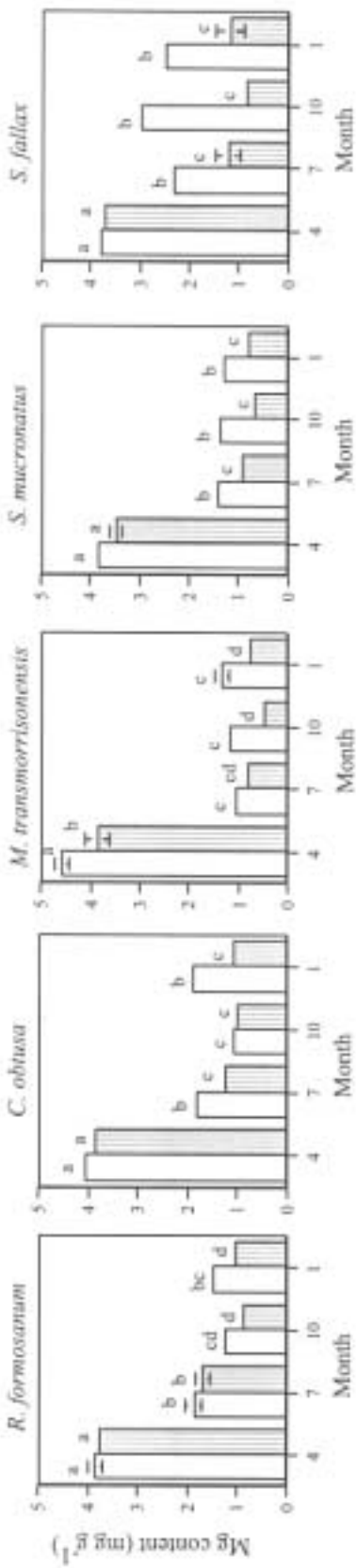

Fig. 4. Magnesium contents of mature (open bars) and senescent leaves (solid bars), sampled in April, July and Oct. of 2002 and Jan. of 2003, of five dominant plant species of YYL Natural Preserve in Taiwan. Statistical test as in Fig. 1.

Table 1. Nutrient lost (Mean ± S.E, %, n = 4), calculated as the average of four samplings, from senescent leaves of five dominant plant species in YYL Natural Preserve.

	N	P	K	Mg
R. formosanum	34.3 ± 3.8	48.8 ± 16.7	80.8 ± 10.8	17.9 ± 7.3
C. obtusa	19.3 ± 8.4	46.8 ± 5.1	89.7 ± 4.6	21.7 ± 9.1
M. transmorrisonensis	61.6 ± 3.2	79.0 ± 2.6	92.6 ± 3.7	34.4 ± 9.4
S. mucronatus	39.8 ± 11.1	67.0 ± 6.0	91.0 ± 4.1	32.8 ± 8.6
S. fallax	31.7 ± 4.2	70.0 ± 3.6	90.4 ± 2.0	43.1 ± 14.8

ecosystem, Chou *et al*. found the greatest leaching of K among the nutrients studied (Chou per. comm.). In a study of the primary productivity of the macrophytes in the YYL, Hwang *et al.* (1996) suggested that the growth of aquatic plants in this environment was limited by potassium supply. Accordingly, potassium leached from leaves might be carried away through the outlets of the lake water resulting in K deficient in the ecosystem.

In general, N and P are not readily leached from leaves (Morton, 1977). For example, soaking of leaves in water leached < 0.6 % of N and P from leaves at autumn senescence when leaves are most susceptible to leaching (Tukey, 1970). In addition, no NO_3^- was found in the leachate collected from the same study described before (Chou per. comm.). Therefore, the decline in N and P contents in senescing leaves in this study was more likely due to resorption from leaves to stems than to leaching loss. Mean N and P resorption from senescing leaves of evergreen and deciduous tree and forbs and graminoids is 50 and 52 %, respectively (Aerts, 1996). The mean percentage of N resorption of the five species in this study varies from 19 to 62 %, the highest was measured in *M. transmorrisonensis* and the lowest in *C. obtuse* (Table 1). The mean percentage of P resorption of the five species ranges from 47 to 79 %. In comparison, the percentage of P resorption of the two terrestrial plants is about the mean, while that of marsh plants is higher than the mean values reported by Aerts (1996) (Table 1). The advantage of high resorption efficiency is clear: the nutrients resorbed from senescing tissues can be re-used directly for new growth or they can be stored until use during the next growing season. Thus, we hypothesize that higher resorption in P would make marsh plants less depend on P uptake than terrestrial plants during new growth.

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鴛鴦湖生態保護區優勢植物葉營養元素比較

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摘　　要

鴛鴦湖生態保護區位於台灣亞高山帶，其植物組成可分為森林植物社會和水、濕生草本植物社會。本文分析此保護區內兩種森林優勢植物(台灣杜鵑、台灣扁柏)和三種水、濕生草本植物(芒草、水毛花、東亞黑三稜，合稱沼澤植物)其葉所含之營養元素。主要目的在比較此五種優勢植物其成熟葉以及老葉主要營養元素(氮、磷、鉀、鎂)之季節性變化。相較於台灣杜鵑和台灣扁柏，沼澤植物其成熟葉具有較多的氮、磷和鉀。在所分析的營養元素中，僅鎂元素具季節性變化：五種植物之成熟葉和老葉其鎂含量在春季(四月)時均呈現大幅增加，顯著高於七、十和一月時葉內鎂含量。五種植物黃化老葉其氮、磷和鉀含量均顯著低於成熟葉，顯示葉子在掉落前其營養元素有流失或被移轉的現象，其中以鉀元素含量減少最多。沼澤植物其老葉所減少之磷元素比例顯著高於台灣杜鵑和台灣扁柏。

關鍵詞：營養元素、老葉、鴛鴦湖生態保護區、台灣杜鵑、台灣扁柏、東亞黑三稜、水毛花、芒草。

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