

# Nutrient contents, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ during leaf senescence in the mangrove, *Kandelia candel* (L.) Druce

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**Abstract.** *Kandelia candel* (L.) Druce is the dominant mangrove species in two nature reserves in Northern Taiwan. We characterized the nutrient quality of the leaf litter originating from *K. candel* and attempted to suggest the extent to which the observed decline of nutrient concentrations in senescing leaves could be attributed to the withdrawal of these nutrients into the main plant before abscission. On a dry weight basis, senescent leaves and leaf litter had significantly lower concentrations of N, P and K and higher concentrations of Na than did younger ones. At one site Ca and Mg contents rose with senescence; at the second site there was no change with age of leaf. Leaf  $\delta^{13}\text{C}$  and C:N ratios suggest that withdrawal into the main plant may not be the major cause for the observed decline of C and N during leaf senescence. The  $\delta^{13}\text{C}$  values of mature leaves ranged from -26‰ to -30‰; senescent leaves and leaf litter were 0.6‰ more negative for  $\delta^{13}\text{C}$  than fresh leaves at the most seaward site. We attribute this decline of  $\delta^{13}\text{C}$  to loss of stomatal control during senescence.  $\delta^{15}\text{N}$  ranged from +4.3‰ to +9.8‰ for individual samples with no significant differences among ages of leaves, indicating no important gaseous N losses during senescence. P was probably not limiting to growth at these sites.

**Keywords:** 13-C; 15-N; *Kandelia candel*; Leaf litter quality; Mangrove.

## Introduction

Mangrove ecosystems in tropical and subtropical coastal areas are highly productive, and mangrove litter is an important food source for vertebrates and invertebrates (Robertson and Daniel, 1989; Osborne and Smith, 1990). Hence, an understanding of the nutrient contents of mangrove leaves can assist in understanding the quality of food resource available to consumers. It is additionally useful to know the fates of putative nutrient losses from mangrove. If, for instance, the nutrients are retained in the plant, they are unavailable to the larger ecosystem while the mangrove lives. If they are leached from leaves into the water, then they are available to other organisms, albeit not as a part of leaf litter.

Although N uptake in *K. candel* has been studied (Kao et al., 2001), the nutrient status of *K. candel* leaves during leaf senescence has not. We aimed to characterize the concentrations of leaf nutrients (C, N, P, K, Na, Ca and Mg) and to use  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , in conjunction with elemental concentrations, to suggest whether decreases in leaf nutrient concentrations were related to withdrawal into the main plant.

## Materials and Methods

Leaves and soil samples were collected from two nature reserves (Figure 1), Watz-wei and Chu-wei swamps (25°9' N, 121°26' E), in May and June of 1998, respectively. Chu-wei swamp contains about 50 ha of pure *K. candel* forest and Watz-wei swamp about 9 ha. Tides are semidiurnal; salinity in Watz-wei Swamp is 5 to 30 psu and ranges from 1.1 to 27.4 psu in Chu-wei Swamp (Shae, 1995). Chu-wei lies further inland than Watz-wei and is closer to the sewage source from Taipei. The pH of water overlying soil at both sites is 7.1 to 7.9 (Shae, 1995). Mean annual temperature is 22°C, and mean annual precipitation is 2,100 mm (Climatological Data Annual Report, Central Weather Bureau, ROC.).

Mature leaves (the second or third pairs of leaves from the terminal bud) and senescent leaves (5 to 6 leaves per sample) were collected from each of 10 trees; leaf litter (as partially decomposed leaves; n = 5 to 6) was collected beneath each tree. Senescent leaves were selected as those which were yellow but still attached to the trees. A five-cm-deep core of the upper mineral soil was collected beneath each tree (n = 10) using a stainless steel hand corer. These were sealed in plastic bags on ice until analysis. Leaf samples were rinsed with distilled water; then leaf and soil samples were oven-dried (70°C) to a constant weight and ground to a fine powder with a mortar and pestle.

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$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were determined by sealed-tube combustion followed by cryogenic distillation (Handley et al., 1991) the isolated gases analyzed using an isotope ratio mass spectrometer (DeltaS, Finnigan Mat, Germany) at the Institute of Botany, Academia Sinica, Taiwan.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were calculated in the usual manner as:

$$\delta X (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000,$$

where R is the ratio of heavy-to-light isotope. The universally agreed standard for  $\delta^{13}\text{C}$  is Pee Dee Belemnite and for  $\delta^{15}\text{N}$  it is the  $\text{N}_2$  of air.

%N and %C were determined using an elemental analyzer (NA 1500, Fisons, Italy). K, Na, Ca and Mg contents of plant materials were determined by HCl (6 M) extraction (Lambert, 1976) followed by flame photometry (Model 410, Corning, England) and atomic absorption (Model 2380, Perkin-Elmer). Total leaf P was determined colorimetrically by the vanadomolybodophosphoric yellow method (Kitson and Mellon, 1944).

Statistical outliers were eliminated (1-3 per variable), and means were compared using Fisher's least significant difference (SYSTAT, Statistical Solutions Limited, Ireland), taking  $P < 0.05$  as significant.

## Results

At Chu-wei and Watz-wei, N, P and K contents in senescent leaves and leaf litter were significantly less than those of fresh leaves (Table 1). Mature leaf contents of P

and K were significantly different ( $P < 0.05$ ) between sites and were the largest at Chu-wei. Senescent leaves at Chu-wei lost 74% of mature-leaf N, 42% of P, and 31% of K. At Watz-wei senescent leaves lacked 65% of mature leaf N, 19% of P, and 61% of K in comparison with mature leaves. Na contents increased significantly in senescent leaves (48% at Chu-Wei and 88% at Watz-wei). Leaf litter contained an additional 28% Na at Chu-Wei and an additional 30% at Watz-wei in comparison with mature leaves. There was no significant difference in the Ca contents of the three ages of leaves at Chu-wei Swamp. Senescent leaves and leaf litter at Watz-wei Swamp had higher Ca contents than did fresh leaves. Leaf Mg contents were similar among all leaves at both sites. At both sites leaf litter contained significantly less P and K than did unfallen senescent leaves.

At Chu-wei Swamp (Table 1), %C declined significantly from mature to senescent stages and in leaf litter significantly increased over that of the mature leaves. At Watz-wei Swamp, %C decreased significantly from mature to senescent leaves and to leaf litter. Compared with mature leaves, the C:N ratio of senescent leaves was greater at both sites. The changes in the C:N ratio were largely determined by the decline of leaf N. The C:N ratio of C and N lost (difference between C:N in mature and senescent leaves; Table 1) was 65 at Chu Wei and 42 at Watz-Wei. There was no significant difference between the C:N of senescent leaves and leaf litter at either site.

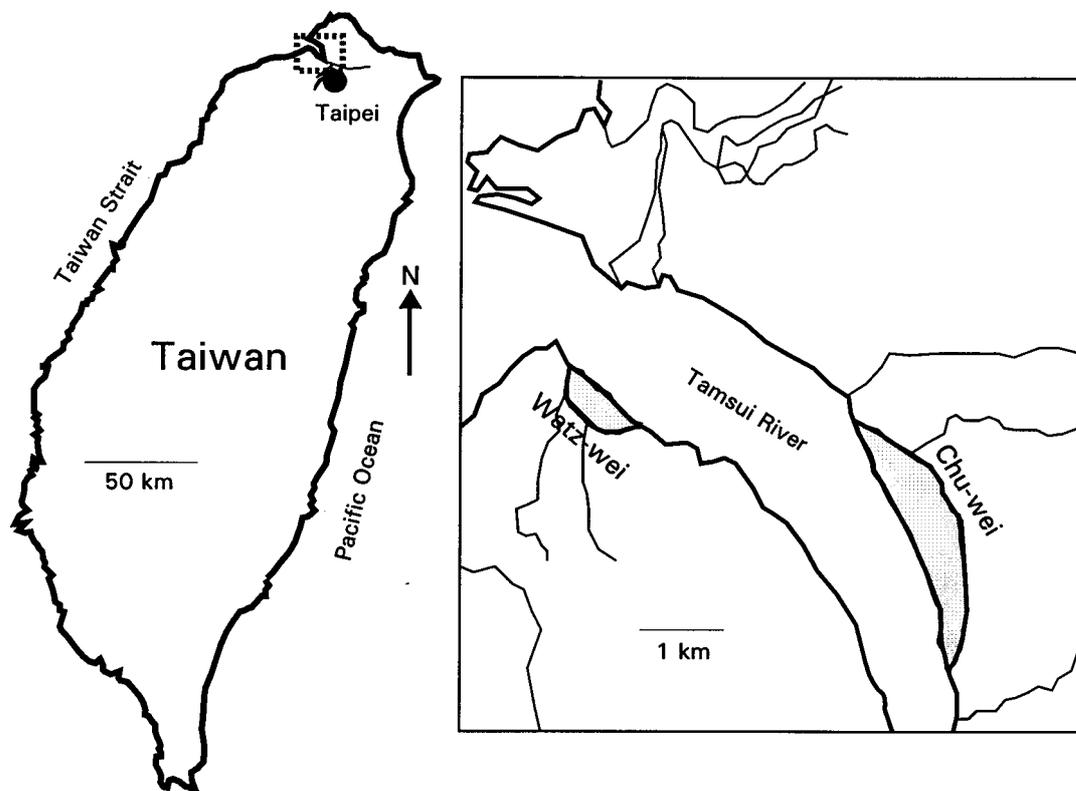


Figure 1. Map of Taiwan showing enlargement of area containing study sites.

**Table 1.** Means  $\pm$  standard errors ( $n = 6-10$ ) of nutrient contents ( $\text{mg g}^{-1}$ ), stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope abundances, carbon (C) and nitrogen (N) contents, and C:N ratio of mature, senescent leaves and leaf litter from *K. candel* and soil from beneath trees. Sampled in two nature reserves, Chu-wei and Watz-wei, in Northern Taiwan. Values on a dry weight basis. Means within columns followed by different superscripts are different at  $P = 0.05$  (LSD procedures).

	% %									
	Na	K	Ca	Mg	P	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C	N	C/N
<b>Chu-wei</b>										
Mature	14.4 $\pm$ 0.8 <sup>a</sup>	6.2 $\pm$ 0.4 <sup>a</sup>	4.6 $\pm$ 0.1 <sup>a</sup>	3.3 $\pm$ 0.1 <sup>a</sup>	2.4 $\pm$ 0.2 <sup>a</sup>	-27.3 $\pm$ 0.2 <sup>a</sup>	6.1 $\pm$ 0.5 <sup>a</sup>	43.2 $\pm$ 0.6 <sup>a</sup>	1.9 $\pm$ 0.1 <sup>a</sup>	23.4 $\pm$ 1.4 <sup>a</sup>
Senescent	21.3 $\pm$ 0.9 <sup>b</sup>	4.3 $\pm$ 0.6 <sup>b</sup>	4.9 $\pm$ 0.2 <sup>a</sup>	3.7 $\pm$ 0.1 <sup>b</sup>	1.4 $\pm$ 0.2 <sup>b</sup>	-27.8 $\pm$ 0.3 <sup>a</sup>	6.0 $\pm$ 0.5 <sup>a</sup>	40.6 $\pm$ 0.8 <sup>b</sup>	0.5 $\pm$ 0.0 <sup>b</sup>	88.3 $\pm$ 6.9 <sup>b</sup>
Litter	25.4 $\pm$ 1.9 <sup>c</sup>	1.0 $\pm$ 0.1 <sup>c</sup>	5.0 $\pm$ 0.3 <sup>a</sup>	3.3 $\pm$ 0.1 <sup>a</sup>	0.9 $\pm$ 0.0 <sup>c</sup>	-27.7 $\pm$ 0.2 <sup>a</sup>	6.1 $\pm$ 0.4 <sup>a</sup>	45.1 $\pm$ 0.7 <sup>c</sup>	0.6 $\pm$ 0.0 <sup>b</sup>	84.9 $\pm$ 6.5 <sup>b</sup>
Soil	*N. A.	*N. A.	*N. A.	*N. A.	*N. A.	-26.7 $\pm$ 0.2 <sup>b</sup>	*N. A.	0.6 $\pm$ 0.0 <sup>d</sup>	0.1 $\pm$ 0.0 <sup>c</sup>	13.8 $\pm$ 0.5 <sup>c</sup>
<b>Watz-wei</b>										
Mature	19.1 $\pm$ 1.3 <sup>a</sup>	4.6 $\pm$ 0.3 <sup>a</sup>	4.9 $\pm$ 0.2 <sup>a</sup>	3.0 $\pm$ 0.2 <sup>a</sup>	1.6 $\pm$ 0.1 <sup>a</sup>	-26.8 $\pm$ 0.1 <sup>a</sup>	6.6 $\pm$ 0.4 <sup>a</sup>	44.4 $\pm$ 0.6 <sup>a</sup>	1.7 $\pm$ 0.1 <sup>a</sup>	27.7 $\pm$ 2.2 <sup>a</sup>
Senescent	36.0 $\pm$ 2.2 <sup>b</sup>	1.8 $\pm$ 0.1 <sup>b</sup>	7.9 $\pm$ 0.6 <sup>b</sup>	3.4 $\pm$ 0.1 <sup>b</sup>	1.3 $\pm$ 0.1 <sup>b</sup>	-27.4 $\pm$ 0.2 <sup>b</sup>	6.8 $\pm$ 0.1 <sup>a</sup>	41.3 $\pm$ 0.7 <sup>b</sup>	0.6 $\pm$ 0.0 <sup>b</sup>	69.8 $\pm$ 5.3 <sup>b</sup>
Litter	41.7 $\pm$ 1.2 <sup>c</sup>	0.9 $\pm$ 0.0 <sup>c</sup>	6.5 $\pm$ 0.3 <sup>c</sup>	3.5 $\pm$ 0.0 <sup>b</sup>	0.7 $\pm$ 0.0 <sup>c</sup>	-27.7 $\pm$ 0.2 <sup>b</sup>	7.3 $\pm$ 0.3 <sup>a</sup>	39.3 $\pm$ 0.4 <sup>c</sup>	0.7 $\pm$ 0.0 <sup>b</sup>	61.4 $\pm$ 5.1 <sup>b</sup>
Soil	*N. A.	*N. A.	*N. A.	*N. A.	*N. A.	-25.3 $\pm$ 0.1 <sup>c</sup>	*N. A.	0.8 $\pm$ 0.1 <sup>d</sup>	0.1 $\pm$ 0.0 <sup>c</sup>	11.9 $\pm$ 0.5 <sup>c</sup>

\*Not available.

At Watz-wei, the  $\delta^{13}\text{C}$  of senescent leaves (-27.4‰) and leaf litter (-27.7‰) were similar and significantly more negative than mature leaves (-26.8‰; Table 1) by 0.6‰. At Chu-wei there were no significant differences among the  $\delta^{13}\text{C}$  of mature leaves, senescent leaves, and leaf litter (-27.3‰, -27.8‰ and -27.7‰, respectively).

Mature leaves from Chu-wei had significantly higher K and phosphorus contents ( $P < 0.05$ ), and lower Na content ( $P < 0.05$ ), than those from Watz-wei (Figure 1), which is nearer the marine coast. However, no significant difference was found between the sites for %N ( $P = 0.1$ ), %Mg ( $P = 0.15$ ) contents, C:N ratio ( $P > 0.05$ ), or  $\delta^{13}\text{C}$  ( $P = 0.09$ ) and  $\delta^{15}\text{N}$  ( $P = 0.24$ ).

The  $\delta^{13}\text{C}$  of soil-sediment C was less negative than that of leaves or leaf litter at both sites.

## Discussion

Nutrient limitations, especially N, P and K, have been thought to limit mangrove growth (Feller, 1995; Lugo and Snedaker, 1974), and withdrawal of nutrients from leaves has been suggested as important for nutrient conservation in some wetland plants (Shaver and Melillo, 1984). We found that senescent leaves of *K. candel* had much lower N, P and K contents than mature leaves and that the relative amounts lost were within the same range found by Rao et al. (1994) for several mangrove species from East Africa. Despite sewage inputs from Taipei, Chen (1998) and Kao & Chang (1998) found evidence of *K. candel*'s being N-limited in some part of the Chu-wei site.

However, the nutrients lost from aging leaves are not necessarily resorbed by the tree. They could be, for instance, leached from the leaves by rainfall, and in the case of N the loss could be as gases to the atmosphere (e.g. Harper and Sharpe, 1995). We used  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and C:N ratios to suggest the extent to which withdrawal could explain declining N and C contents in the leaves. If withdrawal were a plausible, single explanation for declining N and C contents, then it might be a plausible explanation also for the loss of other nutrients such as P and K. If withdrawal explained most of the observed decline of leaf C and N, then we expected: (1) The  $\delta^{13}\text{C}$  of senescent leaves should be less negative than that of mature leaves. This is because non-mobile, structural C is less negative for  $\delta^{13}\text{C}$  than are starch, sugar or fats, which might be easily mobilized during senescence (Brendel, 2001) and (2) The C:N ratio of the lost C and N should fall within the range of 4 to 5. This range is characteristic of typical plant amino acids which are continually exported from leaves *via* the phloem during the life of the leaf. Leaf  $\delta^{15}\text{N}$ , which is probably unrelated to withdrawal for the reason given below, should increase if gaseous loss is a major factor; all known forms of gaseous N losses are isotopically lighter than their N sources (Handley and Raven, 1992) and enhance  $\delta^{15}\text{N}$  in the remaining source.

Leaf N is continually exported to the main plant *via* the phloem during the life of the leaf. We are aware of only one report for the direct measurement of phloem  $\delta^{15}\text{N}$ , and

this was for wheat in the grain-filling stage (Yoneyama et al., 1997). Yoneyama et al. (1997) found no significant difference in the  $\delta^{15}\text{N}$  of phloem N, leaf blade N or leaf sheath N. This suggests that the occasionally reported variations of leaf  $\delta^{15}\text{N}$  with age (e.g. Handley and Scrimgeour, 1997; Domenach et al., 1989) were caused by variations of N isotopic source and not by isotopic fractionations during withdrawal from the leaf.

In *K. candel* the  $\delta^{13}\text{C}$  values of mature leaves of *K. candel* either became more negative (by 0.6‰) in senescence (Watz-wei) or did not significantly change (Chu-wei). Leaf  $\delta^{13}\text{C}$  is chiefly controlled by the amount of stomatal opening in the leaf (Farquhar and Richards, 1984), leaf  $\delta^{13}\text{C}$  becoming more negative with greater stomatal opening. Stomata commonly lose their ability to close completely during senescence (Wilmer, 1983), and this is the simplest explanation for senescent leaf  $\delta^{13}\text{C}$  being more negative than that of mature leaves. Our interpretation is consistent with the greater Na contents of leaves at Watz-wei. Open stomata incur large amounts of transpiration, which would bring more water and dissolved Na into the leaves. Our leaf  $\delta^{13}\text{C}$  data are within the range of those reported by Rao et al. (1994) for mangrove in W. Africa, where  $\delta^{13}\text{C}$  of mangrove leaves became increasingly negative with senescence (by 0.6‰ to 2.6‰) for seven species; three other species became less negative with senescence (by 0.7‰ to 1.1‰) and the  $\delta^{13}\text{C}$  of one species did not change in senescence.

We found  $\delta^{15}\text{N}$  in mature leaves of *K. candel* to be +4.3‰ to +9.8‰. This is the same range of values reported by McKee et al. (2002) for P-limited *Rhizophora mangle* L. in Belize (+0.1‰ to -5.8‰), and a narrower range than that reported by Fry et al. (2000) for *R. mangle* growing in South Florida (-5‰ to +15‰). The Florida trees were exposed to sewage-derived N as were *K. candel* at our study sites. Leaf  $\delta^{15}\text{N}$  of *K. candel* did not change with senescence. We can therefore conclude that no large gaseous losses of N occurred and that the lost N had the same  $\delta^{15}\text{N}$  value as the whole leaf N. The lack of age-related change in leaf  $\delta^{15}\text{N}$  is consistent with withdrawal of leaf N, but insufficient to demonstrate it as a mechanism. Reports of mangrove  $\delta^{15}\text{N}$  are few, and we are unaware of any other reports of mangrove leaf  $\delta^{15}\text{N}$  related to leaf age.

Mean annual rainfall at the two sites studied is high (2100 mm), and it is likely that at least some N and C is lost from mangrove leaves through leaching.

The quality of the leaf litter (as newly fallen, partially decomposing leaves) was influenced by changes in nutrient content before leaf-fall and by proximity to the sea. The leaf litter at the seaward site contained more Na and more Ca than that at the inland site. Concentrations of all other nutrients measured were similar at the two sites. P and K were lost in significant amounts during the early stages of decay.

*Kandelia candel* carbon contributed to the sediment C pool as witnessed by the litter layer, and because the  $\delta^{13}\text{C}$  of sediment C and mangrove litter were similar, we presume that mangrove is a major source of C to the

sediments. However, bulk sediment  $\delta^{13}\text{C}$  was slightly less negative than that of mangrove leaf litter, probably because of C contributions of a marine origin, given the tidal nature of the sites. Although the  $\delta^{13}\text{C}$  of marine C is on average less negative than that of  $\text{C}_3$  terrestrial C, marine macrophytes are reported to have  $\delta^{13}\text{C}$  values ranging from -3‰ to -35‰ (Raven et al., 2002). Hence, it is not possible to quantify the fractional contributions of marine and mangrove sources to sediment C.

Na concentration was greater in senescent leaves than in mature ones. It is a common salt-avoidance strategy of halophytes to load excess Na into senescing leaves, which has been demonstrated for the mangrove *R. mangle* (Werner and Stelzer, 1990). The Na is then lost from the plant when the leaves abscise and fall.

Leaves at Chu-wei contained more P than did those at the more coastal site, Watz-wei. This difference may be related to the proximity of Chu-wei to the sewage source at Taipei. Domestic sewage may contain large amounts of P, because P is a major ingredient in household cleaning agents. P also readily adsorbs onto sediments and would be adsorbed from the water column as it moves from downstream. McKee et al. (2002) found that demonstrated P deficiency in *R. mangle* was associated with low foliar  $\delta^{15}\text{N}$ . We found the reverse relationship for foliar P contents. The  $\delta^{15}\text{N}$  of Chu-Wei leaves was lower than those from Watz-Wei, but contained more P. This suggests that P was not growth-limiting to the trees sampled.

In conclusion, results from this study reveal that *K. candel* leaves lose substantial amounts of nutrients during senescence, producing a nutrient-depleted litter which continues to lose significant amounts of P and K during the early stages of decay.  $\delta^{13}\text{C}$  and C:N values suggest that withdrawal by the trees is possibly not the major mechanism by which these nutrients are lost from senescing, unfallen leaves. We interpret the senescent decline of leaf  $\delta^{13}\text{C}$  as loss of stomatal control under stress. Leaf  $\delta^{15}\text{N}$  indicates that gaseous losses from leaves are not large and that there is little P limitation to growth at these sites. Because the  $\delta^{13}\text{C}$  of sediment C is close to that of mangrove leaf litter, we presume that mangrove contributes a large proportion of sediment C.

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## 水筆仔營養鹽含量及穩定性碳、氮同位素比值

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本文分析台灣北部竹圍和挖仔尾紅樹林保護區之主要樹種水筆仔其掉落葉之營養鹽品質，並嘗試用穩定性碳、氮同位素比值變化來探討水筆仔葉老化時其主要營養鹽含量降低的原因。結果顯示水筆仔老葉和掉落葉其氮、磷和鉀之乾重含量均顯著低於成熟葉。挖仔尾水筆仔葉老化時鈣和鎂含量增加，然而竹圍水筆仔其成熟葉、老葉和掉落葉鈣和鎂含量則無顯著變化。分析葉之碳同位素比值和碳氮比顯示植體再吸收可能不是導致老葉碳、氮含量降低的主因。成熟葉碳同位素比值介於 -26‰ 和 -30‰ 間；老葉和掉落葉其碳同位素比值均較成熟葉為負，我們認為是因為葉老化時其氣孔逐漸失去控制氣體交換能力所致。水筆仔葉之氮同位素比值介於 +4.3‰ 和 +9.8‰ 間，且成熟葉、老葉和掉落葉間無顯著差異，顯示水筆仔葉老化時應無明顯之氣態氮釋出。比較兩保護區水筆仔葉之磷含量和氮同位素比值顯示磷應該不是限制此二保護區內水筆仔生長的因子。

**關鍵詞：**水筆仔；紅樹林；老化；穩定性碳同位素比值；穩定性氮同位素比值。