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Vertical profiles of CO_2 concentration and $\delta^{13}C$ values in a subalpine forest of Taiwan

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Abstract. We investigated the vertical gradients in CO_2 concentration and stable carbon isotope ratio ($\delta^{13}Cco_2$) of the canopy air within a coniferous-hardwood, *Chamaecyparis* and *Rhododendron* dominated, subalpine forest in Taiwan. The stable carbon isotope ratio of vascular plants and a epiphytic bryophyte species (*Bazzania fauriana*) ($\delta^{13}C_{leaf}$) from different heights within the forest were also analyzed. Results revealed that CO_2 and $\delta^{13}Cco_2$ gradients did exist within the forest, with higher CO_2 concentrations and more negative $\delta^{13}Cco_2$ values in air sampled from the lower canopy. The average vertical gradients in CO_2 and $\delta^{13}Cco_2$ value of the CO_2 of the 12 sampling dates were 28.5 ± 6.1 ppm and 1.3 ± 0.3‰, respectively. Seasonal patterns of the relationship between 1/[CO_2] and the corresponding $\delta^{13}C$ were pronounced, with steady decreases in the slopes and increases in the intercepts found from January to August. A decreasing $\delta^{13}C_{leaf}$ with decreasing height was also measured in a bryophyte (ranging from -27.4 to -29.2‰), canopy and understory leaves (ranging from -28.6 to -33.5‰). It was estimated that photosynthetic physiology affected by microclimates within the forest contributed approximately 2.8‰ of variation of the vertical gradient of vascular plant $\delta^{13}C$ values.

Keywords: Bryophyte; CO_2; Subalpine forest; Stable carbon isotope ratio.

Introduction

Forest ecosystems are an important carbon pool and have profound impacts on atmospheric CO_2 concentrations. In particular, soil-respired CO_2 in forests has been reported as a significant component in global carbon cycling (Woodwell et al., 1983). The CO_2 released during respiration and decomposition may diffuse through the forest canopy into the atmosphere or a fraction of this CO_2 may be reassimilated through photosynthesis by the forest ecosystem (Lloyd et al., 1996; Sternberg et al., 1989). Thus, there are two major sources of CO_2 for photosynthesis within forests: one is from bulk air and the other from soil respiration.

Internal carbon fluxes within forest canopies and their interactions with soil and atmospheric exchange processes can be addressed using carbon isotopes. The mean value of atmospheric CO_2 is currently -8‰ but varies seasonally in response to the patterns of photosynthesis and respiration (Conway et al., 1994; Mook et al., 1983). Photosynthesis discriminates against $^{13}CO_2$, thus plants have a lighter carbon isotopic composition in their tissue in comparison to the atmospheric CO_2. The respired CO_2 derived from root respiration and decomposition of soil organic matter has a $\delta^{13}C$ value close to that of the organic matter of the dominant species in the forest community (Flanagan et al., 1996). Accordingly, the two sources of CO_2 within the forest canopy have different isotopic signals.

Vertical gradients in CO_2 and $\delta^{13}C$ values have been studied in different forest ecosystems in different areas of the world. Turbulent mixing between the two sources of CO_2 within the canopy and discrimination against $^{13}CO_2$ during photosynthesis results in $\delta^{13}C$ of ratios of canopy air that are more depleted near the soil surface than at top of the canopy (Broadmeadow et al., 1992; Buchmann et al., 1997a,b; Flanagan et al., 1996; Francey et al., 1985; Quay et al., 1989; Sternberg, 1989; Van der Merwe and Medina, 1989). The range of the gradients depends on forest development, forest structure, and forest types (Buchmann et al., 1997b). To our knowledge, no similar study has been done in any forests of Taiwan. Since 1992, a long-term ecological study (LTER) has been set-up at a subalpine ecosystem within a natural preserve. The LTER study emphasizes the structure and function of the forest ecosystem as well as its carbon and nutrient flux. Understanding variations in the concentration and isotopic composition of CO_2 within and above vegetation could provide insights into ecosystem functioning (Lloyd et al., 1996). In the present study, we investigated the profiles of CO_2 concentration and $\delta^{13}C$ values of the canopy air and vegetation at different heights of the forest stand to understand processes related to carbon flux within the ecosystem. Stable carbon isotope ratios of vascular plants and a moss species ($\delta^{13}C_{leaf}$) from different heights within the forest were also analyzed. The objectives of the present study were to understand: (1) whether a vertical profile in CO_2

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concentration and $\delta^{13}C$ of the subalpine forest ecosystem exists, what the relationship is between these two parameters, and how this compares with other ecosystems; (2) whether a vertical profile in leaf $\delta^{13}C$ of plants of different heights exists and what the causes of the variation are; and (3) whether there is a difference in leaf $\delta^{13}C$ between bryophyte and vascular plants within the forest ecosystem.

Materials and Methods

Study Site

The Yuanyang Lake Natural Preserve (N 24°35' and E 121°24') located in the northeastern part of Hsinchu County is one of five Long-term Ecological Research sites in Taiwan. It consists of coniferous forest, hardwood forest, pteridophytes, epiphytes (such as mosses and liverworts), grassland species and several aquatic plants (Chou et al., 2000). The vegetation of the study area, located in the preserve at an altitude of 1,670 m, is dominated by a mixture of *Chamaecyparis formonensis*, *Chamaecyparis taiwanensis*, and *Rhododendron formosanum* stands. The weather has been classified as temperate heavy moist (Liu and Hsu, 1973). The monthly mean air temperature ranged from 5 to 17.5°C from 1992 to 1995 (Hwang et al., 1996).

Air Sampling

A portable tower 8 m high was set up within a mixed forest of *Chamaecyparis* and *Rhododendron* stands. The leaf area index (LAI) of the forest stand was measured in July with a leaf area index meter (Li-2000, Li-Cor, Lincoln, Nebraska). Forest air samples were collected between 2 and 4 pm at 8, 5, 3, 1, 0.5 and 0.02 m above ground once a month throughout 1995. Air was pumped through a pre-evacuated 2L glass flask (with two high-vacuum stopcocks) at a flow rate of 20 ml s^{-1} for 20 min. CO_2 coming out of the flask was measured with an IRGA (LI-6252, Licor, Lincoln, Nebraska), and then both stopcocks of the flask were closed. CO_2 was extracted by cryogenic distillation at liquid nitrogen temperature. The purified CO_2 samples were sealed with copper pellet in a 6 mm O.D. pyrex tube, then combusted at 500°C for an hour to avoid the interference of N_2O (which has a molecular weight the same as CO_2 and can't be separated from CO_2 by the cryogenic distillation method). After combustion, samples were purified again through an ethanol-dry ice trap and a liquid nitrogen trap.

Organic Materials

Leaf samples of dominant (*Chamaecyparis* and *Rhododendron*) and understory species from different heights of the canopy were collected in July. A dominant moss species (*Bazzania fauriana*) growing epiphytically on the tree trunk at different heights of the canopy was also sampled. Litter and the top 10 cm of the soil were also collected. The samples were dried at 70°C in a oven for at least 48 h, then ground to a fine powder with a mortar and pestle. Two to three mg of grounded leaf material was sealed under vacuum with a 1 g copper oxide pellet and silver foil (2 × 10 mm) in a 6 mm O.D. quartz tubing, then combusted at 850°C for four hours. The resulting CO_2 was purified through an ethanol-dry ice trap and a liquid nitrogen trap (Ehleringer and Osmond, 1989).

The isotopic composition of the carbon was measured with a Finnigan delta S mass spectrometer, and the result was expressed as a per mil (‰) deviation from the PDB standard $\delta^{13}C = \{[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{PDB}]-1\} \times 1000$.

Calculation of Carbon Isotope Discrimination and C_i/C_a for the Leaves

Carbon isotope discrimination (‰) of leaves of trees and understory species (Δ_p) was calculated using foliar $\delta^{13}C$ (δ_{leaf} in ‰) and δco_2 (‰) by the following equation:

$$\Delta_p = (\delta co_2 - \delta_{leaf}) / [1 + (\delta_{leaf}/1000)]$$

The ratio of long-term intercellular CO_2 partial pressure (C_i) and ambient CO_2 partial pressure (C_a) of leaves can be estimated from Δ_p by the following equation (Farquhar et al., 1989):

$$\Delta_p = a + (b - a) \times C_i/C_a,$$

where a is the discrimination during CO_2 diffusion through the stomata and has been estimated to be 4.4‰ (O'Leary, 1988), and b is the isotope fractionation during carboxylation (approximately 27‰ by Farquhar and Richards, 1984).

Results

CO_2 and $\delta^{13}C$ of Forest Air

The LAI of the forest stand measured in July was 3.7 $m^2 m^{-2}$. Carbon dioxide and $\delta^{13}Cco_2$ gradients existed within the forest stand, with higher CO_2 concentrations and more negative $\delta^{13}Cco_2$ values in air sampled from the lower canopy (Figures 1 and 2). The average $[CO_2]$ at 8 and 0.02 m of the 12 sampling dates were 355.6 ± 2.1 and 384.2 ± 6.1 ppm (mean ± s.e.), respectively. And the average $\delta^{13}Cco_2$ value at 8 and 0.02 m of the 12 sampling dates were -8.1 ± 0.1 and -9.3‰, respectively. The largest vertical gradient in the concentration of CO_2 was measured in November, the $[CO_2]$ ranged from 364 to 445 ppm, at 8 m and 0.02 m, respectively, and the corresponding $\delta^{13}Cco_2$ from -8.5 to -11.5‰. In contrast, the smallest vertical gradient was measured in February and July (Figure 1), the gradient in $[CO_2]$ was only 8 ppm. The average vertical gradient in CO_2 and $\delta^{13}Cco_2$ value of the $[CO_2]$ of the 12 sampling dates were 28.5 ± 6.1 ppm and 1.3 ± 0.3‰ (mean ± s.e.), respectively.

There was also temporal variation in $[CO_2]$ and $\delta^{13}Cco_2$ of the forest air. The lowest and the highest CO_2 concentrations of air sampled at 8 m were measured on June and January, 345 and 370 ppm, respectively (Figure 1). The most positive and negative values of $\delta^{13}Cco_2$ of air sampled at 8 m were analyzed in June (-7.6‰) and November (-8.5‰) (Figure 2). In comparison, the lowest and the highest CO_2 concentrations of air sampled at 0.02 m were mea-

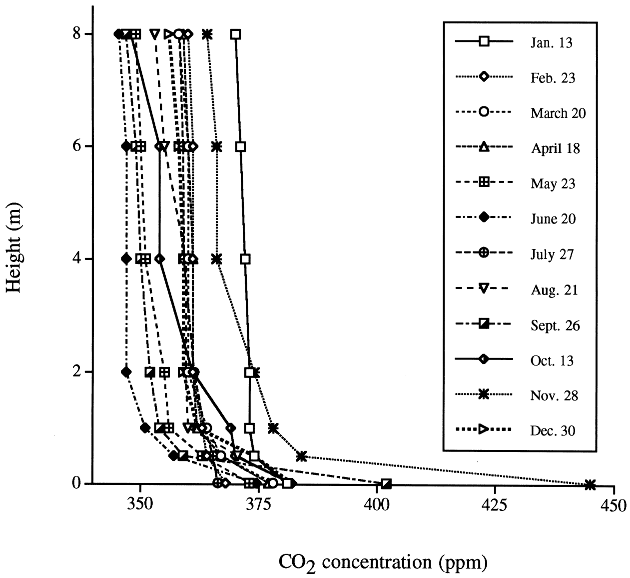

Figure 1. Height profiles of CO_2 concentrations within a mixed forest of *Chamaecyparis* and *Rhododendron* stands.

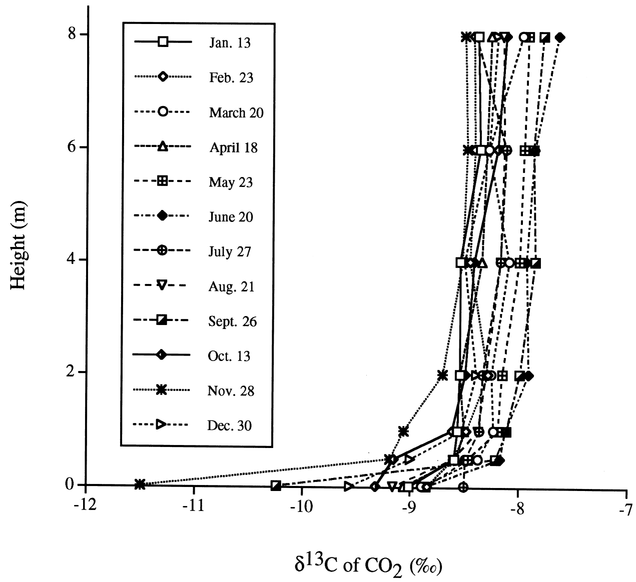

Figure 2. Height profiles of $\delta^{13}Cco_2$ within a mixed forest of *Chamaecyparis* and *Rhododendron* stands.

sured in February and November, 368 and 445 ppm, respectively. And the most positive and negative values of $\delta^{13}Cco_2$ sampled at 0.02 m were analyzed in July (-8.5‰) and November (-11.5‰).

Relationship Between $\delta^{13}Cco_2$ and $[CO_2]$

A significantly positive linear relationship was measured between $1/[CO_2]$ and the corresponding $\delta^{13}C$ values for measurement taken in each month (Table 1). Seasonal patterns of the relationship were pronounced, with steady decreases in the slopes and increases in the intercepts found from January to August. However, the slopes increased and the intercepts decreased again from September to December. Combining data from the 12 sampling dates, the relationship between $1/[CO_2]$ and the corresponding $\delta^{13}C$ values was: $\delta^{13}Cco_2$ (‰) = 5472.8 × (1/$[CO_2]$) - 23.5, r = 0.95 (Figure 3).

$\delta^{13}C$ of Vegetation, Litter and Soil

A vertical gradient in $\delta^{13}C$ values was measured in the moss species *B. fauriana* (Figure 4). The $\delta^{13}C$ of the moss became progressively more negative with decreasing height, ranging from -27.4‰ at 8 m to -29.2‰ at ground.

As with the moss species, a general trend appeared in the leaf $\delta^{13}C$ values of vascular plants: they tended to be more positive in upper canopy leaves and more negative in understory plants, and ranged from -28.6 to -33.5‰ (Figure 4). In comparison between *B. fauriana* and the vascular plants at the same height, the bryophyte always had more positive $\delta^{13}C$ values than the vascular plants.

Table 1. Linear regressions and coefficient of regression (r) between $\delta^{13}Cco_2$ and $1/[CO_2]$ for a mixed forest of *Chamaecyparis* and *Rhododendron* stands throughout the 1995.

Month	Regression	r
January	y = 7830 × x - 29.5	0.98
Febuary	y = 6316 × x - 25.9	0.81
March	y = 5193 × x - 22.6	0.95
April	y = 5550 × x - 23.8	0.95
May	y = 5770 × x - 24.4	0.99
June	y = 4762 × x - 21.6	0.97
July	y = 4889 × x - 21.8	0.89
August	y = 4889 × x - 21.9	0.97
September	y = 6077 × x - 25.2	0.99
October	y = 5453 × x - 23.7	0.96
November	y = 6151 × x - 25.3	0.99
December	y = 6570 × x - 26.7	0.99

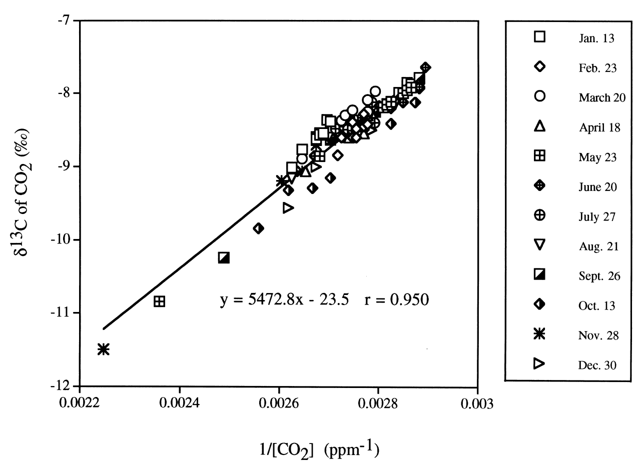

Figure 3. Relationship of the inverse of canopy CO_2 concentrations and their corresponding $\delta^{13}Cco_2$ within a mixed forest of *Chamaecyparis* and *Rhododendron* stands.

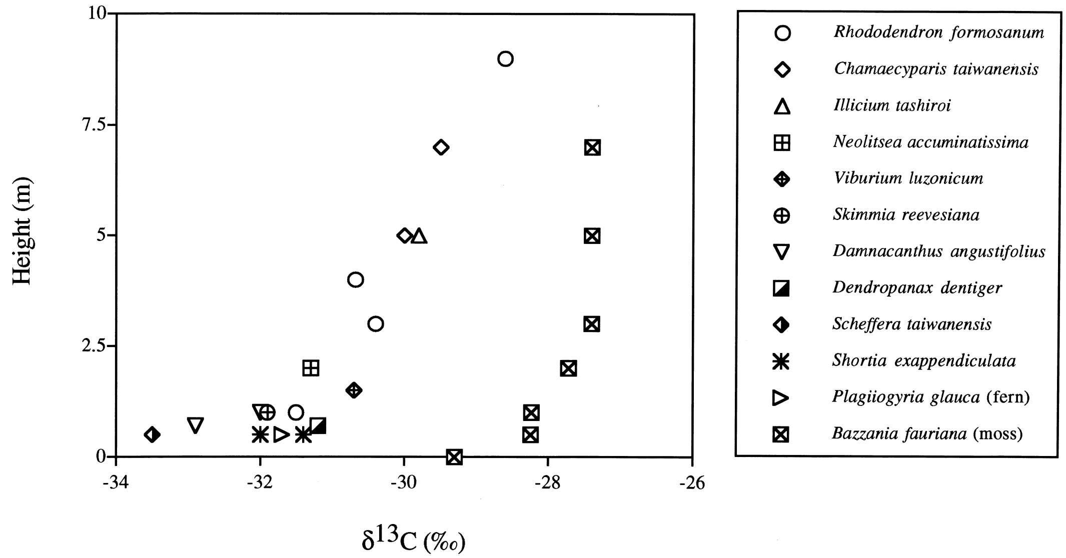

Figure 4. Vertical profile of leaf carbon isotope ratios ($\delta^{13}C$) of a moss species (*B. fauriana*), understory vegetation and the dominant tree species within a mixed forest of *Chamaecyparis* and *Rhododendron* stands.

The $\delta^{13}C$ values of litter and soil were -28.2 ± 0.2 and -27.2 ± 0.2‰ (mean ± s.e., n = 8), respectively.

Calculation of Carbon Isotope Discrimination (Δ_p) and C_i/C_a for the Leaves

For the vascular plant species, carbon isotope discrimination in leaf (Δ_p) decreased with height (Figure 5). The carbon isotope discrimination in leaf varied from 21.5 to 24.3‰. As a result, the estimated C_i/C_a of leaves from different canopy heights also decreased with height and the ratio varied from 0.76 to 0.88 for leaves from 8 to 0.02 m.

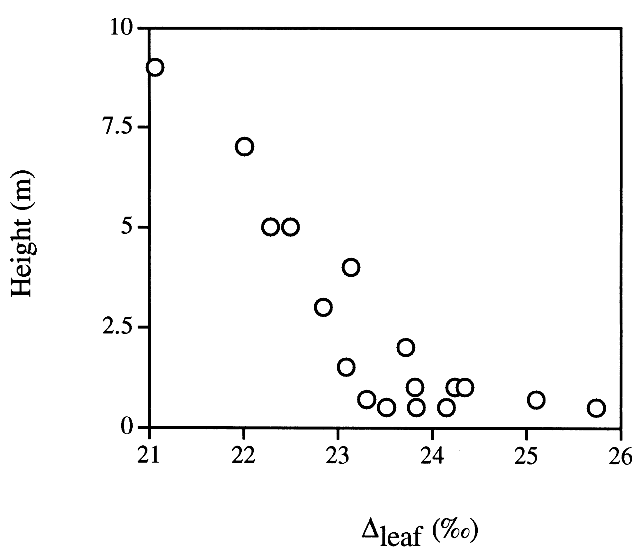

Figure 5. Vertical profile of calculated carbon isotope discrimination in leaf (Δ_{leaf}) of understory vegetation and the dominant tree species within a mixed forest of *Chamaecyparis* and *Rhododendron* stands.

Discussion

Few studies have analyzed the profiles of CO_2 concentration and $\delta^{13}C$ values in tropical rain forests (Medina and Minchin, 1980; Medina et al., 1991) or in temperate forests (Broadmeadow, 1992; Buchmann et al., 1997b; Hanba et al., 1997). To our knowledge, this is the first study investigating the vertical profiles of CO_2 and $\delta^{13}C$ values within a subalpine forest in Taiwan. However, results from this study reveal the subalpine forest to have the same vertical profiles of canopy [CO_2] and $\delta^{13}C$ (Figures 1 and 2) as forests in other climatic zones. Only small differences in CO_2 concentration were detected between 1 m and 8 m within the forest, indicating a high degree of mixing of the forest air above 1 m. However, the gradient between 1 m and ground level was mainly due to the mixing of atmospheric CO_2 and soil respired CO_2. Significant variations in the profile of CO_2 and $\delta^{13}C$ values observed at different sampling dates implies temporal variation in the vertical profile.

The intercept of the linear relationship between 1/[CO_2] and the corresponding $\delta^{13}C_{CO_2}$ values represents the $\delta^{13}C$ of respired CO_2 (Keeling, 1958) and can be used to estimate ecosystem discrimination against the heavier ^{13}C during photosynthesis of the entire stand if the $\delta^{13}C$ value of tropospheric CO_2 is also measured (Buchmann et al., 1997b). The slopes and the $\delta^{13}C$ values of the intercept (Table 1) of this study are similar to those measured in temperate deciduous and evergreen forests (Francy et al., 1985; Buchmann et al., 1997b). Without information in the $\delta^{13}C$ value of tropospheric CO_2, we are unable to calculate the ecosystem discrimination. However, the steady increase in intercepts of the relationship represented increasing $\delta^{13}C$ values of respired CO_2 of the forest ecosystem from January to August. Hardly any data sets exist that show seasonality in the isotopic signature of ecosystem respiration. Buchmann et al. (1997a) reported the intercept of the relationship measured in an Amazonian rainforest was close to the $\delta^{13}C$ of soil respired CO_2 and to the $\delta^{13}C$ of litter and soil organic matter. Though we did not measure the $\delta^{13}C$ values of soil efflux CO_2, the intercepts of the relationship of this study (except the measurement taken in January) are more positive than the $\delta^{13}C$ values of soil organic matter and litter. This could be due to discrimination against ^{13}C during soil respiration, resulting in a $\delta^{13}C$ value of the soil respired CO_2 that is more positive than that of the soil organic matter. A further study analyzing soil respired CO_2 is necessary to understand if this is the reason for the discrepancy.

As in other studies (Medina and Minchin, 1980; Vogel, 1978), the present study also showed that leaves collected from lower canopy or understory plants within a subalpine forest ecosystem usually had a $\delta^{13}C$ value more negative than that of upper canopy leaves. Two factors might be responsible for these lower values. First, they might be due to the recycling of soil respired CO_2, which is more negative than bulk atmospheric CO_2 (Sternberg, 1989; Vogel, 1978). However, due to the effect of microclimates on photosynthetic gas exchange, the ratio of the intercellular CO_2 to the ambient CO_2 (C_i/C_a), and hence the leaf $\delta^{13}C$ values, would also be affected by changes in microclimates within the forest canopy. For example, Ehleringer et al. (1986) reported that low light intensity resulted in plants with a more negative $\delta^{13}C$ value. The contribution of physiological effect and the $\delta^{13}C$ of source air to the variation in vertical profile of leaf $\delta^{13}C$ can be separated by calculation of leaf carbon isotope discrimination (Δ_{leaf}) (Hanba et al., 1997). In this study, the variation in this discrimination was estimated at approximately 2.8‰ from 0.02 to 8 m within the forest canopy. This implies that approximately 2.8‰ of variation in the vertical profile of leaf $\delta^{13}C$ was due to the effect of the changing microclimate on the photosynthetic physiology. This result is in agreement with the study in a temperate Japanese forest by Hanba et al. (1997).

This is the first time that a bryophyte species was shown to have a gradient in $\delta^{13}C$ values similar to coexisting vascular plants. However, the bryophyte's $\delta^{13}C$ value was richer in ^{13}C than those other plants. In addition, the analysis also indicates that the gradient in $\delta^{13}C$ of the bryophyte reflects the $\delta^{13}C$ of the canopy CO_2 better than vascular plants. Due to the absence of stomata in the bryophyte, its photosynthesis might be less affected by the changing microclimates than that of the coexisting vascular plants within the forest. Hence it is possible that the gradient in $\delta^{13}C$ of bryophyte is mainly caused by the gradient of $\delta^{13}C$ of forest CO_2.

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台灣亞高山帶森林內二氧化碳濃度和穩定性碳同位素比值之探討

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本文探討台灣一亞高山帶森林（位於鴛鴦湖生態保留區）內二氧化碳濃度和其穩定性碳同位素比值（$\delta^{13}Cco_2$）之垂直變化；並比較森林內不同高度之維管束植物和一附生苔蘚植體之碳同位素比值($\delta^{13}C_{leaf}$)。目的在了解此森林生態系內之碳通量，並提供建立全球碳循環模式之區域性基本資料。在1995 年間，每個月測量森林內不同高度之二氧化碳濃度並分析其穩定性碳同位素比值。結果顯示：林內愈接近地面之空氣，CO_2 濃度愈高，同時其 $\delta^{13}Cco_2$ 比值也愈負。每個月所測得的林內二氧化碳濃度倒數和其相對之 $\delta^{13}Cco_2$ 比值呈現一顯著線性正相關；此線性正相關的截距具季節性變化，表示系統內呼吸作用有季節性變化。綜合 1995 年整年之測量，得到的線性正相關為： $\delta^{13}Cco_2 = 5472.8 \times (1/[CO_2]) - 23.5$, $r = 0.95$。採自林內不同高度之維管束植物和苔蘚之 $\delta^{13}C_{leaf}$ 也呈現和林內 CO_2 之 $\delta^{13}Cco_2$ 相同趨勢。此外，苔蘚植物之 $\delta^{13}C_{leaf}$ 值（-27.4 到 -29.2‰）較維管束植物之 $\delta^{13}C_{leaf}$ 值(-28.6 到 -33.5‰) 為正。文中並討論影響苔蘚和維管束植物碳同位素比值差異之可能機制。

關鍵詞：鴛鴦湖生態系；亞高山帶森林；二氧化碳；穩定性碳同位素比值；苔蘚。