Research paper

The Importance of Litter Biomass in Estimating Soil Organic Carbon Pools in Natural Forests of Taiwan

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【Summary】

Litter layers store a significant reservoir of carbon in forest ecosystems and are prone to be impacted by climate change and anthropogenic management practices. However, estimating forest litter biomass is commonly neglected in soil surveys. In this study, litter biomass, soil bulk density, fine soil content, and C concentration of the top 20 cm of topsoils were analyzed for 8 natural forests at elevations ranging 390~3000 m located within 4 climate zones (tropical, subtropical, temperate, and cool-temperate climate) to understand the importance of forest litter biomass in estimating soil organic carbon (SOC) pools in Taiwan. Natural temperate forests at high elevations stored 2~3 times the C per hectare than did warm tropical and subtropical ones. The proportion of the litter C pool in topsoils increased with elevation and was highest in the temperate forest (28.8%) and lowest in the tropical forest (4.0%). These results suggest that when estimating the potential of forest C sequestraion and release, temperate and cool- temperate forest litter layers should be of great concern since these C pools are considerably less well protected. The warmth index (WI) was significant positively correlated with litter C pools and SOC stocks ($R = 0.95$), while there was no correlation between the annual precipitation and litter and SOC pools, indicating that litter accumulation and the SOC content in Taiwan are mainly controlled by temperature rather than precipitation.

Key words: forest soil organic carbon, litter layer, C pool, climate zone, warmth index.

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研究報告

枝葉層在台灣天然林土壤碳庫估算之重要性

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摘 要

枝葉層為森林生態系中重要的碳庫，其有機碳也最易受到氣候變遷與人為經營的影響，然而一直以來森林枝葉層生物量在土壤碳庫調查工作上卻常常被忽略。本研究調查分析台灣海拔390~3000 m的四個主要氣候區(熱帶、亞熱帶、溫帶與冷溫帶)中八個天然林之枝葉層生物量、土壤容積密度、細土含量及其碳濃度，以瞭解枝葉層在台灣天然林土壤表層碳庫估算上之重要性。分析結果得知，高海拔溫帶天然林每公頃之碳庫存量為低海拔之熱帶與亞熱帶天然林之2~3倍。台灣天然林枝葉層碳貯存量所佔土壤碳庫比例，以熱帶林最低(4.0%)、而溫帶林最高(38.8%)，可知在台灣中高海拔地區的天然林，枝葉層在表層20 cm土壤碳儲存量中扮演極重要的角色；且在估算溫帶至冷溫帶森林碳吸存與釋放潛能時，更應重視此易於礦化之枝葉層。表層土壤與枝葉層之碳庫存量與溫量指數呈明顯正相關(R = 0.95)，而與雨量無關，顯示台灣天然林枝葉層之累積速率與表土碳庫主要受控於溫度。

關鍵詞：森林土壤有機質、枝葉層、碳庫存、氣候區、溫量指數。

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INTRODUCTION

Litter layers, which result from the annual amount of litterfall accumulation minus the annual rate of decomposition, play an important role in forest C budgets. According to several investigations, forest litter and mineral soils store approximately 3-fold more C than do living plants (Post et al. 1982, Wang et al. 1999), and the litter layer C pool may store 5~20% of the total stand C (Karjalainen 1996). The litter layer and topsoil are prone to impacts by climatic factors such as temperature and precipitation (Batjes 1996, Van de Walle et al. 2001) and anthropogenic management practices (Pastor and Post 1986). For example, Makipaa et al. (1999) found an overall decrease in soil organic C (SOC) stocks of 30% in boreal forests for a rise of 4℃. Since the litter layer is composed of "nonprotected" C (Tremblay et al. 2002), organic C releases would be mainly from the forest floor rather than the soil if the climate changes (Priha and Smolander 1997, Conant et al. 1998, Kurz and Apps 1999, Richter et al. 1999).

In Taiwan, the uncertainty of SOC estimations needs to be improved, and it is also important to assess the C in the forest litter layer. The primary objective of this study was to determine the amounts of C stored in forest litter layers and topsoils (0~20 cm), where the SOC is most vulnerable to the effects of land use practices and climate change. Many factors, such as topography, lithologic substrate, clay content, mineralogy, pH, soil structure, and land use, can influence the SOC content; however it is often considered that the most important factor regulating the SOC content at a large scale is climate (Post et al. 1982, Jobbágy and Jackson 2000). Thus, in this study, the annual precipitation and warmth index (WI) were evaluated to find suitable environmental factors related to SOC pools in Taiwan while disregarding other soil characteristics. No attempt was made here to relate the SOC to different vegetation cover types or to compare the forest SOC pools in Taiwan with global estimates, for which the depth is 1 m (Batjes 1996).

MATERIALS AND METHODS

Study sites and field surveys

Taiwan lies at 21°54'~25°18'N and 120°01'~121°59'E. Due to the seasonal monsoon and several north-to-south mountain chains that stretch almost the entire length of the island, the climate varies from tropic to cool temperate. This climatic gradient together with the orographic and geological complexity create different environmental situations occupied by very diverse forest communities, including evergreen coniferous forests, mixed coniferous-broadleaf forests, subtropical Lauraceae-Fagaceae rainforests and tropical *Ficus*-*Machilus* forests.

Although 58% of Taiwan is covered by forests, most lowland forests have been extensively exploited, and the easy-to-reach middle-elevation forests are highly disturbed by human activities. Hence, in order to ensure that suitable undisturbed sites were selected, the species composition and the diameter at breast height (DBH) were surveyed before soil sampling. Sampling sites were chosen when the DBH distribution presented a J-shape (data not shown). Native forests were surveyed in the Central Mountain Range (CMR) to eliminate geological variances. Eight forests located in 4 climate zones at elevations ranging 390~3000 m (Fig. 1) were examined in this study. For each forest, three 50×50-m plots were established. The soil type was classified according to the *Keys to Soil Taxonomy* (Soil Survey Staff 2006). The overstory species composition was noted. DBH was measured for all trees larger than 5 cm to calculate the basal area of each plot. The basal area ranged 39.8~92.3 m^2 ha^{-1} depending on the different climates (Table 1). For all forests, the mean annual precipitation (MAP) and mean annual temperature (MAT) varied between 2200 and 3300 mm and 7.6 and 22.4℃, respectively (Table 1).

Sampling and C analysis

At each plot, 5 litter layers were collected using a sharpened steel ring (14.5 cm in diameter) and separated into the Oi, Oe, and Oa sublayers. All fractions were dried at 65℃ for at least 48 h, weighed, and pulverized in a vibrating sample mill (CMT TI-100, Tokyo, Japan). Subsamples of pulverized litter were analyzed for total C concentrations by a combustion method using an automatic elemental analyzer (Thermo Finnigan NA1500, Bremen, Germany). The litter biomass is expressed on an oven dry-weight base.

Measurement of the soil bulk density is essential to calculate soil C stocks (Bernoux et al. 1998). In this study, the soil bulk density was measured by an excavation method (Lal and Kimble 2001) using steel cores (6.5 cm in diameter and 25 cm long) to a depth of > 20 cm. Five soil cores were collected at each plot and then driven out from the bottom of the core in the lab. Soil cores were divided into 4 layers 0~5, 5~10, 10~15 and 15~20 cm (the rest of the soil was disregarded). As forest soils in Taiwan normally contain a high percentage of stones, the C content of which is normally considered inorganic C, using the bulk density obtained from the excavation method will overestimate the SOC stock if the SOC concentration of stones is not measured. Thus, 2 soil cores were randomly selected from the 5 samples to measure the soil bulk density (oven-dried at 105℃ for 48 h and weighed), and 3 cores were used to determine the fine soil content to calculate the

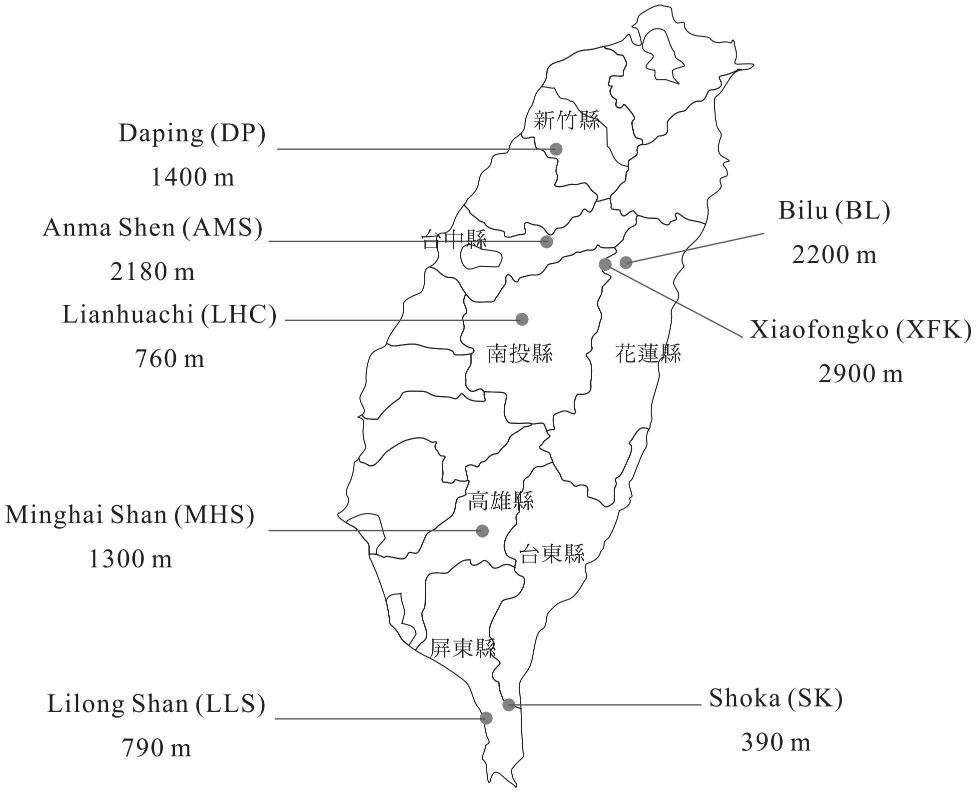

Fig. 1. Location and elevation of the sampling sites.

Table 1. General characteristics of the sampling sites

Site[1]	Elevation (m)	MAT (℃)	MAP (mm)	WI (℃)	Climate zone[2]	Forest type	Soil Classification[3]	Number of individual (ha^{-1})	Max. DBH (cm)	BA (m^2/ha)
SK	390	22.4	3300	211.9	Tropical	*Ficus-Machilus*	Alfisols	1701±524	115	42.0±5.7
LLS	790	21.1	2180	198.4	Subtropical	*Machilus-Castanopsis*	Ultisols	1645±106	97	48.0±4.9
LHC	760	20.8	2180	178.4	Subtropical	*Machilus-Castanopsis*	Ultisols	1524±379	94	58.0±19.8
MHS	1300	18.6	2280	153.7	Subtropical	*Machilus-Castanopsis*	Ultisols	780±80	95	39.8±2.1
DP	1400	16.6	2900	136.3	Subtropical	*Machilus-Castanopsis*	Ultisols	1312±113	112	67.8±28.3
AMS	2180	11.0	2406	86.8	Temperate	*Quercus-Chamaecyparis*	Inceptisols	1365±222	164	69.0±21.0
BL	2200	11.8	2870	96.1	Temperate	*Quercus-Chamaecyparis*	Ultisols	1773±348	155	92.3±15.2
XFK	2960	7.6	2760	33.6	Cool-Temperate	*Tsuga-Picea* and *Abies zone*	Inceptisols	612±213	164	91.0±36.2

MAT, mean annual temperature; MAP, mean annual precipitation (data from Central Weather Bureau, 1990~2000); DBH, diameter at breast height; BA, basal area.

[1] Sites are defined in Fig. 1.

[2] Climate zone is distinguished by the combination of temperature, precipitation and vegetation type according to the concept of the Köppen-Geiger climate classification system.

[3] Soil classification according to *Keys to Soil Taxonomy* (USDA 2006).

total SOC stock. The air-dried soil cores were sieved through a 2-mm mesh and weighed. Roots and stones were collected by hand, oven-dried at 105℃ and weighed. At least 5 g of subsample for each sieved soils was oven-dried at 105℃ for 24 h to calculate the total dry weight. All sieved soils were then milled prior to the C analysis. The SOC concentration was determined by the Walkley-Black method (Nelson and Sommers 1996).

Statistical analysis

The litter layer biomass was determined for 5 samples from each plot, while the fine soil content was determined for 3 samples and the soil bulk density for 2 samples. The organic C content for each depth was expressed as follows: C content = Cc×W; where Cc denotes the organic C concentration (%) and W denotes the fine soil weight. The C content for each forest was the mean value obtained from 3 plots.

Because of the high geological heterogeneity in Taiwan, the warmth index (WI) was used as an environmental parameter in this study to include the influences of elevation and latitude. The WI, which represents an idea of the optimal temperature for the growth of plants, is a function of the accumulated monthly temperature (Tm) minus 5℃ (Kira 1945) and can be calculated by the following equation:

WI = Sum of (Tm - 5), when Tm is above 5℃.

The climate data during the years 1990~2000 were collected from weather stations of the Central Weather Bureau to obtain the monthly average temperatures. Pearson's correlation was used to examine relationships of WI, MAP, and MAT, with characteristics of SOC including biomass, C concentration, etc.

RESULTS AND DISCUSSION

Litter biomass

The litter layer biomass and soil bulk density both varied with the WI (Table 2). As the litter decomposition rate increases with increasing temperature, the Oa-layer disappeared from warm sites but constituted nearly 40~57% of the litter biomass at high-elevation sites. With a decrease in the WI from 211.9℃ in tropical forests to 86.8℃ in

Table 2. Litter biomass, mineral soil bulk density (BD), and fine soil content (mean±SD) of sampling sites with different values of the warmth index (WI)

	WI	211.9	198.4	178.4	153.7	136.3	96.1	86.8	33.6
Litter	Oi	0.66±2.04	4.63±1.29	1.28±1.55	1.95±1.79	2.06±7.54	6.40±4.54	7.11±3.95	11.71±17.41
layer	Oe	2.58±1.06	8.07±7.45	7.29±2.42	5.65±1.07	5.54±8.04	16.94±14.29	26.80±22.50	12.65±10.89
biomass	Oa	–	–	–	7.71±5.72	3.02±4.38	30.82±18.35	25.14±29.38	15.26±9.76
(ton/ha)	Total	3.24±1.39	12.70±4.99	8.57±3.31	15.31±4.38	10.62±4.12	54.16±16.49	59.05±38.18	39.62±32.8
Soil BD	0~5 cm	0.59±0.17	0.59±0.10	0.64±0.13	0.61±0.14	0.39±0.18	0.47±0.20	0.32±0.13	0.45±0.13
($g\ cm^{-3}$)	5~10 cm	0.77±0.14	0.84±0.14	0.92±0.17	0.76±0.18	0.68±0.24	0.84±0.32	0.63±0.23	0.65±0.27
	10~15 cm	1.10±0.24	0.98±0.13	0.95±0.03	0.87±0.20	0.90±0.37	0.97±0.27	0.87±0.39	0.86±0.21
	15~20 cm	1.15±0.23	1.14±0.20	1.02±0.12	0.85±0.10	0.83±0.18	1.18±0.29	0.70±0.13	0.82±0.20
Fine soil	0~5 cm	0.47±0.11	0.59±0.06	0.59±0.14	0.32±0.11	0.20±0.05	0.21±0.07	0.30±0.07	0.19±0.10
content	5~10 cm	0.66±0.08	0.80±0.06	0.85±0.07	0.35±0.08	0.31±0.05	0.49±0.15	0.38±0.12	0.38±0.13
($g\ cm^{-3}$)	10~15 cm	0.82±0.16	0.87±0.11	0.90±0.10	0.46±0.05	0.37±0.10	0.48±0.17	0.45±0.21	0.50±0.17
	15~20 cm	0.92±0.18	1.04±0.19	1.02±0.14	0.43±0.13	0.41±0.13	0.59±0.23	0.47±0.17	0.45±0.19

The sample number (n) for each site: litter biomass n = 15; mineral soil bulk density n = 6; and fine soil content n = 9.

temperate broadleaf-coniferous forests, the litter layer biomass increased almost 20-fold from 3.2 to 59.1 ton ha^{-1}. This finding agrees with those obtained by Mendoza-Vega et al. (2003), who examined a mixed broadleaf-coniferous forest and a *Quercus* forest in Mexico, and found that forests located in the cloud zone could store more C in the litter layer.

Soil bulk density and fine soil content

The soil bulk density ranged 0.32~1.18 g cm^{-3} and generally increased with depth (Table 2). The variance in the bulk density at different elevations was not statistically significant. However, as the litter decomposition rate and soil mineralization rate increase with rising temperature (Townsend and Vitousek 1995, Wang et al. 2005), which may decrease the SOC content of the soil, the soil bulk density was generally higher in tropical to subtropical sites below 1500 m than in high-elevation temperate to cool-temperate forests. Different from the soil bulk density, the fine soil content significantly decreased with an increase in elevation. Due to the higher rock volume at high-elevation sites, differences between bulk density and fine soil content were higher than for sites at lower elevations.

The 0~30-cm depth soil bulk density of Alfisol, Ultisol, and Inceptisol as measured by Chen and Hseu (1997) were 1.15, 1.31 and 0.94 g cm^{-3} respectively, which are relatively higher than our findings. Page-Dumroese et al. (1999) indicated that using different sampling methods, like core, clod, and excavation methods, can lead to variations in results. They found that the soil bulk density measured by the small-diameter core method was significantly higher (by 33~37%) than that by the large-diameter core method and 2 excavation methods. This is similar to our results when compared to the bulk density measured by Chen and Hseu (1997), who used a smaller core (with a diameter of 3.4 cm and 6.8 cm in height) than ours (with a diameter of 6.5 cm and 20 cm in height). Although using small cores may overestimate the soil bulk density, Harrison et al. (2003) found that the average whole-soil bulk density of rocky soils estimated using 31- and 54-mm small cores was 24% lower than that with the 50-cm^2 pit excavation method.

Taiwan forest soils normally contain high proportions of stones, which would be excluded when sampling with small cores and affect the accuracy of the bulk density measurements. For rocky forest soils, Kulmatiski et al. (2003) suggested that the core method is efficient and requires less than 1/2 of the sampling time of the pit method; however, the pit method allows better quantitative measurements. To reduce the sampling bias, the large core and pit excavation methods are strongly recommended for further soil surveys in Taiwan.

Carbon concentration

Carbon concentrations of the litter all decreased from the Oi and Oe layers to the Oa layer (Table 3). C concentrations of the Oi layer in the subtropical (where WI < 178.4℃) and temperate forests were almost consistent (ranging 47.5~48.0%) and were slightly higher than those of tropical and cool-temperate forests (ranging 43.3~44.4%). C concentrations of the Oe and Oa layers, and mineral soils all increased with a decreasing WI and reached the highest concentration in temperate forests. In addition, there was a clear decrease in the C concentration in fine mineral soil with depth (Table 3).

Litter layer carbon pools

With a decrease in WI, more organic C accumulated in the litter layer. In the tropical

Table 3. Carbon concentration (%) of litter and mineral soils (mean±SD) for sampling sites with different values of the warmth index (WI)

	WI	211.9	198.4	178.4	153.7	136.3	96.1	86.8	33.6
Litter	Oi	43.31±0.88	44.36±1.28	47.53±0.18	47.63±0.21	47.78±0.32	47.96±0.37	47.74±0.76	43.52±2.52
(%)	Oe	37.85±1.37	33.77±2.66	37.42±6.47	42.59±1.82	43.59±3.94	46.55±0.72	45.23±2.63	40.99±0.53
	Oa	--	--	--	30.82±1.99	39.70±1.56	44.43±1.40	43.30±2.53	37.01±0.53
Soil	0~5 cm	3.11±0.50	4.14±0.25	4.09±0.25	11.20±2.86	18.08±0.89	18.92±7.47	19.41±7.47	14.80±3.56
(%)	5~10 cm	2.63±0.36	2.37±0.24	2.78±0.27	7.10±1.19	10.02±0.99	6.87±1.22	11.29±2.33	7.22±2.10
	10~15 cm	2.16±0.32	1.63±0.26	2.11±0.33	5.64±1.50	6.73±1.05	4.83±0.78	8.11±0.59	5.01±1.32
	15~20 cm	1.78±0.28	1.44±0.19	1.81±0.11	3.55±0.43	5.64±0.69	3.65±1.28	6.61±0.58	4.71±0.95

The sample number (n) for each site and each depth: litter $n = 15$; soil $n = 9$.

to subtropical forests, the litter layer stored only about 1.4~4.8 ton-C ha^{-1}, while in temperate forests, the C pool of litter was about 5~20-times those of the former (Table 4). Litter layer C stocks accounted for 4.0% of the soil solum (litter + soil) in tropical natural forests and rapidly increased to 28.8% in temperate forests. This result was very similar to other reports. For example, Huntington et al. (1988) found that in the mixed broadleaf-coniferous forests of North America, 30 ton-C ha^{-1} was stored in the litter layer, which was approximately 33.7% of the total C in the first 20-cm depth of soil (89 ton-C ha^{-1}). Van de Walle et al. (2001) also found that in 2 Belgium mixed-deciduous forests, the litter layer stored 31.3% of total SOC in the first 15-cm depth of soil. Homann et al. (2005) estimated the potential ecosystem C stores in an old-growth coniferous forest and found that there was about 28.7% of the 20-cm soil C stored in the forest floor. Because of the existence of coniferous leaves, which generally decompose slower than leaves of broadleaf species, the topsoil can store more SOC in mixed forests and *Quercus* forests than any other forest types (Mendoza-Vega et al. 2003). Our results also suggest that when estimating the potential for forest C sequestration and release, temperate and cool-temperate forest litter layers should garner great concern since these C pools are generally less well protected.

Variations of SOC contents

Traditionally, the soil rock fraction of > 2 mm is screened out when estimating soil C contents. Thus, the fine soil content was chosen to calculate the total C content in this

Table 4. Litter and topsoil carbon contents of different sites calculated by total bulk density and fine soil content

Calculation method	WI (℃)	211.9	198.4	178.4	153.7	136.3	96.1	86.8	33.6
	Litter (ton-C Ha^{-1})	1.35	4.69	3.61	4.75	4.62	24.09	26.75	16.88
By bulk density	0~20 cm soil (ton- C Ha^{-1})	41.34	38.26	45.23	100.51	122.86	117.91	124.36	97.24
	*Total Solum (ton-C Ha^{-1})	42.69	42.95	48.84	105.26	127.48	142.00	151.11	114.12
	% Litter	3.16	10.92	7.39	4.51	3.62	16.97	17.70	14.79
By fine soil content	0~20 cm soil (ton-C Ha^{-1})	32.63	36.66	41.76	45.32	55.60	59.46	70.22	46.90
	*Total Solum (ton-C Ha^{-1})	33.98	41.35	45.37	50.07	60.22	83.56	96.98	63.79
	% Litter	3.97	11.34	7.96	9.49	7.67	28.83	27.59	26.47

* Total solum = litter + soil.

% litter, the percentage of litter in the total solum carbon content.

study since stones and rocks contain only a little SOC. However, for better comparisons with other reports, SOC contents calculated by the total soil bulk density are also listed in Table 4. The SOC contents estimated by total bulk density and fine soil solum (litter + fine soil) varied 38.2~32.6 ton-C ha^{-1} in tropical to subtropical natural forests and 124.4~70.2 ton-C ha^{-1} in temperate natural forests, respectively. As shown in Table 2, soils from high-elevation sites contained more stones; thus it is reasonable that differences in SOC contents estimated by bulk density and fine soil content were much higher than those at low-elevation sites. Lal and Kimble (2001) found that even a slight change in soil bulk density (1.10~1.12 g cm^{-3}) can have a strong impact on the SOC pool estimation (a 4 ton-C ha^{-1} increase). Those reports indicated a potential error when SOC pools are estimated at highly geologically heterogeneous sites.

The SOC concentration and content are mainly controlled by the litter layer accumulation rate, soil physical and chemical properties, dissolved organic carbon leaching, and accumulation rates (Oades 1988, Grigal and Ohmann 1992, Burke et al. 1995). These factors are mostly affected by the climate zone. Homann et al. (1995) found that the SOC content increased with annual precipitation, annual temperature, actual evapotranspiration, clay content, and the available water-holding capacity and decreased with slope in a forested region in western Oregon, USA. Combinations of these variables explained up to 50% of the SOC variability. In San Paulo State, Brazil, Lepsch et al. (1994) developed regression models with different factors including silt, base saturation, annual water deficit, and mean annual temperature to explain SOC contents in different ecosystems. The combination of these factors explained 49~86% of the SOC variability. Hontoria et al. (1999) found that the mean annual precipitation, mean annual temperature, and land use explained 45% of the SOC variability in peninsular Spain, while soil texture, elevation, and slope gradient only explained 2% of the variability.

In general, the SOC content increases with precipitation and decreases with increasing temperature. In temperate regions, SOC contents generally tend to increase with elevation because of lower temperatures and higher precipitation (Tate 1992). In the same climatic zone, coniferous forest soils might store more SOC per hectare than broadleaf forest soils (Howard et al. 1995, Liebens and VanMolle 2003). As the mean annual precipitation of the sampling sites in this study all exceeded 2100 mm (Table 1), there was no statistical correlation between annual precipitation and the litter or SOC contents, while the WI was significant positively correlated with the SOC content (R = 0.95). These results suggest that litter accumulation and SOC contents in Taiwan are mainly controlled by temperature rather than precipitation.

CONCLUSIONS

The litter layer and topsoil C pools including the litter layer of natural forests in Taiwan were estimated in this study. The litter biomass as well as SOC concentration and SOC content all increased with a decrease in the warmth index. Total C storage in the litter layer and topsoils also varied with the warmth index, and the maximum C stock per hectare occurred in the natural temperate forest, which stored 2~3-times more C per hectare than did warm-tropical and subtropical forests. The proportion of the litter C pool increased from tropical (4.0%) to temperate forests (28.8%), indicating that the forest litter layer plays an important role in C stocks.

The warmth index was significant positively correlated with the litter and SOC pools (*R* = 0.95), while there was no correlation between annual precipitation and the litter or SOC pools, suggesting that litter accumulation and SOC stocks are mainly controlled by temperature in Taiwan.

LITERATURE CITED

Batjes NH. 1996. Total carbon and nitrogen in the soil of the world. Eur J Soil Sci 47(2):151-63.

Bernoux M, Cerri C, Arrouays D, Jolivet C. 1998. Bulk densities of Brazilian Amazon soils related to other soil properties. Soil Sci Soc Am J 62(3):743-9.

Burke IC, Elliott ET, Cole CV. 1995. Influence of macroclimate, landscape position, and management on soil organic matter in agroecosystems. Ecol Appl 5(1):124-31.

Chen ZS, Hseu ZY. 1997. Total organic carbon pool in soils of Taiwan. Proc Natl Sci Counc ROC Part B: Life Sci 21(3):120-7.

Conant RT, Klopatek JM, Malin RC, Klopatek CC. 1998. Carbon pools and fluxes along an environmental gradient in northern Arizona. Biogeochemistry 43(1):43-61.

Grigal DF, Ohmann LF. 1992. Carbon storage in upland forest of the Lake States. Soil Sci Soc Am J 56(3):935-43.

Harrison RB, et al. 2003. Quantifying deep-soil and coarse-soil fraction: avoiding sampling bias. Soil Sci Soc Am J 67(5):1602-6.

Homann PS, Harmon M, Remillard S, Smithwick EAH. 2005. What the soil reveals: potential total ecosystem C stores of the Pacific Northwest region, USA. Forest Ecol Manage 220(1-3):270-83.

Homann PS, Sollins P, Chappell HN, Stangenberger AG. 1995. Soil organic carbon in a mountainous, forest region: relation to site characteristics. Soil Sci Soc Am J 59(5):1468-75.

Hontoria C, Rodrguez-Murillo JC, Saa A. 1999. Relationships between soil organic carbon and site characteristics in peninsular Spain. Soil Sci Soc Am J 63(3):614-21.

Howard DM, Howard PJA, Howard DC. 1995. A Markov model projection of soil organic carbon stores following land use changes. J Environ Manage 45(3):287-302.

Huntington TG, Ryan DF, Hamburg SP. 1988. Estimating soil nitrogen and carbon pools in a northern hardwood forest ecosystem. Soil Sci Soc Am J 52(4):1162-7.

Jobbágy R, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10(2):423-36.

Karjalainen T. 1996. Dynamics and potentials of carbon sequestration in managed stands and wood products in Finland under changing climatic conditions. For Ecol Manage 80(1-3):113-32.

Kira T. 1945. A new classification of climate in eastern Asia as the basis for agricultural geography. Kyoto, Japan: Horticultural Institute, Kyoto University. 23 p. [in Japanese].

Kulmatiski A, Vogt DJ, Siccama TG, Beard KH. 2003. Detecting nutrient pool changes in rocky forest soils. Soil Sci Soc Am J 67(4):1282-6.

Kurz WA, Apps MJ. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sectors. Ecol Appl 9(2):526-47.

Lal R, Kimble JM. 2001. Importance of soil bulk density and methods of its importance. In: Lal R, Kimble JM, Follett RF, Stewart BA, editors. Assessment methods for soil carbon. Boca Raton, FL: Lewis Publishers. p 31-44.

Lepsch IF, Menk JRF, Oliveira JB. 1994. Carbon storage and other properties of soils under agriculture and natural vegetation in Sãn Paulo State, Brazil. Soil Use Manage 10(1):34-2.

Liebens J, VanMolle M. 2003. Influence of estimation procedure on soil organic carbon stock assessment in Flanders, Belgium. Soil Use Manage 19(4):364-71.

Makipaa R, Karjalainen T, Pussinen A, Kellomaki S. 1999. Effects of climate change and nitrogen deposition on the carbon sequestration of a forest ecosystem in the boreal zone. Can J For Res 29(10):1490-501.

Mendoza-Vega J, Karltun E, Olsson M, 2003. Estimation of amounts of soil organic carbon and fine root carbon in land use and land cover classes, and soil types of Chiapas highlands, Mexico. For Ecol Manage 177(1-3): 191-206.

Nelson DW, Sommers LE. 1996. Total carbon, organic carbon, and organic matter. In: Page AL et al. editors. Methods of soil analysis, Part 2, 2nd ed, Agronomy. Madison, WI: American Society of Agronomy. 9:961-1010.

Oades JM. 1988. The retention of organic matter in soils. Biogeochemistry 5(1):35-70.

Page-Dumroese DS, Jurgensen MF, Brown RE, Mroz GD. 1999. Comparison of methods for determining bulk density of rocky forest soils. Soil Sci Soc Am J 63(2):379-83.

Pastor J, Post WM. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2(1):3-27.

Post WM, Emanuel WR, Zinke PJ. 1982. Soil carbon pools and world life zone. Nature 298(5870):156-9.

Priha E, Smolander A. 1997. Microbial biomass and activity in soil and litter under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at originally similar field afforestation sites. Biol Fertil Soil 24(1):45-51.

Richter DD, Markewitz D, Trumbore SE, Wells CG, 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400(6739):56-8.

Tate KR. 1992. Assessment based on a climosequence of soils in tussock grasslands of soil carbon storage and release in response to global warming. J Soil Sci 43(4):697-707.

Townsend AR, Vitousek PM. 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecology 76(3):721-33.

Tremblay S, Quimet R, Houle D. 2002. Prediction of organic carbon content in upland forest soils of Quebec Canada. Can J For Res 32(5):903-14.

Soil Survey Staff. 2006. Keys to soil taxonomy, 10th ed. Washington, DC: USDA-Natural Resources Conservation Service.

Van de Walle I, Mussche S, Samson R, Lust N, Lemeur R. 2001. The above- and below-ground carbon pools of two mixed deciduous forest stands located in East-Flanders (Belgium). Ann For Sci 58(5):507-17.

Wang L, Ouyang H, Zhou CP, Zhang F, Song MH, Tian YQ. 2005. Soil organic matter dynamics along a vertical vegetation gradient in the Gongga Mountain on the Tibetan Plateau. J Int Plant Biol 47(4):411-20.

Wang Y, Amundson R, Trumbore S. 1999. The impact of land use change on C turnover in soils. Global Biogeochem Cycles 13(1):47-57.