Department of Environmental Biology

Nutrient Cycling in a Montane Moist Evergreen Broad-Leaved Forest (*Lithocarpus/Castanopsis* Association) in Ailao Mountains, Yunnan, Southwestern China

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DECLARATION

I declare that all work presented in this thesis is that of myself alone unless otherwise acknowledged. The contents of this thesis have not been submitted previously, in whole or in part, in respect of any other academic award.

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March 2001

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DEDICATION

To

My father who passed away on the 7th February, 1978, and my mother and my wife, Liyun and my son, Zhiyu.

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ABSTRACT

This study was conducted at the Ailao Mountain National Natural Reserve (NNR) in natural vegetation described as: *Lithocarpus xylocarpus/Castanopsis wattii* (Oak /Chestnut association) forest. Study sites were located in the Xujiaba area of the reserve at an altitude of ~ 2450 m with slopes of 10-15 °. This type of forest is believed to be unique to the NNR area. The forest is floristically characterized by multiple families and genera. It has two tall tree layers, a well-developed bamboo (*Sinarundinaria nitida*) layer and evergreen fern species. Bryophyte, ferns and lichen occur and abundant epiphytic bryophyte is present on tree boles.

A number of important aspects of nutrient cycling, including patterns of biomass and nutrient accumulation; nutrient return in litterfall and release from decomposing leaf litter; annual nutrient uptake and retention, and nutrient input and output budgets through hydrological flux in natural *Lithocarpus/Castanopsis* forest in the reserve, were investigated.

This natural forest is characterized by high biomass accumulation of living and dead materials. Trees account for >90 % of total biomass. Dead wood comprises a high proportion (9-41 %) of total stand biomass. The sequence of inorganic nutrient element content decreased in the order leaves>branches>roots> stems. Elemental content of the total stand decreased in the order of C>Ca>N>K>Al>Mg>P>Fe>Mn. The elements C, Ca and N were mainly in stems while Al and Fe were mainly in roots.

Litterfall was sampled using traps during the period 1991-1999. High variations in litter production between years were associated with masting years of canopy species, and exceptional physical events (strong winds and snow). The mean annual litterfall is 7.12 t ha^{-1} with a bimodal seasonal pattern in litterfall: the main litterfall peak occurred in April-May and a lesser one in October-November. Woody litter and reproductive parts contribute relatively high proportions in this natural forest compared with other montane forests. Woody litter had low N and P concentrations compared with the leaf and reproductive parts. Elements return to the soil through small litterfall decreases in the order C>N>Ca>K>Mg>Mn>Al>P>Fe.

The standard litter-bag technique was used to determine decomposition of leaf litter from three dominant canopy species (*L. xylocarpus*, *L. chintungensis*, *C. wattii*), one dominant understory species (the bamboo *S. nitida*) and a mixture of dominant bryophytes between Nov. 1997 and Oct. 1999. In each case, fast initial litter decomposition was followed by lower rates. Decomposition rates of canopy species and bamboo leaf litter appear to be controlled by initial concentration of lignin, N and P more than by morphological features of the leaves. P seemed to limit decomposition of all leaf litter, both initially and later. Nutrient release from decomposing leaf litter is in the order of K>Mg>Ca>N>P>Mn>Fe, except for bamboo (*S. nitida*) K>Ca> P>N>Mg>Mn>Fe.

Nutrient fluxes in bulk precipitation, throughfall and stemflow were measured in the natural forest between Jan. 1998 and Dec. 1999. This forest exhibited low interception by the canopy (13 % of total rainfall). N, P, Ca and S annual throughfall inputs were mainly from precipitation, while most of the K and two thirds of the Mg throughfall input was due to canopy leaching. There were significant effects of epiphytes on the amount and chemical composition of stemflow. Water volume and annual amounts of N, Ca and Mg were reduced, while K, P and S were increased in stemflow, after removing epiphytes on boles and branches.

Plot- and catchment level approaches were applied to determine nutrient output from the ecosystem during the study period. The results indicated that this catchment has a subsurface flow system. The amounts of percolation water varied with soil depths. Concentrations of all nutrient elements studied were greater in surface water than in soil solution and stream water. The budgets for all nutrient elements between atmospheric inputs and outputs by both seepage and stream flow were positive, except for calcium (negative).

This forest appears to be characterized by relatively high nutrient return (5.6-8.0 % of the total storage) and low nutrient retention (2.0-2.7 % of the total storage). The relative rate of nutrient cycling occupies an intermediate position between temperate evergreen broad-leaved forest and tropical montane rain forest, it is closer to montane rain forests in rates of nutrient circulation.

DEFINITIONS OF TERMS USED IN THE TEXT

Ailao Mountain NNR:

Ailao Mountain National Nature Reserve.

Xujiaba FERS:

Xujiaba Forest Ecosystem Research Station.

Drip tip:

This term describes the morphological character of leaves that terminate in an extended apex. Most plant species of rain forest have leaves with drip tips.

Natural:

Unaffected by man, not altered, of a pristine nature (synonymous with primary).

Evergreen:

A plant that retains green foliage all year.

Broad-leaved forest:

Forest is composed of species with relatively broad leaves as compared to pines.

Throughfall:

Precipitation which passes through the canopy and falls to the ground is called throughfall (net or effective rainfall).

Stemflow:

An additional portion of precipitation reaches the ground by running down the branches and trunk, depositing at the base of the tree. This portion is called stemflow (trunk or stem runoff).

Lucidophyll:

Trees that have leathery and smooth leaves that reflect sunshine.

Dwarf mossy forest:

Forest is composed mainly of species of *Lithocarpus* (Fagaceae) and *Rhododendron* (Ericaceae). This type of forest has short stems (height <5 m) and well developed epiphytic moss. This forest type occurs generally on several peaks (altitudes 2,600-3,000m) of Ailao Mountains and other upper montane areas in subtropical Yunnan.

Montane moist evergreen broad-leaved forest:

Forest is composed mainly of evergreen species of oak and chestnut, occurs on tropical and subtropical mountainous areas in Yunnan, with altitudes 1,800-2,800 m (2,000-2,600 m on Ailao Mountains) and high rainfall (1,500-3,000 mm) and humidity and mean annual temperature of 10-17 °C (coldest month <10 °C).

Monsoon evergreen broad-leaved forest:

This forest type is also called the "southern subtropical evergreen broad-leaved forest ". It is composed mainly of species from *Quercus* and *Lithocarpus* of Fagaceae, and *Schima* and *Anneslea* of Theaceae, and is distributed mainly in tropical and subtropical mountain areas in Yunnan at altitudes 1,100-1,500 m, where is influenced by the monsoon season, with rainfall of 1,100-1,700 mm and mean annual temperature of 17-19 °C (coldest month 10-12 °C).

Semi-moist evergreen broad-leaved forest:

This type of forest is composed of species of *Castanopsis, Cyclobalanopsis* and *Lithocarpus* of Fagaceae. It occurs mainly on lower mountainous regions of subtropical areas in Yunnan, with altitudes of 1500-2500 m and relatively low rainfall (800-1,100 mm) and mean annual temperature of 14-17 °C (coldest month 6-10 °C).

tonne (t) =1000kg

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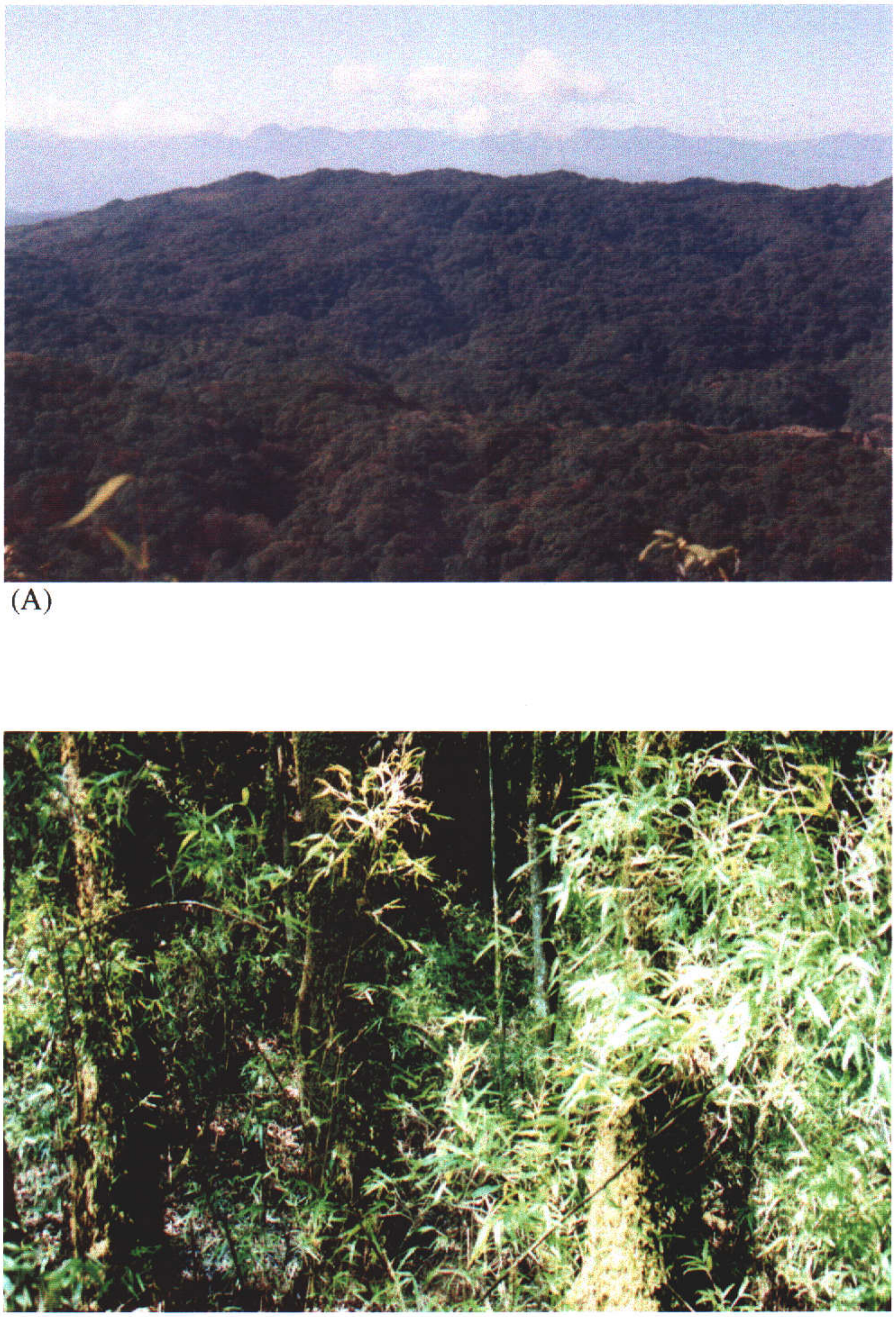

(A)

(B)

Plate 1. Continuous patch of the primary evergreen broad-leaved forest on the crest of Ailao Mountains (A), and well developed bamboo understory in the forest (B).

(A)

(B)

Plate 2. (A): Xujiaba Reservoir in the centre of the natural evergreen broad-leaved forest.

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(A)

(B)

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Chapter 1 Introduction

1.1 Geographical distribution of evergreen broad-leaved forest

The term "evergreen broad-leaved forest" refers to a humid or moist forest consisting of evergreen broad-leaved dicotyledonous trees, mainly of the families *Fagaceae, Lauraceae, Theaceae, Magnoliaceae, Hamamelidaceae,* in humid climatic regions (Jin, 1979; Wu, 1980, 1987; Kira, 1991; Tagawa, 1997). Leaves in this type of evergreen broad-leaved forest tend to be leathery and smooth with surfaces that reflect sunlight. These forests have a wide distribution in the temperate, subtropical and tropical regions of Asia, New Guinea, Macronesia, southeastern North America, Central and South America (Richards, 1952; Kira, 1991; Tagawa, 1997). The combination of species differs from place to place. Consequently, there have been different terminologies applied to this form of forest, such as: terms showing distribution: High mountain hardwood forest (Davis, 1964); Montane evergreen forest (Ogawa, Yoda & Kira, 1961); Tropical lower montane rain forest (Kitayama, 1987); Montane cloud forest (Kitayama, 1995); terms showing combination of climate zone and character of leaves: Temperate rain forest (Schimper, 1898); Temperate broad-leaved evergreen forest (Olson, 1983); Subtropical evergreen broad-leaved forest (Wu, 1980, 1987); terms showing leaf character: Lucidophyll forest (Kira, 1977); and terms based on species composition: Laurisilval/Laurisi/Laurel forest (Brochmann-Jerosch & Rübel, 1912); Oak forest (Stamp, 1924); Oak-laurel forest (Whitmore, 1975); Lauro-Fagaceous forest (Ohsawa, 1983). Based on leaf character, species composition and vertical distribution, Tagawa (1997) proposes a new nomenclature, "evergreen lucidophyll oak-laurel forest" for the evergreen broad-leaved forest dominated by laurel (Lauraceae) and/or oak (Fagaceae) species in warm-temperate and mountain areas of subtropical and tropical regions.

According to Tagawa (1997), the lucidophyll oak-laurel forest has a wide latitudinal range from 9° S to 40° 34′ N and in altitude, ranges from sea level in the cool-temperate zone to about 3000 m in the Asian humid tropics. A suggested distribution of the lucidophyll forests in Asia by Tagawa (1997) is shown in Fig. 1.1.

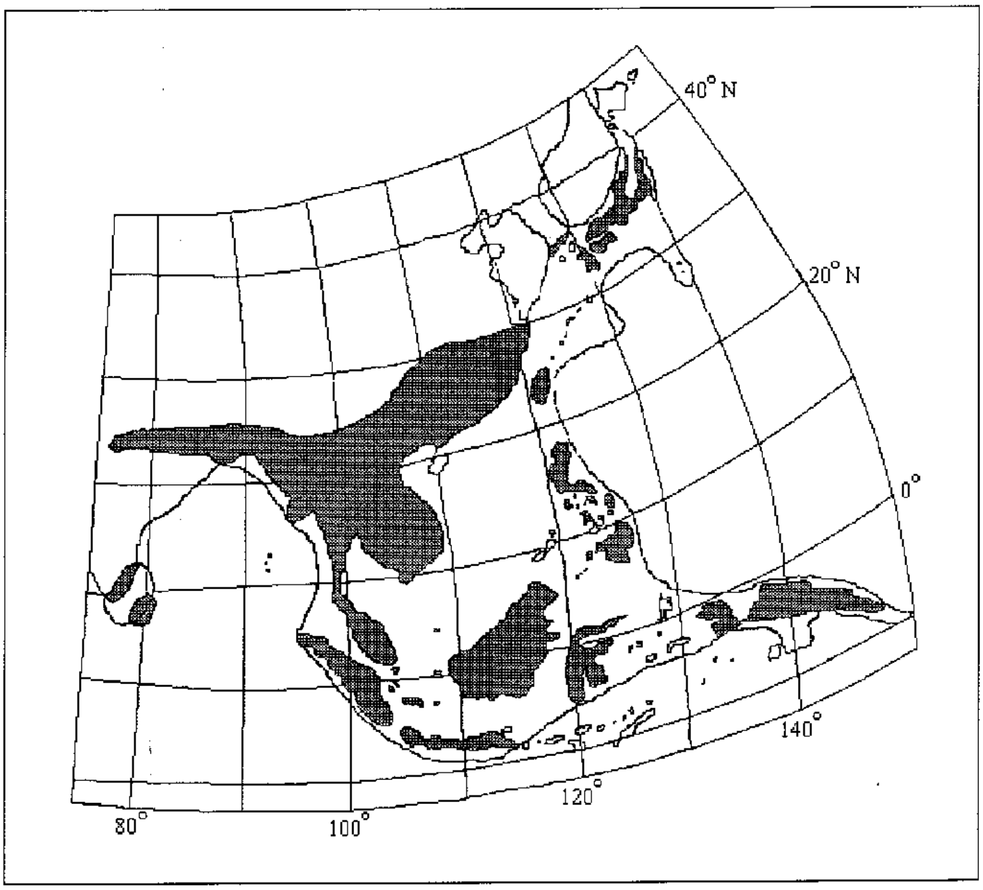

Fig. 1.1. Suggested distribution of lucidophyll oak-laurel forest in Asia by Tagawa (1997).

Evergreen broad-leaved forest or the lucidophyll oak-laurel forest is the most extensive of forest biomes in China. The distribution range covers ~2.4 million km^2 (ca 25 % of the total land area), with a range of approximately 12° latitude and 28°

longitude (Wu, 1980; Davis, Heywood & Hamilton, 1995; Fig. 1.2). The northern boundary is the Qinling mountain range, near Hui River, at latitude 34°00 N. The southern boundary is near the Tropic of Cancer, extending eastwards towards Taiwan. The western boundary is formed by the eastern slopes of the Qinhai-Xizhang (Tibet) Plateau. To the south, the vegetation continues into the Indian Subcontinent, including North Myanmar (Burma) and the foothills of the Eastern Himalayas in India. About 105° longitude is considered as the boundary of the western and the eastern types of evergreen broad-leaved forest in China (Wu, 1980). In the west, these forest types are affiliated floristically with the Sino-Himalaya flora, and in the east, with the East Asian flora (Jin, 1979; Wu, 1980).

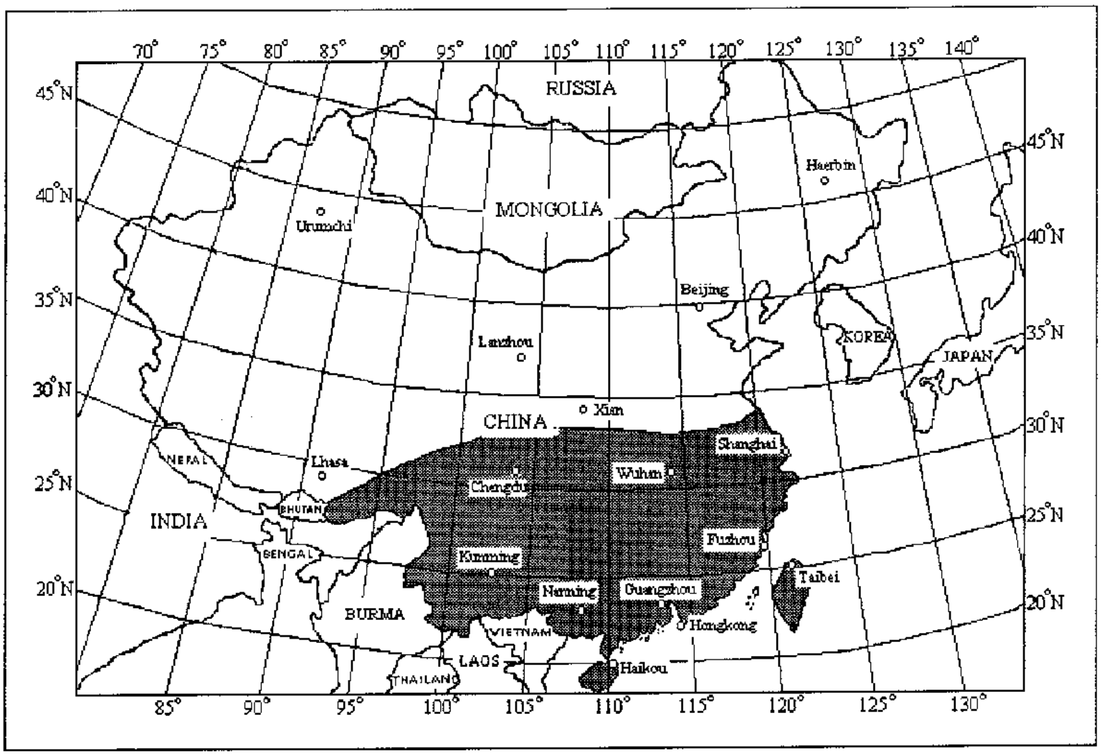

Fig. 1.2. Distribution of subtropical evergreen broad-leaved forest in China (after Wu, 1980).

In China, the topography of the forest distribution areas is varied, including plains, basins, hills, plateaux and mountains. Most of the region is limestone. In the east, part of the region is influenced by the Pacific Monsoon. Cold air penetrates from Siberia. In the west, the climate is influenced by the Indian Ocean Monsoon, bringing high rainfall in summer and autumn. Continental dry air ensures that winter and spring are warm and dry. Mean annual temperatures over the region as a whole are 15-21 °C. In winter, temperature can be as low as –10 °C in the north and –6 °C in the south. Annual rainfall exceeds 1000 mm and is sometimes > 2000 mm. Although the region has had a long history of cultivation, most vegetation on the mountains is still intact. More than 200 Nature Reserves have been established in the region (Davis *et al.*, 1995).

Yunnan Province in southwestern China is a region of exceptional interest to biologists, not only because it is in a transitional position from the southern Himalayas to east Asia and from tropical southeast Asia to subtropical China, but also because it is at the junction of the Indo-Burmese plates of Gondwanaland and the Eurasian plate of Laurasia (Audley-Charles, 1987). Moreover, Yunnan Province is one of the few regions of China with considerable natural forest cover remaining (Hsiung & Johnson, 1981; Richardson, 1990). Evergreen broad-leaved forest, dominated by evergreen oaks of the Fagaceae (*Lithocarpus, Castanopsis* and *Quercus*), is widely distributed in the warm-temperate zone of Yunnan at altitudes from 1500 to 3000 m above sea level (Wu, 1980, 1987; Li & Walker, 1986; Tagawa, 1997). The *Lithocarpus/Castanopsis* association is considered representative of this forest vegetation in subtropical, mountainous central and southern Yunnan, with an altitudinal range of 2000-2900 m above sea level (Jin, 1979; Wu, 1987; Peng & Wu, 1998; Qiu, Xie & Liu, 1998).

These montane evergreen broad-leaved forests in Yunnan have a lot of similarities in terms of physiognomy, structure and environment (Wu, 1980, 1987; Jin, 1979, 1983; Peng & Wu, 1998). They are characterized by a tall tree layer dominated by evergreen species of the genera *Lithocarpus and Castanopsis*, with companion species from Fagaceae, Lauraceae, Magnoliaceae, Theaceae, Hamamelidaceae, Aquifoliaceae and Ericaceae; a well-developed bamboo layer; and abundant epiphytes (mainly moss, lichen and ferns).

The most extensive stands of evergreen broad-leaved forests comprise the main components of natural reserves or parks in Yunnan Province. To 1997, 11 Nature Reserves or Parks, mainly of montane evergreen broad-leaved forests, had been established in Yunnan province, with a total area of 2,648 km^2. Among these four are of national significance. Ailao Mountain National Nature Reserve (NNR) of 504 km^2 is the largest such reserve. An extensive area of intact evergreen broad-leaved forest (33,349 ha) occurs in the northern portion of Ailao Mountain NNR (Yunnan Forestry Planning & Design Institute, 1987; Bureau of Environment Conservation of Yunnan, 1997).

1.2 Previous studies on montane moist evergreen broad-leaved forest in Yunnan, SW China

The montane moist evergreen broad-leaved forests of Yunnan Province, southwestern China had not been investigated in detail until the 1980s because of poor access and security problems (Wu, 1983; Qiu *et al.*, 1998). Since the 1980s, the Chinese government and provincial agencies have made efforts to protect forest lands and have issued a series of forest conservation measurements. The first investigations were to survey composition, area and distribution of the different forest types, and to assess their conservation values, providing basic information for assessing and establishing natural reserves or parks (Yunnan Forestry Planning & Design Institute, 1987; Bureau of Environment Conservation of Yunnan, 1997). Under the influence of the IBP (International Biological Program), ecological research on structure and function of the principal forest ecosystems in China has been undertaken from 1980, organized by the Chinese Academy of Sciences

A field research station was established in 1981 at Xujiaba, Ailao Mountain NNR by Kunming Institute of Ecology, the Chinese Academy of Sciences (Wu, 1983). Research undertaken from this station focuses on the dynamics of structure and function of natural, evergreen, broad-leaved forest. Some of this work is summarized in Chapter 2, below. The station facilities are located in a cleared area that adjoins undisturbed forest and the Xujiaba Reservoir (reconstructed in 1980). A meteorological observation facility is at the station, and a second set of instrumentation is located inside the adjoining forest. Permanent plots were established within the adjoining forest. Data concerning the vegetation, soil, climate and fauna in the natural forest ecosystem were accumulated in the first phase 1981-1983. Studies included plant species composition and community structure (You, 1983; Jin, 1983); growth characteristics of dominant tree species (Xie, Qiu & Jin, 1983); composition and distribution of fauna (mammals, insects, birds, amphibians and reptiles) and soil-microbes in the natural forest (Wu, 1983, He, Hu & Li, 1983; Ma, Chen & Li, 1983; Wang & Wei, 1983); distribution of soil types and their physical and chemical properties (Deng *et al.*, 1983); and characteristics of the mountain climate (Zhang, 1983; Liu, 1993).

Subsequently, studies of biomass and productivity of evergreen broad-leaved forest have been conducted (Qiu, Xie & Jin, 1984; Xie, Liu & Li 1996). Comparative studies of secondary and primary forest structure and composition have been undertaken (Young & Wang, 1989; Young, Carpenter & Wang, 1992; Young & Herwitz, 1995). From 1991 to 1996, a research project that monitored dynamics of structure and function of the montane moist evergreen broad-leaved forest at Ailao Mountain NNR were carried out, and an associated book has been published (Qiu *et al.*, 1998). Results of these studies are summarized in Chapter 2. That project provided the foundation for further research on dynamics of the forest ecosystem in Ailao Mountain, including this present thesis.

Studies of nutrient uptake and cycling are important components for understanding the long-term dynamics of structure and function of forest ecosystems (Vitousek & Sanford, 1986; Tamm, 1995; Nilsson *et al.*, 1995). Moreover, forest growth depends on the cycling of nutrient elements, and as forest management practices and environmental factors can result in changes in soil structure and nutrition, it is necessary to understand the cycling of nutrients for forest management (Nys, Stevens & Ranger, 1990; Nilsson *et al.*, 1995). Although there have been studies on vegetation, climate and soil in the area, very little information is available on nutrient uptake, accumulation, allocation and cycling in the natural forest. In addition, the Ailao Mountain forest is likely to differ from other forests in the pattern of nutrient cycling, because it lies in an area of high rainfall and humidity at high altitudes that may retard decay rates of litter.

1.3 History of forest nutrient cycling research

Scientific studies of nutrient cycling can be said to have originated with the work of Liebig (1840), on the way that plants satisfy their needs for nutrients. A landmark study of forest nutrient cycling was that of Ebermayer (1876). This presented a survey of litter and its importance for chemical stability in the context of forest management. Increased interest in mineral nutrition of forests appeared in the 20th century. Wiedemann (1932), summarized the results of earlier German experiments, most of them simple tests of liming or application of waste products. Hesselman (1937), described the reaction of mature spruce forests to the application of ammonium nitrate solution. He concluded that nitrogen is the limiting factor for growth and regeneration in the boreal forest. Mitchell & Chandler (1939), summarized the effect of nitrogen nutrition on growth of deciduous trees in the northeastern United States, using a variety of methods. These included extensive nursery work, nitrogen dosage experiments on large plots in mixed stands, and leaf analysis.

Rennie (1955) rediscovered the work of Ebermayer, following this much data on nutrient cycling among standing tree species were accumulated (e.g. Ovington, 1962). Bazilevich & Rodin (1966) and Rodin & Bazilevich (1967) had summarized knowledge of biological cycles of minerals in the principal ecosystems of the world; they recognized a zonal distribution of biomass and nutrient content and circulation, parallel to the zonation of plant formations. The International Biological Program (IBP), 1965-1975, put the productivity of world ecosystems in focus (Reichle, Franklin & Goodall, 1975). The IBP brought together large amounts of information from a great variety of forests and woodlands (Reichle, 1981). The study of nutrient cycling was considered almost as important as that of net primary production, at least in the context of forest ecosystems. In Europe Ovington (UK) and Duvigneaud & Denaeyer-De Smet (Belgium) together with Ellenberg (Germany) undertook fundamental studies (Ovington, 1959a, b, 1962, 1968; Duvigneaud & Denaeyer-De

Smet, 1968, 1970; Ellenberg, 1971). Biomass and nutrient cycling has been studied in different forest types in the United States (Woodwell & Whittaker, 1968; Whittaker & Woodwell, 1969), and in Japan (Kira & Shidei, 1967; Tsutsumi, Kawahara & Shidei, 1968). There has been much criticism of the IBP, from both ecologists and silviculturists. The achievements of the IBP might have been far greater if there had been a deeper understanding of tree nutrition in its planning, in relation to both nutrient cycling and site conditions (Tamm, 1995). Combining nutrient cycling studies with biomass (the Solling project; Ulrich, Mayer & Khanna, 1979), the hydrological approach (the Hubbard Brook Project; Likens *et al.*, 1967, 1970), and site conditions were recognized as good examples of forest nutrient cycling studies during the IBP phase (Tamm, 1995). These studies provided a substantial foundation for research on forest productivity and nutrient cycling in forest ecosystems.

Studies of nutrient cycling in tropical forests have also been popular. Many authors report that the rates of primary production and the amounts of nutrients cycled in moist tropical forests exceed those of temperate zone forests (Nye, 1961; Zonn & Li, 1962; Vitousek & Sanford, 1986). Nutrient cycling in tropical forests is described as "tight" or "effective" relative to temperate forests (Vitousek, 1984), and patterns of nutrient cycling in tropical forests are diverse and differ among forests on different soils (Vitousek & Sanford, 1986). Generally, forests on more fertile soils support more productive forests that appear to cycle larger quantities of nutrient elements than those on soil of lower fertility. Montane tropical forests appear to be low in nitrogen, and upper montane forests cycle substantially less nitrogen than do lower montane forests (Grimm & Fassbender, 1981; Grubb &Edwards, 1982; Tanner, 1985). These patterns influence physiology, community ecology, and population biology of tropical forests (Vitousek & Sanford, 1986).

Understanding of the role of nutrient uptake and cycling in forest ecosystems has become increasingly important. Both cycling and uptake of nutrients have been shown to be critical processes for the health of forest ecosystems (Waring & Schlesinger, 1985; Nilsson *et al.*, 1995). A series of international symposia, with a common focus on processes in the plant-soil continuum system of forest ecosystems has been held, beginning in South Africa (1984) and continuing in Canberra, Australia (1987), in Freiburg, Germany (1989), and in Halmstad, Sweden (1993). The general aim of these was to evaluate and discuss the important problem of 'Nutrient uptake and cycling in forests'. Nutrient uptake and cycling studies in forest ecosystems are important aspects of the recommendations for future research of the Halmstad symposium (Nilsson *et al.*, 1995). On the other hand, it is necessary to carry out long-term nutrient budget studies, in order to obtain accurate budgets of nutrient flux in forest ecosystems. Nutrient input and output budgets are considered key indicators of variation of soil fertility and of sustainability of forest management (Ranger & Turpault, 1999).

An undisturbed forest can be considered as a vast bioassay of site-specific nutrient status. Developing an understanding of ecosystem functions and reactions to ecosystem disturbances should be relatively easy in an undisturbed forest ecosystem (Nilsson *et al.*, 1995). However, atmospheric pollution and other human activities have altered natural element cycles over large regions of the world. Much of our current understanding of nutrient dynamics in temperate region ecosystems has been gained from such biogeochemically altered areas. It has become increasingly difficult to find regions that are free from human influence. Studies of unpolluted and undisturbed areas can provide important information about natural patterns of nutrient cycling, insight into biogeochemical conditions prior to the advent of regional-scale human impacts and allow for evaluation of biogeochemical theories that have been developed in areas subject to strong human influence (Hedin *et al.*, 1995). Examples of such theories are the "N saturation hypothesis" (Abert *et al.*, 1989), that N-limited forests receiving chronic anthropogenic N inputs will accumulate and retain that N for a long period of time; the "nutrient retention hypothesis", that net biotic retention of elements should be minimal in old-growth forest ecosystems (Vitousek & Reiners, 1975). Natural, old growth stands of evergreen broad-leaved forest in Ailao Mountain, a remote, unpolluted montane region, can provide an opportunity to understand and contribute to nutrient uptake and cycling in forests in SW China. On the other hand, the Ailao Mountain lies in a transitional zone between the southern and northern forest formations in Yunnan, and is also in the climatic boundary between the south and north of Yunnan province. It was hypothesized that this forest would likely have nutrient cycling characteristics that differ from those described elsewhere.

1.4 Thesis objectives

The preceding review has demonstrated that pattern of nutrient cycling are considered important to understanding how forests function. Studies have been conducted in many forest formations, but, to date, little has been reported from the evergreen broad-leaved forests of China. The objectives of this thesis were to investigate:

1) Quantification of nutrient inputs in rainfall, nutrient leaching through canopy and nutrient output by runoff in the natural forest.

2) Measurement of absorption, accumulation and distribution of nutrients within different stories of the natural forest.

3) Levels of nutrient return by litterfall and litter decomposition and the levels of nutrient dynamics in the natural forest.

4) Any relationships between uptake and retention of nutrients in plants and nutrient storage in soils in the natural forest.

5) Establishment of a model of biological cycling of nutrients in the natural forest.

1.5 Thesis Outline

This thesis is organized into 9 chapters. In Chapter 1, I present a general introduction, including an account of the geographic distribution of montane, moist, evergreen broad-leaved forest. I briefly describe the history of nutrient research with relevance to this type of vegetation and then outline the objectives of my thesis.

In Chapter 2, firstly, I provide a brief description of my general study site, including previous studies on the vegetation association, general geology and soil types, and the local climate and I then present physiognomic and floristic characteristics, species diversity and stand productivity of natural *Lithocarpus /Castanopsis* forest undertaken in the area in the past.

In Chapter 3, I present biomass and nutrient contents of living plants and dead materials in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain, and elucidate the characteristics of biomass and nutrient accumulation among different structural layers within high and low density stands of the forest.

In Chapter 4, I describe temporal and spatial variation in small litterfall and large wood fall in the forest over 9 years, and examine nutrient contents in different components of litterfall and litter on the forest floor.

In Chapter 5, I report decomposition and nutrient dynamics of leaf litter from important species in the natural forest, and present an analysis of the relationship between chemical composition and lignin concentration of litter fractions and their respective decay rates.

In Chapter 6, I describe nutrient fluxes in bulk precipitation, throughfall and stemflow in the forest. I also test the effects of epiphytes on the amount and chemical composition of stemflow.

In Chapter 7, I present information on annual uptake and retention by plants, and annual nutrient return to the soil in the forest, using materials collected in Chapters 3, 4, 5 and 6.

In Chapter 8, I describe nutrient input and output budgets of the forest through the hydrological flux in the natural forest.

In Chapter 9, I provide a general discussion synthesizing results from earlier chapters.

Chapter 2 Environment of the Study Site and Characteristics of Structure and Composition of Natural *Lithocarpus /Castanopsis* Forest at Xujiaba, Ailao Mountain NNR

2.1 Introduction

Ailao Mountain NNR is located between latitudes 23°35′ - 24°44′ N and longitudes 100°54′ - 101°30′ E, with a total area of 504 km^2 (Qiu *et al.*, 1998; Fig. 2.1). It lies between the Yungui Plateau, Henduan Mountain Ranges and the Tibetan Plateau (Zhao, 1983). It divides Yunnan Province into east and west parts. It traverses the climatic boundary between the south and north of Yunnan province (Zhang, 1983). It is also a transition zone from north to south in the region of subtropical vegetation (Wu, 1987; Young & Wang, 1989; Qiu *et al.*, 1998). Thus, this area is not only an ideal base for scientific research into biodiversity conservation, but is also of ecological value in relation to the study of the local climate, soil and water conservation and water storage, in relation to sustainable agricultural development of the lowlands that derive their water supplies from the ranges (Qiu *et al.*, 1998; Young & Herwitz, 1995).

2.2 Location

2.2.1 Locality

The study site is at Xujiaba, on the northern crest of the Ailao Mountains in Jingdong County, Yunnan (24°32′N, 101°01′E; Fig. 2.1). Xujiaba occupies an area of 5400 ha of primary forest and is a key part of the Ailao Mountain NNR that includes the largest tract of native old growth evergreen broad-leaved forest (33,400 ha) in China (Young & Herwitz, 1995).

Outside the Nature Reserve, the original forest cover has been removed for agricultural purposes. This location has an undulating topography, ranging from

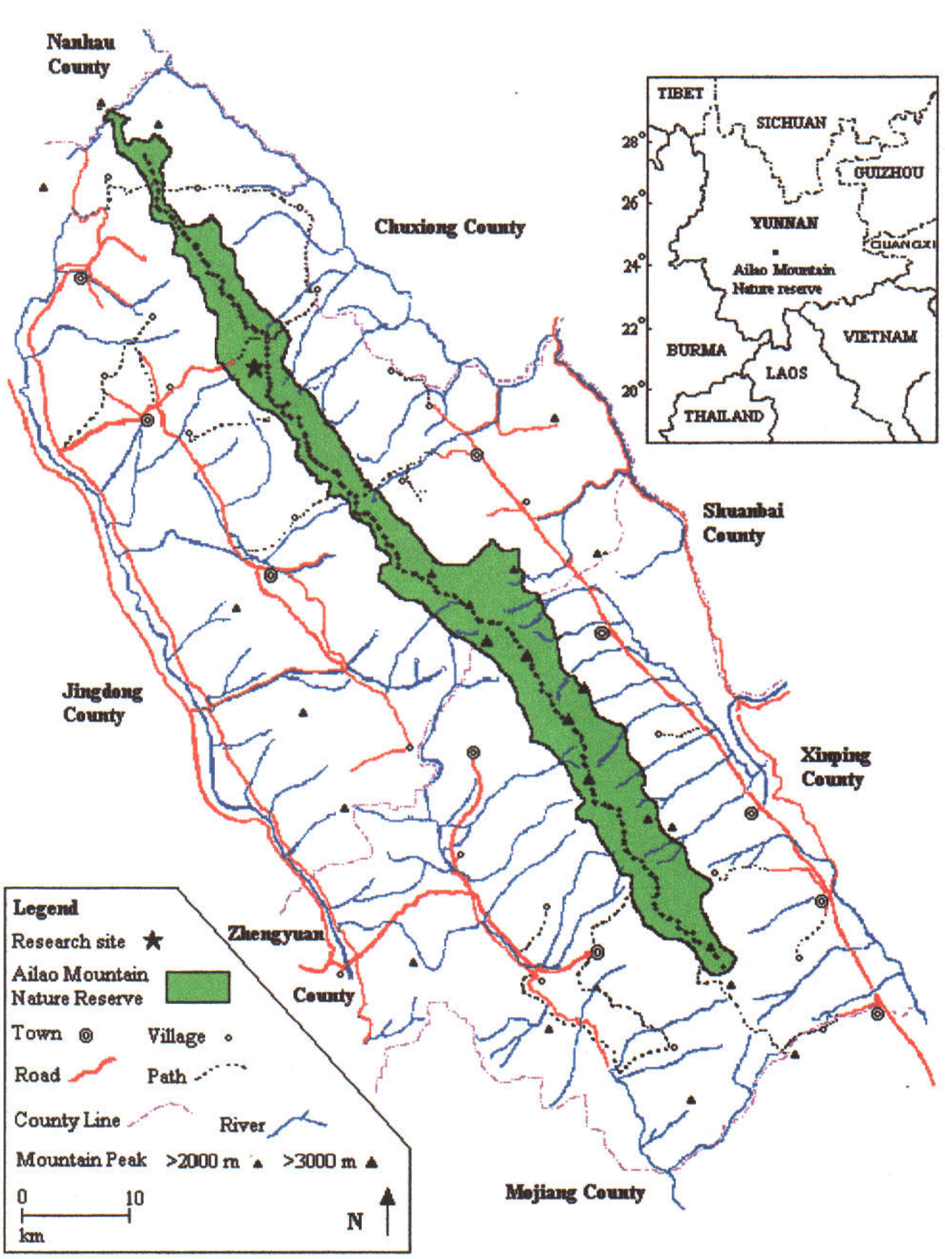

Fig. 2.1. Location of the Ailao Mountain National Nature Reserve (After Wang, Carpenter & Young, 2000).

approximately 2400 m to 2600 m (Qiu *et al.*, 1998). It is about 700 km southwest of Kunming, the provincial capital of Yunnan, and about 60 km southeast from Jingdong town.

2.2.2 Climate

The climate of this area is warm-temperate and is controlled by both the south-east monsoon and the south-west monsoon (Zhang, 1983; Qiu *et al.*, 1998). Meteorological observations (1991-1995) at the Forest Ecosystem Research Station (FERS), Xujiaba (24°32′ N, 101°01′ E, 2450 m altitude) show: the annual mean precipitation is 1931 mm (85 % in the rainy season from May to October, Fig. 2.2); annual evaporation 1485.5 mm (23 % less than precipitation); annual mean relative humidity 86 %; and, annual mean air temperature 11.3 °C (from 5.4 °C in January to 16.4 ° C in July). The ≥ 10 °C accumulative temperature was about 3420 °C, placing this area as similar to the warm temperate zone (Liu, 1993). The temperature in winter, however, is not so low, thus explaining why evergreen broad-leaved forest is developed at Xujiaba (Qiu *et al.*, 1998). Natural disturbances most commonly affecting forests in the Ailao Mountain are strong winds and the occasional cold spell, that may be accompanied by snowfall (about every 8-10 year).

The Xujiaba region is moist throughout the year and fog-covered days are frequent, despite alternations of dry and wet periods. Mist occurring in the dry season decreases light level. The total annual sunshine at Xujiaba (2450 m altitude) is 1268.6 hours, comprising only 60.2 % of that in the piedmont (Jingdong Town, 1162m altitude) where annual rainfall is only 45 % of that at Xujiaba (Zhang, 1983; Ma *et al.*, 1992). The mean daily hours of sunshine are longer in the dry season (Jan.-May) than in the wet season (June-Oct.).

Mean and maximum air temperatures inside the forest are lower (0.3-1.2 °C and 0.8 °C) than those outside the forest. The mean minimum air temperature in the forest is greater (1.0 °C) than outside. Annual mean relative humidity in the forest is 5 % higher than outside (Liu, 1993, Fig. 2.3).

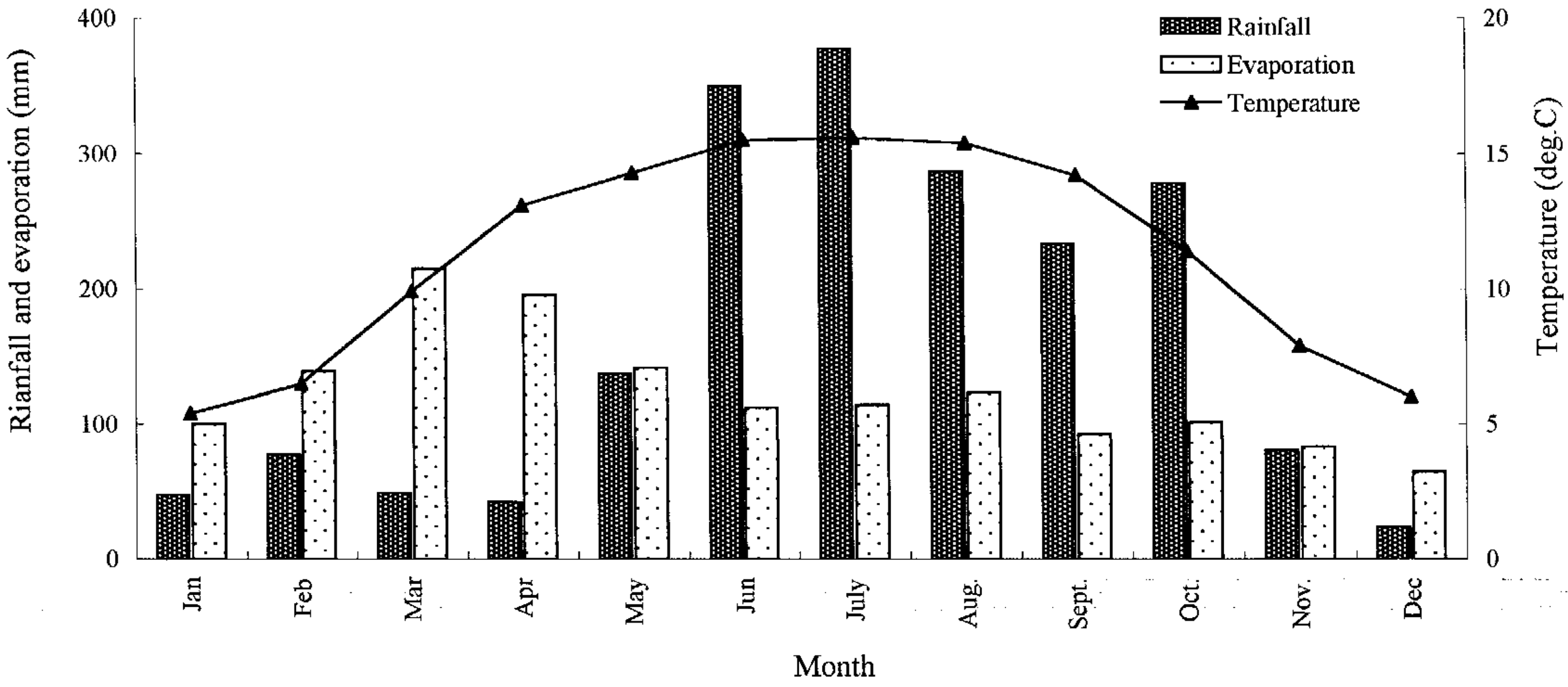

Fig.2.2. Mean monthly rainfall, evaporation and temperature (1991-1995) at Xujiaba FERS, Ailao Mountain NNR, altitude 2450m. Data are from records of Kunming Institute of Ecology, Chinese Academy of Sciences.

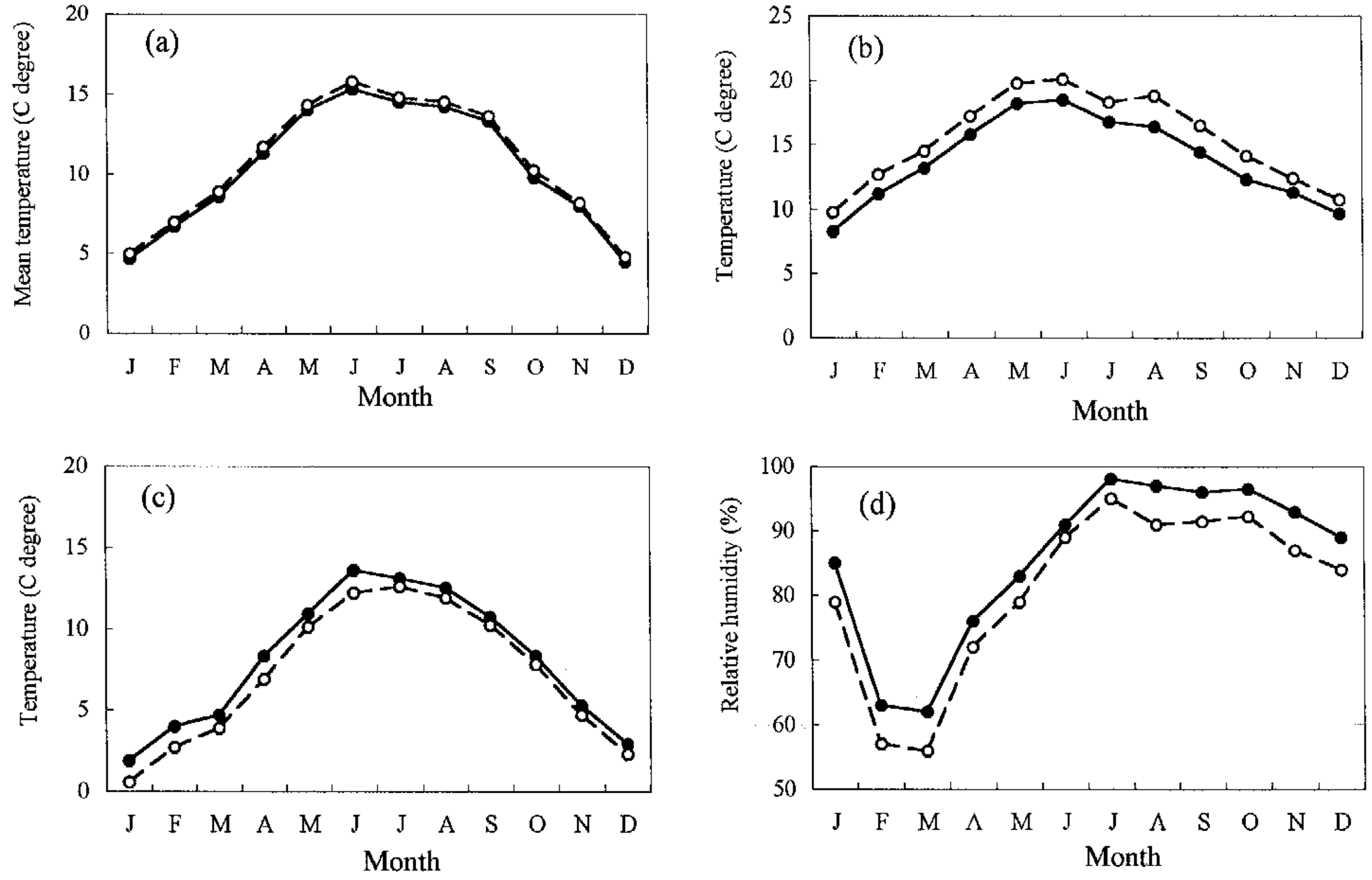

Fig. 2.3. Monthly variation in means of temperature and humidity inside and outside the forest during 1986-1987 at Xujiaba FERS, Ailao Mountain NNR. Open circles: outside; closed circle: inside; (a) to (c) = air temperature (degree C), (a) = mean, (b) = maximum, (c) = minimum; (d) = means of relative humidity (%). Data are from Liu (1993).

2.2.3 Geology and topography

As with other regions of Yunnan Province, geomorphic development of the northern segment of the Ailao mountains is characterized by a relatively stable period of crustal movement, after land formation by the folding of the Yanshan Movement (Zhao, 1983b). The land surface has experienced a long process of erosion, denudation and gradation, giving rise to a peneplain of wave-formed relief. The mean altitude of the northern segment of Ailao Mountains exceeds 2000 m, with main peaks > 2600 m and the highest peak in the Xujiaba region at ~ 2700 m.

Based on analysis of background geologic tectonics, geomorphologic types and features of neotectonic movements, Zhao (1983b) found the northern segment of Ailao Mountains to be a metamorphic zone, jointly composed of a series of complicated structural formations and diversified magmatic and metamorphic rocks. The northern segment of Ailao Mountains was formed by uplifted blocks, confined by faults on both sides. The valleys, basins, and high and moderately-high mountains are composed of deeply or slightly metamorphosed zones. From the Pliocene up to the Pleistocene, the peneplain of Yunnan province was uplifted into the Yunnan Plateau, under the effect exerted by tectonic movement of the Himalayas. The present geomorphology of the northern segment of Ailao Mountains results from the joint effect endogenic and allogenic forces from since the Pleistocene epoch (Qiu *et al.*, 1998).

2.2.4 Soils

An altitudinal sequence of soils identified by Deng *et al.* (1983) used color (Munsell, 1954), to differentiate broad soil groups of Ailao Mountains. These are as follows: at altitudes <1300 m: lateritic red earth; at 1300-1900 m: yellow red earth; at 1900-2600 m: yellow brown earth; and at >2600 m: brown earth. Main soils under the *Lithocarpus xylocarpus* and *Castanopsis wattii* natural forest are yellow-brown in colour, of hues 7.5 YR/6/8 – 5/8; between reddish yellow and strong brown. Parent rocks of the yellow-brown earths consist of schist, gneiss and diorite. Soil texture is generally loam, with pH values of 4.2-4.9 (1:5 soil: water). A 3-7 cm litter layer covers the soil surface. Surface organic C, total N and total P are reported as 12.91%, 0.52 % and 0.06 %, respectively. The exchangeable K is 0.75 $\mathrm{cmol^{+}\,100g^{-1}}$. C/N ratio varies slightly from 14.4 at the surface to 15.3 at 30-50 cm depth (Deng *et al.*, 1983; Qiu *et al.*, 1998). Physical and chemical properties of the yellow brown soil are summarized in Appendices 1, 2.

2.3 Biotic environment

2.3.1 Vegetation

2.3.1.1 Vertical distribution

The Ailao Mountains stretch approximately 250 km from the northwest to the southeast, rising straight up between the Yuanjiang River (Honghe River) and the Lanchang River (the upper course of the Mekong River). It forms the border between the two main physiographic regions of Yunnan (Qiu *et al.*, 1998): the western Valleyland to the west, a region of deep valleys and high mountains; and the Yunnan-Guizhou plateau to the east, a region of hills above a high plateau (average elevation approximately 2,000 m). The eastern slopes experience a greater range in temperature and are influenced by the cold winter air masses of central Asia while the western slopes experience milder temperatures and more humid conditions (Zhang, 1983). Differences in climate on the two sides affect the distribution of vegetation types. On the south-west slopes, the vegetation is monsoon, with evergreen, broad-leaved forest (mainly of *Castanopsis hystrix, C. indica, Lithocarpus truncatus, L. microspermus and Schima wallichii*) and also carries *Pinus kesiya* var. *landbianensis* forest. On the north-east slopes, the vegetation cover is semi-moist, evergreen, broad-leaved forest (mainly of *Castanopsis orthacantha, Castanopsais. delavayi, Cyclobalanopsis glaucoides, Cyclobalanopsis. delavayi and Lithocarpus dealbatus*) with *Pinus yunnanensis* forest and some hot-dry valley vegetation at lower altitudes. On the top of the Ailao Mountain, the vegetation is dwarf mossy forest, dominated by *Lithocarpus pachyphylloides* and *Rhododendron irroratum* (Fig. 2.4). The lower limit of montane moist evergreen broad-leaved forest is higher on the north-east slopes than that on the south-west slopes, indicating that moisture is greater on the south-west slope than on the north-east slope. The south-west slope belongs to the upland type of the southern subtropics of Yunnan and the north-east belongs to the upland type of the northern subtropics of Yunnan. In terms of vegetation distribution, Xujiaba is situated at the transition area the between the southern and northern subtropics.

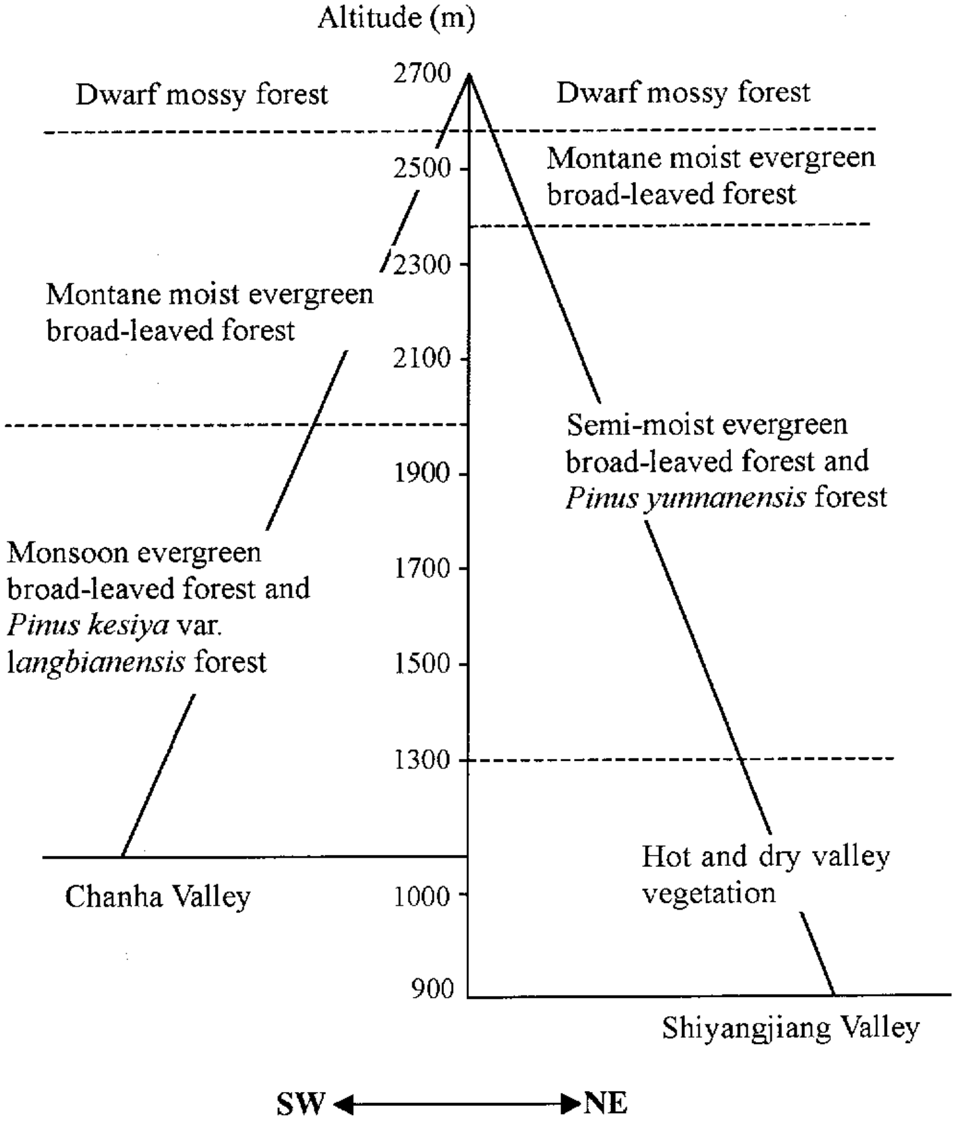

Fig. 2.4. Vertical vegetation zones on the mountain slopes in Xujiaba, Ailao Mountain NNR (from Li, 1983).

2.3.1.2 Composition of forest types

In describing the vegetation of the Xujiaba area, You (1983) used the reléve method and recognized seven different associations. He described the main association as (1) *Lithocarpus xylocarpus - Lithocarpus chintungensis - Castanopsis wattii* (oak/chestnut forest). This occupies some 80 % of the area illustrated in Fig 2.5 and represents the main natural forest. At high altitudes on steep slopes he described a shorter-statured natural community; (2) *Lithocarpus pachyphylloides - Rhododendron irroratum* (dwarf oak/rhododendron elfin forest). Low-lying moist areas carry an alder community with bracken fern; (3) *Alnus nepalensis - Pteridium revolutum*. This may represent a seral stage following disturbance. You (1983) reported that some small areas of primary forest had been destroyed and had formed secondary communities; (4) Regrowth of oak. Other secondary associations he identified are: (5) *Populus bonatii - Pteridium revolutum* (Poplar and bracken fern or *Sinarundinaria* short bamboo); (6) *Pinus yunnanensis - Pteridium revolutum* (Pine and bracken); (7) *Pteridium revolutum- Yushania niitakayamensis* (Bracken and dwarf bamboo).

2.3.2 Fauna

The large area of natural evergreen broad-leaved forests in Ailao Mountains provides diversified habitats for various wildlife. It was estimated that there were 20 species of amphibians and reptiles (Kou & Xing, 1983; Ma, Chen & Li, 1983); 43 species of small mammals (Wang *et al.*, 1983; Wu *et al.*, 1983); 214 species of birds (Wang, 1983; Wang & Wu, 1983; Wang & Wei, 1983; Wei *et al.*, 1983; Wang *et al.*, 2000); 24 species of large and medium sized mammals (Zhao, 1983a); and representatives of some 58 families of insects (He *et al.*, 1983) in the primary forest.

2.3.3 Microbes

Surface soil and litter are rich in microorganisms. Researchers have isolated 217 strains of fungi, belonging to 2 orders, 4 families and 30 genera of *Ascomycetes* and

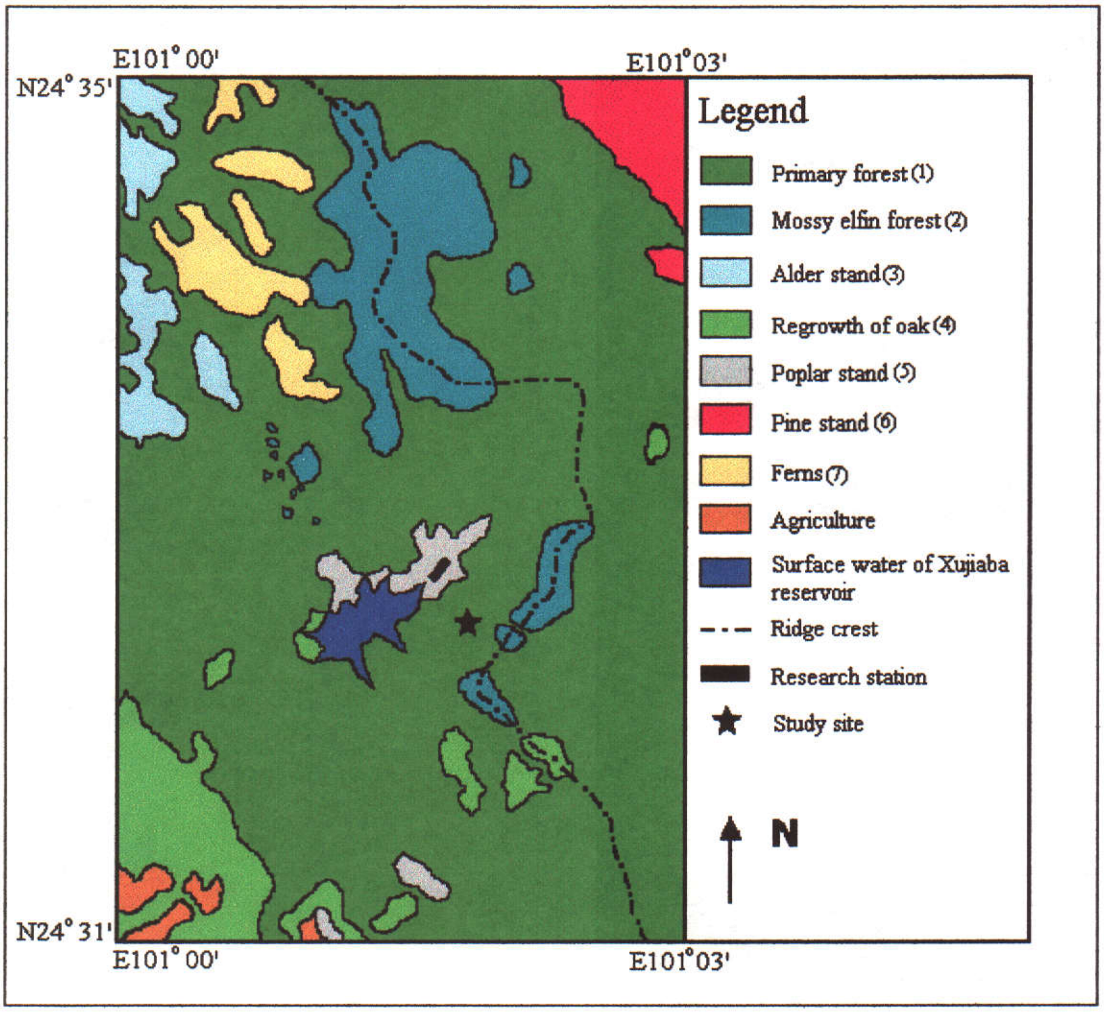

Fig. 2.5. Vegetation types at Xujiaba, Ailao Mountain NNR (modified from You, 1983)

fungi imperfecti in the natural forest, of which strains of *Moniliaceae* and *Dematiaceae* dominate the composition (Xue *et al.*, 1983; Sheng *et al.*, 1983; Jiang & Xu, 1983; Zhou *et al.*, 1983). The quantity of strains decreased with soil depth. The litter layer is richest in number of strains, reaching 6.38 x 10^4 per gram, compared with 0.68-1.71 x 10^4 per gram dry soil in the surface soil.

2.3.4 Human-induced disturbance

In general, the impact of human activities on the natural forest is light in the Xujiaba region. However, a variety of human-induced disturbances at the small scale, including the collection of herbs, fruits and bamboo by local people, does occur in parts of the Xujiaba region. Timber harvesting for local use occurs at edges of the primary forest. Some domesticated animals and feral pigs use both open- and closed-canopy forests.

On the other hand, a reservoir, which stores water for rice irrigation on the mountainsides, occupies the interior of Xujiaba. In Chinese Xujiaba means "Xu family dam". When the reservoir and dam were constructed about 100 years ago, some surrounding forested areas were cut and these are now regenerating into a variety of associations depending on their location. Kunming Institute of Ecology maintains a research station (Xujiaba FERS) with four full-time employees, recruited from local villages. Numerous visiting researchers from various institutes in Kunming and other Chinese cities, and also from other countries, spend time at Xujiaba FERS.

2.3.5 Study site

The research reported in this thesis was conducted during 1991-1999 in the natural forest association of *Lithocarpus/Castanopsis*, near Xujiaba FERS. A 4 ha (200 x 200m) research plot was selected as a site for litterfall, litter decomposition, throughfall, stemflow and runoff studies. The area had a uniform slope of ca. 10°

with a south-eastern aspect. To avoid sampling effects of harvesting on measurements in this permanent plot, another two 50 x 50m plots of similar species composition, soil and slope were selected for biomass and nutrient content studies (Chapter 3). Studies of floristic composition and species diversity in the natural forest were conducted within representative patches of the old growth forest in Xujiaba region (next section, 2.4).

2.4 Characteristics of structure and composition of natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR

2.4.1 Floristic composition and community structure

A total of 139 species in 107 genera and 63 families were present in a set of eight plots of 20 x 20 m (Qiu *et al.*, 1998, Appendix 3). Mean number of species per 400 m^2 plot was 62. Important families containing two or more genera and species (2:2) are Lauraceae (6:10), Theaceae (5:7), Fagaceae (3:5), Magnoliaceae (2:2), Araliaceae (3:5), Rosaceae (6:7), Ericaceae (4:7), Rutaceae (3:3), Myrsinaceae (2:2), Vacciniaceae (2:4), Caprifoliaceae (2:2), Cornaceae (2:2), Urticaceae (2:2), Melastomataceae (2:2), Vitaceae (3:3), Smilacaceae (2:4), Gesneriaceae (2:2), Dryopteridaceae (2:2), Polypodiaceae (2:2) and Liliaceae (5:5).

Evergreen trees of Lauraceae, Theaceae, Fagaceae and Magnoliaceae are the main floristic components of temperate broad-leaved forest (Ovington, 1983). These also comprise the principal families of subtropical evergreen forests of continental China and Japan generally (Kira, 1991; Wu, 1980; Tagawa, 1997). However, due to the low latitude of Ailao Mountains, species composition here is enriched with some tropical floral elements. A subtle combination of tropical, temperate and endemic elements characterize species composition of the forest.

Eleven generic-level and six specific-level geographical groups are recognized within the evergreen broad-leaved forest by Qiu *et al.* (1998), based on the floristic element classification of Chinese seed plants (Wu, 1991; Table 2.1). At a generic level, tropical types (1-6) have 58 genera that contribute 54 % of the total, while temperate distribution types (7-10) have 46 genera that contribute 43 %. Of these, East Asian and North American distribution types comprise 28 %. At a specific level, endemic types account for 40 % of the total species, temperate types 38 % and tropical types 21 %. In the three groups, Chinese Himalayan species are the major constituent (27 %), next are endemic species of south-western China (22%) and East Himalayan species (11%). This pattern of floristic composition indicates the forest consists of Sino-Himalayan endemics together with components of tropical south-east Asian distribution.

Table 2.1. Geographical elements of the middle mountain moist evergreen broad-leaved forest at Xujiaba, Ailao Mountain NNR[a].

A: Geographic element of genera	No. of genera	% of genera
1. Pantropic	24	22.4
2. Tropical Asia to Tropical America disjunct	2	1.9
3. Old world tropics	2	1.9
4. Tropical Asia to Tropical Australia	5	4.7
5. Tropical Asia to Tropical Africa	2	1.9
6. Tropical Asia	23	21.5
7. North Temperate	11	10.3
8. East Asia & North America disjunct	12	11.2
9. Old world Temperate	5	4.7
10. East Asia	18	16.8
11. Endemic to China	3	2.8
Total	107	100
B: Geographic element of species	**No. of species**	**% of species**
1. Pantropic	1	0.7
2. Tropical Asia to Tropical Africa	1	0.7
3. Tropical South East Asia	(29)	(20.9)
a. Tropical Himalaya to S. China	1	0.7
b. East Himalaya to S. China	15	10.8
c. Burma, Thailand to S. China	4	2.9
d. Vietnam to S. China	4	2.9
e. Mainland S. E Asia	5	3.6
4. Eastern Asia	(53)	(38.1)
a. China Himalaya to S.W. China	38	27.3
b. China and Japan	7	5.0
c. Mainland East Asia	8	5.8
5. Endemic to S. China	40	28.8
6. Endemic to Yunnan	15	10.8
Total	139	100

[a] The data are from Qiu *et al.*(1998)

The forest reaches 20-25 m in height. Canopy tree species are mainly comprised of *Castanopsis wattii*, *Lithocarpus xylocarpus*, *Schima noronhae* and *L. chintungensis* (Fig. 2.6). These dominants have highest importance values (Table 2.2; Appendix 4). They have most stems, are the tallest trees with largest trunk diameters and are also evenly distributed within the forest. A subcanopy occurs with an estimated cover of >50 % (Qiu *et al.*, 1998). *Vaccinium duclouxii*, *Manglietia insignis*, *Hartia sinensis* and *Machilus viridis*, with next highest importance values, are dominant species in the subcanopy layer, reaching heights of 10-15 m and cover of 15-25 %. Other important species listed comprise the main tree species in the forest. A suite of deciduous tree species, including *Acer heptolobum*, *Styrax perkinsiae*, *Acanthopanax evodeaefolius* and *Tapiscia yunnanensis* account for a small proportion of the total number of plant species in the forest.

The understory bamboo, *Sinarundinaria nitida*, 1-3.5 m high, with a cover of 70 %, dominates the shrub layer in the forest. While true shrubs are not abundant, the most common species are *Daphne cannabina*, *Mahonia mairei*, *Ardisia crenata* and *Skimmia arborescens*. The herb layer, to 0.5 m high with cover of 30 % mainly consists of the ferns *Plagiogyria communis* and *Leptorumhora quadripinnata*; the sedge *Carex teinogyna* and the geophyte *Oxalis griffithii*. Woody lianas are abundant, mainly represented by the genera: *Smilax*, *Kadsura*, *Jasminum*, *Euonymus*, *Tetrastigma* and *Millettia*. The most common species are *Smilax lebrunii*, *Jasminum duclouxii*, *Euonymus vagans*, *Tetrastigma hypoglaucum*, *Kadsura coccinea*, *Rosa longicuspis* and *Parthenocissus himalayana*. Epiphytes are also abundant, the most common species are *Elatostema diversifolium*, *Briggsia longifolia* and *Agapetes manni*. Common epiphytic ferns are *Lepisorus scolopendrium*, *Vittaria flexuosoides* and *Asplenium planicaule*. The lichens *Anaptychia ciliaris*, *Usanea* spp. and the bryophytes *Homaliodendron scalpellifolium*, *Symphyodon perrottetti*, *Herberta longifolissa* and *Bazzania albicans*, are also abundant.

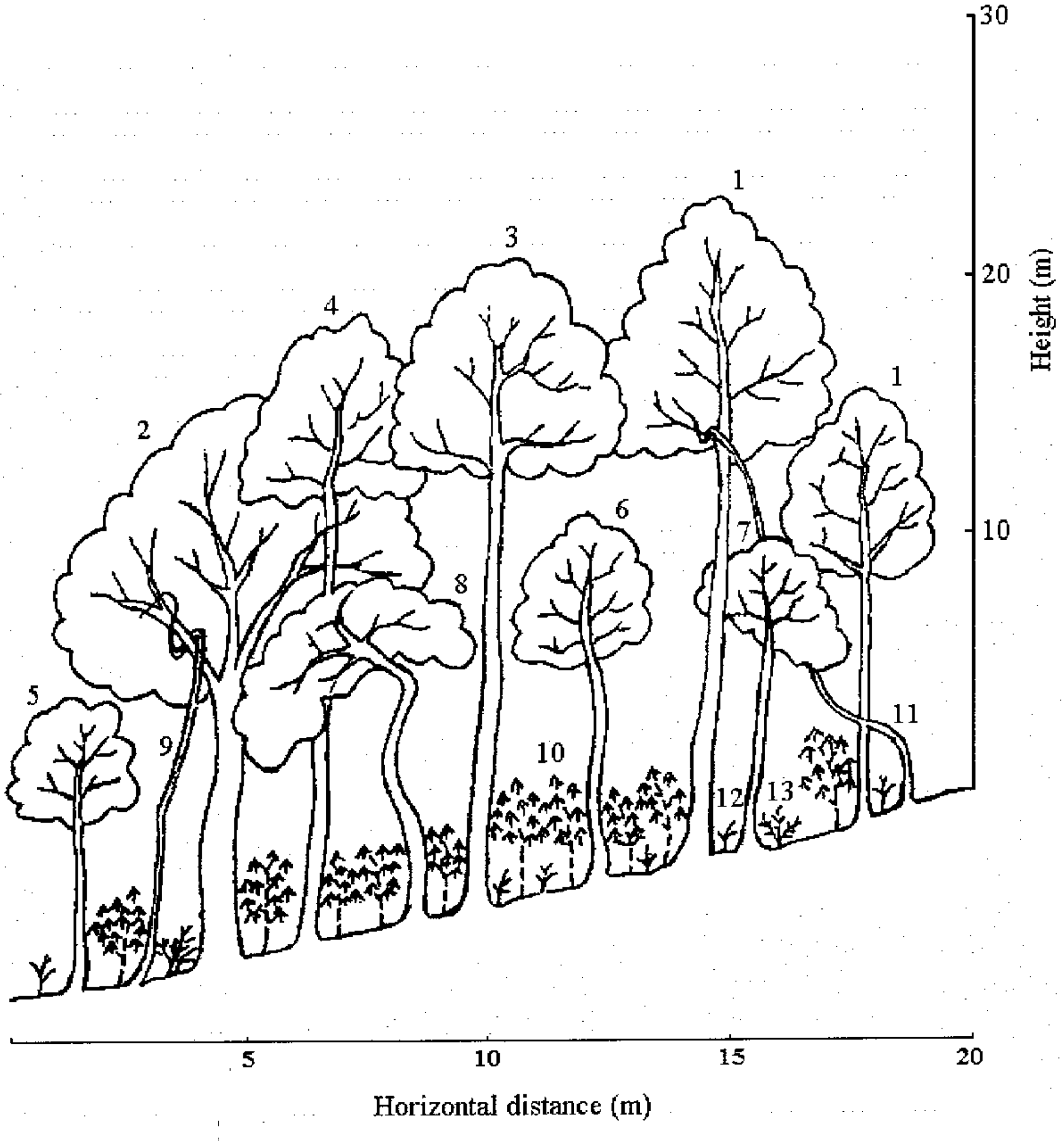

Fig. 2.6. Profile diagram of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR. 1.*Lithocarpus xylocarpus*; 2. *Castanopsis wattii*; 3. *Schima noronhae*; 4. *Acer heptalobum*; 5. *Illicium macranthum*; 6. *Neolitsea polycarpa*; 7. *Lindera thomsonii*; 8. *Eurya obliquifolia*; 9. *Rosa longicuspis*; 10. *Sinarundinaria nitida*; 11. *Kadsura coccinea*; 12. *Carex teinogyna*; 13. *Plagiogyria communis* (Qiu *et al.*, 1998).

Table 2.2. The 20 tree species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR with highest importance values.

No.	Tree species	No. of trees	Mean height (m)	Mean DBH (cm)	Abundance (%)	Dominance (%)	Relative freq. (%)	IV[a]
1	*Castanopsis wattii*	71	24	68	5.2	21.0	5.6	31.7
2	*Lithocarpus xylocarpus*	98	25	42	7.1	8.0	5.3	20.4
3	*Schima noronhae*	94	23	35	6.8	5.6	5.3	17.7
4	*Lithocarpus chintungensis*	82	22	39	6.0	6.9	4.7	17.6
5	*Vaccinium duclouxii*	128	7.7	8.2	9.3	0.3	2.9	12.6
6	*Manglietia insignis*	56	21	23.5	4.1	2.5	4.7	11.3
7	*Hartia sinensis*	76	18	19.8	5.5	1.8	3.2	10.5
8	*Machilus viridis*	53	20	22	3.9	2.2	4.4	10.5
9	*Camellia forestii*	77	4.4	5.7	5.6	0.1	3.5	9.3
10	*Eriobotrya bengalensis*	68	12	14	4.9	0.9	3.2	9.1
11	*Michelia floribunda*	50	18	22	3.6	2.2	2.9	8.8
12	*Cyclobalanopsis sterwardiana* var. *longicaudata*	34	19	26.8	2.5	3.3	2.9	8.7
13	*Rhododendron leptothrium*	78	6	8.5	5.7	0.3	2.1	8.1
14	*Symplocos ramosissima*	38	11	11.5	2.8	0.6	3.5	6.9
15	*Lindera thomsonii*	29	16.2	17.9	2.1	1.5	3.2	6.8
16	*Lithocarpus hypoviridis*	17	19	28.8	1.2	3.8	1.5	6.5
17	*Tapiscia yunnanensis*	2	25	35	0.1	5.6	0.6	6.3
18	*Illicum macranthum*	21	17	21	1.5	2.0	2.6	6.2
19	*Eurya obliquifolia*	31	3.9	4.4	2.3	0.1	3.5	5.9
20	*Acanthopanax evodiaefolius*	3	23	32.5	0.2	4.8	0.9	5.9

[a] IV, Importance value (Abundance + Dominance + Relative frequency).
Data are from Qiu *et al.* (1998.).
See Appendix 4 for more details.

2.4.2 Physiognomy

The physiognomy of a forest community is mainly determined by life form composition. Based on the classification system of Raunkiar (1934) applied to eight representative plots, Qiu *et al.* (1998) indicate that the natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR is dominated by phanerophytes (45.2 % of total species; Fig. 2.7). Epiphytes and hemicryptophytes are especially abundant (15.8 and 17.3 % of total species). Evergreen species, mainly mesophanerophytes, contribute 38.1 % of total species, while deciduous species comprise only 7.1 %. A group of woody liana phanerophytes makes up 11.5 %. Therophytes are uncommon (only 3.6 %). In comparison with tropical rain forests, the natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR has fewer mega- and meso-phanerophytes, more hemicryptophytes and more epiphytes (Fig. 2.8). Woody lianas are more abundant in this forest than in subtropical forest, at Jiande, east China (Chen, 1992), lowland rain forests in Brazil (Cain & Castro, 1959) and Guiana (Richards, 1952), but less than in tropical seasonal rain forest of south Yunnan (Zhu, 1997).

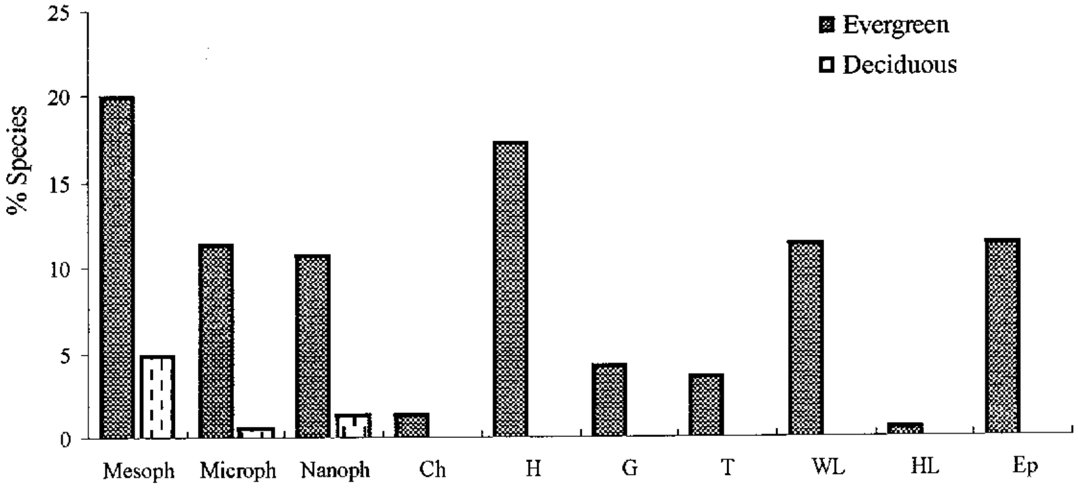

Fig. 2.7. Life form spectrum of the middle-mountain moist evergreen broad-leaved forest at Xujiaba, Ailao Mountains. Mesoph, Mesophanerophyte; Microph, Microphanerophyte; Nanoph, Nanophanerophyte; Ch, Chamaephyte; H, Hemicryptophyte; G, Geophyte; T, Therophyte; WL, Woody Liana; HL, Herbaceous Liana; Ep, Epiphyte.

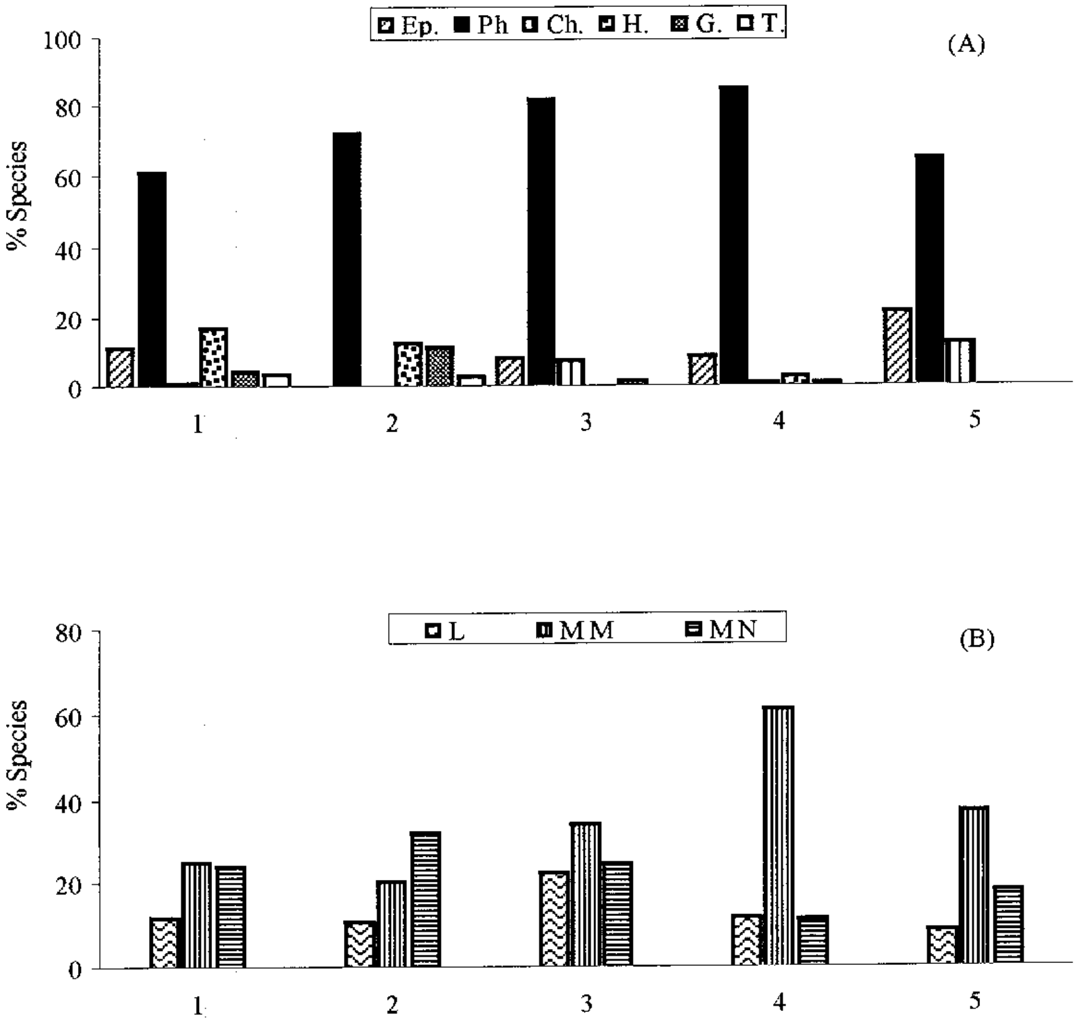

Fig. 2.8. Comparison of life form spectra. (A) For all vascular plant species in the communities; (B) For phanerophytes. 1. Middle-mountain moist evergreen broad-leaved forest, Ailao Mts.; 2. Subtropical evergreen broad-leaved forest, Jiande, east China (Chen, 1992); 3. Tropical seasonal rain forest, south Yunnan (Zhu, 1997); 4. Lowland rain forest, Brazil (Cain & Castro, 1959); 5. Lowland rain forest, Guiana (Richards, 1952).
Ep, Epiphyte; Ph, Phanerophyte; Ch, Chamaephyte; H, Hemicryptophyte; G, Geophyte; T, Therophyte; L, Liana; MM, Mega- and Meso-phanaerophyte; MN, Micro- and Nano-phanerophyte.

Of the leaf size spectra, mesophytes comprise 40.3 % of total species and have the highest percentage in the upper tree layer, while microphylls are most frequent as shrubs and lianas. Leptophylls are least frequent, at 5.7 %, and megaphylls are absent (Qiu *et al.*, 1998). Fig. 2.9 provides a comparison of leaf-size spectra between tropical and subtropical forests. Tropical forests are mostly dominated by mesophyll species, while tropical, upper montane, rain forest and subtropical lowland forests are dominated by micropylls. The Ailao mountain forest has abundant mesophylls, comparable with the tropical upper montane forest in Sumatra; subtropical/warm temperate forest in Japan (Ohsawa & Ozaki, 1992); and, subtropical evergreen broad-leaved forest in east China (Chen, 1992). However, the percentage of mesophyll species in the forest is considerably less than in tropical lowland forests (Richards, 1952; Ohsawa & Ozaki, 1992; Zhu, 1997). The leaf size spectrum of this forest represents an intermediate pattern between tropical and subtropical montane forests, and exhibits affinities with tropical montane rain forests and subtropical and warm temperate rain forest.

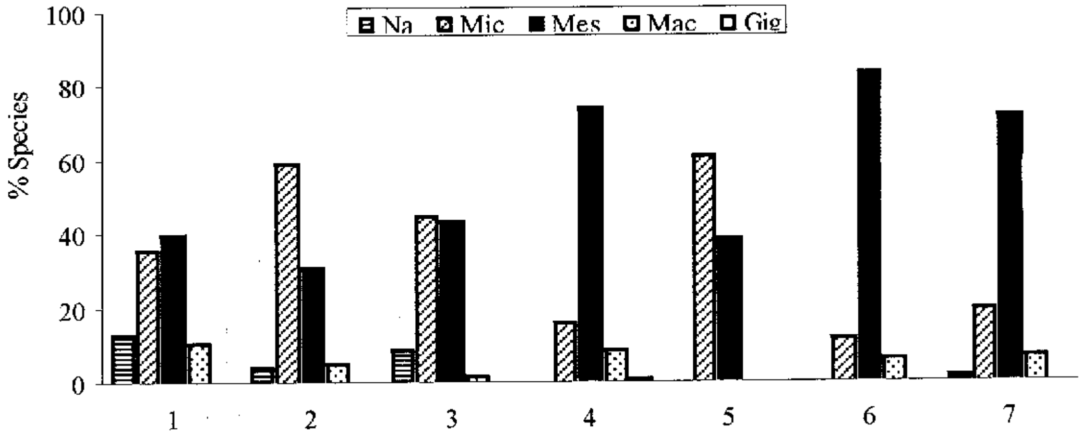

Fig. 2.9. Comparison of leaf-size classes. 1. Montane moist evergreen broad-leaved forest at Xujiaba, Ailao Mts.; 2. Subtropical evergreen broad-leaved forest, Zhijiang, China (Chen, 1992); 3.Subtropical warm-temperate forest, Japan (Ohsawa & Ozaki, 1992); 4. Tropical rain forest, south Yunnan (Zhu, 1997); 5. Tropical upper montane rain forest, Sumatra (Ohsawa & Ozaki, 1992). 6. Wet evergreen forest, Nigeria (Richards, 1952); 7. Tropical lowland montane rain forest, Sumatra (Ohsawa & Ozaki, 1992).
Lep, Leptophyll; Na, Nanophyll; Mic, Microphyll; Mes, Mesophyll; Mac, Macrophyll; Gig, Gigantophyll.

Within the forest, epiphytes and herbaceous plants have various leaf sizes whereas most woody plant species have simple leaves that are mainly leathery. Leaves with drip tips are common, present on 62.4 % of all tree and shrub species (Qiu *et al.*, 1998, Appendix 3). Some trees, such as *Manglietia insignis*, *Lithocarpus chintungensis* and *Castanopsis wattii* have slight buttresses.

2.4.3 Species diversity

Based on data from eight 20 x 20 m plots, species diversity indices were calculated for natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR by Qiu *et al.*(1998), using Shannon-Wiener' index, $H' = -\Sigma p_i \ln p_i$; Simpson's index, $d' = 1 - \Sigma p_i^2$; Evenness index, $E = H' / \ln S$ (Magurran, 1988; Cao & Zhang, 1997), where p_i is the proportion of the number of individuals of the i-th species with N individuals of S species in total, i.e. $p_i = (N/N_i)$; N is the total number of individuals recorded in the sample; N_i is the number of the individuals of the i-th species in the sample, and, S is the number of species recorded in the sample. Results revealed significant differences in species richness among sites (Appendix 5), and between the different structural layers (Appendix 6). Generally, the stands estimated as mature, but still capable of good growth had lower values for species diversity than those of juvenile and over-mature stands growing in the same environmental conditions. Species richness decreased in the order of grass layer > shrub layer > tree layer B > tree layer A (Table 2.3). However, species diversity indices and evenness showed no such tendency, although differences between structural layers and between plots were also significant. Species diversity was greatest in the herb layer, while the shrub population had lowest species diversity with a high coefficient of variation due to the dense bamboo (*S. nitida*) layer. Evenness of the upper tree layer was highest, while that of the shrub layer was lowest.

Table 2.3. Diversity indices (mean ± SD) of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Layers	Total individuals	Total species	H'	d'	E
Tree A	20	8d	1.87±0.11c	0.82±0.03b	0.91±0.04a
Tree B	42	16c	2.45±0.31b	0.88±0.06a	0.89±0.08a
Shrub	601	18b	1.08±0.56d	0.39±0.22c	0.37±0.16c
Herb	1184	20a	2.93±0.45a	0.89±0.05a	0.80±0.10b

[a] H', d' and E are respectively Shannon-Wiener, Simpson index and evenness index. The data in the table are the means for eight 20 x 20 m2 plots. Same letters indicate samples which are not significantly different ($p<0.05$) within a column, using Fisher's LSD test.
Data are from Qiu *et al.* (1998). See Appendix 5 and 6 for more details.

Among tree diameter classes, the smallest (2.5-7.5 cm) class had highest species richness, and the largest (≥17.5 cm) had least. Diversity exhibited a similar tendency, decreasing from the smallest diameter class to the largest diameter classes (Table 2.4, Appendix 7). The coefficient of variation (37 %) of diversity of the largest diameter class (≥17.5 cm) was significantly higher than that of other diameter class.

Table 2.4. Diversity by diameter class of woody plants in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Diameter class (cm)	Total individuals	Total species	H'	d'	E
2.5-7.5	68	20	2.56±0.32a	0.91±0.03a	0.85±0.07b
7.6-12.5	45	17	2.52±0.33a	0.88±0.05ab	0.90±0.05a
12.6-17.5	34	13	2.27±0.33b	0.87±0.04b	0.91±0.07a
≥17.5	25	10	2.06±0.76c	0.78±0.30c	0.91±0.30a

[a] Legend as for Table 2.3. Some woody species occur in more than one diameter class in the plots.

Mean species diversity indices of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR are: Shannon-Wiener index 2.83; Simpson index 0.87; and, Evenness 0.71 for the eight plots (Qiu *et al.*, 1998 Appendix 5). Species diversity of the Ailao Mountain forest is close to that of tropical montane evergreen broad-leaved forest in Xishuangbanna, south Yunnan (Shannon-Wiener index 2.60, Simpson index 0.9; Cao & Zhang, 1997), and subtropical lowland montane evergreen broad-leaved forest in Dinghushan Biosphere Reserve, south China (Kong *et al.*, 1997, Shannon-Wiener index 2.54). The diversity of genera of the forest in Ailao Mountain is higher than that of evergreen broad-leaved forest in other areas of Yunnan province (Yunnan Forestry Investigation and Planning Institute, 1987).

2.4.4 Phenology

Phenological observations on fourteen species, revealed that the growth rhythm of the *Lithocarpus/Castanopsis* forest is similar to that of tropical forest (Qiu *et al.*, 1998). Plants flower and bear fruits almost all year, with the major flowering (70 % of the total species observed) and fruit bearing (75 %) periods between March-April. For *Lithocarpus xylocarpus, L. chintungensis, Castanopsis wattii* and *Schima noronhae*, flowering is in March-April and fruiting August-October of the next year. Although evergreen species have no obvious season of leaf fall, two peaks occur in April-May and October-November. Change of leaves on deciduous species occurs mainly in September-November (Fig. 2.10).

Most dominant species share phenological patterns that are characteristic of warm temperate floras (Qiu *et al.*, 1998). Three important patterns were observed: Firstly, warm temperate species are most common, with 82 % of the fourteen species observed. Species are *Lithocarpus xylocarpus, L. chintungensis, Castanopsis wattii, Machilus viridis, Manglietia insignis, Hartia sinensis, Skimmia arborescens, Styrax perkinsiae, Acer heptolobum, Populus bonatii* and *Lyonia ovalifolia*, with some herbs, epiphytes and ferns. These species tend to flower from March to June when air temperatures are rising. Secondly, a group of temperate species accounts for 12 %, including *Schima noronhae* and *Litsea elongata*, with some lianas and herbs. These species flower from July to September when air and soil temperatures start to fall. Thirdly, a smaller suite of cool temperate species (6 %), including *Illicium macranthum* and other species, such as *Camellia forrestii* and *Daphne cannabina*. These species flower from December to February at the coolest period of the year.

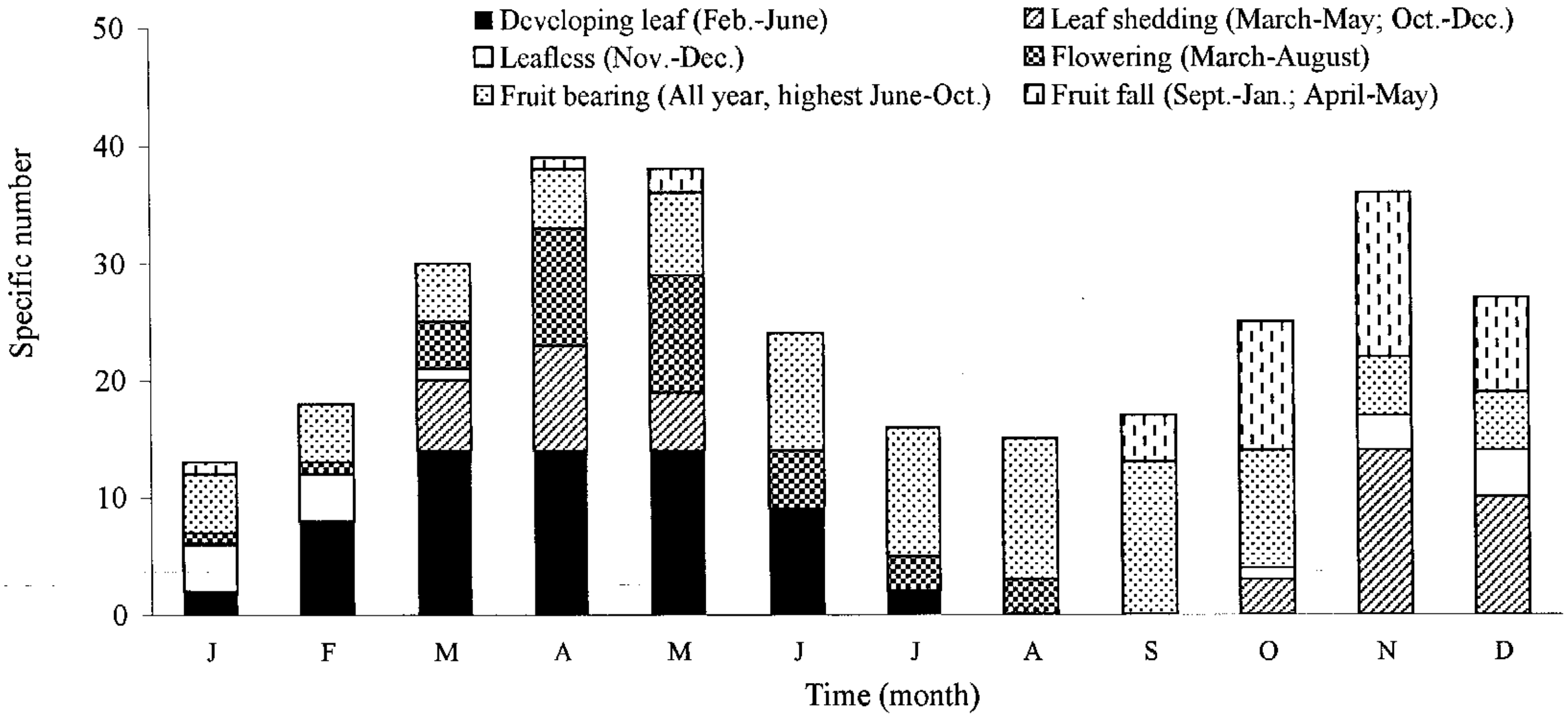

Fig. 2.10. The phenological spectrum of dominant tree species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR (Qiu *et al.* , 1998).

Environmental factors appear to affect the growth rhythm of this forest. Mean temperature and ≥ 5 °C accumulated temperature are considered to be the main meteorological factors that are most closely related to phenological performance of these trees (Xie, Sheng & Li, 1997). Light duration and temperature play important roles in the induction of flowering, and new leaf production is associated with precipitation and light.

2.4.5 Productivity

Studies on biomass estimates of the natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR were initially undertaken by Qiu *et al.* (1984). Their work was conducted in a 0.1 ha plot with high tree density at Xujiaba. All trees with DBH ≥10.0 cm in the plot (Σ = 108) were enumerated and measured for stem diameter at breast height and tree height in April-May 1982. DBH range of trees in the plot was divided into six classes (<10.0 cm, 10.1-20.0 cm, 20.1-30.0 cm, 30.1-40.0 cm, 40.1-50.0 cm and >50.0 cm), and 2-3 sample trees from each class for each species were felled. Fresh weight of all tree components (leaves, branches and stems) were determined in the field, and samples of each component were collected for dry weight. Tree roots were obtained from cores. Shrubs and herbs were sampled from quadrats. Least squares regression analysis, on the basis of the sample tree data was used to develop allometric equations of dry weight (w) on diameter at breast height (D) and tree height (H) as $W = a(D^2 H)^b$ (a and b are coefficients). Formulae were established for six dominant tree species: *Lithocarpus xylocarpus, Castanopsis wattii, L. chintungensis, Machilus viridis, Manglietia insignis* and *Schima noronhae* (Table 2.5). In Chapter 3, I will use these formulae to estimate biomass of these dominant trees.

According to Qiu *et al.* (1984), there were apparent differences in biomass distribution among species (Table 2.6). Stand biomass was dominated by five tree species (*Lithocarpus xylocarpus, Machilus viridis, Castanopsis wattii, Schima noronhae* and *Manglietia insignis*) whose estimated aboveground biomass exceeded 10 t ha^{-1}, indicating their importance in the community. The forest was estimated to contain 499.8 t ha^{-1}, with the tree layer contributing 98.3 % of total biomass (Table 2.7.).

Table 2.5. Regression equations between biomass (ton) of different organs and D (cm), H (m) of dominant trees in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Dominant Species	Leaf	Branch	Stem	Samples number
Lithocarpus xylocarpus	$W = 0.0072\ (D^2H)^{0.6893}$ $R^2 = 0.8606$	$W = 0.0053\ (D^2H)^{0.9112}$ $R^2 = 0.9197$	$W = 0.0347\ (D^2H)^{0.9740}$ $R^2 = 0.9944$	12
Castanopsis wattii	$W = 0.1533\ (D^2H)^{0.2948}$ $R^2 = 0.7616$	$W = 0.0364\ (D^2H)^{0.6530}$ $R^2 = 0.9686$	$W = 0.0177\ (D^2H)^{1.0168}$ $R^2 = 0.9962$	12
L. chintungensis	$W = 0.0045\ (D^2H)^{0.3893}$ $R^2 = 0.7856$	$W = 0.0032\ (D^2H)^{0.5435}$ $R^2 = 0.8212$	$W = 0.0226\ (D^2H)^{0.6193}$ $R^2 = 0.8765$	12
Schima norohae	$W = 0.0204\ (D^2H)^{0.3310}$ $R^2 = 0.9428$	$W = 0.2093\ (D^2H)^{0.4741}$ $R^2 = 0.5635$	$W = 0.3595\ (D^2H)^{0.3471}$ $R^2 = 0.9845$	10
Machilus viridis	$W = 0.0601\ (D^2H)^{0.4320}$ $R^2 = 0.7564$	$W = 0.0285\ (D^2H)^{0.6756}$ $R^2 = 0.9333$	$W = 0.0283\ (D^2H)^{0.9560}$ $R^2 = 0.7494$	9
Manglietia insignis	$W = 0.0225\ (D^2H)^{0.6260}$ $R^2 = 0.9952$	$W = 0.0072\ (D^2H)^{0.9219}$ $R^2 = 0.9948$	$W = 0.5029\ (D^2H)^{0.5682}$ $R^2 = 0.9245$	9

[a] These formula are from Qiu *et al.*(1984).

Table 2.6. Estimated biomass (t ha^{-1}) of above-ground parts for tree species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Tree species	Stem	Branch	Leaf	Total
Lithocarpus xylocarpus	90.63	15.34	1.47	107.44
Machilus viridis	82.91	6.97	0.79	90.67
Castanopsis wattii	78.53	5.46	0.58	84.57
Schima noronhae	17.81	4.76	0.26	22.83
Manglietia insignis	13.85	3.32	0.64	17.81
Hartia sinensis	8.49	1.14	0.16	9.79
Acer heptalobum	5.78	0.58	0.05	6.41
Meliosma kirkii	2.79	0.35	0.03	3.17
Symplocos stapfiana	1.60	0.27	0.03	1.90
Eurya obliquifolia	1.34	0.31	0.11	1.75
L. chintungensis	0.94	0.19	0.03	1.16
Camellia forrestii	0.53	0.11	0.03	0.67
Cyclobalanopsis stewardiana var. *longicaudata*	0.32	0.22	0.06	0.60
Ilex corallina var. *aberrans*	0.41	0.04	0.01	0.46
Litsea coreana var. *lanuginosa*	0.15	0.01	0.005	0.017
Other species	1.26	0.70	0.10	2.06

[a] These data are from Qiu *et al.*(1984).

Table 2.7. Estimated biomass of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Components	Biomass ($t\ ha^{-1}$)				
	Leaf	Branch	Stem	Root	Total
Tree layer	4.35	32.62	307.34	146.84	491.15
Shrub layer	0.82	0.55	4.98	1.12	7.47
Herb layer	0.33	0.10	0.23	0.48	1.14
Total	5.50	33.27	312.55	148.44	499.76

[a] These data are from Qiu *et al.*(1984).

Subsequently, a preliminary approach to net productivity of the forest was made by Xie *et al.* (1996) using the mean growth yield method (Whittaker & Marks, 1975). Firstly, mean age of each tree was estimated using the regression of tree age and diameter at breast height, developed previously by Xie *et al.* (1983; Appendix 8). The mean annual net accumulation of the woody component of the tree layer was determined as the cumulative quotients of biomass of each species to mean age of that species in the plot. Mean annual accumulation of foliage was determined as the sum of one-year old leaves of evergreen species and all leaves of deciduous species. For shrub (mainly bamboo) and herb (mainly fern) layers, the biomass of current tissues was roughly estimated as net mean annual accumulation. Estimated mean annual accumulation of the forest is summarized in Table 2.8. Although the estimated mean annual net accumulation of evergreen broad-leaved forest may be rough or even inadequate in methodology, it represents a first attempt to study net productivity of the forest. It is difficult to obtain such data in a remote region at high altitude. In Chapter 7, I will use the mean annual net accumulation of different components and mean nutrient concentration of each component to determine retention of nutrients in the forest.

Table 2.8. The mean annual net accumulation in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Layer	Mean net accumulation ($kg\ ha^{-1}\ yr^{-1}$)				
	Leaf	Branch	Stem	Root	Total
Tree	1670	1542	3493	1980	8685
Shrub	180	123	323	190	816
Herb	182	-	-	251	433
Total	2032	1665	3816	2421	9934

[a] These data are from Xie *et al.* (1996).

2.4.6 Management and conservation of evergreen broad-leaved forest in Yunnan

Some 94 % of the total land area of Yunnan Province is mountainous. Yunnan is China's second most forested area after the northeast (Hsiung & Johnson, 1981; Wu, 1980; Young & Wang, 1989). The complex geography and climatic conditions have given rise to varied vegetation from tropical rain forests in the south to temperate forests in the north (Li & Walker, 1986). Different forest ecosystems span tropical, subtropical and temperate vegetation zones (Wu, 1987). Yunnan has more than 50 % of China's plants and over 55 % of the total animal species.

In earlier times a dense broad-leaved forest shrouded the majority of Yunnan. In the early 1950s, forests still covered some 55 % of the total area of the province. Over the past few decades, increased population, road construction and development of new markets have led to destruction of much of the valuable natural forest in Yunnan. This has resulted in many barren, eroded areas along with increased cultivated land, shelter-belts and plantations. By 1975, forest cover had fallen to 30 % and continues to decline (Smil, 1983). Deforestation in Yunnan has led to ecological problems in both sustaining agricultural development, and potential loss of species diversity. Since the 1980s, a series of forestry policies and conservation measures has been promulgated and a number of natural reserves or parks has been established (Yunnan Forestry Investigation and Planning Institute, 1987; Bureau of Environment Conservation of Yunnan, 1997). By 1997, six national natural reserves, 49 state natural reserves and 56 local preserves or reserves had been established in Yunnan Province, the highest number in China. Together they occupy nearly 19,932 km^2, comprising some 5.06 % of the total land area of Yunnan Province (Bureau of Environment Conservation of Yunnan, 1997). Evergreen broad-leaved forest is the main vegetation in these reserves.

Ailao Mountain NNR is one of the important natural reserves in southwest China. It lies at the border between China's two principal monsoon systems (southwestern and southeastern), and between northern and southern subtropical vegetation types of Yunnan (Young & Wang, 1989; Qiu *et al.*, 1998). The flora in this area is a subtle combination of tropical and temperate elements with high diversity, and some dominant species are unique to Yunnan (Qiu *et al.*, 1998). The forest provides various habitats for wildlife, allowing different species to coexist.

Some 87 % of the population of Yunnan lives in mountainous areas (Liang, 1983). The relationship between protection and use of forest resources is one of the most important problems in the management of Ailao Mountain NNR. Traditionally, people living near the reserve have taken their requirements from forest areas. Such people usually have relatively low incomes. Therefore any conservation program must consider human needs. A number of cases of successful sustainable uses of natural forest ecosystems have been documented (e.g. Boom, 1985; Yim, 1997). Primary forests must be effectively protected and monitored whereas there is a better case for the more common forest types to be utilized. Ailao Mountain old growth forest of *Lithocarpus/Castanopsis* has greater species diversity than that of the associated secondary pine forests (Young & Wang, 1989). In order to satisfy local needs and relieve pressure on primary forests, denuded areas on the edge of Ailao Mountain NNR could be used for plantations of economic species (such as pine or fruit trees). On the other hand, a conservation education program is also needed to inform local people about the importance and benefits of intact forests and thus encourage them to maintain the forest cover.

A well-developed bamboo understory influences the forest floor micro-environment in ways that lead to the reduction of tree-seedling species emergence and establishment. Similar inhibition of establishment of canopy tree seedlings, by understory cover (bamboo, fern, rhododendron) has been found in other forests (Nakashizuka, 1987; Clinton, Boring & Swank, 1994; Taylor, Qin & Lin, 1995; George & Bazzaz, 1999a, b). A dense shrub/herb stratum in forest provides habitat and shelter for both seed and seedling predators, which lead to reduced seedling densities (Wada, 1993). Controlled harvesting of bamboo by local people could improve microenvironment, density, species composition and spatial distribution of the seed bank.

Dominant species or functional groups may dictate nutrient uptake in more diverse communities, and disproportionately affect available nutrient pools and nutrient cycling in the ecosystem (Tilman, 1988; Hooper and Vitousek, 1998). Floristic analysis has revealed a high proportion of canopy tree species to be of the

Fagaceae, Lauraceae, Magnoliaceae, Theaceae and Araliaceae, although the forest has multi-dominant species. Species with highest importance values are *Castanopsis wattii* (Fagaceae), *Lithocarpus xylocarpus* (Fagaceae*),* *Schima noronhae* (Theaceae), *L. chintungensis* (Fagaceae), *Manglietia insignis* (Magnoliaceae) and *Machilus viridis* (Lauraceae). The 3 dominant Fagaceae (*Castanopsis wattii, Lithocarpus xylocarpus* and *L. chintungensis)* comprise more than 55 % of canopy tree basal area. In the shrub and herb layers, well developed bamboo (*Sinarundinaria nitida*) and ferns (especially *Plagiogyria communis*) are common. I have selected these dominant species as representative species for studying the pattern of nutrient accumulation and cycling in this forest (Chapters 3, 5 and 6).

Chapter 3. Biomass and Nutrient Accumulation in Natural *Lithocarpus/Castanopsis* Forest at Xujiaba, Ailao Mountain NNR

3.1 Introduction

A knowledge of the accumulation of biomass and distribution of nutrients among plant components is important for understanding nutrient fluxes and cycling as well as other ecosystem processes (Likens *et al.*, 1977; Pearson, Knight & Fahey, 1987; Archibold, 1995). Moreover, an understanding of nutrient cycling in forest ecosystems is critical for continued long-term forest use and management (Turner, Cole & Gessel, 1976). Within a natural forest ecosystem biomass consists of both living and dead materials (Pearson *et al.*,1987). Dead wood is an important biomass component of natural forest ecosystems (Harmon *et al.*, 1986; Pearson *et al.*, 1987). The patterns of biomass accumulation and nutrient cycling are strongly dependent on stand successional status as well as climate and soils (Schlesinger, 1978; Vitousek, 1982; Sprugel, 1984; Vitousek & Sanford, 1986; Pearson *et al.*, 1987; Archibold, 1995). Stand-level disturbance has been shown to be an important factor affecting biomass and nutrient cycling (Garwood, Janos & Brokaw, 1979; Sanford *et al.*, 1985; Vitousek & Sanford, 1986). The pattern of nutrient cycling and nutrient use efficiency of plants differs in forests on different soils (Vitousek, 1982; Waring & Schlesinger, 1985; Vitousek & Sanford, 1986). On the other hand, nutrient availability affects composition of plant communities. It is widely recognized that community biomass is controlled by N and P (DiTomasso & Aarsen, 1989; Morris, 1991; Vitousek & Howarth, 1991; Koerselman & Verhoeven, 1995). The N:P ratios in forest vegetation may serve as indicators of the nature of nutrient limitation in a community (Koerselman & Meuleman, 1996).

In light of the particular environment and floristic composition of the natural *Lithocarpus /Castanopsis* forest in Ailao Mountain, it was hypothesized that stand dynamics would differ from other forests and that nutrient patterns could also be unique. Moreover, within the natural forest, different successional stages occur with stands of differing density, basal area and age structure within the ecosystem as a whole (You, 1983; Young *et al.*, 1992; Young & Herwitz, 1995; Qiu *et al.*, 1998). These may result in differences in distribution and cycling of nutrients among sites (Schlesinger, 1978; Gorham, Vitousek & Reiners, 1979; Bormann & Likens, 1979; Sprugel, 1984; Pearson *et al.*, 1987). Therefore, it was also hypothesized that different canopy characteristics might affect patterns of biomass and nutrient accumulation. In addition, the Ailao Mountains occur in the transition area between the southern and the northern subtropical vegetation types (Jin, 1983; Wu, 1987; Young & Wang, 1989; Qiu *et al*, 1998). Although considerable information is available on biomass and nutrient dynamics of both conifer and hardwood forest ecosystems and plantations in temperate and tropical climate zones (Rodin & Bazilevich, 1967; Vitousek & Sanford, 1986), biomass and nutrient cycling has not been previously examined in the montane evergreen broad-leaved forest, especially in this transition zone where tropical, temperate and endemic species occur together in an environment of high rainfall and humidity at high elevations (Wu, 1987; Young *et al.*, 1992; Qiu *et al.*, 1998).

The objectives of the study were twofold: first, to quantify litter, dead wood and living plant biomass and associated nutrient contents of the dominant forest type (*Lithocarpus/Castanopsis* association), and second, to compare biomass accumulation and nutrient cycling with other forest types elsewhere. It was anticipated that information generated would be useful for future management of Ailao Mountain NNR.

3.2 Materials and methods

3.2.1 Study site

This study was conducted in natural *Lithocarpus/Castanopsis* forest, near Xujiaba FERS in April to May 1994. The climate, species composition and soil of this area are described in Chapter 2.

The forest described is a special area and one that will require considerable vigilance in future to maintain in the natural state. Patches of really old trees are not common over large areas and these are especially worthy of preservation while a complete account of their ecology is being assembled. The China National Nature Reserve system includes strict rules and regulations as to how much destructive sampling of residual remnant natural vegetation is appropriate in the light of the national scientific body setting good examples for nature conservation for the village peoples of the area. Many studies examine species associations elsewhere in non-destructive ways.

Within the natural forest, the relative density and dominance of the main species vary among sites. To sample forest biomass, two typical stands of different density and apparent age structure were selected. Because it is hard to measure the age of trees, diameter at breast height (stems < 10 cm DBH were not included) was used to represent the age. One stand was considered to be younger. It had relatively high density and corresponding lower mean tree diameter. The second stand was presumed older, with relatively low density and relatively high mean diameter (Table 3.1). Subsequently, I use "plot" and "stand" interchangeably to describe these two plots.

Table 3.1. The structure and composition of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Plot No.	Density [a] (No. ha^{-1})	DBH (cm)		Mean tree height (m)	Basal area (m^2 ha^{-1})	Trees cover (%)	Shrubs cover (%)	Herbs cover (%)	Standing dead trees (No. ha^{-1})	Fallen dead trees (No. ha^{-1})
		Mean	Max.							
Plot 1	1100	37.0	68	24.1	58.4	95	40	20	100	10
Plot 2	510	45.5	150	25.0	29.8	80	70	30	10	20

[a] Including all ≥ 10.0 cm DBH living trees, bamboo excluded.

3.2.2 Biomass of living plants

All trees in both plots were enumerated in 1994 and measured for stem diameter at breast height (DBH) and tree height. Biomass of six dominant tree species *Lithocarpus xylocarpus, Castanopsis wattii, L. chintungensis, Machilus viridis, Manglietia insignis* and *Schima noronhae* was estimated using allometric equations

(Qiu *et al.*, 1984; Table 2.5). These formulae are of the form $W = a(D^2H)^b$, where W = biomass (in tonnes either for leaves, branches or stems) of a species; a and b are constants; D = DBH (cm); and H = tree height (m). For example, leaf biomass of *L. xylocarpus* is derived from $W = 0.0072\ (D^2H)^{0.6893}$ ($r^2 = 0.8606$, n = 12).

For subordinate layer trees, of which there were 14 species (plot 1+ plot 2), sample trees were harvested by felling (Whittaker & Marks, 1975). Most subordinate trees were less than 20 cm DBH. A total of 33 trees from a total of 44 in both plots was harvested. For root biomass, twenty vertical columns of 50 x 50 cm (0.25 m^2) were excavated to 1.5 m depth. These were taken every 2 m along a transect through the center of each plot. All roots were removed from each cylinder to provide fresh weight. Due to difficulty in distinguishing roots of each tree species, root weight was estimated as total underground biomass of trees.

In each plot, five random 2 x 2 m subplots were used to sample above- and below-ground biomass of shrubs. Subplots were clipped and materials weighed fresh. Bamboo dominated the shrub layer. There were apparent differences in morphological characters between current and perennial bamboo individuals (current individuals have no leaves or twigs). The two components were separately measured. Herb biomass was harvested from ten 1 x 1 m random quadrats in each plot. Samples of components from trees, shrubs and herbs were oven-dried at 80 °C to constant weight. Fresh weights were converted to dry weight using the respective fresh weight-dry weight ratios.

3.2.3 The standing crop of dead wood and litter on the forest floor

The standing crop of dead wood, including dead trees (≥ 5 cm), fallen dead trees and large branches (> 2.5 cm) was measured in April to May 1994. Two 50 m transect lines were used in each plot in a diagonal pattern. Five 2 x 2 m quadrats were established at 10 m intervals along each transect line. The fallen dead wood was collected and weighed fresh in four diameter classes: 2.5-5.0 cm; 5.1-10.0 cm; 10.1-30.0 cm; and >30.0 cm. For large pieces of dead wood too heavy to remove, a chain saw was used to take subsamples and materials were weighed on a steelyard in the field.

All ≥ 5.0 cm dead standing trees (snags) in each stand were respectively recorded and measured by species, DBH and height. The volume of dead standing trees was computed using the formula for a cone: $\pi r^2 ht/3$. Different decay classes (sound, moderate and decayed) of standing dead trees were sampled to determine mean density value for each species (e. g. dead wood density ranged from 0.61-0.68 g cm^{-3} for *Lithocarpus xylocarpus*; 0.48-0.52 g cm^{-3} for *Castanopsis wattii*). Biomass of standing dead trees was calculated as the sum of the product of mean density and volume of each dead tree. On each plot, litter on the forest floor was determined using ten 50 x 50 cm quadrats randomly positioned. Litter collections will be described in Chapter 4.

Samples of each component of dead wood and litter were taken to determine dry weight at 80 °C constant weight. The standing crop of dead wood (t ha^{-1}) was estimated on the basis of the sum of moist content multiplied by fresh weight. Samples of dry weight for each component were used for chemical analysis.

3.2.4 Chemical analysis

The six dominant tree species mentioned above (*Lithocarpus xylocarpus, Castanopsis wattii, L. chintungensis, Machilus viridis, Manglietia insignis* and *Schima noronhae*), bamboo (*Sinarundinaria nitida*) and an evergreen fern (*Plagiogyria communis*) were selected to determine nutrient concentrations of living plants in the forest. Three samples of each tissue for each species were taken from samples collected from different size class individuals of both stands. Fractions of dead material used in chemical analysis were taken from mixed dead wood and litter on the forest floor, respectively.

All samples were dried as above, and ground to pass through a 20 mm mesh screen. Total N was determined by the micro-Kjeldahl method after digesting 0.5 g subsamples in $K_2Cr_2O_7$-H_2SO_4 (Institute of Soil Academia Sinica, 1978). Samples for P, K, Ca, Mg, Mn, Al and Fe were wet digested in a mixture of HNO_3, H_2SO_4 and

$HClO_4$ solution. Concentration of P was obtained colorimetrically by the chloro-molybdophosphoric blue colour method (Institute of Soil Academia Sinica, 1978), and concentrations of K, Ca, Mg, Mn, Al and Fe were obtained by atomic absorption spectrophotometer (AAS-932, GBC Scientific Equipment Pty. Ltd. Australia).

Elemental contents (kg ha^{-1}) of each tissue for each dominant species were calculated as biomass and nutrient concentration in each tissue. For other trees, elemental content of each tissue was calculated as the product of mean tissue nutrient concentration of the six dominant tree species and biomass of that tissue. The amounts of nutrient (kg ha^{-1}) in each component for dead wood, litterfall and litter on the forest floor were respectively calculated by multiplying the nutrient concentration in each component by the dry weights of each component.

3.2.5 Statistical analysis

Standard deviations of different component biomasses between both stands were calculated, with the exception of above ground biomass of trees, which were census values. Nutrient concentrations of different organs of dominant species were statistically analyzed using one way analysis of variance followed by Fisher's LSD (least significant difference) test at $p<0.05$ to detect whether significant differences occurred between means of these species. All statistical analyses were performed using StatView^{TM}(Abacus Concepts, Inc., 1986).

3.3 Results

3.3.1 Biomass of living plants

The biomass of living plants differed considerably between sites (Table 3.2). Standing biomass was 503.1 t ha^{-1} in Plot 1, and 285.1 t ha^{-1} in Plot 2, with tree layer biomass accounting for 98.3 % and 85.3 % of the totals, respectively. The biomass ratio of stem-wood to branch-wood was 10:1 in the former and 14:1 in the latter.

Similarly, the ratio of stem-wood to leaf biomass was 43.4:1 and 29.7:1, respectively.

The contributions of dominant tree species to total biomass also differed. The six dominant tree species (*Lithocarpus xylocarpus, Castanopsis wattii, L. chintungensis, Machilus viridis, Manglietia insignis* and *Schima noronhae*) comprised 91.3 % of the aboveground biomass in Plot 1 and 70.1 % in Plot 2. The two large tree species *Lithocarpus xylocarpus* and *Castanopsis wattii* contributed >50 % of the aboveground biomass, despite their overall density being < 35 % of the total in both stands (Table 3.3). However, Plot 1 had 30 % biomass in *Lithocarpus xylocarpus* (+ 24 % in *Castanopsis wattii*); whereas Plot 2 had 44 % biomass in *Castanopsis wattii* (+ 12 % in *Lithocarpus xylocarpus*). The proportion of *Machilus viridis* was higher in Plot 1 whereas *L. chintungensis* was higher in Plot 2.

Table 3.2. Biomass composition and its distribution among living plants in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Aialo Mountain NNR.

	Plot 1		Plot 2	
Components	Biomass (t ha^{-1})	%	Biomass (t ha^{-1})	%
Tree layer				
Leaf	7.08	1.41	5.46	1.92
Branch	30.74	6.11	11.77	4.13
Stem	307.34	61.08	162.24	56.91
Total aboveground	345.16	68.60	179.47	62.95
Root	149.45 (28.47)	29.70	63.73 (16.65)	22.36
Total	494.61	98.31	243.20	85.31
Shrub layer				
Leaf	0.79 (0.33)	0.16	1.83 (0.44)	0.64
Branch	0.55 (0.20)	0.11	5.09 (1.30)	1.79
Stem	4.98 (1.75)	0.99	22.32 (5.10)	7.83
Root	1.07 (0.28)	0.21	9.11 (2.58)	3.20
Total	7.39	1.47	38.35	13.45
Herb layer				
Aboveground part	0.66 (0.21)	0.13	1.19 (0.38)	0.42
Underground part	0.48 (0.19)	0.10	2.34 (0.51)	0.82
Total	1.14	0.23	3.53	1.24
Sum	503.14	100	285.08	100

Note: values in parentheses are standard deviations (SD). Data for aboveground biomass of tree layer are census values.

Table 3.3. Density and aboveground biomass of dominant tree species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Species	Plot 1				Plot 2			
	Density		Biomass		Density		Biomass	
	No. ha^{-1}	%	t ha^{-1}	%	No. ha^{-1}	%	t ha^{-1}	%
Lithocarpus xylocarpus	140	16.3	104.24	30.20	16	5.6	21.58	12.02
Castanopsis wattii	140	16.3	82.39	23.86	72	25.4	79.38	44.51
L. chintungensis	20	2.3	1.17	0.34	16	5.6	10.38	5.78
Machilus viridis	200	23.3	87.48	25.34	28	9.9	2.75	1.53
Manglietia insignis	100	11.6	17.72	5.13	24	8.5	5.70	3.23
Schima noronhae	200	23.3	22.08	6.4	12	4.2	6.83	3.80
Other [a]	60 (6 spp.)	7.0	30.13	8.73	116 (8 spp.)	40.8	52.30	29.13
Total	850	100	345.21	100	284	100	179.5	100

[a] 6 'other' tree species in plot 1, 8 in plot 2.

Differences were considerable between the two stands in biomass distribution of shrub and herb layers. The biomass of these layers contributed only 1.7 % of the total living plant biomass in Plot 1, but 14.7 % in Plot 2, where relatively low tree density and correspondingly higher light level allowed more understory development. Bamboo (*Sinarundinaria nitida*) contributed 99.2 % of the shrub biomass in Plot 1 and 94.6 % in Plot 2. The amount of bamboo due to current individuals was 0.24 t ha^{-1} in Plot 1 and 1.39 t ha^{-1} in Plot 2. The two plots had similar proportions (3.2-3.6 %) of current individuals contributing to total bamboo biomass. Ferns, dominated by *Plagiogyria communis*, comprised 60 % of herb biomass in Plot 1 and 67 % in Plot 2.

3.3.2 Biomass of dead materials

Density of standing dead trees was greater in Plot 1, whereas there were more fallen dead trees in Plot 2 (Table 3.1). The standing crop of dead wood in Plot 1 was about half of that in Plot 2. Fallen dead wood was the main component of dead wood, comprising 78 % in Plot 1 of the total dead wood biomass and 86 % in Plot 2. The ratio of dead wood biomass to total living trees was 0.09 in Plot 1, and 0.40 in

Plot 2 (Tables 3.2, 3.4). Litter on the forest floor mainly constitutes newly fallen leaves and fragmented litter. There was no apparent difference in litter on forest floor between the two stands. The relative contribution of partially and more decomposed litter to the total forest floor was greater than that of fresh litter all the year round.

Table 3.4. Estimated biomass of dead materials in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Components	Plot 1		Plot 2	
	Biomass ($t\ ha^{-1}$)	%	Biomass ($t\ ha^{-1}$)	%
Standing dead trees	5.65	10.00	8.83	7.93
Fallen dead trees	36.03 (7.76)	63.86	84.45 (11.30)	75.87
Dead branches	4.49 (1.24)	7.96	5.18 (1.56)	4.65
Litter mass	10.25 (1.30)	18.17	12.86 (1.88)	11.55
Total	56.42	100	111.31	100

Note: values in parentheses are SD. Data for biomasses of standing dead trees are census values.

3.3.3. Nutrient concentration in living plants

Nutrient concentrations as percent of dry weights are summarized for six canopy species, bamboo understory and the fern *Plagiogyria communis* (Table 3.5). Nutrient concentration varied significantly ($p<0.05$) among species and organs. Carbon percent was least in leaves and greatest in stems (Table 3.6). Within dominant tree species, *Manglietia insignis* stems had the highest carbon. Apart from carbon, the general trend for nutrient element concentration among components was highest for concentrations in leaf, then branch followed by root and stem. More mobile nutrients (N, K) tend to be highest in concentration in leaves (more active organs/parts), whereas higher concentrations of the less mobile elements (P, Ca) occur in older organs. N in leaves ranged from 1.04-1.44 %. *Lithocarpus chintungensis* leaf had the highest N concentration, followed by *Castanopsis wattii, Machilus viridis* and *L. xylocarpus*. N concentration in branches was less than half that in leaves. K in leaves

Table 3.5. Nutrient concentration in dominant species in natural *Lithocarpus /Castanopsis* forest at Xujiab, Aialo Mountain NNR. Values are mean, n=3 with SD in parentheses.

Species	Organs	Nutrient concentration (% of dry weight)								
		C	N	P	K	Ca	Mg	Mn	Al	Fe
Tree species										
Lithocarpus xylocarpus	Leaf	41.161bc (0.93)	1.420a (0.132)	0.095b (0.017)	0.592c (0.110)	0.550b (0.032)	0.162c (0.035)	0.041de (0.005)	0.065b (0.013)	0.018a (0.001)
	Branch	49.869a (0.83)	0.47a (0.165)	0.054bc (0.015)	0.548a (0.157)	0.620b (0.047)	0.172bc (0.044)	0.013de (0.005)	0.055b (0.010)	0.016b (0.003)
	Stem	50.830bc (1.99)	0.139c (0.022)	0.008c (0.003)	0.110d (0.016)	0.349b (0.096)	0.019c (0.012)	0.008d (0.001)	0.031b (0.005)	0.006d (0.004)
	Root	48.362b (1.08)	0.428ab (0.083)	0.068a (0.01)	0.251c (0.090)	0.242d (0.078)	0.150b (0.009)	0.006c (0.001)	0.139cd (0.023)	0.110c (0.008)
Lithocarpus chintungensis	Leaf	43.310a (1.02)	1.440a (0.062)	0.121a (0.006)	0.858b (0.106)	0.550b (0.020)	0.182c (0.021)	0.038e (0.009)	0.055b (0.005)	0.012c (0.003)
	Branch	48.261b (0.90)	0.486a (0.082)	0.089a (0.005)	0.520a (0.137)	0.604bc (0.016)	0.179b (0.015)	0.011e (0.001)	0.056b (0.004)	0.011d (0.001)
	Stem	52.111bc (1.25)	0.201b (0.016)	0.018a (0.004)	0.220b (0.005)	0.560a (0.045)	0.025bc (0.007)	0.009c (0.001)	0.039a (0.004)	0.018a (0.002)
	Root	48.318b (0.98)	0.360bc (0.038)	0.054c (0.004)	0.199c (0.021)	0.558b (0.036)	0.074d (0.025)	0.015bc (0.006)	0.169c (0.015)	0.278a (0.012)
Castanopsis wattii	Leaf	40.381c (0.87)	1.433a (0.135)	0.115a (0.017)	0.430d (0.112)	0.709a (0.139)	0.491a (0.028)	0.045cd (0.006)	0.086a (0.019)	0.013c (0.002)
	Branch	44.330c (2.11)	0.452ab (0.036)	0.058bc (0.004)	0.340b (0.043)	0.806a (0.061)	0.161cd (0.058)	0.018d (0.005)	0.069a (0.002)	0.013c (0.002)
	Stem	46.230d (1.22)	0.231a (0.023)	0.010b (0.002)	0.288a (0.021)	0.121d (0.013)	0.036a (0.003)	0.008d (0.002)	0.018d (0.004)	0.011c (0.002)
	Root	45.005c (1.18)	0.468a (0.042)	0.055c (0.007)	0.302bc (0.086)	0.728a (0.121)	0.087d (0.006)	0.102a (0.008)	0.006e (0.001)	0.011c (0.003)
Machilus viridis	Leaf	41.051bc (2.38)	1.274ab (0.290)	0.082b (0.010)	0.591c (0.077)	0.490bc (0.064)	0.348b (0.049)	0.049c (0.006)	0.084a (0.009)	0.014c (0.005)
	Branch	49.227ab (0.53)	0.352bc (0.110)	0.048bc (0.017)	0.318b (0.068)	0.605bc (0.136)	0.232a (0.041)	0.028c (0.009)	0.044c (0.011)	0.013c (0.003)
	Stem	50.640c (1.32)	0.229a (0.015)	0.008c (0.002)	0.130c (0.012)	0.489a (0.085)	0.026bc (0.002)	0.008cd (0.002)	0.026c (0.006)	0.007d (0.001)
	Root	49.851a (1.09)	0.419ab (0.048)	0.051c (0.011)	0.411ab (0.049)	0.492bc (0.010)	0.096cd (0.035)	0.009a (0.001)	0.102d (0.004)	0.110c (0.009)
Manglietia insignis	Leaf	41.842abc (1.02)	1.122bc (0.116)	0.084b (0.020)	0.889b (0.122)	0.450c (0.039)	0.363b (0.092)	0.065b (0.008)	0.082a (0.009)	0.017ab (0.002)
	Branch	49.906a (1.36)	0.544a (0.058)	0.043c (0.020)	0.320b (0.057)	0.582bc (0.049)	0.133d (0.050)	0.037b (0.002)	0.041c (0.004)	0.011d (0.001)
	Stem	52.250a (1.30)	0.128c (0.025)	0.011b (0.004)	0.088e (0.008)	0.201bc (0.012)	0.028ab (0.003)	0.023b (0.005)	0.021cd (0.006)	0.014b (0.003)
	Root	45.069c (1.10)	0.421ab (0.047)	0.048c (0.008)	0.462a (0.102)	0.220d (0.031)	0.191a (0.010)	0.016bc (0.002)	0.362a (0.031)	0.270a (0.022)
Schima noronhae	Leaf	42.505ab (2.38)	1.038c (0.015)	0.086b (0.013)	1.019a (0.153)	0.493bc (0.032)	0.331b (0.012)	0.072a (0.008)	0.110c (0.010)	0.015bc (0.001)
	Branch	50.166a (0.95)	0.308c (0.019)	0.065b (0.017)	0.592a (0.104)	0.533c (0.026)	0.137cd (0.009)	0.051a (0.005)	0.058b (0.005)	0.018a (0.001)
	Stem	51.671ab (1.32)	0.150d (0.012)	0.009bc (0.002)	0.111d (0.015)	0.129cd (0.011)	0.023bc (0.002)	0.038a (0.005)	0.007e (0.001)	0.006d (0.001)
	Root	50.928a (1.18)	0.289c (0.015)	0.065b (0.008)	0.530a (0.112)	0.428c (0.035)	0.131bc (0.012)	0.018b (0.009)	0.307b (0.020)	0.152b (0.003)
Understorey species										
Sinarundinaria nitida	Leaf	36.512 (0.98)	2.138 (0.062)	0.089 (0.008)	0.932 (0.120)	0.220 (0.031)	0.081 (0.010)	0.034 (0.002)	0.025 (0.001)	0.023 (0.002)
	Branch	43.710 (2.11)	0.757 (0.048)	0.061 (0.007)	0.649 (0.115)	0.191 (0.022)	0.048 (0.003)	0.033 (0.005)	0.059 (0.002)	0.046 (0.003)
	Stem	47.429 (1.16)	0.281 (0.016)	0.022 (0.008)	0.690 (0.059)	0.122 (0.018)	0.028 (0.003)	0.065 (0.005)	0.033 (0.002)	0.023 (0.002)
	Root	45.730 (1.83)	0.388 (0.026)	0.033 (0.007)	0.711 (0.103)	0.106 (0.016)	0.045 (0.005)	0.038 (0.002)	0.389 (0.018)	0.211 (0.012)
Plagiogyria communis	Above-ground	40.448 (0.95)	1.733 (0.152)	0.053 (0.008)	0.303 (0.112)	0.221 (0.032)	0.190 (0.003)	0.074 (0.013)	0.091 (0.008)	0.019 (0.005)
	Under-ground	40.931 (1.02)	1.029 (0.121)	0.110 (0.010)	0.529 (0.115)	0.131 (0.022)	0.272 (0.018)	0.021 (0.004)	0.309 (0.023)	0.130 (0.012)

Note: In each organ, values with same letters in a column, across tree species, are not significantly different ($p<0.05$), using Fisher's LSD test.

varied from 0.25-1.02 %. *Schima noronhae* leaf had the highest K concentration among the sampled tree species. Range of Ca concentration in leaves was 0.45-0.71 %. *Castanopsis wattii* had the highest leaf Ca concentration. P and Mg concentrations in leaves and branches were higher than in stem and roots. Concentrations of Al and Fe in roots of all species were greater than in above-ground parts.

Most elemental concentrations in *Sinarundinaria nitida* (except stem, with highest carbon concentration) decreased in the order of leaf > branch >stem > root. The concentrations of N, P and K in branch were only 35-68 % of that of leaf, and for Ca and Mg, 40-60 % of leaf concentrations. Most element concentrations in root were lower than in aboveground parts, with the exception of Al and Fe, which had highest concentrations in root. Concentrations of N, Ca and Mn in aboveground parts of *Plagiogyria communis* were relatively high. Other element concentrations in aboveground parts were lower than for underground parts.

3.3.4. Nutrient concentration in dead materials

Concentrations of most elements in fallen litter were lower than in living organs (especially K), except for Ca, Al and Fe (Table 3.6). This is a reflection of translocation of mobile elements from senescing tissues to young, actively-growing material. Forest floor litter concentrations were higher than in fresh leaf litter. Concentrations of all elements studied were lower in dead wood materials compared with those in litter on the forest floor, except for C. Dead and living wood had similar concentrations of organic carbon but other nutrient elements were lower in dead than living wood. Concentrations of most elements were higher in large branches compared with the other two dead materials. Standing dead trees had higher concentrations of C and K. Generally, nutrient concentrations of dead wood decreased in the order: standing dead trees >large branches >fallen dead trees (Table 3.6).

Table 3.6. Nutrient concentration in dead materials in natural *Lithocarpus/ Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Values are means (n=3) with SD in parentheses.

Components	Nutrient concentration (% of dry weight)								
	C	N	P	K	Ca	Mg	Mn	Al	Fe
Standing dead trees	51.53a (1.25)	0.275c (0.028)	0.016c (0.005)	0.082b (0.012)	0.497b (0.038)	0.035b (0.004)	0.005bc (0.000)	0.006c (0.001)	0.007c (0.002)
Fallen dead trees	48.55b (2.18)	0.221c (0.022)	0.012c (0.002)	0.037b (0.003)	0.153c (0.021)	0.024c (0.004)	0.004c (0.000)	0.005c (0.000)	0.008c (0.002)
Large branches	50.54ab (1.92)	0.376b (0.035)	0.025b (0.002)	0.069b (0.007)	0.531b (0.042)	0.040b (0.003)	0.017b (0.002)	0.056b (0.007)	0.043b (0.008)
Litter mass	43.19c (1.06)	1.178a (0.102)	0.084a (0.020)	0.214a (0.058)	0.738a (0.026)	0.115a (0.003)	0.078a (0.012)	0.534a (0.053)	0.469a (0.032)

Note: values with similar letters in a column across dead material fractions are not significantly different ($p<0.05$), using Fisher's LSD test.

3.3.5 Nutrient content and distribution in living plants

3.3.5.1 Nutrient content of dominant tree species

Most nutrients were in the dominant tree species. However, there were important differences in nutrient content (kg ha^{-1}) and distribution among dominant tree species and between sites (Table 3.7). Greater proportions of nutrients were contained within *Lithocarpus xylocarpus* and *Castanopsis wattii* in both stands, due to the greater biomass of these species.

Biomass/nutrient ratios (t/kg) are indicators of within-stand nutrient use efficiency (Vitousek, 1982). In this forest, the procedure reveals differences among dominant species (Table 3.7). P, K, Mg, and Fe were used most efficiently by *Machilus viridis* and *Lithocarpus xylocarpus*, while N was used most efficiently by *Schima noronhae*. *Castanopsis wattii* had highest Ca and Mn, but low use efficiencies of N and P. Nutrient use efficiencies of most elements by *L. chintungensis* and *Manglietia insignis* were lower than by other species. In general, use efficiency of nutrients in Plot 1 was slightly greater than in Plot 2.

Table 3.7. Elemental distribution in aboveground part of dominant tree species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Values in parentheses are efficiencies of nutrient use in biomass (t biomass / kg nutrient; after Vitousek 1982).

Plot	Species	Nutrient content (kg ha^{-1})								
		C	N	P	K	Ca	Mg	Mn	Al	Fe
Plot 1	*Lithocarpus xylocarpus*	52758a	193a	15a	175b	400a	41a	9.1a	35a	7.9a
			(0.54)	(6.95)	(0.60)	(0.26)	(2.54)	(11.45)	(3.00)	(13.03)
	L. chintungensis	589g	3.4c	0.4d	3.4e	6.6c	0.7b	0.1b	0.5d	0.2b
			(0.34)	(2.93)	(0.34)	(0.18)	(1.67)	(11.70)	(2.34)	(5.85)
	Castanopsis wattii	38000c	203a	10b	239a	126b	36a	7.3a	17c	9.0a
			(0.41)	(8.24)	(0.34)	(0.65)	(2.29)	(11.29)	(4.85)	(9.26)
	Machilus viridis	44186b	211a	9.0b	124c	432a	33a	8.0a	24b	6.1a
			(0.41)	(9.72)	(0.71)	(0.20)	(2.65)	(10.94)	(3.65)	(13.34)
	Manglietia insignis	9132f	41b	3.4c	27de	49c	9.9b	4.7b	4.7d	2.5b
			(0.43)	(5.21)	(0.66)	(0.36)	(1.79)	(3.77)	(3.77)	(7.09)
	Schima noronhae	11334e	41b	4.5c	46d	46c	10b	8.9a	3.8d	1.9b
			(0.54)	(4.91)	(0.48)	(0.48)	(2.21)	(2.48)	(5.81)	(11.62)
Plot 2	*Lithocarpus xylocarpus*	10921b	40b	3.1b	36b	83b	8.5b	1.9bc	7.3b	1.6c
			(0.53)	(6.96)	(0.60)	(0.26)	(2.54)	(11.36)	(2.96)	(12.69)
	L. chintungensis	5236c	29b	3.4b	30b	59c	5.7bc	1.0cd	4.4c	1.8bc
			(0.36)	(3.05)	(0.35)	(0.18)	(1.82)	(10.38)	(2.36)	(5.77)
	Castanopsis wattii	36863a	197a	10a	232a	122a	35a	7.1a	17a	8.6a
			(0.40)	(7.99)	(0.34)	(0.66)	(2.28)	(11.26)	(4.70)	(9.29)
	Machilus viridis	1389e	6.7c	0.3c	3.9c	14d	1.0d	0.3d	0.7d	0.2d
			(0.41)	(9.17)	(0.71)	(0.20)	(2.75)	(9.17)	(3.93)	(13.75)
	Manglietia insignis	2932d	14c	1.1c	9.0	16d	3.4cd	1.5c	1.5d	0.8cd
			(0.41)	(5.18)	(0.63)	(0.36)	(1.68)	(3.75)	(3.80)	(7.13)
	Schima noronhae	3502d	13c	1.4c	14c	14d	3.3cd	2.8b	1.2d	0.6d
			(0.53)	(4.88)	(0.46)	(0.49)	(2.07)	(2.44)	(5.69)	(11.38)

Note: values with similar letters in a column across species in each stand are not significantly different ($p<0.05$), using Fisher's LSD test.

3.3.5.2 Nutrient content and distribution of living materials

Distribution of nutrient content (kg ha^{-1}) of different components in the two stands suggests overall nutrient contents in Plot 1 were greater than in Plot 2 (Table 3.8). Nutrients in the tree layer comprised 98 % of the total nutrients of living biomass in Plot 1 compared with 86 % in Plot 2. However, total nutrient content of shrubs and herbs in Plot 1 was lower than in Plot 2, with 2 % and 14 %, respectively.

Table 3.8. The content of nutrients and their distribution in living materials in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Plot No.	Components	Nutrient (kg ha^{-1})								
		C	N	P	K	Ca	Mg	Mn	Al	Fe
Plot 1	Tree layer									
	Leaf	1746	55	4.0	28	23	13	2.1	3.2	0.7
	Branches	14703	130	16	139	187	51	7.3	16	4.5
	Stem	154587	581	28	509	909	83	36	74	26
	Root	71616	595	90	538	665	182	63	271	232
	Total	242652	1361	138	1214	1784	329	108	364	263
	Shrub layer									
	Leaf	288	17	0.7	7.4	1.7	0.6	0.3	0.2	0.2
	Branch	240	4.2	0.3	3.6	1.1	0.3	0.2	0.3	0.3
	Stem	2362	14	1.1	34	6.1	1.4	3.2	1.6	1.2
	Root	489	4.2	0.4	7.6	1.1	0.5	0.4	4.2	2.3
	Total	3379	39	2.5	52	10	2.8	4.1	6.3	4.0
	Herb layer									
	Aboveground	196	11	0.4	2.0	1.5	1.3	0.1	1.5	0.7
	Underground	267	4.9	0.5	2.5	0.6	1.3	0.5	0.6	0.1
	Total	463	16	0.9	4.5	2.1	2.6	0.6	2.1	0.8
	Sum	246494	1416	141	1271	1796	334	113	372	268
	Biomass/nutrient ratio 1)		0.36	3.57	0.40	0.28	1.51	4.38		
Plot 2	Tree layer									
	Leaf	1099	35	2.6	19	15	8.7	1.3	2.1	0.4
	Branch	6871	64	8.7	65	93	23	3.3	8.2	1.9
	Stem	78925	320	18	345	376	49	21	36	17
	Root	30539	254	38	229	284	78	23	115	99
	Total	117435	673	66	658	768	159	49	161	118
	Shrub layer									
	Leaf	668	39	1.6	17	4.0	1.5	0.6	0.5	0.4
	Branch	2225	39	3.1	33	9.7	2.4	1.7	3.0	2.3
	Stem	10586	63	4.9	154	27	6.3	15	7.4	5.1
	Root	4161	35	3.0	48	9.7	4.1	3.5	35	19
	Total	17640	176	13	252	51	14	21	46	27
	Herb layer									
	Aboveground	958	21	0.6	12	2.6	2.3	0.5	7.2	3.0
	Underground	481	24	2.6	3.6	3.1	6.4	0.9	1.1	0.2
	Total	1439	45	3.2	16	5.7	8.7	1.4	8.3	3.2
	Sum	136513	894	82	926	825	182	71	215	148
	Biomass/nutrient ratio 1)		0.32	3.48	0.31	0.35	1.56	3.80		

1). Biomass is expressed in t ha^{-1}; nutrient in kg ha^{-1}.

Nutrient contents in tree components generally decreased from stem, root and branch to leaf, reflecting biomass amounts but with variation among components. Stems, branches and roots held a larger proportions of organic carbon, followed by Ca, N, K and Mg, whereas the roots held large proportions of K, followed by Al, Fe and P. Nutrient contents in leaves were lower than other components. Nutrient content in trees decreased in the order of C>Ca>N>K>Al>Mg>Fe>P>Mn.

Carbon also had the highest content among elements sampled in shrubs and herbs as well as litter. The aboveground shrub component had a large proportion of N followed by K, Ca, Mn, Mg and P while the underground component held more Al and Fe. The herb layer held large proportions of N followed by K, Ca, Mg and Al.

3.3.6 Nutrient storage and distribution in dead materials

Although dead wood had low concentrations of nutrient elements, total nutrient storage in dead wood was high because of its comparatively large contribution to the standing crop. Thus, fallen dead trees stored most nutrients (Table 3.9). Nutrient storage in fallen dead trees of Plot 1 accounted for 77.0 % of the total. The level was 85.0 % in Plot 2. Standing dead trees and large branches comprised 12.9 % and 10.1 % of the total nutrient storage in Plot 1 and 9.5 % and 5.5 % in Plot 2, respectively. Carbon was highest in dead wood, accounting for 98.9 % of the total nutrient content. N, Ca and K were relatively high, being 112-230 kg ha^{-1} for N, 107-200 kg ha^{-1} for Ca and 21-42 kg ha^{-1} for K, but storage of Mn, Al and Fe in dead wood was less than 10 kg ha^{-1}. Comparison of nutrient storage in dead wood between the two stands showed that the proportion of nutrient storage contained in dead wood tended to increase from Plot 1 to Plot 2. The total storage of nutrients in dead wood in Plot 2 comprised 40.6 % of the total nutrients in living trees compared with 9.2 % in Plot 1. Compared to the dead wood, most elemental contents in litter were low, with the exception of Al and Fe, which were higher than dead wood (litter on forest floor has more contamination from mineral soil than dead wood, Chapter 5). Nutrient content in litter was lower in Plot 1 than Plot 2.

Table 3.9. The content of nutrients and their distributions among dead materials in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Plot No.	Components	Nutrient (kg/ha)								
		C	N	P	K	Ca	Mg	Mn	Al	Fe
Plot 1	Standing dead trees	2911	15	0.9	4.6	28	2.0	0.3	3.4	0.5
	Fallen dead trees	17493	79	4.3	13	55	8.7	1.4	1.8	2.9
	Dead branches	2269	16	1.1	3.1	24	1.8	0.8	2.5	1.9
	Total dead wood	22673	110	6.3	21	107	13	2.5	7.7	5.3
	Litter	4427	121	8.6	22	76	12	8.0	55	48
	Sum dead materials	27100	231	15	43	183	25	11	63	53
Plot 2	Standing dead trees	4550	24	1.4	7.2	44	3.1	0.4	0.5	0.7
	Fallen dead trees	41000	187	10	31	129	20	3.4	4.2	6.7
	Dead branches	2618	19	1.3	3.6	28	2.1	0.9	2.9	2.2
	Total dead wood	48168	230	13	42	201	25	4.7	7.6	9.6
	Litter	5554	151	11	28	95	15	10	69	60
	Sum dead materials	53722	381	24	70	296	40	15	77	70

3.4. Discussion

3.4.1 Biomass of live trees and dead wood

The aboveground biomass of this natural forest appears to be greater than that reported for temperate forests (Whittaker & Likens, 1975; Pastor & Bockheim, 1984; Monk & Frank, 1985; Archibold, 1995; Rapp *et al.*, 1999), but lower than in tropical rain forests (Archibold, 1995; Vitousek & Sanford, 1986). The data are similar to the values reported for tropical montane rain forests elsewhere (Grimm & Fassbender, 1981; Grubb & Edwards, 1982; Tanner, 1985; Table 3.10).

Table 3.10. Aboveground biomass and nutrient content in a range of montane forests.

Site	Elevation (m)	Annual rainfall (mm)	Biomass (t ha^{-1})	Reference
New Guinea	2500	4000	310	Grubb & Edwards, 1982
Puerto Rico	-	-	197	Ovington & Olson, 1970
Venezuela	2250	1500	348	Grimm & Fassbender, 1981
Jamaica-mull	1600	3000	337	Tanner, 1985
Jamaica-mor	1600	3000	209	Tanner, 1985
Yunnan, China	2450	1930	210-352	This study

Dead wood is an important component of the natural forest. The standing crop of dead wood is higher in the Ailao mountain forest than reported from other broad-leaved forests (Harmon *et al.*, 1986; MacMillan, 1988; Muller & Liu, 1991; Delaney *et al.*, 1998). The moist and relatively cold environment of Ailao Mountain is an important factor for conserving more dead wood. There is less biological activity and low metabolic rates of decomposing organisms under low temperature (Vitousek & Sanford, 1986; Archibold, 1995). High values for dead wood mass, especially for fallen dead trees, in Ailao Mountains reflect slow decomposition of the dead wood, and little or no past disturbance in the natural forest. Spies & Frankling (1988) report that more dead wood in moist environments than in drier sites is related to greater production, larger tree boles; higher mortality rates; slower decay rate; and less fire. However, in comparison to old growth coniferous forests of California (200 t ha^{-1}; Binham & Sawyer, 1988) and the Pacific Northwest (143-215 t ha^{-1}; Harmon & Chen, 1991), my values are much lower.

Dominant species are important contributors to live and dead biomass and its distribution in the natural forest ecosystem. 70-91 % of the aboveground biomass of the tree layer here is contributed by the six dominant tree species. 78-85 % of fallen dead trees is composed of material from the three species *Lithocarpus xylocarpus, Castanopsis wattii* and *Machilus viridis*. This is a function of longevity, canopy development and complex age structure of these trees (Xie *et al.*, 1983, Qiu *et al.*, 1998). The hard wood of these dominants decomposes slowly under the prevailing climate.

Accumulation of live and dead wood biomass is influenced by stand density, age and environment (Long, 1982). Low stand density limits accumulation rates of both living and detrital biomass in Wyoming lodgepole pine forests (Pearson *et al.*, 1987). In the Xujiaba region, due to differences in relative density, basal area and complex age structure, there are greater differences in living and dead wood biomass and in the ratio of stem-wood to branch biomass. Natural thinning amongst younger patches may explain differences in relative biomass of branch-wood and foliage while the stem-wood biomass increases (Qiu *et al.*, 1998). The biomass ratios of stem-wood to branch-wood are 10:1 in a high density stand and 14:1 in a low density stand respectively. Similarly, the ratios of stem-wood to leaf biomass are 43:1 and

30:1 respectively.

Many of the structural parameters suggest that low density stands contain some trees considerably older than those in higher density stands. Greater amounts of dead wood in the low density stand than at high density are explained by the successional stage of each set of stand components. The stand history and exogenic disturbances are the main factors that explain variation in dead wood (Harmon *et al.*, 1986; Pearson *et al.* 1987). This natural forest is uneven-aged, and whereas no previous stand-replacing disturbance has been noted, the mean diameter, basal area and density of dominant trees differ considerably between component stands. Fluctuation in dead wood associated with gap-phase dynamics results from disturbance in evergreen broad-leaved forests (Qiu *et al.*, 1998). In natural stands, death of older, large trees not only produces recruitment peaks of dead wood, but also contributes to large-size gaps. Such small-scale, gap-phase fluctuations in mortality and subsequent recruitment of deadwood seem to be typical for many types of boreal old growth forests (Liu & Hytteborn, 1991; Jonsson & Dynesius, 1992; Siitonen *et al.*, 2000). The proportion of dead wood of the total stand biomass (living + dead) is similar to the range reported for boreal mesic forest in southern Finland (13-43 %; Siitonen *et al.*, 2000).

Different species tend to contribute different qualities of dead wood in this natural forest. Over 70 % of the dominant tree species *Lithocarpus xylocarpus, Castanopsis wattii* and *Machilus viridis*, are of large stem diameter in the sampled stands. Most subordinate species contribute standing dead mainly of small diameter. The proportion of small diameter standing dead trees is higher in the high density stand, whereas large diameter fallen dead trees are greater in the low density stand. Natural thinning, disease damage and insect epidemics may contribute to the quotient of small diameter standing dead trees. In contrast, old age, strong winds and occasional massive snow damage are probably responsible for large diameter fallen dead trees in the low density stand, from among large trees.

More dead wood, lower density of trees and greater gap areas in natural old stands contribute to more light inside the stand that in turn, allows for greater understory development (Harmon *et al.*, 1986; Liu & Hytteborn, 1991. Qiu *et al.*, 1998). In the

Lithocarpus/Castanopsis forest the bamboo layer is an important component. In this study, greater biomass of bamboo occurs in the low density stand. However, the similar proportions of current individuals in the total bamboo biomass in both stands indicates that canopy effects on sprouting capacity of bamboo are less than on growth after sprouting, because more dead individuals of newly sprouted (young) bamboo occur in the high density stand than in the low density stand.

3.4.2. Nutrient content in plants

The N: P ratio of the vegetation directly indicates the nature of nutrient limitation at a community level (Chapin, Vitousek & Van-Cleve, 1986; Koerselman & Meuleman, 1996). High foliage N: P ratios are usually associated with P limitation in soil (Medina, 1984). In this study, the N: P ratio in the leaves of dominant species is 1: 11.9-15.5, with mean about 13.4. Carten (1976) and Singh & Singh (1991) report N: P ratio means of 1: 10 and 1: 15 respectively. Foliage N: P quotients of all species combined from a range of Amazonian forest types is 1: 20 (Medina, Garcia & Curvas, 1990). The N: P ratios of the forests in Maraca Island, Brazil vary (38 species) from 9.1 to 28.6, with substantial differences within species (Thompson *et al.*, 1992). These results are comparable with my data that the N:P ratio varies among species. Carten (1976) notes that an N: P ratio of 10 in vegetation indicates a good supply of P, and higher ratios limit plant growth by P deficiency. Koerselman & Meuleman (1996), based on 40 fertilization studies, reveal that an N: P ratio > 16 indicates P limitation at a community level, while an N: P <14 is indicative of N limitation. At N: P ratios between 14 and 16, plant growth is co-limited by N and P together. In my study, the ratios of N: P in dominant species suggests that the growth of most plants may be more limited by P than by N because of lower P concentration in the soil (Deng *et al.*, 1983; Qiu *et al.*, 1998). Tanner, Vitousek & Cuevas (1998) indicate that Jamaican montane trees are limited both by N and by P, and Venezuelan montane trees are limited by N. Nutrient limitation is widespread in montane soils (Tanner *et al.*, 1998).

The nutrient content and distribution in different components differ considerably, and foliage concentrations of N, P, K and Mg are much higher than in other components, while Ca is high in branch-wood and Al and Fe are high in roots. This is in agreement with the observation of Ranger *et al.* (1995) that smaller biomass components tend to have greater concentration of nutrients. Plant parts of younger age are more active metabolically and have higher nutrient concentrations than plant tissues of older age. For distributions of nutrient in different components, the greatest total amounts of nutrients are present in stem and root components, although the stem has the lowest concentration of nutrient. The relative contribution of tree components to the total standing crop of nutrients is in the order: stem>root>branch>leaf for organic C, N, K and Ca, and root>stem>branch>leaf for P, Mg, Mn, Al and Fe. Of nutrient content in each vegetation component, most nutrient is stored in stems but all vary in the order of other compartments (Grubb & Edwards, 1982; Singh & Singh, 1991). Ranger *et al.* (1995) show that young Douglas fir retains most nutrients in the tree crown. In my study, the largest quantities of all nutrients are found in the trunk and root components. This pattern reflects tree age and is likely to be characteristic of mature primary forests.

It has been hypothesized that early-successional tree species may be especially effective as nutrient sinks because of more rapid growth and nutrient uptake and greater retention of nutrients in perennial tissues than in late-successional species (Vitousek & Reiners, 1975; Vitousek, 1977; Bormann & Likens, 1979; Boring, Monk & Swank, 1981). In this study, although both stands are of natural forest, I note considerable differences in the tree components. In the natural forest, younger trees have relatively high growth rates and greater productivity than older trees (Xie *et al.*, 1983). There is greater retention of nutrients in perennial tissues in the high density stand (Table 3.8). Nutrient use efficiencies of this stand are higher than in the low density stand, with the exception of Ca (Table 3.8).

Compared to living tissues, concentrations of N, P and K in leaf and twig litter of dominant tree species are obviously lower, indicating effective recycling of these elements. Efficient retranslocation, particularly of essential elements in short supply, is a typical feature of climax forest tree species (Staaf & Berg, 1981; Staaf, 1982). This conservation mechanism has typically evolved in tropical and subtropical forests, especially on soil of poor nutrient availability (Medina, 1984; Vitousek & Sanford, 1986).

Dead wood contributes significantly to the total amount of organic material in the forest and affects carbon storage, energy flow and nutrient cycling in the natural forest. The magnitude of nutrient storage in dead wood is equivalent to 9-41 % of the nutrient in living trees in the natural forest. Storage of nutrient in dead wood plays an important role in nutrient cycling within natural forest ecosystems, especially in carbon cycling. (Harmon *et al.*1986; Siitonen *et al.*, 2000). It is necessary to consider the quality and quantity of dead wood in studying nutrient budgets and cycling within natural forest, especially these undisturbed ancient stands. On the other hand, the proportions of dry matter and nutrients contained in understories in the total stand biomass and nutrients tend to increase with stand age. However, collection of herbs, fruits and bamboo by local people do occur frequently in these natural forests, and these activities may make local impacts on nutrient cycling. No information is available of the possible impact on nutrient budgets, cycling and conservation of species diversity. The effects of these activities should be quantified with a view to understanding the magnitude of effects on nutrient turnover, and, ultimately, the continued integrity of the forest.

3.4.3 Comparison of nutrient accumulation with other montane forests

On a world scale, Ailao Mountain forest is, for its latitude and altitude, relatively rich in terms of stature and species diversity. The forest is more developed than other forests in mountainous areas of central Yunnan at the same altitude. Aboveground biomass of Ailao Mountain forest is similar to montane forests in New Guinea, Venezuela and Jamaica. In comparison with these three montane forests, the Ailao Mountain forest has intermediate quantities of N, P, K, Ca and Mg in aboveground biomass, being most similar to Jamaican montane forests. The Venezuela montane forest has most (except for Ca) and the New Guinean montane forest least nutrients (most for Ca; Table 3.11). The four forests have similar concentrations of N, P and Mg. K is higher in the Venezuelan forest, whereas Ca is higher in New Guinea. The differences may be due to variations in climate, species composition and soil among sites as well as differences between laboratories and techniques used (Tanner, 1985). On the other hand, the Ailao mountain forest, similar to other montane forests, has lower nutrient concentrations (especially for N and P) in comparision with lowland forests elsewhere (Table 3.11). This is agreement with other studies that N and P limited in montane forests (Grubb & Edwards, 1982; Vitousek & Sanford, 1986).

Table 3.11. Mean concentrations and contents of nutrient in aboveground biomass in a range of montane forests and lowland forests.

Site	Concentration (%)					($kg\ ha^{-1}$)					Reference
	N	P	K	Ca	Mg	N	P	K	Ca	Mg	
Montane forrests											
New Guinea	0.22	0.012	0.22	0.41	0.06	683	37	664	1281	185	Grubb & Edwards, 1982
Puerto Rico	0.41	0.022	0.26	0.45	0.17	814	43	517	894	340	Ovington & Olson, 1970
Venezuela	0.25	0.015	0.38	0.21	0.06	876	53	1321	745	215	Grimm & Fassbender, 1981
Jamaica-mull	0.25	0.120	0.25	0.28	0.06	857	41	829	940	193	Tanner, 1985
Jamaica-mor	0.20	0.014	0.13	0.17	0.07	426	30	272	353	155	Tanner, 1985
Yunnan, SW China	0.25	0.017	0.25	0.29	0.04	696	44	683	850	122	This study
Lowland forests											
Panama	-	0.050	0.96	1.23	0.13	-	158	3020	3900	403	Golley *et al.*, 1975
Ghana	0.72	0.048	0.32	1.02	0.14	1685	112	753	2370	320	Nye, 1961
Brazil	0.60	0.015	0.11	0.11	0.06	2430	59	435	432	201	Klinge,1984
Venezuela	0.32	0.012	0.09	0.08	0.02	1084	40	302	260	69	Jordan & Escalante, 1980; Jordan *et al.*, 1982

Nutrient content and its distribution in forest vegetation is an important foundation for studying nutrient cycling. To examine nutrient cycling in the natural forest (Chapter 7), I will use mean values for each element content in the stand components determined in this chapter as the basis of total storage of nutrients in the natural forest.

4.5. Conclusion

This natural forest of *Lithocarpus/Castanopsis* at Xujiaba, Ailao Mountain NNR is more developed than other forests in mountainous areas of central Yunnan at the same altitude. It is characterized by high biomass accumulation of living and dead materials. The aboveground biomass of living plants is similar to those of tropical montane rain forests elsewhere. Dead wood comprises a high proportion (9-41 %) of total stand biomass. This forest has intermediate quantities of N, P, K, Ca and Mg in the aboveground biomass compared with montane rain forests. Foliage has highest concentrations of N and K, whereas P and Ca are of higher concentration in woody tissues. Roots of all species have higher concentrations of Al and Fe than in aboveground parts. The patterns of accumulation of biomass and nutrient and their distribution in living plant and dead wood vary considerably with stand density. Density and basal area are the main factors affecting the accumulation of biomass and nutrients. Dead wood accounts for a significant amount of organic material on the forest floor, contributing to carbon storage, energy flow and nutrient cycling.

As this forest is a multi-dominant, uneven-aged natural ecosystem, this study provides useful information on accumulation of biomass and nutrients. Nevertheless, due to the limited number of stands examined the results obtained present a limited range of the standing crop and nutrient content and their distribution. Long-term studies are necessary to examine the dynamics of accumulation and allocation of biomass, nutrient uptake and cycling among younger and older trees to contribute to a better understanding of structure and function in this unique natural forest.

Nutrients are lost when foliage and other plants fall from the plant to the soil. In studies of nutrient cycling of forest ecosystem, litterfall from the aboveground vegetation to the soil surface is considered as an important component. In the next chapter, I will describe the pattern of litterfall dynamics and associated nutrient return in the natural forest.

Chapter 4 Litterfall and Nutrient Returns in Natural *Lithocarpus /Castanopsis* Forest at Xujiaba, Ailao Mountain NNR

4.1 Introduction

Litterfall is the main pathway for the return of organic matter and nutrients from aerial portions of the plant community to the soil surface (Vitousek, 1982; Spain, 1984; Vitousek & Sanford, 1986; Klinka, Wang & Kayahara, 1994; Palma *et al.*, 1998; Arunachalam *et al.*, 1998). It can be considered as an input-output system of nutrients and energy sources for an array of micro-organisms (Vogt *et al.*, 1986; Vitousek & Sanford, 1986; Cuevas & Medina, 1986; Sundarapandian & Swamy, 1999; Garkoti & Singh, 1995). Litterfall and decomposition processes maintain effect nutrient pools in the soil, influence primary production, regulate energy flow, and nutrient cycling in forest ecosystems (Waring & Schlesinger, 1985). Nutrient cycling rates in a forest ecosystem can be inferred through comparing concentrations and amounts of nutrient elements in fresh litterfall and in forest floor litter (Proctor *et al.*, 1983; Proctor, 1987; Vitousek & Sanford, 1986; Scott, Proctor & Thompson, 1992; Burghouts *et al.*, 1998).

Within natural forest ecosystems, litterfall dynamics have been shown to be strongly influenced by a number of factors including species composition, tree density, basal area, and tree size (age) (Stolgren, 1988; Arunachalam *et al.*, 1998; Sundarapandian & Swamy, 1999). Other factors include altitude (Reiners & Lang, 1987), latitude (Bray & Gorham, 1964) and season. Physical disturbance to forests, such as fire, wind and hurricanes, may also induce pulses of litterfall (Bruederle & Streans, 1985). The amounts of litter on the forest floor have been strongly correlated with amounts of litterfall (Proctor, 1987; Vitousek & Sanford, 1986). Although litterfall in tropical and subtropical forests has received special attention over the last two decades (Vitousek, 1984; Vitousek & Sanford, 1986), few data are available on litterfall for montane evergreen broad-leaved forests in subtropical areas of southwestern China. The natural *Lithocarpus/Castanopsis* forest ecosystem was hypothesized to differ from other forests in patterns of litterfall and nutrient return under the particular environmental conditions of high altitude and rainfall within its warm temperate climatic regime.

In Chapter 3, I have described the patterns of biomass and nutrient accumulation in the natural forest. In this Chapter, I present results of quantifying the annual litterfall and its nutrient content, by seasonal pattern and relative contribution of each component of the litter over a nine year period (1991-1999). The standing crop of litter on the forest floor and nutrient accumulation were sampled to provide an insight into turnover rates of dry matter and elements in litterfall and forest floor litter at Xujiaba, Ailao Mountain NNR.

4.2 Material and Methods

4.2.1 Study site

This study was conducted in a typical stand of natural *Lithocarpus/Castanopsis* forest, using a permanent research plot (200 x 200 m, 4 ha), adjacent to Xujiaba FERS. It is at an altitude of 2450 m and has slopes of 10-15°, and is of southwest aspect. The general characteristics of this forest type have been described earlier (Chapter 2). The upper canopy of 18-25 m includes large trees of *Castanopsis wattii*, *Lithocarpus xylocarpus*, and other species. It is floristically similar to the stand with large trees used in biomass and nutrient distribution (Chapter 3) and has a density of 516 stems ha^{-1} ($\geq$10 cm DBH). There is a variable second story of smaller trees and tall shrubs 3<12 m tall, the bamboo (*S. nitida*) is locally abundant, to 3 m tall. Moss, ferns and lichen occur and abundant epiphytic moss is present on tree boles.

4.2.2 Litterfall measurement

Litterfall collection commenced in January 1991 and continued through December 1999. Collection of litterfall was made in two classes: small litterfall; and large wood fall ($\geq$2.5 cm in diameter).

Small litterfall was collected in fifteen 1 x 1 m traps placed randomly to give a 0.15 % sample within an area of 1 ha (100 x 100 m) in the central zone of the 4 ha plot. These traps were made of four pieces of wood 15 cm deep with a fine 2 mm mesh nylon screen nailed to the base and were supported on four legs so that the top was 1 m above the ground. During the 9-year period, a few traps were broken, mainly by fallen large branches. Damaged traps were replaced. Traps were emptied monthly. All litter was oven-dried to a constant weight at 80 °C and sorted into leaf, twig (<2.5cm in diameter), reproductive litter (flower and fruits) and a miscellaneous fraction (unrecognizable plant debris <2mm and frass).

Eight 4 x 2 m subplots, demarcated by bamboo culms were randomly placed on the forest floor in the one ha plot. Large wood (diameter ≥2.5 cm) litterfall was collected at monthly intervals from these subplots. The large wood litterfall was weighed fresh in three diameter classes: 2.5-5.0 cm, 5.1-10.0 cm and >10.0 cm. Samples of each component were taken to determine dry weight at 80°C constant weight. The monthly value for large wood fall was calculated on a unit area basis (t ha^{-1}).

4.2.3 Litter on the forest floor

The gradual transformation from litter to soil organic matter is an important ecosystem characteristic in montane forests (Anderson, Proctor & Vallack, 1983; Edwards, 1977). Estimates of litter turnover depend very much on the distinction made between forest floor and soil organic matter (Burghouts *et al.*, 1998).

Litter on the forest floor was collected according to the method of Scott *et al.* (1992) who define ≥2 mm in diameter as litter and below 2 mm as soil organic matter. Litter on the forest floor was determined at three-monthly intervals for the period from June 1997 to December 1999. On each occasion, ten 0.5 x 0.5 m quadrats were used to collect litter samples from random locations. The location of each collection was marked with a peg to avoid repeated collection from the same place. Litter samples were taken in fabric bags to the FERS laboratory and dried as above. All collections were sorted into leaves, wood and reproductive parts (as described for small litterfall). There was no trash fraction because it was impracticable to sort out from the soil organic matter any fragments <5mm in their longest dimension. Fractions of litter layer were treated following the procedures described for the litterfall.

4.2.4 Chemical analysis

Each component of litterfall was sampled from respective mixed collections for the dry months (March to May) and wet months (July to October) in order to determine seasonal change of nutrient concentration. Each of the three samples of large wood fall and litter on the forest floor were used for chemical analysis were taken from respective mixed samples. After drying and grinding, to pass a 20 mesh screen, samples were analyzed as described in Chapter 3 (Section 3.2.4).

4.2.5 Data processing and statistical analysis

The mean concentrations (as % of dry weight) of each element from 12 samples analyzed for litterfall components, were used to weight the litterfall values (t ha^{-1}) in order to obtain the nutrient content (kg ha^{-1}) per litter component per month and per year. The nutrient accumulation of litter on the forest floor was calculated as the mass-weighted mean concentration times the standing crop of litter.

Turnover rates (k) for each litter component and each element were calculated by the equation of Scott *et al.*(1992):

$$k = A/F$$

Where A is the annual small litter input to the forest floor and F is the mean standing crop of small litter. Turnover time (t) is the reciprocal of turnover rate and is expressed as $t = 1/k$. Turnover rates and turnover time for litter components (leaves; twigs; flowers/fruits; and total small litter) and each nutrient element were calculated. Amount of nutrient element returned to the soil was calculated by dividing mineral element content (kg ha^{-1}) of standing crop of litter by turnover time (year) (Rochow, 1975).

In addition, nutrient cycling efficiency for each element was calculated using the ratio of litterfall mass to nutrient return in litterfall (Bridgham *et al.*, 1995). This is used to compare my data with results from other montane forests.

The data for seasonal variation in litterfall components, nutrient concentration and content, were statistically analyzed using one way analysis of variance to detect whether any differences between the five leaf types were significant. This was followed by Fisher's LSD test (at $p<0.05$) to distinguish between means of these components. Correlation analysis between total small litterfall and environmental factors (rainfall, temperature) was made. All statistical analyses were performed using StatView^{TM}(Abacus Concepts, Inc., 1986).

4.3 Results

4.3.1 Litter production

4.3.1.1 Small litterfall

The total annual litterfall in the natural forest (mean ± SD) was 7.12 ± 0.96 t ha^{-1} yr^{-1}. Significant differences in each component of litterfall existed among years. Higher values of leaf litterfall occur when flower/fruit fall is high. Leaf litterfall with fruit occurs in *Castanopsis wattii, Lithocapus xylocarpus* and *L. chintungensis*. Higher values of leaf and flower/fruit fall, occurred in 1992 and in 1998, and lower values in 1991 and in 1995. Of the mean total annual small litterfall, the leaf litter constituted 65.4 %, twig 18.6 %, flower/fruit 14.4 % and miscellaneous parts 1.6 %, respectively (Table 4.1).

Of contribution of dominant tree species to the total annual litter production, *Castanopsis wattii, Lithocarpus xylocarpus* and *L. chintungensis* contribute 40-45 %

of total leaf litterfall and more than 60 % of total fruit fall.

Table 4.1. Annual production (mean ± SD; n=15) of litterfall components in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR (1991-1999). Values in parentheses are percentage of the total.

Years	Litterfall (t ha^{-1} yr^{-1})				Total
	Leaf	Twig	Flower/fruit	Miscellaneous	
1991	3.611±0.222h (66.34)	0.975±0.091d (17.91)	0.762±0.075d (14.00)	0.095±0.010ef (1.75)	5.443±0.262h (100)
1992	5.179±0.359ab (64.24)	1.463±0.178bc (18.15)	1.320±0.174a (16.37)	0.100±0.010de (1.24)	8.062±0.472a (100)
1993	4.583±0.250e (65.34)	1.324±0.161c (18.88)	1.023±0.137b (14.58)	0.084±0.009f (1.20)	7.014±0.339e (100)
1994	4.655±0.252de (69.30)	1.042±0.107d (15.51)	0.902±0.108c (13.43)	0.118±0.013bc (1.76)	6.717±0.297f (100)
1995	3.942±0.288f (67.36)	1.025±0.121d (17.52)	0.796±0.078d (13.60)	0.089±0.011ef (1.52)	5.852±0.323g (100)
1996	5.087±0.303b (64.72)	1.592±0.256a (20.25)	1.033±0.163b (13.14)	0.148±0.026a (1.88)	7.860±0.594b (100)
1997	4.879±0.306c (63.74)	1.559±0.280a (20.37)	1.085±0.170b (14.18)	0.131±0.025b (1.71)	7.654±0.647c (100)
1998	5.193±0.308a (63.66)	1.475±0.267abc (18.08)	1.331±0.318a (16.32)	0.158±0.037a (1.94)	8.157±0.666a (100)
1999	4.753±0.301d (65.22)	1.377±0.232c (18.89)	1.048±0.129b (14.38)	0.110±0.015cd (1.51)	7.288±0.541d (100)
F	233.42	29.59	34.48	30.35	177.77
p	0.0001	0.0001	0.0001	0.0001	0.0001

Note: Values with same letters are not significantly different ($p<0.05$) within a column, using Fisher's LSD test.

4.3.1.2 Seasonal variation of small litterfall

There was a distinctly seasonal pattern of litterfall in the natural forest. Although litterfall was continuous during the 9 year period (Fig. 4.1), two peaks of litterfall in each year were observed: the main one in the late dry season (April-May) and a lesser one in early winter (October - November). Seasonal patterns of total and leaf litterfall were similar, with high litterfall in the dry season and early winter and low litterfall in the wet season. Higher values of litterfall peaks were observed in the dry seasons (March-May) of 1992, 1994 and 1996. Small branch litterfall mainly occurred in the dry season. The fall of flowers and fruits peaked in March-May and August-October, with higher values of flower and fruit litterfall in 1992 and 1998.

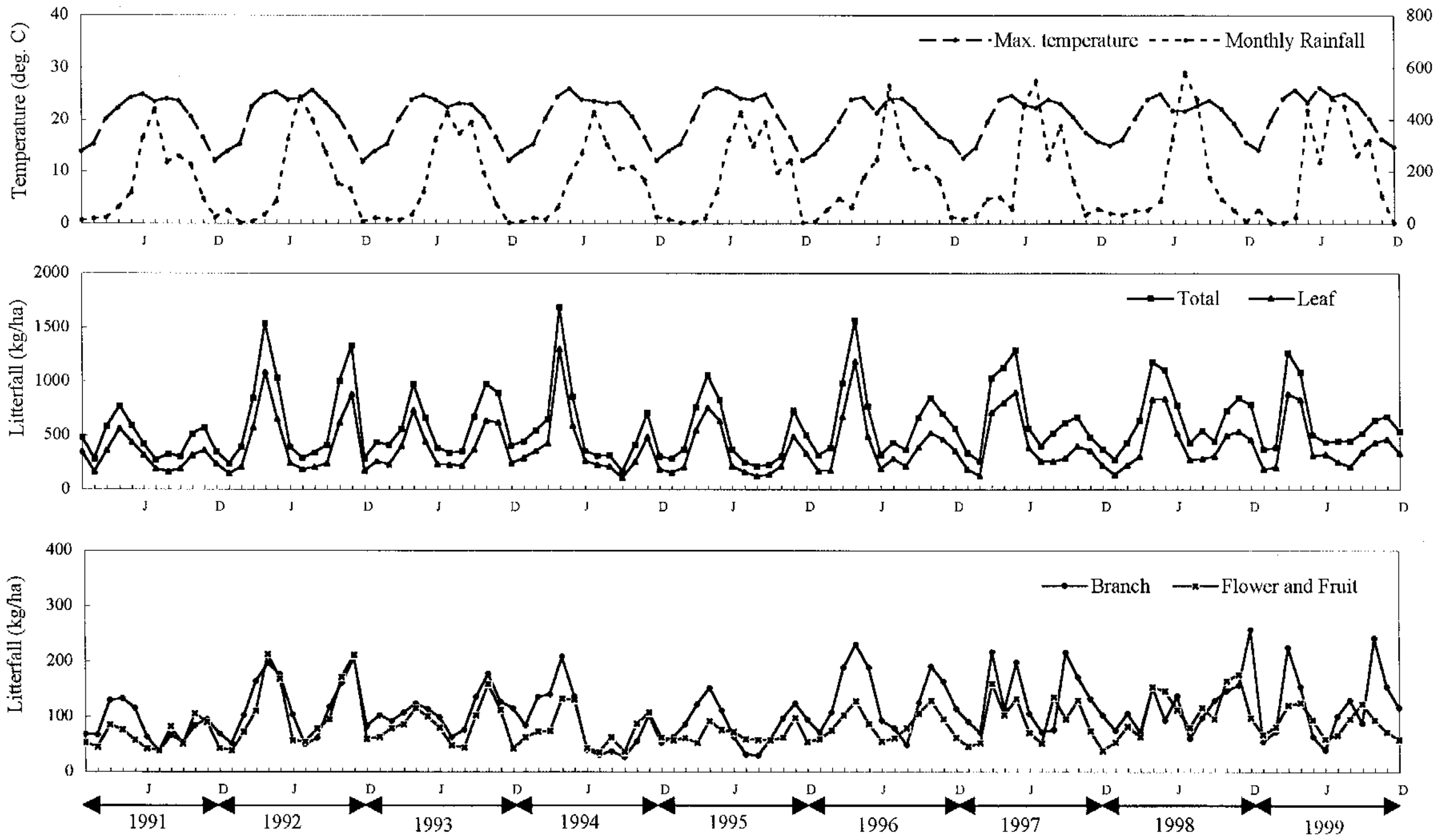

Fig. 4.1. Monthly rainfall and maximum air temperature at the Xujiaba Field Station and litterfall in natural *Lithocapus/Castanopsis* forest, at Xujiaba, Ailao MountainNNR (1991-1999).

Correlation coefficients between total litterfall and some climatic vaiable are shown in Table 4.2. Litterfall correlated positively with monthly maximum air temperature and negatively with monthly rainfall. No significant correlation existed between relative humidity and litterfall at Xujiaba, Ailao Mountain NNR.

Table 4.2. Correlation coefficients between total monthly litterfall of natural *Lithocarpus/Castanopsis* forest and monthly maximum air temperature and monthly rainfall at Xujiaba field station from 1991 to 1999 (n=108).

Climatic variables	Correlation coefficients (monthly litterfall)	F
Monthly max. temperature (°C)	0.2936	4.96**
Monthly rainfall (mm)	-0.3017	5.23**
Monthly relative humidity (%)	-0.1962	2.45

** Significant ($p<0.01$) ($F_{(0.01)} = 4.83$),
($p<0.05$) ($F_{(0.05)} = 3.10$).

4.3.1.3 Large wood litterfall

Considerable variation was found in the annual large wood fall during the 9-year period, ranging from 213 to 1405 kg ha^{-1}yr^{-1} with a mean of 522 kg ha^{-1}yr^{-1} (Fig. 4.2). The coefficient of yearly variation (79%) of large wood fall was greater than

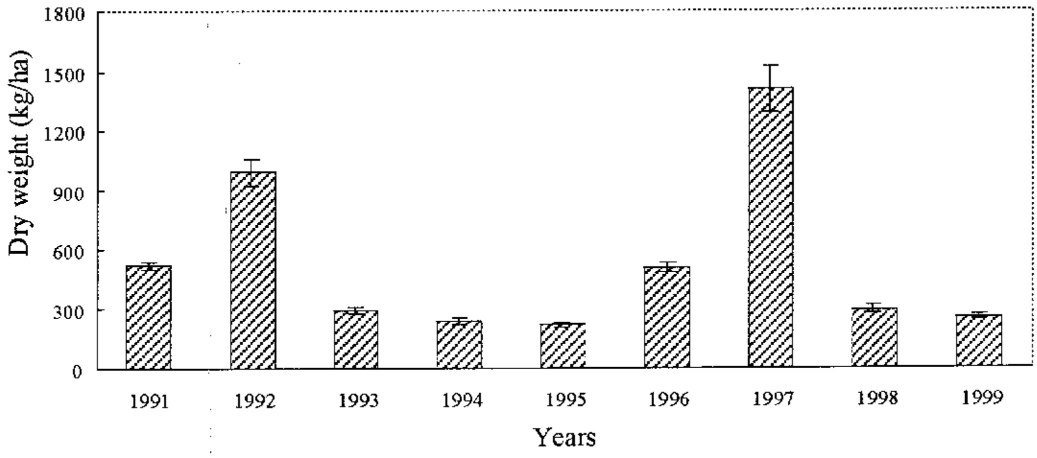

Fig. 4.2. Yearly variation in large wood fall in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR over nine years (1991-1999). Bars denote standard error (n = 8).

that of small litterfall (14%). Branch-fall of the 2.5-5.0 cm diameter class contributed over 80 % of the annual total large wood fall. Occurrence of branch fall was significantly greater during the dry seasons (March-May) and October-December, comprising respectively 37 % and 39 % of the mean annual large wood fall.

4.3.2 Litter on the forest floor

The estimated values for standing crop of the small litter layer (Table 4.3) reveal that litter on the forest floor was greatest late in the dry season (April), and least, late in the wet season (October). The mean standing crop of the litter layer was 12.69 t ha^{-1}. The relative contribution of partially and more decomposed litter to the total forest floor litter was greater than that of fresh litter all the year round. Turnover rates and turnover time for the various components of small litter indicate reproductive material has fastest turnover and twigs the slower, with leaves intermediate (Table 4.4).

Table 4.3. Estimated litter (t ha^{-1}, mean ± SD, n=10) on the forest floor at four dates in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Litter fraction	Collection date				Mean
	20 Apr	10 July	10 Oct	30 Dec	
Leaf litter mass	9.23±0.33	8.62±0.36	7.85±0.29	8.45±0.36	8.54
Twigs	3.42±0.35	3.26±0.33	2.88±0.38	3.23±0.31	3.20
Flowers/fruits	0.75±0.10	0.88±0.11	1.25±0.11	0.94±0.12	0.96
Total	13.40	12.76	11.98	12.62	12.69

Table 4.4. Estimated turnover rate (k_L) and turnover time (years) for different components of small-litter in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

	Leaves	Twigs	Flowers/Fruits	Total
Turnover rate (k_L)	0.54	0.38	1.24	0.58
Turnover time (years)	1.85	2.63	0.81	1.72

4.3.3 Element input to forest floor by litterfall

Although there were no significant differences between the mean seasonal nutrient concentration values of elements in leaf and twig litter parts, concentrations of all elements in leaf and twig litter were greater in wet months than dry months, except for C and K which were greater in dry months (Table 4.5). The mean concentrations for organic C were greater in twig litter; leaf and flower/fruit had similar values. Mean concentration of N in the litter components was similar in leaf and flower/fruit, but twig litter had a lower concentration. Mean concentrations of P and K were greater in the flower/fruit and the trash parts than in either the leaf or twig litter. The highest concentrations of Ca in the litter parts were found in the twig, then leaf and then trash and flower/fruit litter. Mg concentrations were greater in leaf and trash than twig and flower/fruit. Mean concentrations for Fe and Al were greater in miscellaneous and twig litter; leaf and flower/fruit had similar values.

Nutrient element accession of leaf litter and twig litter was significantly higher ($p<0.05$) in the dry season than in the wet season (Table 4.6). The annual nutrient accession varied among different components of litterfall. Two thirds of the total nutrient mass was returned to the forest floor through leaf litter, followed, in order by twigs, reproductive parts and the trash fraction. Nutrient accession to the forest floor through litterfall followed the decreasing sequence C>N>Ca>K>Mg>Mn>Al>P>Fe.

The ratio of litterfall mass to nutrient return in litterfall provide indicators of nutrient use efficiency in litterfall (Vitousek, 1984; Bridgham *et al.*, 1995). Within the forest N and Ca use efficiencies were low in litterfall, while P, Mg and K were relatively greater (Table 4.6).

Table 4.5. Mean (± SD) seasonal concentration of elements of small litterfall components in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Elements	Mean concentration in litter components (%)							
	Leaf			Twig			Flower/fruits	Miscellaneous
	Dry season	Wet season	Mean	Dry season	Wet season	Mean		
C	49.242 ±1.421	48.931 ±1.027	49.087	51.223 ±2.120	49.861 ±1.875	50.542	47.132 ±2.456	49.124 ±1.850
N	1.136 ±0.107	1.179 ±0.119	1.158	0.610 ±0.093	0.632 ±0.089	0.621	1.478 ±0.134	1.347 ±0.108
P	0.068 ±0.006	0.070 ±0.007	0.069	0.048 ±0.005	0.050 ±0.004	0.049	0.102 ±0.030	0.117 ±0.014
K	0.428 ±0.019	0.380 ±0.025	0.404	0.202 ±0.009	0.228 ±0.012	0.215	0.740 ±0.023	0.469 ±0.034
Ca	0.839 ±0.082	0.873 ±0.077	0.856	1.096 ±0.120	1.178 ±0.117	1.137	0.226 ±0.032	0.520 ±0.023
Mg	0.178 ±0.020	0.185 ±0.017	0.182	0.119 ±0.015	0.121 ±0.012	0.120	0.099 ±0.018	0.148 ±0.032
Mn	0.112 ±0.012	0.116 ±0.013	0.114	0.060 ±0.007	0.064 ±0.005	0.062	0.047 ±0.008	0.073 ±0.010
Al	0.079 ±0.007	0.082 ±0.008	0.081	0.089 ±0.008	0.093 ±0.006	0.090	0.072 ±0.005	0.092 ±0.006
Fe	0.012 ±0.004	0.013 ±0.005	0.013	0.016 ±0.006	0.017 ±0.003	0.017	0.014 ±0.003	0.021 ±0.006

Dry season: November-April. Wet season: May-October.
Sample size (leaves and twigs) = 12 for dry and wet seasons respectively. For flower & fruit, and miscellaneous, n = 12, respectively.

Table 4.6. Nutrient accession of small litterfall components in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Elements	Elemental accession in litter components (kg $ha^{-1}yr^{-1}$)									
	Leaf			Twig			Flower /fruit	Miscellaneous	Total (All parts)	Nutrient use efficiency
	Dry season	Wet season	Total	Dry season	Wet season	Total				
C	1316.0±179.3* (57.6)	969.3±191.6 (42.4)	2285.3±264.0 [65.3]	378.4±55.8* (56.2)	294.5±77.5 (43.8)	672.9±126.2 [19.2]	487.1±94.3 [13.9]	56.4±12.9 [1.6]	3501.7±478.6 [100.0]	
N	31.0±4.2* (57.0)	23.4±4.6 (43.0)	54.4±6.4 [68.4]	4.5±0.7* (54.9)	3.7±0.9 (45.1)	8.2±1.6 [10.3]	15.3±3.0 [19.3]	1.6±0.5 [2.0]	79.5±10.8 [100.0]	89.6
P	1.8±0.3* (56.3)	1.4±0.4 (43.7)	3.2±0.4 [61.5]	0.4±0.1 (57.1)	0.3±0.1 (42.9)	0.7±0.1 [13.5]	1.2±0.3 [23.1]	0.1±0.0 [1.9]	5.2±0.7 [100.0]	1369.2
K	11.5±1.6* (60.5)	7.5±1.5 (39.5)	19.0±2.2 [62.9]	1.5±0.2* (51.7)	1.4±0.3 (48.3)	2.9±0.5 [9.6]	7.7±1.8 [25.5]	0.6±0.2 [2.0]	30.2±4.1 [100.0]	235.8
Ca	22.5±3.1* (56.7)	17.2±3.4 (43.3)	39.7±4.7 [68.3]	8.1±1.2* (54.0)	6.9±1.8 (46.0)	15.0±2.9 [25.8]	2.8±0.5 [4.8]	0.6±0.1 [1.0]	58.1±7.9 [100.0]	122.5
Mg	4.8±0.7* (56.5)	3.7±0.7 (43.5)	8.5±1.0 [75.2]	0.9±0.1* (56.3)	0.7±0.2 (43.7)	1.6±0.3 [14.2]	1.0±0.2 [8.9]	0.2±0.0 [1.8]	11.3±1.5 [100.0]	630.1
Mn	3.0±0.4* (56.6)	2.3±0.5 (43.4)	5.3±0.6 [79.1]	0.4±0.1* (50.0)	0.4±0.1 (50.0)	0.8±0.2 [11.9]	0.5±0.1 [7.5]	0.1±0.0 [1.5]	6.7±0.9 [100.0]	1062.7
Al	2.1±0.3* (56.8)	1.6±0.3 (43.2)	3.7±0.4 [63.8]	0.7±0.1* (53.8)	0.6±0.1 (46.2)	1.3±0.2 [22.4]	0.7±0.1 [12.1]	0.1±0.0 [1.7]	5.8±0.8 [100.0]	1227.6
Fe	0.3±0.0 (50.0)	0.3±0.0 (50.0)	0.6±0.1 [66.7]	0.1±0.0 (50.0)	0.1±0.0 (50.0)	0.2±0.0 [22.2]	0.1±0.0 [11.1]	0.0±0.0 [0.0]	0.9±0.1 [100.0]	7911.1

Dry season, November-April. Wet season, May-October.

Values in parenthesis are percentage per season for each element. Values in square brackets are percentage of total annual input per element per litter component.

Nutrient use efficiency in litterfall is the ratio of litterfall mass to nutrient return in litterfall.

* Differences between the dry and wet months in nutrient accession of leaf and twig fall were significant ($p<0.05$).

4.3.4 Element accession from large wood fall

Concentrations of nutrient elements in large wood fall (Table 4.7) were lower compared with twig litterfall. Mean annual nutrient element accession by large wood fall ranged from 0.1 kg ha^{-1} $year^{-1}$ for P or Fe to 2.8 kg ha^{-1} $year^{-1}$ for Ca.

Table 4.7. Mean nutrient concentration (mean ± SD, n=3) and accession of large wood in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

	C	N	P	K	Ca	Mg	Mn	Al	Fe
Concentration (%)	50.542 ±1.532	0.376 ±0.026	0.025 ±0.004	0.069 ±0.007	0.531 ±0.048	0.240 ±0.005	0.117 ±0.003	0.043 ±0.008	0.026 ±0.004
Accession (kg ha^{-1})	263.8	2.0	0.1	0.4	2.8	1.3	0.6	0.2	0.1

4.3.5 Element accumulation and turnover rate in litter

Concentrations of N, P, Mn, Al and Fe were slightly higher in litter components on the forest floor, and lower in concentrations of C, K and Ca than litterfall. Mg concentrations in fresh litterfall components were similar to those in litter fractions on the forest floor (Table 4.8). Accumulation of nutrient elements in the litter ranged from 10.2 kg ha^{-1} for P and 149.5 kg ha^{-1} for N. Element content in the standing crop of litter on the forest floor decreased in the order of C>N>Ca>Al>Fe>K>Mg>P>Mn (Table 4.9).

Table 4.8. Mean concentration of elements in litter on the forest floor collected over 12 months in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Values are mean (± SD; n=3).

Fraction	Element concentration (%)								
	C	N	P	K	Ca	Mg	Mn	Al	Fe
Leaves	42.642 ±1.256	1.385 ±0.188	0.092 ±0.010	0.234 ±0.035	0.763 ±0.052	0.126 ±0.012	0.135 ±0.016	0.751 ±0.122	0.685 ±0.056
Twigs	45.331 ±2.130	0.668 ±0.095	0.042 ±0.004	0.110 ±0.017	0.828 ±0.112	0.102 ±0.021	0.065 ±0.007	0.097 ±0.015	0.022 ±0.003
Flowers/ Fruits	41.052 ±1.854	1.030 ±0.168	0.106 ±0.012	0.412 ±0.028	0.212 ±0.015	0.058 ±0.010	0.042 ±0.005	0.052 ±0.032	0.026 ±0.003

Table 4.9. Element accumulation of litter on the forest floor of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Fraction	Element content (kg ha^{-1})								
	C	N	P	K	Ca	Mg	Mn	Al	Fe
Leaves	3642	118.3	7.9	20.0	65.2	10.8	11.5	64.1	58.5
Twigs	1441	21.2	1.3	3.5	26.3	3.2	2.1	3.1	0.7
Flowers/fruits	398	10.0	1.0	4.0	2.1	0.6	0.4	0.5	0.3
Total	5482	149.5	10.2	27.5	93.6	14.6	14.0	67.7	59.5

Turnover rates for nine different elements in total small litter are given in Table 4.10. Organic C and Ca showed turnover rates that were similar to those for organic matter in the small litter. K and Mg showed higher turnover rates than organic matter, but those of N, P, Mn, Al and Fe were lower, indicating relative enrichment. The turnover of Mg was faster than that of Ca. The estimated amount of mineral element returned from litter to the soil ranged from 1.2 kg ha^{-1}yr^{-1} for Fe to 80.0 kg ha^{-1}yr^{-1} for N.

Table 4.10. Mean turnover rate, turnover time and amount returned to the soil for mineral elements in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

	C	N	P	K	Ca	Mg	Mn	Al	Fe
Turnover rate (k)	0.63	0.53	0.52	1.11	0.59	0.75	0.48	0.08	0.02
Turnover time (year)	1.58	1.87	1.92	0.90	1.69	1.33	2.08	12.50	50.00
Amount returned to the soil (kg ha^{-1} yr^{-1})[a)]	3469.62	79.95	5.31	30.56	55.38	10.66	6.73	5.42	1.19

[a)] Amount returned to the soil was calculated by dividing mineral element content (kg ha^{-1}) of standing crop of litter by turnover time (year) (Rochow, 1975).

4.4. Discussion

4.4.1 Litterfall and seasonal pattern

There were significant differences ($p<0.0001$) in annual litterfall in the natural forest during the 9-year period. Year-to-year variation in litter production is a feature of many forest ecosystems and has been reported by many researchers (e.g. Bray & Gorham, 1964; Egunjobi & Onweluzo, 1979; Briggs & Maher, 1983; Rai & Proctor, 1986; Dantas & Phillipson, 1989; Lisanework & Michelsen, 1994; Sundarapandian & Swamy, 1999). This emphasizes the need for long-term litterfall studies (Chapman, 1979; Lisanework & Michelsen, 1994). In the present study, variation in litterfall is thought to be mainly associated with masting year (gregarious fruiting) of canopy species, and exceptional physical events (such as strong winds, snow) in the area. Most canopy trees such as *Lithocarpus xylocarpus, L. chintungensis* and *Castanopsis wattii* have a fruit yield peak at intervals of 3-5 years. Two peaks (1992 and 1998) of greater fruiting years occurred during the 9 year period, which resulted in higher (annual) litterfall. The higher litter production of winter 1992 is attributable to heavy snow fall, that caused considerable branch and leaf fall to soil. The results suggest that understanding the intricacies of variation in litterfall production between years is important for explaining long term dynamics in this forest ecosystem. Long term observations are necessary to cover cyclical events (masting) and weather extremes.

The seasonal pattern of litterfall largely follows annual environmental changes (Swift *et al.*, 1979). In the present study one major peak of litterfall occurs consistently late in the dry season (April-May) with a second peak also consistently at the beginning of winter (October-November). The climatic records for Xujiaba show that April-May is characterized by low humidity, low rainfall and higher temperatures with evaporation greater than rainfall (Fig. 1). Qiu *et al.* (1998) suggest that rainfall, temperature and light might play an important role in leaf fall and flushing among dominant canopy species in the forest. Phenological observations show that April to May is a period of leaf development and expansion for most evergreen species in the area (Qiu *et al.*, 1998). That seasonal litter production is highest in dry months is consistent with results from tropical forests in India

(Arunachalam *et al.*, 1998; Sundarapandia & Swamy, 1999). The negative correlation (Table 4.2) between litterfall and rainfall in the site corresponds to most results from litterfall studies in other forests (Songwe, Fasehun & Okali, 1988; Matínez-Yrízar & Sarukhan, 1990; Lisanework & Michelsen, 1994). The correlation is explained by the effect of water stress on abscission of leaves and small branches (Songwe *et al.*, 1988, Swift & Anderson, 1989). Water stress, which is usually greatest at the end of the dry season, may be an important factor influencing dry season leaf fall (Jackson, 1978; Okeke & Omaliko; 1994; Sundarapandian & Swamy, 1999). Moore (1980) reports that water stress triggers *de novo* synthesis of abscissic acid in plant foliage, which in turn can stimulate senescence of leaves and other parts. The other minor peak in November could be attributed to strong winds, reduced rainfall and low temperature, combined with regular leaf fall of some deciduous species. Deciduous species in the forest include *Acer heptolobum*, *Betula luminifera*, *Tapiscia yunnanensis*, *Acanthopanax evodiaefolius* and *Lyonia ovalifolia.* Litterfall mainly occurs in autumn and early winter for these deciduous species (Qiu *et al.*, 1998).

4.4.2 Litterfall and associated element inputs

The mean litterfall of the forest of 7.12 t $ha^{-1}yr^{-1}$ (with a range of 5.4-8.2 t $ha^{-1}yr^{-1}$), lies in the low to middle part of the range recorded for tropical moist forests (Vitousek & Sanford, 1986: 5.5-12.0 t $ha^{-1}yr^{-1}$). However, few data exist of litterfall in montane forests exposed to rainfall comparable in size and seasonal distribution of the forest studied. The data are similar to those of New Guinea montane rain forest (7.6 t ha^{-1} $year^{-1}$; Edwards, 1982); Hawaiian montane rainforest on the most fertile soil (7.0 t $ha^{-1}year^{-1}$; Vitousek *et al.*, 1995) and Colombian montane rain forest (7.0 t ha^{-1} yr^{-1}; Veneklaas, 1991). The proportion of leaf litter (65.1 %) in the natural forest is comparable with the reported values of Vaneklaas (1991; 65.6 %) and Scott *et al.* (1992; 67.9 %).

The result for twig litter at Xujiaba (18.6 %) is greater than data reported by Edwards (1982; 15.9 %), Mehra *et al.* (1985; 9-20 %) and Arunachalam *et al.* (1998; 9-16 %), but less than those reported by Bray & Gorham (1964; 21-23), Christensen

(1978; 19-36 %) and Fahey (1983; 17-46 %). The obvious reason for the low values is exclusion of twigs beyond 2.5 cm diameter. The proportion of flower/fruit litter in the study (14.4 %) is slightly greater than the 13.0 % reported by Scott *et al.* (1992) in lowland evergreen rain forest on Maracá Island, Brazil. The difference may be due to the size and heavy weight of oak tree fruits or nuts. A higher proportion of reproductive parts (mainly fruits; 15.9 %) was observed in a bush fallow at Ozala, Nigeria (Okeke & Omaliko, 1994).

In comparison with other montane forests, annual nutrient inputs and nutrient use efficiency in litterfall in this forest are in the middle range of values reported for montane rain forests (Table 4.11). Annual N input in litterfall appears highest (but least N use efficiency) in New Guinea forest, while P and K inputs are highest (but least use efficiencies of P and K) in Colombian forest. Highest annual inputs of Ca and Mg (lowest use efficiencies of Ca and Mg) are reported from litterfall in Hawaiian montane forest but lower inputs of N, P and K. The Ailao mountain forest has similar concentrations, accession and use efficiencies of N, P and K in litterfall to those of montane forest in New Guinea (Edwards, 1982), while the values for Ca and Mg appear to be equivalent to those of montane forest in Jamaica at Mull Ridge (Tanner, 1977). Apart from species composition and climate, soil fertility is the more likely cause of the difference (Vitousek & Sanford, 1986; Herbohn & Congdon, 1998).

The mean seasonal concentrations of the elements studied at Xujiaba are similar to those of Edwards & Grubb (1982) in New Guinea. Although not significant, concentrations of most elements appears to be slightly greater in the rainy season than in the dry season, except for K. Higher K concentrations during the dry season may be due to a lower intensity of leaching (Edwards and Grubb, 1982; Brasell & Sinclair, 1983; Okeke & Omaliko, 1994). However, Swift *et al.* (1981) indicate that lower mean concentration values of K occur in the dry season in a bush fallow. The difference may be due to differences in climate, aspect, altitude and latitude. These factors can greatly affect variations in litter production in different locations (Bray & Gorham, 1964).

Table 4.11. Litterfall mass and associated nutrient return in range of montane forests. Values in parentheses are of nutrient use efficiency (litterfall/nutrient ratio) in litterfall.

Site	Altitude (m)	Rainfall (mm)	Dry mass (tha^{-1}yr^{1})	Concentration (%)					Accession (kg ha^{-1}yr^{-1})					Reference
				N	P	K	Ca	Mg	N	P	K	Ca	Mg	
New Guinea	2500	4000	7.6	1.18	0.07	0.37	1.25	0.25	90 (84)	5.0 (1520)	28 (271)	95 (85)	19 (400)	Edwards, 1982
Venezuela	2250	1500	7.0	0.99	0.06	0.48	0.61	0.20	69 (101)	4.0 (1750)	33 (212)	43 (163)	14 (500)	Fassbender & Grimm, 1981
Jamaica-mull	1600	3000	5.5	0.89	0.03	0.71	0.91	0.31	49 (112)	1.5 (3667)	39 (141)	50 (11)	17 (324)	Tanner,1977
Jamaica-mor	1600	3000	6.6	0.59	0.02	0.23	0.52	0.29	39 (169)	1.3 (5077)	15 (440))	34 (194)	19 (347)	Tanner, 1977
Hawaii-Olaa	1220	2900	7.0	0.96	0.07	0.11	0.23	1.29	67 (104)	4.6 (1522)	8 (875)	16 (438)	90 (78)	Vitousek *et al.*, 1995
Hawaii-Puu Makaala	1220	4000	5.2	0.69	0.03	0.23	1.62	0.19	36 (144)	1.3 (4000)	12 (433)	84 (62)	10 (520)	Vitousek *et al.*, 1995
Hawaii-Saddle Road	1400	3200	5.2	0.54	0.02	0.10	2.62	0.17	28 (186)	1.1 (4727)	5 (1040)	136 (38)	9 (578)	Vitousek *et al.*, 1995
Hawaii-Turston	1190	2500	5.2	0.48	0.03	0.15	1.31	0.19	25 (208)	1.8 (2889)	8 (650)	68 (76)	10 (520)	Vitousek *et al.*, 1995
Colombia	2550	-	7.0	1.17	0.09	0.84	-	-	82 (85)	6.1 (1148)	59 (119)	-	-	Veneklaas, 1991
	3370	-	4.3	0.79	0.04	0.30	-	-	34 (126)	1.9 (2263)	13 (331)	-	-	Veneklaas, 1991
Yunnan, China	2450	1930	7.1	1.12	0.07	0.44	0.80	0.15	80 (89)	5.1 (1396)	30 (238)	58 (123)	11 (647)	This study

Note: nutrient use efficiency is the ratio of litterfall mass (kg ha^{-1} yr^{-1}) to nutrient return in litterfall (kg ha^{-1} yr^{-1}).

Large wood litterfall or branch-fall (≥ 2.5 cm in diameter) is an important component of litterfall in natural forest ecosystems. However, very few data are available on large wood fall in montane forests for comparison of results from this study. Mean annual total large wood litterfall (522 kg $ha^{-1} yr^{-1}$) in the Ailao mountain forest is low. 1320 and 1540 kg ha^{-1} yr^{-1} branchfall (large wood fall) are reported for two sites in Panama (Golley *et al.*, 1975). Kira (1977) reports 3300 kg ha^{-1} yr^{-1} branchfall in tropical lowland rainforests in Malaysia. In tropical rainforests on the Atherton Tableland in north – eastern Australia, branchfall ranges from 464 to 1580 kg ha^{-1} yr^{-1} (Brasell & Sinclair, 1983). Apart from differences between forest types and climatic conditions, a reason for my lower values could be the greater diameter class (≥2.5cm) for collection and the estimation of branchfall. On several occasions during the study, comparatively large falls of wood material occurred. It would appear that these large wood falls were due to high winds bringing down either material in advanced stages of decomposition that had been held up in the canopy or, in the case of heavy snow-fall, fresh material. This observation is consistent with that of Edwards (1977), who found that twigs tend to fall in a highly decomposed condition although the smaller twigs, being easily knocked down or actually shed with the leaves, are the most intact. Both Frangi & Lugo (1986) and Herbohn & Congdon (1998) have also reported increased wood-fall associated with high winds.

4.4.3 Litterfall and element turnover

Litter on the forest floor varies seasonally with litterfall. The estimated mean standing crop of the litter layer (12.69 t ha^{-1}) is less than that obtained in a Bornean rain forest (Burghouts *et al.*, 1998; 20.32 t ha^{-1}). The data are close to the upper part of the range reported for Jamaican montane rain forest (Tanner, 1981; 8.1-11.7 t ha^{-1}), but considerably greater than in the studies of Edwards (1982; 6.5 t ha^{-1}) and Scott *et al.* (1992; 4.6 t ha^{-1}). Higher standing crops of litter layer on the forest floor in forest at higher altitudes are associated with low temperature and slow decomposition of litter (Tanner, 1981, Vitousek & Sanford, 1986). The differences in definition and sampling of litter layer mass on the forest floor may have resulted in differences in estimates of the litter standing crop (Edwards, 1977; Anderson *et al.*, 1983; Proctor, 1987; Coleman, Oades & Uehara, 1989; Young, 1989; Burghouts *et al.*, 1998).

Turnover rates for leaf litter of the Ailao Mountain forest are similar to results obtained for Jamaican montane rain forests (Tanner, 1981; 0.44-0.68), but are considerably less than the values reported for tropical forests elsewhere (Scott *et al.*, 1992; Anderson & Swift; 1983; Proctor, 1987; Burghouts *et al.*, 1998). The turnover rates for litter dry mass are 1.0-3.3 in low tropical rain forests (Anderson & Swift, 1983), 1.5-2.9 and 1.1-2.2 for leaf and total small litterfall in Amazonian forests (Scott *et al.*, 1992). Turnover rates for nine elements studied in small litter at Xujiaba, Ailao Mountain are lower than tropical forests (Scott *et al.*, 1992; Burghouts *et al.*, 1998) but higher than oak-hickory forest in Missouri, U.S. (Rochow, 1975). For those elements studied, K has a higher turnover rate than organic matter and other elements, indicating rapid leaching from the litter. It is usually the most mobile element. P, N and Mn clearly exhibit immobilization, while Mg had a higher turnover rate than Ca, suggesting that Mg is more susceptible to leaching than Ca. Enrichment in the litter is shown for Al and Fe, which may be attributed to contamination from mineral soil (Wesemael & Van-Wesemael, 1993) because the two elements are richer in the soil (Deng *et al.*, 1983). The magnitude of turnover rates of elements and organic matter (OM) is in the order K>Mg>C>Ca>OM>N>P>Mn>Al>Fe. This ranking is similar to temperate forest studies (Nihlgård, 1972; Swift *et al.*, 1979; Duchaufour, 1982) and also Bornean tropical forest (Burghouts *et al.*, 1998).

4.5 Conclusion

This study reveals significant differences in annual litterfall among years. Year to year variation in litterfall is mainly related to the masting years of canopy species, and exceptional physical events (strong winds and snow) in the natural forest. The results suggest that understanding the intricacies of variation in litterfall production between years is important for explaining long term dynamics in the forest ecosystem. Monthly variation in litterfall pattern is marked by two peaks, the main one in the late dry season (April-May) and a lesser one in early winter (October-November). The mean annual litterfall (7.12 t $ha^{-1}yr^{-1}$) is comparable with values observed from montane rain forests elsewhere. Leaf litter accounts for 65 % of total litterfall. Twig and reproductive parts contribute 18.6 and 14.4 % of the total litterfall. Large branch fall is an important component of the natural forest. The ratios of leaf litterfall and total annual litterfall to leaf litter and total litter on the forest floor were 0.54 and 0.58 in this forest.

Differences between the mean seasonal values of elements in leaf and twig litter parts reveals no significance, but concentrations of all elements in leaf and twig litter are greater in wet months than dry months, except for C and K which are greater in dry months. Woody litter has low N and P concentrations compared with the leaf and reproductive parts. Nutrient return to the soil through small litterfall decreases in the order C>N>Ca>K>Mg>Mn>Al>P>Fe, while nutrient reserves in litter on the forest floor are in the declining sequence C>N>Ca>K>Mg>P>Fe>Al>Mn.

In this thesis, I approached the estimation of rates of litter decomposition from two methods. That described in this chapter used a comparison of data for litterfall and the standing crop of litter on forest floor (Waring Schlesinger, 1985). The second, was from direct measurements of the rate of decomposition of freshly-fallen leaves of different species using litterbag method (Swift *et al.*, 1979; Waring & Schlesinger, 1985). The first method, based on a mass-balance approach, only provides overall and mean rates of litter decomposition. The actual litter decomposition and nutrient release may be very different from that implied by turnover coefficients that are calculated from mean values for litterfall and forest floor mass. The litterbag technique is recognized as an effective way for understanding weight loss of decomposing litter and its nutrient release. In the next Chapter, I examine leaf litter decomposition of several important species and nutrient dynamics using the litterbag method.

Chapter 5 Leaf litter Decomposition of Canopy Trees, Bamboo and Bryophytes in Natural *Lithocarpus/Castanopsis* Forest at Xujiaba, Ailao Mountain NNR

5.1 Introduction

Litter decomposition and nutrient mineralization presents an important source of nutrients for primary production in terrestrial ecosystems (Swift *et al.*, 1979; Vitousek, 1984; Berg, Berg & Bottner, 1993; Köchy & Wilson, 1997). It is estimated that nutrients released by litter decomposition make up 70-90 % of the total nutrient requirement of plants (Waring & Schlesinger, 1985). The rate of decomposition is an important determinant of the biomass and productivity of terrestrial forest ecosystems. Litter decomposition and mineralization are affected by physico-chemical factors (temperature, moisture, and pH), litter quality and decomposer organisms (Swift *et al.*, 1979; Schlesinger & Hasey, 1981; Melillo, Aber & Muratore, 1982; Anderson & Swift, 1983; Songwe *et al.*, 1995). Decomposition rate varies considerably between forest types and within sites (Anderson & Swift, 1983; Swift & Anderson, 1989; Lisanework & Michelsen, 1994). There is more organic matter in the soil and a greater standing crop of litter in forests at higher altitudes on tropical and subtropical mountains (Grubb, 1971; Edwards, 1977; Tanner, 1981; Qiu *et al.*, 1998). The accumulation of organic residue on the soil surface allows for the formation of humus that is characteristic of particular ecosystems and represents a provisional accumulation of elements which are released gradually, thereby guaranteeing a permanent contribution of nutrients to the soil (Cuevas & Medina, 1988; Palma *et al.*, 1998).

In Yunnan, SW China, montane evergreen broad-leaved forest, dominated by trees of the genera *Lithocarpus* and *Castanopsis*, is the major vegetation type of subtropical mountainous areas. As in many other natural forests, a major proportion of nutrients in these ecosystems is tied up in organic matter (Edwards, 1977; Tanner, 1981; Jordan, 1982; Vitousek & Sanford, 1986), so that decomposition constitutes a critical path for maintenance of ecosystem production. Although there have been many studies on litter dynamics in other temperate and tropical forests (Swift *et al.*, 1979; Vitousek & Sanford, 1986; Klinka *et al.*, 1994; Palma *et al.*, 1998); information on litter decomposition and nutrient dynamics in montane forest of the subtropical mountainous areas in southwestern China is limited.

Particular features of high altitude and high humidity include a well developed bamboo understory and abundant epiphytic bryophyte populations in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR. These components not only have apparently different leaf morphological characteristics, but were considered likely to have different nutrient cycling characteristics. Additionally, the local climatic regime with cool winters and an alternation of dry and wet seasons was hypothesized as resulting in different litter decay patterns, through affects on soil microorganism activity, and leaching of nutrients and labile elements (Meentemeyer, 1978; Moore, 1986).

In this study, decomposition rates and nutrient dynamics of dominant canopy species, an understory species and epiphytic bryophytes were examined in the natural forest at Xujiaba, Ailao Mountain NNR, SW China. The objectives were to characterize variation in amount and quality of leaf litter, decay rates and release of nutrients through litter decomposition to the soil, within this particular environment and forest where nutrient cycling had not been studied before.

5.2 Material and methods

5.2.1 Materials used

The study site is described in Chapters 2 and 4.

Decomposition and nutrient release were examined for fresh foliage of five important ecosystem components. These were firstly, leaves of three canopy dominants: *Castanopsis wattii, Lithocarpus xylocarpus* and *L. chintungensis*, that collectively comprise 62 % of above-ground biomass, 47 % of total leaf biomass and

45 % of total leaf litter (Chapter 4). Secondly, the understory bamboo, *Sinarundinaria nitida*, that accounts for a high proportion of total shrub layer biomass (Chapter 3). Finally, mixed bryophytes growing on tree stems. Of these, You (1983) identified the four main species as: moss (*Homaliodendron scalpellifolium* and *Symphyodon perrottetti*), and liverworts (*Herberta longifolissa* and *Bazzania albicans*).

The site for this study was the permanent plot (200 x 200 m, 4 ha) close to Xujiaba FERS used for litterfall measurement (Chapter 4). By 1997, litter taken monthly from the traps used in that experiment (1991-1999) had revealed a bimodal seasonal pattern of litterfall with peaks in April-May and October-November each year. On 30 October 1997, freshly fallen foliage of the three canopy species and bamboo was taken from the traps for use in this study. Simultaneously, relatively dry bryophyte was collected randomly from the bark of 20 trees in samples of 20 x 20 cm at 1-1.5 m above ground.

5.2.2 Decomposition

The litterbag method was employed in the study. This method has been recognized as a most useful procedure for understanding decomposition and nutrient dynamics of litter in forest ecosystems (Swift *et al.*, 1979; Berg *et al.*, 1993), although the decay rate measured by this method may be underestimated because of the restriction of macrofauna entry into the litterbags (Ewel, 1976, Sundarapandian & Swamy, 1999).

All collected materials were dried to constant weight in a 60°C oven for 48 hours. Samples of 5 g (weighed to the nearest 0.01 g) for dried leaves and mixed mosses (or 3 g for the lower specific gravity bamboo leaves) were placed in 2 mm mesh nylon bags of 15 x 20 cm. These were then sewn with thread, 50 bags for each litter type. Three samples of each litter type were set aside for determination of initial oven dry weight and initial leaf nutrient concentrations. On 28 November 1997, ten litterbags of each type were placed in each of five, 10 x 10 m blocks, pegged out on the ground in the research plot. Blocks were placed approximately 100 m apart. One litterbag of each type was retrieved randomly from each of the five blocks at intervals: one each three months for 12 months and thereafter one each two months for 10 months (i. e. five bags of each leaf type were removed at each retrieval). Bags were cleaned to remove extraneous materials, arthropods, and sand. Litter was dried at 80 °C to constant mass and weight. From the mean dry weight the decomposition rate constant (k) was calculated for each species using the exponential relationship $X_1/X_0 = e^{kt}$ (Olson, 1963), where X_0 is initial dry weight, X_1 is the dry weight remaining at collection time (t) in years. Decomposition rate constants were determined to compare decomposition rates among the five litter types.

5.2.3 Chemical analysis

Initial samples and residual samples for six collection times over a 22 month period were milled to yield 3 g of finely ground samples for chemical analysis. Three samples taken from mixed whole litter of five litterbags were analyzed of each leaf type at each retrieval. Concentrations of N, P, K, Ca, Mg, Mn and Fe in samples were analyzed as described in Chapter 3 (Section 3.2.4). Lignin concentrations were determined gravimetrically, after acid digestion (72% H_2SO_4) and correction for ash content following the Van Soest method (Cotrufo *et al.*, 1999).

5.2.4 Statistical analysis

The initial chemical composition and the weight loss of decomposing litter were analyzed statistically using one way analysis of variance followed by the multiple comparison Fisher' test at $p<0.05$ to detect whether significant differences occurred between the five leaf types. All statistical analyses were performed using StatView^{TM}(Abacus Concepts, Inc., 1986).

5.3 Results

5.3.1 Leaf litter quality

Initial foliar nutrient levels differed among leaf types and in several cases differences were significant (Table 5.1). Canopy trees had similar levels of foliar nitrogen, but moss had most nitrogen. *Lithocarpus* species had most carbon and highest C: N ratio. *L. chintungensis* had most lignin. *C. wattii* had most foliar P, least lignin and lowest Lignin: P and N: P ratios. Bamboo foliage had least N, P and C with highest lignin: N, lignin: P and N: P ratios. Bryophytes (with most N) had lowest lignin: N and C: N ratios.

Table 5.1. Initial chemical composition of five leaf types in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Values are means (n = 3) with SD in parentheses.

Species	Lignin (%)	N (%)	P (%)	C (%)	Lignin/N	Lignin/P	C : N	N : P
Lithocarpus xylocarpus	42.29 b	1.25 ab	0.091 b	48.64 b	34.05 b	466.37 c	39.13 a	13.76 c
	(1.99)	(0.10)	(0.008)	(0.91)	(3.12)	(33.34)	(2.59)	(1.34)
L. chintungensis	47.86 a	1.29 a	0.074 c	50.62 a	37.31 ab	647.84 b	39.48 a	17.37 b
	(1.35)	(0.09)	(0.005)	(1.00)	(1.90)	(28.41)	(2.28)	(0.44)
Castanopsis wattii	33.60 c	1.30 a	0.101 a	42.23 d	25.98 c	333.95 e	32.67 b	12.70 c
	(1.18)	(0.06)	(0.006)	(1.11)	(1.22)	(17.79)	(0.83)	(0.94)
Sinarundinaria nitida	42.55 b	1.08 b	0.054 d	36.31 e	39.51 a	789.92 a	33.77 b	20.96 a
	(1.84)	(0.14)	(0.006)	(0.95)	(3.28)	(35.26)	(3.31)	(0.40)
Bryophyte	34.16 c	1.39 a	0.083 bc	43.38 c	24.71 c	410.24 d	32.12 b	16.61 b
	(0.98)	(0.09)	(0.004)	(0.78)	(1.63)	(17.39)	(1.56)	(0.52)
F	82.140	4.452	39.007	140.415	24.785	186.599	8.489	40.440
P	0.0001	0.0347	0.0001	0.0001	0.0001	0.0001	0.0056	0.0001

Note: Same letters indicate samples which are not significantly different ($p<0.05$) within a column, using Fisher's LSD test.

5.3.2 Litter decomposition

Changes in mean dry weight of litter of all leaf types during the decomposition period were recorded (Table 5.2). Differences between bags at each sampling occasion for all leaf types tended to increase with time. In general, there were lower values of the coefficient of variation taking five leaf types and all sampling times, ranging from 0.01 to 0.18. Higher coefficients of variation between bags were found at the 18th month of exposure when the litter weight had increased significantly. *C. wattii* had had the highest coefficient of variation.

Table 5.2. Mean dry weight (g) ± S.D. (n=5) of decomposing litter of five leaf types in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Figures in parentheses are proportions of the initial weight remaining at different intervals.

Time (months)	*Lithocarpus xylocarpus*	*L. chintungensis*	*Castanopsis wattii*	*Sinarundinaria nitida* [1)]	Bryophyte	F	P
0	5.00	5.00	5.00	5.00	5.00		
3	4.26±0.06a	4.16±0.11ab	3.92±0.11 c	4.07±0.30abc	4.00±0.16bc	2.843	0.059
6	3.44±0.11b	3.81±0.08a	3.30±0.11 b	3.93±0.21a	4.00±0.16a	21.870	0.0001
9	2.76±0.13b	3.38±0.19a	2.74±0.11 b	3.57±0.35a	3.66±0.24a	20.496	0.0001
12	1.91±0.13d	2.48±0.18c	1.92±0.24 d	2.90±0.15b	3.38±0.28a	43.101	0.0001
14	1.70±0.28c	2.28±0.27b	1.73±0.05 c	2.42±0.29b	2.99±0.20a	23.788	0.0001
16	2.06±0.19c	2.56±0.29b	2.22±0.28bc	3.20±0.32a	3.48±0.33a	26.480	0.0001
18	2.38±0.42b	2.64±0.15b	2.58±0.46ab	2.80±0.42ab	3.04±0.16a	2.755	0.0644
20	1.76±0.48c	2.37±0.30b	1.57±0.14 c	2.22±0.11b	2.86±0.28a	35.865	0.0001
22	1.44±0.11c	1.72±0.18c	1.21±0.18d	1.93±0.15b	2.46±0.17a	51.372	0.0001

[1)] In the case of *S. nitida*, the original dry weight was 3.00 g. Values in this table have been converted in proportion, as if the original weight was 5.00 g. Actual mean weight of decomposing litter was in the order 2.44, 2.36, 2.14, 1.74, 1.45, 1.92, 1.68, 1.33 and 1.16 g.

Same letters indicate samples which are not significantly different ($p<0.05$) within a row, using Fisher's LSD test.

Loss of dry weight followed the same trend for all leaf types (Fig. 5.1). Decomposition was more rapid in the first 12 months, in which the mean monthly decomposition rates were 0.053-0.074 $g.g^{-1}$ for the three canopy species, 0.048 $g.g^{-1}$ and 0.045 $g.g^{-1}$ for bamboo and mixed moss, respectively. Between 14 and 18 months all leaf types increased in weight. In the subsequent 4 months, the rates of decomposition of all leaf types decreased rapidly. The mean monthly decomposition rate within the 14-22 month period decreased to 0.044-0.057 $g.g^{-1}$ for canopy species, 0.039 $g.g^{-1}$ for bamboo and 0.029 $g.g^{-1}$ for bryophyte.

Castanopsis wattii leaf litter decomposed faster than other species (Table 5.2; Fig. 5.1). The lowest decomposition was found in mixed mosses. After 22 months, 49 % of moss mass remained while *C. wattii* had only 24 %. Although bamboo (*Sinarundinaria nitida*) has thin and less rigid leaves (density 0.017 ± 0.001 g cm^{-2}), its decomposition rate was lower than the canopy species with thicker and tougher leaves (densities of foliage of 0.030 ± 0.002 g cm^{-2} - 0.035 ± 0.002 g cm^{-2}).

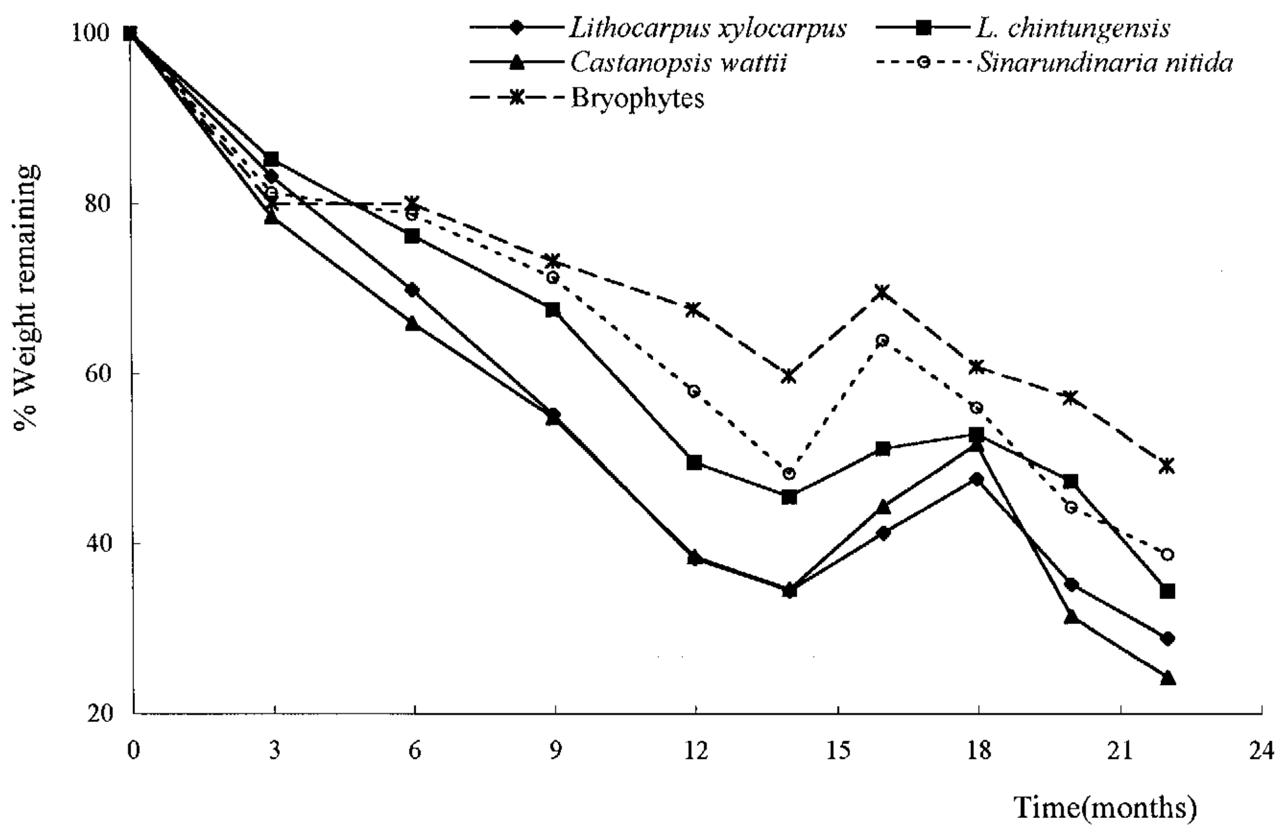

Fig. 5.1. Dry weight remaining as a percentage of the initial mass in decomposing litter of five leaf types in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Using Olson's (1963) model, *C. wattii* leaf litter had the highest decomposition rate constant (k), with a turnover time (1/k) of 1.6 years and the time required for 95% loss of 4.5 years. *Lithocarpus xylocarpus*, *L. chintungensis* and bamboo followed in order. The mixed bryophyte material decayed more slowly, requiring 9.4 years for 95% decomposition (Table 5.3).

Table 5.3. Coefficients of regressions used to estimate decomposition rate constants (k), turnover time (1/k) and time required for 95% loss for the five leaf types. The regression was of the form $X_t = X_0e^{-kt}$, where X_t is the percentage of the mass remaining at time t (years), X_0 is the initial mass in percent dry weight, and k is the decomposition rate constant. ** $p<0.01$.

Species	Regression coefficient			Turnover time (1/k) (year^{-1})	Time (years) required for 95% loss
	X_0 (%)	K (year^{-1})	r^2		
Lithocarpus xylocarpus	91.8356	0.6211	0.8526**	1.61	4.68
L. chintungensis	95.2019	0.4964	0.8864**	2.01	5.94
Castanopsis wattii	91.5513	0.6447	0.8237**	1.55	4.51
Sinarundinaria nitida	91.5513	0.4513	0.8754**	2.22	6.44
Bryophyte	93.5223	0.3118	0.8913**	3.21	9.39

5.3.3 Concentration of nutrients in decomposing litter

Concentrations of N, Mn and Fe in residual tissue increased steadily over the 22 months. There was a slighter increase of N and Mn for tree foliage compared with bamboo and moss (Fig. 5.2). The P concentration in all species also increased in the first 12 months, followed by a gradual decrease later.

Although initial K levels differed among leaf types, the changes in concentration of this element were similar for all five leaf types. Major reductions in K occurred in the first 6 months, followed by little change subsequently. The Ca concentration of bamboo was half that of other leaf types, except for *C. watti*. Despite some fluctuation, the Ca levels were fairly constant. Changes in Mg concentration were variable, but increased levels occurred at 12-14 months, and as with Ca decreased to

12 months and then increased to 16 months, except for bamboo.

5.3.4 The absolute amount of nutrient in decomposing litter

The observed change in concentrations of most nutrient elements did not correspond to net immobilization of nutrients. Change in the absolute amount of nutrient during decomposition is a function of loss in mass and change in relative nutrient concentration in remaining litter. Change in the absolute amount of each nutrient is expressed by percentage of the initial amount remaining (Fig. 5.3). Canopy species showed initial N immobilization and then later release, while bamboo and bryophyte had a net release of N over 22 months. By 22 months the net release levels of N from *Lithocarpus xylocarpus*, *L. chintungensis*, *Castanopsis wattii*, *Sinarundinaria nitida* and moss were 43, 47, 60, 30 and 39 % of the initial amount, respectively. With the exception of *C. wattii* and *L. xylocarpus*, P in decomposing litter increased in the first 12 months, especially for moss, reaching 152% at 6 months and 130% at 12 months, of the initial level. By 22 months, the net release levels of P from the five litter types were 57, 62, 72, 44 and 40 %, respectively, of the initial amount. More than 60% of K was released from all species within 6 months, and > 75% by 12 months with little subsequent loss. By 22 months, the net release levels of K from the five litter types were 81, 82, 91, 85 and 77 %, respectively, of the initial amount. During the 22 month period there was a net release of Ca from all the litter types with rapid initial loss, followed by a more gradual release. Both Ca and Mg increased from 12 to 14 months, after initial declines. At 22 months, the net release levels of Ca were 73, 69, 83, 63 and 53 % respectively, and the net release levels of Mg were 61, 53, 81 and 46% for canopy species and bryophyte respectively, however Mg in bamboo litter increased slightly (Fig. 5.3). Mn in canopy species followed an initial release and then had small increases at 18 months, while Mn in bamboo and bryophyte material was greater, reaching 118 % and 171 % of the initial amounts, respectively. Fe was an accumulative element in this experiment: some 264-1425 % of the initial amount was accumulated in all leaf types over the 22 month period.

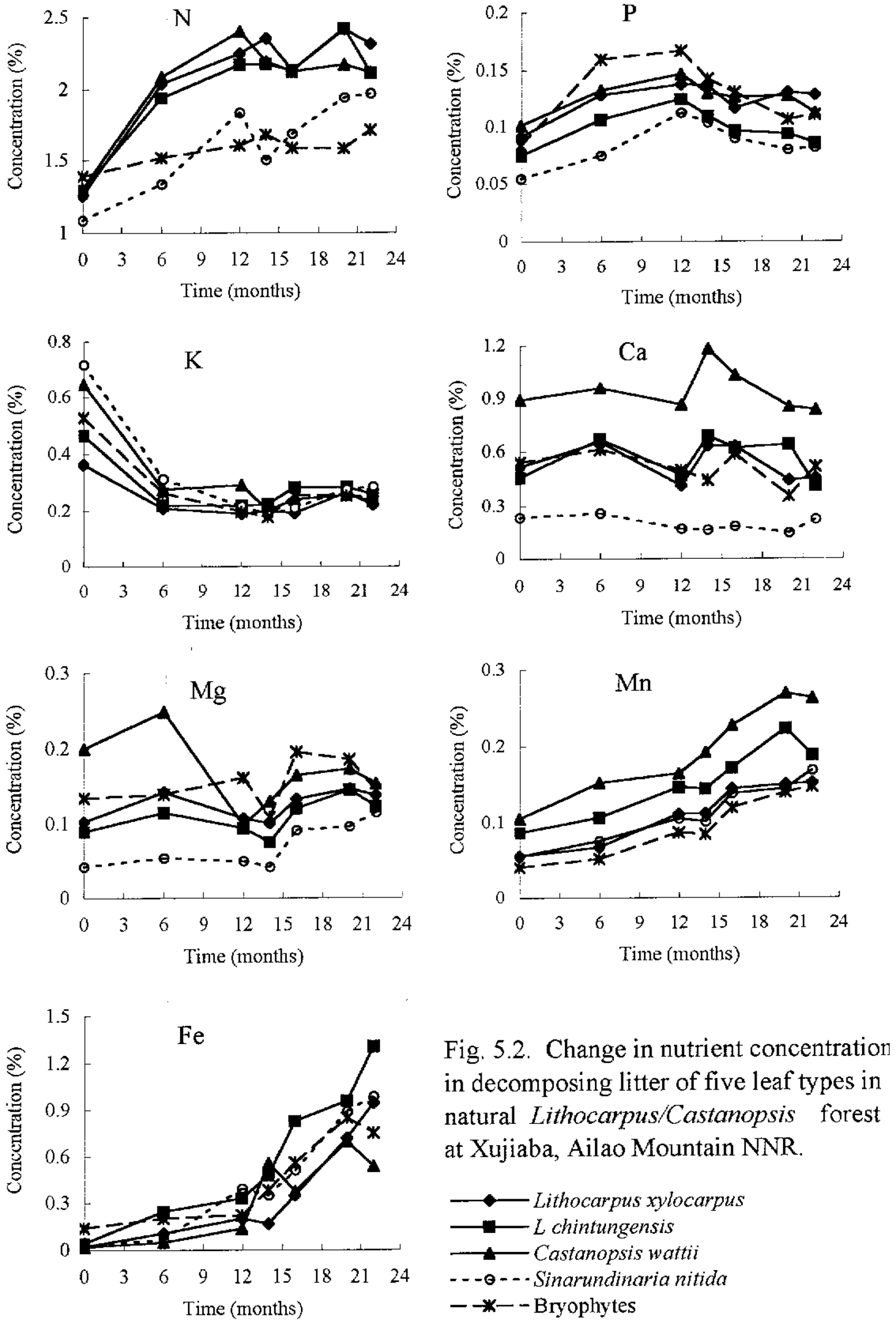

Fig. 5.2. Change in nutrient concentration in decomposing litter of five leaf types in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

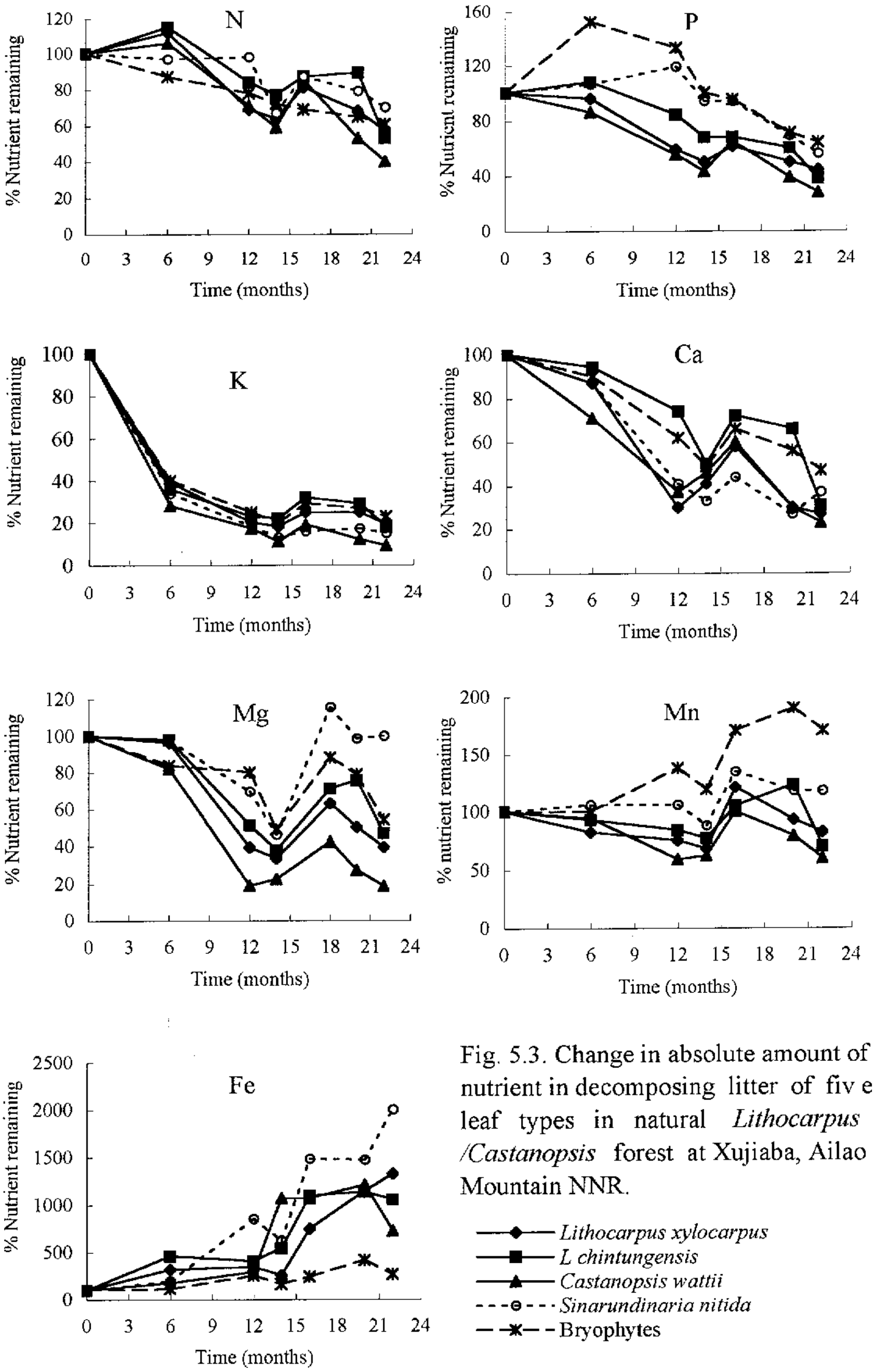

Fig. 5.3. Change in absolute amount of nutrient in decomposing litter of five leaf types in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

For the 22 month period, the aggregate rate of nutrient release for all leaf types followed the sequence of K>Ca>Mg>P>N>Mn>Fe, except for bamboo (*Sinarundinaria nitida*) where the corresponding order was K>Ca> P>N>Mg> Mn>Fe.

5.4 Discussion

5.4.1 Initial composition and decomposition rates

Litter decomposition of all leaf types is initially rapid, followed subsequently by a slower rate. Faster initial decay rates may reflect easily decomposable tissues and readily mineralisable elements (Swift *et al.*, 1979; Swift & Anderson, 1989; Kumar & Deepu, 1992; Songwe, Okali & Fasehun, 1995; Sundarapandian & Swamy, 1999). Residual tissues decompose less readily. Relatively slower decay rates in later stages may be attributable to accumulation of more resistant or stable constituents in residual litter mass (Sundarapandian & Swamy, 1999). Leaching is the main factor influencing weight loss of litter during initial stages (Swift *et al.*, 1979; Blair, 1988; Berg *et al.*, 1993; Songwe *et al.*, 1995). Pardo, Gil & Pardos (1997) report that leaching and decomposition are halted during summer dryness. Higher relative loss of mass during the rainy season than in the dry season is a feature of tropical forest (Sundarapandian & Swamy, 1999). Timing of placement of litterbags is an important factor that affects decomposition rates in regions where distinct dry and wet seasons alternate. In Xujiaba the rainy season occurs from June to October and the dry season from November to May (Fig. 2.2). *Lithocarpus* species litterfalls are highest in April-May and October-November. The decomposition experiment of leaf litter commenced early in the dry season. During the study period, samples taken at 6 and 18 months coincided with change from dry to wet weather. Loss of dry weight of decomposing litter is generally higher in the rainy period than that in the dry period, although some rainfall events early in the dry season, result in higher decomposition rates. During the height of the dry season (between 3 and 6 months, and 14 to 18 months, respectively, or March-May 1998, 1999) lower decomposition rates of litter occurred for all leaf types, presumably because with scarce moisture, less leaching can occur at those times.

Decomposition rates between leaf types differ significantly. Varying rates of decomposition have been related to initial nutrient composition and lignin concentration in leaves (Singh & Gupta, 1977; Melillo *et al.*, 1982; Upadhyay, 1993; Lisanework & Michelsen, 1994; Couteaux, Bottner & Berg, 1995; Bubb *et al.*, 1998; Murphy, Klopatek & Klopatek, 1998; Cotrufo *et al.*, 1999). Other authors have attributed variability to morphological characters of foliage (Edwards, 1977; Songwe *et al.*, 1995). Wedderburn & Carter (1999) emphasize that N and lignin concentration and the lignin: N ratio in leaf litter appear to be likely controls of the rate of decay. Of the three canopy species in the present study, *Castanopsis wattii* and *Lithocarpus xylocarpus* have lower lignin and higher N and P concentration in initial leaves and these decompose faster than that of *L. chintungensis*, which has higher lignin concentration and lower N and P concentration (Table 2; Fig. 2). It has also been shown that the proportion of lignin, N and P in litter affects decomposition rate (Melillo *et al.*, 1982; Lisanework & Michelsen, 1994; Couteaux *et al.*, 1995). P deficiency, higher N: P and lignin: P ratios in decomposing leaf litter are associated with lower decomposition rates (Lisanework & Michelsen, 1994; Gallardo & Merino, 1999). Bamboo leaves decompose more slowly than canopy species leaves. Bamboo leaves are thinner, less rigid and of lower density than are leaves of canopy species, but they are distinguished by higher lignin: N, lignin: P and N: P ratios although lignin in bamboo leaves is not least among the tested litter species. These results suggest that decomposition rates of canopy species and bamboo in the same environmental conditions may be controlled more by nutrient composition and lignin concentration than by their morphological characters.

In the case of bryophyte, the decomposition rate seems less related to initial nutrient concentration. Daubenmire & Prussco (1963) found poor intraspecific correlation between N content and decomposition rates. Lower decomposition rates in species with higher N and P concentration also occur in tropical forest (Sundarapandian & Swamy, 1999). Bryophyte has higher N and P concentration in initial material. After an initial rapid weight loss, bryophyte subsequently decomposes more slowly. Lower decomposition of bryophyte may be associated with higher content of repellent tissues (Nakatsubo *et al.*, 1997). That bryophytes are effective in uptake and slow release of nutrients in humid mossy forest is reported elsewhere (Li & Vitt, 1997; Nakatsubo, 1997; Nakatsubo *et al.*, 1997). Higher initial nutrient concentration of bryophytes could be attributed to presence of many microbes (fungi, acarids, arthropods, etc.) in bryophyte tissues and to atmospheric deposition captured by such species (Coxson & Nadkarni, 1995). These loosely attached nutrients would be readily leached in the first stage, leaving more resistant structural materials that may decay slowly. Resistance to decomposition and low potential to immobilize nitrogen for bryophyte litter is in agreement with results reported elsewhere (Coxson & Nadkarni, 1995; Hobbie, 1996; Nakatsubo *et al.*, 1997).

Dry weight of decomposing litter appears to have increased 8-20 % within 12-18 months of the start of the experiment. Apparent increases of bagged leaf litter weights between some months are reported for five species of tropical forest in Cameroon (Songwe *et al.*, 1995). This could be due to entry of organisms or other contaminants excluded by the mesh size employed (Swift *et al.*, 1979; Songwe *et at.*, 1995). At 19 months, dry weight of decomposing litter decreases at the time of onset of the summer wet season. The increased moisture may have washed out the debris.

Decomposition rates of canopy species in the present study are high, compared to values reported for temperate forests. Decomposition constants of some temperate hardwood species range from 0.08 to 0.47 (Melillo *et al*, 1982); and for pine species from 0.307 to 0.46 (Das & Ramakrishnan, 1985). Songwe *et al.* (1995) report that mean decomposition constants of five species with different leaf morphological characteristics in tropical forest vary from 1.60 to 4.18. These generate times required for 50 % decay of 1.8 to 4.6 months and turnover time (1/k) of 2.2 to 7.7 months. In the present study the time required for 95 % decay ranges from 4.5 to 9.4 years, higher levels than other reported ranges. Thus my decomposition rates for canopy species in the middle mountain humid evergreen broad-leaved forest lie in the upper part of the range for temperate forest and in the lower part of the range recorded for montane tropical forest. This is consistent with the present understanding of the status of these forests as in a transitional or intermediate category, in relation to environmental conditions.

5.4.2 Nutrient dynamics of decomposing litter

N and P concentrations in litter of all species reveal an increase in the first 12 months, followed by a decrease corresponding with subsequent loss in mass. The absolute amounts of these two elements in decomposing litter vary with different decay rates between species, as elsewhere (Palm & Sanchez, 1990; Lisanework & Michelsen, 1994; Songwe *et al.*, 1995). High concentrations of N and P in decomposing litter are affected by atmospheric deposition, leaching, insect frass and fungal accumulation (Swift *et al.*, 1979; Lisanework & Michelsen, 1994). N, and especially P concentration in decomposing residues increase in P deficient substrates (Alexander, 1976). The high accumulation of P in decomposing litter in the initial stage has also been observed in forests elsewhere (Upadhyay & Singh, 1989; Palm & Sanchez, 1990; Lisanework & Michesen, 1994). Songwe *et al* (1995) note high initial build up of N and P in decomposing litter might reflect the degree of limitation of these elements in litter and soil. At Xujiaba, P concentration in the soil is relatively low (Appendix 2). Fresh leaf litter of canopy species and bamboo has a higher N: P ratio. In decomposing litter this ratio decreases initially and then subsequently increases with decreased decay rate. High N: P ratio in fresh litter in soils where P is limited, affecting litter decomposition is not unusual (Lugo & Murphy, 1986; Lisanework & Michelsen, 1994). This suggests P limitation in the soil substrates, a hypothesis supported by the low available P found in all soils (Michelsen *et al.*, 1993). The high ratio of N: P indicates that P may limit litter decomposition of natural forest in the Ethiopian highlands in the beginning and at the end (Lisanework & Michesen, 1994). Vogt *et al.* (1986) note that the ideal N: P ratio for decomposers is 10 and higher ratios limit litter decomposition. In this study P seems to limit decomposition of canopy species, bamboo and bryophyte litter both initially and later.

K is released rapidly, with more than 75% mineralization occurring in the first 12 months. Subsequent slow K release reflects low residual levels (Songwe *et al.*, 1995). Both Mg and Ca are also relatively rapidly mineralized, similar to that shown in other forests (Swift *et al.*, 1981; Anderson & Swift, 1983; Palm & Sanchez, 1990; Lisanework & Michelsen, 1994). Loss of Mg is attributed to leaching, while release of Ca is mainly associated with cellular decay (Lisanework & Michelsen, 1994). Mn and the absolute levels of Fe increase dramatically in decomposing litter. The net accumulation of Fe, Al and Mn may be associated with contamination from mineral soil (Wesemael & Van-Wesemael, 1993).

The natural forest is characterized by tall canopy tree species, well developed bamboo and abundant epiphytes. Varying decomposition rates of leaf litter and nutrient dynamics of dominant species in each story suggests that the role or importance of litter decomposition and nutrient dynamics in each story on whole nutrient dynamics of the old growth forest ecosystem may be different. In my study difference between stories in the old growth forest may be insignificant. However, it is recommended that a study of decomposition and nutrient dynamics of the different stories be need in order to better understand whole nutrient dynamics and its cycling in the forest ecosystem.

5.5 Conclusion

All species studied have a pattern of fast initial litter decomposition that is followed by lower rates. Although there are apparent differences in leaf morphological characteristics among species studied, decomposition rates of canopy species (*Lithocarpus xylocarpus*, *L. chintungensis* and *Castanopsis wattii*) and bamboo leaf litter appear to be controlled by initial concentration of lignin, N and P more than by morphological features of the leaves. The decay rate of bryophyte litter is less correlated with nutrient composition and lignin concentration in initial mass. The order of decomposition rates is *Castanopsis wattii* > *Lithocarpus xylocarpus* > *L. chintungensis* > bamboo > bryophyte. Decomposition rate constants (k) of leaf litter for canopy species range from 0.50 to 0.64, and 0.40 and 0.22 for bamboo and bryophyte.

N and P concentration in decomposing leaf litter increases in the first 6 months and thereafter decreases over the remaining period. K has a relatively rapid initial loss, followed by a slight increase. Each of Ca and Mg decrease with time, whereas Fe and Mn increase with time to some extent. Nutrient release from decomposing leaf litter is in the order of K>Mg>Ca>N>P>Mn>Fe, except for bamboo (*Sinarundinaria nitida*) K>Ca> P>N>Mg>Mn>Fe.

Within this natural forest ecosystem, nutrients are derived from the decomposition of plant parts, which release nutrients to the soil solution from which plant roots may access them. Atmospheric input is also an important source of nutrients to natural forest ecosystems. In the next Chapter, I will describe patterns of nutrient input through water fluxes within this natural forest ecosystem.

Chapter 6 Nutrient Fluxes in Bulk Precipitation, Throughfall and Stemflow in Natural *Lithocarpus/Castanopsis* Forest at Xujiaba, Ailao Mountain NNR

6.1 Introduction

In humid environments, nutrient cycles are closely tied to hydrological linkages (Bormann & Likens, 1967; Likens *et al.*, 1977; Parker, 1983). Nutrients are deposited in both wet and dry deposition (McColl & Bush, 1978; Pehl & Ray, 1983; Parker, 1983); produced or retained by the forest canopy; flushed into groundwater, as throughfall and stemflow infiltrates the soil profile; and, exported from the catchment in stream water (Likens *et al.*, 1977; McDowell, 1998).

Estimation of the fluxes of elements in precipitation, throughfall and stemflow is a routine part of nutrient budget studies in forests (Corlin, 1971; Tsutsumi, 1971; Likens *et al.*, 1977; Schlesinger & Hasey, 1980; Sollins *et al.*, 1980; Parker, 1983; Crockford & Richardson, 1998). Throughfall, the portion of precipitation that interacts with vegetation, is enriched by washing deposited materials from plant surfaces and by nutrients leaching from plant tissues (Switzer & Nelson, 1972; Bernhard-Renverat, 1975; Rolfe, Akhtar & Arnold, 1978; Parker, 1983). Stemflow, the portion of the rainfall reaching the forest floor via plant stems, is similarly enriched by nutrient leaching and washing of the stems (Gersper & Holowaychuk, 1971; Switzer & Nelson, 1972; Rolfe *et al.*, 1978; Parker, 1983). Throughfall and stemflow have ecological significance because all nutrients of these fluxes are soluble, particularly foliar leachates being readily reabsorbed by plants (Tukey, Tukey & Wittwer, 1958; Parker, 1983; Bellot & Escarre, 1991) and being available to microbes in the forest floor (Lodge, McDowell & McSwiney, 1994).

Interactions between hydrological and nutrient cycles are well documented for many temperate forests (Likens *et al.*, 1977), but much less is known about such interactions in montane moist forests at high altitude (Parker, 1983; Vitousek & Sanford, 1986). The chemistry of throughfall and stemflow may be affected by cryptogamic epiphytes through selective uptake or release of elements within montane moist forests (Barkman, 1959; Lang, Reiners & Heier, 1976; Knops & Nash, 1996). However, little information is available for mountainous regions at high elevation, regarding precipitation interception and subsequent nutrient changes on passing through forested canopies and thick epiphyte growth, although such inputs have been shown to be important for maintaining tree growth in natural forests (Lang *et al.*, 1976; Parker, 1983; Knops *et al.*, 1991).

The forest type studied in this thesis, on the remote western slopes of the Ailao Mountains, is essentially a mossy forest, with well-developed epiphytic moss and liverworts. This forest has not been subject to air pollution or other significant anthropogenic influence (Young & Wang, 1989; Qiu *et al.*, 1998). Precipitation is believed to be the source of major nutrient inputs to the natural forest. Additionally, this forest has provided an opportunity to discover baseline information on patterns of nutrient fluxes in undisturbed natural forest. The purpose of this Chapter is to characterize the magnitude of nutrient fluxes via precipitation, throughfall and stemflow in the montane moist evergreen broad-leaved forest at Xujiaba, Ailao Mountain NNR during the 24 month period (January 1998 to December 1999).

6.2 Materials and methods

6.2.1 Study site

This study was conducted within the previously described 4 ha (200 x 200 m) research site near Xujiaba FERS. Site characteristics were described earlier (Chapter 2, 4). The plot is on a southwestern-facing *Lithocarpus xylocarpus* stand, with two tree layers, subordinate shrub and herb layers, and with abundant epiphytes. The stand density (trees with DBH ≥10.0 cm) was 516 stems per hectare with 90 % of canopy cover, is similar to the 2 low density site of the biomass study reported in Chapter 3.

6.2.2 Rainfall and throughfall

Rainfall was collected from two rain gauges (20 cm diameter) positioned 1 m above ground in the meteorological observatory of Xujiaba FERS, at about 100 m from the forest edge. Intensity of each rainfall event was obtained from continuous records of an automatic rain gauge installed at Xujiaba meteorological station. A large funnel and collector in the same area provided samples for elemental analysis. A subplot of 50 x 50 m was established and fenced using deer-proof fencing within the centre of the 4 ha research plot. Throughfall was obtained in this subplot from 12 collectors. Each collector consisted of a 20 cm diameter polyethylene funnel attached with tubing to a 2 l glass collection bottle. Fiberglass mesh window screen was used to cover the funnel tops to prevent the entrance of insects and particles. Regular measurements of rainfall and throughfall were taken at 8:00, 14:00 and 20:00 hr each day. Samples of throughfall were pooled after measuring the 12 individual throughfall volumes and subsamples were taken from the mixed samples for chemical analysis.

6.2.3 Epiphytic biomass on boles and stemflow

Two groups of sample trees were selected to examine the influence of epiphytes on the amount and chemistry of stemflow. Each group consisted of a total of 12 stems (different diameter classes), which included three stems of small (<20 cm), moderate (20-40 cm) and larger (40-60 cm) bole diameter classes for each of the three dominant species *Lithocarpus xylocarpus*, *L. chintungensis* and *Castanopsis wattii*, and one moderate diameter stem for each of three other co-dominant tree species (*Machilus viridis*, *Manglietia insignis* and *Schima noronhae*). For one group, all 12 sample trees were stripped of all epiphytes living on the bark of stems and large branches of the trees in late November to early December 1997. Epiphytes on small branches were not removed. For the other group, all 12 sample trees were keep intact as the control. All epiphytes scraped from each stem were weighed fresh and then stored in plastic bags. Samples of epiphytes were oven-dried at 80 °C to constant weight. Fresh weights were converted to dry weight using the respective fresh weight-dry weight ratios. Epiphytic biomass per hectare was estimated as the sum of the product of mean biomass per tree times the numbers of trees for each diameter class. To examine water-holding capacity of the epiphytes, dried epiphyte samples were immersed in water for 48 hours, and then weighed. The maximum water-holding capacity of moss was estimated as the difference between moist and dry weight.

Stemflow collections were made under the stems of the two groups (with and without epiphytic bryophytes). Stemflow for each tree was collected using spiral polyethylene collars around the tree trunk, connected to plastic containers. Stemflow volumes were measured on site three times a day (as described for rainfall and throughfall). Stemflow samples taken from 12 trees of each treatment group were combined, and subsamples taken for chemical analysis.

To minimize growth of microorganisms in the collectors (rainfall, throughfall and stemflow) a few (2-3) drops of 0.05 % chloroform were added (Kellman, Hudson & Sanmagadas, 1982).

6.2.4 Chemical analysis

During the two year period from 1 January 1998 to 30 December 1999, 100 ml samples of precipitation, throughfall and stemflow, were transferred each two months into high-density polyethylene bottles and sent to Kunming Institute of Ecology for chemical analysis. All samples were first filtered through a 0.5 um Whatman No. 42 filter paper, stored in a refrigerator and analyzed as quickly as possible. pH was measured electrochemically. Cation concentrations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) were determined by flame atomic absorption spectrophotometry (AAS: Atomic Absorption Spectrum – 932, GBC Scientific Equipment Pty. Ltd. Australia). Sulfate (SO_4^{2-}-S) sulphur was determined by Inductively Coupled Plasma Atomic Emission Spectrum (ICP-AES, IRIS Advantage-ER, Thermo Jarrell Ash Corporation USA). Phosphorus was determined using the molybdenum blue colorimetric procedure (Institute of Soil Academia Sinica, 1978). Total N was obtained by Kjeldahl digestion followed by analysis of NH_4-ions (micro-Kjeldahl distillation and titration with 0.001 N HCl). NO_3^--N was determined after reduction to NO_2^--N by colorimetric methods (sulphanilamide/N-1-napthylethylene-diaminedihydrochloride; Institute of Soil Academia Sinica, 1978).

6.2.5 Flux calculations

The reliable estimation of throughfall nutrients, demands a good forest hydrological budget. The components of the forest hydrological budget were expressed as the following equation (after Parker, 1983): $Pr = I+Tr+St$, Where Pr, I, Tr and St are incidental precipitation, interception loss, throughfall and stemflow respectively. Incident precipitation that does not appear on the forest floor by either throughfall or stemflow is called the interception loss, The sum of throughfall and stemflow is the total forest water or net rainfall (Parker, 1983).

Hydrological fluxes for the two-year period were calculated for rainfall, throughfall, stemflow, runoff and summed as the volume-weight unit based on three measurements each day. Elemental fluxes for each component were calculated by multiplication of the volume-weighted mean nutrient concentrations by the respective water volumes. The amount of nutrients leached from leaves and boles was calculated as the total amount in throughfall and stemflow minus the input in precipitation. In order to compare Xujiaba FERS values with other montane rain forests, elemental net flux was taken as the difference between the flux in throughfall and the flux in bulk precipitation. The deposition ratio was the flux in throughfall divided by the flux in bulk precipitation (Parker, 1983).

6.2.6 Statistical analysis

Concentrations of nutrient elements in rainfall and throughfall and two treatments for stemflow from stems with and without epiphytes, were analyzed statistically, based on the respective 12 samples for each component, using one way analysis of variance (ANOVA). All statistical analyses were performed using StatView^{TM}(Abacus Concepts, Inc., 1986).

6.3 Results

6.3.1 Monthly distribution of rainfall

The two year experimental period had a much higher mean annual rainfall (2165 mm, Table 6.1) than the mean (1931 mm) over the period 1991 to 1995 (Section 2.2.2). The total annual rainfall in 1999 exceeded this five-year mean by 435 mm. The higher rainfall results in greater water movement from canopy to forest floor, and then infiltration and drainage in the catchment.

The rainfall distribution pattern of the study site is strongly seasonal (Fig. 6.1). Rainfall from May to October comprised 88.3% of total annual rainfall in 1998 and 92.1% in 1999. The maximum monthly rainfall was 581.8 mm in July 1998. During the two-year period, there were nine months when rainfall exceeded 200 mm. The amount of rainfall in the dry season (November to April) was 230.3 mm in 1998 and 187.6 mm in 1999. The minimum monthly rainfall was 1.5 mm in Feb. 1999, and the mean monthly rainfall in the dry season was 32.9 mm during the two-year period.

6.3.2 Dynamics of canopy interception

Crown interception by the forest canopy was characterized by a distinct seasonal pattern, a low capacity for water storage, and was greatly influenced by total rainfall and rainfall intensity. The amount of rainfall intercepted by the forest canopy was 13.6 % in 1998 and 12.6 % in 1999 (Table 6.1). Monthly interception ranged from 8.7 to 17.3 % in rainy months and 22.4 to 84.2 % in dry months. In ten months, interception exceeded 30 mm in the rainy season during the two-year period. The greatest monthly interception was 62 mm in August 1998. During the dry months of December to March 1998 and 1999, most of the incidental precipitation was low rainfall with low intensity and was intercepted by the canopy. Heavy storm events were infrequent in that period (Fig.6.1).

In general, the amount of interception loss by the canopy increased with rainfall. However, the rate of interception, expressed as the ratio of interception by canopy to

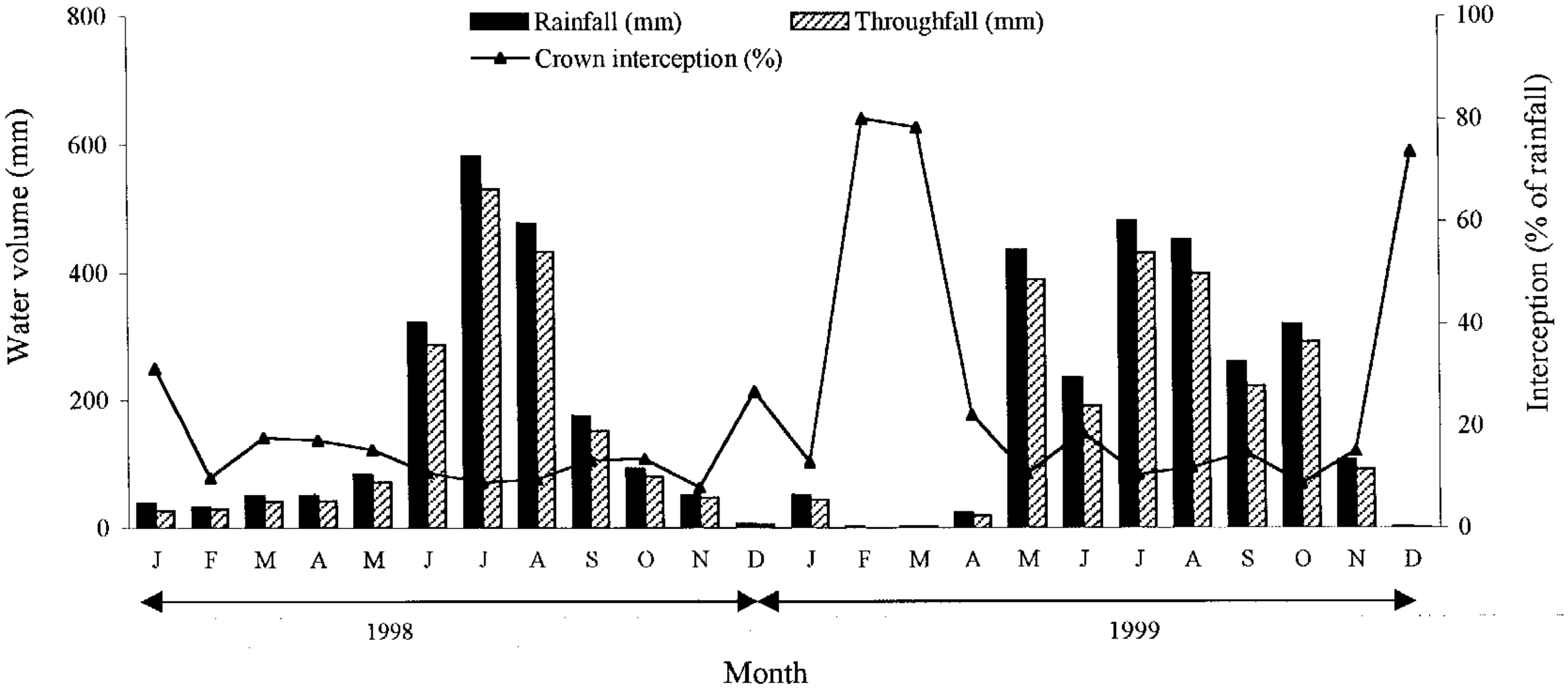

Fig. 6.1. Monthly distribution of rainfall, throughfall and interception in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR (1998-1999).

Table 6.1. Annual total amount of precipitation, throughfall and interception by canopy in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Years	Precipitation (mm)	Throughfall		Crown interception	
		(mm)	(%)	(mm)	(%)
1998	1964.6	1697.4±48.2	86.37	267.2±48.2	13.64
1999	2365.0	2067.3±42.6	87.41	297.6±42.6	12.58
Mean	2164.8	1882.2	86.94	282.7	13.06

rainfall, decreased with increased rainfall. It correlated negatively with rainfall and intensity of rainfall (Fig. 6.2).

6.3.3 Dynamics of stemflow

6.3.3.1 Epiphytic biomass and its water-holding capacity

Mean biomass of epiphytes in the natural forest was estimated at 1360 kg ha^{-1}. Moss (*Homaliodendron scalpellifolium* and *Symphyodon perrottetti*), liverwort (*Herberta longifolissa* and *Bazzania albicans*) were the dominant species on tree stems, contributing more than 85 % of total biomass of bryophytes on the bark of boles and branches of trees. The total dry weight of bryophytes (mean ± SD) was 1223 ± 1043 g tree^{-1}. Variation in total moss biomass for individual trees was very high, with 85 % coefficient of variation for individual trees. The maximum water-holding capacity of the moss was determined to be 10-13 times greater than its own dry weight.

6.3.3.2 Comparison of stemflow from stems with and without epiphytes

Within the natural forest, the amount of stemflow comprised only 2.0 % of annual rainfall. The stemflow was significantly increased by removal of epiphytic bryophyte (40 % increase, Table 6.2). Some 16.9 mm of stemflow water volume was calculated as intercepted and absorbed by epiphytic bryophytes each year. The observed results also showed differences in seasonal variation of stemflow between the two bryophyte treatment groups (with and without epiphytic bryophytes). The

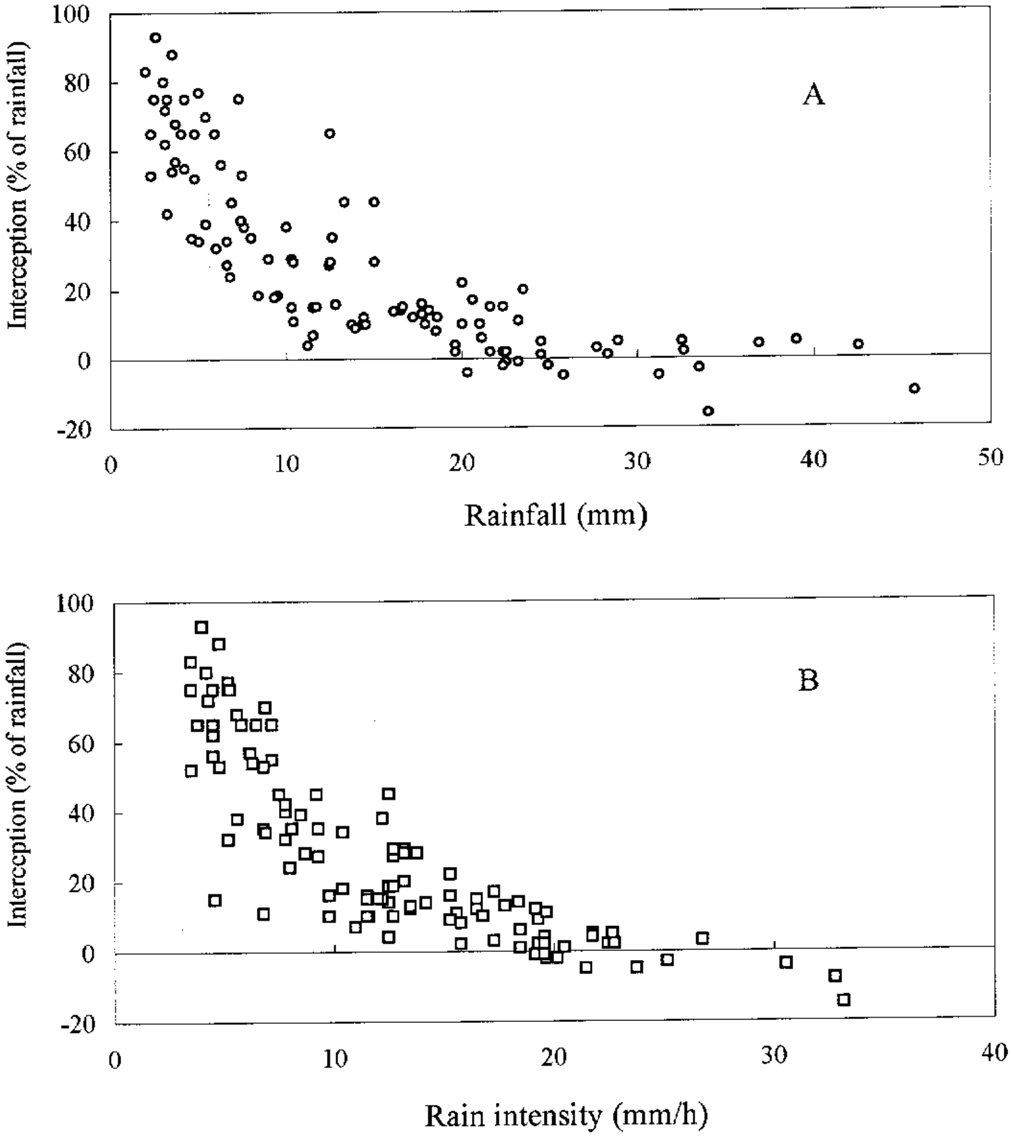

Fig. 6.2. Relationships of A, interception rate with rainfall (indicated by circles) and B, rainfall intensity (indicated by squares) in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountains.

Table 6.2. Annual amount of stemflow from two treatments in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Years	Precipitation (mm)	Stems with bryophytes		Stems without bryophytes	
		(mm)	(%)	(mm)	(%)
1998	1964.6	38.0±25.9	1.93	56.1±35.4	2.86*
1999	2365.0	46.9±29.7	1.98	62.6±40.7	2.65*
Mean	2164.8	42.5	1.96	59.4	2.76

* Significant ($p<0.05$).

maximum monthly stemflow occurred in July 1998, with 14.4 mm (2.5 % of that month's rainfall) from stems with bryophytes, and 21.4 mm (3.7 %) from stems without bryophytes. In the dry months (December to March) there was little stemflow, following several storms (Fig. 6.3).

6.3.4 Nutrient inputs

6.3.4.1 Nutrient concentration in precipitation, throughfall and stemflow

The weighted monthly pH values (6.2 to 6.5) for precipitation are close to neutrality. Within any sampling date, throughfall was observed to be significantly ($p<0.05$) acidified as compared to rainfall, and there was a positive relationship in pH values between rainfall and throughfall. The pH value of stemflow was considerably lower than for precipitation and throughfall, with pH values between 5.5 and 6.1. Seasonal variation of pH in precipitation revealed maximum pH values in the rainy season and minimum values in the dry season.

The chemical composition of precipitation in the area was dominated by nitrogen and calcium. Elemental concentration in precipitation and throughfall exhibited seasonality (Table 6.3). Concentrations of total N, NO_3^--N, K, Mg and SO_4^--S in precipitation were higher in the dry season than in the rainy season, whereas NH_4^+-N, P, Ca and Na concentrations were relatively high in the rainy season.

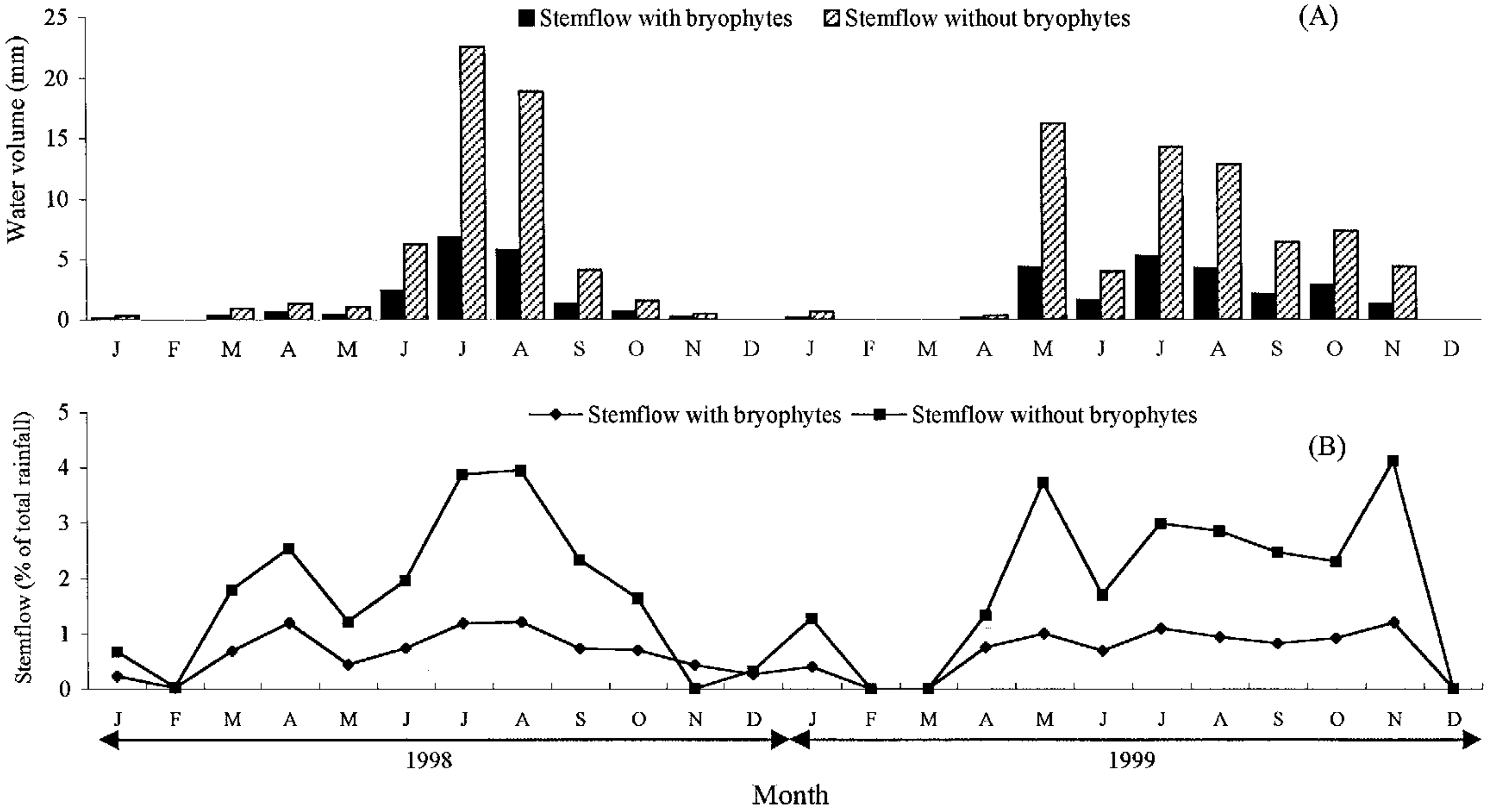

Fig. 6.3. Monthly distributions of stemflow from stems with and without epiphytes in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR during the study period (1998-1999). (A). Stemflow water volume (mm); (B). Stemflow rate (% of total annual rainfall).

Table 6.3. Volume-weighted mean concentration (± SD) in precipitation and throughfall in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR in dry season (n = 4) and wet season (n=8). Nutrient concentrations in throughfall vs. precipitation are compared in analysis of variance and the F values associated with the treatments are given.

Items	Season	pH	Nutrient concentration (mg/l)								
			Total N	NH_4^+-N	NO_3^--N	P	K	Ca	Mg	Na	SO_4^--S
Precipitation	Dry	6.20	0.484	0.083	0.053	0.041	0.193	0.286	0.075	0.069	0.158
		±0.22	±0.128	±0.035	±0.012	±0.012	±0.076	±0.093	±0.030	±0.020	±0.046
	Wet	6.52	0.491	0.130	0.035	0.060	0.134	0.380	0.158	0.082	0.130
		±0.13	±0.153	±0.058	±0.008	±0.016	±0.054	±0.092	±0.057	±0.024	±0.037
	Annual	6.42	0.489	0.114	0.041	0.054	0.154	0.349	0.129	0.078	0.139
		±0.22	±0.144	±0.052	±0.013	±0.018	±0.069	±0.103	±0.061	±0.023	±0.043
Throughfall	Dry	6.10	0.750	0.172	0.185	0.061	2.536	0.435	0.372	0.049	0.220
		±0.16	±0.212	±0.068	±0.063	±0.014	±0.514	±0.173	±0.058	±0.012	±0.039
	Wet	6.25	0.632	0.190	0.075	0.079	1.685	0.841	0.532	0.121	0.199
		±0.08	±0.213	±0.062	±0.20	±0.020	±0.188	±0.246	±0.101	±0.019	±0.057
	Annual	6.20	0.672	0.184	0.121	0.073	1.968	0.739	0.483	0.097	0.206
		±0.13	±0.211	±0.062	±0.065	±0.019	±0.520	±0.263	±0.115	±0.039	±0.051
F value[1)]		20.645	12.09	44.534	19.87	11.054	152.858	41.130	106.433	2.687	13.747
p		0.0008	0.0052	0.0001	0.001	0.0068	0.0001	0.0001	0.0001	0.1294	0.0035

[1)] F values were calculated based on all samples (n=12) of dry and wet seasons for each element.

Table 6.3. Volume-weighted mean concentration in precipitation and throughfall in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR in dry season (n = 4) and wet season (n=8). Nutrient concentrations in the throughfall vs. the precipitation are compared with an ANOVA and the F values associated with the treatments are given.

Significant differences ($p < 0.05$) were observed between precipitation and throughfall in concentrations of nutrient elements, and enrichment occurred within the natural forest for all nutrient elements. The ratios of nutrient concentration in throughfall to precipitation were 1.4 for total N; 1.6 for NH_4^+-N; 3.0 for NO_3^--N; 1.3 for P, 12.8 for K; 2.1 for Ca; 3.7 for Mg; 1.2 for Na and 1.5 for SO_4^--S (Table 6.3).

An incremental enrichment factor relative to rainfall was observed in stemflow after throughfall. The solution flowing along the trunk surface already contained the elements caught in the canopy but also collected large amounts of elements from contact with stembark and bryophytes. Stemflow composition differed significantly ($p<0.05$) from throughfall for all nutrient elements (Tables 6.3, 6.4). The enhancement in concentration with respect to rainfall was about 2-5 times for P, Na, SO_4^--S and total N, and much higher and variable (from 10 to 48 times) for NH_4^+-N, NO_3^--N, Ca, Mg and K.

Epiphytic bryophytes significantly affected chemical composition of stemflow ($p< 0.05$). Total N, NH_4^+-N, Ca, Mg, Na and SO_4^--S exhibited higher concentrations in stemflow from stems with bryophytes. The reverse was observed for NO_3^--N, P and K, which were significantly higher in stemflow from stems without bryophytes (Table 6.4).

6.3.4.2 Annual nutrient input

Annual input of each element from precipitation was calculated as the sum of the product of mean concentration and rainfall amounts in different seasons. Total annual nutrient inputs reaching the forest floor indicated that each nutrient amount was increased by the canopy. However, the amount differed among nutrients (Table 6.5). 91 % of the total annual K and 67 % of the total annual Mg throughfall input was due to canopy. However, 87 % the total N, 86 % of the P, 52 % of the Ca and most of the Na, SO_4^--S, NH_4^+-N and NO_3^--N annual throughfall inputs came from precipitation. The amounts of NH_4^+-N and NO_3^--N in annual precipitation were smaller and more variable than total N. The input of total N was more than twice the sum of the two inorganic-N forms.

Table 6.4. Volume-weighted mean concentration (± SD) in stemflow from two treatments in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR in dry season (n=4) and wet season (n=8). The two stem treatments in nutrient concentration are compared in analysis of variance and the F values associated with the treatments are given.

Treatment	Season	pH	Nutrient concentration (mg/l)								
			Total N	NH_4+-N	NO_3^--N	P	K	Ca	Mg	Na	SO_4^--S
	Dry	5.70	3.442	0.785	0.595	0.145	5.255	3.665	0.551	0.196	0.270
		±0.16	±1.271	±0.142	±0.217	±0.080	±1.504	±0.482	±0.169	±0.091	±0.056
Stems with	Wet	5.82	1.859	1.315	0.330	0.089	3.250	1.184	1.105	0.121	0.217
bryophytes		±0.23	±0.542	±0.524	±0.086	±0.020	±1.190	±0.418	±0.171	±0.049	±0.041
	Annual	5.78	2.386	1.138	0.418	0.108	3.908	2.011	0.920	0.146	0.235
		±0.22	±1.112	±0.498	±0.206	±0.053	±1.569	±1.291	±0.317	±0.072	±0.051
	Dry	5.67	2.175	0.578	0.755	0.119	9.855	4.470	0.535	0.175	0.257
		±0.13	±0.903	±0.099	±0.125	±0.059	±1.810	±0.886	±0.103	±0.089	±0.048
Stems without	Wet	6.09	1.166	1.004	0.465	0.062	6.034	1.942	0.834	0.104	0.208
bryophytes		±0.28	±0.332	±0.241	±0.072	±0.020	±1.088	±0.602	±0.114	±0.030	±0.037
	Annual	5.95	1.502	0.862	0.562	0.081	7.308	2.785	0.734	0.127	0.224
		±0.31	±735	±0.386	±0.167	±0.042	±2.277	±1.412	±0.182	±0.063	±0.046
F values 1)		4.275	6.222	3.235	6.740	9.380	45.607	14.598	11.177	1.486	0.812
p		0.063	0.0298	0.0995	0.0249	0.0108	0.0001	0.0028	0.0066	0.2484	0.3869

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*1) F values were calculated based on all samples (n=12) of dry and wet seasons for each element

Table 6.5. Seasonal and annual input of nutrients through precipitation in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Items	Season	Nutrient input (kg ha^{-1} $year^{-1}$)								
		Total N	NH_4^+ -N	NO_3^- -N	P	K	Ca	Mg	Na	SO_4^- -S
Precipitation	Dry	0.88	0.15	0.23	0.08	0.35	0.52	0.14	0.12	0.29
	Wet	9.60	2.54	0.68	1.17	2.62	7.43	3.09	1.60	2.54
	Total	10.48	2.69	0.91	1.25	2.97	7.95	3.23	1.72	2.83
Throughfall	Dry	1.11	0.26	0.27	0.09	3.77	0.91	0.55	0.08	0.37
	Wet	10.96	3.29	1.30	1.37	29.21	14.43	7.49	2.08	3.42
	Total	12.07	3.55	1.57	1.46	32.98	15.34	8.04	2.16	3.79

Although stemflow nutrient concentrations for individual storms were higher than throughfall and precipitation, total annual stemflow nutrient inputs to the forest floor on a per hectare basis were a minor component, accounting for only 8.5 % of that for throughfall due to the small amount of water flowing through them (Tables 6.5, 6.6). Relative to trees without bryophytes, the annual stemflow nutrient inputs of stems with bryophytes was enhanced for total N, Ca and Mg, but decreased for K, P, NO_3^--N, NH_4^+-N, and SO_4^--S.

Table 6.6. Comparison of nutrient content in stemflow from two treatments (with and without epiphytes) in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Treatments	Season	Nutrient input (kg ha^{-1} $year^{-1}$)								
		Total N	NH_4^+-N	NO_3^--N	P	K	Ca	Mg	Na	SO_4^--S
Stems with bryophytes	Dry	0.10	0.02	0.02	0.00	0.15	0.10	0.02	0.01	0.01
	Wet	0.74	0.52	0.13	0.04	1.29	0.47	0.44	0.05	0.09
	Total	0.84	0.54	0.15	0.04	1.44	0.57	0.46	0.06	0.10
Stems without bryophytes	Dry	0.08	0.02	0.03	0.01	0.38	0.17	0.02	0.01	0.01
	Wet	0.65	0.56	0.26	0.03	3.35	1.08	0.46	0.06	0.12
	Total	0.73	0.58	0.29	0.04	3.73	1.25	0.48	0.07	0.13

6.4 Discussion

6.4.1. Throughfall and nutrient inputs

In the present study, annual throughfall of 1886 mm corresponds to 87.1 % of total rainfall. The amount of interception loss by the canopy is higher compared with montane evergreen broad-leaved forests elsewhere (Parker, 1983). High throughfall in this forest may reflect the relatively high rainfall during the study period. Parker (1983) indicates that the amount of precipitation controls the magnitude of throughfall. Interception rate increases with decreased rainfall and rainfall intensity (Fig. 6.2).

The proportional amount of throughfall in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR, lies in the upper range of values recorded for tropical montane and lowland rain forests. In Ghanaian lowland forest, Nye (1961) reports throughfall as 84 % of rainfall (1850 mm), while Manokaran (1979) found it to be 78 % in Malaya (rainfall 2380 mm). Working in lower montane rain forest at El Verde in Puerto Rico (rainfall 3760 mm), Jordan (1970) estimates throughfall as about 70 % of rainfall. Edwards (1982) obtained a range of 60-74 % of rainfall (3700-3900 mm), for a montane rain forest in New Guinea, while Brasell & Sinclair (1983) record 76-88 % in rainforests on the Atherton Tablelands, Australia, with annual rainfall of 2256-3805 mm. The Xujiaba value reported here is similar to the 88 % of rainfall for montane tropical rain forests at 2550 m altitude with rainfall of 2112 mm in Colombia (Veneklaas, 1990).

Although these overall values provide a useful basis for comparison, the proportion of throughfall depends on the intensity of rainfall and the conditions for evaporation (Edwards, 1982). In the Xujiaba region, a lower proportion of throughfall occurs in the drier months (e.g. 51 % for the period March to April 1998, where the mean rainfall was 31.8 mm per month). These much reduced amounts of throughfall may have important effects on the seasonal distribution of litterfall (Chapter 4). Similar results are observed in New Guinea montane rain forest (Edwards, 1977).

The nature of the intercepting canopy and climatic conditions affect interception (Eaton, Liken & Bormann, 1973; Tsutsumi, 1977; Parker, 1983). High interception by montane rain forest in New Guinea is associated with abundance of tree foliage in the smaller classes of leaf-size (mainly microphyll and notophyll, and mainly without drip tips) plus abundant epiphytes in the forest canopy, as well as long sunny periods (Edwards, 1982). In the Xuijaba region, mesophylls comprise 40.3 % of total species and leaves with drip tips are common, present on 62.4 % of all tree and shrub species (Qiu *et al.*, 1998). This area is characterized by high humidity throughout the year and fog-covered days are frequent, despite alternations of dry and wet periods (Zhang *et al.*, 1994). These differences may reduce canopy moisture storage compared with other montane rain forests.

The rainfall composition of this site ranks it as a pristine area. The "pristine" state is associated with low sulphur and nitrogen concentration; neutral pH values (range: 6.2-6.5) of rainfall water, and no significant difference between rainy and dry season pH values. Differences detected in pH values and sulphur concentrations between rainfall and throughfall or stemflow were also low for this natural forest. Fan *et al.* (1999) report that the pH values in rainfall, throughfall and stemflow in a polluted Chinese fir plantation in Fujian, southeastern China were 5.6-6.5, 5.2-6.4 and 2.8-5.6, respectively, and suggest that there are due to acidifying effects of sulphur dioxide on precipitation.

In a wide variety of environments, alteration of precipitation bypassing the canopy appears to be similar. Based on studies of temperate forests, Parker (1983) concluded that throughfall tended to be enriched in base cations and dissolved organic carbon, and depleted in NH_4^+ and NO_3^- relative to precipitation. The results of this study and others in tropical montane rain forests reveal a clear pattern of increased base cation and fluxes in throughfall compared to precipitation (Table 6.7). This is particularly true for K; fluxes of K in throughfall are typically 5-10 times higher than those in rainfall (Edwards, 1982; Veneklaas, 1990; Forti & Moreira-Nordemann, 1991; Sinun *et al.*, 1992; Asbury *et al.*, 1994; Strigel *et al.*, 1994; McDowell, 1998). The enrichment of elements in throughfall has been attributed to the dissolution and washout of atmospheric materials deposited on the canopy (Eaton *et al.*, 1973; Parker, 1983) or due to the exchanges between rainfall and elements in internal plant parts (Tukey, 1970; Marques & Ranger, 1997; McDowell, 1998). The external origin (dry deposition) and internal cycling (leaching process) can take place for most of the elements, with different intensities. The quantities of nutrient elements leached are related to the levels of exchangeable elements in the foliage (Mecklenburg, Tukey & Morgan, 1966; Yawney, Leaf & Leonard, 1978). According to Franke (1967), these exchangeable nutrients are free ions translocated outside the cytoplasm. The extent to which individual nutrients are leached appears to be dependent not only upon the mineral nutrient status of the plant, but also on the balance that exists between elements (Yawney *et al.*, 1978). The increase in K content of throughfall would indicate that the level of exchangeable K is related to the overall K economy within the foliage.

Differences between the flux of sodium in precipitation and throughfall are indicative of the magnitude of dry deposition of marine aerosols (Parker, 1983). The high humidity of this montane forest should be conducive to high rates of dry deposition, but throughfall is enriched in sodium by only 26 % on a flux basis (Table 6.5) because this site is a large distance from the ocean. Wet deposition appears to be the dominant pathway for deposition of marine aerosols at this site. However, the amount of sodium in the precipitation and throughfall is considerably less than for montane rain forests elsewhere (Table 6.7). This indicates that the origin of nutrients in the precipitation at Xujiaba, Ailao Mountain is from sources other than marine aerosols, such as the atmosphere, smoke, and dust (Parker, 1983). Nitrogen (total N, NH_4^+-N and NO_3^--N), P, Ca and SO_4^--S are mainly from precipitation, while over 80 % of the total K and two thirds of the total Mg probably leach from the canopy. This is in agreement with results reported for montane rain forests elsewhere (Table 6.7) and other forest sites (Brinson *et al*, 1980; Pehl & Ray, 1983; Marques & Ranger 1997; Friedland & Miller, 1999). The total annual inputs of elements in throughfall are either intermediate or in the lower range reported for montane rain forests (Table 6.7).

Table 6.7. Annual fluxes of nutrient (kg ha^{-1}) in bulk precipitation (R) and throughfall (T) in a range of montane rain forests.

Site	Precipitation (mm)		Total N	NH_4^--N	P	K	Ca	Mg	Na	SO_4^--S
Puerto Rico (430 m)	R	3500	-	0.69	-	4.69	13.0	8.53	63.3	-
	T	2060	-	3.34	-	51.6	22.7	13.4	81.3	-
Jamaica (1550 m)	R	c. 2600	-	-	-	7.1	5.5	5.0	20.3	-
	T	c. 2385	-	-	-	42.7	13.3	11.5	29.0	-
New Guinea (2450 m)	R	c. 3800	6.5	-	0.5	7.3	3.6	1.3	-	-
	T	c. 2585	36.1	-	3.0	78.4	22.6	12.2	-	-
Venezuela (2300 m)	R	1576	9.9	-	1.10	2.6	5.6	5.2	3.3	-
	T	1260	8.5	-	1.38	69.7	6.9	3.3	4.4	-
Colombia (2550 m)	R	2115	18.0	18.3	0.72	7.9	10.1	3.2	24.1	26.2
	T	1845	22.4	21.5	1.67	95.2	27.1	10.7	26.9	40.9
Colombia (3370 m)	R	1453	12.2	11.2	0.48	6.9	7.3	2.5	15.9	16.8
	T	1188	10.5	11.6	0.40	33.0	18.8	7.0	14.4	31.7
Yunnan, SW China (2450 m)	R	2165	10.5	2.7	1.35	3.0	8.0	3.2	1.7	2.8
	T	1886	12.1	3.6	1.46	33.0	15.3	9.8	2.2	3.8

Source: Puerto Rico, McDowell (1998); Jamaica, Tanner (1977), means for four sites; New Guinea, Edwards (1982), means for four sites; Venezuela, Steinhardt (1979); Colombia, Veneklaas (1990).

The extent to which elements are leached from a forest canopy depends upon such factors as temperature, precipitation amount and intensity, the residence time of water on the leaves and leaf index, and indirectly depend upon the availability of minerals in the soil (Edwards, 1982; Parker, 1983). The rainfall and the average temperature (11.3 °C) in the Xujiaba forest are lower than in tropical lowland rain forests; leaf area index (5.8; Qiu *et al.*, 1984) is lower than in most tropical rain forests (Edwards & Grubb, 1977); and the rate of litter decomposition (0.5-0.6) is considerably less than that of tropical forest (Chapter 5). Thus, the throughfall data for this montane forest reflect a generally lower cycling rate of mineral elements than for other tropical montane rain forests.

Net flux and deposition ratios provide information on the effect of the canopy on precipitation chemistry, and are useful for comparisons between forests (Parker, 1983; Adams & Attiwill, 1986; Veneklaas, 1990). The overall amount of annual net flux of nutrients appears higher in New Guinea montane rain forest compared to other montane rain forests (Table 6.8). This may reflect high foliar leaching due to frequent and abundant rainfall or some fundamental difference. K is considered to be the most easily leached element (Tukey, 1970). In this Xujiaba study, however, there appears to be a relatively lower leaching of K compared with montane rain forests in New Guinea (Edwards, 1982) and in Colombia (2550 m; Veneklaas, 1990). A possible explanation is that the amount of leachable K declines with high intensity precipitation. Relatively low foliar K concentration (Chapter 3) is also an important factor. However, in spite of some variation, deposition ratios of K are high in all forests. Ca and Mg are similar in all forests, except the Venezuelan site, which has low net fluxes and deposition ratios. The soil at that site is low in exchangeable Ca and Mg (Table 6.9). Circulation of Ca and Mg is high in forests with well endowed sources of these elements (e.g. in Malaysia, Crowther, 1987). Steinhardt (1979) suggests that Mg is absorbed by the canopy in Venezuelan cloud forest. This would be contrary to the pattern for Mg in most other forests (Parker, 1983). Na has low net fluxes and deposition ratios close to unity, except at the two near-ocean Caribbean sites. Wash-off of marine aerosols, captured by the canopy, probably contributes to the throughfall fluxes at these two sites. Net flux and deposition ratio of P are highest in the New Guinean forest. The availability of P is probably greatest there because soil P reserves and soil pH are high (Table 6.9). Sanchez (1976) found that a large

Table 6.8. Annual net fluxes (throughfall flux – bulk precipitation fluxes) and deposition ratios (throughfall fluxes/bulk precipitation fluxes).

Site	Precipitation (mm)	Total N	NH_4^+-N	P	K	Ca	Mg	Na	SO_4^--S
Annual net fluxes (kg ha-1)									
Puerto Rico	3500	-	2.6	-	46.9	9.7	4.9	18.0	-
Jamaica	c. 2600	-	-	-	35.6	7.8	6.5	8.7	-
New Guinea	c. 3800	29.6	-	2.5	71.1	19.0	10.9	-	-
Venezuela	1576	-1.4	-	0.3	67.1	1.0	-1.9	1.1	-
Colombia(2550 m)	2115	4.4	3.2	0.95	87.3	17.0	7.5	2.8	14.7
(3370 m)	1453	-1.7	0.4	-0.08	26.1	11.5	4.5	-1.5	14.9
Yunnan, SW China	2165	1.6	0.9	0.2	30.2	7.3	6.6	0.5	1.0
Deposition ratios									
Puerto Rico	3500	-	4.7	-	10.9	1.7	1.6	1.3	-
Jamaica	c. 2600	-	-	-	6.0	2.4	2.3	1.4	-
New Guinea	c. 3800	5.6	5.7-	-	10.7	6.3	9.4	-	-
Venezuela	1576	0.9	-	1.3	26.8	1.2	0.64	1.3	-
Colombia (2550 m)	2115	1.2	1.2	2.3	12.1	2.7	3.3	1.1	1.6
(3370 m)	1453	0.9	1.0	0.8	4.8	2.6	2.8	0.9	1.9
Yunnan, SW China	2165	1.2	1.3	1.2	11.1	1.9	3.1	1.3	1.4

Note: Sites and references see Table 7.6.

part of P in soil with low pH is immobilized.

Table 6.9. Soil characteristics at some montane rain forest sites[1].

Site	Depth (cm)	pH	Total N (%)	Total P (%)	Exchangable bases (mmol 100 g^{-1})			
					Ca	Mg	K	Na
Jamaica	30-45	3.6	0.6	-	0.8	1.4	0.4	0.2
New Guinea	30	6.0	1.4	0.17	9.4	2.7	0.9	0.5
Venezuela	40	3.5	0.34	0.05	0.3	0.2	0.2	0.1
Colombia								
2500 m	30	4.0	-	-	0.6	0.4	0.3	0.1
3550 m	25	4.7	0.9	-	0.7	0.7	0.3	0.2
Ailao Mts., SW China	30-50	4.87	0.32	0.06	2.53	0.60	0.15	0.82

[1]. Sources: Jamaica, Tanner (1977), mean for four sites; New Guinea, Edwards & Grubb, 1982, means for four sites; Venezuela, Steinhardt (1979); Colombia, Veneklaas (1990). Ailao Mts., Deng *et al.*, (1983), the soils were sampled in forest close to the present study.

The high deposition of N in throughfall in New Guinea is probably also caused by higher leaching rates related to the greater availability of that element in the soil. However, N-fixation organisms (blue green algae, bacteria) on foliage may capture atmospheric N, giving rise to enrichment of throughfall water (Ruinen, 1965, 1975; Edmisten, 1970). Some 61 kg N ha^{-1} yr^{-1} is trapped by N-fixation organisms in Puerto Rico lower montane forest (Edmisten, 1970). Forman (1975) estimated a biomass of 5.7 kg ha^{-1} of lichens containing bluegreen algae, capable of fixing some 1.5-8 kg N ha^{-1}yr^{-1}. Although the humid environments of montane tropical rain forests seem favorable for the establishment of N-fixation organisms, low temperature, high acidity and shade on the forest floor may limit the occurrence and activity of N-fixing lichens, bacteria and bluegreen algae in the phyllosphere (Gibson & Jordan, 1983), especially at high altitude (Veneklaas, 1990). Bentley (1987) found a net uptake of nitrogen from precipitation by leaves covered with N-fixing epiphylls. Veneklaas (1990) suggested that only a small part of the nitrogen fixed by epiphytic organisms reaches the forest floor via throughfall at high altitude in Colombia. Climate and vegetation of Xujiaba, Ailao Mountains are somewhat comparable with that of the 2550 m site in Colombia. It is probable that a lower proportion of nitrogen fixed by epiphytic organisms enters the throughfall in the Ailao mountain forest.

6.4.2. Effect of epiphytes on nutrient dynamics

The epiphyte biomass in the montane forest at Xujiaba, Ailao Mountain NNR is dominated by bryophytes. The total dry weight of epiphytes in this study (1360 kg ha^{-1}), lies in the lower range (2.0-4.0 t ha^{-1}) obtained in lower montane forest by Frangi & Lugo (1986, 1992). My estimate may be lower because I did not collect smaller species of bryophytes or epiphytic ferns. However, in comparison with estimates from various moist forest ecosystems (Table 6.10), the data for epiphytic biomass are within the middle to lower range of reported values.

Although epiphytic mosses can contribute a substantial amount of biomass to forest canopies, few studies have examined the effect of epiphytes on nutrient cycling. Studies from an oak woodland in California report epiphytic lichens affecting interception by the canopy and as important in deposition of water and nutrients in throughfall (Knops & Nash, 1996). At Xujiaba, I observed that epiphytes significantly affected the amount and chemistry of stemflow. These epiphytes store high quantities of water and nutrients and intercept materials washed from foliage. In this study, 29 % of total annual stemflow had been intercepted by epiphytic bryophytes living on stembark. Canopy epiphytes intercept 8.8 % of the total annual throughfall relative to throughfall underneath trees stripped of their epiphytes in an oak woodland in California (Boucher & Nash, 1990; Knops *et al.*, 1991). Some species (e.g. *Plagiochila* spp.) have been shown to retain more water than the phorophyte itself (Pòcs, 1980). The importance of epiphytes in the hydrological balance and for watershed conservation are obvious (Richards, 1952, 1984).

Nutrient dynamics in the stemflow solution are also associated with epiphytes. Some elements (total N, NH_4^+-N, Mg, Na and SO_4^--S) are enriched in stemflow solutions, but others are impoverished (NO_3^--N, P, K and Ca) as a consequence of epiphyte interactions. Barkman (1959) and Lang *et al.* (1976) suggest that cryptogamic epiphytes might affect the chemistry of precipitation collected below the canopy (throughfall) and at tree bole bases (stemflow) by selective uptake or release of elements. Enrichment of stemflow water has been attributed to inputs from mosses, lichens and other organisms living on the surface of boles and branches of trees (Nye, 1961; Yawney *et al.*, 1978). Coxson (1991) and Coxson & Nadkarni (1995) note that epiphytes have an enormous surface area available to capture nutrient elements. Epiphytes reportedly increase total atmospheric inputs in tropical montane forests to values up to 2.5 times higher than for low elevation forests (Bate & Farmer, 1992). Nutrient scavenging from rainwater by epiphytes was described by Jordan *et al.* (1980). Although the mechanism of nutrient uptake and release by epiphytes is not clear at the ecosystem level, the importance of epiphytes in nutrient cycling of forest ecosystem is recognized (Lowman & Nadkarni, 1995).

Table 6.10. Biomass estimate for epiphytes in some montane forest ecosystems

Ecosystem	Location	Biomass (t ha^{-1})	Source
Montane moist forest	Ailao Mountain, SW China	1.36	This study
Dry forest	Guanica, Puerto Rico	0.14	Murphy & Lugo, 1986
Moist forest	Manaus, Brazil	0.05	Klinge *et al.*, 1975
Lower montane wet forest	Luquillo Experimental forest Puerto Rico	0.05	Weaver & Murphy, 1990
Lower montane forest	Costa Rico	0.017[a]	Romero,1999
Lower montane wet forest	Luquillo Experimental forest Puerto Rico	2.0-4.0	Frangi & Lugo, 1986, 1992
Lower montane rain forest	Jamaica	2.8	Tanner, 1980
Lower montane rain forest	New Guinea	3.4	Edwards & Grubb, 1977
Submontane forest	Uluguru Mountains, Tanzania	2.13	Pócs, 1980, 1982
Mossy elfin forest	Uluguru Mountains, Tanzania	13.6	Pócs, 1980, 1982
Elfin woodland	Monteverde, Costa Rica	4.7	Nadkarni, 1984
Upper montane cloud forests	Columbia	33.0	Hofstede *et al.*, 1993

[a]: The value represents the pendant non-vascular epiphytic material available for harvest (1-3 m above the ground).

By subtracting nutrient elements in stemflow under stems without bryophytes from that of the stems with mosses, I calculate the epiphyte contribution to stemflow as 0.11 kg ha^{-1}year^{-1} for N, 0.21 kg ha^{-1}yr^{-1} for Ca and 0.05 kg ha^{-1}yr^{-1} for Mg. These values were enhanced by epiphytes. In contrast, values of 1.29 kg $ha^{-1}yr^{-1}$ for K, 0.03 kg $ha^{-1}yr^{-1}$ for P and 0.03 kg $ha^{-1}yr^{-1}$ for S suggest these nutrients were conserved in stemflow by epiphytes.

6.5 Conclusion

The results of this study reveal that low rainfall interception (13 % of total annual rainfall) by the forest canopy could be attributed to the high rainfall and humidity, combined with leaf architecture: median size leaves (mainly mesophylls) with drip tips.

The rainfall composition at this site indicates that the natural forest has not been subject to air pollution inputs and can be considered to be a pristine area.

Base cations and fluxes are increased in throughfall, while NH_4^+-N and NO_3^--N are reduced, compared to precipitation. N, P, Ca and S annual throughfall inputs are mainly from precipitation, while most K and two thirds of the Mg throughfall input is due to canopy leaching. Inputs of Na in precipitation and both throughfall and stemflow are low in this forest.

Net flux (throughfall flux minus bulk precipitation) and deposition ratios (ratio of throughfall flux to bulk precipitation flux) are in the lower part of the range reported for other tropical montane rain forests. The throughfall data for this forest show a generally low cycling rate of mineral elements. The patterns described in the present study are in agreement with other studies that reduced rates and limited availability of nitrogen and phosphorus occur in high altitude rain forests.

Epiphytic bryophytes on bole bark is shown to affect the chemical composition of stemflow by selective uptake or release of elements. Relative to trees without epiphytic bryophytes, the annual amounts of total N, NH_4^+-N, Mg, Na and SO_4^--S are enhanced, while NO_3^--N, K, P and Ca are depleted in stemflow.

Although atmospheric inputs supply important sources of available nutrients to plant growth, it provides a small percentage of the annual requirement of nutrients. The remaining nutrients must be supplied by intrasystem cycling, including efficient retention of nutrients in trees and return of nutrients in decomposition of dead plant parts. In the next Chapter, I will describe annual uptake and retention of nutrients in the natural forest.

Chapter 7 Uptake and cycling of nutrient in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR

7.1 Introduction

Nutrient movement within natural forest ecosystems includes intra- and inter-system cycles (Waring & Schlesinger, 1985; Attiwill & Leeper, 1987). The uptake of essential nutrients and their return to soil constitute the intra-system cycle, the biological cycle, in a forest ecosystem (Duvigneaud & Denaeyer-DeSmet, 1970; Cole & Rapp, 1981; Waring & Schlesinger, 1985). The biological cycle of nutrients is one of the principal processes supporting the production of organic matter (Duvigneaud & Denaeyer-De Smet, 1970). Nutrient cycling in forests is an important parameter affecting productivity (Waring & Schlesinger, 1985).

The biological cycle involves the phenomena of uptake, retention and restitution (Cole & Rapp, 1981). During growth, forest ecosystems show selective uptake and retention of essential nutrients from the biogeochemical flux. Nutrients are retained effectively within the system considering the amount of annual circulation (Melin *et al.*, 1983; Waring & Schlesinger, 1985; Li, 1996). Compared to the amounts received or lost from most forests, the biological cycle involves rather large movements of nutrient within a forest ecosystem (Feller, 1977; Sollins *et al.*, 1980). However, if forest biomass is not accumulating or the nutrients are not in short supply, the long-term retention of nutrients would be low. Atmospheric inputs supply only a small proportion of the annual requirement of nutrients and the remainder is derived from other sources, e.g. decomposition of plant parts and rock weathering (Cole & Rapp, 1981; Waring & Schlesinger, 1985; Pearson *et al.*, 1987; Ranger *et al.*, 1995). Rodin & Bazilevich (1967) reviewed the rates of the known biological cycles of minerals in the principal types of ecosystem in the world. Many reports suggested that the rates of biological cycling vary among soil conditions, climate and vegetation types, as well as being affected by physical disturbances (Duvigneaud & Denaeyer De Smet, 1970; Cole & Rapp, 1981; Waring & Schlesinger, 1985). Soil fertility, availability of nutrients and water are important within the same climate range (Waring & Schlesinger, 1985; Vitousek & Sanford, 1986).

In forest ecosystems, the macronutrient elements N, P, K, Ca, Mg and S are required in relatively high concentration to sustain plant growth and deficiencies of N and P commonly limit the productivity of forest ecosystems (Warning & Schlesinger, 1985). Plants also require the micro-elements Fe, Mn, Cu, Zn, B, and Mo, but in much smaller quantities. These tend to be available in adequate quantities in most forest soils. In my study Cu, Zn, B and Mo were not analyzed in plant and water samples because of the financial restrictions. S was not studied with the vegetation samples matter (due to the cost of doning so), but was considered in the water analysis because the quality of water is affected by the concentration of S. In the previous Chapter (Chapter 6), I described the sources of nutrients in natural forest of *Lithocarpus/Castanopsis*. In this present Chapter, I emphasize macronutrients and seek to elucidate the biological cycling of nutrients by analyzing amounts of nutrient requirements, plant uptake, retention and return to the soil. The results are compared with other montane rain forests.

7.2 Methods

The annual circulation of nutrients in forest can be modeled using the mass-balance approach (Duvigneaud & Denaeyer-De Smet, 1970; Waring & Schlesinger, 1985). In this study, uptake of nutrients was calculated as the following equation: Uptake = annual retention + litterfall + leaching. The annual retention of nutrient was calculated as the product of nutrient concentration and incremental production of wood tissue. For an evergreen forest, the incremental production of each component was determined as the sum of the net accumulation of each tissue and annual litterfall of that component. Uptake is less than the annual requirement by the amount reabsorbed from leaf tissues before abscission. The annual requirement is equal to the nutrient content in annually produced tissues plus the leaching losses through the year (Waring & Schlesinger, 1985). In this study, the net annual accumulation of nutrients was calculated as the product of the annual production of each component and nutrient concentration in that component. The annual production was determined as the sum of mean net productivity reported by Xie *et al.* (1996; Table 2.8) and mean annual production of flower/fruit fall (mean 1153 kg ha^{-1} yr^{-1}, Table 4.1, Chapter 4), which had not been collected in the Xie *et al.* (1996) study. Nutrient concentrations of each tissue for tree, shrub and herb layers were respectively determined using average concentration of nutrient in each component of biomass from six tree species, bamboo and fern (Chapter 3). Considering that nutrient concentrations in newly produced tissues are usually higher than those of the biomass, the results will underestimate the actual values for annual increment.

In Chapter 3. I described nutrient accumulation and allocation of two stands of *Lithocarpus/Castanopsis* forest with different densities. Nutrient storage in the forest was determined using the mean of the nutrient storage in the two stands. The mean annual amounts of nutrients in litterfall returned to the soil (Chapter 4) and the annual amounts of nutrients leached from canopy and boles (Chapter 6) were respectively used to produce the annual requirement, which is assumed equal to the replacement of litterfall and leaching losses (Waring & Schlesinger, 1985). The annual absorption of nutrient was computed from the sum of the tree accumulation values and the litterfall (Harmbuckers & Remacle, 1990).

7.3 Results

7.3.1 Annual accumulation of nutrients

The forest has a low net relative productivity (about 3 % of total biomass). The annual total accumulation of macro-nutrients (N, P, K, Ca and Mg) in the forest is estimated as 182 kg $ha^{-1}yr^{-1}$. Of these the tree layer contributes 87.1 % of the total accumulation (Table 7.1). Foliage, flowers and fruits hold the greatest proportion of nutrients, although they represent only 28.7 % of the total annual biomass increment (Table 2.8). The annual retention of nutrients in woody tissues ranges from 3 kg ha^{-1} yr^{-1} for P to 30 kg $ha^{-1}yr^{-1}$ for Ca, with a magnitude sequence of Ca>N>K>Mg>P.

7.3.2 Nutrient storage and annual flux

Internal storage and the annual transfer of nutrients in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountains, based on the mass-balance approach, are shown (Table 7.2). Within the forest, a greater proportion of nutrients is retained within the woody tissues (branches, boles and roots) compared to nutrient storage in short-lived tissues. Nutrient storage in the forest ranges from 112 kg ha^{-1} for P to 1333 kg ha^{-1} for Ca, with a magnitude sequence of Ca>N>K>Mg>P.

Table 7.1. Annual nutrient accumulation in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Layer	Component	Annual nutrient accumulation (kg ha^{-1}yr^{-1})				
		N	P	K	Ca	Mg
Tree layer	Leaf	23.2	2.0	12.2	9.0	3.6
	Flower/Fruit	15.3	1.2	7.7	2.8	1.0
	Branch	6.7	0.9	6.9	9.6	2.6
	Stem	6.2	0.4	5.5	10.8	0.9
	Root	10.3	1.4	7.1	8.8	2.4
	Total	61.7	5.9	39.4	41.0	10.5
Shrub layer	Leaf	3.9	0.2	1.7	0.4	0.2
	Branch	0.9	0.1	0.8	0.2	0.1
	Stem	0.9	0.1	2.2	0.4	0.1
	Root	0.7	0.1	1.4	0.2	0.1
	Total	6.4	0.4	6.1	1.2	0.5
Herb layer	Aboveground	3.2	0.1	0.6	0.4	0.4
	Underground	2.6	0.3	0.3	0.3	0.7
	Total	5.8	0.4	0.9	0.7	1.1
Sum		73.9	6.7	46.4	42.9	12.1

Leaching losses are dominated by throughfall, but the annual return in leaching is relatively small (14-48 % of the total return) except for K, which has high leaching from canopy and boles, comprising 53 % of the total return. Litterfall is the dominant pathway (77-86 %) for the return of N, Ca and P to the soil. In the forest, the annual uptake is 8-10 % of the total storage in vegetation, but 69-80 % of the uptake is returned each year. The annual requirement, which is a combination of the nutrient accumulation in newly produced tissues and the leaching losses through the year (Waring & Schlesinger, 1985), comprises 7-12 % of the total storage. There appears to be substantial reabsorption of N, P, K and Mg each year, comprising respectively 15 %, 13 %, 11 % and 7 % of the total annual requirement. Ca is rather immobile in plant cells, and shows no reabsorbtion.

Table 7.2. Storage and annual circulation of macro-nutrients in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

	N	P	K	Ca	Mg
Storage (kg ha^{-1})					
Foliage	45	33	24	19	11
Branches	97	12	102	140	37
Bole	450	22	427	665	66
Roots	425	64	484	475	130
Understory	138	10	162	34	14
Total	1155	112	1099	1333	258
Annual requirement (kg ha^{-1} yr^{-1})					
Foliage	84.5	5.5	33.4	49.3	12.1
Flower and Fruits	15.3	1.2	7.7	2.8	1.0
Wood increment in					
Boles	7.1	0.5	7.7	11.2	1.0
Branches	7.6	1.0	7.6	9.8	2.7
Roots	8.4	1.5	8.5	9.0	2.5
Total increase	23.1	3.0	23.8	30.0	6.2
Leaching					
Throughfall	12.1	1.5	33.0	15.3	8.0
Stemflow	0.8	0.04	1.4	0.6	0.5
Total leaching	12.9	1.54	34.4	15.9	8.5
Total requirement	135.8	11.24	99.3	98.0	27.8
Annual uptake (kg ha^{-1} yr^{-1})					
Wood increment	23.1	3.0	23.8	30.0	6.2
Returns					
Leaching	12.9	1.54	34.4	15.9	8.5
Litterfall	79.5	5.2	30.2	58.1	11.3
Total return	92.4	6.74	64.6	74.0	19.8
Total uptake	115.5	9.74	88.4	104.0	26.0
Reabsorption (kg ha^{-1} yr^{-1})	20.3	1.5	10.9	-6.0	1.8
Comparison of annual turnovers And flux (%)					
Litterfall/return	86.0	77.2	46.7	78.5	57.1
Return/uptake	80.0	69.2	73.1	71.2	76.2
Return/total storage	8.0	6.0	5.9	5.6	7.7
Uptake/total storage	10.0	8.7	8.0	7.8	10.1
Reabsorption/requirement	14.9	13.3	11.0	0	6.5

7.4 Discussion

Within the natural forest, the rank by mass of total nutrient return (litterfall plus aqueous) to the forest floor in the present study of N>Ca>K>Mg>P, is consistent with levels reported for montane rain forest in New Guinea (Edwards & Grubb, 1982), mixed deciduous forests at Hubbard Brook (Eaton *et al.*, 1973) and English oak forest (Carlisle, Brown & White, 1967). However, large amounts of K and Ca in litterall and throughfall are found within tropical lowland forests (Greenland & Kowal, 1960; Nye, 1961; Golley *et al.*, 1975).

The ratio of annual return to total nutrient storage in vegetation is considered an indication of the relative rate of cycling of nutrients stored in the vegetation (Edwards & Grubb, 1982; Vitousek & Sanford, 1986). Table 7.3 presents percentages of annual return in litter and throughfall for total storage in above-ground standing crops of a range of rain forests. New Guinea montane rain forest shows relatively high rates of N and P (18 and 21 % respectively), as a proportion of amounts in aboveground vegetation, while Ghanain tropical moist forest exhibits relatively high rates of K and Mg (37 and 20 % respectively). Very high relative turnover of K is associated with the large amount present in throughfall. The relative rates for nutrients in Ailao Mountain forest vegetation are within the lower ranges reported for tropical forests. The amount of nutrient cycling annually is small compared with most tropical forests. The rate of nutrient cycling is also slower at Xujiaba, Ailao Mountain NNR than in most tropical forests, especially the tropical lowland forests. Although tropical forests tend to have relatively high rates of nutrient cycling, only a small proportion of the annual uptake of nutrients is thought to be incorporated into new wood (Edwards & Grubb, 1982).

The annual nutrient uptake, which may be considered as a means of evaluating the nutrient requirements of the forest, is the sum of the annual return and annual retention (Duvigneaud & Denaeyer-De Smet, 1970; Waring & Schlesinger, 1985). No information is available on the annual uptake in tropical montane forests, but a number of studies of nutrient uptake and cycling were conducted in temperate forests involved in the International Biological Program (IBP) of the 1960s & 70s (Cole & Rapp, 1981). Table 7.4 compares annual return, retention and uptake in the Ailao

Table 7.3. Comparison of the storage of nutrient in above-ground standing crop of vegetation and that returned annually in the litter and throughfall in the Ailao Mountain forest, with some tropical rain forests.

Site		N	P	K	Ca	Mg	References
Lower montane rain forest, New Guinea	Storage (kg ha^{-1})	683	37	664	1281	185	Edwards & Grubb, 1982
	Return (kg ha^{-1}yr^{-1})	120	13.8	99	114	30	
	Return/storage (%)	17.6	20.5	14.9	8.9	16.2	
Lower montane rain forest, Venezuela	Storage (kg ha^{-1})	876	53	1321	745	215	Fassbender & Grimm, 1981; Grimm & Fassbender, 1981a, b
	Return (kg ha^{-1}yr^{-1})	77	5.4	103	50	17	
	Return/storage (%)	8.8	10.2	7.8	6.7	7.9	
Tropical moist forest, Ghana	Storage (kg ha^{-1})	1685	112	753	2370	320	Greenland & Kowal, 1960; Nye, 1961
	Return (kg ha^{-1}yr^{-1})	211	11.0	287	235	63	
	Return/storage (%)	12.5	9.8	38	9.9	19.7	
Tropical moist forest, Panama	Storage (kg ha^{-1})	N.D.	158	3020	3900	403	Golley *et al.*, 1975
	Return (kg ha^{-1}yr^{-1})[A]	N.D.	8.6	129	240	22	
	Return/storage (%)	-	5.5	4.3	6.2	5.5	
Montane moist evergreen forest, Yunnan, China	Storage (kg ha^{-1})	696	45	684	850	122	This study
	Return (kg ha^{-1}yr^{-1})	92.4	6.7	64.6	74.0	19.8	
	Return/storage (%)	13.3	14.9	9.4	8.7	16.2	

[A]. Return is only litterfall

N. D. = not determined

Table 7.4. Comparison of the macronutrient cycles in the Ailao Mountain forest with several different forest ecosystems involved in IBP.

Forest type	Site	Cycling (kg ha^{-1} yr^{-1})	N	P	K	Ca	Mg	References
Mixed hardwood forest (*Liriodendron tulipifera, Quercus*)	Oak Ridge, Tennessee USA	Return	48.2	3.1	37.5	80.2	11.7	Cole & Rapp, 1981 (Stand No. 23)
		Retention	9.9	0.3	2.5	7.6	0.7	
		Uptake	58.1	3.4	40.0	87.8	12.4	
		Return/uptake	0.83	0.92	0.94	0.91	0.94	
Northern hardwood forest (*Acer, Betula, Fagus*)	Hubbard Brook, New Hampshire, USA	Return	59.4	4.7	47.8	46.1	7.5	Cole & Rapp, 1981 (Stand No. 27)
		Retention	30.1	4.6	12.8	23.5	3.0	
		Uptake	89.5	9.3	60.6	69.6	10.5	
		Return/uptake	0.66	0.51	0.79	0.66	0.71	
Mixed oak forest (*Quercus*-mixed)	Virelles, Belgium	Return	61.4	3.4	39	66	10.4	Cole & Rapp, 1981 (Stand No. 28)
		Retention	30.0	3	18	34	4	
		Uptake	91.4	6.4	47	100	14.4	
		Return/uptake	0.67	0.53	0.83	0.66	0.72	
Beech forest (*Fagus silvatica*)	Solling Project, Germany	Return	74.6	4.6	39.4	43.6	5.4	Cole & Rapp, 1981 (Stand No. 30)
		Retention	20.0	3.2	7.6	30.8	2.2	
		Uptake	94.6	7.8	47.0	74.4	7.6	
		Return/uptake	0.79	0.59	0.84	0.59	0.71	
Red alder (*Alnus rubra*)	Washington, USA	Return	95.9	7.2	51.6	77.2	15	Cole & Rapp, 1981 (Stand No. 35)
		Retention	19	3.1	34.5	14	4.4	
		Uptake	114.9	10.5	86.1	81.2	19.4	
		Return/uptake	0.83	0.69	0.60	0.95	0.77	
Mixed deciduous (*Quercus-Betula*)	Meathop Wood, UK	Return	72.7	3.33	54.1	111.3	24.0	Cole & Rapp, 1981 (Stand No. 33)
		Retention	13.9	0.9	11.5	27.1	2.7	
		Uptake	86.6	4.23	65.6	138.4	26.7	
		Return/uptake	0.84	0.79	0.82	0.80	0.90	
Mediterranean evergreen oak forest (*Quercus ilex*)	Rouquet, France	Return	34.5	4.7	44.0	95.0	9.0	Cole & Rapp, 1981 (stand No. 36)
		Retention	13.2	2.6	8.9	25.7	2.2	
		Uptake	47.7	7.3	52.9	120.7	11.2	
		Return/uptake	0.72	0.64	0.83	0.79	0.80	
Montane evergreen forest (*Lithocarpus-Castanopsis*)	Yunnan, China	Return	92.4	6.74	64.6	74.0	19.8	This study
		Retention	23.1	3.0	23.8	30.0	6.2	
		Uptake	115.5	9.74	88.4	104.0	26.0	
		Return/uptake	0.80	0.69	0.73	0.71	0.76	

Mountain forest with some hardwood forests in temperate regions. The amounts of annual uptake of N, P and K are higher in the Ailao Mountain forest (104, 8 and 81 kg $ha^{-1}yr^{-1}$ respectively) than most other hardwood forests, but are comparable with those in red alder forest (115, 11 and 86 kg $ha^{-1}yr^{-1}$ respectively) in Washington, USA. The Washington Alder stand may have eco-physiological similarities with Ailao Mountain NNR as Alder grows in wet swamp sites at Xujiaba (Chapter 2). Large amounts of Ca are taken up in mixed deciduous forest (138 kg ha^{-1} yr^{-1}) at Meathop Wood, UK; Mediterranean evergreen oak forest (121 kg ha^{-1} yr^{-1}) in France; and mixed oak forest (100 kg ha^{-1} yr^{-1}) in Belgium (Cole & Rapp, 1981). The high amount of Ca taken up in these forests is due to the large amounts present in the soil (Duvingneaud & Denaeyer-De Smet, 1970). The amount of annual uptake of Mg is higher in the Ailao mountain forest compared to most oak forests in temperate regions, and it is similar to that of mixed deciduous forest in UK. On the other hand, application of the return/uptake ratio as an indicator of turnover rate shows that the Ailao mountain forest has relatively slow turnover rates of nutrients compared with mixed oak forest in Tennessee, USA and mixed deciduous forest in UK, but is higher than in other hardwood forests. The turnover rates of nutrients are within the same ranges as found in other forests.

Relatively low turnover rates of nutrients in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR compared with tropical rain forests are associated with the mountainous environment of lower temperature and high moisture. There is a general reducation of microbial activity at lower temperatures in montane forests (Edwards, 1977). This is coupled with a complexing of the organic matter by soil colloids (Edwards & Grubb, 1982) so that although nitrogen continuously accumulates it is relatively unavailable to plants. The plants have lower concentrations of nitrogen in their leaves and wood than plants in most lowland forests (Chapter 3 this thesis), which might be taken as evidence of a shortage of available nitrogen (Edwards & Grubb, 1982). Vitousek & Sanford (1986) indicate that there is relatively low mineralization and a greater shortage of nitrogen in montane rain forest than in lowland rain forests.

The availability of nutrients in soil is important to plant growth. Within the natural forest, the total amount of N and P in the top 30 cm of the mineral soil (6,600 and 737 kg ha^{-1} respectively; Table 7.5) is much greater than that in the vegetation, but probably only small proportions of the reserves of these two elements are in forms readily available to plants. As described for other montane forests (Grubb & Edwards, 1982; Tanner, 1985), limitations of N and P were found in the forest (Chapter 3 this thesis), providing evidence for such a hypothesis. The quantities of exchangeable Ca and Mg in the top 50 cm of soil (3,953 and 672 kg ha^{-1} respectively), indicate that these elements are abundant and available. However, the amount of exchangeable K in the top 50 cm soil (381 kg ha^{-1}) is a little over four times that in the annual litter and throughfall and it appears that this element is rapidly and tightly recycled.

Table 7.5. Total N and P, and exchangeable K, Ca and Mg in soil from natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[1].

Depth (cm)	Soil (t ha^{-1})	Nutrient storage (kg ha^{-1})				
		N	P	K	Ca	Mg
3-10	420	2184	252	122	683	178
10-30	1380	4416	485	155	1468	352
30-50	1780	3916	340	104	1802	142
Total (3-50)	3580	10516	1077	381	3953	672

[1] Data after Deng *et al.* (1983).

7.5 Conclusion

On an annual basis, this forest is characterized by relatively high nutrient return (5.6-8.0 % of the total storage) and low nutrient retention (2.0-2.7 % of the total storage). The rate of nutrient cycling in the forest occupies an intermediate position between temperate evergreen broad-leaved forest and tropical montane rain forest, it is closer to the latter.

The total annual nutrient return is dominated by litterfall, except for K, which has high leaching from canopy and boles. Total annual nutrient return through litterfall and aqueous flux to the forest floor ranks in the order of N>Ca>K>Mg>P. this is similar to levels reported for other tropical montane rain forests. The relative cycling rates (ratio of total annual return to nutrient storage in vegetation) of nutrients in the Ailao Mountain forest are generally within the low part of the range reported for tropical montane rain forests elsewhere.

Within the natural forest, the annual uptake of element is 7-12 % of the total storage, while annual retention is less than 3 % of the total storage in the vegetation. Annual uptake of N, P, K and Mg are higher in the Ailao mountain forest than hardwood forests in temperate regions. Low uptake of Ca in the forest is attributed to low amount present in the soil. The return/uptake ratio (as indictor of turnover rate) of nutrients indicate that the Ailao Mountain forest has relative high turnover rate of nutrients compared with other temperate hardwood forests.

Although the total amounts of N and P are vastly greater in the soil than that in the vegetation, some proportions of the two elements' reserves these elements are unavailable to plants. Ca and Mg are abundant and may be available. K is rapidly and tightly recycled in the forest.

The movement of nutrients within a forest ecosystem not only includes nutrient uptake, retention by plants and nutrient return to the soil, but also involves nutrient loss by geological process, such as runoff, seepage and streamwater. The gains and losses of nutrients in a forest result in the exchange of nutrients with other ecosystems. In the next chapter, I will describe nutrient budgets for the forest ecosystem is attempt to compare and balance the inputs and outputs by the processes.

Chapter 8 Nutrient Budget of Natural *Lithocarpus/Castanopsis* Forest Ecosystem at Xujiaba, Ailao Mountain NNR

8.1 Introduction

Nutrient inputs and outputs are directly related to the flux of water moving into and out of an ecosystem, resulting in the exchange of nutrients with other ecosystems (Lickens & Bormann, 1974; Waring & Schlesinger, 1985). The temporal and absolute limits of biogeochemical activities within the ecosystem are markedly influenced by the hydrological regimes (Bormann & Lickens, 1967; Stanhill, 1970; Turvey, 1974; Parker, 1983; Miller, Blum & Friedland, 1993; Marques *et al.*, 1997). In natural forest ecosystems with high precipitation, the dominant pathway for nutrient loss from ecosystems is via ground surface runoff and subsurface drainage (Nelson, 1970; Likens *et al.*, 1977; Waring & Schlesinger, 1985; Hornung, 1990; Reynolds, Hudson & Leeks, 1990; Cavelier *et al.*, 1997). Thus, estimations of the output of nutrients through these hydrological fluxes is now a routine part of nutrient budget studies in forest ecosystems (Jordan, 1982; Marques & Ranger, 1997; Marques *et al.*, 1997; McDowell, 1998). On the other hand, nutrient input-output budgets in undisturbed forest ecosystems provide a conceptual and empirical framework, both for examining ecosystem function in diverse geographic regions and for evaluating the impact of human activity on the natural landscape (Waring & Schlesinger, 1985; Swank & Waide, 1988; Hedin *et al.*, 1995).

Nutrient budgets for forest ecosystems have been studied from the end of the last century, are now commonplace and increasing in number. In the past, interest was directed at quantification of nutrient inputs and outputs under various climates and in different forests, and the examination of factors and processes controlling nutrient budgets, seasonality and heterogeneity. Recently, much attention is being focused on the geochemical implications of nutrient balance for forest ecosystems including internal causes and effects of human disturbance (Jordan, 1982; Hedin *et al.*, 1995; Marques *et al.*, 1997) and the implications of input-output budgets for sustainable forest management (Ranger & Turpault, 1999).

Most information on nutrient budgets is from temperate forests of the more populated areas in Europe and America (e.g. Likens *et al.*, 1977); much less is known for forests in China, especially for the subtropical mountainous areas of southwestern China. On the larger world scale, there is still relatively poor understanding of nutrient budgets for tropical and subtropical forests compared to temperate forests (Vitousek & Sanford, 1986; Bruijnzeel 1990). In the current study, the fluxes of nutrient elements in water movement from atmospheric input to output via ground runoff, percolation and stream flow are examined for a natural stand of *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain. In this chapter, I develop a budget for inputs and outputs to characterize this forest by accounting for nutrients in precipitation, runoff and water drainage. Due to most plant roots being distributed within the upper 70 cm of soil depth, I selected the output of nutrients in percolation water from 70 cm soil depth as the reference level, while nutrient loss through streamflow was considered during a two-year period of data collection.

8.2. Methods and materials

8.2.1. Site characterization

This study was conducted within the fenced plot (0.25 ha) used for measuring throughfall and stemflow. Information on species composition and community structure within the site is described in Chapter 6. Precipitation collection is also described in Chapter 6.

8.2.2. Measurement of runoff and percolation

Within the 0.25 ha plot, ground surface runoff was collected from two 2 x 5 m runoff subplots surrounded on all four sides with plastic sheeting hammered deep in the soil (to 30 cm) and connected with polyethylene tubes to plastic 50 l containers situated downslope.

Gravitational percolation water was measured using zero-tension plate lysimeters, suitable for study of input-out budgets in ecosystems (Haines, Waide & Todd, 1982; Kellman & Roulet, 1990; Marques *et al.*, 1996; Marques & Ranger, 1997). Although there are different opinions of soil water fluxes measured by lysimeters, Marques *et al.* (1996) indicate significant correlation between measured water from zero-tension lysimeters and estimated water fluxes in soil. In this study, soil percolation water was collected in the plot at depths of 10, 30, 50 and 70 cm from three replicates of the zero-tension plate lysimeter, respectively. Each zero-tension lysimeter consisted of a plastic plate, 40 x 40 cm in surface area with a thickness of 5 cm. These were introduced into the soil profile from a pit that was backfilled after installation with soil horizons replaced in their correct order. The plates were covered with polyethylene mesh containing 0.5 mm apertures. The bottom of the tray was attached with polyethylene tubing to a 20 l plastic container. Soil solutions from different depths were collected in the respective containers.

Sample containers for ground surface runoff and soil solutions were placed in closed pits downhill where they were protected from light and temperature variations. Choroform was used in all containers to inhibit bacterial growth as in chapter 7 (after Kellman *et al.*, 1982). Rainfall, runoff and soil water volumes were measured at 8:00, 14:00 and 20:00 each day between 1 Jan. 1998 and 31 December 1999.

8.2.3 Streamflow in the catchment

Stream flow represents the net out flow from a catchment (Turvey, 1974; McDowell, 1998). Fortunately, a water reservoir occupies the area below the Xujiaba study area, with a 28.5 km^2 catchment area, mainly of natural forest (Picture 2). A local hydrological management office, Water Conservancy Department, is responsible for recording rainfall and water storage and for management of dammed water. The annual stream flux was calculated based on the catchment area and amount of water storage obtained from the Xujiaba reservoir. The streamflow was calculated using the following formula:

Streamflow = rainwater on total catchment area - rainwater on water surface - minimal water storage.

Data for maximum water surface area and minimal storage of the reservoir were obtained from the hydrological office. All values were expressed as water depth (mm) on the basis of water storage (m^3) on unit area. Monthly values of stream water entering the reservoir were summed to give the annual total stream water.

8.2.4. Chemical analysis

As percolation water and streamflow mainly occur in the rainy season, samples of these components were taken monthly for chemical analysis during the rainy seasons only. Precipitation samples were taken in clean 100 ml polythene bottles. At each sample collection, three samples from each of the respective collectors of ground runoff and soil solutions at different depths were combined proportionally to make one sample. Samples were taken to the laboratory one or two day afterwards.

During the two-year period, a total of 12 water samples for each component (ground runoff, percolation water at different soil depths, and stream water) was analyzed. The concentrations of nutrient elements (total N, NH_4^+-N, NO_3^--N, P, K, Ca, Mg, Na and SO_4^--S) for these components were obtained. The corresponding chemical analysis methods are summarized above (Chapter 6). Data on chemical composition of rainfall, throughfall and stemflow are in Chapter 6.

8.2.5. Nutrient fluxes and budget

All elemental fluxes are based on annual volume - weighted concentrations multiplied by the water volume flux. Soil-water fluxes were estimated based on measured water volumes. Stream flow was based on the measurements of water storage provided by the Xujiaba Reservoir Hydrological Office.

Nutrient budgets were established for major elements. Percolation water from 70 cm soil depth in the plot and stream water in the catchment were considered as the output of two reference levels. The terms of these budgets were as follows:

Input = throughfall (T_r) + stemflow (S_t); Output = input – leaching out of the soil (70 cm) or loss through stream water.

Output of nutrients through streamwater is considered as the most obvious means by which nutrients are lost from forest ecosystems (Waring & Schlesinger, 1985). In this study, nutrient loss from streamwater is considered as the total output of the forest watershed.

8.2.6. Data analysis

Based on the 12 samples analyzed for each component, elemental concentrations between different components were compared statistically using one way analysis of variance, followed by the multiple comparison Fisher' test at $p<0.05$ to detect whether significant differences occurred among runoff, percolation and stream water. All statistical analyses were performed using StatView^{TM}(Abacus Concepts, Inc., 1986).

8.3. Results

8.3.1. Dynamics of surface runoff

Within this particular natural forest, surface runoff measured was slight (< 1 % of annual precipitation). During the period 1998-1999, annual runoff varied between 8.5 and 13.8 mm with a mean of 11 mm: 0.51 % of mean annual rainfall (Table 8.1). Surface runoff mainly occurs in June to October, with maximum monthly runoff of 3.2 mm in July 1999 (Fig. 8.1).

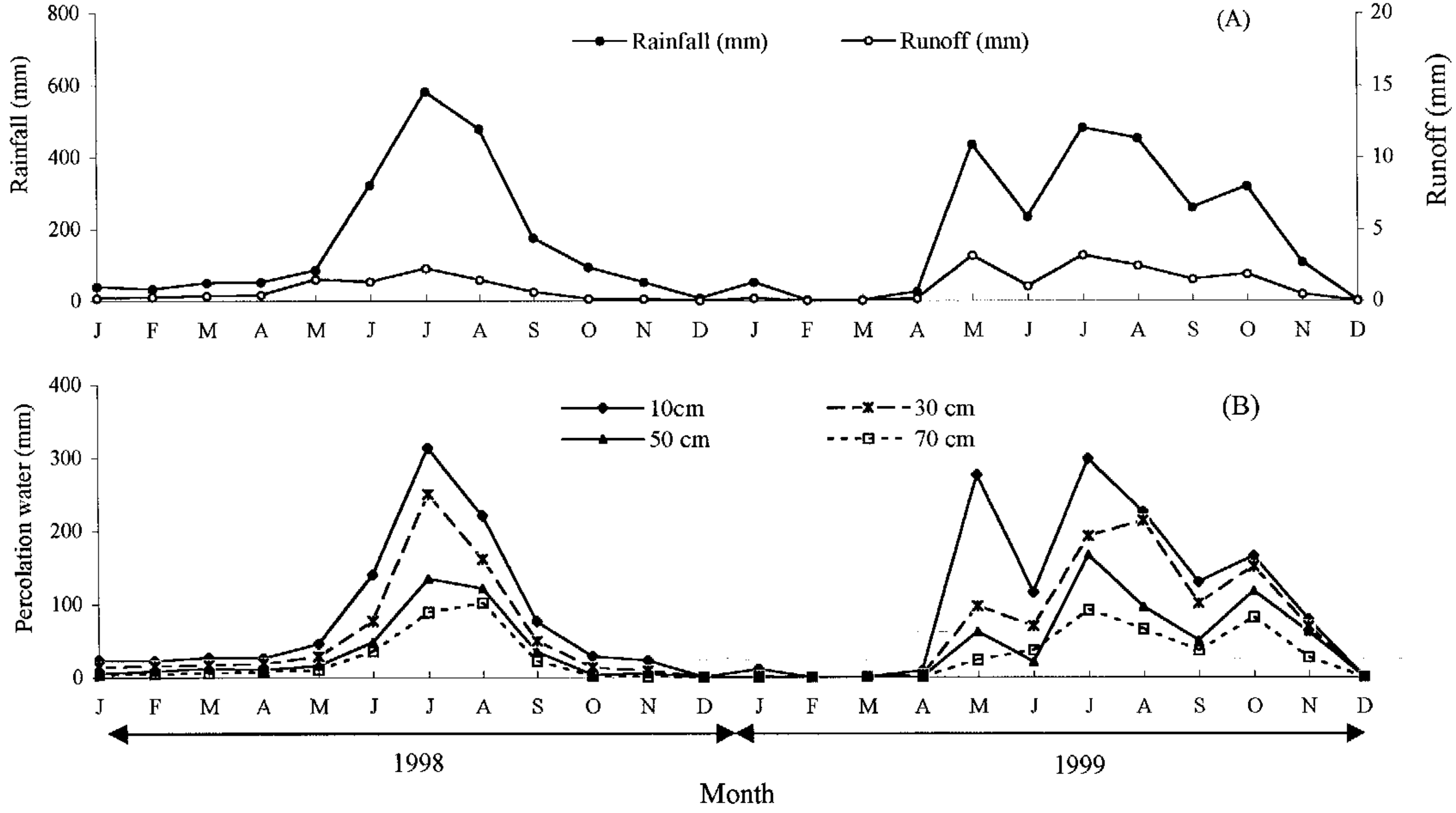

Fig. 8.1. Monthly fluxes of precipitation and surface runoff (A), and percolation water from different soil depths (B) in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Table 8.1. Annual runoff in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR (1998-1999).

Year	Rainfall (mm)	Surface runoff (mm)	% of rainfall
1998	1964.6	8.5	0.43
1999	2365.0	13.8	0.58
Mean	2164.8	11.2	0.51

8.3.2 Percolation water and streamflow

That surface runoff was only 0.51 % of total rainfall suggests the catchment is a subsurface flow system. The quantity of percolation water from the soil profile rose with increased rainfall. Percolation water tended to occur on any day in which rainfall exceeded 10 mm. Monthly percolation was highest in July, 1998 when rainfall was greatest (Fig. 8.1).

The mean annual percolation water at 10 cm soil depth was 1125 mm or 51.9 % of total rainfall. At 70 cm depth, percolation water was 322 mm, comprising 14.8 % of total rainfall. The difference of percolating water between 10 cm and 70 cm was 803 mm (Table 8.2).

Table 8.2. Annual fluxes of percolating water from different soil depths and streamflow (mm) in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Year	Precipitation (mm)	Soil depths								Streamflow	
		10 cm		30 cm		50 cm		70 cm			
		(mm)	(%)^{a}	(mm)	(%)^{a}	(mm)	(%)^{a}	(mm)	(%)^{a}	(mm)	(%)
1998	1964.6	942	47.92	652	33.19	395	20.11	281	14.30	920	46.83
1999	2365.0	1307	55.20	897	37.93	574	24.22	362	15.31	1180	49.89
Mean	2164.8	1125	51.90	775	35.56	485	22.17	322	14.81	1050	48.36

a: This term accounting for percentage of the annual rainfall.

A comparison of different curves suggests that the percolation water decreased exponentially with soil depths (Fig. 8.2). The exponential equations are, for 1998 data: $y = 1520.5e^{-0.0249x}$, $r^2 = 0.9415$; and for 1999 data: $y = 1983.7^{e-0.0249x}$, $r^2 = 0.9708$, where y is percolation (mm), x is soil depth (cm). These formulae indicate that variations in annual rainfall result in changes in soil water fluxes at different depths.

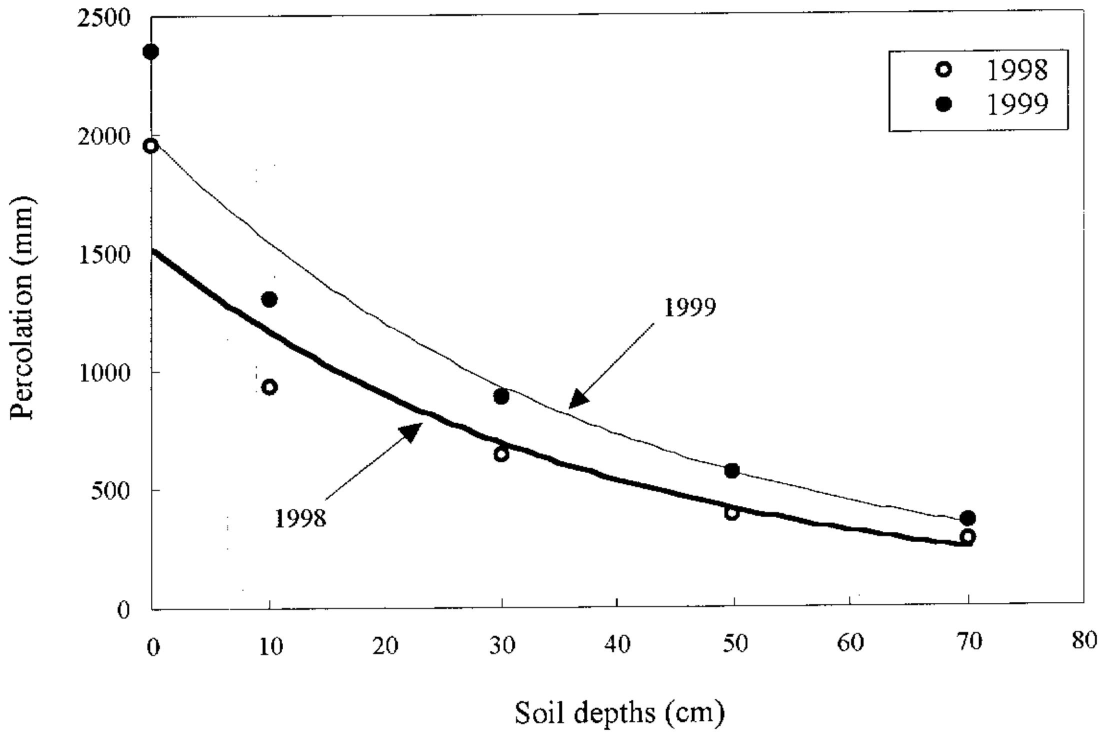

Fig. 8.2. Relationships between percolation water and soil depths in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR during two year period (1998-1999).

Stream water represents a net loss of water from the catchment. The annual amount of stream water in the catchment increased with annual rainfall. The net annual water loss averaged 1050 mm, comprising 48.4 % of the total rainfall (Table 8.2). Monthly stream water volume was least in the latter part of the dry season (May-June). The peak values of stream water occurred in August or October depending on rainfall amount. There were more months of higher stream water volume (exceeded 200 mm per month) in 1999 than in 1998 (Fig. 8.3).

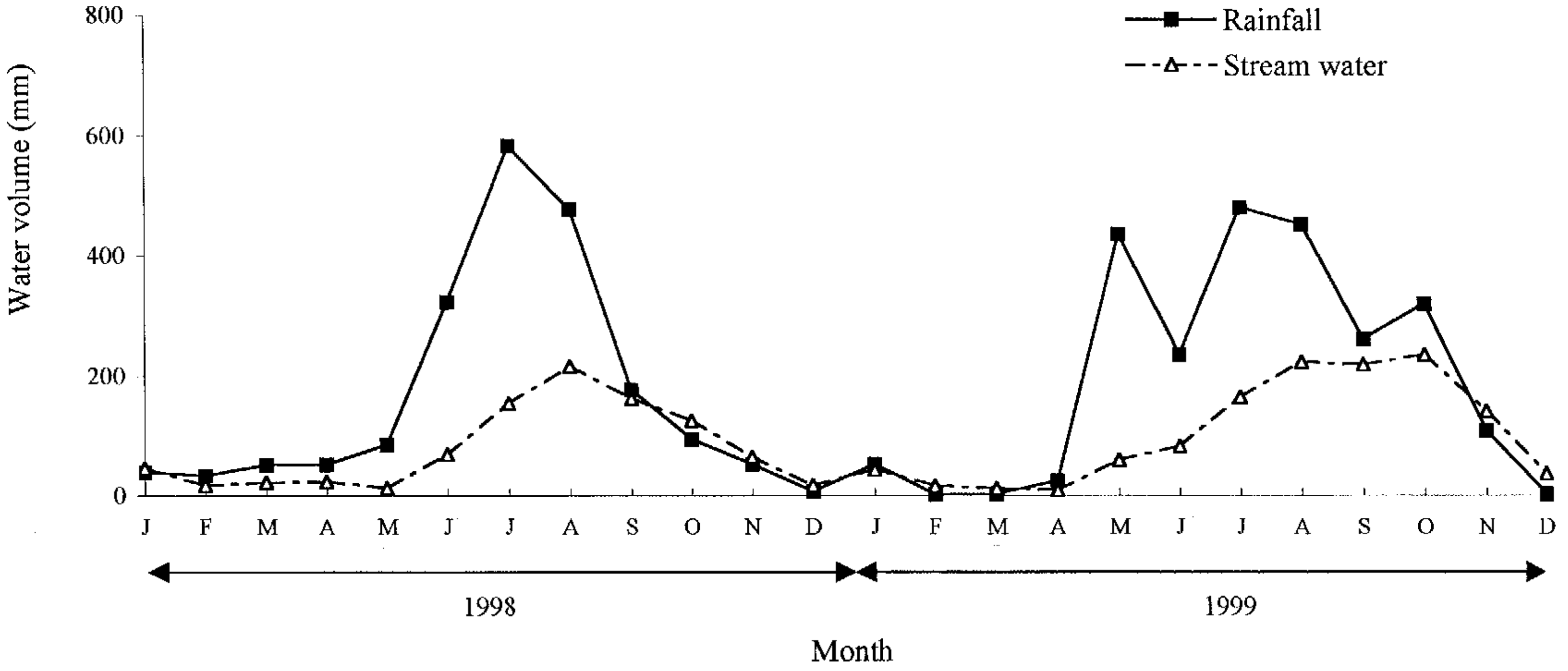

Fig. 8.3. Monthly flux of stream water in catchment of the Xujiaba Reservoir, Ailao Mountain NNR (1998-1999).

8.3.3 Nutrient input through rainfall

This information is available in chapter 6.

8.3.4. Nutrient output through runoff and percolation water

8.3.4.1 Nutrient concentration

Volume-weighted nutrient concentrations of surface runoff, percolation water from different depths and stream water are summarized (Table 8.3). Concentrations of all nutrients studied in runoff and drainage water were higher than in atmospheric precipitation (Chapter 7). K, P, Ca and Mg concentrations were considerably higher, 61, 6, 8 and 14 times greater respectively in surface runoff than in atmospheric precipitation. For other nutrients, increases in concentration were between 0.7 to 5 times. Concentrations of all nutrient elements were lower in soil solution and stream water than in surface runoff. Nutrient concentrations of soil solution decreased with soil depth. However, concentrations of base cations (K^+, Ca^{2+} and Mg^{2+}) in the soil solution collected at 70 cm were considerably higher than at 50 cm depth. Although concentration of total N and NH_4^+-N were considerably higher than in stream water, K^+, Ca^{2+} and Mg^{2+} concentrations were all much lower in soil solution than in stream water.

8.3.4.2 Nutrient fluxes

Annual nutrient fluxes through surface runoff, soil solution and stream water from the forest are summarized (Table 8.4). The mean annual fluxes of nutrients in runoff were low, ranging from 0.01 kg ha^{-1} yr^{-1} for NO_3-N to 0.77 kg for K.

The fluxes of nutrient elements from the soil profile decreased with depth and appeared to be regulated by soil sorption processes. Moreover, there were differences in the amount of nutrient flux among elements in soil solution. Annual fluxes of all nutrient elements were highest in the 10 cm layer. Although there were low annual

Table 8.3. Volume-weighted mean concentration (± SD, n=12) in surface runoff and soil solution at different depths in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR. Same letters indicate samples which are not significantly different ($p<0.05$) within a column, using Fisher' LSD test.

Soil depths (cm)	pH	Nutrient concentration (mg/l)								
		Total N	NH_4^+-N	NO_3^-N	P	K	Ca	Mg	Na	SO_4^--S
Surface	6.02ab ±0.16	2.430a ±0.732	0.752a ±0.273	0.076a ±0.021	0.315a ±0.101	6.952a ±1.709	3.161a ±1.108	2.038a ±0.738	0.134ab ±0.044	0.660a ±0.203
10	5.64d ±0.27	1.833b ±0.549	0.424b ±0.119	0.032b ±0.006	0.125b ±0.033	2.116b ±0.290	1.696b ±0.433	0.880b ±0.143	0.138a ±0.031	0.542b ±0.165
30	5.73cd ±0.24	1.455c ±0.380	0.222c ±0.077	0.018cd ±0.005	0.065c ±0.021	0.239cd ±0.075	0.520c ±0.191	0.316c ±0.095	0.122abc ±0.024	0.282d ±0.033
50	6.03ab ±0.33	1.226c ±0.338	0.135cd ±0.037	0.012d ±0.004	0.042c ±0.010	0.156d ±0.060	0.464c ±0.112	0.212c ±0.035	0.118abc ±0.035	0.206e ±0.078
70	6.10a ±0.29	0.802d ±0.232	0.082d ±0.021	0.016cd ±0.004	0.056c ±0.019	0.470c ±0.072	0.867c ±0.304	0.446c ±0.079	0.110c ±0.022	0.182e ±0.024
Steamflow	5.85bc ±0.18	0.415e ±0.089	0.032d ±0.009	0.022c ±0.008	0.075c ±0.020	1.618b ±0.390	3.225a ±0.642	0.826b ±0.124	0.112bc ±0.017	0.370c ±0.068
F value	7.387	37.18	51.057	62.596	64.767	149.117	69.241	54.650	2.091	62.127
P	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0803	0.0001

Table 8.4. Annual mean nutrient fluxes (kg ha^{-1} yr^{-1}) through surface runoff, percolation water and stream flow in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Components	Total N	NH_4^+-N	NO_3^--N	P	K	Ca	Mg	Na	SO_4^--S
Surface runoff	0.27	0.08	0.01	0.04	0.77	0.35	0.23	0.02	0.07
Percolating water									
at 10 cm	20.61	4.77	0.36	1.41	23.79	19.07	9.89	1.55	6.09
30 cm	11.27	1.72	0.14	0.50	1.85	4.03	2.45	0.95	2.19
50 cm	5.94	0.65	0.06	0.20	0.76	2.25	1.03	0.57	0.99
70 cm	2.58	0.26	0.05	0.18	1.51	2.79	1.43	0.35	0.59
Stream water	4.36	0.34	0.23	0.79	16.99	33.86	8.67	1.18	3.83

fluxes of total N, NH_4^+-N, NO_3^--N, P, Na and SO_4^--S at 70 cm depth, annual fluxes of K, Ca and Mg were greater at that depth than at both 30 and 50 cm depths. The annual amounts of nutrients from the deepest soil layer (70 cm) ranged from 0.05 kg $ha^{-1}yr^{-1}$for NO_3^--N to 2.8 kg for Ca (Table 8.4).

There were large amounts of net nutrient losses through stream flow in the catchment where mean annual net loss amounted to 33.9 kg $ha^{-1}yr^{-1}$ for Ca, 17.0 kg for K, 8.7 kg for Mg and 4.4 kg for total N (Table 8.4).

Nutrient in solution was absorbed effectively by shallow soil collected at the site. The amount of nutrient retained by soil or absorbed by roots varied with soil depth. Within the 0-70 cm soil layer, annual total nutrient retained in the soil profile ranged from 0.3 kg $ha^{-1}yr^{-1}$ for NO_3-N to 23.0 kg for K. 90 % of the K, over two thirds of the Ca, Mg, P, SO_4^--S, NH_4^+-N and NO_3^--N, and half of the total N and Na was retained or sorbed in the 10-30 cm soil layer. At 70 cm depth, however, there was some increase of K, Ca and Mg, compared with the upper layer, reflecting these elements being leached from the upper soil layer in seepage (Table 8.5).

8.3.5 Nutrient budget

Annual nutrient budgets calculated for the natural *Lithocarpus/Castanopsis* forest ecosystem (Table 8.6) were made considering two criteria for output (a) from the soil profile (at 70 cm depth) and (b) the catchment (stream water). At 70 cm soil depth, the budgets were generally positive. Annual atmospheric inputs for all elements were sufficient to compensate for output by the seepage from 70 cm depth. The budgets of stream water in the catchment showed large accumulations of nitrogen and potassium. For magnesium and sodium, the input from throughfall and stemflow was slightly higher than the loss through drainage, but there was a net loss of calcium during the period of the study. Phosphorus and sulfur appear to be in close balance, with annual net gain or loss of less than 1 kg $ha^{-1}yr^{-1}$ (Table 8.6).

Table 8.5. The amount of nutrient retained in different soil layers through percolation in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Soil depth (cm)	Nutrient retention (kg ha^{-1} yr^{-1})								
	Total N	NH_4^+-N	NO_3^--N	P	K	Ca	Mg	Na	SO_4^--S
10-30 cm	9.34	3.05	0.22	0.91	20.77	15.04	7.44	0.60	3.90
30-50 cm	5.33	1.07	0.08	0.30	2.26	1.78	1.42	0.38	1.00
50-70 cm	3.36	0.39	0.01	0.02	-0.75	-0.54	-0.40	0.22	0.60
Total (0-70 cm)	18.03	4.51	0.31	1.23	23.03	16.82	8.86	1.20	5.50

Note: elemental retention is defined as the difference between the element in the upper and the element in lower soil layers.

Table 8.6. Annual nutrient budgets (kg ha^{-1}yr^{-1}) of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

Item	Total N	NH_4^+-N	NO_3^-N	P	K	Ca	Mg	Na	SO_4^--S
Precipitation (Pr)	10.48	2.69	0.91	1.25	2.97	7.95	3.23	1.72	2.83
Throughfall (Tr) +Stemflow St)	12.91	4.09	1.72	1.50	34.42	15.91	10.22	2.22	3.89
Output at 70 cm	2.58	0.26	0.06	0.18	1.51	2.79	0.47	0.35	0.59
Output by stream water	4.36	0.34	0.23	0.79	16.99	33.86	8.67	1.18	3.83
Budget at 70 cm	10.33	3.83	1.66	1.32	32.91	13.12	9.75	1.87	3.30
Budget stream water	8.55	3.75	1.49	0.71	17.43	-17.95	1.55	1.04	0.06

8.4 Discussion

8.4.1 Hydrological fluxes

Differences have been observed between plot and catchment level measurements used in calculation of hydrological and nutrient fluxes. McDowell (1998) suggests that it is not ideal to combine both levels of measurements in estimating nutrient fluxes. Catchment-level estimates of stream flow are generally the most appropriate means of obtaining minimum estimates of soil water and groundwater fluxes (Turvey, 1974; McDowell, 1998). Considerable spatial variability in rates of saturated and unsaturated flow may occur in a catchment, and thus these rates are difficult to predict at any particular plot without extensive hydrological monitoring (McDowell, 1998). For the Xujiaba Reservoir, the catchment consists mainly of natural forests together with scattered regeneration stands. Despite these uncertainties, I believe that the values presented at plot and catchment level here provide a useful estimate of the relative magnitude of internal element fluxes in this montane forest.

Surface runoff rarely occurs on forested watersheds (Rothacher, 1971; Waring & Schlesinger, 1985). In this study, surface runoff comprised only 0.53 % of the total rainfall, similar to a forested catchment in Kumaun Himalaya, India (Pandey, Pathak & Singh, 1984), indicating that the catchment has a subsurface flow system. At plot level, apparent gradient variations in seepage water occur with soil depth. The difference in annual water flux between shallow soil (10 cm) and the deepest sampled depth (70 cm) was 803 mm, exceeding the maximum amount of soil water holding capacity and soil evaporation, and suggesting considerable quantities of water are exported from the forest.

Stream water is a combination of surface runoff, subsurface flow and groundwater (Bormann & Likens, 1967, 1979; Turvey, 1974). It represents net loss from a catchment. Compared to other forested catchments, the estimated annual net flux of stream flow (48.4 % of total annual rainfall) is similar to that reported for a rain forest in Puerto Rico (50 % of total rainfall; McDowell, 1998), and less than that of Papuan rain forest (54.8 % of total; Turvey, 1974).

8.4.2 Nutrient fluxes

Within the natural forest, nutrient fluxes appear to be least through surface runoff although high nutrient concentrations occur in the water. Annual nutrient fluxes are greatest in the surface soil layer (10 cm depth) and decrease with soil depth following the pattern of water flux. This suggests that nutrient fluxes are mainly associated with hydrological flow. This pattern of decreasing fluxes with soil depth has been observed in many forest ecosystems (Feller, 1977; Edmonds, Thomas & Rhodes, 1991; Marques *et al.*, 1997; McDowell, 1998) and is variously attributed to reduction in water flux, plant uptake and adsorption processes by mineral and organic phases in the soil (Marques & Ranger, 1997; McDowell, 1998).

The higher concentrations and fluxes of nutrients in solution in the 0-10 cm layer appear related to nutrient release, i.e. litter leaching and organic matter mineralization (Friedland & Miller, 1999). My study site may be characterized by its well developed litter layer, high rainfall, and relatively high weathering rates (Qiu *et al.*, 1998). In a comparative experiment (with and without litter layer treatments) in an evergreen broad-leaved forest in central Yunnan, a significant increase in the concentration of K was found by Liu, Liu & Zheng (1991), who suggest that this increase is largely from litter layer leaching. Similar results are reported elsewhere (Daldoum & Ranger, 1994; Marques et al., 1998; Li, 1998). At deeper soil levels, reduction in the concentrations of nutrient elements are related to plant uptake and mineralization. Marques *et al.* (1997) suggests that local mineralization rather than nutrient transport from upper layers is the main process contributing to the quality of solutions throughout the soil profiles. In this present study, the higher concentrations of base cations in soil solution at the deepest depth, compared with the upper soil layer (30 cm and 50 cm) may be attributable to leaching and weathering of these elements from the soil profile.

Chemical composition of soil solution in the Ailao Mountain forest is comparable with that observed from tropical montane forest in the Luquillo Mountains of Puerto Rico (McDowell, 1998). The concentrations of base cations are within the middle to lower range observed in soil solution of tropical rain forests. Four forested sites are reported from sub-Sahelian Africa that all have higher concentrations of base cations in soil solution (Roose & Lelong, 1981) than those observed here. Concentrations of Ca^{2+}, for example, are 4-8 mg l^{-1} in African forests and only 0.4-1.2 mg l^{-1} in Ailao Mountains. Amazonian forests have considerably lower soil solution concentrations of Ca, with values of 0.1 to 1 mg l^{-1} (Forti & Neal, 1992).

Differences between soil solution and stream water in both concentration and fluxes (especially for Ca^{2+} and Mg^{2+}), are reported (Waring & Schlesinger, 1985; McDowell, 1998). Similar results apply to this study. Feller (1977) noted that the chemistry of a stream is extremely complicated and a result of many processes. Nutrients in a stream may be enriched through surface runoff, throughfall, evaporation and litter decomposition, within or at the edge of the stream, and released from adsorption sites on organic or inorganic materials. Nutrient concentrations may be diluted as a result of uptake of organisms, adsorption reactions, or inputs of low concentration waters in the forms of lateral seepage, tributary streams, or direct precipitation. Increases of Ca^{2+} and Mg^{2+} concentrations in stream water are the net result of these variable, disparate processes.

On the other hand, weathering is considered to be the main process for increase of base cations in stream water (Bormann & Likens, 1967; Waring & Schlesinger, 1985; McDowell, 1998; Friedland & Miller, 1999). Relatively high concentrations of weathering products in stream water compared to soil solution may be attributed to the result of accumulation of weathering products in the riparian zone (McDowell, 1998). Silver *et al.* (1994) found that standing stocks of Ca^{2+}, Mg^{2+} and K^+ were 2-3 times greater in riparian soils than on ridgetop soils.

Annual output of K^+ through steam flow from the catchment of the Xujiaba Reservoir appears to be relatively high and Na^- is least, compared with other experimental areas (Table 8.7). The extreme range of sodium export in New Zealand and Puerto Rico indicates the marine influence in contrast to the continental sources such as Hubbard Brook and Ailao Mountain. Other nutrient element outputs lie within the range of those observed in stream flow at experimental areas elsewhere.

8.4.3 Input-output budget

Atmospheric inputs into the natural *Lithocarpus/Castanopsis* forest are among the medium to low ranges observed for forest ecosystems elsewhere (Chapter 6). Positive budgets occur for all nutrients between atmospheric inputs and outputs by both seepage and stream flow. The exception is calcium, for which annual Ca output through stream flow apparently exceeds atmospheric input (including leaching from canopy and stems). Negative budgets for calcium have been reported for other forest ecosystems (Federer *et al.*, 1989; Johnson *et al.*, 1994; Friedland & Miller, 1999). Calcium is considered to be the element most threatened by leaching and also by removal in biomass from logging (Waring & Schlesinger, 1985; Federer *et al.*, 1989). Within a natural ecosystem, there must be release of some calcium to the ecosystem due to the weathering of parent material (Friedland & Miller, 1999). Jordan (1982) noted that leaching loss of elements from an ecosystem would have to be compensated by weathering for the system to remain in a steady state. On the other hand, net gains of nitrogen, potassium, magnesium and sodium in an ecosystem mean that weathering of parent material does not play an important role in the economy of these elements for the forest, and these elements could be replaced through atmospheric input. The phosphorus and sulfur balances for the ecosystem also indicate that rock weathering is not contributing to these two elements' budget in the ecosystem.

Annual variations in the nutrient budget are seen to have been large during the two years of investigation. Annual deficits and gains of nutrient elements are correlated with the amount of rainfall: 1998<1999. Year to year variation in nutrient fluxes has been reported by some researchers (Marques *et al.*, 1997; Li, 1998; McDowell, 1998). These results suggest that the study of multiple plots stratified by different topographic position and long-term observation, would be necessary to obtain values representative of the entire catchment.

Since the nutrient budget is so closely tied to the hydrological budget, the relatively low interception, and high drainage water in this montane humid forest is responsible for the high output of nutrient through drainage water. This pattern represents an internal dynamic equilibrium in the ecosystem. It is rather fragile and relatively easily disrupted by the activities of man (Bormann & Lickens, 1967, 1979; Hedin *et al.*, 1995; Qiu *et al.*, 1998). Human activities in the natural forest ecosystem should be minimal in order to preserve the structure and function of the ecosystem.

Table 8.7. Comparison of nutrient output (kg $ha^{-1}yr^{-1}$) from different experimental areas.

Site	N	P	K	Ca	Mg	Na	SO_4-S	Reference
Hubbard Brook, USA	-	-	1.8	12.8	2.6	5.9	-	Likens *et al.*, 1967; Bormann, Fisher & Cleaves, 1968
Pennine Mooreland, UK	17.7	0.86	10.4	58.6	-	45.5	-	Crisp, 1966
Finnish Rivers	1.87	0.26	4.57	12.0	4.35	5.6	14.2	Viro, 1953
New Zealand	1.8	0.03	13	27	13	63	40	Miller, 1963
Puerto Rico	1.3	-	4.9	87.9	60.0	113	-	McDowell, 1998
Ailao Mountain	4.4	0.8	17.0	33.9	8.7	1.2	3.8	This study

8.5 Conclusion

It is seen that the Xujiaba reservoir catchment is a subsurface flow system. There are apparent gradient variations in percolation water with soil depth. The estimated net flux of stream water is 48 % of total annual rainfall. Nutrient concentrations are lower in soil solution and stream water than in surface runoff. K^+, Ca^{2+} and Mg^{2+} concentrations are all lower in soil solution than in stream water, although soil solution has higher concentrations of total N and NH_4^+-N.

Annual nutrient fluxes are greatest in the surface soil layer (10 cm depth) and decrease with soil depth following the pattern of water flux. Annual net nutrient losses from stream flow in the catchment is in the order of Ca>K>Mg>total N>SO_4-S>Na>NH_4-N>NO_3-N. The budgets for all nutrient elements between atmospheric inputs and outputs by both seepage and stream flow are seen to be positive, whereas a negative budget exists for calcium. Leaching losses of that element could be compensated by weathering. Net gains of nitrogen, phosphorus, potassium, magnesium, sodium and sulfur could be replaced through atmospheric inputs.

Annual gains and deficits of nutrient in the natural forest are strongly correlated with the hydrological budget. High yearly variations in nutrient fluxes suggest that long-term observation is necessary in order to obtain values representative of the entire catchment, on a sustainable basis.

Chapter 9 General Discussion

In combination with methods of plot analysis and the small-watershed approach, this study provides a comprehensive view of the status and behavior of individual elements within natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR, SW China. Data generated from the study increase our understanding of fundamental nutrient relationships of the natural forest. This chapter presents a general discussion on the main aspects of biological cycling of nutrients, and seeks a synthesis of the relationships among these aspects within the natural forest ecosystem.

9.1 Overall characteristics of nutrient cycling in the natural forest

The Ailao Mountain forest is characterized by relatively low annual retention and relatively high return of nutrients. The different pathways of nutrient cycling between plant and soil in the forest are summarized in Fig. 10.1. In the forest, the annual increment is: 73.9, 6.7, 46.4, 42.9 and 12.1 kg $ha^{-1}yr^{-1}$ for N, P, K, Ca and Mg, respectively, representing 6.6, 6.1, 4.3, 3.2 and 4.8 % of the nutrients accumulated in the total biomass. The annual retention of nutrients in perennial tissues is very small, comprising 2.0-2.7 % of the total nutrient storage in the vegetation. This forest has a relatively high uptake of N, Ca and K in comparision with other elements. Annual uptake is 115.5, 9.7, 88.4, 104.0 and 26.0 kg $ha^{-1}yr^{-1}$ for N, P, K, Ca and Mg, respectively. Annual nutrient return comprises 80.0, 69.2, 73.1, 71.2 and 76.2 % respectively of the nutrients comprising the annual uptake. The annual return of N, P and Ca derive from litterfall, while K and Mg are from both litterfall and leaching. The nutrient requirements and turnover rates of this montane oak forest seem to be much greater than those of other oak forests in temperate regions (Duvigneaud & Denaeyer-De Smet, 1970; Cole & Rapp, 1981), but lower than those of tropical lowland forests (Vitousek & Sanford, 1986), and it is close to that of tropical montane rain forests (Edwards, 1982; Vaneklaas, 1991). The characteristics of nutrient cycling observed are in agreement with the understanding of the status of

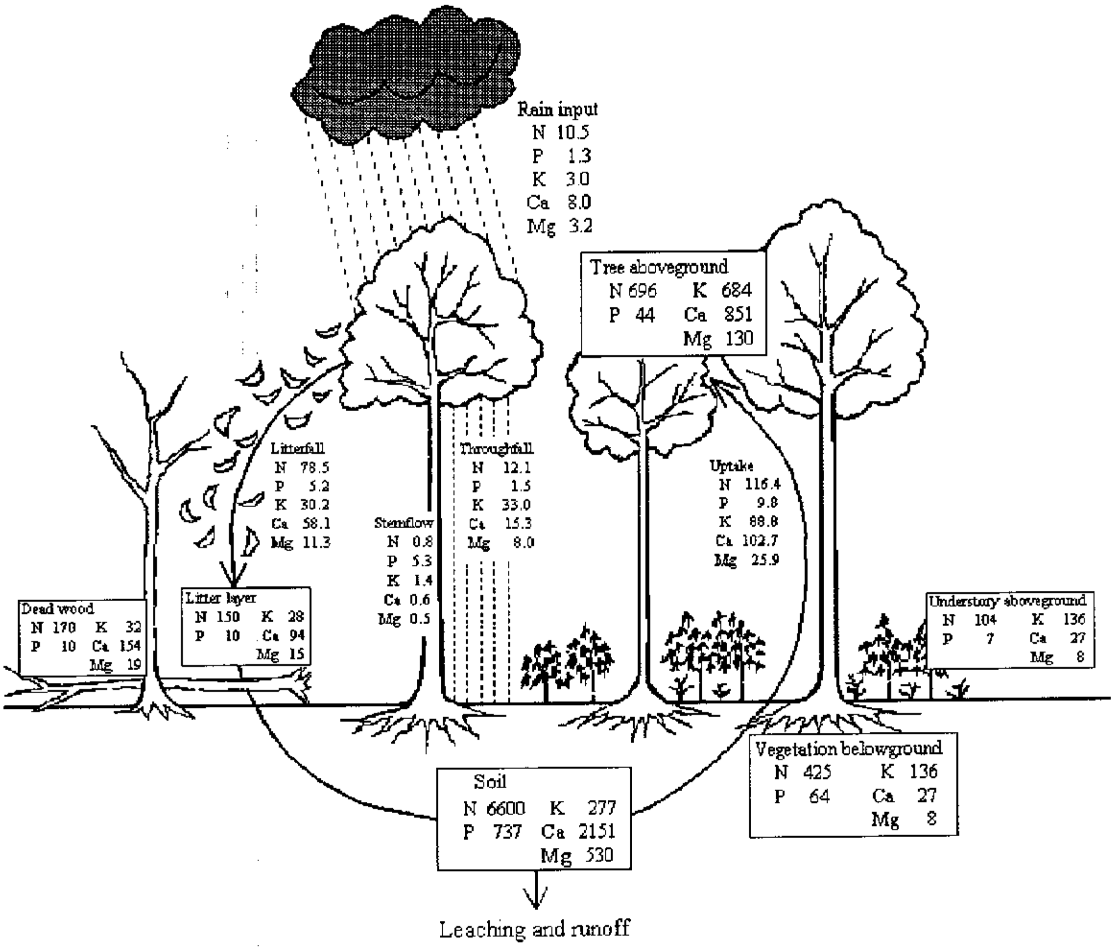

Fig. 9.1. Summary diagram of nutrient cycling in a montane moist forest at Xujiaba, Ailao Mountains, Yunnan, SW China. Data for the dry weight of organic matter and nutrient capital in various components of the ecosystem are presented within rectangles (kg ha^{-1}). Imported: by incident rainfall (kg ha^{-1}yr^{-1}). Returned: by litterfall, litter layer and leaching from canopy and stemflow (kg ha^{-1}yr^{-1}). Retained: in the annual increment of woody tissues (kg ha^{-1}yr^{-1}). Soil nutrient pool (30 cm depth): exchangeable cations and total nitrogen and total phosphorus (kg ha^{-1}yr^{-1}).

these natural forests as in a transitional or intermediate category in relation to environmental conditions (Qiu *et al.*, 1998).

The overall pattern of nutrient cycling in the natural forest is shown to be characterized by low retention and relatively high return of nutrients. The results of this study support the conventional view (Vitousek & Reiners, 1975) that old growth forest ecosystems should exhibit minimal or nil net biotic retention of nutrient inputs.

9.2 Overall input-output balance of macro-nutrients in the natural forest

Forest vegetation is most effective at retaining nutrients (Vitousek & Reiners, 1975; Pastor & Bockheim, 1984). The biological cycling of nutrients leads to the conservation of essential nutrients within forest ecosystems (Attiwill & Leeper, 1987), and large amounts of nutrients are retained in woody tissues through nutrient cycling and plant growth. Within the natural *Lithocarpus/Castanopsis* forest ecosystem, nutrient input-output budgeting indicated that annual losses of K and Ca in streamflow exceeded that of atmospheric input. However, there were larger amounts of these two elements returned from litterfall and leaching from the canopy to the soil each year. The annual amounts of return can sufficiently compensate for the loss of the two elements in streamflow (Table 9.1). Therefore, the long-term budgets for the natural forest ecosystem at Xujiaba seem to be in balance. Similar results were observed within unmanaged hardwood forest at Coweeta, southern Appalachians, USA (Johnson & Swank, 1973; Swank & Douglass, 1977; Henderson *et al.*, 1978).

Table 9.1. A comparison of the amount of nutrient returned annually from plant to soil and nutrient output through stream water in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR.

	Nutrient flux (kg ha^{-1} yr^{-1})				
	N	P	K	Ca	Mg
Return from plant to soil					
by litterfall	80.4	5.3	30.6	56.8	11.1
by leaching	2.4	0.2	31.4	7.9	7.1
Total return	82.8	5.5	62.0	64.7	18.2
Input-output					
Atmospheric input	10.5	1.3	3.0	9.0	3.2
Output by stream	4.4	0.8	17.0	33.9	8.7

9.3 Nutrient limitation of litter decomposition in the natural forest

Decomposition of plant litter regulates recycling of nutrients in ecosystems. Nutrient availability is considered to be the controller of decomposition (Swift *et al.*, 1979). Litter decay rates correlate positively with absolute nutrient concentrations or lignin (Melillo *et al.*, 1982; Taylor, Parkinson & Parsons, 1989). High N: P ratio in fresh litter in soils where P is limited, affecting litter decomposition is not unusual (Lugo & Murphy, 1986; Lisanework & Michelsen, 1994). Vogt *et al.*(1986) noted that the ideal N: P ratio for decomposers was 10 and higher ratios limited litter decomposition. In this study (Chapter 5), I demonstrate that fresh leaf litter of canopy species and bamboo have a higher N: P ratio. Low P concentration was observed in the forest soil by Deng *et al.* (1983). In decomposing litter, this ratio decreases initially and then subsequently increases, with a decreased decay rate. Alexander (1976) noted that N, and especially P concentration in decomposing residues increases in P deficient substrates. Thus, P seems to limit decomposition of plant litter in this natural forest.

9.4. Short-term cycle and long-term cycle

Within natural, old growth forest ecosystems, there are two kinds of nutrient turnover: the short-term cycle and long-term cycle (Edwards, 1982; Waring & Schlesinger, 1985). The short-term cycle is expressed rapidly in small litterfall, and in throughfall and stemflow, while the long-term cycle is a slower cycle of nutrients incorporated into larger woody tissues and subsequent release from them. Obviously, the two processes are not separate and the distinction is somewhat arbitrary. However, there is a correlation between both cycles. The rate of nutrient cycling in leaf litterfall, throughfall and stemflow (the short-term cycles) is likely to be a good guide to the availability of nutrients for wood growth (the long-term cycle). In comparison with lowland forests, Grubb (1977) found that the production of woody parts was reduced more than that of leaf. Therefore, there are similar amounts of nutrients cycling through leaves in a montane and a lowland forest, but much smaller amounts cycling through woody parts.

At Xujiaba, Ailoao Mountain NNR, the natural *Lithocarpus/Castanopsis* forest not only has very great biomass and nutrient accumulation, but also contains considerable amounts of nutrients in dead wood. The short-term cycle through litterfall, throughfall and stemflow supplies available nutrients to plant growth, but nutrient release from dead wood also plays important roles in nutrient cycling, although the mechanism of nutrient release is not very clear (Harmon *et al.*, 1986). Within the forest, most dead wood is derived from the natural death of old trees. Such individuals are partly decomposed before they actually fall down to the forest floor. Nutrient cycling through dead wood are likely to be relatively greater in the Ailao mountain forests than in plantations and other forests with relatively small amounts of dead wood.

9.5 Effect of epiphytes on nutrient cycling

Well-developed epiphytes are important structural features of tropical and subtropical montane forests and temperate wet forests. Epiphytes can contribute a substantial amount of biomass to the forest canopy. Due to their physiology and their location at the atmosphere-vegetation interface, epiphytes can affect the ecosystem in many ways. Pike (1978) states that epiphytes form an important nutrient pool in the montane forest ecosystem, and this can affect the pattern of nutrient cycling through processes of uptake, accumulation and release during the entire period of plant growth.

The Ailao Mountain forest examined in this thesis has abundant epiphytes, with a well-developed synusia of moss species. The biomass of epiphytes is comparable with other montane rain forests. The results of my epiphyte removal experiment show significant effects of epiphytes on the annual flux of nutrients in stemflow. Knops *et al.* (1991) revealed that canopy epiphytes could significantly influence the annual fluxes of nutrient in throughfall in an oak woodland in California. Despite widespread acceptance of effects of epiphytes on nutrient cycling in forest ecosystems, few studies have examined the effect of epiphytes on nutrient cycling. In further research, as suggested by Coxson & Nadkarni (1995), establishing long-term studies to quantify unknown properties such as epiphytic growth rates, death and decomposition rates, and colonization and successional regimes; and to carry out experimental work (e.g. fertilization studies, removal experiments) concerning nutrient cycling including the mechanism of uptake, fixation, release of nutrients by epiphytes should be important considerations in order to gain a better understanding of natural forest ecosystems.

9.6 Nutrient cycling with relation to ecosystem stability

It has been generally accepted that ecosystem stability is related to mineral cycling characteristics (Pomeroy, 1979; Odum, 1970, 1971; Jordan, Kline & Sassces, 1972; Brasell & Sinclair, 1983) and some studies have attempted to provide definitions of relative stability (Webster, Waide & Patten, 1975; Harwell, Cropper & Ragsdale, 1977). Three main factors, important to the functioning and stability of ecosystems, are the size of the abiotic element content, the size of the biotic contents, and the turnover rate of the nutrients. A low turnover rate relative to the content, generally indicates high potential resistance of the ecosystem to perturbation (Brasell & Sinclair, 1983). In this study, the amounts of nutrients in inputs and their relative turnover rates were relatively low compared with nutrient storage in the vegetation (Chapter 7; Table 7.3). Comparing the total nutrient input to the soil with size of the abiotic nutrient pool in the soil (Table 9.1), N, P, Ca and Mg have relatively low rates of flux compared with the abiotic soil content. K has a much larger quotient. This element is much more mobile than Ca, and is cycled mostly in a soluble form in throughfall and stemflow. A more eutrophic soil will probably be more resistant to perturbations (Brasell & Sinclair, 1983). The ratio of the annual nutrient returns to the soil to the available amounts of nutrient in the soil is thought to be an index of resistance (Brasell & Sinclair, 1983). Compared with tropical rain forests, the Ailao mountain forest has relatively low quotients for base cations, and relatively high quotients for N and P (Table 9.2). The greater quotients for N and P are due to low content of these two elements in the soil. Based on the quotients for nutrients, the Ailao mountain forest is likely to be more resistant to perturbation with respect to the less mobile elements, which have lower rates of turnover within the ecosystem.

Table 9.2. Comparison of the amounts of nutrient elements in the top 30 cm of soil and the quotient of total annual inputs of each element (litterfall + throughfall) to the mineral pool in the soil[1].

Site		N	P	K	Ca	Mg	Reference
Montane rain forest, New Guinea	Inputs	120	7.6	99	114	30	Edwards, 1982
	Soil pool	19200	2560	403	3750	682	
	Input/soil pool	0.006	0.003	0.25	0.03	0.04	
Rain forest, Australia	Inputs	-	-	19.2	26.8	6.2	Brasell & Sinclair, 1983
	Soil pool	-	-	70	1046	105	
	Input/soil pool	-	-	0.27	0.03	0.06	
Montane moist forest, Yunnan, SW China	Inputs	92.5	6.7	64.6	74.0	19.8	This study
	Soil pool	7600	737	277	2106	530	
	Input/soil pool	0.012	0.009	0.23	0.03	0.04	

[1] The values for N and P are total amount, while values for K, Ca and Mg are exchangeable.

On the other hand, the cycling and uptake of nutrients have been shown to be critical processes for the health of a forest ecosystem. Loss of nutrients from the ecosystem, disruption of nutrient cycling and uptake, or imbalance in nutrient status may be associated with decline in forest productivity and stability (Waring & Schlesinger, 1985; Attiwill & Leeper, 1987). When the forest is destroyed, for example, by bushfire or by logging, the ecosystem becomes temporarily non-conservative of nutrients. Following destruction of the forest, evapotranspiration decreases and drainage and streamflow increase. Litterfall, which previously maintained a continuing supply to the litter layer of organic matter, comes to a halt. The surface soil becomes better aerated, and warmer than it was under the mature natural, undisturbed forest. All of these factors contribute to an increase in mineralization and to a consequent increase in the concentration of nutrients in drainage waters and in the output of nutrients in streamflow (Bormann & Likens, 1979). In an intensively logged ecosystem, there is no system of nutrient cycling, and the increased rate of mineralization leads to losses of nutrients to drainage waters (Waring & Schlesinger, 1985).

Although no obvious disturbance results, collection of herbs, fungi, fruits and bamboo by local people does occur on a seasonal basis within the natural forest at

Xujiaba, Ailao Mountains. Such activities may make local impacts on nutrient cycling to some extent. From the point of view of nutrient cycling and ecosystem stability, these collecting activities should perhaps be documented to ensure that the ecosystem is able to sustain these activities without being compromised.

9.7 Recommendations

It will be obvious from this study that the pattern of nutrient cycling obtained after 2 years of observation (although data on litterfall were accumulated for 9 years), does not give a definitive picture for the behavior of this natural forest ecosystem. Owing to large temporal variations in nutrient fluxes, monitoring should continue for several years to validate the present trends and to reduce the weight of singular climatic years.

Ailao Mountains is an important boundary area (topographic, climatic and vegetative) in Yunnan (Young & Wang, 1989; Qiu et al., 1998; Wang *et al.*, 2000). The evergreen broad-leaved forests in this area are the richest and potentially most productive ecosystems (Wu, 1980, 1987; Davis *et al.*, 1995; Tagawa, 1997). However, these forest ecosystems are facing pressure from increasing population. It is imperative to develop an integrated approach to forest ecology research and management of this forest ecosystem. Through an ecological understanding of the forest ecosystem, strategies can be developed and policies established which could tap the productivity and diversity of the forest ecosystem so that both humans and forest can survive and prosper.

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APPENDICES

Appendix 1. Physical properties of mountain yellow-brown earth under natural Lithocarpus/Castanopsis forest at Xujiaba, Ailao Mountain NNR[a].

Soil property	Soil depths (cm)				
	3-10	10-30	30-50	50-80	80-130
Bulk density (g/cm^3)	0.60	0.69	0.89	1.09	1.28
Total porosity (%)	71.2	66.8	59.0	52.0	54.6
Saturated water capacity (%)	175.2	145.7	135.5	126.6	-
Maximum water capacity (%)	171.8	139.9	128.7	-	-
Percent particle size (mm)					
<0.001	12.0	14.0	18.0	16.0	19.5
0.001<0.01	16.0	22.0	23.0	27.0	20.0
0.01<0.05	24.0	22.0	19.5	25.0	18.0
0.05<1.00	48.0	42.0	39.5	32.0	42.5

[a] These data are from Qiu *et al.*(1998).

Appendix 2. Chemical properties of mountain yellow-brown earth under natural Lithocarpus/Castanopsis forest at Xujiaba, Ailao Mountain NNR[a].

Chemical composition	Soil depths (cm)				
	3-12	12-45	45-68	68-117	117-174
pH (H_2O)	4.42	4.80	4.86	4.90	4.99
OM (%)	12.91	8.21	5.81	3.59	2.66
Total N (%)	0.52	0.32	0.22	0.13	0.08
C / N	14.4	14.88	15.32	16.07	19.29
Available P (mg/kg)	42	21	29	25	18
Available K (mg/kg)	150.5	101.6	45.15	42.85	44.55
Exchangeable bases ($cmol^+$/100 g)					
Ca^{++}	7.60	5.32	5.05	2.59	1.80
Mg^{++}	3.50	2.11	0.60	0.62	0.91
K^+	0.75	0.29	0.15	0.14	0.16
Na^+	2.93	3.56	0.82	0.95	2.74
Total	10.98	8.62	4.10	4.30	5.61
CEC ($cmol^+$/kg)	37.88	38.71	29.26	20.01	17.99
Base saturation (%)	31.62	27.30	14.31	19.58	33.98
Total chemical composition (% oven-dry weight)					
SiO_2	37.34	41.46	44.24	45.13	48.00
Al_2O_3	15.39	17.84	19.70	20.74	20.50
Fe_2O_3	8.76	10.19	11.30	11.81	11.44
CaO	0.36	0.28	0.20	0.28	0.20
MgO	0.74	0.74	0.77	0.81	0.86
K_2O	1.12	1.21	1.33	1.52	1.57
Na_2O	0.44	0.39	0.42	0.44	0.45
P_2O_5	0.135	0.079	0.043	0.31	0.48

[a] These data are from Deng *et al.*(1983).

Appendix 3. List of vascular plants recorded from eight plots at Xujiaba, Ailao Mountain NNR[a].

No.	Species	Leaf form	Leaf size	Evergreen or Deciduous	Drip tip	Presence classes [a]
	Tree species					
1	*Castanopsis wattii*	MesPh	Mes	E	+	V
2	*Lithocarpus xylocarpus*	MesPh	Mes	E	+	V
3	*Schima noronhae*	MesPh	Mes	E	+	V
4	*Lithocarpus chintungensis*	MesPh	Mes	E	+	V
5	*Vaccinium duclouxii*	MicPh	Mes	E	+	V
6	*Manglietia insignis*	MesPh	Mes	E	+	IV
7	*Hartia sinensis*	MesPh	Mes	E	+	IV
8	*Machilus viridis*	MesPh	Mes	E	+	IV
9	*Camellia forestii*	MicPh	Mic	E	+	IV
10	*Eriobotrya bengalensis*	MesPh	Mes	E	+	IV
11	*Michelia floribunda*	MesPh	Mes	E	+	III
12	*Cyclobalanopsis sterwardiana* var. *longicaudata*	MesPh	Mes	E	+	III
13	*Rhododendron leptothrium*	MicPh	Mes	E	-	III
14	*Symplocos ramosissima*	MicPh	Mes	E	+	III
15	*Lindera thomsonii*	MesPh	Mes	E	+	III
16	*Lithocarpus hypoviridis*	MesPh	Mes	E	+	III
17	*Illicum macranthum*	MesPh	Mes	E	+	III
18	*Eurya obliquifolia*	MicPh	Mes	E	+	III
19	*Machilus bombycina*	MesPh	Mes	E	+	III
20	*Styrax perkinsiae*	MesPh	Mic	D	+	III
21	*Litsea elongata*	MesPh	Mic	E	+	II
22	*Schefflera shweliensis*	MesPh	Mes	E	+	II
23	*Neolitsea homilantha*	MesPh	Mes	E	+	II
24	*Symplocos botryantha*	MicPh	Mes	E	+	II
25	*Lyonia ovalifolia*	MesPh	Mic	D	+	II
26	*Symplocos anomala*	MicPh	Mes	E	+	II
27	*Mahonia mairei*	NaPh	Na	E	+	II
28	*Prunus maximowiczii*	MesPh	Mes	E	+	II
29	*Symplocos poilanei*	NaPh	Na	E	+	II
30	*Acanthopanax evodiaefolius*	MesPh	Mac	D	+	II
31	*Neolitsea polycarpa*	MesPh	Mes	E	+	I
32	*Acer heptalobum*	MesPh	Mes	D	+	I
33	*Elaeocarpus japonicus*	MesPh	Mes	E	+	I
34	*Ilex polyneura*	MesPh	Mes	E	-	I
35	*Ilex corallina*	MesPh	Mes	E	-	I
36	*Tapiscia yunnanensis*	MesPh	Mes	D	+	I
37	*Ilex corallina var. aberrans*	MesPh	Mes	E	-	I
38	*Butula luminifera*	MesPh	Mes	D	+	I
39	*Skimmia arborescens*	MicPh	Mes	E	+	I
40	*Eurya paratetragonoclada*	MicPh	Mic	E	-	I

41	*Populus bonatii*	MicPh	Mic	D	+	I
42	*Ilex szchwanensis*	MesPh	Mes	E	-	I
43	*Symplocos dryophila*	MicPh	Mic	E	-	I
44	*Acer amplum*	MesPh	Mes	D	-	I
45	*Ternstroemia gymnanthera*	MesPh	Mic	E	-	I
46	*Dichapetalum gelonioides*	MesPh	Mic	E	-	I
47	*Viburnum cylindricum*	MicPh	Mic	E	+	I
48	*Rhodoleia parvipetala*	MicPh	Mic	E	-	I
49	*Rhodendron irroratum*	MicPh	Mic	E	-	I
50	*Myrsine semiserrata*	MicPh	Mic	E	+	I
51	*Schefflera delavayi*	MesPh	Mes	E	+	I
52	*Litsea elongata var. subverticillata*	MicPh	Mic	E	+	I
53	*Itea chinensis*	MesPh	Mic	E	-	I
54	*Cinnamonmum pittosporoides*	MesPh	Mes	E	+	I

Shrub species

55	*Sinarundinaria nitida*	MicPh	Mic	E	-	V
56	*Daphne cannabina*	NaPh	Mic	E	-	IV
57	*Aridisia crenata*	NaPh	Na	E	-	III
58	*Zanthoxylum alpinum*	NaPh	Na	D	-	III
59	*Berberis sp.*	NaPh	Na	E	+	II
60	*Aucuba himalaica*	NaPh	Na	E	-	II
61	*Viburnum foetidum* var. *rectangulatum*	NaPh	Na	E	-	II
62	*Ligustrum delavayanum*	NaPh	Na	E	-	II
63	*Plagiopetalum serratum*	NaPh	Na	E	+	I
64	*Rhamnus heterophylla*	NaPh	Na	E	-	I
65	*Helwingia himalaica*	NaPh	Na	E	-	I
66	*Viburnum erubescens*	NaPh	Na	E	-	I
67	*Rubus pinfaensis*	NaPh	Na	E	+	I
68	*Rubus multibracteatus*	NaPh	Na	E	-	I
69	*Pentapanax racemosus*	NaPh	Na	D	-	I
70	*Cythotheca montana*	NaPh	Na	E	-	I

Herb species

71	*Carex teinogyan*	H	Mes		-	V
72	*Leptorumohra quadripinnata*	H	Mac		-	V
73	*Plagiogyria communis*	H	Mac		-	V
74	*Ophiopogon wallichianus*	H	Mes		-	IV
75	*Asparagus filicinus*	G	Mes		-	III
76	*Polysitichum nigropaleaceum*	H	Mes		-	II
77	*Pilea fasciata*	H	Mes		+	II
78	*Elatostema dissectum*	H	Mic		+	II
79	*Ainsliaea henryi*	H	Mes		-	II
80	*Oxalis griffithii*	T	Mic		-	II
81	*Reineckea carnea*	G	Mic		-	II

82	*Tupistra wattii*	H	Mic	-	II
83	*Polygonum strindbergii*	H	Mic	-	II
84	*Pteris nervosa*	H	Mac	-	II
85	*Arisaema erubescens*	G	Mac	-	I
86	*Impatiens rubrostriata*	T	Mic	-	I
87	*Sarcopyramis nepalensis*	T	Mes	-	I
88	*Strobilanthes* sp.	H	Mic	-	I
89	*Allantodia spectabilis*	H	Mac	-	I
90	*Rubia cordifolia*	H	Na	-	I
91	*Selaginella* sp.	H	Mic	-	I
92	*Athyrium dissitifolia*	H	Mac	-	I
93	*Allantodia hirsutepes*	H	Mac	-	I
94	*Impatiens siculifer*	T	Mic	-	I
95	*Athyrium mengtzeense*	H	Mac	-	I
96	*Scutellaria macrosiphon*	T	Mic	-	I
97	*Disporum sessile*	G	Mic	-	I
98	*Paries poplyphylla*	G	Mac	-	I
99	*Dryopteris subfructuosa*	H	Mac	-	I
100	*Huperzia serrata*	H	Mic	-	I
101	*Leycesteria formosa* var. *stenosepala*	Ch	Mes	-	I
102	*Ainsliaea bonatii*	H	Mes	-	I
103	*Ainsliaea triflora* var. *obovata*	H	Mes	+	I
104	*Disporum brachystemen*	G	Mes	-	I
105	*Elsholtzia rugulosa*	Ch	Mic	-	I
106	*Eupatorium edenophorum*	H	Mes	-	I
107	*Melissa axillaris*	H	Mic	-	

Liana species

108	*Tetrastigma hypoglaucum*	WL	Mic	-	V
109	*Heterosmilax japonica*	WL	Mic	-	IV
110	*Smilax ferox*	WL	Mic	-	III
111	*Jasminum duclo*	WL	Mic	-	III
112	*Euonymus vagans*	WL	Mic	-	III
113	*Smilax lebrunii*	WL	Mic	-	III
114	*Embelia procumbens*	WL	Mic	-	II
115	*Rosa longicuspis*	WL	Mic	-	II
116	*Actinidia glaucocallosa*	WL	Mic	+	II
117	*Heterosmilax yunnanensis*	WL	Mic	-	II
118	*Holboellia latifolia*	WL	Mic	-	II
119	*Jasminum dispermum*	WL	Mic	-	II
120	*Aristolochia yunnensis*	WL	Mic	-	I
121	*Parthenocissus himalayana*	WL	Mes	-	I
122	*Kadsura coccinea*	WL	Mic	-	I
123	*Rubus dielsianus*	WL	Mic	-	I
124	*Smilax hayatae*	HL	Mic	-	I

	Epiphyte species				
125	*Lepisorus scolopendrium*	Ep	Mes	-	V
126	*Agapetes mannii*	Ep	Na	-	IV
127	*Lepisrus loriformis*	Ep	Mic	-	IV
128	*Vittaria flexuosoides*	Ep	Mes	-	III
129	*Asplenium planicaule*	Ep	Mes	-	III
130	*Elatostema diversifolia* var. *elegans*	Ep	Mic	-	II
131	*Asplenium ensiforme*	Ep	Mes	-	II
132	*Araiostegia perdurans*	Ep	Mac	-	II
133	*Briggsia longifolia*	Ep	Mes	-	I
134	*Phymatopsis trisecta*	Ep	Mac	-	I
135	*Mecodium microsorum*	Ep	Mac	-	I
136	*Elatostema obtusum*	Ep	Mic	-	I
137	*Aeschynanthus buxifolius*	Ep	Mes	-	I
138	*Cautleya gracilis*	Ep	Mes	-	I
139	*Arthromeris lehmannii*	Ep	Mac	-	I

[a] These data are from Qiu *et al.* (1998).

E, Evergreen; D, Deciduous; MesPh, Mesophanerophyte; MicPh, Microphanerophyte; NaPh, Nanophanerophyte; Ch, Chamaephyte; H, Hemicryptophyte; G, Geophyte; T, Therophyte; WL, Woody Liana; HL, Herbaceous Liana; Ep, Epiphyte.

Mac, Macophyll; Mes, Mesophyll; Mic, Micophyll; Na, Nanophyll; (Raunkiaer, 1934).

"+" Leaf with drip tip; "-"leaf without drip tip.

Presence classes (from Braun-Blanquet, 1932), V (presence in 81-100 % of plots), IV (61-80 %), III (41-60%), II (21-40 %) and I (<20 %).

Appendix 4. The tree species of natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR with their importance values [a].

Tree species	No. of tree	Mean height (m)	Mean DBH (cm)	Abundance (%)	Dominance (%)	Relative freq. (%)	IV
Castanopsis wattii	71	24	68	5.2	21.0	5.6	31.7
Lithocarpus xylocarpus	98	25	42	7.1	8.0	5.3	20.4
Schima noronhae	94	23	35	6.8	5.6	5.3	17.7
Lithocarpus chintungensis	82	22	39	6.0	6.9	4.7	17.6
Vaccinium duclouxii	128	7.7	8.2	9.3	0.3	2.9	12.6
Manglietia insignis	56	21	23.5	4.1	2.5	4.7	11.3
Hartia sinensis	76	18	19.8	5.5	1.8	3.2	10.5
Machilus viridis	53	20	22	3.9	2.2	4.4	10.5
Camellia forestii	77	4.4	5.7	5.6	0.1	3.5	9.3
Eriobotrya bengalensis	68	12	14	4.9	0.9	3.2	9.1
Michelia floribunda	50	18	22	3.6	2.2	2.9	8.8
Cyclobalanopsis sterwardiana var. *longicaudata*	34	19	26.8	2.5	3.3	2.9	8.7
Rhododendron leptothrium	78	6	8.5	5.7	0.3	2.1	8.1
Symplocos ramosissima	38	11	11.5	2.8	0.6	3.5	6.9
Lindera thomsonii	29	16.2	17.9	2.1	1.5	3.2	6.8
Lithocarpus hypoviridis	17	19	28.8	1.2	3.8	1.5	6.5
Tapiscia yunnanensis	2	25	35	0.1	5.6	0.6	6.3
Illicum macranthum	21	17	21	1.5	2.0	2.6	6.2
Eurya obliquifolia	31	3.9	4.4	2.3	0.1	3.5	5.9
Acanthopanax evodiaefolius	3	23	32.5	0.2	4.8	0.9	5.9
Schefflera shweliensis	9	19.6	26	0.7	3.1	2.1	5.8
Machilus bombycina	22	13.7	13	1.6	0.8	3.2	5.6
Symplocos botryantha	39	6.2	5.8	2.8	0.2	2.6	5.6
Styrax perkinsiae	26	21	17.5	1.9	1.4	2.1	5.3
Lyonia ovalifolia	20	20	23	1.5	2.4	1.5	5.3
Litsea elongata	20	10.6	10.3	1.5	0.5	2.4	4.3
Neolitsea polycarpa	8	18.7	22.9	0.6	2.4	1.2	4.1
Acer heptalobum	2	18	28	0.1	3.6	0.3	4.0
Elaeocarpus japonicus	6	17.5	21	0.4	2.0	1.2	3.6
Ilex polyneura	5	20.5	18	0.4	1.5	1.5	3.3
Ilex corallina	15	13.4	12	1.1	0.7	1.5	3.2
Neolitsea homilantha	18	13.4	11.4	1.3	0.6	1.2	3.1
Symplocos poilanei	12	3	4	0.9	0.1	2.1	3.0
Symplocos anomala	9	9.6	8.5	0.7	0.3	1.2	2.2
Ilex corallina var. aberrans	3	18	16	0.2	1.2	0.6	2.0
Butula luminifera	2	22	18	0.1	1.5	0.3	1.9
Skimmia arborescens	9	6	5.2	0.7	0.1	0.9	1.7
Eurya paratetragonoclada	6	5	6.8	0.4	0.2	0.9	1.5
Ilex szchwanensis	2	12.5	13	0.1	0.8	0.6	1.5
Smplocos dryophila	6	3	4.5	0.4	0.1	0.9	1.4
Acer amplum	1	17.5	14	0.1	0.9	0.3	1.3
Ternstroemia gymnanthera	5	8.5	7.8	0.4	0.3	0.6	1.2
Dichapetalum gelonioides	4	9.2	8	0.3	0.3	0.6	1.2
Schefflera hypoleuca	3	6	5.5	0.2	0.1	0.6	0.9
Mahonia mairei	3	2.8	2.2	0.2	0.0	0.6	0.8
Prunus maximowiczii	3	6	8.5	0.2	0.3	0.3	0.8
Viburnum cylindricum	1	9.2	8.5	0.1	0.3	0.3	0.7
Rhodoleia parvipetala	1	8	8.2	0.1	0.3	0.3	0.7
Rhodendron irroratum	1	7	8.5	0.1	0.3	0.3	0.7
Myrsine semiserrata	4	4	3.5	0.3	0.1	0.3	0.6
Schefflera delavayi	1	6.5	7.2	0.1	0.2	0.3	0.6
Litsea elongata var. subverticillata	1	5	6.2	0.1	0.2	0.3	0.5
Itea chinensis	1	5	5.5	0.1	0.1	0.3	0.5
Cinnamonmum pittosporoides	1	6	6.3	0.1	0.2	0.3	0.5

[a] These data are from Qiu *et al.* (1998).

IV, Importance value (Abundance + Dominance + Relative frequency).

All species is present in the eight plots (total area of 8 x 400 m^2). Minor species (<2.5 cm in diameter) are omitted.

Appendix 5. Species diversity of different stands in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR [a].

Plot No.	1	2	3	4	5	6	7	8	Mean ±SD
Area (m^2)	400	400	400	400	400	400	400	400	
Stand	Primary forest	Primary forest	Primary forest	Primary forest	Interior regrowth	Interior regrowth	Forest-edge regrowth	Forest-edge regrowth	
Canopy cover (%)	90	90	90	80	90	80	90	80	
Slope (°)	10	10	15	15	12	10	15	15	
Exposure (°)	SW 10	SW 5	SW 10	SW 15	SW 10	SW 10	NW 30	NW 10	
No. of individual	1474	1425	1368	1602	1793	2000	2774	2407	1855 ±508
No. of species	56	60	55	69	59	63	60	72	62 ±6
H'	2.9653	2.8591	2.3383	3.2760	2.5913	3.0785	2.3658	3.1538	2.8285 ±0.3583
D'	0.8996	0.8819	0.7567	0.9010	0.8806	0.8884	0.8439	0.9347	0.8734 ±0.0535
E	0.7469	0.7308	0.6143	0.7737	0.6409	0.7430	0.6413	0.7982	0.7111 ±0.0690

[a] These data are from Qiu *et al.*(1998).

H', D' and E are respectively Shannon-Wiener, Simpson index and evenness index.

Appendix 6. Species diversity indexes of different layers in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

No. of plot	Layers	Total individual	Total species	H'	D'	E
1	Tree A	17	7	1.7080	0.7866	0.8777
	Tree B	33	11	1.8720	0.7545	0.7807
	Shrub	459	17	1.2365	0.4490	0.4364
	Herb	965	21	2.9754	0.9034	0.8012
2	Tree A	33	9	1.9016	0.8246	0.8455
	Tree B	68	19	2.5124	0.8888	0.8533
	Shrub	463	18	0.9458	0.3204	0.3272
	Herb	861	14	2.8628	0.9091	0.7869
3	Tree A	15	8	1.9336	0.8356	0.9298
	Tree B	33	17	2.6847	0.9220	0.9476
	Shrub	749	18	0.7820	0.2653	0.2705
	Herb	571	12	2.9044	0.9225	0.8716
4	Tree A	13	7	1.7780	0.8046	0.9137
	Tree B	60	16	2.2110	0.8455	0.7974
	Shrub	557	18	0.7894	0.2709	0.2731
	Herb	927	28	3.9180	0.9656	0.9649
5	Tree A	13	7	1.8450	0.8281	0.9481
	Tree B	31	18	2.8886	0.9226	0.9994
	Shrub	630	12	0.5916	0.2065	0.2381
	Herb	1119	22	2.7171	0.8633	0.7224
6	Tree A	45	8	1.7820	0.8021	0.8570
	Tree B	22	14	2.5280	0.9090	0.9579
	Shrub	463	24	2.0262	0.7615	0.6375
	Herb	1470	17	2.8028	0.8406	0.7165
7	Tree A	19	10	2.0060	0.8584	0.9189
	Tree B	49	14	2.4342	0.8996	0.9224
	Shrub	906	16	0.5251	0.1700	0.1894
	Herb	1800	20	2.3000	0.8138	0.6578
8	Tree A	12	8	2.0232	0.8611	0.9730
	Tree B	46	18	2.5170	0.8904	0.8708
	Shrub	586	23	1.7865	0.6659	0.5697
	Herb	1763	23	2.9580	0.9276	0.8535

[a] These data are from Qiu *et al.* (1998).

Some tree species at patches occur in short crown because of local environmental condition. They were recorded as shrub species in some plots.

H000', D' and E are respectively Shannon-Wiener, Simpson index and evenness index. The data in the table are the average of eight 20 x 20 m2 plots.

Appendix 7. Diversity indexes of woody plant species in natural *Lithocarpus /Castanopsis* forest at Xujiaba, Ailao Mountain NNR [a].

No. of plot	Diameter class	Total individual	Total species	H’	D’	E
1	>2.5cm	52	15	1.9292	0.8417	0.7124
	>7.5cm	28	12	2.2637	0.8725	0.9110
	>12.5cm	21	9	1.9543	0.8300	0.8894
	>17.5cm	11	6	1.6417	0.7769	0.9162
2	>2.5cm	102	21	2.6725	0.9145	0.8778
	>7.5cm	85	19	2.6217	0.7784	0.8903
	>12.5cm	62	19	2.6089	0.9095	0.8860
	>17.5cm	54	15	2.4095	0.8931	0.8897
3	>2.5cm	49	23	2.9267	0.9355	0.9334
	>7.5cm	35	18	2.6610	0.9110	0.9206
	>12.5cm	29	14	2.4012	0.8847	0.9099
	>17.5cm	23	10	2.0381	0.8356	0.8851
4	>2.5cm	83	19	2.2960	0.9208	0.7800
	>7.5cm	34	18	2.7650	0.9292	0.9566
	>12.5cm	16	12	2.3050	0.8894	0.9999
	>17.5cm	13	9	2.0960	0.8633	0.9540
5	>2.5cm	46	20	2.6265	0.9311	0.8767
	>7.5cm	35	18	2.7270	0.9359	0.9435
	>12.5cm	29	14	2.4990	0.9102	0.9469
	>17.5cm	20	12	2.3470	0.3899	0.9445
6	>2.5cm	68	17	2.5006	0.8616	0.8826
	>7.5cm	45	11	1.9814	0.8188	0.8263
	>12.5cm	38	7	1.5995	0.7562	0.8220
	>17.5cm	36	7	1.6225	0.7640	0.8338
7	>2.5cm	70	18	2.6422	0.9118	0.9141
	>7.5cm	47	17	2.4777	0.8946	0.8745
	>12.5cm	39	13	2.3188	0.8885	0.9038
	>17.5cm	22	11	2.2087	0.8719	0.9211
8	>2.5cm	77	25	2.8692	0.9283	0.8229
	>7.5cm	50	19	2.6489	0.9324	0.8996
	>12.5cm	34	14	2.4427	0.8856	0.9256
	>17.5cm	22	10	2.1454	0.8678	0.9317

[a] These data are from Qiu *et al.*(1998).

Some woody species occur in more than one diameter class in the plots.

H’, D’ and E are respectively Shannon-Wiener, Simpson index and evenness index. The data in the table are the average of eight 20 x 20 m2 plots.

Appendix 8. Regression equations between tree age (year) and D (cm) of dominant species in natural *Lithocarpus/Castanopsis* forest at Xujiaba, Ailao Mountain NNR[a].

Tree species	Regression	Correlation coefficient	DBH (cm)	Age (yr)
Lithocarpus xylocarpus	A =2.9190 + 2.169D	R^2 = 0.9994	3.0 – 41.1	10 – 93
L. chintungensis	A =5.1775 + 1.9592D	R^2 = 0.9994	2.6 – 27.0	10 – 57
Castanopsis wattii	A =15.7856 + 2.0587D	R^2 =0.9978	2.9 – 39.5	20 – 98
Machilus viridis	A =-7.5532 + 2.7955D	R^2 =0.9968	4.2 – 37.8	10 – 76
Manglietia insignis	A =5.7356 + 2.3812D	R^2 =0.9948	10.6 – 31.5	20 – 85
Schima noronhae	A =1.6592 + 1.9949D	R^2 =0.9980	2.0 – 32.0	10 – 58
Hartia sinensis	A =-13.6000 + 2.8233D	R^2 =0.9718	11.6 – 38.7	20 – 100

[a] These formulae are from Xie *et al.*(1983)

Appendix 9. Publications and Reference Conference Proceedings

Peer-Refereed Journal Publications

Liu W., Fox, J. E. D. & Xu, Z. (2001) Nutrient budgets of a montane evergreen broad-leaved forest at Ailao Mountain National Nature Reserve, Yunnan, SW China. *Hydrological Processes* (Submitted).

Liu, W., Fox, J. E. D & Xu, Z. (2001) Nutrient fluxes in bulk precipitation, throughfall and stemflow in montane subtropical moist forest on Ailao Mountains in Yunnan, SW China. *Journal of Tropical Ecology* (in press).

Liu, W., Fox, E. D. Fox & Xu, Z. (2001) Litterfall and nutrient dynamics in montane moist evergreen broad-leaved forest on Ailao Mountains, SW China. *Plant Ecology* (in press).

Liu, W., Fox, J. E. D. & Xu, Z. F. (2001) Community characteristics, species diversity and management of middle mountain moist evergreen broad-leaved forest in the Ailao Mountains, southwestern China. *Pacific Conservation Biology* **6**: xxx-xxx (in press).

Liu, W., Fox, J. E. D. & Xu, Z. F. (2001) Biomass and nutrient accumulation in montane evergreen broad-leaved forest (*Lithocarpus xylocarpus* type) in Ailao Mountains, SW China. Forest Ecology and Management (in press).

Liu, W., Fox, J. E. D. and Xu, Z. F. (2000) Leaf litter decomposition of canopy trees, bamboo and moss in montane moist evergreen broad-leaved forest in Ailao Mountain of Yunnan, SW China. *Ecological Research* 15: 435-447.

Liu, W., Liu. L. H. & He, A. (2000) Decomposition of leaf litter *in Pinus yunnanensis* forest and evergreen broad-leaved forest in central Yunnan. *Acata Botanica Yunnanica* **22**: 298-306.

Liu, W. (2000) The role of epiphytic material in nutrient cycling of forest ecosystem. *Chinese Journal of Ecology* **19**: 30-35.

Liu, W., Liu, L. H. & Sheng, C. Y. (1999) Adaptability and application of biological engineering for controlling debris flow. *Journal of Mountain Science* **17**: 358-362.

Liu, W., Liu, L. H., Qiu, X. Z., Xie, S. C. & Sheng, C. Y. (1999) Bio-ecological engineering prevention and control of debris flow of Houshan by Nanjian County Town, Yunnan. *Journal of Mountain Science* **17**: 136-140.

Liu, W., Liu, L. H., Qiu, X. Z., Xie, S. C., Sheng, C. Y. & Tang C. (1999) Environmental characteristics and its control of dry-hot degraded mountainous area by Nanjian County, Yunnan Province. *Journal of Soil Erosion and Soil and Water Conservation* **5**: 87-95.

Liu, W., Sheng, C. Y. & Liu, L. H. (1999) Vegetation restoration on degraded mountainous area of dry-hot river valley in Nanjian County, Yunnan Province. *Journal of Beijing Forestry University* 21: 9-13.

Liu, W., Sheng, C. Y. & Liu, L. H. (1999) Analysis of benefit of vegetation restoration on degraded mountainous area of dry-hot river valley in Nanjian County. *Guihaia* 19: 215-220.

Liu, W. (1999) Study on rainfall erosivity and soil erodibility in the Zhaotong Basin, Yunnan Province. *Yunnan Geological Environment Research* 11: 76-82.

Liu, W., Liu, L. H. & Sheng, C. Y. (1999) Experiment on the bio-ecological engineering harnessing of gullies in degraded mountainous region in dry-hot valley in Nanjian of Yunnan. *Yunnan Geological Environment Research* **11:** 38-43.

Liu, W. (1999) Preliminary study of R index of the Zhaotong Basin. *Yunnan Forestry science and Technology* 7: 24-26.

Book Chapters

Liu, W. (1998) Uptake, accumulation and allocation of chemical elements of dominant plants in *Lithocaupus xylocarpus* forest (Seventh Chapter). Pp. 75-83. In *Studies on the Forest Ecosystem in Ailao Mountain, China* (Eds. X. Z. Qiu, S. C. Xie & W. Liu). Yunnan Science and Technology Press, Kunming. pp 135.

Liu, W. (1998) Litterfall, coarse woody debris and nutrient return in *Lithocaupus xylocarpus* forest (Eighth Chapter). Pp. 84-93. In *Studies on the Forest Ecosystem in Ailao Mountain, China* (Eds. X. Z. Qiu, S. C. Xie & W. Liu), Yunnan Science and Technology Press, Kunming. pp 135.

Peer-Refereed Conference Proceedings

Liu W. & Fox, J. E. D. (2000). Litter production and leaf litter decomposition of selected canopy species, bamboo and moss in a montane rain forest on Ailao Mts., Yunnan, SW China. Presented at Conference on "Ecology in a Rapidly Changing World", held in Melbourne 29th Nov. to 1st Dec.

Liu W. (2000). Vegetation restoration of degraded mountainous area of dry-hot valley in the middle southern parts of Yunnan Province, southwestern China. International Conference on the Remediation and Management of Degraded Lands. Fremental, 30th Nov -2 nd, Dec. Western Australia.

Liu, W. (2000). Nutrient accumulation and cycling in a montane moist evergreen broad-leaved forest on Ailao Mts., Southwestern China. (Accepted by Third International Oak Conference, held at The North Carolina Arboretum, Indiana, USA on 28-31 October, 2000.

Liu, W., Liu, L. H., Qiu, X. Z., Xie, S. C. & Sheng, C. Y. (1999) The role of bio-ecological engineering in the biodiversty conservation and sustainable development in mountainous regions and its application prospect analysis.

Proceedings of International Symposium on Biodiversity Management and Sustainable Socia-economic Development in the Upper Mekong River Basin. Xishuangbanna, pp.43-44.