中国西南地区热带季节雨林及山地常绿阔叶林 热值及能量分配格局

林 华^{1,2} 曹 敏^{1*} 张建侯¹

(1 中国科学院西双版纳热带植物园森林生态系统研究中心,昆明 650223) (2 中国科学院研究生院,北京 100049)

摘 要 能量分配格局是研究生态系统能量流动的基础,但是由于热带森林结构的高度复杂性和物种多样性,对它的热值和能量分配格局的全面研究还很少。该文研究的热带季节雨林位于西双版纳,是分布于热带亚洲北缘的一种森林类型,山地常绿阔叶林位于云南省中部的哀牢山,属于我国西部亚热带地区的地带性常绿阔叶林。该研究的目的是探讨这两种重要森林类型的热值和能量分配格局,验证 Golley(1961,1969)提出的世界范围内植被的热值由低纬度向高纬度、由低海拔向高海拔升高的规律。热值的测定采用 SDCM-III a 氧弹测量仪。两个森林样地面积都是 1 hm²,能量分配格局及年固定量根据生物量和生物量增量计算。研究结果表明,热带季节雨林样地的热值低于山地常绿阔叶林,乔木层的热值>灌木层>草本层,所有器官中叶片的热值较高。由于以前种植砂仁(*Amomum villosum*)的影响,热带季节雨林样地的能量现存量小于山地常绿阔叶林,但是因为地处高温高湿、光照充足的地区,热带季节雨林的年固定量高于山地常绿阔叶林。对于热带季节雨林样地来说,97%的能量储存在乔木层中;山地常绿阔叶林样地的乔木层储存了 88%的能量,可见乔木层是维持森林能量结构的关键层。研究结果为 Golley 的结论提供了更加丰富的实验证据。

关键词 热值 能量储存 能量固定 热带季节雨林 山地常绿阔叶林

CALORIC VALUES AND ENERGY ALLOCATION OF A TROPICAL SEASONAL RAIN FOREST AND A MONTANE EVERGREEN BROAD-LEAVED FOREST IN SOUTHWEST CHINA

LIN Hua^{1,2}, CAO Min^{1*}, and ZHANG Jian-Hou¹

¹Forest Ecosystem Research Center, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China, and
²Graduate University of Chinese Academy of Sciences, Beijing 100049, China

Abstract Aims Energy allocation pattern is the basis for understanding energy flow processes in ecosystems. High structure complexity and species diversity of tropical forests, however, have resulted in little research on caloric values and energy allocation patterns in tropical rain forests. Tropical seasonal rain forest (TSRF) in Xishuangbanna, Southwest Yunnan is distributed on the northern edge of tropical Asia, and montane evergreen broad-leaved forest (MEBF) is located in subtropical mountain areas of middle Yunnan. Our objectives are to examine the energy allocation pattern of the two forests and test the hypothesis of Golley (1961, 1969) that caloric values of vegetation tend to increase with the altitude and latitude.

Methods Caloric values were measured with a SDCM-III a oxygen bomb calorimeter. Energy allocation and sequestration were estimated based on biomass and biomass increment in a 1 hm² plot in each forest.

Important findings The caloric value of the TSRF plot was lower than that of the MEBF plot. Caloric values decreased from tree layer to shrub layer to herb layer. Leaves showed the highest caloric values of any plant part. Due to an understory plantation of *Amomum villosum*, which had removed almost all saplings and seedlings, the TSRF plot stored less energy than the MEBF plot, although it still maintained a high energy sequestration rate for tropical habitats with high temperature, humidity and intensive solar radiation. The tree layer stored 97% of the energy in the TSRF plot and 88% in the MEBF plot, suggesting that tree layer plays a key role in the maintenance of energy structure in the two forests. Our results support Golley's hypothesis.

Key words caloric value, energy storage, energy sequestration, tropical seasonal rain forest, montane evergreen broad-leaved forest

The dynamics and translation of energy between environments and organisms are two basic functions of ecosystem. Energy flow and storage serve as two key aspects of energy study (Odum , 1983 ; Zu , 1990). Since caloric value can be both precisely defined and measured in physical units , it is usually used as an equivalent to convert biomass into energy. The approach has been attempted at different levels of ecological organization : individual , population , and ecosystem (Ovington & Heitkamp , 1960 ; Bliss , 1962 ; Hadley & Bliss , 1964 ; Ovington & Lawrence , 1967 ; Kucera *et al.* , 1967 ; Golley , 1969 ; Jordan , 1971 ; Zu , 1991 ; Li & Wu , 1996 ; Lin *et al.* , 1996 , 1999 ; Ren *et al.* , 1999 ; Ren & Peng , 1999 ; Guo *et al.* , 2001a , 2001b).

Measurement of the energy content of organic matter in different parts of the biosphere is becoming increasingly important as the current ecological research lays greater emphasis upon energy flows in ecosystems. Estimation of energy storage and annual sequestration are the first step to determine energy translation in ecosystem. However , the energy studies in tropical rain forest ecosystems were still rarely reported because of the high structural complexity and species diversity of the ecosystems. Although Golley (1969) and Jordan (1971) measured the caloric values of some species in tropical rain forests , their samples were only represented by 2 – 5 species. In China , Li *et al.* (1996) reported caloric values of a tropical mountain forest in Hainan Island , but there still exists a large gap in energy studies between tropical zone and other climate zones .

Tropical seasonal rain forest (TSRF) and montane evergreen broad-leaved forest (MEBF) are two important forest types in Yunnan Province , China. TSRF is distributed in Xishuangbanna , southwestern Yunnan , on the northern edge of tropical Asia. This area is predominated by tropical monsoon climate with a distinct alternation between dry season (from November to April) and rainy seasons (from May to October). This results in the fact that the TSRF is mixed with a small proportion of deciduous tree species (Zhang & Cao , 1995 ; Zhu *et al.* , 2006).

The subtropical region , which covers more than 50% land area of Yunnan Province , is represented by evergreen broad-leaved forest that is dominated by the tree species of Fagaceae , Lauraceae , Theaceae and Magnoliaceae. Montane evergreen broad-leaved forest (MEBF) is distributed on the subtropical mountains , ranging from 1 100 m to 2 700 m above sea level (asl.) (Wu & Zhu , 1987).

This study aims at examining the energy allocation

pattern of the TSRF and MEBF. We also intend to verify the hypothesis proposed by Golley (1961 , 1969) : caloric values of vegetation tend to increase with altitude and latitude.

1 Materials and Methods

1.1 Study sites

The two study sites are all in Yunnan Province , Southwest China (Fig. 1).

Fig. 1 Geographic location of the sites
Site 1 : Tropical seasonal rain forest Site 2 : Montane evergreen broad-leaved forest

1.1.1 Site 1

The climate of Xishuangbanna is dominated by Asian monsoon with high rainfall occurring from November to April. There is a well-defined alternation of rainy and dry seasons. In the Xishuangbanna Tropical Botanical Garden (21°54' N , 101°46' E , 580 m asl.) , the long-term (1959 – 1998) annual mean temperature averaged 21.8 °C , the mean temperature of the coldest month (January) is 16 °C . Annual precipitation averaged 1 493 mm , of which over 84% occurs in rainy season (between May and October , data from Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies). A lateritic red soil occurs below 1 000 m elevation (Cao *et al.* , 2006).

The tropical seasonal rainforest is one of the most luxuriant forests in Xishuangbanna. It is distributed in wet valleys , usually with small streams or on the low hills and flats below 1 000 m altitude. *Pometia tomentosa*-*Terminalia myriocarpa* forest is one of the representative types. The canopy comprises three tree layers (A , B and C). Dominant tree species in layer A (> 30 m) are *Pometia tomentosa* , *Barringtonia macrostachya* , *Terminalia myriocarpa* , *Gironniera subaequalis* , and *Garuga*

floribund. Layer B is between 16 – 30 m and layer C is lower than 16 m. *Barringtonia macrostachya*, *Sloanea cheliensis*, *P. tomentosa*, *Semecarpus reticulata*, *Cleidion brevipetiolatum*, *Chisocheton siamensis*, *Ardisia tenera*, *Mezzettiopsis creaghii*, *Dichapetalum gelonioides*, and *Millettia leptobotrya* are frequently met in these two layers. Saplings dominate the shrub layer, such as *Ardisia tenera*, *Mezzettiopsis creaghii*, *Drypetes yunnanensis* and *Dichapetalum gelonioides* (Cao *et al.*, 1996). There are no obvious dominant species in herb layer, but *Tectaria decurrens*, *Elatostema macintyreii*, *Phrynium capitatum*, *Selaginella* sp. are often found.

1.1.2 Site 2

Climatic records at Ailao Mountains Station for Subtropical Forest Ecosystem Studies (24°32' N, 101°01' E, 2 450 m asl.) indicate that the mean annual temperature is 11.3 °C, the mean temperature of the coldest month (January) is 5.4 °C. The mean annual precipitation is 1 931 mm with more than 85% occurring from May to October (Liu *et al.*, 2002). Soils are alfisols (Qiu *et al.*, 1998).

MEBF is a kind of subtropical forest on the Ailao Mountains. *Lithocarpus xylocarpus*, *L. chintungensis* and *Castanopsis wattii* dominate the forest. The forest canopy is composed of two tree layers (layer A : 18 – 25 m, with 90% coverage, layer B : 5 – 18 m, with 50% coverage). Lower saplings and shrubs (1 – 3 m) cover 70%, and herbs (< 0.5 m) cover 30% (Qiu *et al.*, 1984; Liu *et al.*, 2002). Dominant tree species of tree layer A are *L. xylocarpus*, *L. chintungensis*, *Castanopsis wattii*, *Machilus viridis*, *Manglietia insignis* and *Schima noronhae*. Layer B includes species of *Machilus*, *Litsea*, *Neolitsea* (Lauraceae); *Camellia*, *Eurya* (Theaceae); *Symplocos* (Symplocaceae); *Ilex* (Aquifoliaceae); *Schefflera* (Araliaceae). Sapling and shrub layer are dominated by well-developed bamboo (*Sinarundinaria nitida*). Evergreen fern species are major herb layer components. Epiphytic species comprise mosses, lichens and ferns as well as some other seed plants.

1.2 Sampling

Sample collections for the measurement of caloric values were carried out in November, 2003 (late rainy season) and April, 2004 (late dry season) respectively. Nine subplots of 20 m × 20 m were established for sampling tree layers, which were arranged along diagonals in a plot of 100 m × 100 m for each site (Fig. 2). Tree layers were sorted into three sub-layers according to perimeter at breast height (PBH): tree layer III, 10 – 50 cm; tree layer II, 50 – 100 cm; tree layer I, ≥ 100 cm. Sample trees were determined by the PBH ratio of the three PBH classes. Then we chose the dominant species from each PBH class, based on the abundance representing each species in the subplot. Finally, the

trees were sampled in proportion to the number of individuals in each PBH class for a given species. In consequence, a total of 34 species for TSRF and 23 species for MEBF were sampled, separating leaves, stems, branches and roots. As it was hard to ascribe lianas into a certain plot, we sampled 7 species in TSRF and 3 species in MEBF according to the species abundance of lianas in each site, separating leaves, stems and roots. Shrub and herb samples were taken in five quadrates of 2 m × 2 m arranged in the middle of four edges and in the centre of the plot respectively (Fig. 2). Whole plants were harvested and sorted into leaves, branches and roots samples for shrubs, and aboveground and belowground parts for herbs. Forest floor litter including leaves and woody parts was also collected in the five quadrates.

All the materials were washed with water in order to avoid the contamination of non-plant materials. Leaves were oven-dried at 80 °C for 24 hours and woody parts were oven-dried for 48 hours, and then pulverized.

Fig. 2 Distribution of subplots and quadrates
Nine subplots for tree layer are marked by numbers. Grey blocks represent the quadrates in which shrubs, herbs and litter were sampled

1.3 Caloric values measurement

All samples were dried again at 105 °C for 3 – 4 hours prior to measurement. Duplicated caloric determinations were made for each sample using SDCM-IIIa oxygen bomb calorimeter. The relative variation between the two replicates of each sample was limited below 1%.

Energy storage is given by : $E = B \times GCV$
Where E is energy storage, B is biomass, GCV is caloric value.

Energy sequestration can be obtained as follows :
 $ES = \Delta B \times GCV$
Where ES is energy sequestration, ΔB is the increment

in biomass.

The biomass of the two forest types was estimated by the previous research by Feng *et al.* (1998) (TSRF) and Liu *et al.* (2002) (MEBF).

1.4 Data analysis

Average caloric value of each plot was estimated based on the average caloric values of the nine subplots (for tree layer) and the five quadrates (for shrub layer and herb layer) sampled in the two seasons. ANOVA was applied to test the statistical differences. Difference was considered as significantce if the value of significance level was ≤ 0.05 .

2 Results

2.1 Caloric values

The average caloric value (ACV) ($18\,586.61\text{ J}\cdot\text{g}^{-1}$) of TSRF plot is lower than that of MEBF plot ($19\,431.97\text{ J}\cdot\text{g}^{-1}$). With the exception of the shrub layer, the ACV in each layer (tree layer, herb layer and litter layer) is significantly higher in MEBF than in TSRF plot ($p < 0.01$). Particularly, the ACV of litter layer in MEBF is 10% higher than that in TSRF plot. In general, ACV tends to decrease from tree layers to shrub layers to herb layers, while it keeps at a relatively high level in litter layers for both sites (Table 1). Among all plant parts, leaves maintain the highest ACV in tree layers ($p < 0.05$) (Fig. 3).

2.2 Energy storage and sequestration rate

On the average, the total energy storage in TSRF is

Fig.3 Distribution of caloric values of plant parts in TSRF and MEBF (Mean $\pm$ SE)
a : Tree layer b : Shrub layer c : Liana layer d : Herb layer

Table 1 Caloric values in different layers in the two study plots (Mean $\pm$ SE)		
Layer	TSRF ($\text{J}\cdot\text{g}^{-1}$)	MEBF ($\text{J}\cdot\text{g}^{-1}$)
Tree	$19\,434.36 \pm 59.54$	$19\,841.70 \pm 66.09$
Liana	$18\,502.60$	$19\,251.00$
Shrub	$19\,135.04 \pm 197.81$	$19\,192.39 \pm 134.85$
Herb	$17\,266.89 \pm 197.81$	$18\,243.86 \pm 134.85$
Coarse wood debris (CWD)	$18\,666.40$	$19\,537.18$
Litter	$18\,514.30 \pm 175.25$	$20\,420.51 \pm 154.25$

CWD includes stand dead tree and fallen dead tree

$708.24\text{ MJ}\cdot\text{m}^{-2}$, of which 96.74% is concentrated in tree layer, 1.28% in shrub layer, 0.12% in herb layer,

0.81% in liana layer and 1.04% in coarse woody debris and litter (Fig. 4). Total energy storage in MEBF is $1\,109.02\text{ MJ}\cdot\text{m}^{-2}$ to the exclusion of liana layer. The energy maintained in tree layer accounts for 88.49% of the total, shrub layer 1.28%, herb layer 0.19%, and coarse woody debris and litter 10.04% (Fig. 5). The annual energy sequestration in TSRF plot is higher than that in MEBF plot, largely due to the contributions of shrub layer and herb layer, although the annual energy sequestrations for tree layer of TSRF plot are lower than those of MEBF plot (Table 2).

Fig. 4 Energy storage pattern in TSRF plot ($\text{MJ}\cdot\text{m}^{-2}$) (Revised based on Cao *et al.* (1996))

Table 2 Annual energy sequestration in different layers in the two study plots

Layer	TSRF ($\text{MJ}\cdot\text{m}^{-2}$)	MEBF ($\text{MJ}\cdot\text{m}^{-2}$)
Tree	11.71	11.79
Shrub	0.75	0.24
Herb	0.61	0.08
Litter	11.57	5.38

3 Discussion

3.1 Caloric values of different vegetation types

The average caloric value of the TSRF (18 586.61 $\text{J}\cdot\text{g}^{-1}$) is lower than that of the tropical montane rain forest (19 338.63 $\text{J}\cdot\text{g}^{-1}$) in South China (data given in the brackets exclude herb layer and litter layer). As compared with that of tropical moist forest at Santa Fe, Panama, it is relatively higher (Table 3). Some results from Golley (1961, 1969) suggested that tropical vegetation had lower caloric values than temperate or alpine vegetation did, and there was an ascending gradient in energy content of vegetation from the equator to higher latitudes or altitudes. The TSRF in Xishuangbanna is the northward extension of tropical Asian rain forests, which lies in higher latitude area than Santa Fe, Panama. The caloric values of these forests are ranked as: tropical moist forest < tropical seasonal rain forest < evergreen broad-leaved forest < tropical montane rain forest < montane ever-

green broad-leaved forest (Table 3), which is true of Golley's corollary (1961, 1969), taking regard of latitude and altitude. The caloric value of MEBF plot is significantly higher than that of TSRF ($p < 0.001$). It is postulated that plants in colder habitats maintain more components with higher energy contents to resist coldness, although this deserves future research efforts.

3.2 Caloric values of different layers

The highest caloric values occurred in tree layer, followed by those of shrub layer and herb layer. These are similar to some previous findings (Long, 1934; Golley, 1969; Lin *et al.*, 1996, 1999; Ren *et al.*, 1999; Hou *et al.*, 1997). Further comparison in the caloric values of plant parts among different layers indicates the same trend in general (Fig. 3). As for the lianas, woody lianas are dominant in MEBF, which can reach up to the top of canopy. While in TSRF plot, non-woody and shade-tolerant lianas hold a large portion. For example, the caloric values of *Pothos chinensis* and *Rhaphidophora crassicaulis* are very low. Long (1934) measured the caloric values of 12 species of cultures in different light intensity. His results suggested a strong relationship between caloric values and light availability. So light may be another reason that interprets this trend.

Litter layer shows higher caloric values in MEBF plot than that in TSRF plot ($p < 0.001$) (Table 1). This could be attributed to the rate of litter decomposition. The

Fig. 5 Energy storage pattern in MEBF plot (MJ·m⁻²)(Revised based on Qiu *et al.* , 1998)

Table 3 Caloric values in different vegetation types

Vegetation type	Caloric value (J·g ⁻¹)	Location	References
Tropical moist forest	17 066.00	Santa Fe , Panama (08°04' N 81°57' W ; 463 m asl.)	Golley , 1969
Tropical seasonal rain forest	18 586.61	Xishuangbanna , China (21°50' N , 101°12' E ; 750 m asl.)	Present study
Evergreen broad-leaved forest	18 619.18	Dinghu Mountain , China (23°10' N , 112°33' E ; 300 m asl.)	Ren <i>et al.</i> , 1999
Tropical montane rain forest	19 338.63 ¹⁾	Hainan , China (18°44' N , 108°50' E ; 950 m asl.)	Yi & Wu , 1996
Montane evergreen broad-leaved forest	19 431.97	Ailao Mountain , China (24°32' N , 101°01' E ; 2 400 m asl.)	Present study

1) Excluding herb layer and litter layer

moist and cold environment in the Ailao Mountains could lead to a slow decay rate. As a consequence of this , more energy is retained in litter layer in MEBF plot than in TSRF plot. In addition , the decomposition of litter and coarse woody debris involves a complex set of processes including chemical , physical and biological agents acting upon a wide variety of organic substrates that are themselves constantly changing (Berg & McClaugherty , 2003). So samplings in different depth and seasons strongly affects the caloric value. Taking TSRF plot as an example , the average caloric value of litter in rainy season is 17 780.45 J·g⁻¹ , which is much lower than 19 248.14 J·g⁻¹ in dry season , indicating a strongly seasonal variation. There is also a variation among the five sub-plots. Therefore , the strategy of litter sampling should be further improved.

3.3 Caloric values in different plant parts

Leaves show the highest caloric values among all the

layers of the two sites(Fig. 3). Golley(1969) reviewed the caloric values of the tropical vegetation reported in the earlier studies and came to the conclusion : on an absolute basis , stems and leaves often had a greater caloric value (Golley , 1969). The variance of caloric values in parts can be attributed to the different amount of energy content. The values in high calories for some of the organic compounds contained in plants were found to be as follows : lipid 39.54 kJ·g⁻¹ , resin 35.28 kJ·g⁻¹ , protein 23.94 kJ·g⁻¹ , carbohydrate 17.15 kJ·g⁻¹ , cellulose 16.8 kJ·g⁻¹ , starch 15.96 kJ·g⁻¹ . Therefore , if determinations show high caloric values , it usually indicates the occurrence of the materials containing a large amount of high-energy compounds , such as lipid or resin (Zu , 1990 ; Long , 1934 ; Ovington & Heitkamp , 1960). Another hypothesis suggests that the organs that have high caloric values have particular functions , such as fruits for reproduction and leaves for photosynthesis (Golley ,

1969 ; Pitelka , 1978). Consequently , they both have relative high caloric values .

3.4 Energy storage and annual sequestration

MEBF plot has higher energy storage than TSRF plot does . Previous disturbance in TSRF could be responsible for this . In 1994 , *Amomum villosum* , a shade-tolerant perennial herb whose fruits are used as Chinese traditional medicine , was planted in the understory of TSRF . To promote its growth and fruit yield , some undergrowth was cleared and about 60% – 70% of saplings , shrubs and herbs were thinned . This greatly reduced biomass accumulation of the forest and made a long-term negative consequence on the community structure (Zheng *et al.* , 2003) , although *Amomum villosum* was completely eliminated in 2000 . In MEBF plot , furthermore , energy storage of course wood debris occupies a great ratio due to the

moist , cold environment and rare disturbance . Tree layer is the major contributor to energy storage of forests . It is not only because of the greatest biomass but also of higher caloric value among all the layers . So the disturbance to the tree layers of forests could greatly influent the energy structure of ecosystem .

High temperature and intensive precipitation result in faster growth rate in TSRF compared with MEBF , so TSRF can sequestrate more energy every year . The annual energy sequestrations in the two plots are between the rain green forest and summer green forest and much lower than that in tropical moist forest (Table 4) , which suggests the characteristics of TSRF in northern edges of tropical Asia and subtropical MEBF in terms of annual energy sequestration .

Table 4 Annual energy sequestration in different vegetation types

Vegetation type	Annual sequestration (MJ · m ⁻²)	References
Northern coniferous forest	10.03	Leith & Wittaker , 1975
<i>Pinus taiwanensis</i> forest	13.89	Lin <i>et al.</i> , 1999
Summer green forest	19.23	Leith & Wittaker , 1975
Evergreen broad-leaved forest	22.90	Peng & Ren , 1998
Montane evergreen broad-leaved forest	23.99	Present study
Tropical seasonal rain forest	25.25	Present study
Rain green forest	29.33	Leith & Wittaker , 1975
Tropical rain forest	34.28	Leith & Wittaker , 1975

Because biomass data of lianas in most vegetation types are unavailable , the values of liana layers are excluded in this table

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