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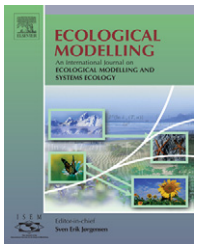

Plant energy storage strategy and caloric value

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ABSTRACT

Jørgensen [Jørgensen, S.E., 2002. Integration of Ecosystem Theories: A Pattern, 3rd ed. Kluwer Academic Publishers, The Netherlands] proposed: Ecosystem attempts to maximize their distance from a thermodynamic reference point by storing exergy. In this research a close relationship between energy storage strategies and caloric value was found. The caloric values of dominant plants in a 1-ha plot in a tropical seasonal rain forest (TSRF) and a 1-ha plot montane evergreen broad-leaved forest (MEBF) of Yunnan Province, southwest China were measured. We found plants growing in different environment and developing stage prefer different energy storage strategy. In the cold environment, plants prefer to condense energy in the limited volume which increases caloric value. And the same strategy is chosen by the top (sun) leaves, so they have higher caloric values than the bottom (shade) leaves. While in the warm environment, structure development dominates which abates caloric value. At the beginning of growth, plants prefer to develop structure. However after matured, they prone to condense energy in the full grown structure. So mature leaves maintain higher caloric values than young shoots do. On all accounts, the two exergy strategies – structural development that decreases caloric value and energy condensation that increases caloric value – interact each other to facilitate energy storage in plants.

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1. Introduction

Caloric value refers to combustion heat of specific dry mass. It was introduced into biological research by Long (1934) and applied to describe energy patterns in ecological processes, such as measurements of energy flow in lake ecosystems (Lindeman, 1942), investigations of energy allocation within individual organisms (Madgwick, 1970; Pitelka, 1977; Meletiou-Christou et al., 1998; Lemenih and Bekele, 2004) and communities (Ovington and Heitkamp, 1960; Golley, 1961, 1969; Ovington and Lawrence, 1967; Cummins and Wuycheck, 1971), measurements of ecological performance (Long, 1934) and construction cost study in forest and grassland ecosystems (Merino, 1987; Williams et al., 1987, 1989; Miller et al., 1990; Kikuzawa and Ackerly, 1999; Jennifer and Kevin, 2001; Villar and Merino, 2001). Caloric value has been believed as a coefficient index when biomass is converted into equivalent energy. However, Verduin (1972) pointed out that the calories of plants measured do not make sense of the energy available to growth or reproduction, and he oppugned establishing connections between stressful environments with higher energy content. Other researchers also indicated the limits of applying caloric value in the explanation of ecosystem processes with certain case studies (Hickman and Pitelka, 1975). Although there are some controversies about caloric value, it is believed to be a useful tool to study energy transfer and flow efficiency.

It probably helps if we look over the mechanism that controls caloric values of plants. Some studies suggested that the plant parts having high caloric values perform particular

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function, for example seeds of reproductive parts and leaves of photosynthesis parts of plants (Golley, 1969; Pitelka, 1978; He et al., 2007). More studies revealed that some other plant parts that produce no organic compounds maintained low caloric values (Hadley and Bliss, 1964; Núñez-Regueira et al., 2004). Environmental factors, in addition, affect the allocation of caloric values in plant parts. Long (1934) found that plants growing in high light environment had higher caloric values. And season subrogation induces change in energy transfer and storage of plant parts, which consequently leads to variations in caloric value of plants (Golley, 1961; Madgwick, 1970; Pitelka, 1978; Meletiou-Christou et al., 1994, 1998; Núñez-Regueira et al., 2004).

These hypotheses mentioned above are variety, and lack a theory to unite. Since caloric value is something about energy storage, can we understand it from thermodynamics aspect? Jørgensen (2002) pointed out that different organisms have different strategies to obtain a certain level of exergy. Although the exergy that calculated by Jørgensen and Mejer (1979, 1981) is biomass multiplying the number of genes that the system is comprised of, it rooted in the basic concept of energy. Caloric value is the primary energy that stored in organism which can be utilized by the up level organism, so we hypothesis that energy storage strategies control allocation patterns of caloric value in plant. There are two energy storage approaches for plants, i.e. structural development, which decreases caloric values, and energy condensation, which increases caloric values. Plants maximize their exergy storage capacity with the development (Jørgensen et al., 2000; Jørgensen and Svirezhev, 2004). The two strategies work together to abet exergy storage. However, plants perform a dominant strategy in particular cases.

The present study investigated the caloric values of dominant plants in a 1-ha plot of a tropical seasonal rain forest (TSRF) and a 1-ha plot montane evergreen broad-leaved forest (MEBF) in Yunnan Province, southwest China. This paper aims at interpreting some trends found in the caloric values with energy storage strategies. And hope to probe a unit theory to explain the caloric value pattern of plants.

2. Methods

2.1. Study site

Xishuangbanna located at the northern margin of tropical SE Asia (21°09′–22°33′N, 91°58′–101°50′E) and is a transitional area between the tropics and subtropics. The climate of Xishuangbanna is dominated by southwest monsoon with high rainfall occurring from May to October, so that there is a well-defined alternation of rainy and dry seasons. Taking Menglun (21°54′N, 101°46′E, alt. 580 m) as an example, the annual mean temperature is 21.8 °C. Annual precipitation averaged is 1493 mm, of which 84% occurs in rainy season (May–October). Although the rainfall is very seasonal, the dry season is not extreme in nature. Fog with an average duration of 6 h occurs on about 130 days, mainly in the dry season. The soil in the area below 1000 m elevation is laterite (Cao et al., 2006).

Tropical seasonal rain forest is the climax forest in Xishuangbanna. This is one of the species-richest forests in China, and is usually distributed in valleys and on low hills below 1000 m altitude (Zhang and Cao, 1995; Cao and Zhang, 1997). The forest canopy is uneven and complex three layers (A, B, and C). Dominant tree species in A layer are *Pometia tomentosa*, *Terminalia myriocarpa*, *Gironniera subaequalis*, and *Garuga floribunda*, which can be beyond 40 m. Layer B is between 16 and 30 m and layer C is less than 16 m. *B. macrostachya*, *Sloanea cheliensis*, *P. tomentosa*, *Semecarpus reticulata*, *Cleidion brevipetiolatum*, *Chisocheton siamensis*, *Ardisia tenera*, *Mezzettiopsis creaghii*, *Dichapetalum gelonioides*, *Millettia leptobotry* are frequently met in the two layers. The shrub layer is dominated by *A. tenera*, *M. creaghii*, *Drypetes yunnanensis* and *D. gelonioides* (Cao et al., 1996). There are no obvious dominant species in herb layer, but *Tectaria decurrens*, *Elatostema macintyrei*, *Phrynium capitatum*, *Selaginella* sp. are often found.

MEBF site is at Xujiaba (24°32′N, 101°01′E, alt. 2400–2600 m) on the northern crest of the Mts. Ailao in central Yunnan, where the Forest Ecosystem Research Station (FERS) of Xishuangbanna Tropical Botanical Garden is located (Fig. 1). It is a kind of well-protected subtropical montane forest, and is a part of the Ailao Mountain Nature Reserve. The climatic records of FERS show that the annual mean temperature is 11.3 °C. Annual precipitation averaged is 1931 mm, more than 85% of which falls from May to October. Soils are alfisols developed over schist, gneiss and diorite.

The forest can be divided into two tree layers. Canopy trees are 18–25 m tall, with 90% coverage; sub-canopy trees are 5–18 m tall with 50% coverage. Dominant tree species are *Lithocarpus xylocarpus*, *L. hancei*, *Castanopsis rufescens*, *Machilus bombycina*, *Manglietia insignis* and *Schima noronhae*. The understorey is composed by shrubs and herbs, which is dominated by a bamboo (*Sinarundinaria nitida*) and some ferns (You, 1983; Qiu et al., 1984).

2.2. Sampling

Plant samples for caloric measurement were collected in November 2003 and April 2004, respectively. A plot of 100 m × 100 m was set for each of TSRF site and MEBF site, within which nine subplots of 20 m × 20 m arranged in diagonals were established (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. Then calculate the PBH ratio of the three ranges in each subplot. The number of sampled trees in each subplot is determined by 10% of the total number in the subplot multiply PBH ratio. If the number <10, we magnify 10% to some extend to ensure at least 8 trees can be sampled. The species sampled in each subplot were based on the abundance in that subplot. Consequently, a total of 34 species in TSRF plot and 23 species in MEBF plot were sampled by distinguishing leaves, stems, branches 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 leaf, branch, and root samples for shrubs, and aboveground and belowground parts for herbs. All forest floor litter including leaves and woody parts was also collected simultaneously in the five quadrates.

Some trees fell down during a road construction project in the Mts. Ailao in 2003 and 2004. This enabled us to collect the

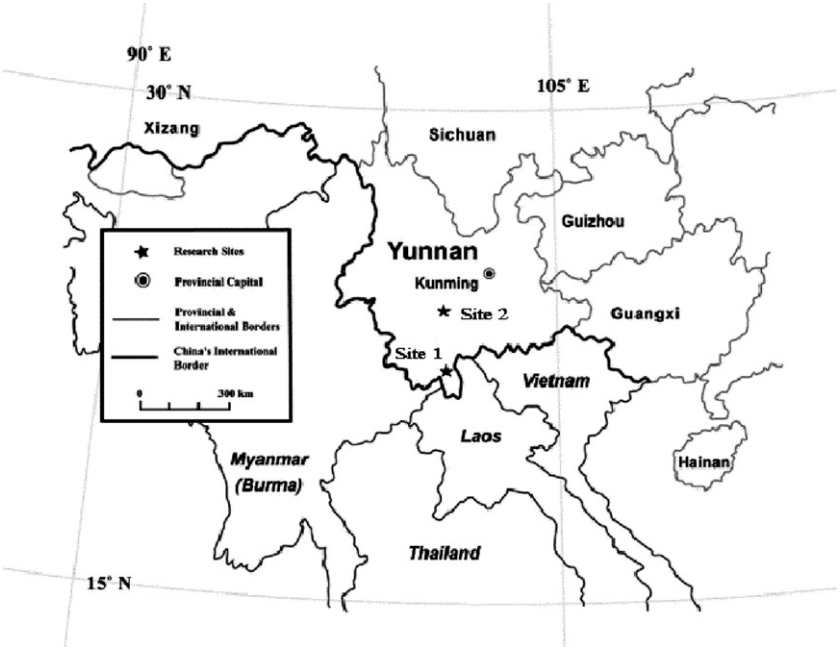

Fig. 1 – Geographic location of the sites. Site 1, tropical seasonal rain forest; Site 2, montane evergreen broad-leaved forest.

very top leaves of the canopy trees. We sampled the top leaves and bottom leaves in tree crowns of four dominant species in MEBF, i.e. *M. insignis*, *S. noronhae*, *C. wattii*, *L. xylocarpus*, respectively. The three individuals of each species sampled were with DBH > 20 cm and occurred in forest canopy.

To remove non-plant materials, all samples were cleaned with water. Leaves were oven dried at 80 °C for 24 h and woody parts were dried for 48 h, and then pulverized.

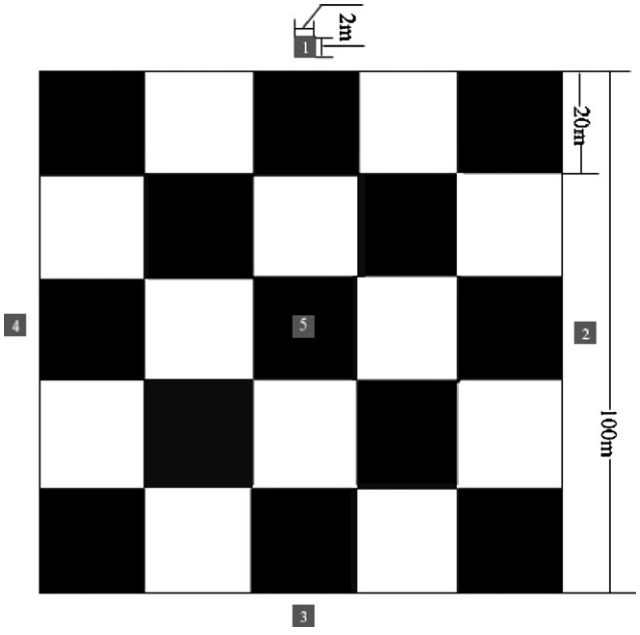

Fig. 2 – Distribution of subplots and quadrates. Black blocks represent the subplots in which trees were sampled (area 20 m × 20 m). Grey blocks represent the quadrates in which shrubs, herbs and litters were sampled (area 2 m × 2 m).

2.3. *Caloric value measurement*

Prior to measurement, the plant samples (powders) were dried again at 105 °C for 2–3 h. Three repetitions were measured for each sample using SDCM-IIIa oxygen bomb calorimeter. The relative variation between the three replicates of each sample was limited below 1%.

2.4. *Data analysis*

One-way ANOVA was applied to test the statistical differences in caloric values between sites, parts and spatial positions of the leaves in canopy. Paired-samples *t*-test was adopted to compare seasonal variances between all the sampled species. All statistical analyses were performed using SPSS 11.5. Average caloric values of the two plots were estimated based on the average caloric values of the nine subplots (for tree layer) and the five quadrates (for shrub layer and herb layer).

3. Results

3.1. *Average caloric values*

The average caloric value (ACV) of TSRF plot was 18586.61 J g^{-1}. It was much lower than 19431.97 J g^{-1} of MEBF plot. Except for shrub layer, the ACVs of tree layer, herb layer and litter layer in MEBF plot were significantly higher than those of TSRF plot ($P < 0.01$). The ACV of litter layer of MEBF was even 10% higher than that of TSRF (Fig. 3).

In general, the ACVs tended to decrease from tree layers to herb layers, but they are relatively high in litter layers of both plots (Fig. 3). The leaves showed the highest ACVs among all parts in the tree layers ($P < 0.05$). But they are not significant higher in other layers (Fig. 4).

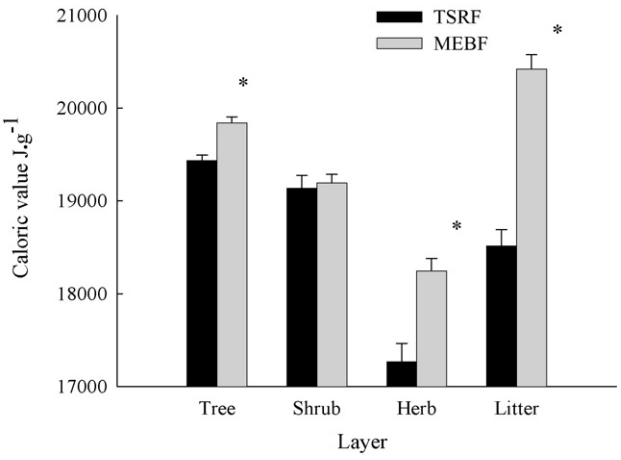

Fig. 3 – Average caloric values among different layers in TSRF and MEBF plot. Significant difference, *P < 0.05.

3.2. *Seasonal dynamic in ACVs*

ACVs were 18411.63 J g^{-1} in November and 18761.6 J g^{-1} in April for TSRF plot. In contrast, MEBF plot showed higher ACV in November (19,587 J g^{-1}) as compared to 19,277 J g^{-1} in April. Exclusive of litter layers, the ACVs of both plots were higher in November than those in April. In MEBF plot, all the layers had higher caloric values in November, except that shrub layer is not significant ($P > 0.05$). In TSRF plot, only litter layer showed significantly higher ACVs in April, while there were no statistically significant seasonal differences in other layers (Fig. 5).

The ACVs for all the parts (leaves, stems, branches and roots) of tree layer in MEBF plot varied significantly between the two seasons ($P < 0.05$), whereas only tree leaves in the TSRF plot demonstrated statistically significant seasonal difference ($P < 0.05$). Besides, significant seasonal differences in ACVs of herb root were observed in MEBF plot ($P < 0.05$) (Fig. 4). Overall, the ACVs of tree leaves changed significantly with season, especially for the species *L. xylocarpus*, *Meliosma arnottiana*, and *C. wattii*, whose seasonal differences in ACVs exceeded

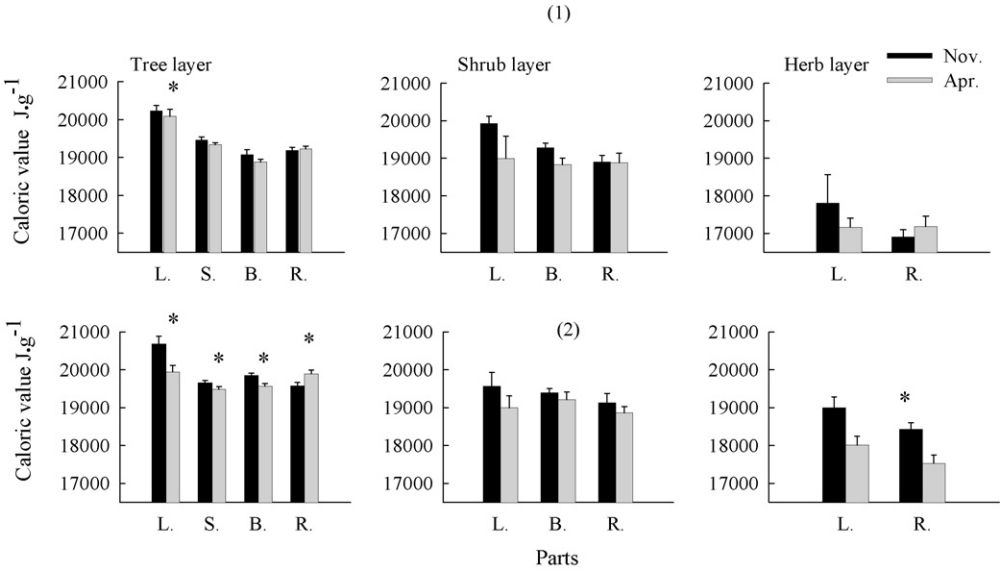

Fig. 4 – Seasonal changes in average caloric value among parts of each layer. (1) TSRF plot and (2) MEBF plot. L., leaf; S., stem; B., branch; R., root. Significant difference, *P < 0.05.

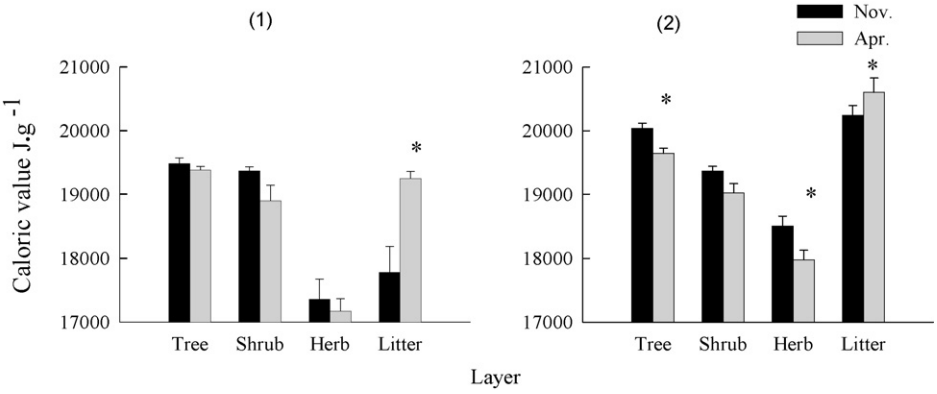

Fig. 5 – Average caloric values of the two seasons in TSRF and MEBF plot. (1) TSRF plot and (2) MEBF plot. Significant difference, *P < 0.05.

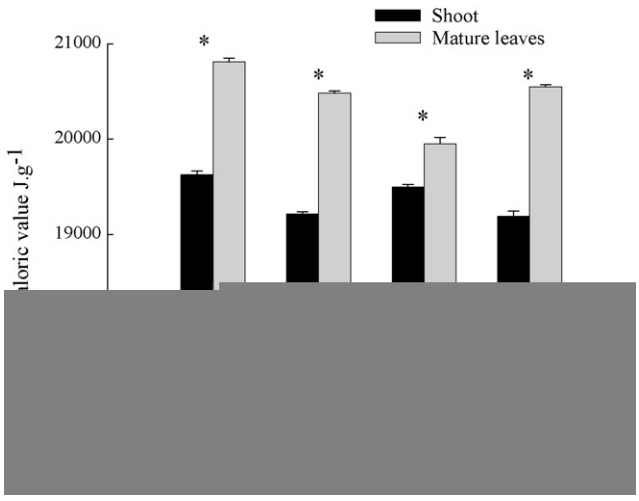

Fig. 6 – Average caloric values of shoots and mature leaves. Significant difference, *P < 0.05.

1000 J g^{-1}. Further comparison in ACVs of shoots with mature leaves for the three species revealed that mature leaves maintained significantly higher values ($P < 0.05$) (Fig. 6).

3.3. *ACVs of top and bottom leaves*

A comparison between the ACVs of top leaves and bottom leaves in the tree crowns of four dominant tree species in MEBF showed that the former showed significantly higher caloric value than the latter did. The ACVs of top leaves ranged from 20779.91 ± 161.31 to 22176.48 ± 52.22 J g^{-1}, while lower leaves ranged from 20559.71 ± 104.16 to 21495.62 ± 257.72 J g^{-1} (Fig. 7).

4. Discussion

The average caloric value of tree layer (19434.36 J g^{-1}) for TSRF plot was similar to that of tropical montane rain forest (TMRF) in Hainan Island, south China (19458.43 J g^{-1}) (Li et al., 1996). However the ACVs of shrub layer and liana layer in TSRF were lower than those in TMRF. While the ACV of tropical rain forests in the world (17154.4 J g^{-1}; Lieth and Whittaker, 1975) was lower than those of TSRF and TMRF. As compared to the ACV of evergreen broad-leaved forest in south China (18619.18 J g^{-1}; Ren et al., 1999), the ACV in MEBF was higher. This pattern is in accordance with the suggestion that there is a corresponding increase in caloric values in high altitude, latitude and low temperature habitats (McNair, 1945; Bliss, 1962; Golley, 1969). From the physiology viewpoint, it has stronger ultraviolet radiation in low temperature and high altitude area, so plants response with low respiration and more active enzyme which enhances the accumulation of non-structural carbohydrates, besides higher proportion of short wave radiation in spectrum occurred at high altitude, as we all know, blue and violet radiation is helpful for synthesizing proteins. In addition, high energy content can increase the resistance of coldness for plants (Long et al., 1993). From the physic viewpoint, in cold habitats, plants tend to grow in cluster and develop small leaves to keep heat. So maximize accumulating high caloric content in small volumes is the prevailing grow strategy for the plants in cold places.

Three facts may be responsible for the caloric value difference between MEBF and TSRF. The first one is that MEBF lies at high altitude with low temperature. The second one is the tree age structure. Taking tree layers as an example, TSRF plot is rich in saplings, while MEBF plot showed fewer saplings under the canopy. The ratio of trees with DBH 2–5 cm was 43.9% in MEBF plot, while it was 64.8% in TSRF plot (Data from Forest Ecosystem Research Station). More saplings growing in TSRF predicate greater potential in the development of forest structures. The last one is forest stratification. TSRF canopy has three tree layers, thus more spaces are available for trees to extend their crows horizontally compared with the even canopy in MEBF plot. Thus energy condensation strategy dominates in MEBF plot, while structural development strategy dominates in TSRF plot. As a result, the caloric value is higher in MEBF than that in TSRF. Our later study showed that caloric values of the dominant species in the climax community were higher than the pioneers (Qiao et al., 2007). In another word, caloric value of community increased with succession. Pioneer communities invest energy on structure expand, while climax community store energy with the strategy of energy condensation to build network and improve information growth. Although climax communities produce less biomass, they can still capture and use energy efficiently (Parresol, 1995; Komarov et al., 2003; Jørgensen and Svirezhev, 2004; Neeff and dos Santos, 2005; Alexandrov, 2008;).

As regard to seasonal dynamic of caloric values, plants accumulate more energy and decrease surface areas in cold season, in order to reduce heat lose. Consequently energy is condensed and caloric values increase.

Exergy storage strategy of leaves in the top canopies differs from that of leaves within bottom canopies. Our observation found that the top canopy leaves are thicker and smaller than bottom leaves. It has been suggested that sun and shade leaves developed different mechanisms to adapt microclimatic conditions. Shade (bottom) leaves usually develop larger leaf areas to improve light capture (Pearcy and Sims, 1994; Niinemets et al., 1998; Mendes et al., 2001). On the other hand, sun leaves, subjected to great evaporation, usually take an avoidance strategy by reducing the water loss, through the decrease

Fig. 7 – Average caloric values of top and bottom leaves. Significant difference, *P < 0.05.