

南亚热带常绿阔叶林 的生产力

PRODUCTIVITY OF THE LOWER SUBTROPICAL
EVERGREEN BROAD-LEAVED FOREST IN CHINA



陈章和 王伯荪 张宏达 著

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Productivity of the lower subtropical evergreen broad-leaved forest in China

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Summary

The lower subtropical evergreen broad-leaved forest in China is distributed in the lower subtropical area, which is located at about $22-24^{\circ}\text{N}$, including most of Taiwan Province and Guangdong Province, the southern part of Guangxi Zhuang Autonomous Region and Yunnan Province. The region has a monsoon climate. Annual mean temperature is about $20-22^{\circ}\text{C}$, the hottest month (July) and the coldest month (January), are about $27-28^{\circ}\text{C}$ and $12-14^{\circ}\text{C}$ respectively. Annual rainfall is about $1600-2200\text{mm}$, with an obvious rainy season (from April to September) and a dry season (from October to March). Relative humidity is about 80% during most of the year. Total annual radiation hours add up to $1400-2000$, and the amount of radiation energy, to $110-120\text{ K cal cm}^{-2}\text{ yr}^{-1}$.

The soil has developed usually on granite and shale etc. and is red in colour, with pH $4.2-4.9$. Organic carbon and element contents vary greatly among sites, with a range of 1%—8% for organic matter, and 0.02%—0.2%, 0.004%—0.06% and 0.6%—3.0% for

N, P and K respectively. Concentrations of Ca, N and P are very low (especially Ca) in the soil studied, as opposed to the phytomass which has higher contents of Ca, N and P and lower contents of Na and Mg (Na and Mg contents are quite high in the soil).

The forest is dominated mostly by Lauraceae, Fagaceae, Theaceae, Hamamelidaceae, Aquifoliaceae, Elaeocarpaceae, Symplocaceae, Moraceae, Myrsinaceae, Myrtaceae, Magnoliaceae, Leguminosae. Tropical and subtropical genera and species dominate the flora (usually 70%—90%). Main dominants include *Endospermum chinensis*, *Ficus microcarpa*, *Cinnamomum camphora*, *Bischoffia javanica*, *Canarium album*, *Aquilaria sinensis*, *Sarcosperma laurinum*, *Sterculia lanceolata*, *Schefflera octophylla*, *Symplocos glauca*, *Chrysophyllum roxburghii*, *Acmena acuminatissima* in the lowland forest; *Cryptocarya concinna*, *Cryptocarya chinensis*, *Altingia chinensis*, *Lithocarpus lohangu*, *Lithocarpus polystachyus*, *Ormosia glaberrima*, *Ormosia pachycarpa*, *Ixonanthes chinensis*, *Artocarpus styracifolius*, *Castanopsis fabri*, *Lindera chunii*, *Neolitsea phanerophlebia*, *Reevesia thyrsoides*, *Xanthophyllum hainanensis* in the lower montane forest; *Castanopsis carlesii*, *Altingia chinensis*, *Exbucklandia tonkinensis*, *Litsea subcoriacea*, *Manglietia moto*, *Michelia foveolata*

in the montane forest. Species densities are great, with usually 70—100 species per 1200 m² forest area. Species diversity (Shannon—Weaver index) usually lies between 4.8—5.4, which is similar to that of the tropical rain forest and tropical montane rain forest in China, and significantly higher than that measured in subtropical and temperate forests in China.

With a very low percentage of deciduous trees based on both species (<7%) and individuals (<5%), the forest is evergreen, although seasonality exists to a certain extent: A higher percentage of the foliage renews in March and April, flowering is more frequent in May and June, and ripening of fruits in November and December.

The forest has a canopy of about 25m (max. 35m) height, a basal area of about 50—60 m² ha⁻¹, a density of trees of about 5000 individuals ha⁻¹ (3000—9000) and that of big trees (D>22.5cm) about 200—300 individuals ha⁻¹. Leaf area index is comparatively high (about 17) in the forest stands studied. Radiation on the forest floor is very low (1%—3%), similar to that of tropical rain forest.

Distribution of the trees shows that small individuals have a more clumpy pattern than the bigger ones, and big trees (DBH>22.5 cm) show a poisson distribution and a tendency towards even distribution pattern.

This distribution spectrum may be favourable to the productivity of the forest.

For the regression of biomass (Y) and diameter (X), four regression models: $Y=a+bX$, $Y=aX^b$, $Y=ae^{bx}$ and $Y=a+\ln X$ could be successfully used in the assessment of the biomass of trunk, branch, root and leaf, with $Y=aX^b$ generally giving slightly better result than the other equations, although for the leaf biomass analysis of the biggest tree class sampled, $Y=a+bX$ was the only significant regression. As to variables, D is better than or comparable to D^2H in our work (D =diameter, H =height).

Total biomass was $360-420 \text{ t ha}^{-1}$ in the stands studied, of which about 97%–99% was accounted for by trees, and about 50%–62% allocated to trunk, about 13%–20% to branch, about 3%–4% to leaf, and about 19%–22% to root. Total biomass and above-ground biomass were about 1.6–1.9 and about 1.3 times trunk biomass respectively for the stands studied, lying in the same range as tropical and subtropical forests and plantations (1.6–2.0 and 1.3–1.5 respectively). Leaf biomass was mostly distributed above 15m, but below this height there was still substantial leaf biomass in comparison with plantations in the area as well as temperate forest, indicating the complex

structure of the lower subtropical forest. LAI (17) and amount of chlorophyll (65 kg ha^{-1}) were high in developed stands even in comparison with tropical rain forest. Root biomass was closely correlated with above-ground biomass in the stand studied. Fine root biomass ($D < 3\text{mm}$, down to $0.7\text{--}1.0\text{m}$ depth in the soil) was $4.8\text{--}12.0 \text{ t ha}^{-1}$ for the mature forests, and 1.3 t ha^{-1} for a young stand. These values are higher than those for the coniferous forest of *Pinus massoniana* (0.601) and plantation of *Eucalyptus exserta* (0.540). Fine root biomass at $1\text{--}5\text{m}$ depth in the soil was 2.30 (cf. 4.82 at $0\text{--}1\text{m}$) in a stand in Heishiding, Guangdong, as estimated from the numbers of fine roots at $0.5\text{--}1.0\text{m}$ and $1.0\text{--}5.0\text{m}$ and the biomass at $0.5\text{--}1.0\text{m}$. Fine root biomass was about $3\%\text{--}9\%$ of the root biomass (excluding fine root), and about $0.7\%\text{--}1.4\%$ of the total biomass of the evergreen broad-leaved forests. The evergreen broad-leaved forest stands had smaller spatial variation of fine root distribution than the coniferous forest and the *Eucalyptus* plantation.

Biomass was closely related to the structure of the forests. For 20 stands of the lower subtropical evergreen broad-leaved forest and other forests in the tropical and subtropical area, above-ground biomass was significantly correlated with basal area, tree density or

the ratio basal area/density. However, basal area and tree density were not always closely related to climatic parameters, elevation and forest age. Volume index [basal area(m^2) \times forest height (m)] instead of basal area and tree density could overcome this problem. Volume index was highly correlated with the biomass of the forest stands studied.

Total biomass of micro - organisms was 0.6324 - 1.4680 g per kg dry soil at 0 - 15 cm depth, in which bacteria biomass accounted for about 70% of the total biomass. Bacteria biomass made up higher percentages in the evergreen broad-leaved forests than in *P. massoniana* forest and coniferous and broad-leaved mixed forest. Micro - organism biomass varied substantially during a year, with generally higher values in spring and summer and lower ones in autumn. The biomass was linearly correlated with organic carbon and nitrogen content in the soil.

Biomass increment was about $10 \text{ t ha}^{-1} \text{ yr}^{-1}$ in the stands studied. In the stand in Heishiding, 8.786 (82.3%) of the biomass increment was allocated to trees, 1.679 (15.7%) and 0.215 (2.0%) to shrubs and herbs respectively. As regards different organs, biomass increment of the trunk was 6.127 (57.4%), of branch 2.195 (20.6%), leaf 0.514 (4.8%), and root

1.844 (17.3%) respectively. The forest canopy ($> 20\text{m}$) accounted for a higher percentage of biomass increment, attributable mainly to the individuals of middle size (DBH 20—40cm).

The values of Pr/Br and K of the equation: $Pa/Ba = K Pr/Br$ which was used in estimating root production (Newbould 1967) were 3.0—9.4 (mean 4.4) and 0.8—2.4 (mean 1.1) respectively (Pr and Pa were below-ground production and above-ground production respectively, and Br and Ba below-ground biomass and above-ground biomass respectively). Both values became higher with the size class.

Litterfall of the evergreen broad-leaved forest was in the range of $5-11 \text{ t ha}^{-1} \text{ yr}^{-1}$, with leaves 52%—72%, branches 15%—21%, flowers and fruits 10%—26%. Peak litterfall occurred in March—April. The seasonal pattern was more similar to tropical montane rain forest in Hainan Island than to tropical semi-deciduous forest in Hainan and subtropical forest in Zhejiang Province. Tree fall and dead trees in the forest in Heishiding amounted to 5.214 and $1.642 \text{ t ha}^{-1} \text{ yr}^{-1}$ respectively (1989—1994), about 1.46% and 0.46% of the biomass of the forest, and about 1.38% and 0.92% of total individuals of the forest. Mortality of the saplings of the forest in Heishiding was 3% over a 5 year

period (1989—1994).

Leaf herbivory was about $0.2 - 0.7 \text{ t ha}^{-1} \text{ yr}^{-1}$, which is about 7%—12% of the total leaf area of the forest. A comparatively higher herbivory percentage was measured from August to November (December) in Heishiding.

Net primary production (Pn) was about $23 - 30 \text{ t ha}^{-1} \text{ yr}^{-1}$ in the stands studied, higher than that of broad-leaved and coniferous mixed forests and plantations of the area ($10 - 21 \text{ t ha}^{-1} \text{ yr}^{-1}$). In a stand in Heishiding, Pn was $29.61 \text{ t ha}^{-1} \text{ yr}^{-1}$, of which biomass increment was $10.68 (36.07\%)$, fine root production $10.68 (36.07\%)$, and of which trunk $8.18 (27.63\%)$, branch $3.40 (11.49\%)$, leaf $4.28 (14.46\%)$, flower and fruit $0.58 (1.97\%)$ and root $13.17 \text{ t ha}^{-1} \text{ yr}^{-1} (44.46\%)$.

Production efficiency of the forest in Heishiding was 1.897 t/t (Pn/leaf biomass) and 1.733 t/ha (Pn/leaf area). Biomass increment (ΔB) efficiency was 0.684 t/t (ΔB /leaf biomass) and 0.625 t/ha (ΔB /leaf area).

Efficiency of radiation utilization was 0.998% (based on total radiation) and 1.996% (based on photosynthetically active radiation), from the latter, energy allocation to the biomass increment (forest growth) was 0.720% (including trunk 0.414% , branch 0.148% , leaf 0.034% and root 0.124%), to litterfall, tree fall,

dead trees and dead fine roots 1.222%, to flower and fruit 0.039%, and to leaf herbivory 0.015%.

Net primary production of the lower subtropical evergreen broad-leaved forest estimated from photosynthesis and respiration was 22–37 t ha⁻¹yr⁻¹, comparable to or higher than the values obtained using the harvest method.

The contribution to Pn of each sublayer of the forest was the highest in the forest canopy (63%–83%) and became lower towards the forest floor. Photosynthetic rate of the forest canopy was also the highest. The photosynthetic rate was positively related to the photosynthetically active photon flux density (PFD), except during the brightest radiation at noon in summer when photosynthesis decreased. Below the forest canopy, photosynthesis was closely positively correlated with the radiation. Night respiration was about 1/3 of the apparent photosynthetic rate for each sublayer.

Mean annual radial growth of the trees in Heishiding was 0.211cm (1984–1989) measured with disc analysis, and 0.074cm and 0.088cm when measured with dendrometers and steel tape (1989–1994) respectively. 17.6% and 15.6% of the individuals showed zero or negative growth during the 5 year period in the measurement with dendrometers and steel tape respectively. Ra-

dial growth seemed to show a fast (1—3yrs) and slow (1—3yrs) rhythm for the individuals measured with disc analysis.

Mean annual height growth was 20—50 cm. Height growth was usually fastest in the age class of 10—30 years, and prevailed over radial growth during the first 30—50 years.

Mean annual growth of the saplings (height 1—3m) was 0.107cm in diameter and 4.76 cm in height (1989—1994). Mean radial growth showed greater yearly variability than mean height growth during the five - year study period. On average, bigger individuals had more growth both in diameter and height (in absolute terms). All 100 saplings measured presented more or less radial growth, although some individuals showed zero or negative height growth because of damage to the top of the stem from tree fall, branch fall or insects.

Relative growth rate (RGR) and unit leaf rate (ULR) of 1—5 year old seedlings in the forest were about $1 \text{ g g}^{-1} \text{ yr}^{-1}$ (max. 3) and $0.5 \text{ g m}^{-2} \text{ day}^{-1}$ respectively. Seedlings of shade intolerant species had higher relative growth rates at higher radiation and poorer soil conditions, and they allocated a higher percentage of biomass to leaf as opposed to root in comparison with shade—tolerant seedlings.

前 言

森林生产力研究与人类所面临的粮食、能源、环境等问题息息相关。由于这些问题对人类影响的长期性，所以，森林生产力的研究也具有长远的意义。

北回归线附近的南亚热带地区，是著名的荒漠带。我国的南亚热带地区，由于特殊的地理位置，发育出世界上独一无二的较大面积的常绿阔叶林。因而对南亚热带常绿阔叶林生产力的研究，在森林生产力的研究中具有特殊的意义。

我国近十多年来，已对森林生产力进行了不少的研究，取得了一定的成果。但至目前为止，仍无有关南亚热带森林生产力研究的专著。本书的出版，对学科的发展，对丰富世界森林生产力理论，将产生积极的作用。

作者对广东黑石顶南亚热带常绿阔叶林生产力的研究从1988年开始。以净第一性生产量为中心，系统地进行了净第一性生产量及其各组成要素：植物生物量、生物量增量、凋落量、枯死量、风倒量、昆虫食叶量以及森林植物的生长特点等的研究。以收获法为基础，共收获样木56株，对全部样木的根系进行挖掘测定，并利用土柱法，进行了林分细根生物量的研究。同时也应用气体交换法进行了光合生产量的测定。使用测树器和游标卡尺对森林植物的生长进行测定研究(至今已进行了5年)。整个研究工作量较大，工作细致，取得了丰富的第一手材料。根系生物量和生产量的研究是至今国内自然林生产力研究中较深入细致的。细根生物量、测树器及游标卡尺的应用等是国内首先开展的。作者在黑石顶等地南亚热带常绿阔叶林的研究成果作为本书的基本的素材。此外，杨家诚(1990)对黑石顶南亚热带常绿阔叶林微生物生物量、林益民(1993)对黑石顶南亚热带常绿阔叶林光合作用的研究成果，屠梦照等(1984, 1989)对广东鼎湖山南亚热带常绿阔叶林凋

落物的研究成果,张祝平等(1989, 1990, 1993)、彭少麟等(1990, 1994)对鼎湖山亚热带常绿阔叶林光合作用及其他方面的研究成果,管东生(1986)对广东流溪河南亚热带幼年常绿阔叶林生物量的研究成果,党承林等(1992)在云南亚热带常绿阔叶林低龄林分的研究成果,也为本书提供了重要的素材,进一步提高了本书的深度和广度。因此,本书实际上是从事亚热带常绿阔叶林生产力研究者们集体智慧的结晶。

为本书的写作提供重要素材的陈章和等人的博士论文,曾得到华南农业大学徐祥浩教授、中山大学傅家瑞教授、南京林业大学熊文愈教授、华东师范大学宋永昌教授、华南植物研究所王铸豪研究员、彭少麟研究员等的细致的审阅,给予许多宝贵的指导,对本书的撰写启发很大。

作者在研究工作期间,得到了华南师范大学植物教研室全体老师的支持与关心。

中山大学张志权副教授、杨家诚博士、林益民博士为作者提供未发表的资料。

中山大学热带亚热带森林生态系统研究中心为研究工作提供了优越的条件。野外工作及生活得到中山大学叶伟南和叶英同志的大力支持和帮助。华南师范大学学生植林、温明、全柱尧和中山大学研究生陈涛、林益民、聂连涛等曾参加部分野外工作。

本书的出版得到华南师范大学人事处、科研处领导的关心。部分出版费由华南师范大学重点教师培养基金和青年科研基金资助。

作者对上述教授们和其他同志们以及有关单位的关心、支持表示衷心的感谢!对所有支持、关心和帮助本书的研究和写作的同志表示衷心的感谢!

由于作者水平不高,错误和不当之处,敬请读者指正。

陈章和

一九九四年九月于华南师范大学

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