

Kun-fang Cao

***FAGUS* DOMINANCE IN
CHINESE MONTANE FORESTS:**

natural regeneration of *Fagus lucida*
and *Fagus hayatae* var. *pashanica*

Ontvangen:

16 JAN, 1995

UB-CARDEX



40951

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and *Fagus hayatae* var. *pashanica*

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op maandag 9 januari 1995
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Cao, Kun-Fang

FAGUS dominance in Chinese montane forests: natural regeneration of *Fagus lucida* and *Fagus hayatae* var. *pashanica* / Kun-fang Cao. -[S.L.: s.n.].-111.

Thesis Wageningen. - With ref. - With summary in English, Dutch and Chinese.

ISBN 90-5485-330-1

Subject headings: beech forests, regeneration, China, forest ecology.

Cover design by: Dr. R. Peters

Printed by: Grafisch Service Centrum Van Gils B.V.

PROPOSITIONS

1. Notwithstanding the actual scarcity of juvenile beeches, *Fagus* dominance in the mixed montane beech forests of southern China will be maintained as long as the actual climate of this beech region persists. (This thesis)
2. In shaded environments within forests, minimizing self-shading is a common and general plant strategy which is followed, however, by means of numerous different modes of plant development. (This thesis)
3. Reiteration strategies in the form of basal sprouting and as mechanism of crown building define an important, frequently occurring but still under-documented developmental pattern allowing numerous tree species to survive in shade. (This thesis)
4. Modelling tree species' or forest ecosystem's responses to global climatic change should consider not only temperature and precipitation but also natural hazards.
5. Because natural events repeatedly open up the forest canopy and so stimulate forest regeneration and interfere with the competitive exclusion of species and also exert selective pressure on plant populations and therefore increase genetic fitness of successive generations for survival, such events should not be considered as "disasters" or 'disturbances' in natural forests.
6. Because chance plays an important role in ecology (c.f. Hubbell & Foster 1986), many natural phenomena are unpredictable.
7. In recent Chinese policy, there have been three major steps towards deforestation: "steel production" in late 1950s, "grain production" between 1960s and 1970s and privatization of forests in 1980s.
8. Today, the Chinese government gives priority to economical development, whereas it can be demonstrated that education, scientific research, conservation of the environment and political reform are equally important.
9. To save natural resources and protect the environment, people in developed countries should limit their living requirements, people in developing countries should control their population growth.
10. Socialist and capitalist systems will have much in common in the next century.

To my parents

BIBLIOTHEEK
LANDBOUWUNIVERSITEIT
WAGENINGEN

PREFACE

The work described in this thesis was initiated in 1987 when the author and Dr. R. Peters worked together in Chinese beech forests. This joint work has been extended into a joint research project between the Institute of Botany in Beijing, Chinese Academy of Sciences, Department of Forestry, Wageningen Agricultural University, and Department of Plant Ecology and Evolutionary Biology, Utrecht University, which focuses on the ecology of Chinese beech forests. The project has been carried out under the Scientific Cooperation Agreement between the Chinese Academy of Sciences and the Royal Dutch Academy of Sciences. The work described in this thesis was part of this joint research project.

First of all, I thank you, Prof. R.A.A. Oldeman and Prof. Xian-pu Wang for your enthusiasm, supervision and support, for valuable discussions and for your friendship. I am indebted to you, Dr. R. Peters for your co-supervising this study, for your valuable advice and discussions, for your cooperation, and for your encouragement and kindness.

I thank you, Dr. P. Schmidt and Dr. F. J.J.M. Bongers for your advice on the research plan and critical comments on parts of the thesis. I am grateful to you, Prof. F. Hallé, Dr. C. Edelin for your advice and discussions on tree architecture, and to you, Dr. B. Thiébaud for your introduction to architectural plasticity of *Fagus sylvatica*. To you, Prof. T. Poulson, I am obliged for your instruction in using Ozalid light-sensitive paper to assess light intensity. Prof. E. Box, Prof. Hsin-shih Chang and two anonymous referees, I am grateful to you for your comments and advice on Chapter 2.

For your reviews, comments and discussions on parts of this thesis, I thank all of you: Ir. H.H. Bartelink, Ir. J. den Ouden, Ir. P. van der Meer, Ir. M.E. van der Zee, Dr. R. van Rompaey, Ir. R.B. Shrestha, Ir. F. Sterk, Prof. Hui-ying Zhen.

Several persons also provided me with discussions and advice. Thank you: Prof. Ling-zhi Chen, Prof. Wei-lie Chen, Prof. J. Fanta, Prof. Miao-guang Hé, the late Prof. Hsioh-yu Hou, Prof. Shun-shi Hu, Dr. W. B.J. Jonkers, Asso. Prof. Shi-zhou Sun, Prof. Zhao-chen Kong, Ir. K.F. Wiersum, Mr. Yi-qin Yang, Mr. Wei-cai Yu, Prof. Tsun-shen Ying.

In China, several people helped me to carry out the fieldwork. Thank you: Mr. Hé-ping Chen, Mr. Ke Guo, Mr. Shi-qiang Hé and Mrs. Xia Li for Daba; Mr. Jin-sheng Hé, Mr. Xiong Lin and Asso. Prof. Yuan-guang Wen for Miao'ershan and Lilio; Mr. Chuan-dong Yang, 'Lao' Yang and 'Xiao' Yang for Fanjingshan; Asso. Prof. De-fa Shi for four sites in Zhejiang Province; Mr. Fan-zhang Du and Mr. Fong-bing Yan for Hupingshan.

Mr. M.H.J.S.M. Hegeman, thank you for your help with the computer network. Mrs. Chun-ying Liu, for your assistance in running the Thornthorn program, Prof. Dian'an Yang, for your assistance in using the EIS (a modified GIS) software, and Ir. P. van der Meer, for your assistance in the light measurement in Wageningen; please accept my warm acknowledgements. Ir. G. Gort and Ir. J.J. Jansen, I am grateful to you for your advice on statistics. Mrs. J. Burrough-Boenish, thank you for editing the English

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of this thesis. Mrs. A.D. Bosch-Jonkers, thank you for your translation of the summary into Dutch. Mrs. Fan-zhi Kong and Mrs. Yi-chuan Yao, I am obliged to you for analysing silica content of bamboo leaves.

For your relevant information, I thank all of you:

Dr. F.J.J.M. Bongers, Prof. Hsin-shih Chang, Dr. Cornelissen, Dr. C. Edelin, Dr. J.Y. Fang, Dr. N.R. De Graaf, the late Prof. Hsioh-yu Hou, Dr. Mo-yi Kang; Dr. T. Kohyama, Asso. Prof. De-zhen Kong, Prof. Zhao-chen Kong, Mr. Ren-ling Liu, Dr. T. Nakashizuka, Dr. T. Ohkubo, Prof. M. Ohsawa, Dr. R. Peters, Prof. R.A.A. Oldeman, Dr. P. Schmidt, Asso. Prof. De-fa Shi, Dr. B. Thiébaud, Prof. Xian-pu Wang, Prof. M. Werger, Asso. Prof. Yuan-guang Wen.

I appreciate the permission to carry out the fieldwork, given by:

Guiling Department of Forestry for Miao'ershan Nature Reserve; Guizhou Department of Forestry for Fanjingshan MAB Nature Reserve; Huangshan National Park for Huangshan; Hunan Department of Forestry for Hupingshan Nature Reserve; Longsheng Department of Forestry for Liluo Forest Station; Nanjiang Forest Service for Daba Forest Station; Yongjia Department of Forestry for Shihai Shan Forest Station; Zhejiang Department of Forestry for Tianmushan National Park, for Longwangshan Nature Reserve and for Baishanzu Nature Reserve.

I sincerely thank you, my colleagues in the Laboratory of plant Ecology and the Laboratory of Quantitative Vegetation Ecology, Institute of Botany in Beijing, Chinese Academy of Sciences, and you, the colleagues in the Departments of Forestry and Ecological Agriculture, Wageningen Agricultural University, for your assistance of all kinds you have offered to me from time to time, your hospitality and friendship.

This study was co-funded by the National Science Foundation of P.R. China (project no. 39070188) and a doctoral fellowship of Wageningen Agricultural University, by the Chinese Academy of Sciences, the Netherlands Ministry of Education and Sciences & the Netherlands Academy of Sciences (KNAW; Scientific Cooperation with China). The Institute of Botany in Beijing provided the regular salary and research facilities. The Department of Forestry, Wageningen Agricultural University, provided working facilities during my three periods of stay in Wageningen. I always felt welcome for the discussions with my promotor at the Department of Ecological Agriculture of Wageningen Agricultural University.

My wife Ling Wang and my daughter Dongna Cao gave me support, freedom and cheerfulness; thank you for all of these.

Wageningen, The Netherlands
September 1994



Kun-Fang Cao

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Chapter 1 Introduction

1.1 Importance of beeches and beech forests

Fagus species occur from cool temperate zones to tropical mountains in humid climates in the Northern Hemisphere (Peters 1992). They dominate in certain mesic temperate broadleaved forests in Europe (Ellenberg 1988), in North America (Braun 1950; Rowe 1992), and in East Asia (Sasaki 1970; Numata 1974; Wu 1980). All yield good-quality hardwood timber. In Europe, silviculture of *Fagus sylvatica* has been practised for several centuries (Mayer 1984), but there is no silvicultural tradition for *Fagus* species in East Asia or in North America. In fact, *Fagus* timber has so far been used hardly commercially in China.

There are eleven recognized species in *Fagus* genus, five of which occur on mountains of southern China (22°–34°N; Chang & Huang 1988; Hong & 'An 1993). The Chinese beech species are important components in the mixed montane forests of subtropical China (*sensu* Nature Zonation Committee 1959; the Chinese subtropical zone is equivalent to the warm temperate zone in Troll & Paffen's (1980) climate classification system). They are often dominating rather steep slopes (around 30°) and ridges. These forests are important in maintaining the stability of watersheds, and in preventing soil erosion.

The forests in southern China have undergone many changes throughout the long history of that country (Wu 1980, Zhao 1989). Here, the lowlands, hills and lower parts of mountains have been converted into farmland or other plantations, and some have subsequently been abandoned. Deforestation has become quite serious in this century because of wars, increasing demand for timber, and mistakes in government policy (Zhao 1989). Many mountainous areas of southern China are now unforested and bare and are therefore susceptible to soil erosion, floods and mud-slides. In this region, natural forests including beech forests are under great pressure and their area continues to shrink because of the spread of felling, charcoal making and other human activities.

Beech is not cultivated in China, and all Chinese beech forests are natural forests growing on mountains located far away from inhabited areas (e.g. Figs. 1.1 & 1.2). These forests are rich in plant and animal species. In the south, Chinese beeches are associated with many subtropical and even tropical trees, e.g. from the families of Fagaceae (*Castanopsis*, *Lithocarpus*, *Cyclobalanopsis*), Lauraceae (*Sassafras*, *Machilus*, *Beilschmiedia*, *Neolitsea*), Magnoliaceae (*Manglietia*, *Michelia*, *Illicium*), Theaceae (*Schima*, *Ternstroemia*, *Camellia*, *Adinandra*, *Cleyera*, *Eurya*), Euphorbiaceae (*Daphniphyllum*), Sabiaceae (*Meliosma*) and Araliaceae (*Acanthopanax*, *Dentropanax*). Mixed Chinese beech forests host many rare, and endangered, plant and animal species. There is an urgent need to conserve these natural forests in China.

Beech has been suggested as being useful for afforestation in montane zones of subtropical China because of its tolerance of a wide range of soil types, and its potential for producing good-quality timber (Qi 1990). Some local foresters have already started using *Fagus* species for afforestation, e.g. in Nanshan Forest Station in Southern Hunan province (Qi 1990) and in Daba Forest Station in northern Sichuan province (pers. obs.). A study of climate in the beech range would be helpful to evaluate areas suitable for beech plantation.

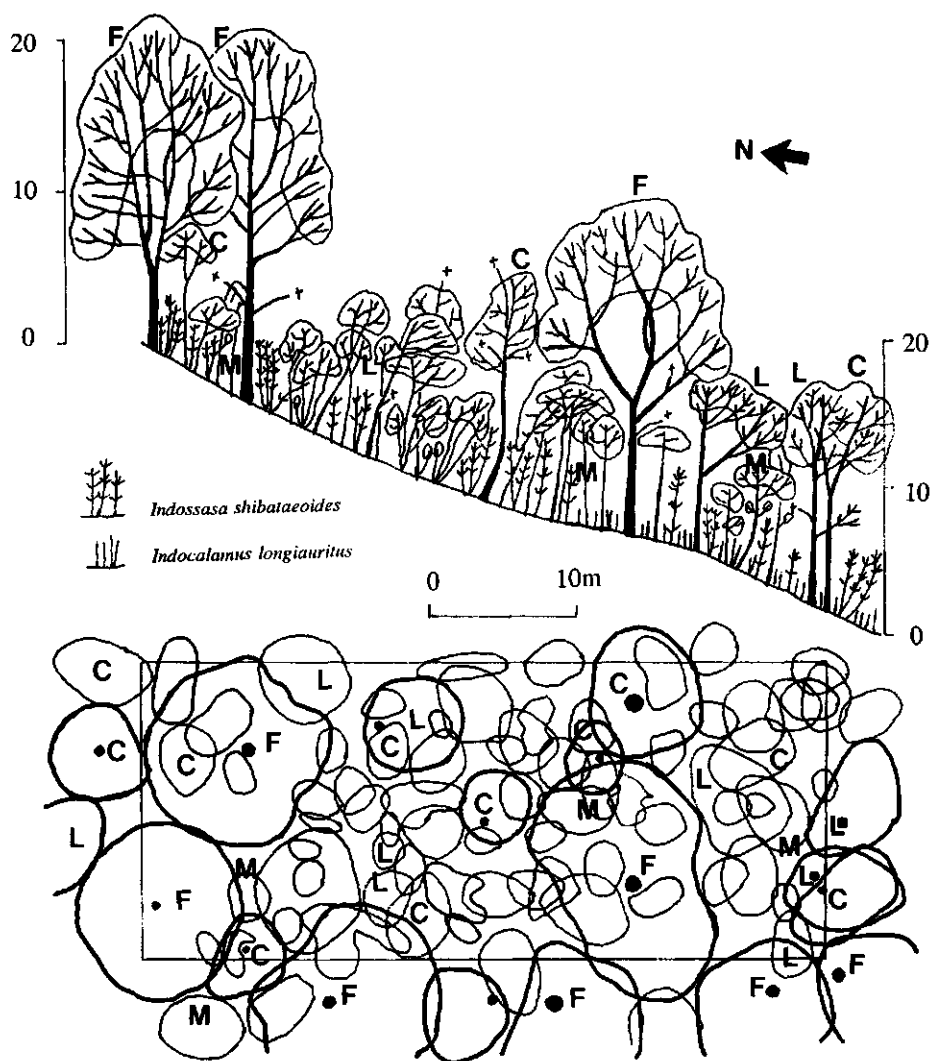


Fig. 1.1 The profile diagram and crown projection map of a sample plot (0.09 ha) at 1650 m altitude in Miao'ershan, on a mid-slope facing south, with trees taller than 5 m. The profile diagram included the bamboos (*Indossasa shibataeoides* and *Indocalamus longiauritus*). On the map, the crowns indicated with thick line and trunk position were trees in or approaching the overstorey canopy, those with thin line were young trees or understorey trees. Only the names of the main species studied in Chapters 4 and 5 are indicated: C = *Castanopsis lamontii*, F = **Fagus lucida*, L = *Lithocarpus hancei*, M = *Manglietia chingii*.

The other species in the order of the basal area per species were: *Ilex ficoidea*, *Lithocarpus* sp., *Cinnamomum* sp., **Rehderodendron kwangtungensis*, *Cinnamomum burmanii*, *Cyclobalanopsis multinervis*, *Symplocos* sp., **Acer davidii*, *Daphniphyllum glaucenscens*, *Machilus leptophylla*, **Acer oliverianum*, *Camellia pitardii*, *Ternstroemia gymnanthera*, **Prunus* sp., *Dendropanax chevalieri*, **Meliosma glandolosa* and *Cleyera pachyphylla*. All are broadleaved, stars indicating deciduous, the rest being evergreen.



Figure 1.2 A forest stand dominated by *Fagus hayatae* var. *pashanica* on a flat ridge at 1700 m altitude in Daba. The understorey is rather sparse, consisting mainly of *Ilex* spp. and *Rhododendron* spp.. Photographed in August 1992.

1.2 Juvenile beeches are rare in southern Chinese beech forests

Many researchers have reported that juvenile beeches are rare in mixed Chinese beech forests in the southern areas of the *Fagus* range (Wang *et al.* 1965; 1983; Chen & Tang 1982; Yuan & Cao 1983; Zhu & Yang 1985; Qi 1990). My own observations in several sites confirm this. This raises the following questions:

1. Will beech dominance in the forest canopy be maintained, or are the current beech-dominated forests a stage in a longer successional cycle or series?
2. If beech remains dominant in the canopy, then where do juvenile Chinese beeches establish themselves, how do they grow up and reach the canopy? How does beech differ from co-dominant species in these aspects?

The second question mainly concerns the regeneration of beech and other co-dominant species. The regeneration of a tree species involves its seed germination, seedling and sapling establishment, and the growing up of saplings. This study focused on saplings.

1.3 Abiotic factors that may affect beech regeneration

Temperature and precipitation are major factors in determining a species' range (Box 1981; Woodward 1987). They also greatly influence the establishment, growth and seed production

of trees. Therefore, they largely determine species composition of forests (Whittaker 1975; Wolfe 1979; Walter 1985).

In mountainous areas, soil properties and micro-climate vary along a toposequence (e.g. Van Rompaey 1993). The micro-climate also varies with aspect (e.g. Weng & Luo 1990). As Chinese beech forests all grow on mountains, site heterogeneity and micro-climate variation probably affect the performance of the beeches (cf. Crawley 1986). The success of European beech regeneration varies among sites on the same mountain (Mayer 1984).

Since Watt's (1947) work in temperate forests and Aubreville's (1938) work in tropical forests, it has been increasingly appreciated that forests are mosaics of different forest patches in different phases of development (e.g. for beech forests: Nakashizuka & Numata 1982; Koop & Hilgen 1987; Koop 1989; Peters 1992; Peters *et al.* 1992). Each of these forest patches started to develop after a forest canopy was opened up (Oldeman 1983; 1990) by external (e.g. storm, waterlogging, ice storm or snow storm in temperate forests, felling) or endogenous factors (e.g. mortality of old trees; Pickett & White 1985).

The opening up of the forest canopy causes the differentiation of micro-climate, soil water and nutrient availability and occasionally of the micro-topography in forests, and activates certain soil micro-organisms (Bormann & Likens 1979; Putz 1983; Platt & Strong 1989). It gives the forest a chance to regenerate. External factors cause the forest canopy to open frequently and are therefore important for forest regeneration and for the maintenance of species diversity of forests (Grubb 1977; Connell 1978; Pickett & White 1985; Platt & Strong 1989; Oliver & Larson 1990; Oldeman 1979, 1990). Because of repeated canopy opening by external factors and canopy closure by forest regrowth, the light environment above the trees in regeneration sites is ever-changing (Koop 1989). Many of the juvenile trees experience periods of shading during the forest regeneration processes (Oldeman 1983; Oldeman & Van Dijk 1990; Oliver & Larson 1990).

1.4 Biotic factors that affect beech regeneration

Chinese *Fagus* species occur over a wide geographical range (Hong & 'An 1993). They co-occur with evergreen broadleaved trees in the south (Wang *et al.* 1965; Zhu & Yang 1985; Qi 1990) and with deciduous broadleaved trees in the north (Zhou 1965; Wuhan Inst. Botany 1980; Peters 1992). Over the wide *Fagus* range, the shade-tolerance of beech species relative to co-dominant species may be different (Peters 1992) and may influence beech regeneration. In the south, the evergreen trees not only co-occur in the canopy, but they also often form a dense understorey. In the north, the forest understorey is rather sparse. Bamboos often cover the forest floor throughout the range of Chinese beech forests. A dense understorey (trees, shrubs and bamboos) certainly limits tree regeneration.

In the changing light environment caused by repeated opening up of the forest canopy, the adjustment of growth and architecture is essential for the survival of juveniles of most shade-tolerant species. Growth may be adjusted by changing relative resource investment in height vs diameter growth and in vertical vs horizontal shoot growth. Architectural adjustment may occur in leaves, shoots and branches, and crowns (Oldeman & Van Dijk 1991).

Trees conform to certain genetic growth models in their growth and architecture (Hallé &

Oldeman 1970). The architecture of trees is built up by differentiation of axes. I focused on one differentiation criterion: the distinction between plagiotropic and orthotropic axes (Hallé & Oldeman 1970). Plagiotropic axes usually pack leaves in two rows in a plane and therefore minimize self-shading. Orthotropic axes arrange leaves radially and possibly generate self-shading (Horn 1971). Givnish (1984) suggests that plagiotropic axes have an advantage in low light intensity and orthotropic axes should be favoured in sunny environments. Ashton (1976) suggests that the plagiotropic axes allow trees to expand their crowns rapidly.

All known *Fagus* species grow conforming to Troll's model (Hallé *et al* 1978; Peters 1992). Their architecture is built up by mixed axes, which are essentially plagiotropic and their basal parts can become erect by secondary growth as in the case of trunk formation. It has been suggested that trees growing in conformity to Troll's model display a highly flexible architecture, so that they are capable of buffering against various inhospitable environments (Hallé *et al.* 1978; cf. Leguminosae, Oldeman 1989). In *Fagus* species, growth and architectural flexibility have been found in *Fagus sylvatica* (Thiébaud 1988) and in *Fagus grandifolia* (Canham 1988). *Fagus sylvatica* in Europe (Ellenberg 1988) and *Fagus grandifolia* in the USA (Bormann & Likens 1979) are the most shade-tolerant of deciduous broadleaved trees. I assumed that Chinese *Fagus* species would also be shade-tolerant, flexible in growth and architecture, and should be able to regenerate in shaded conditions.

1.5 Objectives of the study

The study described in this thesis had four research objectives:

1. To quantify climatic heat and moisture ranges in Chinese beech habitats (Chapter 2).
2. To determine the relation between macro-climate (temperature, precipitation and major climatic hazards) and species composition of Chinese beech forests (Chapter 3).
3. To identify the relations between topography and beech regeneration and between species composition and beech regeneration in two forests, representatives of the Chinese beech forests in the north and in the south of the beech range (Chapter 4).
4. To compare juvenile growth and architectural strategies of beech with other shade-tolerant canopy or subcanopy species in relation to the light environment (Chapter 5). The species selected are all broadleaved, but differ in branch morphology (plagiotropy vs orthotropy) and in leaf longevity (deciduous vs evergreen).

1.6 Time of field work

I started field work in 1987, collecting data on Chinese *Fagus* distribution and species composition of Chinese beech forests. Until 1993, I aggregated the data from ten beech sites. These data were combined with data from literature and are presented in Chapters 2 and 3. Furthermore, two sites, i.e. Daba in the north and Miao'ershan in the south of the *Fagus* range, were selected to study regeneration strategies (see Chapter 4 for description of the two sites), and the growth and architecture of the main tree species in different light environments. The field work in these two sites was done during the growing season: from 1990 till 1992 in Miao'ershan, and in 1991 and 1992 in Daba.

Chapter 2 Climatic range and distribution of Chinese *Fagus* species

2.1 INTRODUCTION

Fagus species are important components in the temperate mesic forests in the Northern Hemisphere (Braun 1950; Numata 1974; Wu 1980; Ellenberg 1988; Peters 1992). In total eleven *Fagus* species are distinguished, five of which are Chinese (Chang & Huang 1988). The Chinese beech species only occur in southern China (Wu 1980; Hou 1983), mainly in the montane zones and occasionally in the lower parts of the mountains (Chang & Huang 1988; Hong & 'An 1993). However, in the northern part of beech range in Japan and Europe, beech species occur in the lowlands (Ellenberg 1988; Peters 1992), and American beech *Fagus grandifolia* Ehrh. can be found in the lowlands throughout its range (Braun 1950; Little 1971; Rowe 1972). Beeches are absent from temperate northern China, i.e. Walter's (1985) zonobiome VI, "typical temperate with a short period of frost". However, in eastern North America and Europe, the zonobiome VI covers a large parts of the beech ranges. To elucidate this difference in ranges, I examined the hypothesis that climatic conditions in Chinese beech zone essentially differ from those in American or European beech zone. I also compared the climatic characteristics of the Chinese temperate zone with those of the Chinese beech habitats.

Specially, the aims of the research described in this chapter were: (1) to quantify the climatic ranges in the habitats of the five Chinese beech species; (2) to clarify the climatic characteristics of Chinese zonobiome VI to evaluate why beech does not occur there; (3) to briefly compare the climatic ranges in Chinese beech habitats with those in other beech habitats.

2.2 METHODS

2.2.1 Distribution of Chinese beeches

There are five *Fagus* species endemic to China: *F. longipetiolata*, *F. lucida*, *F. engleriana*, *F. hayatae* and *F. chienii* (Chang & Huang 1988). To construct a distribution map of these beeches I combined the authors's observations, information from the literature (Table 2.1) and from the Central Herbarium of China in Beijing and the Herbarium of Zhejiang College of Forestry. These distribution data were also used for the analysis of climates in the beech habitats. I roughly divided the Chinese *Fagus* zone along 107 °E longitude into the two regions (Table 2.2) because in southern China the land from around this line to the west rises up to the Yunnan-Guizhou Plateau, and the mountains in the west are higher than in the east. *Fagus* species occur at higher altitudes in the west than in the east. In line with Ellenberg's (1988) definition of montane zone where mean annual temperature is at least 3°C lower than the lowland, I interpreted the montane zone where the elevation is at least 600 m higher than the mountain foot. I defined the submontane zone for the lower parts of a mountain, where the altitudes are between 200 and 600 m higher than the mountain foot.

Table 2.1. Literature consulted for distribution of *Fagus* species in China.

Regions	Species	Literature
Northwestern region	<i>F. hayatae</i> var. <i>pashanica</i> ; <i>F. engleriana</i> ; <i>F. lucida</i> ; <i>F. longipetiolata</i>	Wuhan Inst. Bot. 1980; Wang <i>et al.</i> 1981; Bartholomew <i>et al.</i> 1983; Gan 1986; Shaanxi For. Ed. Committee 1989; Peters 1992.
Eastern region	<i>F. hayatae</i> var. <i>pashanica</i>	Wang 1992.
Eastern region	<i>F. hayatae</i> var. <i>zhejiangensis</i>	Wang 1992.
Eastern region	<i>F. longipetiolata</i> ; <i>F. lucida</i> ;	Jiangxi Branch of CAS 1960; Zhou 1965; Ling 1981, 1986; Wu <i>et al.</i> 1988; Chen & Zhao 1989; Zhang 1990; Zhou and Bao 1991; Wang 1992.
Central, southern & SW regions	<i>F. longipetiolata</i> ; <i>F. lucida</i> ; <i>F. engleriana</i>	Wang <i>et al.</i> 1965; 1983; Tsien <i>et al.</i> 1975; Ed. Comm. Guizhou Flora 1982; Wang YM 1983; Wang XP 1984; Gan 1986; Wu & Jiang 1987; Dayaoshan Exped. 1988; Wu <i>et al.</i> 1988; Fang 1989; Qi 1990; Wang <i>et al.</i> 1991; Liu & Hou 1991; Peters 1992; Yi <i>et al.</i> 1992.
Taiwan	<i>F. hayatae</i>	Hsieh <i>et al.</i> 1987; Su 1988.
Vietnam	<i>F. longipetiolata</i>	Thái van Trúng 1978.

2.2.2 Collecting climatic data

Several climatic factors have been postulated to control *Fagus* distribution: (1) moisture deficits in continental and southern areas (Becker 1981; Peters 1992; Hong & 'An 1993); (2) short growing seasons in northern areas (Hong & 'An 1993); (3) cold (Huntley *et al.* 1989; Hong & 'An 1993) and extreme temperature minima (Sakai 1975) in winter in northern areas; (4) late spring frosts (Becker 1981; Mayer 1986); (5) excessive heat in southern areas (Peters 1992; Hong & 'An 1993). These factors were therefore considered in the analysis.

Mean monthly temperature and precipitation, and extreme temperature minima were collected from 32 standard and 8 temporary montane weather stations in China (Appendix 2.1), all located in the *Fagus* zone. Most of the standard stations have records of about 30 years. The temporary stations have records of 3 to 24 years. I also incorporated another eight beech sites, for which climatic data were available from literature (Bartholomew *et al.* 1983; Anon. 1986b, 1989; Dayaoshan Exped. Team 1988; Qi 1990; Liu & Hou 1991; Zhou & Bao 1991). The data given in the literature were mean annual precipitation, mean annual temperature and sometimes mean temperature of January and July. I included climatic data from 111 standard stations outside the Chinese *Fagus* range, for comparison. I used the results of Chang (1989) to analyse the thermal and moisture conditions in the lowlands, hilly areas and submontane zones in subtropical China, and the results of Fang and Yoda (1990) for Chinese tropical forest areas.

2.2.3 Climatic heat analysis

I followed Kira's (1945) method for climatic heat analysis because good correlations with Kira's temperature indices and vegetation distribution have been found in East Asia (Kira 1977; Yim 1977; Fang & Yoda 1989; Ohsawa 1991; Hong & 'An 1993). I calculated Kira's

Warmth Index (WI) and Coldness Index (CI):

$$WI = \Sigma(t-5), t > 5^{\circ}\text{C};$$

$$CI = \Sigma(t-5), t < 5^{\circ}\text{C},$$

in which t equals mean monthly temperature. The unit of WI and CI is $^{\circ}\text{C} \cdot \text{month}$ (Kira 1945).

Potential evapotranspiration was also used as a thermal index, because at any one site it is a parameter of the thermal energy available for evaporation and transpiration (Thornthwaite 1948).

2.2.4 Climatic moisture analysis

For the analysis of climatic moisture, I calculated potential evapotranspiration and annual moisture index. Although Penman's (1948) method gives a more accurate estimate of potential evapotranspiration than Thornthwaite's (1948), I applied Thornthwaite's method because the necessary data were available for all stations. Also, Thornthwaite's indices made a comparison with other work possible (e.g. Mather & Yoshioka 1968; Chang 1989; Fang & Yoda 1990). I used the THORN.FOR program by Chang (1989) for the calculation. In this program, monthly potential evapotranspiration (PE) is calculated by the following equations:

$$PE = e * CF$$

$$e = 16(10t/I)^4 \text{ mm mo}^{-1}$$

$$a = (0.675I^3 - 77.1I^2 + 17920I + 492390) * 10^{-6}$$

$$I = \Sigma(t/5)^{1.514}$$

in which PE is monthly potential evapotranspiration in mm; e is uncorrected monthly potential evapotranspiration in mm; t is the mean monthly temperature in $^{\circ}\text{C}$; I is annual heat index. CF is a correction factor for the actual number of days per month and the number of daylight hours per day. CF is obtained from the tables established by Thornthwaite and Mather (1957). The annual moisture index (Im) is calculated by the following equations:

$$Im = 100(S - 0.6 D)/\Sigma PE;$$

$$S = \Sigma(P - PE) \text{ (if } P > PE);$$

$$D = \Sigma(PE - P) \text{ (if } P < PE),$$

in which S is the theoretical annual water surplus and D the theoretical annual water deficit, PE is monthly potential evapotranspiration and P is monthly precipitation. Thornthwaite uses Im ranges to define six major moisture zones: perhumid ($Im > 100$), humid (20-100), moist subhumid (0-20), dry subhumid (-33.0 - 0), semiarid (-66.7 - -33.3) and arid climates (-100 - -66.7). A humid climate ($Im > 0$) does not necessarily exclude a water deficit in any one month.

PE and Im were calculated for the 40 weather station sites within the beech range and also for the 111 weather station sites in the bordering areas.

2.2.5 Missing climatic data: data extrapolation

I extrapolated the heat indices, i.e. WI, CI, mean annual potential evapotranspiration (PET), mean temperature of January and July and mean annual temperature, mean yearly precipitation, and annual moisture index (Im) in the middle zone and at the upper and lower

altitudinal limits of every beech range for the 40 sites with weather stations. These climatic indices at the upper and lower altitudinal limits were used to analyse the climatic ranges in the habitats of each beech species. I calculated average climatic indices (avgI) for each of the three widely distributed beech species: *Fagus longipetiolata*, *F. lucida* and *F. engleriana*. Per site i , for each species, the altitudinal range (AR) was introduced as a weighting factor:

$$\text{avgI} = \Sigma(I_i \times \text{AR}_i) / \Sigma \text{AR}_i,$$

in which I_i was the climatic index calculated for the middle zone of site i . AR_i was the altitudinal range of a beech species in 100 m steps at site i . At eight sites, *Fagus longipetiolata* has been only found at one altitude by specimen record; at two other sites *F. engleriana* has been also only known at one altitude. For these 10 sites an AR_i of 2 was used.

I based my estimation of temperature and precipitation on the lapse rate given in the literature (Huang 1982; Zhang & Wang 1983; Li & Fu 1984; Anon. 1986; Gan & Mu 1989; Weng & Luo 1990; Jiang 1991; Xu 1991). The lapse rate for mean annual temperature is around 0.55°C per 100 m altitude, being slightly more for summer months and less for winter months. For each of the 40 sites, I used the annual total potential evapotranspiration (PET) and Im at the weather station as the starting point for estimating the ranges of these indices. I then used regressions based on the 40 stations to estimate PET and Im values in other altitudes of each of these 40 sites. For the other eight beech sites with climatic data given in the literature I calculated PET from Ta, and Im from PRCP and Ta directly by the regression equations. The formulae used were:

$$\text{PET} = 296.28 + 32.44 \text{ Ta}$$

$$(N = 40, r^2 = 97.8\%, P < 0.001)$$

$$\text{Im} = 23.47 + 0.1475 \text{ PRCP} - 9.8829 \text{ Ta}$$

$$(N = 40, r^2 = 98.6\%, P < 0.001),$$

in which Ta is the mean annual temperature (°C) and PRCP is the mean annual precipitation in mm. These formulae predict that per 1°C increase in Ta, the PET increases by 32.44 mm and the Im decreases by 9.9; and per 100 mm increase in PRCP the Im increases by 14.75. Also, using the literature data, I estimated WI and CI for those eight sites from the regression formulae:

$$\text{WI} = -18.5 + 9.2853 \text{ Ta}$$

$$(N = 36, r^2 = 99.0\%, P < 0.001),$$

$$\text{CI} = -41.15 + 2.688 \text{ Ta}$$

$$(N = 36, r^2 = 89.2\%, P < 0.01)$$

2.2.6 Comparison among climates in Chinese and other beech habitats

I compared the climatic ranges in Chinese beech habitats with those in habitats of other widely distributed beeches, i.e. *F. crenata* in Japan, *F. sylvatica* in Europe and *F. grandifolia* in North America. For the comparison between Chinese temperate zone and the temperate zones where other beeches occur, I applied the climate classification of Troll and Paffen (1980) because it goes into greater detail than Walter's (1985) system. The Walter's Zonobiome VI is called the cool temperate zone in Troll and Paffen's system. Troll and Paffen's classification is more general and includes more climatic parameters than either Kira's (1945) or Thornthwaite's (1948). Kira's and Thornthwaite's indices are particularly useful for analysing specific climatic parameters.

2.3 RESULTS

2.3.1 *Fagus* distribution in China

The geographical range of Chinese *Fagus* species lies in the eastern part of southern China (Fig. 2.1). The northern limit of the *Fagus* range roughly coincides with 34.3°N latitude and lies in the Qinling mountain range (Fig. 2.2). The southernmost occurrences are found in mesic tropical mountain slopes (Fig. 2.1). The western limit approximately coincides with 101°E longitude. Chinese beeches only occur in mountains, mainly between altitudes of 700 and 2500 m (Fig. 2.2). *F. longipetiolata* occasionally occur in lower parts of mountains around altitudes of 400-500 m. The upper altitudinal limits of the beeches are higher in the west than in the east of the beech range because the mountains in the west are higher (Table 2.2).

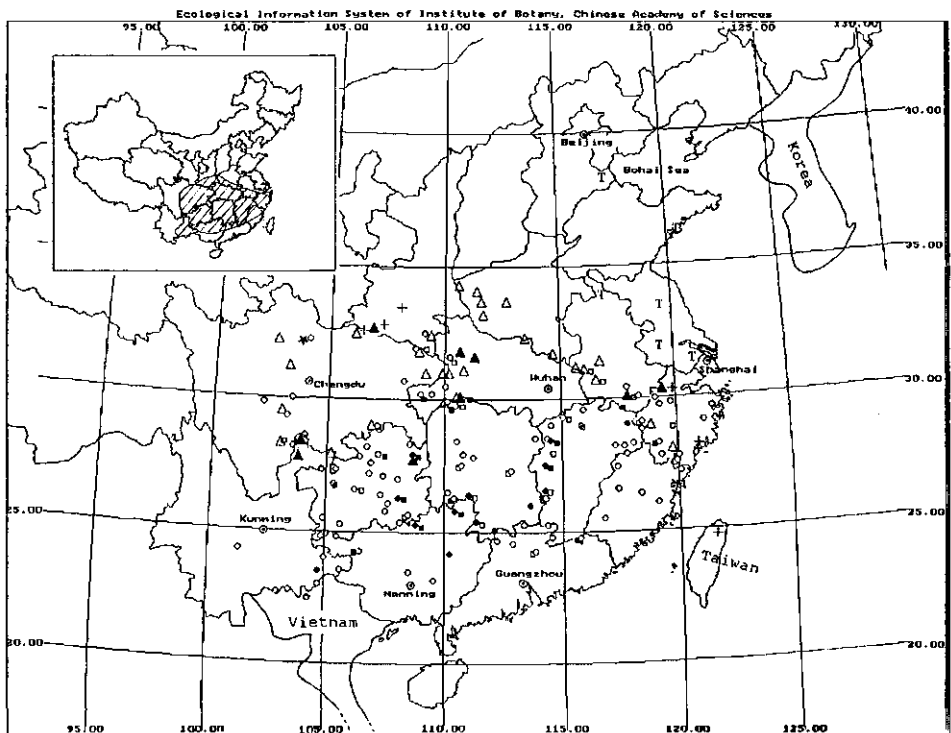


Figure 2.1. Distribution of known present-day *Fagus* localities in China: *F. longipetiolata* (circles), *F. lucida* (squares), *F. engleriana* (triangles), *F. hayatae* (crosses), and *F. chienii* (star). Solid and open symbols indicate abundant and scattered presence respectively. Map inset in upper left shows the rough extent of the actual *Fagus* zone of China. The symbol 'T' indicates the localities near the coast, where *Fagus* pollen fossils have been identified in the Holocene deposits, and where *Fagus* subsequently became extinct. Note: the demarcation of Korea and Vietnam is only roughly indicated.

Table 2.2. Geographical distribution of *Fagus* species in China.

Species	Latitude (°N)	Longitude (°E)	Altitude (m) East of 107°E ^a	West of 107°E ^a
<i>F. longipetiolata</i>	22.3 - 32.7	101.2 - 121.5	400 - 1500	800 - 2600
<i>F. lucida</i>	24.3 - 32.0	103.2 - 120.8	700 - 2000	1800 - 2200
<i>F. engleriana</i>	27.5 - 34.3	102.2 - 119.4	1000 - 2200	1200 - 2500
<i>F. hayatae</i>	24.7	121.4	1300 - 2000	
<i>F. hayatae</i> ¹	28.2	120.8	700 - 1000	
<i>F. hayatae</i> ²	30.3	119.4	1000	
<i>F. hayatae</i> ²	32.7 - 33.5	105 - 107		1200 - 1900
<i>F. chienii</i>	33	104		1300
<i>Fagus</i>	22.3 - 34.3	101.2 - 121.5	400 - 2200	800 - 2600

¹ = var. *zhejiangensis*; ² = var. *pashanica*. ^a the land from about 107°E longitude to the west rises up to the Yunnan-Guizhou Plateau and the mountains are higher than in the east.



Figure 2.2. The map shows the locations of the main mountain systems (indicated with names) where Chinese beech occur. A few mountains (names not indicated) next to the *Fagus* range to the west are indicated to illustrate their north-southward orientation. Note: mountains further to the west and to the north where *Fagus* is absent are excluded on the map; the names ending with 'shan' and 'ling' mean mountains; the demarcation of Korea and Vietnam is only roughly indicated.

Among Chinese beeches, *F. longipetiolata*, *F. lucida* and *F. engleriana* have wide geographical ranges. *F. longipetiolata* has the widest range and occurs as far south as the mesic, usually north-facing, slopes of tropical mountains in northern Vietnam and in the southeast of Yunnan Province of China. *F. engleriana* is inherently multi-stemmed (Fig. 2.3) and is mainly found in the northern part of the *Fagus* range. *F. lucida* somewhat concentrates to the central area of that range. *F. chienii* is only known from Pingwu County in northern Sichuan Province. *F. hayatae* has a disjunct distribution. *F. hayatae* forest patches occur on mountains of northern Taiwan. *F. hayatae* var. *zhejiangensis* forms small forest patches in coastal montane site, i.e. Sihaishan Forest Station (28.3°N, 120.8°E) of Yongjia County in Zhejiang Province. *F. hayatae* var. *pashanica* occur abundantly in Dabashan mountain range in northwest. Its specimen has also been collected from Mt. Tianmushan in the east.

2.3.2 Temperature and moisture in Chinese beech habitats

The five Chinese beech species occur in overlapped moisture and heat ranges (Fig. 2.4; Tables 2.3 & 2.4). All the forest dominated by Chinese beeches lie in the perhumid montane



Figure 2.3. A multi-stemmed *Fagus engleriana* at 1650 m altitude on Mt. Huangshan, about 10 m tall, sprouts regenerated at the root collar of old stems. Photographed by R. Peters in June 1987.

zones with abundant water throughout the year. *F. longipetiolata* habitats cover the widest moisture ranges and the warmest climate on the average. Only in a few cases has *F. longipetiolata* been found in a cool climate. For example, *F. longipetiolata* occurs up to 2500 m altitude in Pingwu County (33°N, 103°E) in Sichuan Province, where the mean annual temperature is around 6°C, WI about 52°C·month and CI about -4.4°C. *F. lucida* experiences an intermediate heat and is confined to perhumid conditions, i.e. Im over 100. *F. engleriana* grows in cooler climate with intermediate moisture level. Its individuals have been found up to 2400 m altitude in Shennongjia mountains, with approximately a mean annual temperature of 4.8°C, a WI of 40°C·month and a CI of -37°C·month. *F. hayatae* occurs in perhumid climates with a wide thermal range (Tables 2.3. & 2.4).

Among all weather stations in the *Fagus* zone, the minimum temperature recorded was -22.5°C on December 28, 1991, at Daba Forest Station (32°42'N, 106°50'E; altitude 1450 m). No frost damage to beech due to this cold was observed in the following summer (pers. obs., Cao).

Table 2.3. Thermal and moisture indices in the geographical ranges of Chinese *Fagus* species.

Species	Number of sites	Thornthwaite's indices				Kira's indices			
		PET (mm)		Im		WI (°C·month)		CI (°C·month)	
		Avg	range	Avg	range	Avg	Range	Avg	Range
<i>F. longipetiolata</i>	26	721.5	520 - 838	125.8	26 - 289	103.1	52 - 140	-3.7	-25 - 0
<i>F. lucida</i>	14	632.0	541 - 749	196.0	111 - 320	80.0	58 - 110	-11.5	-30 - 0
<i>F. engleriana</i>	14	606.1	450 - 640	132.0	61 - 274	72.1	40 - 105	-15.8	-37 - 0
<i>F. hayatae</i>	1		700 - 832		> 200		90 - 132	0	
<i>F. hayatae</i> ¹	1		655 - 725		> 100				
<i>F. hayatae</i> ²	1		500 - 613		148 - 188		56 - 72		-16 - -25
<i>Fagus</i>			450 - 838		26 - 320		40 - 140		-37 - 0

¹ = *F. hayatae* var. *zhejiangensis*; ² = *F. hayatae* var. *pashanica*.

Table 2.4. Mean annual temperature (Ta), mean January temperature (TJan), mean July temperature (TJuly) and mean annual precipitation (PRCP) in each Chinese beech range.

Species	Ta (°C)		TJan (°C)		TJuly (°C)		PRCP (mm)	
	Avg	range	Avg	range	Avg	range	avg	range
<i>F. longipetiolata</i>	13.2	6.0 - 16.7	3.2	-3.0 - 9.8	22.7	15.4 - 25.6	1587	850 - 2770
<i>F. lucida</i>	9.8	7.4 - 14.2	0.1	-4.0 - 5.1	19.7	17.4 - 22.4	1915	1200 - 2700
<i>F. engleriana</i>	9.6	4.8 - 13.9	-1.3	-7.7 - 3.8	19.5	15.0 - 22.4	1419	740 - 2400
<i>F. hayatae</i>		12.5 - 16.5		5.5 - 9.3		17.6 - 20.7		2800 - 3500
<i>F. hayatae</i> ²		6.6 - 9.6		-3.5 - -1.4		17.4 - 20.4		1300 - 1550
<i>Fagus</i>		4.8 - 16.7		-7.7 - 9.8		15.0 - 25.6		740 - 3500

² = *F. hayatae* var. *pashanica*.

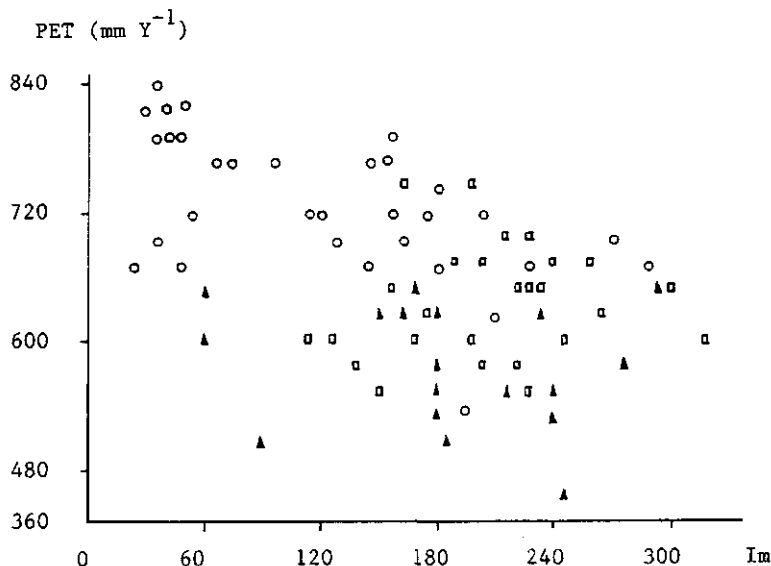


Figure 2.4. Known *Fagus* locations in China and their distribution along the thermal (PET) and climatic moisture (Im) gradients: *F. longipetiolata* (circles), *F. lucida* (squares), and *F. engleriana* (triangles).

2.3.3 Heat and moisture outside the *Fagus* range

The subtropical lowlands are much warmer than the beech habitats (Tables 2.3 & 2.5). These lowlands receive less precipitation and experience certain water deficits during the growing season.

In the northern areas next to the *Fagus* range, climatic moisture is much lower than in the beech habitats. Inland, the Im is below zero both in lowlands and in montane zones (Table 2.5); this is characteristic of dry climates. Compared to the inland areas, the coastal areas are more humid and less cold in winter.

In the mountainous areas next to the *Fagus* range to the west (i.e. west of 101° E, Fig. 2.2), the moisture overlaps to that in the beech habitats (Tables 3.3 & 3.5). These western mountainous areas were described in two parts. In the northern part, only the montane habitats are favourable to beech. In the central and southern parts, because of the rain-shadow effects and because of the weakened impacts by summer monsoons, the habitats are favourable only on the east-facing slopes. Further to the west from this western margin, the lands rise to an alpine plateau, and then to the Himalaya mountains, there the heat is not sufficient for beech.

Chinese tropical forest areas are hotter than the beech habitats. Water deficit occurs in the tropical seasonal rainforest area.

Table 2.5 Heat and moisture in areas bordering the Chinese *Fagus* range.

Neighbour areas	Latitude	Longitude	Number of stations	Altitude stations(m)	PET (mm)	Im
Northern lowland & hilly areas	35-40°N	108-123°E	43	< 1000	619- 800	-23- 25
Northern montane zones	35-40°N	109-113°E	10	1000-1600	520- 665	-23- 4 (117) ^a
NE China: southern coastal area	40-42°21'	123-128°E	13	0- 774	548- 654	24- 83
Western margin: north (highland)	30-35°N	98-104°E	5	2300-3000	500- 680	-2- 51
			12	3000-4000	348- 520	10- 95
middle highland	25-30°N	98-104°E	17	1400-3000	577- 775	-34- 98
south	22-25°N	97-104°E	11	500-1705	757-1100	0- 53
Lowlands & hilly areas						
below <i>Fagus</i> range ^b : north					813- 894	-3- 31
middle					850-1000	25- 75
south					1066-1184	10- 50
Tropical China ^c :						
Seasonal rain forest area					1030-1168	33- 50
Humid rain forest area					1077-1300	62-111

^a figure in parenthesis only found in one station; ^b data from Chang (1989); ^c data from Fang and Yoda (1990).

Table 2.6 Comparison with climates in *Fagus* ranges in China and in other countries.

	Lat. (°N)	Ta(°C)	PRCP(mm)	PET(mm)	Im	WI	CI	Radiation ^e Apr-Sept	Climatic zone ^f
<i>Fagus</i> in China	22.3-34.3	5 - 17	740-2770	450- 838	26-320	40-140	-37-0	270-400	III7, III8, IV7
<i>F. hayatae</i> ^a	24.7	12 - 17	2800-3500	700- 832	270-400	90-132	0		IV7
<i>F. crenata</i> ^b	31.5-42.8	3 - 13	1200-3400	< 700	> 90	33- 98	-54-0		III8, IV7
<i>F. sylvatica</i> ^c	37.5-60	2 - 14	500-2000	480- 800	-14-239	17-114	-69-0	300-400	III2, III3, III4, IV7
<i>F. grandifolia</i> ^d	30- 49	3 - 21	760-2100	530-1080	32-225	49-196	-63-0	400-540	III4, III7, III8, IV7, V2

Data source: ^a Hsieh 1987; ^b Peters 1985 & in prep.; ^c Müller 1982 and Peters in prep., including data for *F. sylvatica* subsp. *orientalis*; ^d Mather & Yoshioka 1968, Rowe 1972, Müller 1982 and Peters in prep. including data for *F. grandifolia* subsp. *mexicana*. ^e in $\text{Ly} \cdot \text{day}^{-1}$ as unit, ^f after Troll and Paffen 1980. See Tables 2.3 and 2.4 for climatic data for each Chinese beech species; see Table 2.3 for units of WI and CI.

2.3.4 Comparison between the climatic ranges in Chinese and other beech habitats

The climatic ranges in the habitats of Chinese and other Northern Hemisphere beeches largely overlap (Table 2.6). There is no clear difference in climatic moisture and in the range of precipitation. However, the beech habitats in China and North America cover greater warm extremes than the beech habitats in Japan and Europe.

2.4 DISCUSSIONS

2.4.1 Heat and moisture characteristics in Chinese beech habitats

Chinese beeches occur in the subtropical evergreen zone, while other beeches mainly grow in temperate deciduous zones. But, the Chinese beeches are confined to the mountains. Therefore, the thermal range in the Chinese beech habitats still belongs to the temperate climate (Troll & Paffen 1980). The heat in the Chinese beech habitats largely overlaps with those in other beech habitats (Table 2.6). The WI of $85^{\circ}\text{C}\cdot\text{month}$ is the lower limit of evergreen broadleaved forest in Japan (Kira 1977) and southeastern Asia (Ohsawa 1991). In China, *Fagus longipetiolata* mainly grows in the climate with WI exceeding $85^{\circ}\text{C}\cdot\text{month}$, and so do other beech species occasionally. In such warm climates the beeches co-occur with evergreen broadleaved trees (e.g. see Wang *et al.* 1983; Wu 1987; Wu *et al.* 1988; Qi 1990). The American beech in its southern range also experiences a warm climate (e.g. in northern Florida, Peters 1992), and there it is also associated with evergreen broadleaved trees (Braun 1950).

Conditions in Chinese beech habitats are indeed very humid. On average, the moisture index in Chinese beech habitats is above 100 (perhumid). Like all mountain climates, the montane Chinese beech zones receive much more precipitations than the lowlands (Weng & Luo 1990). Also, the montane zones are often covered with clouds and mists, and consequently receive less solar radiation than the lowlands. The amount of radiation received in the Chinese beech zone is the same as in the European beech zone and less than in American beech zone (Table 2.6). The frequent mists, cloud cover and rains maintain a high humidity in the Chinese beech habitats. In the same way, frequent mists maintain a high moisture in beech forests in tropical mountains in Mexico (Peters 1994).

At its northern limit in southeastern Canada, *F. grandifolia* occurs in a climate close to boreal and with cold winters (Rowe 1972). Chinese (Tables 3 & 4) and European beeches (Becker 1981; Ellenberg 1988) at upper altitudinal limits also experience cold climates.

2.4.2 Are there suitable habitats for Chinese beeches in the cool temperate China?

2.4.2a Water deficits and cold winters inhibit beech in the continental areas of the cool temperate China

The climate of the cool temperate China is continental, the winter is cold and dry because of the strong influence of continental winds descending from Siberia and Mongolia. According to the climate classification of Troll and Paffen (1980), the western half of the cool temperate zone in China has a steppe climate (Zone III11), or semi-desert and desert climates (Zone III12) with cold winters. The inland part of the cool temperate zone in eastern China also has a steppe climate. Northeastern China such as eastern Inner Mongolia, Heilongjiang, Jiling and northern Liaoning provinces has a very continental climate (mainly in Zone III6), where the winter is too cold and the moisture is insufficient for beeches (see

Xu 1983; and Chang 1989 for the climates). The North China Plain and the eastern part of Loess Plateau are characterized by a humid climate with warm summers (Zone III7). But in the lowlands and in the inland montane zones of this Zone III7 the moisture is low (Table 4) and water deficits are severe in spring and autumn (Zhang 1991). Thus, the climates in most parts of the Chinese cool temperate zone are not suitable for beech as we know.

However, the cool-temperate zone in eastern North America where *F. grandifolia* occurs and the cool-temperate zone in Japan where *F. crenata* grows are mainly in permanently humid climates (Zone III8). In Europe, the cool temperate zone where *F. sylvatica* grows is in sub-oceanic and oceanic climates (Zones III2 and III3; Table 2.6). In the cool temperate zones in Europe and eastern Northern America, precipitations occur more or less evenly throughout the year so that the chances of water deficits are low. In contrast, precipitations in the cool temperate China are largely concentrated on the summer months.

2.4.2b The climate in the Bohai coastal area seems suitable for beech

The only area in the Chinese cool temperate zone that has a climate potentially suitable for beech is the coastal area near the Bohai Sea (Table 2.5). However, beech is absent from this area. Pollen data show that *Fagus* existed in this area during the Holocene Megathermal (c. 5000-8000 BP; Fig. 2.1; Wang YJ & Li 1983; Xu *et al.* 1993). Since then, the temperature and humidity have decreased, the sea level has become lower (Shi & Kong 1992) and human impact has increased (Wu 1980). However, the present temperature and moisture of this coastal area are still within the climatic range of *F. engleriana*. Also, the average date of late spring frost in this area is in mid-May, just as in the upper and northern limits of the Chinese beech range (see climatic diagrams in Wu 1980). Thus, neither the temperatures, nor moisture, nor late spring frost could have caused *Fagus* to become extinct from this area. I therefore suspect that human impact could be a cause of the absence of *Fagus* species from this area (Wu 1980). If this is so, it should be possible to reintroduce beech here.

2.4.3 Possible factors limiting *Fagus* extension downwards to the lowlands and southwards

High temperatures and large water deficits seem to limit the range of Chinese beeches in the lowlands and in further south (Tables 2.3 & 2.5). However, *F. longipetiolata* grows occasionally in the submontane zones where mean annual temperature is around 16°C (Table 2.4) and water deficits occur in some period in the growing season. In northern Florida *F. grandifolia* can grow in a climate with mean annual temperature of about 20°C (Peters 1992) and with occasional water deficits (cf. Müller 1982). So other factors may inhibit beech in the lowlands and the southern areas in China, for example, the inability of beech to compete with evergreen broadleaved trees (Woodward 1987). In these southern areas, evergreen broadleaved trees may outgrow beech because they have higher productivity (Kira & Shidei 1967) as a result of their larger leaf area indices (Satoo 1983), longer active growing seasons (Kusumoto 1957; Jarvis & Leverenz 1983), and their more efficient use of soil nutrients and

water (Chabot & Hicks 1982; Hollinger 1992).

In eastern China, human has affected forests for a long time (Wu 1980). The original forests in the lowlands and in hilly regions have been converted to farmlands or to secondary and planted forests. The disappearance of *Fagus* from the lower parts of mountains in the subtropical China may well be the result of these intense human activities. For example, solitary specimens of *F. longipetiolata* can be found in submontane zones in the eastern and central areas of the *Fagus* range (Wang 1992; herbarium records).

The disjunct distribution of Chinese beech species in montane zones suggests that these species were once much more widespread. For example, palaeobotanical studies have speculated that these beech species survived in mountain valleys during ice ages and spread to higher altitudes and to the north during the inter-glaciations (Kong *et al.* 1977; 1992; Zhu 1979; Zhong *et al.* 1988). During the Holocene Megathermal, in eastern China near the coast *Fagus* spread far more to the north than the present day (Fig. 2.1; Liu & Yi 1977; Wang YJ & Li 1983; Tang & Shen 1992; Xu *et al.* 1993).

2.5 CONCLUSIONS

Chinese beeches are found in a humid or perhumid temperate climate. Although there is some variation between species, the Northern Hemisphere beech species including Chinese ones require a similar climate. The climatic ranges in Chinese beech habitats today suggest that the Chinese beech species could have a wider distribution. Competition from evergreen broadleaved trees and human impact limit the Chinese beeches in the lowlands. The survival of these species probably depends on their effective regeneration. The climate of most of cool temperate China is outside the climatic range occurring in the Chinese beech habitats. However, the climatic conditions near the Bohai Bay in northeastern China is still within the climatic range in the beech habitats. Beech re-introduction to this area might be succeeded.

Chapter 3 Species diversity of Chinese beech forests in relation to warmth and climatic hazards

3.1 INTRODUCTION

Temperature and precipitation are key factors that determine species' ranges (Wolfe 1979; Box 1981; Walter 1985; Woodward 1987). Chinese beech species occur in a wide climatic range (Cao *et al.* in prep.). They co-occur with tree species ranging from coniferous, through deciduous broadleaved, to evergreen broadleaved (Wu 1980). The species composition of Chinese beech forests differs widely.

All forests are influenced by external factors (e.g. storms, heavy rains or fires) that locally change forest structure and function (Pickett & White 1985). These external factors can cause the forest canopy to open up at forest patch level or forest mosaic level. Beneath the canopy openings, the abiotic and biotic resources and sometimes micro-topography differ from those under the closed canopy (Bormann & Likens 1979; Putz 1983; Platt & Strong 1989). The opening up of the forest canopy gives trees the chance to establish their offspring, to resume growth in their already established but suppressed juveniles, and may allow the young trees to grow up and reach the forest canopy. In this way, external factors largely determine the presence and dominance of trees in forests (Connell 1978; Platt & Strong 1989; Oldeman 1983; 1990; Runkle 1982, 1990; Peters & Poulson 1994).

External factors such as climatic hazards act on forests frequently and repeatedly. They exert selective pressure on forest communities and may increase the genetic fitness of successive generations (Harper 1977). They interfere with the exclusion of species by competition and therefore are necessary for the maintenance of species diversity in forests (Grubb 1977; Connell 1978). However, these external factors are called "disturbance", "perturbation" or "disaster" (Pickett & White 1985), which are all terms that have a negative connotation. It would be better to use some purely neutral descriptive terms instead. Chablis is an old European term for the events occurring when a tree is uprooted. Oldeman (1990) coined the term "zero-event" to describe external factors that change forest architecture at the forest patch (eco-unit) level, and the term "shifting event" for the factors that change forest architecture at the level of silvatic mosaic. In this paper, the term "disturbance" has been avoided.

Storms cause the forest canopy to open up at both forest patch and forest mosaic levels in tropical and temperate forests (Pickett & White 1985). Cyclones are important in coastal zones of North America and East Asia (Arakawa 1969; Bryson & Hare 1974), and cause tree-falls in the forests located there. Tornadoes are important in the United States (Bryant 1991), and they cause tree-falls in the American beech forests (Runkle 1990; Peters 1992). In northeastern USA, glaze storms cause branch breakage and sometimes tree-fall at the forest mosaic level in the northern hardwood forests (Downs 1938; Whitney & Johnson 1984; De Steven *et al.* 1991). In Chinese beech forests, tree-falls and branch-breakage may be caused by cyclones, tornadoes and localized strong gusts (Feng *et al.* 1985; Zhang *et al.* 1991), glaze storms (freezing rains and freezing fogs; Jiang 1991), lightning during thunderstorms (pers. comm., X.P. Wang; cf. Brünig & Huang 1989, tropical forests),

torrential rains (Tao 1980; Sun 1988), heavy snowfall, and hailstorms (Wang 1990; Xu 1991). The intensities and frequencies of these climatic hazards vary from the coastal area to the inland (Sun *et al.* 1990).

To identify the climatic factors that may influence beech dominance and species diversity in Chinese beech forests, the study reported in this paper was attempted to: describe the general trends in frequency and intensity of major climatic hazards in Chinese *Fagus* zone, which may cause canopy opening up in the beech forests; and characterize the relation between climate (temperature, precipitation and climatic hazards) and species diversity in Chinese beech forests.

3.2 METHOD

3.2.1 Study sites and transect sampling

Eight beech forests were selected along a thermal gradient in the Chinese *Fagus* range (Fig. 3.1; Table 3.1). Like all other Chinese beech forests, these beech forests developed naturally and lie in montane zones. They are deciduous broadleaved forests in the north and mixed evergreen and deciduous broadleaved forests in the south (Appendix 3.1).

In all eight forests, soils were yellow earth and yellow-brown earth according to Chinese soil classification and had a pH range of from 4.5 to 5.5 (Li & Sun 1990). According to the FAO-UNESCO (1988) soil classification they are dystic and gleyic Cambisols.

To examine the species diversity of these forests, I used own transect data and transect data given in the literature. The sources of the data and certain characteristics of these transects are given in Table 3.1. Own data were collected in Fanjingshan MAB Reserve in 1987, in Miao'ershan Nature Reserve in 1990 and in Daba Forest Station in 1991. Unpublished data collected by X.P. Wang *et al.* in Laoshan in 1982 were used. The data given in literature were collected in the 1960s (Huangshan & Kuankuoshui) and in the 1980s (Jiulongshan & Tianpingshan). These transects were established on mid-slopes, away from ridges or valley bottoms or very steep slopes. They were in mature forest stands dominated by beech and without evidences of felling or burning. Because of variation of beech forest patches in area and variation in the research aims in different studies, the areas of these transects varied from 300 to 2300 m². In every transect, the diameter at 1.3 m height of trees and shrubs taller than 5 m was measured.

3.2.2 Weather stations

Eleven weather stations located in montane zones between 1165 and 2065 m altitude in the *Fagus* range were selected to examine the occurrence of major climatic hazards (Fig. 3.1). Eight stations have records covering between 23 and 30 years (1950 to 1980). Three stations, i.e. Qixianshan, Xuefengshan and Bamianshan stations, have records covering between 9 and 10 years.

Table 3.1. Location, mean annual temperature (T_{mean}) and mean annual precipitation (PRCP) of each sampled forest site, area (projection) of every sample forest unit at a narrow altitudinal range of each site and data sources. The site codes have been used in Figure 3.1.

Name of Site	Code	Lat.	Longi.	Alt. (m, asl)	T_{mean} (°C)	PRCP (mm y ⁻¹)	Plot area (ha)	Number of transects	Source
Daba For. Station	D	32°42'	106°55'	1450	9.2	1500	0.20	3	current study
Mt. Huangshan	HS	30°08'	118°09'	1400	10	2100	0.15	1	Zhou 1965
Mt. Tianpingshan	T1	29°43'	110°	1600	9	1790	0.18	1	Qi 1990
Mt. Tianpingshan	T2	29°43'	110°	1150	11.5	1580	0.23	1	Qi 1990
Mt. Jiulongshan	J	28°18'	118°24'	1560	9.6	2000	0.20	5	Chen & Tang 1982
Kuankuoshui	K	28°14'	107°10'	1600	10.5	1400	0.18	2	Wang <i>et al.</i> 1965
Mt. Fanjingshan	F1	27°55'	108°45'	1785-1860	9-9.5	2550	0.20	5	current study
Mt. Fanjingshan	F2	27°55'	108°45'	1540-1700	10-11	2450	0.15	5	current study
Mt. Miao'ershan	M	25°50'	110°40'	1630	11	2300	0.18	1	current study
Mt. Laoshan	L	24°16'	106°14'	1540-1640	13.7	1660	0.12	3	unpubl. data, XP Wang

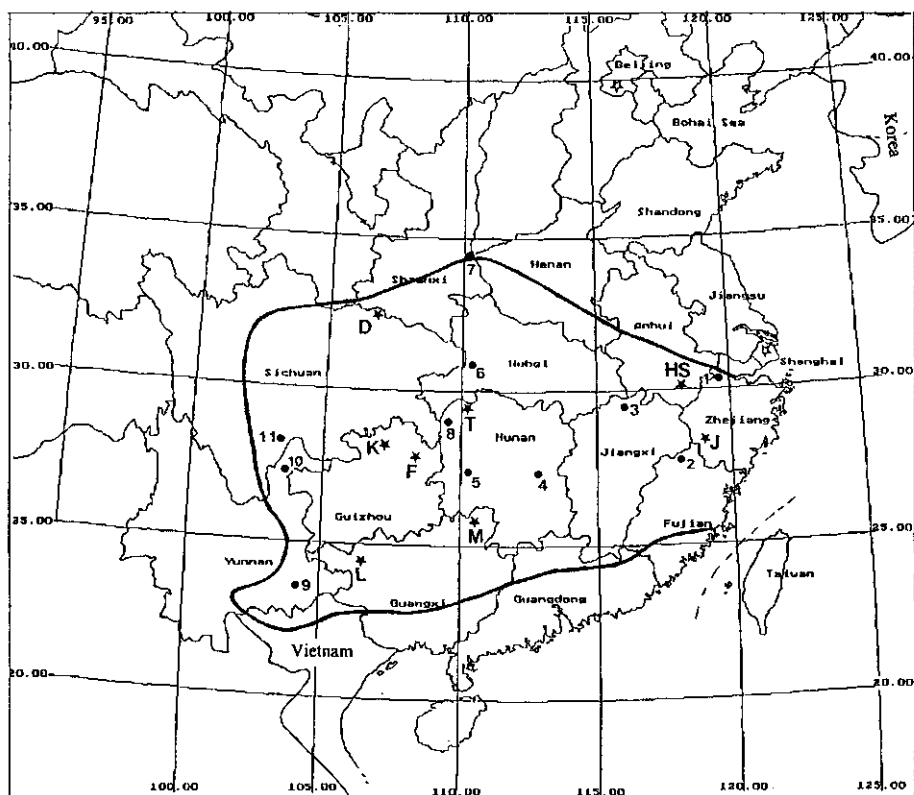


Figure 3.1. Approximate outline of the *Fagus* geographical range in China and northern Vietnam. In reality, *Fagus* distribution is very discontinuous. Geographical locations of eight beech forest sites (stars with code marks) and eleven weather stations (circles with code numbers). The codes for the study sites follow Table 3.1, and code numbers of the stations follow Table 3.3.

Data from three other weather stations, i.e. Huangshan, Laoshan and Daba, were only used for extrapolation of temperature and precipitation. These three stations are situated near the beech stands sampled in these sites. Laoshan and Daba stations are temporary and do not have sufficient records on climatic hazards. Huangshan station is located in an exposed and very windy site, so its data were not used for the analysis of climatic hazards.

3.2.3 Analysis of woody species diversity

In each of six sites, the transects covered a single narrow altitudinal range and the transect data were combined in the analysis. In each of the two remaining sites (T, F), the transects were combined in two narrow altitudinal ranges. Thus, the transect data from eight sites were combined into ten sample units. The Shannon-Wiener index H (Pielou 1975) was calculated for each unit:

$$H = -\sum(p_i \times \text{LOG}_2 p_i)$$

in which $p_i = (n_i/N + BA_i/TBA)/2$; n_i is number of individuals of a species and BA_i is its total stem basal area at breast high; N is the total number of individuals of all species and TBA is the total basal area at 1.3 m high of all species. Here, p_i was the relative importance value of a species, transformed to a percentage. In each sample unit, the sum of p_i of all deciduous species (IDE) was used to indicate the relative importance of deciduous trees, and the sum of the p_i of all light-demanding species (ILD) was used to indicate the relative importance of light-demanding trees. A combination of density, frequency and basal area is often used to measure the relative importance of a woody species in a forest community (Whittaker 1975). Plant frequency index greatly depends on quadrat-size (Crawley 1986) and is a useful index for forest communities whenever the sampling covers a substantially large area. As the sample units were relatively small in area, a combination of density and basal area was used in the analysis. For comparison with other studies, diversity index (H') was also calculated on the basis of plant density alone.

There was some variation in area among the ten sample units (Table 3.1). A extrapolation was done for the number of species and the diversity index H in the sample units smaller or larger than 0.20 ha. This was done by using conversion factors derived from the data on the five transects of Jiulongshan. The following regression equations were derived:

$$\begin{aligned} F_S &= -0.6285 \cdot \ln(x) - 0.0622 \\ (R_{\text{adj}}^2 &= 0.9843, p = 0.0005), \\ F_H &= -0.1277 \cdot \ln(x) + 0.7661 \\ (R_{\text{adj}}^2 &= 0.8857, p = 0.0109), \end{aligned}$$

in which x is the area of a sample unit in ha, F_S is the conversion factor for the number of species and F_H is the conversion factor of diversity index H when a sample unit was smaller or larger than 0.20 ha. The conversion factor for the number of species varied considerably with the area of a sample unit. However, the difference of the conversion factor for the diversity index H was small when the sample areas varied from 0.12 to 0.23 ha (Fig. 3.2). No extrapolation was done for the relative importance of deciduous trees or for the relative importance of light-demanding trees, because the changes were negligible. Neither was the H calculated solely from the number of individuals extrapolated, because this value was only used for comparison with other forests.

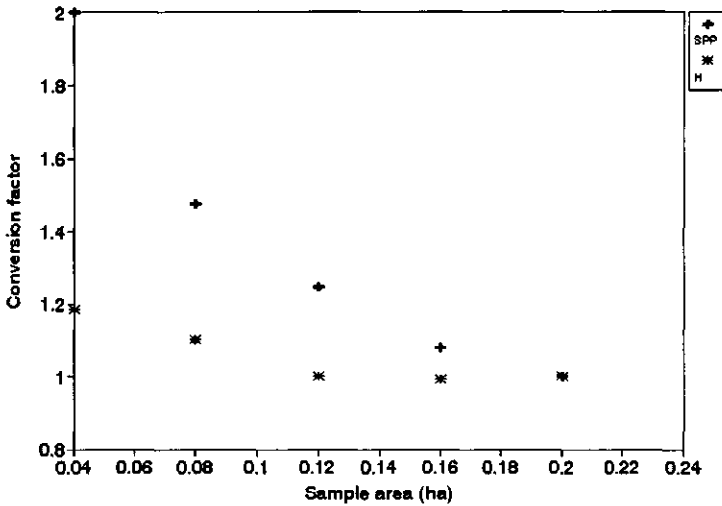


Figure 3.2. Conversion factors for number of species and diversity index H in relation to the area of combined transects of Jiulongshan.

3.2.4 Analysis of frequencies and intensities of climatic hazards

For the eleven weather stations, I compared maximum, minimum and annual average number of days with storms, freezing rains, freezing fogs, hails, thunderstorms and snowfall. Wind with a speed exceeding 17.2 m s^{-1} at any moment is regarded as a storm (Met. Info. Centre Beijing, 1984). The maximum thickness of ice accumulated during a continuing freezing rain or a freezing fog was also compared among stations. In China, 50 mm diel (24 hours) rainfall is regarded as the flooding threshold (Tao 1980). Therefore, the mean annual number of days with diel rainfall greater than 50 mm and the maximum amount of a diel rainfall were examined.

As the amount of snowfall was not recorded at the weather stations, I assessed annual snowfall at each of the eleven stations following Aber and Federer (1992). If the mean temperature (T_{month}) for a month is above 2°C , then all precipitation in that month is considered as rainfall. If T_{month} is below -5°C , then all precipitation is regarded as snowfall. When T_{month} is between -5 and 2°C , then:

$$\text{SnowFrac} = (T_{\text{month}} - 2)/(-7)$$

in which SnowFrac is the fraction of precipitation of a month falling as snow. In southern China, the average density of fresh snow is about $130 \text{ Kg} \cdot \text{m}^{-3}$ (Hé 1988). Thus, the assessed monthly snowfall (S_f) was calculated as:

$$S_f = \text{SnowFrac} \times P_{\text{month}} \times 1000/130$$

in which P_{month} = monthly precipitation; when T_{month} below -5°C , $\text{SnowFrac} = 1$. Of course this method cannot be used to assess snowfall in sites where snowfall actually occurs at mean monthly temperatures over 2°C .

3.2.5 Analysis of the relation between species diversity and climatic factors

For the analysis, mean annual temperature (T_{mean}) was used as the sole parameter of climatic warmth. In the Chinese *Fagus* range T_{mean} correlates closely with other thermal indices such as Kira's Warmth and Coldness indices or Thornthwaite's potential evapotranspiration (Chapter 2; Cao *et al.* in prep.). T_{mean} for the sites in Huangshan, Daba and Laoshan was extrapolated from the climatic data from the montane weather stations near the forest plots sampled. T_{mean} for the two plots in Tianpingshan was extrapolated from data from Bamingshan montane weather station, which is c. 120 km away in the southwest of Tianpingshan (Fig.3.1). T_{mean} for the site of Miao'ershan was extrapolated from unpublished data on Miao'ershan Nature Reserve, which were recorded at an altitude of 1200 m in the 1980s. T_{mean} for the remaining three sites was extrapolated from the data given in the literature per site (Wang *et al.* 1965; Chen & Tang 1982; Huang 1982). For T_{mean} extrapolation, a lapse rate of 0.55°C per 100 m altitude was used (Jiang 1991; Xu 1991). Using data from the same sources, annual precipitation was extrapolated for these study sites. T_{mean} and annual precipitation of the ten plots are given in Table 3.1. All these sites are in perhumid conditions with sufficient water supplied by precipitation throughout the year (Chapter 2; Cao *et al.* in prep.).

For the analysis, the parameters used for climatic hazards were the mean annual numbers of days on which storms, freezing rains, freezing fogs, snowfall, diel rainfall over 50 mm, thunderstorms and hailstorms occurred. Using the data from the eleven weather stations, the gradients of the mean numbers of such days were interpolated and mapped for the *Fagus* zone by means of SURFER software (the Kriging method; normal searching). Using these gradient maps, the mean numbers of such days were interpolated for the eight study sites (Appendix 3.2). Using the lapse rates given by Jiang (1991), these means were adjusted for the two sites (Tianpingshan & Fanjingshan) whose transects had been sampled at two narrow altitudinal ranges.

A preliminary correlation analysis showed that there were several interrelated climatic parameters, hence, I applied Factor Analysis to extract some common factors from them. Two common factors were extracted from the six climatic parameters. The factor 1 is mainly influenced by T_{mean} (negative) and the mean numbers of days per year (positive) with freezing rains, freezing fogs and snowfall (Table 3.2); and the factor 2 is mainly influenced by the mean numbers of days per year with storms and with diel rainfall over 50 mm. Bartlett's test of sphericity ($p = 0.0092$) and the Kaiser-Meyer-Olkin measure ($\text{KMO Measure} = 0.5948$) of sampling adequacy indicated that the factor extraction was appropriate.

The relations between the diversity indices (dependent variables: H, SPP, IDE, ILD) and the extracted common factors or individual climatic parameters (independent variables) were analysed by multiple linear regression. Partial correlation coefficients resulting from the regressions were used to show the degree of association. Analysis of the residuals suggested that the linear regressions were appropriate.

Table 3.2. Principal component analysis: factor loading (rotated) of two common factors extracted from mean annual temperature (T_{mean} : °C), mean annual days with occurrences of freezing rain, freezing fog, snow, storm and heavy rain (diel rainfall over 50 mm); eigenvalue of the two factors, and percentage of total variance explained by the two factors.

	Factor 1	Factor 2
T_{mean}	-0.8669	-0.1689
Freezing rain	0.8021	0.2505
Freezing fog	0.8768	0.4143
Snowfall	0.8776	0.0449
Storm	0.0341	0.8712
Heavy rain	0.3122	0.8461
Eigenvalue	3.5475	1.2247
Variance %	59.1	20.4

3.3 RESULTS

3.3.1 Trends in the frequency and intensity of climatic hazards

In the Chinese *Fagus* range, the areas near the coast experience storms more frequently than the western interior (Table 3.3; Fig. 3.3). Diel rains of over 50 mm are more frequent in the eastern and central areas than in the rest of Chinese *Fagus* range (Fig. 3.4). The frequency of thunderstorms increases towards the equator (Fig 3.5). However, I found no clear trend in thunderstorm frequency from east to west. Hailstorm occurs most frequently in the central part in the *Fagus* range (Fig.3.6).

Freezing rains and freezing fogs are most frequent and intense (thicker ice accumulation) in the centre of the *Fagus* range (Table 3.3; Figs. 3.7 & 3.8). Near the coast, freezing rains and freezing fogs are slightly less frequent than in the centre but are more frequent than in the western interior. The frequency of snowfall decreases from north to south (Fig. 3.9). The amount of annual snowfall in the *Fagus* range varies from 0 to 70 cm (Table 3.3). It is larger in the northeastern and central areas and absent from the southernmost parts (e.g. Wenshan & Laoshan).

3.3.2 Relation between species diversity and climatic factors

The diversity indices (H, SPP, IDE & ILD) of the ten sample units are given in Table 3.4. The regression analysis showed that H and SPP were related to the common factors, and ILD and IDE were related to individual climatic hazards. The diversity index H was strongly and negatively associated with the factor 1 and to a lesser degree was positively associated with the factor 2 (Table 3.5). This indicated that the diversity index H in the beech stands

Table 3.3. Comparison of major climatic hazards in the Chinese *Fagus* range. Stations are arranged from east to west. Code numbers have been used in Figure 3.1.^a

Code No. Station ^a Altitude (m)	1 Tianmushan 1497	2 Qianshan 1414	3 Lushan 1165	4 Nanyue 1266	5 Xuefengshan 1405	6 Lucongpo 1819	7 Hushan 2065	8 Bamianshan 1346	9 Wenshan 1246	10 Zhaoteng 1950	11 Leibo 1475
Storm	120.6	73.3	117.6	108.4	38.6	29		29.1	15	17.2	12
Freezing rain	89-160	50-107	84-168	26-152	20-97	4-85		9-44	0-66	0-11	3-25
mean days y ⁻¹	47.8	30.3	39.6	58.5	54.1	61.5	19.8	55.5	0	9.9	18.2
range	30-63		25-58	27-83	42-69	24-90	4-47	43-65	0	0-26	6-40
max. thickness of glaze (mm)	246		299	1200	648	711	124	448	0		57
Freezing fog	63.3	36.8	42.5	63.5	53	74.4	60.5	53.1	0	2.9	0.4
mean days y ⁻¹	47-90	24-57	25-67	41-88	40-66	51-98	37-86	35-44	0	0-6	0-3
range	153		93	350	90	272	9	10	0		
max. thickness of glaze (mm)	1.2	0.8	1	0.6	1.6	2.8	2.3	3.6	1.1	1.2	0.2
Hailstorm	0-3	0-5	0-4	0-3	0-3	0-8	0-9	2-6	0-4	0-4	0-1
mean days y ⁻¹	53.9	75.1	51	54.3	57.3	48.6	29.1	62.8	79.1	56	56
Thunderstorm	30-84	54-99	35-75	40-73	42-79	21-67	11-49	56-76	52-104	39-76	33-75
range	32.1	16.8	22.4	17.6	16.7	51.1	48.7	28.5	0.8	15.1	16.7
Snowfall	19-48	6-28	11-32	13-27	6-27	33-65	31-71	19-38	0-3	6-28	6-26
mean days y ⁻¹	70	2.2	23	25	30	69	20	23		20	0.4
range	3.7	7	6.7	6.4	5.6	6.4	1.7	4.4	1.3	0.5	0.7
Diel rain > 50 mm	218	241	330	340	219	192	120	125	148.6	93.2	92.6
Max. diel rainfall (mm)											

^a Climatic data from Xuefengshan station were recorded from 1971 through 1980, Bamianshan from 1971 through 1979, and the remaining stations from the 1950s through 1980 for 23-30 years (Met. Info. Centre Beijing, 1984).

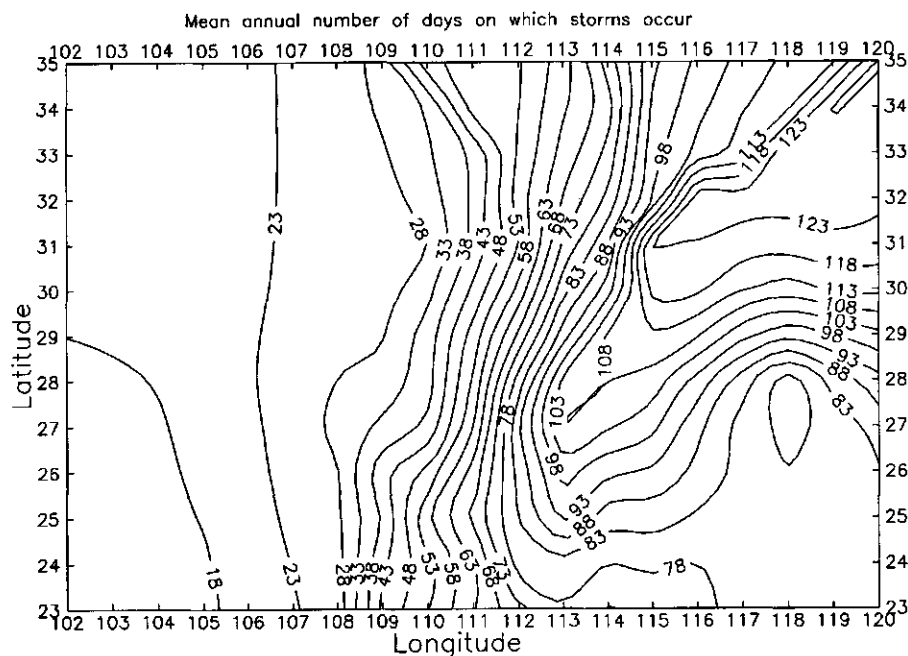


Figure 3.3. Distribution map of mean annual number of days on which storms occur in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

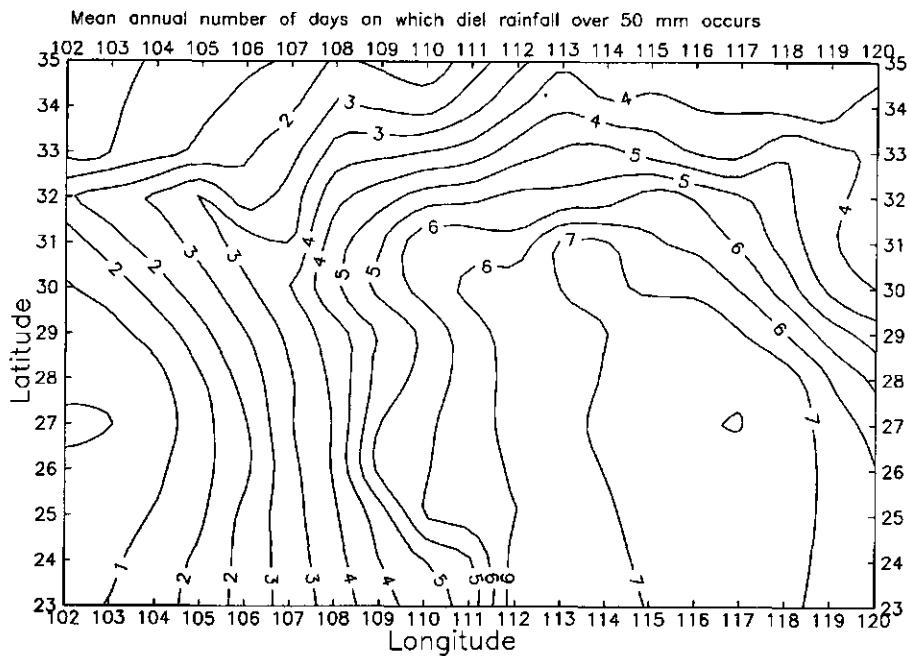


Figure 3.4. Distribution map of mean annual number of days on which diel rainfall over 50 mm occurs in the beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

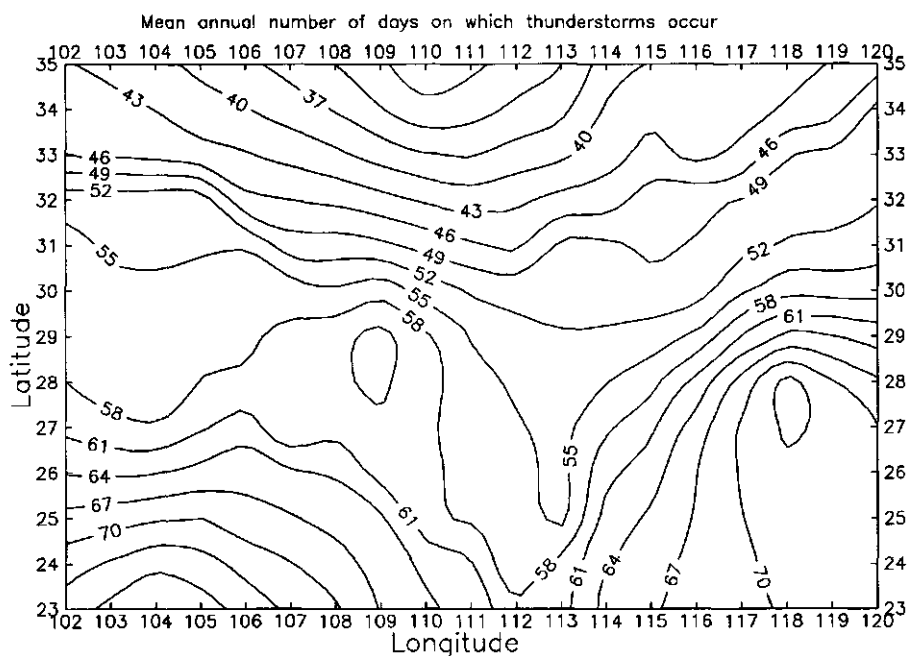


Figure 3.5. Distribution map of mean annual number of days on which thunderstorms occur in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

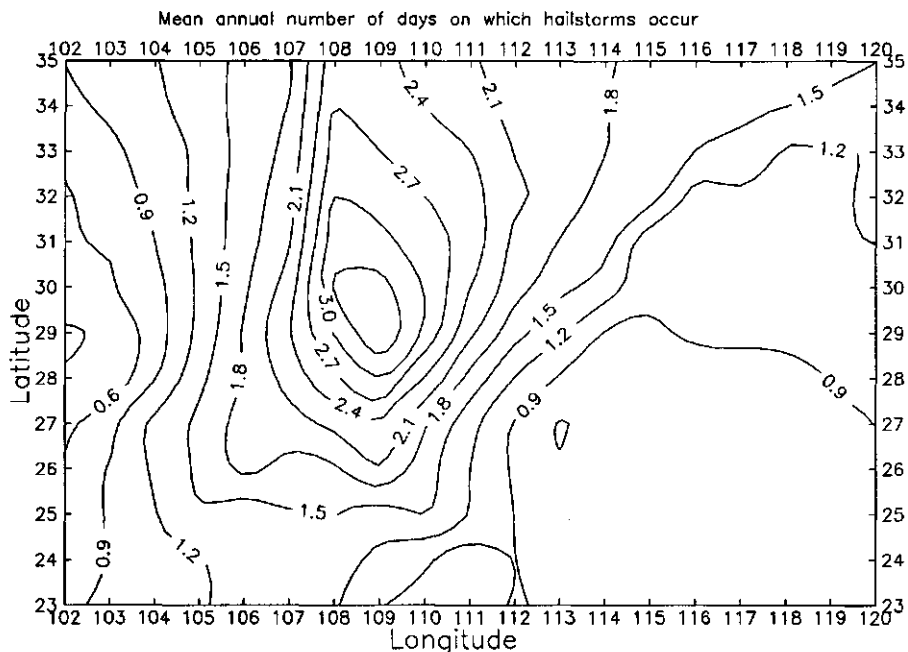


Figure 3.6. Distribution map of mean annual number of days on which hailstorm occurs in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

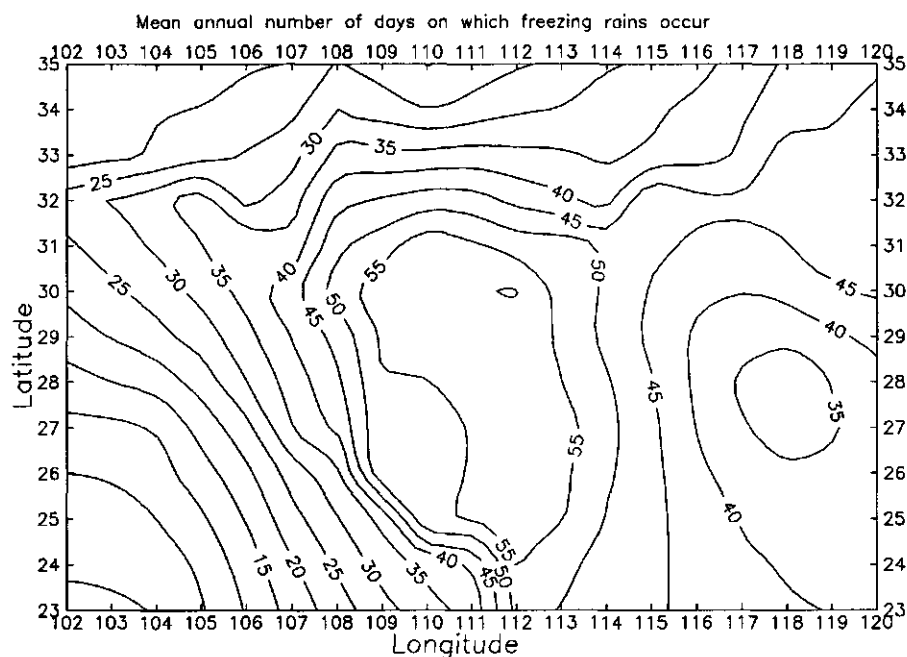


Figure 3.7. Distribution map of mean annual number of days on which freezing rains occur in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

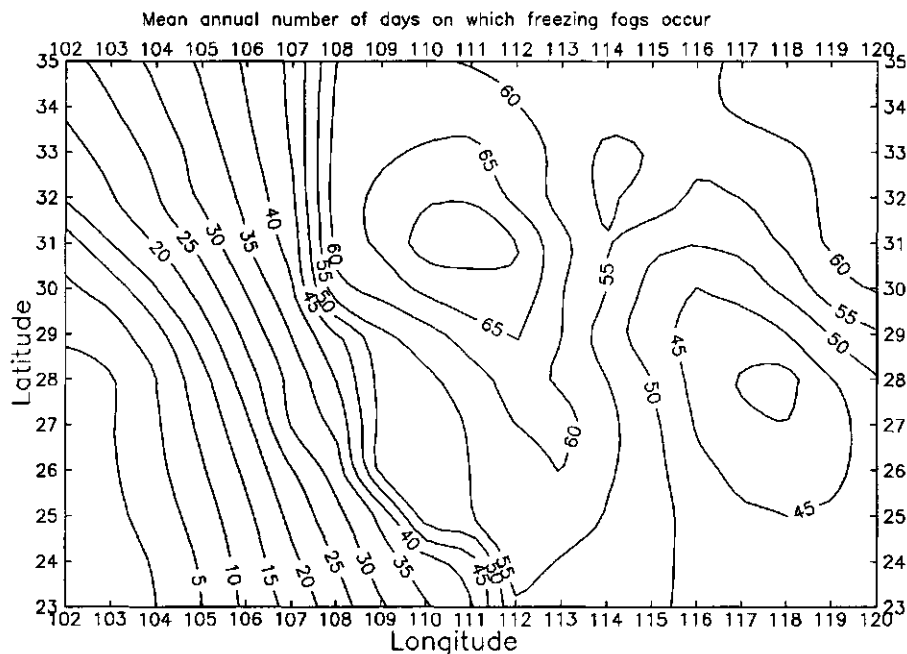


Figure 3.8. Distribution map of mean annual number of days on which freezing fogs occur in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

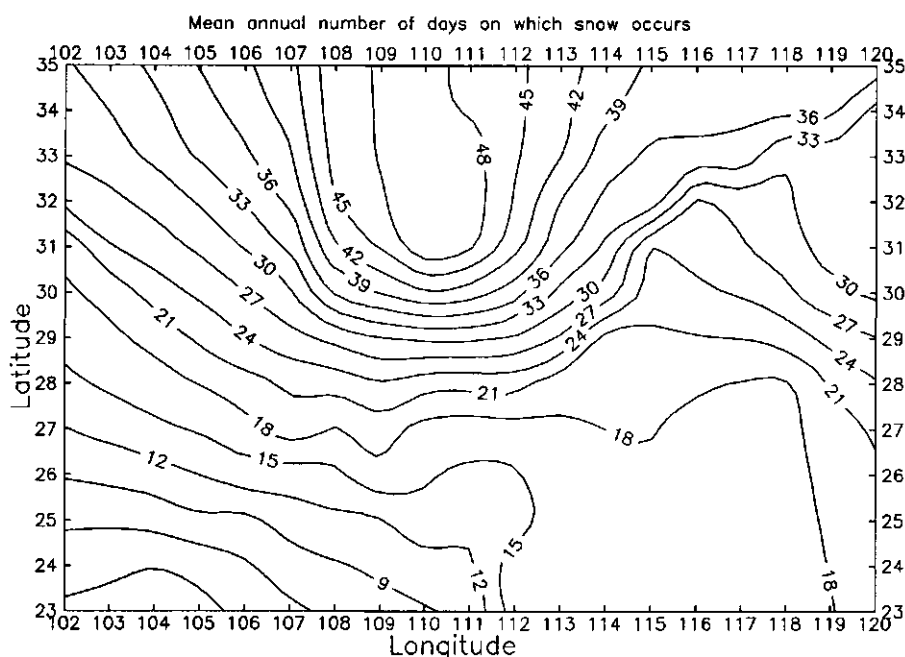


Figure 3.9. Distribution map of mean annual number of days on which snow occurs in the montane beech zones, interpolated from the data of 11 weather stations located between 1165 and 2065 m altitude.

Table 3.4. Number of species (SPP), total importance value of all deciduous trees and shrubs (IDE), total importance value of light-demanding trees (ILD), Shannon-Wiener diversity index (H) in the ten beech units. Data are original indices and indices (SPP' and H') interpolated to 0.20 ha.

Sites	Lat.	SPP	SPP'	IDE	ILD	H ^a	H' ^a	H ^b	
Daba	32.7	16		98	19	2.46		2.74	
Huangshan	30.1	20	23	97	27	3.91	3.94	3.93	coastal
Tianpingshan	29.7	18		87	12	1.94		2.84	higher altitude
Tianpingshan	29.7	44	38	59	24	4.68	4.46	4.55	lower altitude
Jiulongshan	28.3	56		31	22	4.48	4.43	4.36	coastal
Kuankuoshui	28.2	35	36	45	10	3.74		4.39	
Fanjingshan	27.9	19		39	4	2.88		2.96	higher altitude
Fanjingshan	27.9	24	24	53	13	3.46	3.49	3.95	lower altitude
Miao'ershan	25.8	28		27	5.5	4.22		4.43	
Laoshan	24.3	62	79	27	14	5.07	5.26	5.28	

^a calculated on the basis of combination of individuals and basal area.

^b calculated solely on the basis of individuals.

Table 3.5. Multiple linear regressions of relations between diversity index (H) or number of species (SPP) and two extracted factors, and the relations between the relative importance of light-demanding trees (ILD) or the relative importance of deciduous woody species (IDE) and individual climatic hazards (mean annual number of days with each of these hazards). Only the results with statistical significance are shown. The indices are interpolated according to the sample unit area of 0.20 ha. Data are partial correlation coefficients unless indicated otherwise.^a

	H	SPP	ILD	IDE
Regression with extracted factors:				
Factor 1	-0.930***	-0.887***		
Factor 2	0.673*			
Regression with individual climatic variables:				
Storms			0.837**	
Freezing rains			-0.755*	
Hailstorm			0.686 ^b	
Snowfall				0.870***
R_{adj}^2	0.844	0.760	0.592	0.726
p (model)	< 0.001	< 0.001	< 0.05	< 0.001

^a Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ^b $p = 0.0603$.

primarily increases towards warmer climates (see factor loading, Table 3.2); to a lesser degree it increases towards the areas with more frequent storms and heavy rains. The diversity index was not related to annual precipitation, nor to mean annual number of days with hailstorm or with thunderstorms.

The number of species in the sampled stands was found to be strongly and negatively related solely to the factor 1 (Table 3.5). Thus the number of species in the stands increased towards warmer climates. The relative importance of light-demanding trees was related to the annual number of days of storms (positive) and of freezing rains (negative; Table 3.5). The relative importance of deciduous trees was positively related solely to mean annual number of days with snowfall (Table 3.5). None of the diversity indices (H, SPP, IDE & ILD) were related to annual precipitation.

3.4 DISCUSSION

3.4.1 Trends of major climatic hazards in the *Fagus* range

Storms and the heavy rains occurred more frequently in the east than elsewhere in the Chinese *Fagus* range (Table 3.3, Figs. 3.3 & 3.4) because the eastern area is exposed to tropical cyclones. Between 1951 and 1980, 210 cyclones in total hit China, 43 of which had wind speeds between 17.2 and $24.4 \text{ m} \cdot \text{s}^{-1}$, 64 had wind speeds between 24.5 and $32.6 \text{ m} \cdot \text{s}^{-1}$, and 103 had wind speeds exceeding $32.6 \text{ m} \cdot \text{s}^{-1}$ (Feng *et al.* 1985). These tropical cyclones

usually hit the coastal southeastern China, and generally penetrate 500 km inland on average (Chai 1990). Based on Feng *et al.* (1985), I estimated that about 30-40% of these cyclones probably hit the eastern area of the *Fagus* range. However, cyclones often bring heavy rainfall and occasionally induce tornadoes and hailstorms, not only in the areas directly in their path but also in the surrounding areas (Tao 1980; Zhu 1988). Therefore, heavy rains and tornadoes also occur more often in the east than in the west of southern China (Sun *et al.* 1990). Although tornadoes usually occur locally, they are usually very destructive. Tornadoes also occur in the western regions, e.g. in Jin'yunshan Nature Reserve (29°50'N, 106°26'E; Cornelissen 1993) and in Jiuwanshan Forest Station (25°18'N, 108°49'E) in Northwestern Guangxi (pers. comm., P.S. Wei).

In the mountainous areas of eastern China, heavy rainfall of over 100 mm during 24 hours has the power to cause landslides and mud-flows, even in forested sites (Sun 1988; Zhu 1988; Liu & Xu 1991). In the eastern area of the Chinese *Fagus* range, diel rainfalls of over 300 mm have been recorded (Table 3.3). The heavy rains can certainly cause single or multiple tree-falls, due to waterlogging plus strong winds (Liu & Xu 1991; Zhou *et al.* 1991).

Freezing rains and freezing fogs occurred more frequently and more intensively in the middle and lower reaches of the Chang-Jiang (Yangtze) River than elsewhere in the *Fagus* range (Table 3.3; Figs. 3.7 & 3.8). Freezing rain, freezing fog, and snowfall may occur together or consecutively, which increases ice load and so becomes more destructive (Jiang 1991). These cold hazards occasionally cause severe damage to forests throughout a large area (e.g. Wang 1984, in southern Hunan). Compared to freezing fogs, freezing rains usually accumulate on plants with a thicker and denser ice layer, and remain longer (Jiang 1991). Therefore, freezing rains are usually more destructive to forests than freezing fogs.

The increasing frequency of thunderstorms towards lower latitudes in the Chinese beech zone (Fig. 3.5) is in accordance with the world-wide trend of thunderstorms (Nieuwolt 1977; Bryant 1991). The frequency of thunderstorms in the Chinese beech zone is comparable to that in some tropical regions (Nieuwolt 1977). Lightning during thunderstorms killing canopy trees and thus creating canopy gaps has been reported in tropical rain forest in Borneo (Brünig & Huang 1989). In mountainous areas of Great Xiang'an and Lesser Xiang'an in Northeastern China, many forest fires, up to 30% of forest fires in some boreal forests, are triggered by lightning (Ge 1990; Zhang *et al.* 1991). But lightning is an unlikely cause of forest fires in the humid forests in southern China (Zhang *et al.* 1991). There, trees killed directly by lightning have been observed (pers. comms. Prof. X.P. Wang, X. Ling, an old inhabitant near Miao'ershan).

Hailstorm is most frequent in the central part in the *Fagus* range (Fig. 3.6). It is intense in the Yunnan-Guizhou Plateau (Xu 1991; Zhang *et al.* 1991) and in the southern provinces such as Fujian, Guangdong and Guangxi (Lu *et al.* 1991). In the Yunnan-Guizhou Plateau, single hailstones weighing over 8 kg have been recorded (Xu 1991). Close to extensive beech forests on Mt. Fanjingshan, a hailstorm severely damaged a *Tsuga chinensis* stand (pers. comm. C.D. Yang). In the long run, hailstorm influences the Chinese beech forest dynamics in some areas.

To sum up, storms, freezing rains, freezing fogs, snow storms and heavy rains can cause forest canopies to open in the Chinese beech forests at the levels of forest patches and forest mosaics. Storms and heavy rains are more frequent and intense in the east than elsewhere in the Chinese *Fagus* range. Freezing rains, freezing fogs and snowstorms were found to be rare in the southernmost parts; they are more frequent and intense in the central and the northeastern areas than in the rest of the *Fagus* range. Hailstorm and lightning seem to have minor impacts on Chinese beech forests.

3.4.2 Relation between warmth and species diversity

One of the major rules in biogeography is that species diversity increases towards warmer climates or towards lower latitudes (Whittaker 1975). This is confirmed by Chinese beech forests. Compared to other beech forests in the Northern Hemisphere, Chinese beech forests in the southern subtropics have a greater diversity (Table 3.6), comparable to the diversity of some tropical rain forests (Table 3.6). Great species diversity in the Chinese beech forests is also favoured by the floristic history. In southern China, the lowlands and certain mountain valleys remained largely unaffected by the glaciers during the Ice Ages. Hence many tropical, subtropical and temperate plants survived in these areas during then (Wu 1980; Zhong *et al.* 1988; Qi 1990). Indeed, many subtropical and tropical trees are associated with Chinese beeches in the southern areas (Appendix 3.1).

A positive relation was found between the importance of deciduous trees and the mean annual days with snowfall (Table 3.5). The temperature minimum in winter is the major factor controlling the distribution of evergreen broadleaved trees (Sakai & Larcher 1987). In Japan, most evergreen broadleaved trees cannot tolerate cold extremes below -15°C (Sakai 1975). In the Chinese *Fagus* range, the mean snowfall frequency increases with latitude. In that range as elsewhere in the northern hemisphere, the further to the north, the greater the probability of occurrence of a low temperature harmful to evergreen broadleaved trees in

Table 3.6. Comparison of number of woody species (SPP) and Shannon-Wiener index (H) of Chinese beech forests with those of other forests. In this table, H has been calculated solely on the basis of individuals. Contrary to Table 3.4, SPP and H in this table were not interpolated.

Forests	Area(ha)	Size limit	SPP	H
Chinese beech forests	0.12-0.23	>5m high	16-62	2.74-5.07
American beech forests ^a	0.15-0.24	>5m high	13-19	1.46-3.17
Japanese beech forests ^a	0.25-0.32	>5m high	14-38	0.88-2.94
Mexican rain forest ^b	0.25	DBH > 3.3cm	61-78	3.65-4.76
Rain forest in Puerto Rico ^c	0.72	DBH > 4cm	51	4.0

Data sources: ^a modified from Peters (in prep.); ^b from Bongers *et al.* (1988); ^c from Crow (1980).

winter, because of the greater exposure to cold continental winds. In the northernmost study site, Daba, a temperature minimum of -22.5°C occurred within a three-year period with climatic records (unpubl. data, Daba For. Station). There, the beech forest was almost completely composed of deciduous broadleaved trees (Table 3.4), with only some small evergreen trees and shrubs in the understorey. In the Chinese *Fagus* range, there are sites with a similar T_{mean} , but the further south (i.e. in the higher altitudes) the more important evergreen trees become in the mixed beech forests (Tables 3.4 & 3.5). This is probably explained by the temperature minima in winter (Sakai & Larcher 1987).

3.4.3 Species diversity in the beech forests was not related to precipitation

Although mean annual precipitation varies from 1500 to 2550 mm among the beech sites (Table 3.1), the species diversity of these sites did not correlate with this precipitation. In neotropical forests, Gentry (1982) found a positive correlation between species richness (in per 1000 m^2 plot) and rainfall for trees with a diameter above 2.5 cm, but no correlation for trees above 10 cm diameter. In the West African rain forests, Van Rompaey (1993) showed a decrease of species richness of large trees ($d > 70$ cm) with increasing rainfall. The lack of association between species diversity of Chinese beech forests and amount of precipitation is probably attributable to all these forests living in perhumid climates and all enjoying sufficient water supply throughout the year from precipitation (Chapter 2).

3.4.4 Relation between species diversity and climatic hazards

The species diversity of Chinese beech forests increased towards the areas in the east where storms and heavy rains occur more frequently (Figs. 3.3 & 3.4.; Tables 3.4 & 3.5). Also the importance of light-demanding trees of the forests increased towards the more stormy areas. This appears to support Connell's (1978) hypothesis: species diversity should be greatest in the forests where 'disturbances' are of intermediate frequency and intensity; in a little 'disturbed' site the forest has a low diversity and is dominated by long-lived and shade-tolerant tree species; in a frequently or intensively 'disturbed' site the forest has a low diversity and is dominated by short-lived and light-demanding trees.

Indeed, the low diversity in the inland beech forest of Daba (Fig. 3.10; Table 3.4) coincides with a low degree of impacts by climatic hazards (Table 3.3). Here the forest is dominated by *Fagus hayatae* var. *pashanica* and *Fagus engleriana*. In Europe, *Fagus sylvatica* is the most shade-tolerant among deciduous broadleaved trees (Ellenberg 1988). I assumed that the two beech species in Daba are probably the most shade-tolerant deciduous trees in the forest. Storms and heavy rains are less frequent and less intense in this interior region than in the eastern areas (Table 3.3; Figs. 3.3 & 3.4).

In a similar T_{mean} , but being exposed to more frequent storms, the beech forests near the coast have much greater diversity and are composed of larger numbers of light-demanding and intermediate trees than those in the western inland (Table 3.4; Fig. 3.10). On Mt. Huangshan near the coast, the light-demanding trees *Magnolia cylindrica*, *Prunus serrulata*, *Quercus stewardii*, and the intermediate *Castanea seguinii* are important in the montane

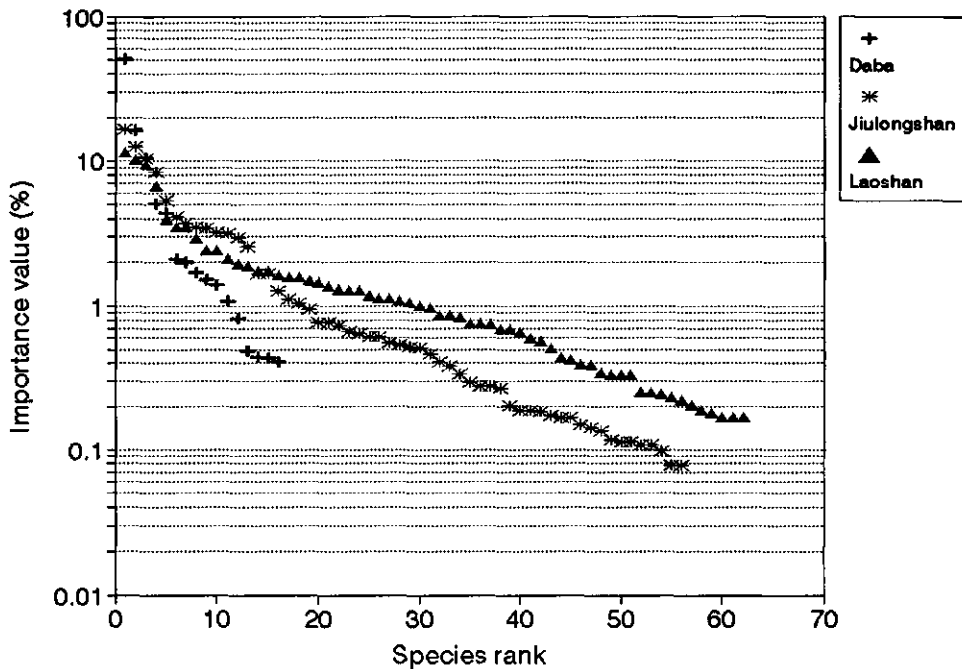


Figure 3.10. Dominance-diversity curves of three beech forests. In Laoshan, the southernmost site, the forest was the most species-rich. With a similar mean annual temperature, the forest in Jiulongshan near the coast had a greater diversity than the forest in Daba in the northwest of the beech range. The sample area was 0.12 ha in Laoshan, and 0.20 ha in both Jiulongshan and Daba.

mixed *Fagus engleriana* forest (Appendix 3.1; Zhou 1965). On Mt. Jiulongshan also near the coast, light-demanding *Liriodendron chinensis*, *Magnolia cylindrica* and intermediate *Schima argentea* are co-dominants in the mixed *Fagus lucida* forest (Appendix 3.1; Chen & Tang 1982).

Other work has demonstrated a positive relation between species diversity or importance of light-demanding trees in forests and frequency of storms. In northern Florida, the beech forests experience rather frequent storms; light-demanding trees such as *Liquidambar styraciflua* and *Pinus glabra* are important in these forests (Peters & Poulson 1994; Peters & Platt in prep.). Mexican rain forest in Los Tuxtlas has a lower species diversity than other tropical rain forests because the forest is relatively less disturbed (Bongers *et al.* 1988).

If Connell's (1978) hypothesis were true, the great diversity of Chinese beech forests near the coast implies that impacts of climatic hazards, particularly storms, in these forests are

neither very intense nor very frequent. Otherwise, these forests would have a low diversity. The best example of a forest that has a relatively low diversity because of being intensively and frequently influenced by storms is a tropical rain forest in Puerto Rico (Crow 1980), which is hit by hurricanes once every 10 years on average (Basnet 1993). Although tropical cyclones hit southeastern China six or seven times each year on average, most of them pass over southernmost China, which is outside the *Fagus* range. The Chinese beech forests near the coast are indeed probably exposed to "intermediate" impacts of climatic hazards.

The species diversity of Chinese beech forests was found to be negatively related to the cold hazards, i.e. freezing rains, freezing fogs and snowfall (Table 3.2). These cold hazards are closely related to the temperature of a site. More frequent occurrence of these cold hazards implies a lower temperature of a site and hence a lower diversity. The physical impacts of these cold hazards upon trees are somewhat different from those of storms and heavy rains. Heavy rains and destructive storms such as intense cyclones and tornadoes mainly occur during the growing season, when all trees are in leaf. Ice storms and snow storms occur in winter or in early spring, when deciduous trees are leafless. Wang (1984) and Hé (1988) reported that evergreen broadleaved trees are more sensitive to ice and snow load than deciduous hardwoods. In the beech forest of Miao'ershan, I observed that exposed evergreen broadleaved trees, both in the canopy and in canopy gaps, had small and broken crowns. Also, the fast growing deciduous trees *Liquidambar acalycina* and *Sassafras tzumu* often had broken crowns. The broken branches are probably caused by ice storms and snow storms. Broken branches allow access to wood-rot fungi and cause branches and trunks to rot (Shigo 1986). I observed that in the beech forest in Miao'ershan about 60 to 70% *Castanopsis lamontii* trees in the overstorey had rotten trunks.

In contrast to the evergreen broadleaved trees, *Fagus lucida* canopy trees usually have large unbroken crowns in the forest. The reasons for the relative resistance of the beeches to ice or snow breakage are: (1) by comparison with some evergreen broadleaved trees or fast-growing deciduous trees, slow-growing beeches have a denser wood and are therefore physically stronger; (2) evergreen broadleaved trees with leaves in the winter carry a heavier load, accumulating more ice or snow plus the weight of their own leaves, than deciduous trees during an ice or snow storm. In the montane zone of Mt. Tianpingshan, *Fagus lucida* crowns form extensive mono-specific forest canopies (Qi 1990). This site (cf. Bamianshan Station, Table 3.3) receives relatively frequent and intense glaze storms. The negative relation between the importance of light-demanding trees and the mean frequency of freezing rains (Table 3.5) could be explained by the sensitivity of many fast-growing, light-demanding trees to freezing rains. It appeared that the cold hazards favour a limited number of trees in dominance of forest overstories (Downs 1938; Wang 1984; Hé 1988).

Although I did not find statistically significant relations between species diversity and frequency of thunderstorms or hailstorms, these climatic hazards probably affect the Chinese beech forests to some extent.

This study only used average frequencies of the climatic hazards to analyse their relation to the species diversity. In fact, the extremes of these climatic hazards are more important. The annual means do not give sufficient information about intensities of freezing rains, freezing fogs and snow storms. For example, there are sites with a similar mean annual number of days of freezing rain or freezing fogs, but the maximum number of such days or the

maximum thickness of ice accumulation still vary largely among these sites (Table 3.3). Likewise, a similar mean frequency of snowfall may hide a different amount of snowfall and different snow depth. Also, the topography of a site may affect the frequency and intensity of occurrences of some climatic hazards. In the same geographical area or even on the same mountain, some sites are more sheltered than others, so impacts of climatic hazards on the forests do indeed vary locally. To analyse the relation between species diversity of forests and the climatic hazards that open up the forest canopies, the quantification of intensities of the hazards needs further investigation.

Based on the findings of this study, it becomes clear that statistical modelling on tree species distribution (e.g. Austin 1992) and species composition of natural forests in relation to climate should not only take heat and moisture into account but also climatic hazards.

3.5 CONCLUSIONS

Storms, heavy rains, freezing rains, freezing fogs and snow storms seem to be the major climatic factors that can open up forest canopies of Chinese beech forests at the levels of forest patches and forest mosaics. Storms are more frequent and intense in the east than in the west of the Chinese beech range. Heavy rains are more frequent and more intense in the eastern and central areas than in the rest. Freezing rains, freezing fogs and snowfall are most frequent and intense in the middle and lower reaches of the Chang-Jiang River (the Yangtze River) in the *Fagus* range. Hailstorms are most frequent in the centre. Thunderstorms increase towards lower latitudes. Hailstorms and lightning seem to have minor impacts on the Chinese beech forests.

Climatic heat and climatic hazards are key factors affecting the dominance and species diversity in Chinese beech forests. The species diversity of Chinese beech forests increases towards warmer climates, and towards the coast, where storms and heavy rains occur more frequently and more intensely. The relative importance of deciduous broadleaved trees in the beech forests decreases towards the areas with less snowfall. The relative importance of light-demanding trees in the forests is positively related to the frequency of storms but negatively related to frequency of freezing rains. Both evergreen broadleaved trees and deciduous light-demanding trees are susceptible to freezing rains, freezing fogs and snow storms. Beech was found to be relatively resistant to these cold hazards because of its deciduous habit and dense wood. Hence, the cold hazards negatively affect the species diversity of Chinese beech forests. Precipitation did not correlate to the species diversity of Chinese beech forests as all these forests are in perhumid conditions.

Climatic hazards were shown to be important in the dynamics and in the maintenance of the species diversity of Chinese beech forests. To conserve biodiversity, nature reserves should be established to cover a range of sites with different frequencies and intensities of natural hazards, to enable most of the associated species adapted to the related environments to be conserved.

Chapter 4 Regeneration sites and population structures of *Fagus lucida* and *Fagus hayatae* var. *pashanica* in two Chinese beech forests

4.1 INTRODUCTION

Natural regeneration is a crucial process for a tree species to maintain a population in the forest community. It involves the establishment and survival of its juveniles in the forest. The site requirements for a tree's regeneration depend on the tree's temperament (Grubb 1977; Oldeman & van Dijk 1990). The sites themselves are regulated by many abiotic (e.g. light, soil water and nutrient) and biotic factors (e.g. competition, grazing) and their interactions (Bormann & Likens 1979; Oliver & Larson 1990). In turn, these are largely affected by species composition and architecture of forests, e.g. via shading and competition.

Chinese beech forests in the northern and southern parts of their ranges differ in their tree species composition (Appendix 3.1). In the northern areas, canopy beeches grow among deciduous broadleaved trees. In the southern areas, canopy beeches are associated with evergreen broadleaved trees. Important differences between evergreen and deciduous broadleaved trees are crown density (Kira & Shidei 1967) and leaf longevity. These affect light climate in the understorey, and thus influence the chances for juvenile trees to establish themselves in forests. Further, different combinations of tree species in forests may affect the relative performance of dominant species, e.g. the growth rate and relative shade-tolerance of beech vs deciduous and beech vs evergreen in Chinese beech forests. This also influences the establishment of seedlings and the survival of saplings in forests.

All Chinese beech forests grow on mountains (Chapter 2; Wu 1980; Cao *et al.* in prep.). The micro-climates and certain soil properties vary along a toposequence from ridge and upper and lower slopes (van Rompaey 1993). The micro-climate usually varies with slope aspects (Weng & Luo 1990). This site and micro-climate heterogeneity affects the relative chances of forest trees establishing and surviving in the sites.

Several authors have reported that beech regeneration is poor in Chinese beech forests in the southern areas (Wang *et al.* 1965; 1983; Chen & Tang 1982; Yuan & Cao 1983; Zhu & Yang 1985; Qi 1990). However, the seedlings and saplings of evergreen co-dominants are common in these beech forests. My observations in several sites confirmed that beech seedlings and saplings are rare here. This raises the question of where the juvenile Chinese beeches establish themselves and survive in the southern beech forests. Beech regeneration in northern part of the Chinese *Fagus* range (e.g. Daba) was observed being more abundant than in the southern areas (pers. obs.). This study compared beech regeneration sites in a southern beech forest with those in a northern beech forest.

The study described in this paper aimed to describe suitable regeneration sites for *Fagus hayatae* var. *pashanica* in a northern area and for *Fagus lucida* in a southern area of the Chinese *Fagus* range. For this research, regeneration sites were defined as sites where juvenile trees (seedlings and saplings) succeed in establishing and surviving. Further, it aimed at analysing differences in types and availability of beech regeneration sites in the northern and southern beech forest, and the presence of juveniles of other canopy or subcanopy tree species in the regeneration sites.

4.2 METHODS

4.2.1 Study sites and time of field work

The study was conducted in two Chinese beech forest sites, i.e. Daba Forest Station in the north (32°42'N, 106°55'E) and Miao'ershan Nature Reserve in the south (25°50'N, 110°49'E; Fig. 4.1) of the Chinese *Fagus* range. The field work was done in the growing season mainly in 1992 in both sites. Some data were collected in 1991 in Daba and in 1990 and 1991 in Miao'ershan. The northern site is a mixed deciduous beech forest and the southern site is a mixed deciduous and evergreen broadleaved forest (e.g. Figs. 1.1-1.2; Appendix 3.1). The northern site is in a mountain complex which is in the western part of the Daba mountain range which runs east-west. The southern site is also in a mountain range running east-west, being a part of Nanling mountain range.

In both sites the beech forest occurs in the montane zone between 1300 and 1900 m altitude. The soils in both sites have developed mainly from granites, shales and sandstones, and are characteristically clayey loam soils with a pH of 4.5-5.5 (Guiling For. Dept. 1979; Anon. 1980). According to the FAO-UNESCO (1988) soil classification they are Cambisols. Annual temperature and precipitation were estimated for both sites, extrapolating from the climatic data recorded between 1990 and 1991 at montane station (1400 m asl) close to the beech forest of Daba and from the unpublished climatic data recorded in 1980s at a site (1200 m asl) near the beech forest of Miao'ershan. In Daba the annual temperature in the beech zone ranges from 6.5 to 10°C and the annual precipitation is about 1500 mm; in Miao'ershan the annual temperature is between 9 and 12.5°C and the annual precipitation is c. 2300 mm.

The main tree species in the beech forest in Daba are *Fagus hayatae* var. *pashanica*, *F. engleriana*, *Carpinus cordata* var. *chinensis* and *Quercus aliena* var. *acuteserrata*, and in Miao'ershan are *Fagus lucida*, *Castanopsis lamontii*, *lithocarpus hancei* and *Manglietia chingii* (Wang & Li 1986). In each site, regeneration sites and population structures of these main species were studied except *F. engleriana* in Daba because of lacking of its juveniles of seed origin. The variety names are omitted in the following text.

In both sites, the beech forests usually have a undergrowth of bamboos. In Daba, the main bamboo species in the beech forest are *Indocalamus latifolius* which is about 1 to 2 m tall, and *Arundinaria fargesii* which is about 3 to 4 m tall. In Daba, stands with patches of dead bamboo were regularly found; the bamboo was probably killed mainly by extreme cold, ice and snow storms in winter (pers. comm, Y Zhao). In Miao'ershan, the main bamboo species in the beech forest are *Indocalamus longiauritus* which is about 1.5 to 2 m tall, and *Indosassa shibataeoides* which is about 4 to 5 m tall (Figs. 4.3 & 4.7). *Indocalamus longiauritus* usually covers the forest floors in the upper slopes and ridges. *Indosassa shibataeoides* mainly covers the middle and lower slopes, valleys and flat sites.

In both sites, until the 1940s, forest fires were used to prepare ground for pasture. In Miao'ershan, abandoned fields with low vegetation or invaded by beech and other trees still persist. In Daba, most such abandoned fields have been planted with pines. Evidence of felling was occasionally observed in both sites during the field work. However, the study plots were selected in stands without traces of burning or other human influences.

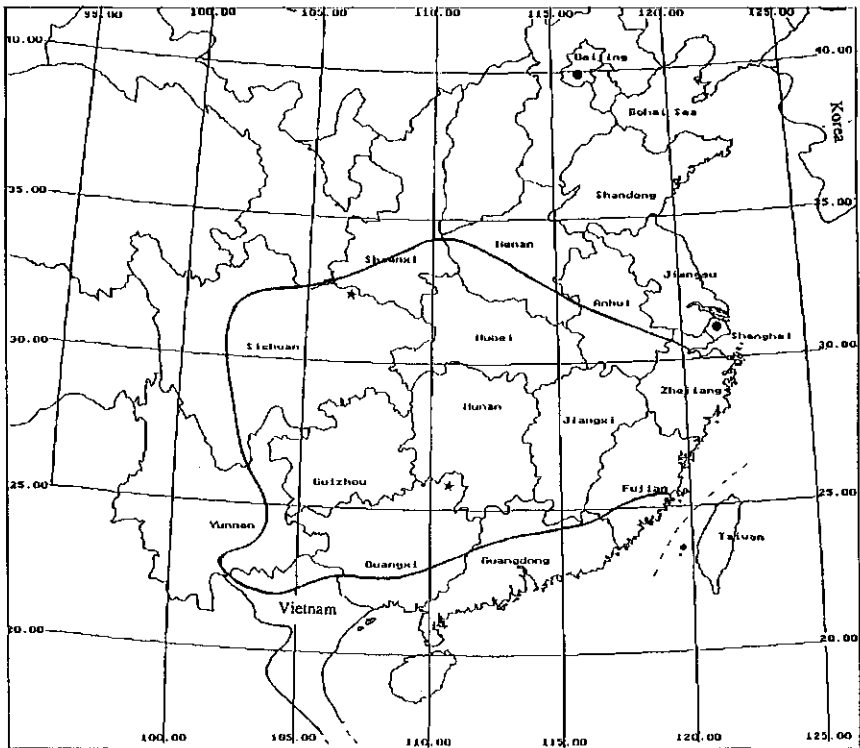


Figure 4.1. Approximate outline of the *Fagus* geographical range in China and northern Vietnam. In reality, *Fagus* distribution is very discontinuous. Geographical locations of two study sites (stars): Daba Forest station in the north and Miao'ershan Nature Reserve in the south.

4.2.2 Working definitions

Juveniles shorter than 0.5 m of overstorey or subcanopy species were regarded as seedlings, and juveniles between 0.5 and 5 m tall as saplings. Tall trees that had reached their full height at a given site and could no longer be suppressed by surrounding trees were classed as overstorey canopy trees. Trees that still had a potential in height growth and had not reached their full height at a given site were termed potential trees. Thus, potential trees included seedlings, saplings and trees of a pole phase in the case of overstorey or subcanopy species.

To describe regeneration sites in forest mosaics, I applied the term eco-unit (Oldeman 1983, 1990). An forest eco-unit is defined as a forest patch on which at one moment in time a vegetation has begun, of which the architecture, ecological functioning and species composition are ordained by one set of trees until the end (Oldeman 1990). I roughly classified the developmental phases of forest eco-units into growing, mature and degrading phases. In a growing phase, height growth was important for an eco-unit and the eco-unit

was dominated by potential trees. Growing eco-units were divided into two sub-groups, i.e. shorter than 5 m and taller than 5 m. In a mature eco-unit, the dominating trees had reached the forest overstorey and could no longer be suppressed by neighbouring crowns. In the study areas, forest overstorey height varies along a slope, usually being between 10 and 12 m on ridges and between 20 and 25 m on slopes in both sites. In a degrading eco-unit, the dominant trees were senescent.

In the beech forests of Miao'ershan I classified mature forest eco-units into beech, evergreen and mixed eco-units. In Daba, mature forest eco-units were classified into those dominated by beeches, those dominated by other deciduous tree and those dominated by a mixture of beeches and other deciduous broadleaved trees.

4.2.3 Regeneration site survey

During the field work in both sites, a general survey was conducted to gather information on overall species presence in the forests. During the surveys, sites with abundant seedlings and saplings of the dominant species were particularly noted. To describe the regeneration sites in detail, four strip transects (10 m wide) with a total (projection) area of 1.04 ha in Daba and two such transects with a total area of 0.57 ha in Miao'ershan were established. The strip transects were sampled from ridge to valley bottom. The length of each transect depended on the length of the slope being surveyed. In Daba, a 10 x 800 m transect which sometimes crossed small ridges was established on a long continuous northeast-facing slope ranging from 1400 to 1860 m altitude. The other three transects in Daba were 10 x 50 m between 1600 and 1640 m altitude on a north-facing slope, 10 x 150 m between 1350 and 1430 m on a west-facing slope and 10 x 200 m between 1450 and 1560 m on a southeast-facing slope. In Miao'ershan, a 10 x 400 m transect was established on a southwest-facing slope between 1320 and 1500 m altitude on the southern flank of the mountain. Another transect of 10 x 200 m was located on a north-facing slope between 1650 and 1740 m altitude on the northern flank of the mountain.

The central line of each strip transect was made to run perpendicular to contour lines and was oriented with a compass. Along the central line in each strip transect, eco-unit types and developmental phases were distinguished according to species composition and height of the vegetation. In each eco-unit, the vegetation height, canopy coverage and dominant species of different vegetation layers (overstorey and understorey) were recorded in a field table. Diameter at breast height and height of each individual of the main species studied in the transects were measured. The locations of regeneration sites on the slopes were classified into ridges plus upper slopes, mid-slopes, and lower slopes.

To analyse the site conditions of beech regeneration in abandoned fields next to forest stands, three 5 x 20 m and two 10 x 20 m block transects were established in Miao'ershan on such fields. The vegetation heights in these sampled sites were between 5 and 7 m tall. In these transects, the height and basal diameter of juvenile trees taller than 0.5 m were measured. Seedlings (shorter than 0.5 m) of the main species in the transects were counted. Abundance and coverage of bamboos and other vegetation lower than 0.5 m were recorded (Braun Blanquet method). In each block transect on abandoned fields, the relative importance of each woody species was assessed by combining the relative abundance and relative basal area of

individuals taller than 0.5 m. In Daba, no such natural regeneration sites were observed on abandoned fields because these fields had been planted with pines.

4.2.4 Data analysis

Regeneration site conditions were characterized according to (1) type and phase of an eco-unit, (2) presence or absence of a bamboo thicket, and (3) on ridge or mid-slope or lower slope. The data showed that the three evergreen species studied in Miao'ershan had similar site requirements for their regeneration. Therefore, these three species were treated as one group in the analysis of regeneration sites. As there was no very dense regeneration in either site except on the abandoned fields, the density of seedlings or saplings was classified into "moderate density" or "low density" with the threshold between these classes being 3 individuals per 100 m².

In each study site the strip transect data were combined and the height class distributions of the main species studied were analysed. Potential and canopy trees of the main species were analysed separately. These transects covered very heterogeneous sites and sometimes they crossed small ridges. Forests on mid-slopes and ridges differed greatly in the overstorey canopy heights. Thus, for the analysis, overstorey trees were classed by their heights in the site where they were found (upper, mid- or lower slope).

4.3 RESULTS

4.3.1 Regeneration sites of the main species

Daba

In Daba the beech juveniles occurred frequently in growing eco-units in all sites and in mature or degrading eco-units only on the ridges (Table 4.1; Fig. 4.2.). They occurred rarely in mature eco-units on slopes and bottoms. To some extent they were restricted by bamboos, except on ridges. Degrading eco-units were rare. Dead trees were often *Betula luminifera*, *Carpinus cordata* and *Quercus aliena*. Occasionally, some young eco-units about 400 m² in area, usually colonized in sunny parts by *Rubus* sp. and other species such as *Aralia chinensis*, *Viburnum* spp. were found on mid-slopes. In the relatively shaded sites of these young eco-units, *Rubus* was sparse or absent and saplings of *Carpinus cordata*, *Acer* sp. and *Daphniphyllum* sp. were found.

When a bamboo layer was absent, *Carpinus cordata* juveniles occurred in young growing eco-units (< 5 m high) in all sites, but its saplings were rare in young growing eco-units on ridges and upper slopes (Table 4.1). They also occurred in degrading eco-units in all sites when bamboos were absent. They were rare or absent in other cases. *Quercus aliena* seedlings and saplings were very rare in all sites.

Table 4.1. Summary of regeneration sites of *Fagus hayatae* var. *pashanica* and *Carpinus cordata* var. *chinensis* and *Quercus aliena* var. *acutiserrata* in Daba Forest Station. Seedlings and saplings: 'p' = present at a density of more than 3 individuals per 100 m², 'r' = present at a density of less than or equal to 3 individuals per 100 m², '-' = absent.

Juvenile trees	Bamboo layer			Growing eco-units < 5m			Growing eco-units > 5m			Basch mature eco-units			Other mature eco-units			Degrading eco-units		
	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope
<i>Fagus</i> seedlings	p	p	-	p	p	p	p	p	p	p	r	r	p	r	p	p	p	p
<i>Fagus</i> saplings	absent	p	p	p	p	p	p	p	p	p	r	r	p	r	p	p	p	-
<i>Fagus</i> seedlings	present	p	p	p	p	p	p	p	p	p	-	-	p	-	p	r	-	-
<i>Fagus</i> saplings	present	p	-	p	-	p	-	p	-	p	-	-	p	-	p	r	-	-
<i>Carpinus</i> seedlings	absent	p	p	p	r	r	p	r	r	p	r	r	p	r	p	p	p	p
<i>Carpinus</i> saplings	absent	p	p	-	-	r	-	-	-	-	-	-	-	-	-	-	-	-
<i>Carpinus</i> seedlings	present	p	p	p	p	p	p	p	-	p	r	r	p	r	p	-	-	-
<i>Carpinus</i> saplings	present	r	-	-	-	r	-	-	-	-	-	-	-	-	-	r	-	-
<i>Quercus</i> seedlings*	absent	r	-	-	r	r	-	r	-	r	r	-	r	-	r	r	-	-
<i>Quercus</i> saplings*	absent	-	-	-	-	-	-	-	-	r	-	-	r	-	-	-	-	-

* *Quercus aliena* seedlings and saplings were absent from all phases and all types of forest eco-units with a bamboo layer.

Table 4.2. Summary of regeneration sites for *Fagus lucida* and three main co-dominant evergreen broadleaved trees (*Castanopsis lamouitii*, *Lithocarpus hancei* and *Manglietia chingii*) in Miao'ershan Nature Reserve. Seedlings and saplings; see Table 4.1 for explanation of 'p', 'r' and '-':

Juvenile trees	Bamboo ³ layer			Growing eco-units < 5m			Growing eco-units > 5m			Basch mature eco-units			Evergreen mature eco-units			Mixed mature eco-units		
	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope	ridge	mid-slope	lower slope
<i>Fagus</i> seedlings	p	r	-	p	r	-	p	r	-	r	-	-	-	-	-	-	-	-
<i>Fagus</i> saplings	absent	p	-	p	-	-	p	-	-	p	-	-	-	-	-	-	-	-
<i>Fagus</i> seedlings	present	p	-	p	-	-	p	-	-	p	-	-	-	-	-	-	-	-
<i>Fagus</i> saplings	present	p	-	p	-	-	p	-	-	p	-	-	-	-	-	-	-	-
Evergreen seedlings	absent	p	p	p	p	p	p	-	-	p	-	-	r	r	r	p	p	p
Evergreen saplings	absent	p	p	p	p	p	p	p	p	p	r	r	r	r	r	p	p	r
Evergreen seedlings	present	p	p	p	p	p	p	p	p	-	-	-	r	r	r	-	-	-
Evergreen saplings	present	p	p	p	p	p	p	p	p	-	-	-	r	r	r	-	-	-

³ Bamboos surveyed are *Indocalamus longiauritus* on the ridges and upper slopes, and *Indocalamus thibetensis* on the middle and lower slopes.



Figure 4.2. A group of *Fagus hayatae* var. *pashanica* saplings were growing beneath a canopy gap and the gap edges, where other understorey plants were sparse, at 1650 m altitude in Daba. Photographed in August 1992.

Miao'ershan

In Miao'ershan the beech juveniles were almost restricted to ridges and upper slopes, where they were found in growing eco-units and in some mature beech eco-units on ridges (Table 4.2). On the ridges, presence or absence of *Indocalamus longiauritus* in the understorey did not matter for the beech regeneration. In all sites except the upper slopes and ridges, the forest floors of growing and mature eco-units were often densely colonized by *Indosassa shibataeoides*, and juvenile trees were rare. When the density of *Indosassa shibataeoides* exceeded 10 culms per m², regeneration of all trees or shrubs was inhibited (Fig. 4.3). In some canopy gaps where bamboo was sparse or absent, juveniles of the three evergreen species and many other small evergreen trees and shrubs were often abundant. Juvenile beeches were nearly absent in these sites.

The three evergreen species showed similar site preferences for their regeneration. Their seedlings and saplings occurred in growing eco-units in all sites, even in the presence of sparse or moderately dense bamboos (Table 4.2). In the absence of a bamboo layer, the evergreen seedlings and saplings occurred in mature beech eco-units on or near ridges, and they also occurred, but rarely, in mature mixed eco-units along the slopes (Table 4.2).

On the abandoned fields next to forest stands, both pioneer (e.g. *Betula*, *Clethra* and deciduous *Rhododendron*) and late successor woody species (*Fagus lucida*, *Acer oliverianum*, *Castanopsis lamontii* and many evergreen small trees and shrubs) invaded at the same moment (Table 4.3). *Rhododendron* species were often important here. Bamboos were present in these fields but they probably arrived after the woody species had established. In these abandoned fields, the beech regeneration was the best, i.e. a high density and good growth (e.g. Fig. 4.4).

In neither Miao'ershan nor Daba did I find any clear relation between regeneration of the main species and slope aspect.

Table 4.3. Total number of woody species, relative importance (IV: %) of woody species (individuals taller than 0.5 m), and coverage of bamboos in five block transects on abandoned fields bordering mature beeches or beech forest stands in Miao'ershan. + indicates presence of an individual.

Plot number→	1	2	3	4	5
Plot size (m)	5 x 20	5 x 20	5 x 20	10 x 20	10 x 20
Vegetation height (m)	2-5	2-5	2-7	2-4	3-8
Number of woody species	14	14	14	14	25
species ↓	IV	IV	IV	IV	IV
<i>Fagus lucida</i>	28.7	45.9	71.7	47.8	18.9
<i>Rhododendron orbiculare</i>	28.7	+		28.8	7.6
<i>R. farrerae</i>					6.5
<i>R. miao'ershanensis</i>	12.6	5.9		3.0	4.3
<i>R. simsii</i>					6.1
<i>Enkianthus serrelutus</i>					6.1
<i>Castanopsis lamontii</i>	7.1				10.6
<i>Acer oliverianum</i>	6.6				
<i>Hydrangea</i> sp.	6.7	+	+		
<i>Betula insignis</i>	3.6	20.7		3.6	+
<i>Clethra kaipoensis</i>	3.7	12.3	+	3.7	+
<i>Lyonia formosa</i>			8.2		2.8
<i>Cunninghamia lanceolata</i>			4.2		
<i>Sorbus</i> sp.			3.6		
<i>Symplocos</i> sp.			1.9		+
<i>Illicium majus</i>					10.3
<i>Cleyera japonica</i>					7.9
<i>Eurya brevistyla</i>					3
<i>Lithocarpus hancei</i>					1.5
others	1.8	15.2	10.4	13.1	14.4
<i>Indosassa</i> coverage (%)	10	10		5	5
<i>Indocalamus</i> coverage (%)		40		60	30



Figure 4.3 Left: a moderately dense undergrowth of *Indosassa shibataeoides* (4-5 m tall), growing on a mid-slope at 1450 m altitude in Miao'ershan, inhibited regeneration of all woody species. Photographed in October 1992. Right: a superficial leptomorph rhizome of *Indosassa shibataeoides*. Photographed in April 1993.



Figure 4.4 A *Fagus lucida* regeneration patch (foreground), mixed mainly with *Rhododendron* spp., on an open site next to mature beeches, at 1650 m altitude on Mt. Miao'ershan. Photographed in September 1991.

4.3.2 Height class distribution of the main species

In Daba, the height class frequency distribution of *Fagus hayatae* had a large peak at seedling height and small peak at overstorey height, although the overstorey height varied at different sites (Fig. 4.5). The beech was most important in the overstorey. *Carpinus cordata* had a peak at heights between 6 and 10 m (Fig. 4.5). Tall *Carpinus cordata* individuals were only found in the overstories of some ridge sites and in some forest patches dominated by this species on gentle and lower slopes. In sites dominated by *Fagus hayatae* and *Quercus aliena*, adult *Carpinus cordata* individuals were usually found in the sub-canopies. *Carpinus cordata* had fewer saplings than the beech. *Quercus aliena* mixed with the beech in overstories, but its seedlings and saplings were nearly absent from the forest (Fig. 4.5).

In Miao'ershan, height class distribution of *Fagus lucida* had a large peak in canopy height class, although the overstorey height varied at different sites, and a small peak in sapling class (Fig. 4.6). The height class frequency of the three evergreen species decreased from the height of seedling and saplings to canopy height (Fig. 4.6). The tall *Manglietia chingii* individuals only attained the sub-canopy height.

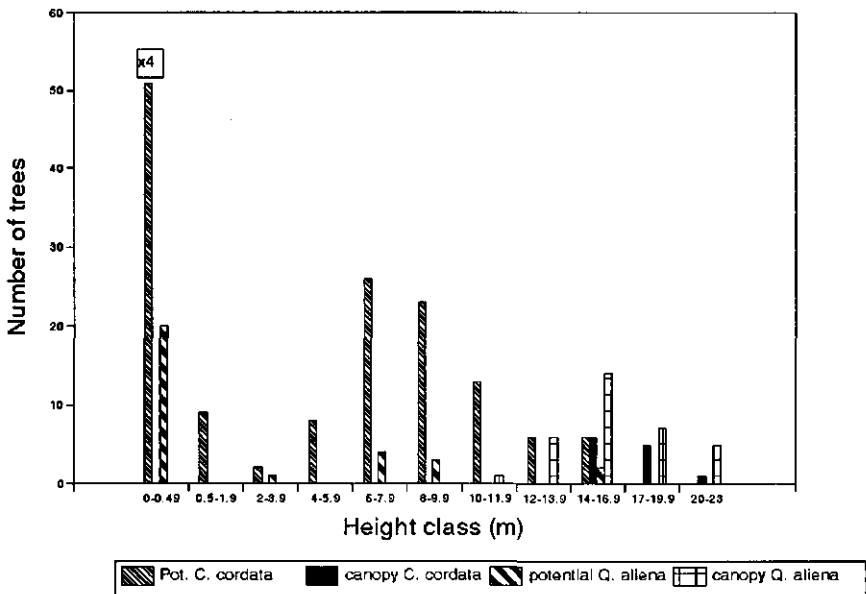
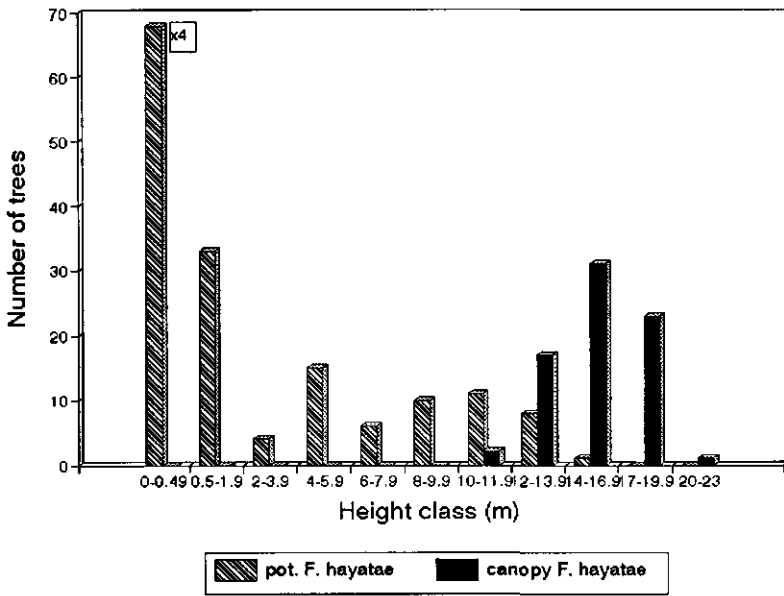


Figure 4.5. Above: height class frequency distribution of *Fagus hayatae* var. *pashanica*. Below: height class frequency distribution of *Carpinus cordata* var. *chinensis* and *Quercus aliena* var. *acuteserrata*. Data are summed from four strip transects on slopes of different aspect. The total area (corrected to projection) of these transects is 1.04 ha.

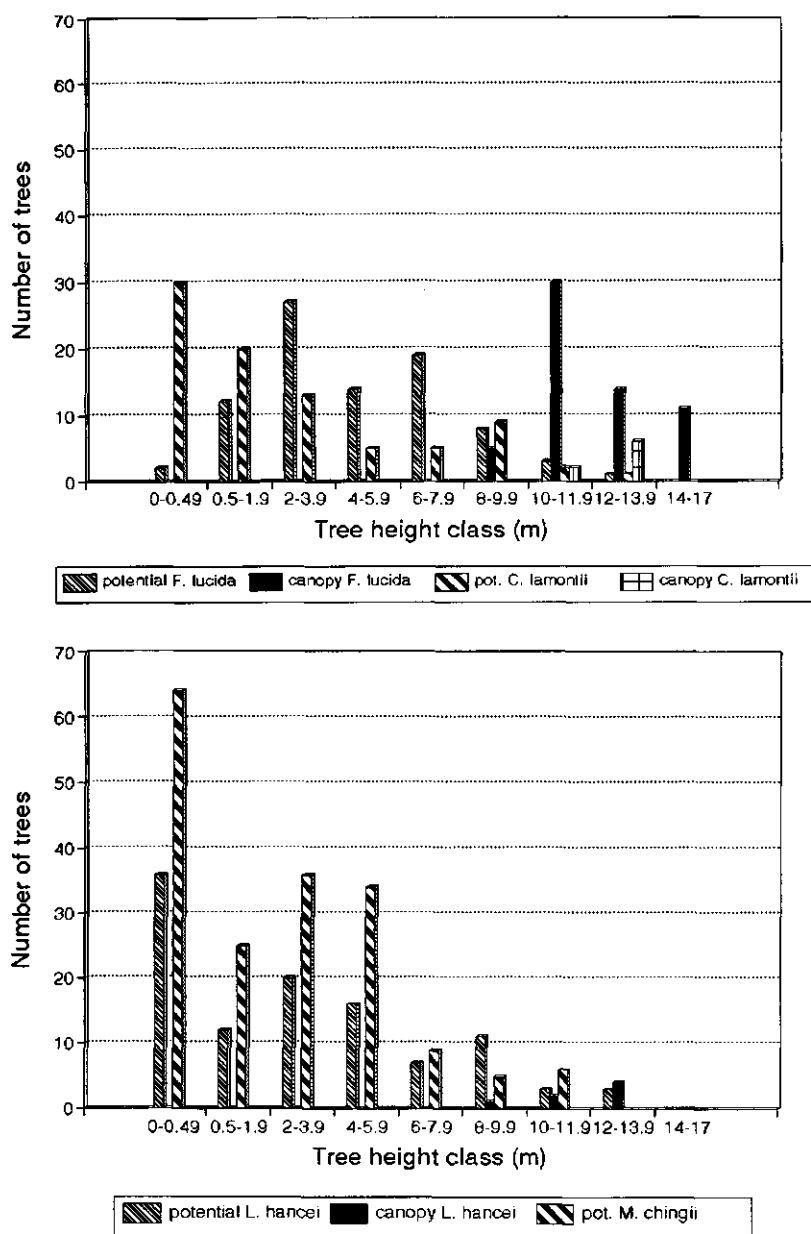


Figure 4.6. Above: height class frequency distribution of *Fagus lucida*, *Castanopsis lamontii*. Below: height class frequency distribution of *Lithocarpus hancei* and *Manglietia chingii*. Data are summed from two strip transects of Miao'ershan. The total area (corrected to projection) of these transects is 0.57 ha.

4.4 DISCUSSIONS

4.4.1 Bamboos and beech regeneration

In both sites, bamboos largely restricted beech regeneration (Tables 4. 1 & 4. 2). This is also observed in other Chinese beech forests (Wang *et al.* 1965; Zhu & Yang 1985; Qi 1990), in Japanese beech forests (Nakashizuka & Numata 1982; Nakashizuka 1988) and in *Nothofagus* forests in Chile (Veblen 1982). A dense bamboo thicket casts much shade on the forest floor (Chapter 5) and probably consumes much water and nutrients (Numata 1979). Bamboo litter (dead leaves mainly) usually contains more silica than the litter of many tree species (Hou 1982). For example, dead leaves of *Indosassa shibataeoides* contain 3-4.8% of SiO₂ and those of *Indocalamus longiauritus* contain 5-8% of SiO₂ (unpubl. data). However, the leaves of *Fagus longipetiolata* contain 1.5% of SiO₂ (Hou 1982). These silica-rich bamboo litters decompose slowly and accumulate on the forest floor (pers. comm. F.Z. Kong, 1993; pers. obs. Cao; cf. Veblen 1982, Chile) and probably inhibit the germination of tree seeds. Further, Veblen (1982) has reported that bamboo litter is rather nutrient-poor. Also, a dense bamboo thicket forms a dense rhizome system in the upper soil layer, which strongly inhibits other plants from establishing themselves from seeds (Zhu & Yang 1985).

However, bamboos may flower and wither simultaneously over a large area once or twice a century (Numata 1970). Bamboo mice which eat bamboo culms, and rooting wild pigs can cause minor disturbances to bamboo thickets (Wang *et al.* 1965; pers. obs.). The death of understorey bamboos gives beech an opportunity to regenerate. In Japan, after the simultaneous death of understorey dwarf bamboo *Sasa kurilensis*, the regeneration of *Fagus crenata* improved (Nakashizuka 1988).

In northern areas, the distribution and growth of bamboos are largely controlled by temperature minima in the winter (Numata 1979). Located in the northern subtropics, the montane forests in Daba are exposed to cold continental winds descending from northern China. In this area, extreme cold and also ice and snow storms may occasionally cause bamboos to die (pers. comms. Y. Zhao, a local forester). These cold weather events are particularly harmful to bamboos growing on exposed sites, e.g. ridges, isolated mountain tops, deep valleys, slopes facing cold winds (cf. ice storms, Wang 1984) and in large canopy gaps (cf. Veblen 1982, Chile). Hence, cold weather events probably largely explain the dead bamboo patches and forest patches without bamboos found regularly in the northern site. More frequent death or absence of bamboos in the northern site than in the southern site certainly makes it easier for *Fagus hayatae* to regenerate in the northern site.

In contrast, in the southern site, no dead bamboo patches were observed and stands without bamboos were rare. There, a dense thicket of 4-5 m tall *Indosassa shibataeoides* inhibited woody plants from regenerating (Fig.4.3). However, on ridges, upper slopes and steep slopes, *Indosassa shibataeoides* usually gives way to *Indocalamus longiauritus*. Ridges and steep slopes are often relatively dry and nutrient-poor, with shallow or rocky and unstable soils. Ridges are usually windy but receive more light than elsewhere on a slope (Weng & Luo 1990). Leptomorph rhizomes of *Indosassa shibataeoides* (Fig 4.7; cf. McClure 1966) and its rather tall culms, make it unsuitable to grow in rocky and unstable sites.

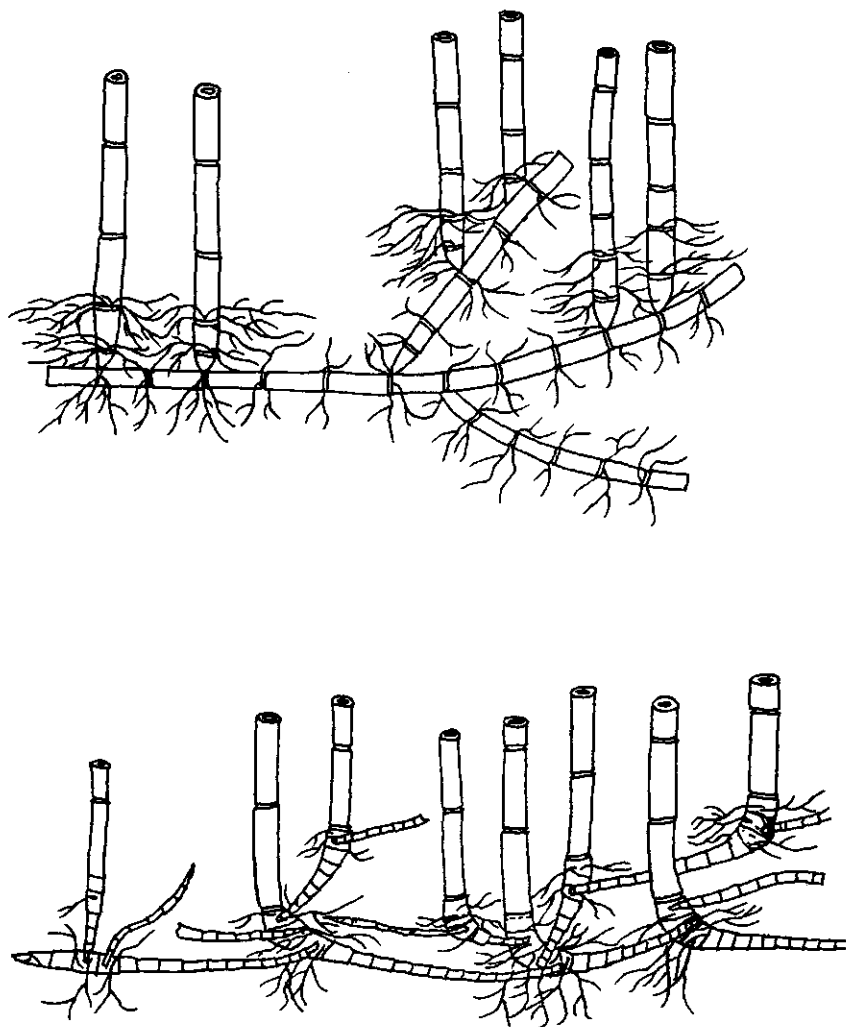


Figure 4.7. Above: leptomorph rhizome with solitary culms of *Indosassa shibataeoides*. Below: long-necked pachymorph rhizome with tillering culms of *Indocalamus longiauritus*, both in Miao'ershan.

Indocalamus longiauritus is much smaller than *Indosassa shibataeoides*. Its long-necked pachymorph rhizomes with tillering culms (Fig. 4.7) and its small size, make it suitable to grow in rocky sites. When it encounters a rock, it may be able to produce a long rhizome to pass over it. When a micro-site is favourable, it may stabilize there, form a small clump, and be prepared from there for further invasion. On the other hand, because of its pachymorph rhizome and small size, *Indocalamus longiauritus* may leave some space (Soderstrom & Calderón 1979) for trees to establish themselves through the bamboo clones. On ridges or upper slopes, juvenile beeches were indeed found growing through the *Indocalamus longiauritus* thickets (Table 4.2).

4.4.2 Other important factors related to beech regeneration

In both sites, the beeches regenerated better on ridges and upper slopes regardless of presence of bamboos (Tables 4.1 & 4.2). In fact, the current beech regeneration in Miao'ershan is confined to ridges plus upper slopes and abandoned fields (Tables 4.2 & 4.3). In other beech forests in the southern areas, beech juveniles are also found mainly on ridges plus upper slopes and abandoned fields next to beech stands (Yuan & Cao 1983; Qi 1990). Ridges and upper slopes where understories are often sparse seem to favour beech regeneration and growth over the other main species.

In the species-rich southern site, not only bamboos but also other trees, shrubs and lianas limit the regeneration of *Fagus lucida* (e.g. Fig.1.1). In this southern area, evergreen overstorey or subcanopy species grow faster than *Fagus lucida* (Chapter 5) because of their higher productivity (Kira & Shidei 1967) resulting from their larger leaf area indices (Kira & Shidei 1967; Satoo 1983) and longer active growing seasons (Kusumoto 1957; Li & Wang 1984; Yang *et al.* 1992). Further, the evergreen *Castanopsis lamontii* and *Lithocarpus hancei* have larger seeds than *Fagus lucida* (pers. obs) and are probably better able to germinate and establish their seedlings through understorey vegetation (Canham & Marks 1985). Thus, these evergreen juveniles are more competitive than the beech juveniles. In contrast, in the northern site, other trees and shrubs did not significantly inhibit the regeneration of *Fagus hayatae*.

In the southern site, *Manglietia chingii* and *Castanopsis lamontii* form root collar sprouts in their understorey saplings to replace suppressed stems so as to survive longer (Chapter 5). Clearly, this strengthens their capacity to compete with other plants in regeneration sites. In coping with the harsh climate in the northern range or upper montane limits, *Fagus grandifolia* in North America produces root suckers to regenerate (Held 1983; Jones & Raynal 1986). However, root suckers and basal sprouts were rare in *Fagus hayatae* and *Fagus lucida* in both study sites (pers. obs.).

The good beech regeneration on abandoned fields in the southern site (Table 4.3) suggests that large forest openings without or with very sparse prior established are the best conditions for *Fagus lucida* regeneration (also cf. Yuan & Cao 1983; Qi 1990). In forest stands dominated by *Fagus lucida* and evergreen oaks on Mt. Badagongshan in northwestern Hunan, the beech regeneration was poor (Yang 1982). However, in that site, good beech regeneration was found in a forest stand dominated by the beech and *Betula insignis*, with an undergrowth

of dwarf bamboo *Sinarundinaria nitida* and other woody plants (Fang & Jiang 1982). The stand mixed with birch was probably originated from a large forest opening and the canopy was probably still rather sparse. This is consistent with my findings that stands with a sparse canopy plus a rather sparse understorey allow beech regeneration to occur if the seed sources are available (Tables 4.1 & 4.2).

In both sites, ice storms, tornadoes, localized strong gusts and heavy rains can cause the forest canopy to open up (Chapter 3). Evergreen broadleaved trees are particularly susceptible to ice storms (Wang 1984; Cao & Peters in prep.; Chapter 3). In Miao'ershan the evergreen trees often have broken crowns and are much less important in the forest canopies than *Fagus lucida* (Fig. 4.6). In both sites, if bamboo death over a large continuous area coinciding with intense canopy opening up in the forest, or after an accidental man-made forest fire, beech regeneration can probably occur in all sites along the slopes.

4.4.3 Population structure and regeneration

In a very heterogeneous montane zone, the performance of a species and its related vegetation may differ greatly in different sites, e.g. ridges vs valleys, upper vs lower slopes and south- vs north-facing slopes. The population structures of the species studied (Figs. 4.5 & 4.6) should not be interpreted as homogeneous patterns occurring evenly in the forest mosaics because many juvenile trees were confined to specific sites (Tables 4.1 & 4.2).

The population structure of *Quercus aliena* (Fig. 4.5) can be interpreted as the emergent type of regeneration, which is described by Ohsawa (1991) for giant emergent trees and pioneer trees in tropical montane rain forests of Southeast Asia. Many deciduous oak species are light-demanding. Deciduous oak species are often dominants in secondary forests in the temperate and subtropical zones in China (Wu 1980) and in the USA (Rogers *et al.* 1993). In montane zones of Qinling mountain range, *Quercus aliena* var. *acuteserrata* forms mono-species forest stands (Wu 1980; Zhu 1983). Inside these oak stands, juvenile oaks are nearly absent (Zhang 1989). However, oak juveniles are abundant in pine stands next to the oak stands (Zhu 1980; Zhang 1989). In deciduous broadleaved forests mixed with oaks in Europe, regeneration of oak species is usually lacking too (Mayer 1984). It seems that in the forest mixed with the beeches in Daba, *Quercus aliena* requires large forest openings for its regeneration.

The population structure of *Carpinus cordata* probably reflects its nature as a sub-canopy species in the mixed beech forest (Fig. 4.5). My field observations suggest that it prefers to regenerate in moist sites (also see Table 4.1). Many *Carpinus* species are subcanopy species in mixed temperate forests and prefer to grow in moist sites. Examples are *Carpinus cordata* in northeastern China (Wu 1980), *Carpinus cordata* in Ogawa Forest Reserve of Japan (Masaki *et al.* 1992), *Carpinus caroliniana* in eastern USA (Braun 1950), and *Carpinus betulus* in central Europe (Mayer 1984; Ellenberg 1988). However, in the study site, adult or pole trees of *Carpinus cordata* were found in all sites along slopes. But juveniles of *Carpinus cordata* in gaps on ridges or upper slopes often had a low vitality and poor growth (pers. obs.) possibly because of inadequate soil moisture. It is not clear whether the present macro-climate or the forest environment in which beeches predominate in the canopy is

unfavourable for *Carpinus cordata* regeneration on sites other than those on lower slopes and valleys.

The population structures of both beech species studied suggest a sporadic regeneration pattern (Figs. 4.5 & 4.6). This is probably due to the sporadic availability of open patches for the beech regeneration and the climatic fluctuation which may influence the performance and reproduction of the trees. Indeed, beech seed production is sporadic, particularly in the northern site.

The population structure of the three evergreen species in the southern site showed a declining curve (Fig. 4.6). This indicates that these species regularly regenerate in the forests, and their regeneration is not dependent on sporadic canopy opening up. However, although the evergreen juveniles were more abundant than *Fagus lucida* juveniles, the beech was more abundant in the canopy than the evergreens. This is largely because the evergreens are susceptible to ice storms and snow storms (Chapter 3).

4.5 CONCLUSIONS

In two sites, a dense bamboo thicket is the major factor inhibiting beech regeneration. However, bamboos died more frequently in the northern site than in southern site, probably because of cold. In the northern site, the understorey vegetation was often sparse. There, *Fagus hayatae* regenerated in growing and degrading eco-units in all sites and in some mature eco-units on ridges only, and the beech regeneration was denser and more frequent on ridges and upper slopes than elsewhere on the slopes. In the southern site, the forest understorey is denser than in the northern site, and bamboos, many evergreen trees and evergreen shrubs, often densely covered the forest floors either under forest canopies or in canopy gaps. There, *Fagus lucida* regeneration was mainly confined to large growing eco-units or large canopy gaps on ridges and upper slopes. Ridges and upper slopes seem to favour beech regeneration in both sites, because there the understories are rather sparse.

In both sites, the beech populations indicate the sporadic regeneration pattern, suggesting sporadic opening up of the forest canopy are essential for the beech regeneration. In the northern site, the co-dominant *Quercus aliena* was present only as tall trees and its regeneration was lacking. This oak species probably requires large forest openings for its regeneration. At that site, *Carpinus cordata* mainly attained the subcanopy height and preferred moist sites for its regeneration. In the southern site, the population structures of the three evergreen species suggest these evergreens regenerate continuously in the forest and do not require major disturbances for their regeneration. However, because they are susceptible to ice or snow storms they fail to dominate in the overstorey. In both sites, sporadic canopy opening up caused by climatic events such as tornadoes, torrential rains and ice or snow storms and simultaneous withering of bamboos are probably prerequisites for abundant beech regeneration. These climatic events need to be more intense in the south than in the north if the beech regeneration is to succeed.

Chapter 5 Growth and architecture of evergreen and deciduous shade-tolerant trees in different light environments in two Chinese beech forests

5.1 INTRODUCTION

Light is one of the critical factors in the regeneration processes of forest trees (e.g. Canham *et al.* 1990). The light environment in a forest understorey is ever-changing (Koop 1989), largely because of the successive development of forest eco-units (forest patches) and their interactions (Hartshorn 1978; Denslow 1980; Whitmore 1982; Runkle 1982, 1985; Nakashizuka 1984, 1987; Oldeman 1974b, 1979, 1983 & 1990). Two extreme growth strategies can be recognized in juvenile forest trees: 1. to grow fast in order to reach the canopy before the canopy opening closes; 2. to persist in the understorey until a new opening occurs or growing slowly and gradually reaching the canopy.

The shade-tolerant juvenile trees may experience several periods of different light environments before reaching the forest canopy (e.g. Canham 1985, 1990; Peters & Poulson 1994). In these different light environments, the juvenile trees of many shade-tolerant canopy species often adjust their growth and architecture. Growth can be adjusted by changing relative resource investment in height vs diameter growth and in vertical vs lateral branch expansion. Architectural adjustment can occur at various levels in the tree system: leaves, shoots and branches, and crowns (Oldeman & van Dijk 1991), e.g. by the well-known morphological and physiological differentiation into sun and shade leaves (Schulze 1970; Strasburger *et al.* 1978), a change in branch angles (Fisher 1986), branching reiteration (Oldeman 1978; Hallé *et al.* 1978) and architectural metamorphosis (Edelin 1977).

Branching patterns have great ecological significance because they determine foliage and shoot arrangement and display and eventually determine the overall crown architecture. Trees have two basic types of branch morphology (Hallé & Oldeman 1970; Hallé *et al.* 1978): plagiotropy and orthotropy, largely as distinguished by 19th century German physiologists (Frank 1868). The leaves on orthotropic branches are arranged radially, and self-shading is possible (Horn 1971). The leaves on plagiotropic branches are arranged in two rows in a plane and self-shading is minimized at branch level. Plagiotropic mixed axis is a special type of plagiotropy, which is essentially plagiotropic but in which the basal part can become erect by secondary growth as in the case of trunk formation (Hallé *et al.* 1978). Based on support-supply analysis, Givnish (1984) has hypothesized that orthotropic axes with spiral phyllotaxis have an advantage in sunny environments and plagiotropic axes are favoured in shady environments. As both orthotropy and plagiotropy (including plagiotropic mixed axes) are found in the shade-tolerant species in Chinese beech forests, this study tested two hypotheses: that the architecture of trees characterized by these different types of branch morphology differs in different light environments; and if this is so, this different architecture affects the growth of saplings.

In a warm climate, evergreen broadleaved canopy tree species may outgrow deciduous canopy trees because of their longer leaf persistence, longer active growing season (Kusumoto 1957; Li & Wang 1984; Zhou 1990; Yang *et al.* 1992) and more efficient use of carbon, water and nutrients (Chabot & Hicks 1982; Schulze 1982; Hollinger 1992). In the

north of the Chinese *Fagus* range, Chinese beeches are mixed with deciduous broadleaved trees, but in the south of that range they are mixed with evergreen broadleaved trees. In the beech forest in the northern site, Daba Forest station, beech seedlings and saplings are more abundant than those of other co-occurring deciduous species (Chapter 4). However, in the south, juvenile beeches are rare, whereas the juveniles of evergreen canopy and subcanopy species are abundant. Below, the relative effects of architecture and leaf persistence (evergreen vs deciduous) on the establishment of juvenile trees are discussed.

This study reported in this chapter aimed to identify architectural and growth strategies in young trees of three evergreen and three deciduous broadleaved shade-tolerant species in two Chinese beech forests. Special emphasis was on branch morphology and leaf persistence (evergreen vs deciduous).

5.2 METHOD

5.2.1 Study sites and time of field work

Study sites are the same as in Chapter 4.

The field work described in this chapter was mainly done in August 1992 in Daba and between September and October 1992 in Miao'ershan. The data on growth collected in 1990 and 1991 from Miao'ershan and in 1991 from Daba were also used.

5.2.2 Tree species studied

In the northern site, Daba, the dominant canopy species *Fagus hayatae* var. *pashanica* and the subcanopy species *Carpinus cordata* var. *chinensis* were selected for the study. Their branching patterns are characterized by plagiotropic mixed axes. For growth comparison, poles of the canopy species *Quercus aliena* var. *acuteserrata* (light-demanding) were included too, but hardly any saplings were available in the forest. In the southern site, Miao'ershan, two canopy species with plagiotropic branches (*Fagus lucida* and *Castanopsis lamontii*) and one canopy species with orthotropic branches (*Lithocarpus hancei*), and one subcanopy species with orthotropic branches (*Manglietia chingii*) were selected. *Carpinus cordata* belongs to Betulaceae, *Manglietia chingii* belongs to Magnoliaceae, and the remaining species belong to Fagaceae. All these species are shade-tolerant except *Quercus aliena*. In the subsequent text the variety names are omitted.

5.2.3 Sample tree selection and measurements

The architecture and growth of a forest tree are controlled at three levels (Waller 1986): 1. genetic, 2. developmental, and 3. physiological. In this study, the genetic control was considered to be the tree's inherited architectural model (Hallé Oldeman 1970; Hallé *et al.* 1978). When considering the developmental influence on growth, the saplings and pole trees were separated in the study. The saplings were defined as juvenile trees between 0.5 m and 5 m tall of the canopy or subcanopy species. The pole trees were defined as being taller than 5 m but lower than the forest canopy. In fact, this study concentrated on the saplings between

1 and 5 m tall in the northern site and on the saplings between 2 and 5 m tall in the southern site. The physiological control on growth and architecture is greatly influenced by the direct environment above a tree. This study was restricted to the influence of one environmental factor: light intensity.

Following Hallé *et al.* (1978), the basic architectural properties of juveniles of the species studied were characterized and genetic architectural models of these species were distinguished (Table 5.1; also Figs. 5.1-5.5). The trees conforming to Troll's model (*Fagus hayatae*, *Fagus lucida* & *Carpinus cordata*) are programmed to form sympodial axes because of the continual superposition by mixed axes. The trees conforming to Massart's (*Castanopsis lamontii*), Scarrone's (*Manglietia chingii*) and Rauh's models (*Lithocarpus hancei*) genetically form monopodial trunks (Hallé *et al.* 1978). This is so in the saplings of the latter three species when growing in open sites (Table 5.1). However, in shaded understories, the saplings of all the six species had sympodial trunks and sympodial main-line axes of lateral branches because distal terminal shoots are replaced by axillary shoots.

To minimize the effects of site heterogeneity, saplings on mid-slopes were selected. These saplings were free from crowding by equally tall neighbouring plants. In Daba, the analysis was restricted to saplings 1-5 m tall without a bamboo undergrowth. In Miao'ershan, saplings were often associated with a dense undergrowth of bamboos. There, saplings 2-5 m tall growing together with dense *Indocalamus longiauritus* were selected for the study; saplings shorter than 2 m were excluded because it was expected that their growth would be greatly affected by bamboos.

The height and trunk diameter at the base of the selected saplings were measured. Their crown projection areas were assessed as an ellipse from two perpendicular crown diameters. Free height of the trunks (height of lowest living branch, h_0) was recorded and leaf-bearing shoots were counted for each sapling. Average elongation during the last five years in the top shoot and the three longest lateral branches, located in the upper, middle and lower parts of a crown were measured for each sapling. The angle from vertical was measured for the top shoot and for the distal parts of the selected branches per sapling.

In Daba, a forest area about 3 ha, located in three locations at altitudes around 1450 m was searched for the saplings; 36 *Fagus hayatae* saplings and 28 *Carpinus cordata* saplings were measured. In Miao'ershan, a forest area about 5 ha, located in six locations at latitudes between 1500 and 1600 m, was searched for the saplings; 26 *Fagus lucida* saplings, 32 *Castanopsis lamontii* saplings, 31 *Lithocarpus hancei* saplings and 26 *Manglietia chingii* saplings were measured.

Some of the saplings were harvested to collect stem disks for measuring radial trunk growth and age. Fresh leaves (around 20 g per deciduous sapling and between 40 to 60 g per evergreen sapling) were sampled from some of the harvested saplings and weighed. Leaves of the two beech species and *Carpinus cordata*, were sampled separately from long and short shoots. A short shoot had only one fully developed bud, while a long shoot had two or more fully developed buds (*sensu* Thiébaud 1988). Increment cores were taken from some of the other, unharvested, saplings. To minimize asymmetry, the increment cores were taken from the stem sides at a right angle to the direction of the slope (Fritts 1976).

Table 5.1. Basic architectural characteristics of the species studied in the two Chinese beech forests.

Species	Arch. Model	Trunk components	Trunk formation* In the open	Branching Sequence	Branch Morphology	Evergreen or Deciduous
<i>Fagus</i> spp.	Troll	plagiotropic mixed axes	sympodium	diffuse	plagiotropic	Deciduous
<i>Carpinus cordata</i>	Troll	plagiotropic mixed axes	sympodium	diffuse	plagiotropic	Deciduous
<i>Castanopsis lamontii</i>	Massart	orthotropic, rhythmic axes	monopodium	diffuse	plagiotropic	Evergreen
<i>Lithocarpus hancei</i>	Rauh	orthotropic, rhythmic axes	monopodium	rhythmic	orthotropic	Evergreen
<i>Manglietia chingii</i>	Scarrone	orthotropic, rhythmic axes	monopodium	rhythmic	orthotropic	Evergreen

* In all species studied, regardless of their architectural models, trunks are sympodial when grown in shaded understories, as the result of weakened top shoots being replaced by axillary shoots.

The age was determined by counting bud scars on smaller saplings whose yearly bud scars were visible. Otherwise, it was determined by counting the tree rings of increment cores or of stem disks. Shoot density was determined by dividing the total number of leaf-bearing shoots of a sapling by its crown projection area. The ratio of free trunk height of a sapling to its total height (h_f/h_t) and ratio of its height to its basal diameter (h/d) were calculated.

To compare radial trunk growth in pole trees, one increment core per tree was taken from some poles of the main species (see Table 5.7 for the number of the poles sampled). These selected poles were growing under canopy trees or in canopy gaps.

The ring width in the increment cores and in the stem disks was measured with a binocular microscope (in 0.01 mm; Digitalpositionimeter, Kutschenreiter, Vienna). Each stem disk was measured at two radials, which were chosen avoiding either the widest or the narrowest side when the disk was asymmetrical. The ring width was averaged from the measurements from the two sides per stem disk.

The leaf samples were first air-dried. Individual leaf surface area was measured with the Delta-T Image Analysis System and the total leaf area of a leaf sample was summed. Afterwards the leaf samples were oven-dried (65°C, 24 hours) to determine dry weight. Specific leaf area (SLA: $\text{cm}^2 \text{g}^{-1}$) was then determined by dividing the total leaf area (cm^2) of a leaf sample by its oven-dry weight (g).

5.2.4 Light assessment with ozalid paper

Ozalid light-sensitive paper was used to assess the percentage of daylight reaching each selected sapling (Friend 1961). In a darkroom, the ozalid paper was cut into small squares which were then wrapped in aluminium foil and packed in small bags. Each bag contained 16 stacked squares of ozalid paper and was covered by two pieces of aluminium foil; a round window was made in each inside foil. In the field, light assessment was done only on clear days, because the light on a clear day was expected to be much more important for sapling growth than the light on a overcast day. Also, the percentage of daylight reaching the forest understorey differs between on a clear day and on an overcast day (Minckler *et al.* 1973; Chazdon & Fetcher 1984).

The light assessment was done between 15 and 25 August 1992 in Daba and between 25 September and 8 October 1992 in Miao'ershan. Either in the early morning or in the late afternoon, small bags of ozalid paper were attached to horizontal branches or horizontal leaves at the top of each sapling with double-sided sticky tape. The window on the inside foil of each bag was open vertically towards the sky. Shading by neighbouring leaves or shoots was avoided. As a control, three bags of ozalid papers were placed in fully open places (e.g. on the roof of a building). All bags were left in situ for 24 hours. Afterwards, the exposed papers in each bag were counted in a dim light. In each stack, several papers were found to be fully exposed and one to three papers were only partly exposed. Each partly exposed paper was counted as a fraction of a fully-exposed paper. To establish the context of the light assessment, I recorded whether a measured sapling was growing under a dense or sparse canopy, or in canopy gaps of large or intermediate or small size, whether a subcanopy was present or not, and the slope aspect.

Calibration of the light assessment was done in September 1993 in Wageningen (the Netherlands) with an LI-1000 Datalogger light meter following Friend (1961). An empirical regression equation was established:

$$\text{Log}_{10}\text{PAR} = 0.3281X + 4.0454$$

$$(N = 25; R^2 = 97.38\%; p < 0.001)$$

in which PAR was light intensity ($\mu\text{mol m}^{-2} \text{ day}^{-1}$) measured by the light sensor; X was the number of exposed ozalid papers found after the same duration at the same spot as the light sensor. Using this equation, the percentage of daylight (on a clear day) reaching each sapling was calculated, based on the number of exposed ozalid papers on each sapling in contrast to those in the fully open places exposed the same day. Note that to minimize errors, during an experiment including the calibration, the exposed papers should be counted by the same person.

The measured saplings of *Fagus hayatae* were mainly in less than 2% of daylight (Table 5.2), either on the edges of gaps or in small gaps on slopes not facing south and in the absence of bamboo thickets. The saplings of *Fagus hayatae* were able to grow in deeper shade than those of *Carpinus cordata*. The saplings of the main species in Miao'ershan mostly grew in the sites with a larger percentage of daylight than those in Daba (Table 5.2). Only when a bamboo thicket or other shrubs or small trees were sparse or absent were the saplings in Miao'ershan able to grow in less than 2% of daylight. In both sites, the saplings growing under the closed canopy received less than 2% of daylight; they often received less than 1% when growing under the closed canopy on the slopes that did not face south. In Miao'ershan, about 0.7% of daylight reached the ground under a thicket of *Indosassa shibataeoides* without any overtopping forest canopy.

Table 5.2. The range of percentage of daylight directly above the measured saplings in the two study sites.

Species	N	Light range %	average %	sd %
Daba:				
<i>Fagus hayatae</i>	36	0.38- 4.70	1.35	0.92
<i>Carpinus cordata</i>	28	0.51- 4.80	2.38	1.27
Miao'ershan:				
<i>Fagus lucida</i>	26	0.63-50.66	11.33	14.13
<i>Castanopsis lamontii</i>	32	1.45-40.39	10.00	11.20
<i>Lithocarpus hancei</i>	31	0.68-68.54	11.69	15.00
<i>Manglietia chingii</i>	26	0.86-68.54	7.67	12.83

5.2.5 Validation of light assessment with ozalid paper

The variation of the percentage of daylight above the saplings fitted well with my field record: less than 2% of daylight was found under closed canopy; between 2% and 5% daylight was usual in small canopy gaps (projected area c. < 50 m²) and edges of gaps; between 5% and 10% daylight represented the relative light intensities in moderate-sized gaps

(projected area c. 50-200 m²); between 10% and 20% daylight indicated the relative light intensities in the bright zones of gaps that were between 200 and 300 m² in projected area. These percentages are similar to the results found in other temperate and tropical forests (Chazdon & Fetcher 1984; Canham *et al.* 1990). However, I expected some bias in the light assessment of the present study because it was only based on a single measurement on a clear day, which neglected the seasonal change in the path of the sun, the change in canopy cover and the differences between percentages of daylight reaching the understorey under a clear and an overcast sky (Minckler *et al.* 1973; Chazdon & Fetcher 1984).

In the mixed evergreen and deciduous forest in Miao'ershan, the evergreen trees are able to photosynthesize and grow before deciduous trees start flushing in spring and after they shed leaves in autumn (cf. Kusumoto 1957; Li & Wang 1984; Yang *et al.* 1992). Also, the deciduous saplings usually flush their leaves between 1 and 2 weeks earlier and shed their leaves later than con-specific adult trees (pers. obs.). In this study, light was assessed during the season when all canopy trees were in leaf. Thus, it is certain that over the year the saplings actually received a larger percentage of direct sunlight than the proportion I assessed. To the saplings, particularly the deciduous ones, their longer active growing season is certainly important for their survival in the understorey (cf. Janzen 1970, Costa Rica).

The Ozalid method is practical and cheap (also see MacDougall & Kellman 1992), and it provided enough precise data to answer the questions posed at the start of this study.

5.2.6 Data analysis

When considering the effects of climatic fluctuation and random events (e.g. insect or animal herbivory) on growth (Fritts 1976), the average growth rates over the last five years per sapling were used for the analysis of the relation between growth and light (cf. Canham 1988). These growth rates were: radial trunk growth rate, extension growth rates of top shoot and upper branch, and branch extension growth rate averaged over the selected branches.

A preliminary analysis of the data collected in this study indicated that the average growth rates over the last five years correlated positively with the percentage of daylight received by a sapling and often also with its height. To establish the relation between growth and percentage of daylight, size-dependent effects on growth should be perceived, measured and removed. Therefore multiple linear regression analysis was applied, in which the average growth rates during the last five year per species were dependent variables and logarithmic percentage of daylight and logarithmic sapling height were two independent variables. Residual analysis indicated that variance was homogeneous and linear regression was appropriate. Then partial correlation coefficient of either logarithmic percentage of daylight or logarithmic sapling height against average growth rates was calculated to reveal the strength of the relationship.

To compare the sapling growth rates of the studied species in a similar light range, I arbitrarily divided the percentage of daylight above the saplings into three classes: less than 5% daylight, between 5% and 10%, and above 10%. The class of above 10% daylight mainly involved saplings grown between 10% and 20% daylight and a few saplings grown in above 20% daylight. Average growth rates of the saplings over the last five years corresponding to the three light classes were analysed per species. However, no further

analysis of significance of the difference in average growth rates among the three light classes of the same species was done, because the significance of light had already been revealed by the regression analysis. The significance of difference in architectural parameters (angles, h_t/d ratio, h_t/h_l ratio and shoot density) was analysed among the three light classes for each of the main species in Miao'ershan, by one-way ANOVA (Duncan's multiple-range comparison) for samples of more than seven and by non-parametric test (Kruskal-Wallis test) for samples of less than seven. Significance of difference in average single leaf-area and in specific leaf area (SLA) between the saplings grown in either lower than or above 10% daylight was analysed for *Fagus lucida* and *Castanopsis lamontii* respectively (Mann-Whitney U test).

Significance of difference in average radial trunk growth over the last five years between poles per species grown either under forest canopy or in gaps was examined (T-test). Significance of difference in stem-radial growth of poles among the studied species per site grown in the two types of conditions was analysed (oneway-ANOVA with Duncan's multiple-range test).

Variance homogeneity was analysed using the Fmax test for the T-test and the Bartlett-box test for the ANOVA test. The data from samples with heterogeneous variance among compared groups were transformed, otherwise non-parametric tests were used. The SPSS statistical package was used for data processing.

5.3 RESULTS

5.3.1 Architectural adjustments and size characteristics

In Miao'ershan, saplings of *Lithocarpus hancei* and *Manglietia chingii* often had smaller crowns, whereas saplings of *Fagus lucida* and *Castanopsis lamontii* often had wider crowns (Figs. 5.1-5.6). Among equally tall saplings of the main species in Miao'ershan, *Manglietia chingii* saplings tended to have the narrowest crowns and *Castanopsis lamontii* saplings tended to have the widest crowns (Fig. 5.6). These tendencies were more pronounced when the saplings growing in low light intensities. Saplings of *Fagus lucida* and *Lithocarpus hancei* had a smaller h_t/h_l ratio (Table 5.3), i.e. deeper crowns, in brighter than in shadier sites. However, the h_t/h_l ratio was not statistically significantly different in *Castanopsis lamontii* saplings in these different light classes.

In Miao'ershan, only *Fagus lucida* showed statistically significant differences in the angles of top shoots and of upper and middle main lateral branches in its saplings growing in higher and lower light classes (Table 5.3). The upper-lateral branches in *Lithocarpus hancei* saplings tended to extend more erectly than those in *Fagus lucida* and *Castanopsis lamontii* saplings.

The top shoots of the two beech species and *Carpinus cordata* became very bent when growing under a closed canopy (Fig. 5.2). Some released saplings demonstrated that these bent top shoots usually bore newly reiterated units with upright leaders after canopy openings had been created. Lateral branches were usually more ramified in the species with



Figure 5.1. Above: a *Fagus lucida* sapling (Troll's model), 4.5 m tall, growing in an open site, showing its straight top shoot, abundant lateral branches, and erect upper branches. Photograph taken in September 1991. Below: a lateral branch complex from an understorey *Fagus lucida* sapling, viewed from above, showing the foliage arranged in a plane and ramified branches. Photographed in October 1992.

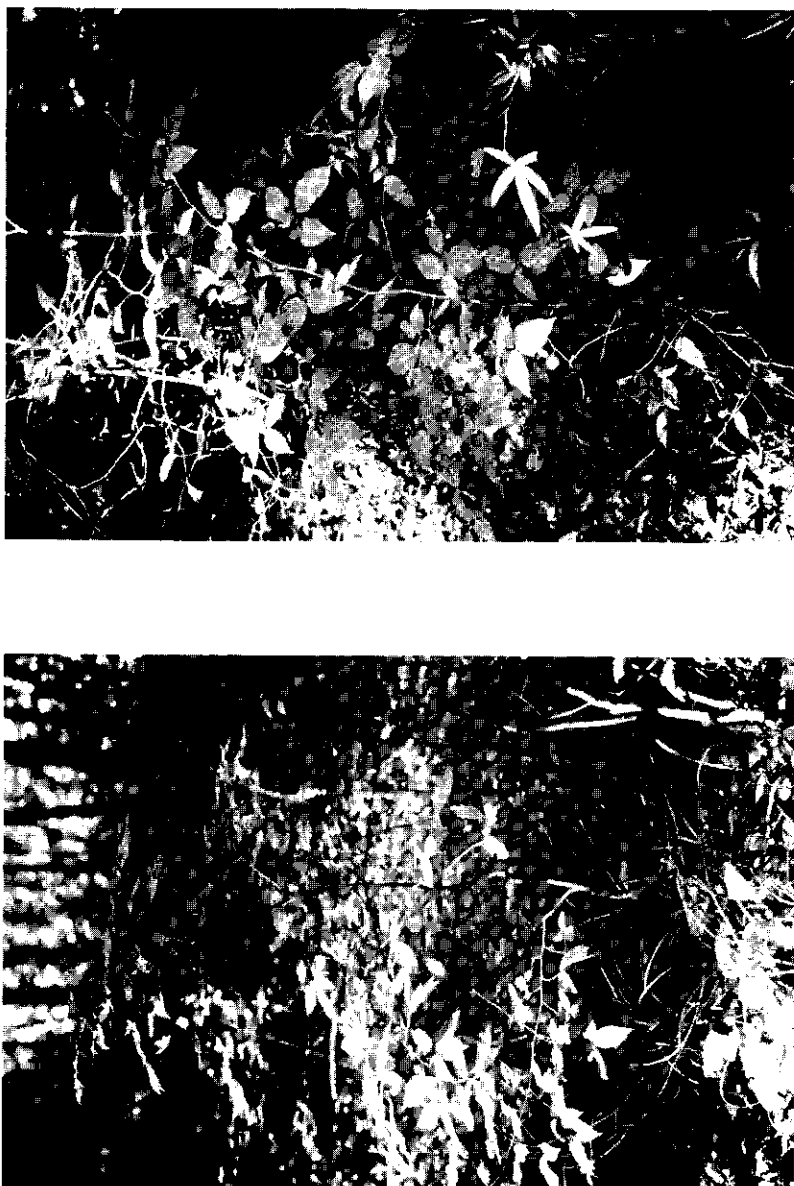


Figure 5.2

Left: an understorey *Fagus hayatae* sapling (1 m tall, Troll's model), showing its bent top shoot and horizontal lateral branches. Photographed in September 1991.
Right: an understorey *Carpinus cordata* sapling (0.8 m tall, Troll's model), showing its horizontal branches and bent top shoot. Photographed in September 1992.

plagiotropic branches than in those with orthotropic branches (Figs. 5.1, 5.3-5.5). *Manglietia chingii* saplings with large leaves were poorly branched, and in shaded understorey they often had only few leaf-bearing shoots at their tops.

In Miao'ershan, only *Fagus lucida* saplings significantly reduced leaf-bearing shoot density when growing in sites with less than 5% daylight (Table 5.3). The leaves of *Fagus lucida* saplings usually became thinner and had a larger SLA (specific leaf area: $\text{cm}^2 \text{g}^{-1}$) in shadier than in brighter sites (Table 5.4). This was not so in the evergreen *Castanopsis lamontii* saplings growing in different light intensity classes. In neither *Fagus lucida* nor *Castanopsis lamontii* was leaf size light-dependent (Table 5.4).

In Miao'ershan, the saplings of all the species studied except *Manglietia chingii* had a greater h_d/d ratio when growing in low light intensity than in high light intensity (Table 5.3). Among the saplings in Miao'ershan, in a similar height, *Castanopsis lamontii* saplings tended to have the largest diameter (Fig. 5.7).

Among twenty-six sampled saplings of *Manglietia chingii*, eight were root collar sprouts originated from older stems growing under the canopy with less 6% daylight (e.g. Fig. 5.5), and one was a sprout formed from an older fallen stem growing in a large gap. Some of the older stems in *Manglietia chingii* sprouts were dead. The older stems were growing very slowly and were much shorter than their sprouts. Basal sprouts also occurred occasionally in the shade-suppressed saplings of *Castanopsis lamontii*. The sprouts of *Manglietia chingii* had often formed before the older stems had died. However, the sprouts of *Castanopsis lamontii* were observed to have formed after the older stems had died back. These basal sprouts in both species usually grew much faster than the previous stems.

Captions to Figures 5.3-5.5.

Figure 5.3 (p.66):

a. A *Castanopsis lamontii* sapling (Massart's model), 4 m tall, which was removed from the forest and had been growing under *Fagus lucida* canopy, showing its straight top shoot and diffusely growing planar lateral branches. Its lower branches were self-pruned because of space competition from *Indocalamus longiauritus*, otherwise, more lower branches could possibly be maintained, as observed elsewhere. Photographed in October 1991.

b. A *C. lamontii* sapling, 1 m tall, growing beneath a closed canopy but not crowded in the same height, showing its wide and decurrent crown, and its plagiotropic shoots. Photographed in October 1992.

c. A branch complex from an understorey *C. lamontii* sapling (removed from the forest), viewed from above, showing its foliage arranged in a plane and well-developed second order branches. Photographed in October 1992.

Figure 5.4 (p.66). Crown part of a *Lithocarpus hancei* (Rauh's model) sapling (4 m tall), removed from the forest, which had been growing in a canopy gap without bamboos in the understorey, showing its straight top shoot, rather narrow crown, rhythmic branching and sympodial trunk (arrow). Photographed in October 1992.

Figure 5.5 (p.67):

a. A *Manglietia chingii* sapling (Scarrone's model), 4.5 m tall, growing in a large gap, showing its wide and deep crown, and its orthotropic branches which are poorly ramified. Photographed in October 1991.

b. An understorey *M. chingii* sapling 2 m tall, regenerated from an older stem (arrow), showing only few shoots bearing large leaves near the top. Photographed in October 1992.

c. Crown part of a *M. chingii* sapling 4 m tall, growing in a canopy gap, showing its narrow crown, few un-ramified shoots, and rhythmically branching. Photographed in September 1992.

d. Top part of the former sapling (Fig. 5.5c), showing its sylleptic, orthotropic shoots and sympodial trunk (arrow).

Fig. 5.3a



Fig. 5.3b



Fig. 5.3c



Fig. 5.4



Fig. 5.5



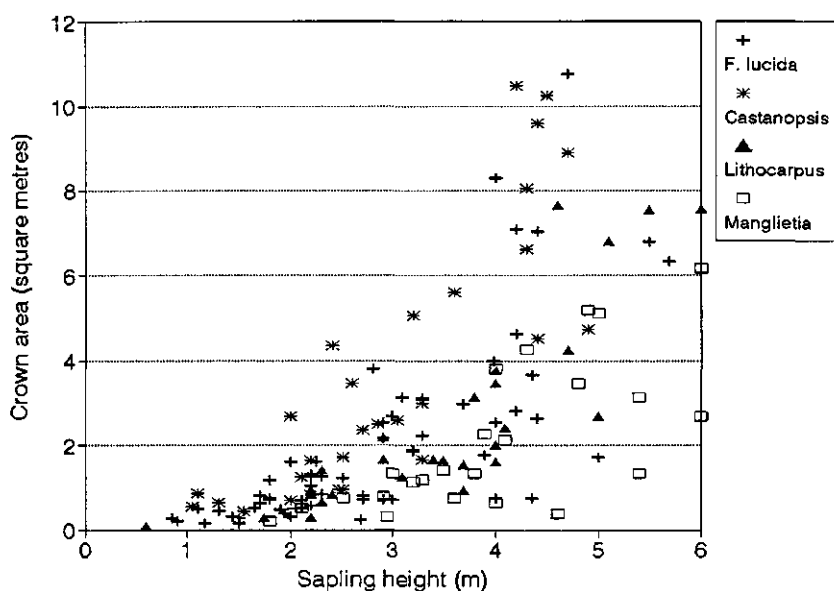


Figure 5.6. Comparison of crown areas (projection) in relation to height among the saplings of *Fagus lucida*, *Castanopsis lamontii*, *Lithocarpus hancei* and *Manglietia chingii*, growing in less than 20% daylight.

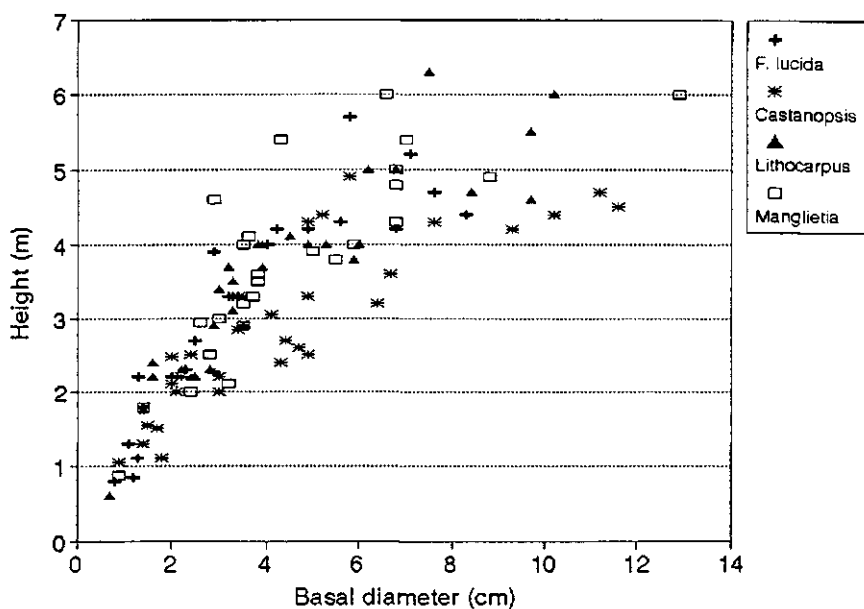


Figure 5.7. Comparison of relations of height and trunk diameter among the saplings of *Fagus lucida*, *Castanopsis lamontii*, *Lithocarpus hancei* and *Manglietia chingii*, growing in less than 20% daylight.

Table 5.3. Comparison of some architectural parameters of the saplings in Miao'ershan in the three light classes.^a

	< 5% daylight			5-10% daylight			> 10% daylight		
	avg	se	N	avg	se	N	avg	se	N
<i>Fagus lucida</i> (by ANOVA test)									
Top shoot angle (°)	24.9 ^a	6.0	12	5.6 ^b	4.0	9	0 ^b	0	12
Upper branch angle	55.4 ^a	4.1	12	59.5 ^a	2.5	10	37.3 ^b	4.1	12
Mid-branch angle	63.3 ^a	3.7	12	67.0 ^a	3.4	10	47.6 ^b	5.7	12
Lower branch angle	70.8 ^a	4.9	12	75.5 ^a	3.9	10	63.9 ^a	4.8	12
h_t/h_l ratio (m m ⁻¹)	0.43 ^a	0.05	13	0.37 ^a	0.03	10	0.22 ^b	0.06	14
h_t/d ratio (m cm ⁻²)	1.07 ^a	0.08	13	0.96 ^a	0.05	11	0.65 ^b	0.05	16
Shoot density (no. m ⁻²)	140.1 ^a	12.7	12	199.7 ^b	18.2	9	242.9 ^b	31.0	10
<i>Castanopsis lamontii</i> (by NPAR test)									
Upper branch angle	70.6 ^a	4.3	8	53.0 ^b	4.6	5	60.4 ^a	3.7	12
Mid-branch angle	73.1 ^a	4.5	8	64.0 ^a	8.9	5	68.8 ^a	4.2	12
Lower branch angle	78.1 ^a	4.6	8	67.0 ^a	8.0	5	67.0 ^a	6.2	12
h_t/h_l ratio	0.43 ^a	0.03	8	0.36 ^a	0.06	7	0.39 ^a	0.04	12
h_t/d ratio	0.91 ^a	0.07	10	0.69 ^b	0.08	7	0.64 ^b	0.06	14
Shoot density	58.0 ^a	8.8	8	59.0 ^a	3.8	4	63.7 ^a	10.1	10
<i>Lithocarpus hancei</i> (by NPAR test)									
Upper branch angle	32.5 ^a	12.5	2	43.8 ^a	9.0	4	42.5 ^a	10.3	4
Mid-branch angle	51.0 ^a	12.8	5	51.7 ^a	5.9	6	65.0 ^a	13.2	3
Lower branch angle	68.0 ^a	6.3	5	63.0 ^a	8.1	6	62.0 ^a	9.6	6
h_t/h_l ratio	0.52 ^a	0.05	10	0.53 ^a	0.06	6	0.44 ^b	0.04	4
h_t/d ratio	1.00 ^a	0.07	10	1.01 ^a	0.09	7	0.70 ^b	0.06	7
Shoot density	95.9 ^a	11.7	10	122.3 ^a	20.3	7			
<i>Manglietia chingii</i> (by NPAR test)									
h_t/h_l ratio	0.36 ^a	0.05	9	0.30 ^a	0.04	9			
h_t/d ratio	0.85 ^a	0.07	9	0.85 ^a	0.07	9			
Shoot density	22.5 ^a	2.6	8	30.0 ^a	4.0	8			

^a Significance of difference in mean or median among groups corresponding to the three light classes was tested by one-way ANOVA or NPAR tests for each species and indicated by superscripts: a different letter indicates a statistically significant difference between two groups per item per species ($p < 0.05$).

5.3.2 Light and growth

In the saplings of all species studied except in *Carpinus cordata* and *Fagus lucida*, their radial trunk growth rate was more strongly related to light than the elongation growth rates of top shoot and lateral branch (Table 5.5). In Miao'ershan, the two species with orthotropic branches, *Lithocarpus hancei* and *Manglietia chingii*, showed a stronger relation between either top shoot elongation rate or radial trunk growth rate and the percentage of daylight than the two species with plagiotropic branches, *Fagus lucida* and *Castanopsis lamontii*.

In Daba, in less than 5% of daylight, the saplings of *Fagus hayatae* and *Carpinus cordata* showed similar growth rates of either radial trunk or top shoot or lateral branch extension (Table 5.6). Also, in overtopped poles the radial trunk growth rates of the three species in Daba was not statistically significantly different (Table 5.7). In canopy gaps, the radial growth rate of *Fagus hayatae* poles was statistically significantly greater than those of *Carpinus cordata* and *Quercus aliena* poles.

Table 5.4 Average single-leaf area (cm^2) and Specific leaf area (SLA: $\text{cm}^2 \text{g}^{-1}$) in saplings of the main species growing in less than and more than 10% daylight. Data are means and standard deviations based on average value per sapling, N = number of saplings. Superscripts indicate significance of differences between either single-leaf area or SLA per species in the two light classes ($P < 0.05$; Mann-Whitney u test). See the definition of long and short shoots in the text.

Species		< 10% daylight					> 10% daylight				
		N	Leaf area		SLA	sd	N	Leaf area		SLA	sd
			Avg	sd				Avg	sd		
<i>Fagus hayatae</i>	Long shoots	7	14.30	1.66	268.09	31.08					
	Short shoots	7	11.29	1.54	295.04	25.50					
<i>Carpinus cordata</i>	Long shoots	4	22.05	9.61	233.73	25.11					
	Short shoots	5	14.33	6.79	267.81	32.10					
<i>Fagus lucida</i>	Long shoots	4	23.20 ^a	1.57	227.55 ^a	50.35	4	23.92 ^a	3.18	142.19 ^b	32.50
	Short shoots	5	20.68 ^a	1.88	223.35 ^a	12.77	4	22.15 ^a	4.08	168.20 ^b	42.70
<i>Castanopsis lamontii</i>		4	29.32 ^a	9.25	80.71 ^a	6.93	5	31.62 ^a	9.65	74.59 ^a	5.90
<i>Lithocarpus hancei</i>		3	13.09	2.12	81.78	6.11	1	16.62		86.90	
<i>Manglietia chingii</i>		2	60.20	11.60	81.28	3.76					

Table 5.5. Partial correlation coefficients (Pr_i^2) of mean growth rates over the last five years of saplings per species against logarithm of relative light intensity and logarithm of sapling height.¹

Species	Independent variables	radial trunk gr.		Trunk elong.		Branch exten.		Upper branch exten.	
		Pr_i^2	N	Pr_i^2	N	Pr_i^2	N	Pr_i^2	N
<i>Fagus hayatae</i> ^a	Ln(Light %)	0.533**	32	0.389*	34	0.384*	32	ns	32
	Ln(Height)	0.540**	32	0.438**	34	ns	32	0.460*	32
<i>Carpinus cordata</i> ^a	Ln(Light %)	ns ^c	17	0.386*	27	0.487**	26	0.540**	26
	Ln(Height)	0.705*** ^c	17	0.527**	27	ns	26	0.493**	26
<i>Fagus lucida</i> ^b	Ln(Light %)	0.592**	18	0.543*	19	0.516*	16	0.535*	16
	Ln(Height)	ns	18	0.744***	19	0.495*	16	0.560*	16
<i>Castanopsis</i> sp. ^b	Ln(Light %)	0.590**	20	0.450*	22	0.589*	20	ns	20
	Ln(Height)	0.590**	20	ns	22	ns	20	ns	20
<i>Lithocarpus hancei</i> ^b	Ln(Light %)	0.789***	22	0.601**	23	ns	18	ns	18
	Ln(Height)	ns	22	ns	23	0.552*	18	0.541*	18
<i>Manglietia chingii</i> ^b	Ln(Light %)	0.739	14	0.610**	13	ns	9	0.583 ^d	9
	Ln(Height)	ns	14	ns	13	0.763**	9	0.592 ^d	9

¹ units used: m for height, $\text{mm} \cdot \text{y}^{-1}$ for radial trunk growth rate, $\text{cm} \cdot \text{y}^{-1}$ for the top-shoot elongation rate and for the branch and upper branch growth rates.

^a bamboos were unimportant in the undergrowth.

^b with dense bamboos in the undergrowth.

^c growth rate was transformed to natural logarithm.

Two-tailed significance: ns = not significant ($p > 0.05$); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

^d $p = 0.09$, the two Pr_i^2 were retained because they originated from small samples.

Table 5.6. Average growth rates of radial trunk, top shoot extension, average lateral branch extension (from the selected branches of between 1 and 3 branches per sapling) and upper lateral branch extension over last five year of saplings between 2 to 5 m tall of the main species studied, in less than 5%, 5 to 10% and above 10% of daylight, in the two Chinese beech forests.^a

Species	Light level	N	Trunk radial avg	sd	Top shoot exten. avg	sd	Branch exten. avg	sd	Upper branch exten. avg	sd
Daba										
<i>Fagus hayatae</i> ^b	< 5%	20	0.51	0.19	16.2	6.3	11.5	5.5	15.0	6.9
<i>Carpinus cordata</i> ^b	< 5%	19	0.59	0.13	16.1	4.4	11.7	4.5	13.1	4.9
Miao'ershan										
<i>Fagus lucida</i> ^c	< 5%	13	0.74	0.27	15.2	4.7	10.3	3.4	12.1	4.4
	5-10%	11	0.98	0.36	18.4	3.8	14.1	1.7	14.9	2.9
	> 10%	11	1.75	0.76	23.2	3.3	15.4	1.7	18.3	3.7
<i>Castanopsis</i> sp. ^c	< 5%	10	1.09	0.45	14.2	2.8	13.2	3.4	14.5	4.3
	5-10%	7	1.47	0.32	17.7	7.4	17.2	3.1	21.2	4.3
	> 10%	14	2.03	1.11	20.9	6.2	17.9	2.6	19.3	3.2
<i>Lithocarpus hancei</i> ^c	< 5%	10	0.81	0.21	14.5	2.6	12.0	3.0	12.7	2.7
	5-10%	7	1.32	0.37	17.4	4.4	13.6	2.2	15.5	4.4
	> 10%	6	2.25	1.14	29.5	7.6	20.0	3.6	23.1	4.4
<i>Manglietia chingii</i> ^c	< 5%	9	1.24	0.49	15.9	8.1	6.3	2.6	6.3	2.6
	5-10%	8	1.89	0.52	22.4	3.9	9.7	4.1	12.5	7.2
	> 10%	2	1.33-2.25	30.2-41.7	16.8		28.7			

^a see Table 5.5 for units of the growth rates. ^b without a dense lower vegetation in the undergrowth.

^c with a dense undergrowth of *Indocalamus longiauritus*.

Table 5.7. Comparison of average radial trunk growth rates over the last five years in pole trees taller than 5 m among the dominant species per study site, growing under forest canopy or in canopy gaps.¹

Species	Under canopy			In gaps		
	N	avg mm y ⁻¹	sd	N	avg mm y ⁻¹	sd
Daba						
<i>F. hayatae</i>	10	0.47 ^a	0.25	11	1.73 ^a	0.90
<i>Carpinus cordata</i>	7	0.48 ^a	0.21	8	0.97 ^b	0.26
<i>Quercus aliena</i> ²	4	0.37 ^a	0.03	5	1.07 ^b	0.36
Miao'ershan						
<i>Fagus lucida</i>	13	0.62 ^a	0.39	12	1.72 ^a	0.62
<i>Castanopsis lamontii</i>	7	1.23 ^b	0.47	6	3.05 ^b	0.97
<i>Lithocarpus hancei</i>	6	1.09 ^b	0.24	10	2.38 ^{abc}	0.89
<i>Manglietia chingii</i>	8	1.03 ^b	0.26	5	1.90 ^{ac}	0.37

¹ One-way ANOVA significance of difference was indicated by superscripts: a different superscript between two means indicating a statistically significant difference in a same light class ($p < 0.05$). An analysis by T-test showed that for each species the growth rate was statistically significantly larger when growing in gaps than growing under a canopy ($p < 0.05$).

² *Quercus aliena* was usually not completely covered by a forest canopy.

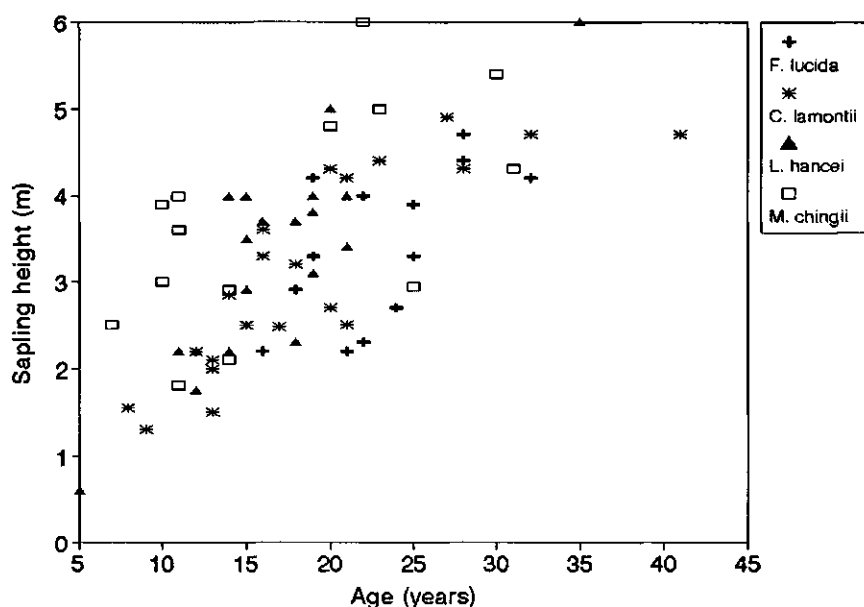


Figure 5.8. Comparison of height in relation to age among the saplings of *Fagus lucida*, *Castanopsis lamontii*, *Lithocarpus hancei* and *Manglietia chingii*, growing in less than 20% daylight.

In Miao'ershan, under all three light classes, the trunk-radial growth rates of the saplings of the three evergreen species were greater than that of *Fagus lucida*. In all three light classes the top shoot elongation rates in the beech saplings were comparable to those of the evergreen saplings. However, in the shaded understorey, the bent distal parts of the trunks reduced absolute height growth in the beech saplings. Thus, in the forest understorey the beech saplings were often shorter than the evergreen saplings of the same age (Fig. 5.8). In less than 10% of daylight the saplings of *Manglietia chingii* extended their branches more slowly than those of other three canopy species (Table 5.6). Therefore, *Manglietia chingii* had the narrowest crowns (Figs. 5.5 & 5.6). Under the canopy, the poles of the three evergreen species had significant greater trunk radial growth rates than the beech poles (Table 5.7). In canopy gaps only *Castanopsis lamontii* poles had significant greater radial growth rate than the beech poles.

5.4 DISCUSSIONS

5.4.1 Architectural adjustment: minimizing self-shading

The studied species with different branching patterns made somewhat different architectural adjustments to different light environments. The trees with plagiotropic branches tended to

form wider crowns than those with orthotropic branches. This tendency became more pronounced in shaded conditions (Figs. 5.3.-5.5). In shaded conditions, the plagiotropic branches usually extended in different directions and formed several layers in taller saplings so as to minimize self-shading among the branches of a sapling. Minimizing self-shading is beneficial for survival in forest understories. A low degree of self-shading has a large impact on net photosynthesis near the compensation point, whereas the additional transpirational costs resulting from more direct exposure are negligible (Givnish 1984).

Compared to the orthotropic lateral branches in the saplings of *Lithocarpus hancei* and *Manglietia chingii*, the plagiotropic branches in the saplings of *Fagus lucida* and *Castanopsis lamontii* were usually more ramified (Figs. 5.1, 5.3-5.5). This tendency also became more pronounced in shaded conditions. This formation of "green fans" (Figs. 5.1 [below] & 5.3c) is certainly beneficial for light interception in understories. In contrast, in the understory, orthotropic branches of *Lithocarpus hancei* were less divided and the lower branches were more frequently self-pruned. In this way the saplings reduced self-shading and maintenance cost and improved survival.

The evergreen *Manglietia chingii* bearing large leaves adjusted its architecture differently. In low light intensities *Manglietia chingii* limited its shoot and leaf production and bore a limited number of large leaves, mainly on the apical part of the sapling (Fig. 5.5). This poorly branched and large-leaved crown form is also found in other understory saplings in mesic tropical and subtropical forests (Kohyama 1987; Kohyama & Hotta 1990; Oldeman & Van Dijk 1990). These are shade-tolerant species. However, Brünig (1976) suggests that large-leaved and sparsely branched crowns are typical in light-demanding trees in humid tropical forests on fertile sites.

The trees with plagiotropic mixed axes (Troll's model) have another way to avoid shading: they bend distal parts of their trunks in a certain direction (Fig 5.2; Table 5.3). Hallé *et al.* (1978) suggest that trees conforming to Troll's model are particularly flexible in architecture because all their axes are plagiotropic mixed and they have the potential of either horizontal or vertical extension. Architectural flexibility is indeed seen in the two Chinese beech species and in *Carpinus cordata*, which conform to Troll's model. The architectural flexibility is also found in other trees conforming to Troll's model, e.g. in *Fagus sylvatica* L. (Thiébaud 1988), and in *Fagus grandifolia* Ehrh. (Canham 1988), and in leguminous trees (Oldeman 1989a).

Not only plagiotropic axes but, in some trees, also orthotropic axes may arrange leaves in a planar single layer and minimize self-shading; for example, plagiotropy by apposition and by secondary plagiotropy of orthotropic axes (Hallé *et al.* 1978, their Fig. 12). One example of organizing leaves in a single layer in orthotropic axes is *Acer saccharum*. When growing in the understory, the petioles of *Acer saccharum* twist around so that the opposite, lobed leaves are displayed in a planar array on the horizontal branches (Steingraeber *et al.* 1979). In contrast, when growing in sunny environments its branches are usually more erect, the leaf petioles extending directly outwards. Similar horizontal arrangement of foliage by axes orthotropic in nature are observed in many other trees, e.g. *Acer* spp. in Europe, *Cyclobalanopsis multinervis* and *Betula insignis* in China (pers obs.). A further example of horizontal foliage occurs in *Neea amplifolia* (Nyctaginaceae), a medium-sized tree native to the coast of Central America; the vertical growth of its twigs along an oblique branch axis

can be corrected in such a way that all leaf-bearing distal twigs remain at the same horizontal level (Fisher 1986). The architectural flexibility related to branch orientation and leaf display is important for plant adaptation to different light environments.

5.4.2 Basal sprouting

Basal sprouting in the saplings of *Manglietia chingii* (Fig. 5.5b) and *Castanopsis lamontii* is a reiteration strategy for survival in forest understorey. Similarly, in shade *Ilex opaca* (Florida) makes basal sprouts that replace suppressed and dying trunks (Peters & Platt in prep.). Vegetative sprouting as a strategy for survival in shade is also known in tropical forest trees (pers. comm. Oldeman). Basal sprouting seems to be a common strategy in shrubs for survival in shade (Koop 1987). However, although much has been published about vegetative sprouting in trees as a strategy for survival in other adverse environments (e.g. Fanta 1981; Held 1983; Mayer 1984; Jones & Raynal 1986; Koop 1987) or after physical injury (e.g. Oldeman 1974a; Putz & Brokaw 1989; Basnet 1993), the literature on vegetative sprouting in trees as a strategy for survival in shade is scarce.

5.4.3 Leaf-size adjustments

Leaf adjustments in relation to light intensity were found in the deciduous *Fagus lucida* but not in the evergreen *Castanopsis lamontii* (Table 5.4). Increased SLA in low light intensity in *Fagus lucida* suggests the formation of shade leaves (Strasburger *et al.* 1978) but its single-leaf surface area remained unchanged. After examining 61 woody species in the rain forest at Los Tuxtlas of Mexico, Bongers and Popma (1988) concluded that within species, sun-grown leaves commonly have a smaller surface area and a higher specific leaf weight. The relatively constant leaf size and SLA of *Castanopsis lamontii* in relation to light may be explained by assuming that the shade in the understorey in Miao'ershan is not deep enough to induce shade-leaf formation in the evergreen species. However, some juvenile trees, particularly light-demanding, do not form shade leaves (Kramer & Kozlowski 1979). Strong competition from the undergrowth for water and nutrients probably limits the leaf growth of the deciduous *Fagus lucida* in the low light intensity.

5.4.4 Growth adjustment

The findings of this study suggest that juveniles of overstorey or subcanopy tree species follow a common strategy in low light intensity, by investing relatively more resources in height growth by comparison with diameter growth, so as to reach brighter environments. In Miao'ershan, the height/diameter ratio of saplings of all the studied species except *Manglietia chingii* increased with decreasing light intensity classes (Table 5.3). This was also supported by the finding that height growth rate of the saplings in both study sites was related to the relative light intensity less strongly than diameter growth rate (Table 5.5). Oldeman (1974a, 1990) has reported that nearly all model-conforming trees in French Guiana have the

ratio $h_t/d = 100$, in which h_t is total height (cm) of a sapling and d is basal trunk diameter (cm); whereas trees that have regenerated from broken trunks show $h_t/d > 100$ and the trees with crown expansion by abundant reiteration have a ratio in the interval: $h_t/d < 100$. In the present study the saplings in the forest understorey had a ratio of $h_t/d = 100$ as in the "model-conforming" trees (Table 5.3). However, the saplings growing in large canopy gaps or in open sites usually had a ratio of $h_t/d < 100$ although they were often still in model-conforming phase. They then had decurrent crowns with abundant branches. This confirms Oldeman's hypothesis of a shorter $h_t/d = 100$ period when trees grow in open sites and are widely spaced (Oldeman 1974a & his Fig. 26). This shortened $h_t/d = 100$ period in the saplings of this study is mainly due to increasing photosynthesis inside the model itself as the result of abundant branches. The height-diameter relation in the saplings in different light classes is consistent with the pipe-model theory (Shinozaki *et al.* 1964; Oldeman 1974a; 1978; 1989; Cannell & Dewar 1994). Compared to understorey saplings, the well illuminated saplings have wider crowns, bear more abundant branches and leaves, and thus gain more carbon which enhances cambium and root growth. In the meantime they require more water, more nutrients and more mechanical supporting organs. Therefore they develop larger trunks (faster diameter growth).

5.4.5 Growth in relation to architecture and leaf persistence

A stronger relation between light intensity and growth rate of either diameter or top shoot was found in the saplings with orthotropic branches than in those with plagiotropic branches (Table 5.5). Also, among the evergreen trees the saplings with orthotropic branches tended to have more slender trunks than those with plagiotropic branches (Fig. 5.7). Compared with the saplings with wider crowns and plagiotropic branches, the saplings in the understorey which have narrower excurrent crowns with orthotropic shoots apparently intercept less light. Their growth is more strongly dependent on light, and height growth is vital for them to reach brighter environments.

The absolute growth rates of the saplings and poles in the southern site were strongly affected by leaf persistence. The evergreen saplings and poles grew faster in height and diameter than the deciduous beech ones, regardless of their architecture (Tables 5.6 & 5.7). In a warm climate, evergreen trees retain their leaves throughout the year and thus are able to photosynthesize and grow in a longer season (Kusumoto 1957; Li & Wang 1984; Yang *et al.* 1992). They also use nutrients and carbon more efficiently (Chabot & Hicks 1982; Schulze 1982; Hollinger 1992). This makes them more tolerant of conditions in the shaded understorey and they grow faster than deciduous trees. In many tree genera, evergreen species are more shade-tolerant than deciduous species of the same genus; e.g. as in *Quercus* (here including *Cyclobalanopsis*), *Rhododendron*, *Symplocos*, *Lindera* and *Litsea* (pers. comm. XP Wang; 1991).

The shade-tolerant trees of canopy and subcanopy species probably have different growth programmes (e.g. Xie *et al.* 1983; Mayer 1984), which determine their response to light in their different developmental phases. In Daba the subcanopy tree *Carpinus cordata* and the

canopy species *Fagus hayatae* had comparable growth rates in their sapling phases. However, in the canopy gaps, *Carpinus cordata* poles grew much slower in diameter than *Fagus hayatae* poles (Table 5.7). In contrast to the subcanopy trees, the fact that *Quercus aliena* poles had slower diameter growth in canopy gaps than *Fagus hayatae* ones implies that the *Quercus aliena* demands more light because much larger radial-growth rates were found in other better illuminated poles or canopy trees of this species (unpubl. data).

Basal sprouts also affected sapling growth. Basal sprouts in understorey *Manglietia chingii* saplings have rapid initial height growth although the light remained similar (pers. obs.). These sprouts certainly profited from an existing root system. Rapid initial height growth is also found in root sprouts of *Liquidambar styraciflua* in northern Florida (Peters & Platt in prep.).

5.4.6 Regeneration and dominance

In Miao'ershan, the predominance of *Fagus lucida* in the forest canopy contrasts to its poor regeneration (Chapter 4) and its growth lagging behind the evergreen species in their sapling and pole phases (Tables 5.6-5.7). Beeches can grow in a wide range of site conditions (Braun 1950; Ellenberg 1988; Peters 1992). The Chinese beeches are able to dominate poor rocky mountain ridges and steep slopes, where the growth conditions are difficult for many other trees. These beeches produce durable beech seed sources. Thus, once suitable sites are available, adequate beech regeneration becomes possible. Also, probably largely benefiting from their efficient architecture (cf. Leguminosae, Oldeman 1989), the Chinese beeches are able to resume their growth when released after surviving a long shade suppression (Fig. 5.9). In the USA, *Fagus grandifolia* can survive suppression for more than 120 years (Canham 1990; Peters 1992).

Like other Northern Hemisphere beeches, by persisting in the understorey and benefiting from periodic canopy openings, some juvenile Chinese beeches eventually grow up to reach the overstorey (Fig. 5.9; Cf. Canham 1988; Peters & Poulson 1994). The branching system of plagiotropic mixed axes allows the beeches to build up large and wide crowns, shading out trees underneath (cf. Ashton 1976; Hilgen & Van den Brenk 1984). In montane Chinese beech zones ice storms frequently break exposed crowns of evergreen broadleaved trees, but usually leave beech crowns undamaged (Chapter 3). These broken crowns give access to wood-rot fungi in the supporting trunks (Shigo 1986; Zabel & Morrell 1992). The broken crowns, together with rotten trunks cause many evergreen trees to fail to dominate the canopy. The beeches are leafless in winter, have a high wood density and slender, supple plagiotropic twigs, and so are better protected against ice storms and against pathogens. Moreover, if injured, the beeches repair their crowns better by vigorous reiteration than the other dominants (pers. obs). Therefore, ice storms in Chinese beech forests favour beeches rather than evergreen broadleaves to dominate the forest canopy.

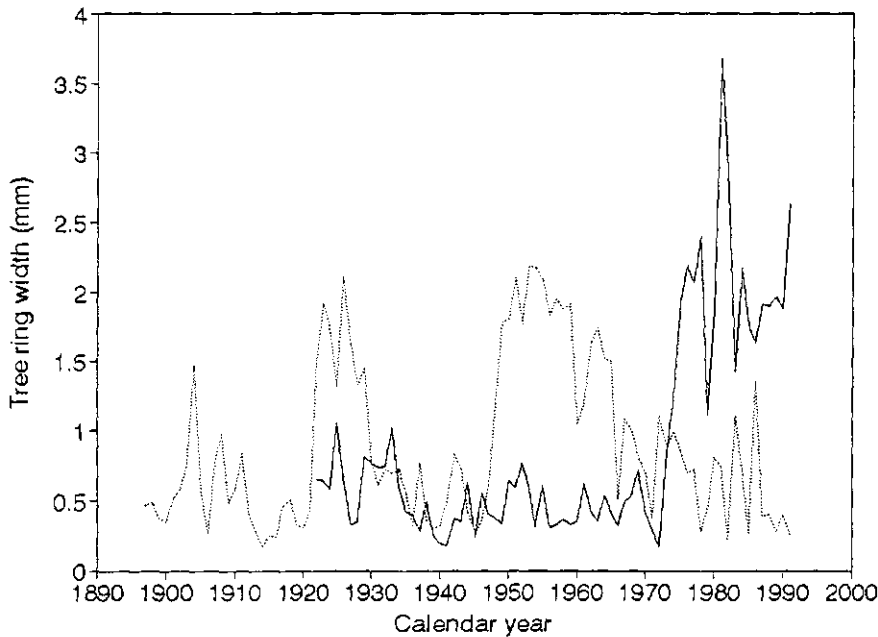


Figure. 5.9. Examples of suppressed and released radial trunk growth of *Fagus lucida*: the older one having reached the overstorey, the other one being released after some 50 years' suppression.

5.5 CONCLUSIONS

In the six species studied, saplings with orthotropic branches tended to grow narrower and shallower crowns and trunks more slender than those with plagiotropic branches. The trees conforming to Troll's model characterized by plagiotropic mixed axes were highly flexible in architecture. In the understorey, the evergreen subcanopy species *Manglietia chingii*, with large and entire leaves and orthotropic shoots, had the narrowest crowns with poorly ramified branches. Basal sprouting as in *Manglietia chingii* and *Castanopsis lamontii* was found to be a reiteration strategy for survival in shaded understoreys.

The growth rates of the saplings studied correlated with their architecture, but correlated even more strongly with leaf persistence. The shade-tolerant saplings bearing orthotropic branches had stronger relations between the growth rates and light intensity than those bearing plagiotropic branches. The evergreen juveniles grew faster than the deciduous beech ones, regardless of their architecture.

However, future canopy dominance in Chinese beech forests cannot be predicted with certainty from growth rates and the overall abundance and frequency of juvenile trees. Although the young evergreen trees are abundant and grow faster than the young beeches in Miao'ershan, the success of *Fagus lucida* in dominating the forest canopy is largely due to availabilities of open patches and a durable seed source.

Chapter 6 Synthesis and conclusions

6.1 SYNTHESIS

6.1.1 Main factors limiting Chinese *Fagus* distribution

Among the Northern Hemisphere beeches, only the Chinese species are confined to the south. However, as they mainly occur in the montane zones between 700 and 2500 m in altitude, they enjoy a climate very similar to that experienced by the other beeches in the north of the Northern Hemisphere (Chapter 2). In most of northern China, the climate is very continental. Water deficits and cold winters prevent beech from growing there. However, along the coastal area of Bohai Bay in northeastern China, the climate is still within the climatic range of *Fagus* habitats. During the Holocene Megathermal (5,000-8,000 B.P.), *Fagus* did occur in this area (Wang YJ & Li 1983; Xu *et al.* 1993), but, intense human activities throughout the long history of China probably caused beech to become extinct here. However, re-introduction is possible in view of our present knowledge.

In the lowlands below the montane Chinese beech zones, the hot climate with occasional water deficits in the growing season is unfavourable for beech. However, *Fagus longipetiolata* is occasionally found below 700 m (at about 400-500 m) in the eastern and central areas of the *Fagus* range. The findings presented in Chapters 2 and 5 suggest that factors other than heat or moisture probably also prevent beech from occurring in the lowlands. The zonal vegetation in the lowlands below the Chinese *Fagus* range is an evergreen broadleaved forest. In the warm climate of this subtropical zone, evergreen trees of overstorey or subcanopy species usually grow faster (Chapter 5) than deciduous beech. Compared to beech, these evergreens are equally or more shade-tolerant. The disjunct occurrences of Chinese beeches reveal that these beeches were once much more widespread, e.g. during the Inter-glacials (Kong *et al.* 1977; 1992; Zhu 1979; Zhong *et al.* 1988). At present, the climate in the lowland favours evergreen broadleaved trees over beech. These evergreen trees have probably outcompeted beeches and have crowded them out from the lowlands.

In short, this study confirms that not only heat and moisture but also species competition and human activity influences the present range of Chinese *Fagus* species.

6.1.2 Climatic factors and species diversity

This study has shown that species diversity in Chinese beech forests correlates primarily with warmth and to a lesser degree with climatic hazards that cause the forest canopy to be opened up locally (Chapter 3). Increase of species diversity toward warmer climates is the master gradient in biogeography (Whittaker 1975). In Chinese beech forests, species diversity correlated positively with frequency of storms in combination with heavy rains. If the

"intermediate disturbance" hypothesis (Connell 1978) were true, this implies that the impacts of storms and heavy rains on Chinese beech forests are neither very frequent nor very intense.

Ice storms and snow storms cause major impacts in the Chinese beech forests in the central and northern areas of Chinese *Fagus* range. These cold hazards adversely affect the species diversity of the beech forests. They favour beech but not evergreen broadleaved trees nor fast-growing deciduous trees in canopy dominance. The strong resistance of beech is linked to its leaflessness in winter, which reduces its surface exposed to snow and ice, and to its dense wood.

6.1.3 Major factors related to beech regeneration

Beech regeneration is more abundant and frequent in the northern site (Daba) than in the southern site (Miao'ershan; Chapter 4). Bamboo is a common factor limiting beech regeneration in both sites. However, in the northern area of the Chinese *Fagus* range, bamboos die of cold regularly. In the northern site, beeches are mixed with deciduous broadleaved trees which can be shown to be less competitive than beech (Chapter 5), and in the understorey, plants other than bamboos are rather sparse. This opens the biotope for beech to regenerate there. In the southern site, beeches are mixed mainly with evergreen broadleaved trees, and the forest understorey is often dense. There, beech regeneration is strongly limited by the understorey vegetation (trees, shrubs and bamboos).

In the southern mixed beech forest, abundant juveniles of the evergreen broadleaved overstorey and subcanopy tree species contrast with their limited number in the overstorey or subcanopy. This is probably because of their sensitivity to ice or snow storms that break exposed crowns of the evergreen trees.

Beech adapts to a wide range of soils. Chinese beeches often predominate on nutrient-poor ridges and steep slopes which are probably inhospitable for many other co-dominants. In these sites, sources of vital beech seeds are durably maintained in the forests.

Storms, heavy rains, ice storms and snow storms are major factors that open the canopies of Chinese beech forests at the system levels of both eco-units and forest mosaics. Bamboos are likely to flower and die simultaneously once or twice a century (Numata 1970). If major disturbances coincided with the simultaneous death of bamboos over a large area, abundant beech regeneration could occur in Chinese beech forests in the north or in the south of the *Fagus* range, as long as there is a durable seed source of beech. Forest fires occurred in many of Chinese beech forests in the past. These fires created suitable sites for beech regeneration. Accidental man-made fires will probably still occur in Chinese beech forests, even in nature reserves, and may induce abundant beech regeneration if the timing is right with respect to beech fruiting.

Beech is known as a late successor or climax species (Braun 1950; Ellenberg 1988). However, Chinese beeches hardly regenerate beneath closed canopy largely because of suppression by the understorey vegetation. Instead, they usually regenerate beneath canopy

openings. The regeneration of *Fagus lucida* was found to be most abundant and also the growth of its saplings was found to be fast in large abandoned field next to beech stands or mature beech trees (Chapter 4). This suggests that the Chinese beeches have certain properties of pioneer species (cf. Whitmore 1989). However, many other late successional species also regenerate in the abandoned fields and large forest opening (Chapter 4). In secondary forest succession, early successional species are usually among the first to appear and to dominate, probably because their seeds disperse over longer distances than those of late successional species (Oliver & Larson 1990). The ecological amplitudes of certain late successor species for light and nutrients can be large.

6.1.4 Growth and architecture in relation to success of regeneration

The present study showed that in low light intensities juveniles of overstorey and subcanopy tree species usually invested relatively more resources in height growth than diameter growth (Chapter 5). The studied overstorey species are *Fagus lucida*, *Fagus hayatae*, *Castanopsis lamontii* and *Lithocarpus hancei*; the subcanopy species are *Manglietia chingii* and *Carpinus cordata*. The two beech species and *Carpinus cordata* are deciduous, the others are evergreen. In all the species studied, except for *Carpinus cordata*, height growth depends less than diameter growth on light. Extension and diameter growth in the species with orthotropic branches both depend more on light than is the case in the species with plagiotropic branches. However, leaf persistence (evergreen vs deciduous) is judged to have a stronger effect on the growth performance of saplings than their architecture. In the understorey, the species with orthotropic branches tend to optimize height growth so as to reach brighter environments, whereas the species with plagiotropic branches tend to persist in the understorey by efficiently spreading their assimilative organs, so intercepting light falling through the canopy. Basal sprouting was revealed as a reiteration strategy for survival in the understorey.

Fagus species all grow according to Troll's model, which is characterized by plagiotropic mixed axes (Hallé & Oldeman 1970). Their growth and architecture are very flexible in response to change of light and growing space and to physical injury. Flexibility in growth and architecture contributes greatly to the success of the natural regeneration and dominance of Chinese beeches in the forests. Furthermore, their deciduous habit and dense wood make beech particularly successful in the habitats with frequent glaze storms and snow storms because risks of permanent strain due to physical injury and biotic attack are significantly diminished.

6.2 CONCLUSIONS

Natural regeneration of Chinese beech species is both regulated by and adapted to many abiotic and biotic factors, e.g. heat, moisture, climatic hazards, species competition, site heterogeneity and human activity. The present scarcity of juvenile beeches in southern beech forests of the Chinese *Fagus* range does *not* foreshadow a diminishing beech dominance in the canopy, or the future replacement of beech by the other tree species which have abundant

juveniles at present. The opening up of beech forest canopies at forest mosaic level by external factors and simultaneous bamboo death can allow abundant beech regeneration to occur suddenly at any, unpredictable moment. Furthermore, beech is a genus adapted to many inhospitable habitats, e.g. nutrient-poor ridges and steep slopes, windy sites, and habitats with frequent freezing rains, freezing fogs and snow storms. Another survival property of beech is the plagiotropy of its axes, which enhances its flexibility in growth and architecture in response to frequent and/or abrupt change in available light and growing space, and to physical injury.

On the basis of the findings presented in this thesis, *I predict that beech dominance will be maintained in Chinese beech forests, both in the north and in the south of the present range, if the macro-climate remains similar.*

The study revealed the following plant strategies: (1) in low light intensities, juvenile trees invest relatively more resources in height growth than in diameter growth; (2) the growth of species with orthotropic branches depends on the light more than the growth of species with plagiotropic branches; in the understorey, species with orthotropic branches tend to optimize height growth, whereas species with plagiotropic branches tend to persist in the understorey by efficiently spreading their light-intercepting assimilative organs; (3) minimizing self-shading is a common strategy in the understorey juvenile trees, but this may happen in different ways; (4) basal sprouting is beneficial for survival of saplings suppressed by shade.

These plant strategies are worth further investigation. Based on the findings of this study, I suggest that the aims of biodiversity conservation are best served by establishing nature reserves over a wide geographical range of sites, which experience different frequencies and intensities of natural hazards, so as to conserve most of the associated species adapted to their related environments. This study has also shown that beech is useful for afforestation in the montane zones of subtropical China, and that beech might be successfully planted in the area near Bohai Bay in northeastern China.

SUMMARY

Fagus species are important components of certain mesic temperate forests in the Northern Hemisphere. Of eleven *Fagus* species distinguished, five are found in China. Chinese beeches are restricted to the mountains of southern China. In the montane zones of the northern subtropics beeches (*Fagus engleriana* in the north, and *Fagus hayatae* var. *pashanica* in the northwest) often predominate in the forests: they are mixed with several other deciduous broadleaved tree species. In these forests the understorey is rather sparse. In the montane zones of the middle and southern subtropics beeches (*Fagus lucida* at higher altitudes and *Fagus longipetiolata* at lower altitudes) dominate in many forests and are mixed mainly with evergreen broadleaved trees. There, in contrast, the forest understorey is often very dense and consists of evergreen trees or shrubs and bamboos. Bamboos often cover the forest floor throughout the range of Chinese beech forests.

All Chinese beech forests are natural forests, and they are rich in plant and animal species, many of which are rare or endangered. Mixed beech forests are major forest communities in many nature reserves or national parks established in subtropical China, and are important in biodiversity conservation. Because they are located on mountain slopes and ridges, Chinese beech forests are also important in the prevention of soil erosion and in the maintenance of the stability of watersheds. Beech yields good-quality hardwood timber, and has been suggested as being useful for afforestation in mountainous areas of subtropical China.

In the forests where Chinese beeches co-occur with evergreen broadleaved trees, adult beeches are common, whereas juvenile beeches are rare. This gave rise to the following research questions:

1. Will beech dominance in the forest canopy in these mixed forests be maintained, or are the current beech-dominated forests a stage in a longer successional cycle or series?
2. If beech remains dominant in the canopy, then where do juvenile beeches establish themselves, and how do they grow up and reach the canopy? How does beech differ from co-dominant tree species in these aspects?

The regeneration processes of trees in natural forests are regulated by many abiotic and biotic factors, e.g. climate, disturbances, species composition, architecture of the forests, and site heterogeneity. The temperament, growth performance and architecture of trees largely influence their success in regeneration. Therefore, the four aims of this study were:

1. To quantify climatic heat and moisture ranges in Chinese beech habitats (Chapter 2).

2. To determine the relation between macro-climate (temperature, precipitation and major climatic hazards) and species composition of Chinese beech forests (Chapter 3).
3. To identify the relations between topography and beech regeneration and between species composition and beech regeneration in two forests, representatives of the Chinese beech forests in the south and in the north of the beech range (Chapter 4).
4. To compare juvenile growth and architectural strategies of beech and other shade-tolerant canopy or subcanopy species in relation to the light environment (Chapter 5).

In chapter 2, data from herbaria, from literature and personal observations in ten beech sites are combined, and the occurrence and geographical range of each Chinese beech species are described and mapped. Using climatic data from 40 weather stations located in the montane zones of the beech range, the heat and atmospheric moisture ranges in the beech habitats were characterized using Thornthwaite's (1948) moisture index and annual potential evapotranspiration and Kira's (1945) Warmth and Coldness indices. To identify the climatic factors that limit beech distribution, the heat and moisture ranges in beech habitats were compared with those in the surrounding areas outside the beech range and in the lowlands below the beech range, using data from 111 weather stations in the surrounding areas and from the literature (Chang 1989; Fang & Yoda 1990). Also, the heat and moisture ranges in Chinese beech habitats were compared with those in beech habitats elsewhere in the world.

Chinese beeches occur in southern China (22.3-34.3° N; 101-121.5° E), mainly in the montane zones between 700 and 2500 m altitude. *Fagus longipetiolata*, *Fagus lucida* and *Fagus engleriana* have wide geographical ranges. *Fagus longipetiolata* has the widest range and occurs as far south as the tropical mountains in southeastern Yunnan province of China and in northern Vietnam. It occasionally occurs below 700 m in altitude (400 to 500 m) in lower parts of mountains in the eastern and central areas. *Fagus engleriana* is mainly found in the northern part of the whole *Fagus* range and is multi-stemmed. *Fagus lucida* is somewhat concentrated in the central area of that range. *Fagus chienii* and *Fagus hayatae* occur locally.

Chinese beeches experience a mean annual temperature ranging from about 5 to 17 °C, a Kira's Warmth Index of 40-140 °C·month, and annual potential evapotranspiration of 450-840 mm. They enjoy a humid to perhumid climate, Thornthwaite's moisture index (Im) lying between 26 and 320. They are found in areas with an annual precipitation of between 740 and 2800 mm largely concentrated in the growing season. Chinese beech forests mainly lie in perhumid climates (Im over 100), where water is sufficiently supplied throughout the year from precipitation. The heat requirements of Chinese and foreign beeches largely coincide. However, the warmth extremes in the American and Chinese beech habitats are larger than in the European and Japanese beech habitats. The conditions in the montane Chinese beech habitats are more humid than those in lowland beech habitats in Europe and North America. Northwards, Chinese beeches are limited by moisture deficits. But the climate of the area near the Bohai Bay in northeastern China is still within the climatic range of beech habitats. Southwards and at lower altitudes, high temperature and relatively low moisture are unfavourable to beech. However, like other beeches, Chinese beeches tolerate a certain water deficit occurring occasionally during the growing season. The failure of *Fagus* species to

compete with evergreen broadleaved trees probably largely determines their southern geographical and lower altitudinal limits.

In Chapter 3 the trends of occurrences of climatic hazards in the Chinese beech range are described using climatic data of eleven montane weather stations; and relations between climatic parameters (heat, moisture, hazards) and species diversity of Chinese beech forests were characterized. The climatic hazards studied are storms, heavy rains, freezing rains, freezing fogs, snow, thunderstorms, and hailstorms. They influence the development of the beech forests. Using the SURFER software (the Kriging method), the mean number of days per annum on which these hazards occur were interpolated and extrapolated for eight beech forests. The Shannon-Wiener diversity index, the number of woody species with individuals taller than 5 m, the relative importance of light-demanding trees and the relative importance of deciduous broadleaved trees were analysed in ten combined forest sample units (between 0.12 and 0.23 ha in area) in the eight beech forests, by combining the number of individuals and the basal area of each tree species represented by individuals taller than 5 m in each unit. These indices in the forest units smaller or larger than 0.20 ha were converted according to 0.20 ha. The relations between these indices and climatic parameters (temperature, annual precipitation and frequencies of major climatic hazards) were ascertained by multiple linear regression. For the analysis, factor analysis (method: PCA) was applied to extract common factors from some interrelated climatic parameters.

Storms, heavy rains, freezing rains, freezing fogs and snow storms can cause forest canopies of Chinese beech forests to open up at the levels of forest patches and forest mosaics. Storms and heavy rains cause the forest canopies to open up throughout the beech forest range. Storms and heavy rains are more frequent in the east than in the west. Freezing rains, freezing fogs and snow storms are most frequent and intense in the centre and the northeast. These cold hazards are rare in the southernmost parts of the beech range. Lightning and hailstorms seem to have minor impacts on Chinese beech forests.

The species diversity of Chinese beech forests increases towards warmer sites. To a lesser degree, it also increases towards coastal areas that experience more frequent storms and heavy rains. The importance of evergreen broadleaved trees increases towards the sites with less snowfall. Ice storms (freezing rains and freezing fogs) and snow storms favour beeches but not evergreen broadleaved trees nor fast-growing deciduous trees in the canopy dominance, because beech is resistant to these cold hazards, thanks to its deciduous habit and dense wood. The amount of annual precipitation was not related to any diversity index of the beech forests.

In Chapter 4, using transect sampling (from ridge to valley bottom), the regeneration sites and population structures of *Fagus hayatae* var. *pashanica* and *Fagus lucida* are characterized and compared with those of other main species in two beech forests: one in the north (Daba) and one in the south (Miao'ershan) of the Chinese *Fagus* range. Besides the beech species, the species compared are two deciduous broadleaved species *Carpinus cordata* var. *chinensis* and *Quercus aliena* var. *acuteserrata* in Daba, and are three evergreen broadleaved species *Castanopsis lamontii*, *Lithocarpus hancei* and *Manglietia chingii* in Miao'ershan. To characterize regeneration sites, forest eco-units of different types in different phases of development were distinguished, following Oldeman's concept (1983, 1990).

Beech regeneration sites were more abundant in Daba than in Miao'ershan. In both sites a dense bamboo layer restricted beech regeneration. However, in Daba, patches of dead bamboos and forest patches without bamboos occurred regularly, probably because of the cold; the forest understorey was rather sparse. There, *Fagus hayatae* regenerated in growing (or canopy gaps) and decaying eco-units in all sites, and in some mature eco-units on ridges. *Quercus aliena* saplings were absent and *Carpinus cordata* mainly regenerated in moist sites. In Miao'ershan, a dense undergrowth of bamboos, evergreen trees and shrubs limited *Fagus lucida* regeneration. There, the beech regeneration was confined to large growing eco-units (or canopy gaps) located on ridges and upper slopes, where plants other than bamboos were sparse. Beech regeneration and growth performance of juvenile beeches were best in large abandoned sites next to beech stands, which were probably created by felling in combination with burning or clearing. This implies that large abandoned sites without prior established vegetation are optimal for beech regeneration.

Population structures suggested a sporadic regeneration pattern in both *Fagus hayatae* and *Fagus lucida* and a continuous regeneration pattern in the three evergreen species studied. *Quercus aliena* was represented by tall trees only. *Fagus lucida*'s dominance over the evergreens in the overstorey in Miao'ershan was probably due to its tolerance of glaze or snow storms.

In Chapter 5, the growth and architectural strategies of three evergreen and three deciduous broadleaved shade-tolerant canopy or subcanopy tree species in the two beech forests (Daba & Miao'ershan) are described. The species studied are the same as in Chapter 4 except for *Quercus aliena* (saplings). The relative light intensity directly above the sampled saplings (1-5 m tall) was assessed using Ozalid paper following Friend (1961). The six species studied were grouped according to two types of branch morphology, i.e. orthotropy and plagiotropy (including plagiotropic mixed axes; see GLOSSARY), and their basic architectural characteristics were described following Hallé & Oldeman (1970). These species include both trees that typically form monopodial trunks and trees form sympodial trunks when conforming to their architectural models. However, sympodial trunks formed by axillary replacement, i.e. reiteration of the model, were common in shaded saplings of all six species.

Shoot growth rates over the last five years in the saplings, and radial stem growth rates over the last five years in some of the saplings studied and in some poles per species were measured. The relations between growth rates and percentage of daylight above the saplings were analysed using multiple linear regression, in which mean growth rates over the last five years were considered as dependent variables and the logarithm of percentage of daylight and the logarithm of sapling height were used as independent variables.

In low light intensities, juvenile trees of the species studied followed a common strategy by investing relatively more resources in height growth than in diameter growth, in order to grow up and reach brighter environments. The light affected extension and diameter growth more strongly in saplings with orthotropic branches than in those with plagiotropic branches. In the shaded understorey, the species with orthotropic branches tended to optimize their height growth so as to reach brighter environments, whereas the species with plagiotropic branches tended to persist in the understorey by efficiently spreading their interceptive and assimilative organs. Root collar sprouting in the saplings of *Manglietia chingii* and

Castanopsis lamontii appears to be a reiteration strategy for survival in the shaded understorey. These diverse strategies should allow diverse tree species to co-exist in the forest.

In the southern forest, the young trees of all three evergreen species had faster top-shoot and diameter growth rates than the deciduous *Fagus lucida* in all light environments they encountered. Obviously, this favours the evergreen trees over the beech to grow up and reach the forest canopy. However, these evergreen trees were so susceptible to ice and snow storms that they failed to dominate in the forest canopy.

Chinese beeches are adapted to a wide range of habitats. The resistance to ice storms and snow storms favours their dominance in the canopy. Major "disturbances" and simultaneous bamboo mortality over a large area can allow beech regeneration at any, unpredictable moment. The plagiotropic mixed axes give beech flexibility in growth and architecture in response to change of light and growing space, and to physical injury.

Because of the beeches' wide ecological amplitude, growth and architectural flexibility and its resistance of ice and snow storms, it seems probable that beech dominance in the canopy will be maintained in the Chinese beech forests in the northern areas and also in most of the southern areas, despite the present scarcity of juvenile beeches in the southern beech forests, if the macro-climate remains similar.

Based on findings of this study, it is suggested that the aims of biodiversity conservation are best served by establishing nature reserves over a range of sites which experience different frequencies and intensities of climatic hazards, so as to conserve most of the associated species adapted to different degrees of forest dynamics and the related environments. It is also suggest that statistical modelling on tree species or forest response to global climatic change should not only account temperature and precipitation but also climatic hazards. This study confirms that beech is useful for afforestation in montane zones of subtropical China, and that it is feasible to plant beech in the area near the Bohai Bay in northeastern China.

SAMENVATTING

Fagus (Beuken) soorten vormen een belangrijke component in verschillende loofbossen van de gematigde streken van het Noordelijk halfrond. Van de elf onderkende *Fagus* soorten in de wereld komen er vijf in China voor. Het verspreidingsgebied van deze Chinese beuken is in de bergen van subtropisch China (ten zuiden van 35°N). In het noordelijke verspreidingsgebied zijn de beuken (*Fagus engleriana* in het noorden, en *Fagus hayatae* var. *pashanica* in het noordwesten) vaak dominant. Ze komen hier gemengd voor met andere loofverliezende loofbomen. In deze bossen is de ondergroei nogal schaars. Ook in het midden en zuiden van het verspreidingsgebied zijn beuken (*Fagus lucida* op grote hoogte en *Fagus longipetiolata* op lagere hoogte) overheersend in vele bossen; zij zijn hier geassocieerd met voornamelijk groenblijvende loofbomen. In contrast met het noordelijke gebied is in deze bossen de ondergroei vaak erg dicht; ze bestaat uit altijd groene bomen of struiken en bamboes. In veel van de gemengde Chinese beukenbossen wordt de bodem bedekt door bamboe.

Alle Chinese beukenbossen zijn natuurbossen. Ze zijn rijk aan planten- en diersoorten, waarvan er veel zeldzaam of bedreigd zijn. In veel natuurreservaten of nationale parken in subtropisch China zijn gemengde beukenbossen de belangrijkste bosgemeenschappen. Deze bossen zijn derhalve belangrijk voor het behoud van biodiversiteit in China. Omdat ze vaak voorkomen op berghellingen en -kammen zijn deze beukenbossen ook belangrijk voor de preventie van bodemerosie en voor de handhaving van de stabiliteit van de hydrologische kringloop. Tevens leveren beuken een goede kwaliteit hardhout en worden ze aangeraden voor herbebossing in de berggebieden van subtropisch China.

In het zuidelijke verspreidingsgebied komen volwassen beuken algemeen voor, terwijl jonge beuken er zeldzaam zijn. Deze vegetatiestructuur gaf de aanleiding tot de volgende probleemstelling voor deze studie:

1. Zal de huidige dominantie van de beuk in het kronendak gehandhaafd blijven of vormen de huidige bossen stadia in een langere successiecyclus of successie-reeks?
2. Als beuken blijven domineren in het kronendak, waar kunnen de jonge beuken zich dan vestigen, hoe groeien ze op en hoe bereiken ze het kronendak? Onderscheidt de beuk zich in dit opzicht van de co-dominante boomsoorten?

De verjongingsprocessen van bomen in natuurbossen worden gereguleerd door vele abiotische en biotische factoren, zoals klimaat, mate van verstoringen, soortensamenstelling, bosarchitectuur en variatie in standplaats. Het temperament, de groei dynamiek en de boomarchitectuur beïnvloeden grotendeels het succes van de verjonging. Derhalve had dit onderzoek de volgende vier doelstellingen:

1. Het bepalen van de klimatologische randvoorwaarden qua warmte en vocht voor het natuurlijke voorkomen van de Chinese beuk (hoofdstuk 2).
2. Het bepalen van de relatie tussen macro-klimaat (temperatuur, neerslag en kans op optreden van klimatologische extremen) en soortensamenstelling van de Chinese beukenbossen (hoofdstuk 3).
3. Het identificeren van de relatie tussen topografie en beukenverjonging en tussen

soortensamenstelling en beukenverjonging in twee beukenbossen die representatief zijn voor het zuidelijke en noordelijke verspreidingsgebied (hoofdstuk 4).

4. Het vergelijken van de jeugdgroei en architectuurstrategieën van de beuk met andere schaduwverdragende boomsoorten in en onder het kronendak in relatie tot de lichtomgeving (hoofdstuk 5).

In hoofdstuk 2 wordt op basis van informatie uit herbaria, literatuur en persoonlijke waarnemingen in tien beukenbossen het voorkomen van iedere Chinese beukensoort en diens geografische herkomstgebied beschreven en in kaart gebracht. Door toepassing van de Thornthwaite's (1948) verhoudingsindex tussen neerslag en jaarlijkse potentiële verdamping en van Kira's (1945) Warmte-en-Koude index wordt de variatie in warmte en de atmosferische vochtigheid in het natuurlijke herkomstgebied van de beuk gekarakteriseerd. Hierbij werd gebruik gemaakt van klimaatgegevens van 40 weerstations in de berggebieden waar de beuk voorkomt. Voor de identificatie van de beperkende klimatologische factoren voor de verspreiding van beuken zijn warmte en vochtigheid in de natuurlijke omgeving van de beuk vergeleken met die in de omliggende gebieden waar geen beuk voorkomt en in de lagergelegen gebieden. Hierbij is gebruik gemaakt van informatie van 111 weerstations in de omliggende streken en van literatuurgegevens (Chang 1989; Fang & Yoda 1990). Ook zijn de warmte en neerslag in de natuurlijke herkomstgebied van de Chinese beuken vergeleken met die in andere beukenarealen in de wereld.

Chinese beuken komen voor in Zuid China (22.3-34.3° N; 101-121.5° E), hoofdzakelijk in berggebieden tussen 700 en 2500 meter hoogte. *Fagus longipetiolata*, *Fagus lucida* en *Fagus engleriana* hebben een grote geografische verspreiding. *Fagus longipetiolata* beslaat het grootste areaal; deze soort komt voor tot in het zuiden van de tropische bergen in het Zuid-Oosten van de Provincie Yunnan in China, alsmede in het noorden van Vietnam. In de berggebieden van zijn oostelijke en centrale verspreidingsgebied komt deze soort soms ook voor onder de 700 meter hoogte, namelijk van 400 tot 500 meter. De meerstammige *Fagus engleriana* wordt voornamelijk aangetroffen in het noordelijke gedeelte van het *Fagus* gebied. Het herkomstgebied van *Fagus lucida* ligt geconcentreerd in het centrale deel van het *Fagus* gebied. *Fagus chienii* en *Fagus hayatae* komen alleen lokaal voor.

Chinese beukenbossen komen voor in gebieden met een gemiddelde jaarlijkse temperatuur variërend van 5° tot 17°C, een Kira's warmte-index van 40° tot 140°C per maand en een potentiële jaarlijkse verdamping van 450 tot 840 mm. Ze prefereren een humide tot perhumide klimaat met een Thornthwaite's vochtigheidsindex (Im) tussen 26 en 320. Meestal liggen zij in perhumide klimaten waar Im meer is dan 100 en waar het hele jaar door voldoende regen valt. De jaarlijkse neerslag in de herkomstgebieden ligt tussen de 740 en 2800 mm, voornamelijk geconcentreerd in het groeiseizoen. De warmte-eisen van beuken in en buiten China komen sterk overeen. Echter, Amerikaanse en andere Chinese beuken komen in een warmer klimatologisch gebied met warmere zomers voor dan Europese en Japanse beuken. De montane beukengebieden in China zijn vochtiger dan die in het laagland van Europa en Noord Amerika. In het noorden wordt het voorkomen van Chinese beuken beperkt door een vochtgebrek. Het klimaat van het gebied dichtbij de Bohai Bay in noordoost China ligt echter nog steeds binnen het klimatologisch gesproken natuurlijke verspreidingsgebied van de beuk. In de zuidelijke gebieden en op lagere hoogten is een hoge temperatuur in combinatie met lage neerslag nadelig voor de beuk. Evenals andere beuken zijn echter Chine-

se beuken in staat een beperkt watertekort, dat meestal optreedt gedurende het groeiseizoen, te overleven. Het gebrek aan concurrentie vermogen van de *Fagus*-soorten met groenblijvende loofbomen bepaalt waarschijnlijk grotendeels de grens van hun voorkomen in zuidelijke gebieden en op lagere hoogten.

In hoofdstuk 3 wordt de aanwezigheid van diverse klimatologische risico's in de Chinese beukenbossen beschreven aan de hand van informatie van elf weerstations. Ook wordt de relatie aangegeven tussen klimatologische parameters (warmte, vochtigheid, risico's) en de soortenrijkdom van de Chinese beukenbossen. De bestudeerde risico's betreffen stormen, zware regenval, ijzel, rijp, sneeuw, onweer en hagel. Deze factoren beïnvloeden de ontwikkeling van de beukenbossen. Door ruimtelijke interpolatie en extrapolatie met behulp van de Kriging methode is voor acht beukenbossen het gemiddelde aantal dagen per jaar bepaald waarin deze effecten optreden. Op basis van de gegevens van tien percelen (tussen 0,12 en 0,23 hectare in grootte) in de acht bestudeerde bossen werd een analyse uitgevoerd betreffende de Shannon-Wiener diversiteitsindex, het aantal boomsoorten met individuen hoger dan vijf meter, de relatieve betekenis van lichteisende bomen en de relatieve betekenis van bladverliezende bomen. Hiervoor werden de gegevens van het aantal individuen hoger dan 5 meter en hun grondvlak van iedere boomsoort in elk perceel gecombineerd. De indexcijfers in de percelen kleiner of groter dan 0,20 hectare zijn omgerekend naar een perceelgrootte van 0,20 hectare. De relatie tussen deze indices en de bestudeerde klimatologische parameters (temperatuur, jaarlijkse neerslag en de frequentie van het optreden van klimatologische extremen) zijn bepaald door een multiple lineair regressie. Een factoranalyse volgens de PCA-methode is toegepast om de invloed van specifieke klimatologische factoren te onderscheiden.

Wind- en sneeuwstormen, zware regenval, ijzel en rijp kunnen er de oorzaak van zijn dat het kronendak van Chinese beukenbossen geopend wordt; hierdoor ontstaan verjongingseenheden en bosmozaïeken. In het gehele beukengebied veroorzaken stormen en zware regenval een sterke verstoring in de bossen. Ze zijn meer frequent in het oosten dan in het westen. IJzel, rijp en sneeuwstormen komen het meest frequent en intensief voor in het midden en noordoosten. Deze koude risico's zijn zeldzaam in het zuidelijkste gedeelte van het beukengebied. Onweer en hagelstormen hebben daarentegen weinig invloed op de dynamiek van het Chinese beukenbos.

De soortendiversiteit van de Chinese beukenbossen neemt toe met een stijgende temperatuur. In mindere mate neemt deze ook toe in de richting van kustgebieden met frequente stormen en zware regenval. Het belang van groenblijvende loofbomen neemt toe in de gebieden met minder sneeuwval. IJzel, rijp en sneeuwstormen bevoordelen de dominantie van de beuken in het kronendak ten opzichte van bladverliezende bomen en snelgroeiende loofverliezende bomen. De beuk is bestand tegen deze koude factoren als gevolg van zijn bladverlies en hoge houtdichtheid. Er werd geen correlatie gevonden tussen de hoeveelheid jaarlijkse neerslag en de verschillende diversiteitsindices.

In hoofdstuk 4 zijn voor twee beukenbossen (één in het noorden - Daba - en één in het zuiden - Miao'ershan - van het Chinese *Fagus*-areaal) de verjongingseenheden en populatiestructuren van *Fagus hayatae* var. *pashanica* en *Fagus lucida* bestudeerd en vergeleken met die van enige andere hoofdboomsoorten. Deze soorten waren respectievelijk de bladverliezende soorten *Carpinus cordata* var. *chinensis* en *Quercus aliena* var. *acuteserrata*

in Daba en de groenblijvende loofsoorten *Castanopsis lamontii*, *Lithocarpus hancei* en *Manglietia chingii* in Miao'ershan. Hierbij is gebruik gemaakt van de transect methode; de bestudeerde transecten lagen loodrecht op de helling. Voor de herkenning van verschillende verjongingseenheden is conform het concept van Oldeman (1983, 1990) een onderscheid gemaakt tussen eco-eenheden van verschillende typen in verschillende ontwikkelingsfasen.

Beukenverjonging komt vaker en overvloediger voor in Daba dan in Miao'ershan. In beide gebieden beperkt een dichte bamboelaag de verjonging van beuken. Echter, waarschijnlijk door de kou, komen in Daba regelmatig plekken met dode bamboe en plekken zonder bamboe voor; de ondergroei is daardoor vrij schaars. In dit gebied komt op alle groeiplaatsen verjonging van *Fagus hayatae* var. *pashanica* voor; deze wordt aangetroffen in eco-eenheden die zowel in de groei- en aftakelingsfase verkeren. Op bergkammen komt tevens verjonging voor in eco-eenheden die in een volwassen fase verkeren. Jonge bomen van *Quercus aliena* var. *acuteserrata* zijn hier afwezig en *Carpinus cordata* var. *chinensis* verjongt zich voornamelijk in vochtige lokaties. In Miao'ershan beperkt de dichte ondergroei van bamboe, juveniele groenblijvende bomen en struiken de verjonging van *Fagus lucida*. Daar beperkt de beukenverjonging zich tot grote eco-eenheden op bergkammen en hogere hellingen die in een groeifase verkeerden. Hier komen nauwelijks niet-bamboesoorten voor. De verjonging en groei van jonge beuken is het best in grote, bijna kale eco-eenheden nabij bestaande beukenbossen. Deze zijn waarschijnlijk ontstaan door het vellen van bos in combinatie met branden of met houtexploitatie. Dit geeft aan dat eco-eenheden zonder reeds opgegroeide vegetatie optimaal geschikt zijn voor regeneratie van de beuk.

De populatiestructuur suggereert een sporadisch verjongingspatroon voor *Fagus hayatae* var. *pashanica* en *Fagus lucida* en een regelmatig verjongingspatroon voor de drie bestudeerde groenblijvende soorten. Van *Quercus aliena* waren alleen grote bomen aanwezig, geen jonge. De overheersing van *Fagus lucida* ten opzichte van de groenblijvende soorten in het kronendak in Miao'ershan is waarschijnlijk toe te schrijven aan zijn tolerantie ten opzichte van rijp of sneeuwstormen.

In hoofdstuk 5 wordt een beschrijving gegeven van de groei- en architectuurstrategieën van drie groenblijvende en drie bladverliezende schaduwverdragende boomsoorten in of onder het kronendak van de twee bestudeerde beukenbossen (Daba en Miao'ershan). De bestudeerde soorten waren dezelfde als in hoofdstuk 4 met uitzondering van *Quercus aliena*. Boven boompjes in de jonge-stakenfase (1 tot 5 meter hoog) werd de relatieve lichtintensiteit gemeten volgens de methode van Friend (1961) met behulp van Ozalid lichtgevoelig papier. De zes bestudeerde soorten zijn gegroepeerd op basis van twee typen van takmorfologie, namelijk orthotropie en plagiotropie (inclusief plagiotrope meng-assen; zie GLOSSARY). Hun basis-architectuurkenmerken zijn beschreven volgens Hallé en Oldeman (1970). Zolang de bomen zich conform hun architectuurmodel ontwikkelen, kunnen de soorten onderscheiden worden in bomen met typische monopodiale stammen en bomen met sympodiale stammen. Echter, bij alle zes soorten komen bij beschaduwde bomen in de stakenfase als gevolg van reïteratie sympodiale stammen voor.

Per soort zijn gedurende vijf jaar van bomen in de jonge-stakenfase de hoogtegroeï gemeten; tevens werd bij een deel van deze bomen evenals bij enkele bomen in de oude-stakenfase de diametergroei bepaald. De relatie tussen de groei en het percentage daglicht boven de jonge

boompjes is geanalyseerd volgens de multiple lineaire regressie methode. Hierbij is de gemiddelde groei over de laatste vijf jaar beschouwd als afhankelijke variabele en de logaritme van het percentage daglicht en de logaritme van de hoogte van de jonge boompjes als onafhankelijke variabelen.

Bij lage lichtintensiteit volgen jonge boompjes van alle bestudeerde soorten eenzelfde strategie door relatief meer te investeren in topscheutgroei dan in diametergroei. Hierdoor groeien ze sneller omhoog en bereiken betere lichtcondities. Het licht beïnvloedt de hoogte- en diametergroei sterker in jonge boompjes met orthotrope takken dan in die met plagiotrope takken. In de schaduwrijke ondergroei neigen de soorten met orthotrope takken ertoe hun hoogtegroeit te maximaliseren zodat ze een lichtere omgeving bereiken, terwijl soorten met plagiotrope takken ertoe neigen zich in de ondergroei te handhaven door het effectief spreiden van hun lichtonderscheppende en fotosynthetische organen. Reïteratie in de vorm van wortelopslag van de jonge boompjes van *Manglietia chingii* en *Castanopsis lamontii* is een andere overlevingsstrategie in de ondergroei. Door deze verschillende strategieën zijn verschillende boomsoorten in staat samen te leven in het bos.

In de zuidelijke bossen hebben de jonge bomen van alle groenblijvende soorten onder elke lichtomstandigheid een snellere hoogte- en diametergroei dan de bladverliezende *Fagus lucida*. Hierdoor zouden de groenblijvende bomen sneller moeten kunnen groeien en eerder het kronendak bereiken dan de beuken. Echter, doordat de groenblijvende bomen zo gevoelig zijn voor ijzel- en sneeuwstormen, zijn zij niet in staat het kronendak te domineren.

Chinese beuken zijn aangepast aan een groot aantal groeiplaats-omstandigheden. Hun resistentie tegen ijzel en sneeuwstormen bepaalt hun dominantie in het kronendak. Als gevolg van grote verstoringen en simultane bamboesterfte kan beukenverjonging op elk willekeurig moment optreden. Door de plagiotrope meng-assen is de beuk flexibel in termen van groei en architectuur en kan hij reageren op veranderingen in lichtcondities en groeiruimte evenals op fysieke beschadigingen.

Vanwege de grote ecologische amplitude van de beuk, de flexibiliteit in groei en architectuur en de hoge resistentie tegen ijs- en sneeuwstormen, lijkt het waarschijnlijk dat in de Chinese beukenbossen bij een gelijkblijvend macroklimaat de dominantie van deze soort in het kronendak gehandhaafd zal blijven. Dit is niet alleen het geval in de noordelijke gebieden, maar waarschijnlijk ook in de meeste zuidelijke streken, ondanks het feit dat jonge beuken daar schaars zijn.

Als conclusie van dit onderzoek wordt gesuggereerd dat conservering van biodiversiteit het best bereikt kan worden, indien er natuurreservaten worden gevestigd in verscheidene bosgebieden met een verschillende intensiteit en frequentie in klimatologische extremen. Hierdoor kunnen de diverse boomsoorten die elk zijn aangepast aan een verschillende mate van bosdynamiek en specifieke omgevingsfactoren het best behouden worden. Dit onderzoek bevestigt tevens dat de beuk potentieel nuttig is voor bebossing in de berggebieden van subtropisch China en dat het haalbaar is beuken te planten in het gebied vlakbij de Bohai Bay in noordoost China.

摘 要

壳斗科水青冈(山毛榉)属植物,分布于北半球,是温带湿润气候下的重要森林树种。该属约有11种,5种分布于中国。中国水青冈不分布于温带,而分布于湿润的南方山地。在亚热带北部山区,水青冈与落叶阔叶树混生形成混交林,下木层较稀。在亚热带中部和南部山区,水青冈多与常绿阔叶树混生形成混交林,下木层茂密,并以常绿的乔灌木在下层占绝对优势。中国水青冈林都是原生性的森林。林下常有茂密的竹子层。林中含有丰富的动植物,其中不少是珍稀、濒危的物种以及名贵药材。水青冈林是我国亚热带山区许多自然保护区重要森林群落,它们对于维持这个地区的生物多样性起着重要作用。由于中国水青冈林分布于山坡,山脊,对于涵养水源,防止水土流失起着重要作用。水青冈耐瘠,且生产优质硬材。

在水青冈与常绿阔叶树混交的林中,林下水青冈的幼苗幼树很少,而共生的常绿阔叶树幼苗幼树却颇多。由此作者提出了如下问题:

1. 在这些水青冈混交林中,水青冈的优势地位能否长久维持下去?它们是否会被常绿阔叶树取代?或者现时水青冈在这些林中的优势地位只是较长时间尺度森林动态中的一个发育阶段?
2. 假如水青冈的优势地位能够长期维持下去,那么水青冈在林中何处更新呢?更新的幼树又怎样生长起来达到林冠层?水青冈与林中共生树种相比在更新及幼树生长方面有什么优劣势?

天然林中树木的更新受许多环境因子和生物因子的影响,如气候,干扰因素,地形,森林的物种组成,结构等的影响。树木内在的耐荫性,生长及形态特征很大程度上决定其更新的策略,更新的成败。

为了解答上面的问题,本项研究着重于:

1. 确定中国各种水青冈的分布范围及其分布区内的气候特征(第二章)。
2. 研究水青冈林的树种组成及物种多样性与气候(温度,降雨,主要气象灾害)的相关关系(第三章)。
3. 查明水青冈更新与地形,与森林的物种组成的关系(第四章)。
4. 比较水青冈及其它耐荫的共生上层树种的幼树对于适应不同光环境在生长及形态建成方面的对策(第五章)。

论文第二章报道了对水青冈分布与气候关系的研究成果。通过查阅大量水青冈标本及有关文献,以及本人在10处水青冈分布地点的调查,绘制了中国各种水青冈的分布图,确定了它们的分布范围。利用40个位于水青冈分布区内的气象站的资料,根据 Thorntwaite(1948)的方法,计算潜在蒸发散和湿度指数。利用 Kira (1945)的方法计算温暖指数和寒冷指数,确定了五种水青冈的分布区内的热量和湿度数量特性。为了分析限制水青冈分布的气候因子,利用水青冈分布区外围地区111个气象站的资料,以及已发表的气候资料(张新时, 1989; Fang 和 Yoda, 1990),对比了水青冈分布区内与其外围地区(温带地区,亚热带低地,

热带地区)的热量和湿度差异。同时对比了欧洲,北美和日本水青冈分布区的热量和湿度。

中国水青冈分布于北纬22.3至34.3度,东经101.2至121.5度的范围内。主要分布于海拔700至2500米的中山地带。长柄水青冈(*Fagus longipetiolata*)分布范围最广,最南分布到越南北部及云南东南部的热带山区。在华东,华中地区长柄水青冈零星分布到海拔400至500米的低海拔地带。亮叶水青冈(*Fagus lucida*),米心水青冈(*Fagus engleriana*)的分布区稍窄。米心水青冈为多主干丛生状,集中于北部地区。亮叶水青冈主要分布于中部地区。台湾水青冈(*Fagus hayatae*)分布于台湾北部山区及浙江永嘉县四海山林场。巴山水青冈(*Fagus hayatae* var. *pashanica*)分布于大巴山区。平武水青冈(*Fagus chienii*)仅分布于四川平武县山区。

中国水青冈分布区内的年平均温度介于5至17摄氏度;该区Kira的温暖指数为40至140摄氏度/月,全年潜在蒸发散总量介于450至840毫米。区内年降水量介于740至3500毫米,Thorntwaite湿度指数介于26至320,为潮湿和过湿气候。水青冈林生长的地方湿润度都大于100,为过湿气候。中国水青冈分布区与世界其它水青冈分布区的热量在很大程度上相似。但是中国水青冈及北美水青冈分布区的热量幅度都较日本的水青冈,欧洲的水青冈的分布区宽。中国水青冈和北美水青冈都能分布到比较暖热的地方,如北美水青冈可分布到年均温20摄氏度的佛罗里达北部。长柄水青冈也可分布到年均17摄氏度的地方。北美水青冈分布的北界接近寒温带。其它水青冈在山区分布的上限的气候也有类似寒温带气候的情况。

在中国温带地区水分不足是限制水青冈分布的首因,在其北部地区冬季寒冷也使水青冈不能在那里分布。但是渤海湾地区的热量,湿度条件还在水青冈分布的低限范围内。在亚热带低地及热带地区热量偏高,低地在生长季还发生干旱,都不利于水青冈分布。但是分析表明,欧洲,北美及中国水青冈是能够忍受短时间缺水的,并且北美水青冈,长柄水青冈也可分布到较热的地区。作者认为,与常绿阔叶树相比,水青冈竞争力弱是限制其在亚热带低地分布的主要因素。

论文的第三章,阐明了中国水青冈林物种组成和物种多样性与热量因子,与气候干扰因子的关系。根据11个(海拔与水青冈林类似的)气象站的数据,分析了中国水青冈林区主要气象灾害发生率的梯度。这些灾害有:暴风,暴雨,冻雨,冻雾,雷暴,雪暴及冰雹。它们可致水青冈林中形成倒木,断冠,断枝,而产生大大小小的林窗,驱动森林的更新。利用类似等高线计算及制图技术(SURFUR软件,Kriging方法),绘制了水青冈林区这些灾害的年均日数分布图,根据这些分布图查算作出了样方取样的八个水青冈林区(十个地块)这些灾害的年均日数。根据样方资料,计算了八个水青冈林中共十个地块的物种丰富度,及Shannon-Wiener多样性指数,落叶树重要值,喜光树种的重要值。利用多元线性回归技术,分析了这些指数是否与年平均温度,年降雨量,以及上述各种气象灾害年均日数具相关关系。分析气候因子时,采用了因子分析技术(主分量分析方法),选出了两个综合气候因子:因子一主要代表热量(含年均温,冻雨,冻雾,降雪);因子二主要代表暴风暴雨。年降雨量,雷暴,冰雹与其它气候因子关联度小,为独立因子。

结果表明：中国水青冈林中主要气候干扰因子是暴风，暴雨，冰凌（冻雨，冻雾）及雪暴。暴风，暴雨可在整个水青冈林区形成强度干扰。但是它们的频度和强度都是沿海地区为高。洞庭湖周边地区冰凌最重，水青冈分布区的东北部次之。东北部，中部地区雪灾较重。冰凌及雪灾在最南部地区（如云南文山，广西田林老山）基本缺如。雷暴及雹灾仅在水青冈林中形成弱干扰。雹灾在云贵高原地区最强烈（雹粒大），湖南西部，两广地区次之。

中国水青冈林物种多样性首先随热量梯度递增。年平均温度愈高，冰凌降雪愈少，则林中物种多样性愈高。其次与暴风和暴雨的综合梯度呈正相关。在相同年平均温度条件下，沿海地区水青冈林的物种多样性及丰富度比西部内陆地区高得多。林中喜光树种重要值不与综合气候因子相关而与年均暴风日数呈正相关，与年均冻雨日数呈负相关。沿海地区暴风较频繁，那里水青冈林喜光树种比西部地区多得多，重要得多。水青冈林中常绿阔叶树的重要值指数与年降雪日数呈负相关。野外观察表明常绿阔叶树及生长快的喜光落叶树都不耐冰凌及雪暴的危害。水青冈生长较慢，材质密度高，冬季无叶，发生冰凌及雪暴时在树上积冰和积雪较少，因此比较耐冰凌及雪灾。在冰凌或雪灾较重地区，利于水青冈在林中形成优势种。在气温较低且干扰较少的地区，林中物种多样性低，水青冈处于竞争的有利地位，利于水青冈在林中形成单优势种，如大巴山区。水青冈林中物种多样性与年雨量无相关关系。

论文第四章对比了亮叶水青冈在广西兴安猫儿山，巴山水青冈在四川南江大坝林区水青冈混交林中的更新情况，揭示了水青冈更新与地形，与森林类型的关系。在两处水青冈林中，采用长样条取样（从山脊沿山坡到山谷），研究了猫儿山及大坝林区水青冈林中主要树种的种群结构，及幼树的生长立地的特征。大坝林区水青冈林以巴山水青冈和米心水青冈为主，混生锐齿栎（*Quercus aliena* var. *acuteserrata*）和华鹅耳枥（*Carpinus cordata* var. *chinensis*）。猫儿山水青冈林中，亮叶水青冈为建群种，混生常绿的铁锥栎（*Castanopsis lamontii*），亮叶柯（*Lithocarpus hancei*）等树种。常绿的桂南木莲（*Manglietia chingii*）为乔木亚层主要树种之一。

大坝林区巴山水青冈混交林中巴山水青冈幼树较常见。猫儿山亮叶水青冈混交林中亮叶水青冈幼树较少。而常绿阔叶树的幼树却丰富。无论是猫儿山还是大坝林区，茂密的竹子层都阻碍水青冈的更新。然而，在大坝林区由于地理位置偏北，冬季严寒常使竹子冻死。因小地形以及有无林冠层遮盖有关，冻死的竹子常常呈斑块状，比如在中大型林窗中。竹子的死亡，加之下木层较稀，利于水青冈更新。在大坝林区巴山水青冈在生长的嵌块或林窗和林冠层较稀的老朽的嵌块下都可以更新。在大坝水青冈林中，锐齿栎的幼树几乎缺如，华鹅耳枥的幼树主要生长在潮湿的地方，它们不构成对水青冈幼树的竞争。

在猫儿山水青冈林下，竹子因寒冷冻死的机会少，竹子层在林下很普遍。在山脊，上坡及陡坡多为箬竹（*Indocalamus longiauritus*），高1-2米。在下坡，山谷及平缓的地方常生摆竹（*Indosassa shibataeoides*），高4-5米。并且林下常有茂密的下木层。在一般情况下，无论在郁闭的林冠下还是在林窗中水青冈都难以更新。然而，在山脊及其附近，下木层较稀，竹子层以箬竹为主，它们不能完全阻碍水青冈的更新，且山脊附近往往透光较好，因此这里水青冈幼树比较常见。在林缘撩荒地，可见茂密的水青冈更新，并且生长快。这说明伐除大

树并清除竹子及其它植物，具有充足的光照是亮叶水青冈最理想的更新生境。种群结构表明亮叶水青冈，巴山水青冈皆为间断更新。而林中常绿树为连续更新。在猫儿山，尽管常绿树的幼树较多，但是它们的上层大树却较少，这与它们不耐冰凌，雪灾有关。

论文第五章，探讨了三个常绿阔叶树种：铁锥栲，亮叶柯及桂南木莲，和三个落叶树种：亮叶水青冈，巴山水青冈及华鹅耳枥，在不同光条件下的生长及形态建成对策。研究地点仍在大坝林场和猫儿山。利用光敏感纸方法 (Friend 1961)，估测了所测定的幼树顶部的相对光强。这六种树种具有两种侧枝形态：直立型枝放射状叶序，平生或斜侧向枝平面状叶序。根据 Halle 和 Oldeman (1970) 的树形分类系统，确定了六种树的生长模式和基本形态特征。根据生长模式，有三个树种，应该形成单轴型主干，三种树形成合轴型主干。但是六种树的幼树在荫闭的条件下都形成合轴型主干。这是由于荫闭条件下，幼树的顶端优势减弱，顶梢一次又一次地被侧梢取代所形成。

研究表明，与强光条件下相比，在弱光条件下，幼树普遍优先将光合产物投入高生长，以便尽最大可能地增高，尽早脱离荫闭的环境。这种现象在直立枝放射型叶序的树种中更加明显。它们的直立枝，易形成自我遮荫，因此它们在林冠下的幼树树冠往往狭小。而平生枝平面状叶序树种的幼树，自我遮荫较少，在荫闭条件下形成较前者较大的树冠，能较好地接受利用从林冠层透射下来的光，这有利于它们在荫闭条件下生存。直立型枝的树种的幼树的高生长和年轮生长与光的相关度，普遍比平生型枝的幼树的为高。研究还发现桂南木莲的幼树在荫闭条件下常在树干基部抽生萌枝以取代衰弱的主干，延续生存。类似现象在铁锥栲的幼树中也偶见。作者认为，萌蘖分枝是在荫闭条件下维持生存的一个重要对策。这些多样化的植物对策，利于多种树种在林中共生。

在猫儿山，无论在强光或弱光条件下，常绿树种的幼树的高生长及直径生长都比亮叶水青冈的幼树快。而且它们的幼树也比水青冈幼树丰富。似乎常绿阔叶树在这个林中比水青冈处于更有利地位。然而不耐冰凌，雪灾和寒害是常绿阔叶树致命弱点。

水青冈耐荫，耐瘠，较抗冰凌及雪害。因此它们在亚热带中山地带，特别是山脊及其附近，形成上层优势种。这里保存了水青冈的种源，一旦林中发生强度干扰，如果再伴随竹子的死亡，水青冈就有可能形成丰富的更新幼树。水青冈在形态上有较大的可塑性，利于它幸存于多种生境。因此作者推断，无论在大坝林区还是在猫儿山水青冈林中，假如大气候维持现状，水青冈的优势地位可以长期维持下去；在猫儿山常绿阔叶树不可能取代亮叶水青冈。

根据本项研究的结果，作者提出，为了保护生物多样性，自然保护区应该建立在受自然干扰程度不同的多个地区，既包含受自然干扰多的地区，也包含受中等程度干扰和少干扰地区。因为通过长期进化，这些地区的生态系统及其所含物种对不同强度的干扰，以及不同类型干扰及其相关生境，形成了特定的适应机制。本研究表明，水青冈是亚热带中山造林的理想树种。根据对气候的对比研究，作者推断，在渤海湾地区引种水青冈，比如作为城市绿化树种是可能成功的。

GLOSSARY

(Terms are defined by the present author, otherwise the sources are given.)

Architectural model of trees: Generalized growth program which determines successive architectural phases of a tree (Hallé *et al.* 1978). The architectural models that were distinguished for the tree species studied in the present study were (Hallé *et al.* 1978):

Massart's model (*Castanopsis lamontii*): An orthotropic, monopodial trunk with rhythmic growth which consequently produces regular tiers of branches at levels established by the growth of the trunk meristem. Branches are plagiotropic either by leaf arrangement or symmetry, but never by apposition. The position of flowers is not significant in the definition of the model.

Rauh's model (*Lithocarpus hancei*, *Quercus aliena*): A monopodial trunk which grows rhythmically and so develops tiers of branches, the branches themselves morphogenetically identical to the trunk. Flowers are always lateral.

Scarrone's model (*Manglietia chingii*): An orthotropic rhythmically active terminal meristem produces an indeterminate trunk bearing tiers of branches, each branch-complex orthotropic and sympodially branched as a result of terminal flowering.

Troll's model (*Carpinus cordata* and all *Fagus* species): Axes are all plagiotropic with continual superposition; main-line axes contribute part trunk, part branch, the proximal part becoming erect, most often secondary after leaf fall. The distal part of each axis is then a branch with or without determinate growth, bearing lateral axes which often do not form a basal erect portion.

Architecture of a living system: Its spatial and functional build-up at a well-defined hierarchical systems' level, i.e. with the omission of more detailed or more encompassing structural features than those operational at that level (Oldeman 1989b).

Architecture of a tree: The visible, morphological expression of the genetic blueprint of a tree at any time (Hallé *et al.* 1978).

Autocorrelation: Sample points spatially close together tend to be more similar than points further apart, but often without easy, direct relation between sample site location and the value of the attribute (Burrough 1987). Important in *Kriging.

Axis: Supporting part of an organ or complex, e.g. leaf axis, stem (Hallé *et al.* 1978).

Beech forest: Forest where at least one *Fagus* species dominates the forest canopy or is the main co-dominant (Peters 1992).

Branch (of a tree): A stem growing from the trunk or from a limb of a tree (Webster's Dictionary 1981). The axes taking over the functions which the *trunk ceases to assume: photosynthesis and formation of sexual organs (Hallé *et al.* 1978).

Canopy gap: A forest opening between *mature forest eco-units (Peters 1992).

Competition of plants: The tendency of neighbouring plants to utilize the same quantum of

light, ion of a mineral nutrient, molecule of water, or volume of space (Grime 1979).

Co-dominant species: See ecological dominance.

Degrading forest eco-unit: An eco-unit dominated by senescent trees.

Dominance: See ecological dominance.

Dominant species: See ecological dominance.

Differentiation of axes: Morphological specialization either as sequential expression of meristematic speciation or growth correlation (e.g. from orthotropic to plagiotropic shoots; Hallé *et al.* 1978).

Ecological dominance: The ecological role of a species or a species group which largely controls the energy flow and strongly affects the environment of all other species or species groups of a community (Odum 1971). In the present study, relative importance assessed on the basis of number of individuals (taller than 5 m) and basal area in sample units was used as an index of dominance of a species. In the plots dominated by mature eco-units, an overstorey species by definition with an importance value greater than 15% was defined a dominant species, whereas a co-dominant species had an importance value between 5 and 15 %.

Factor ([Latin], = maker): Something that actively contributes to the production of a result (Webster's Dictionary 1981). Something that makes something else happen (Oldeman 1990).

Forest architecture: Spatio-temporal structure linked to well-defined hierarchical levels of forest ecosystems (Oldeman 1990).

Forest canopy: Aggregate of tree crowns belonging to overstorey tree species, which have reached their full height at a given site.

Forest eco-unit: A forest patch in which at one moment in time a vegetation has begun, of which the architecture, eco-physiological functioning and species composition are ordained by one set of trees until the end (Oldeman 1990).

Freezing fogs: Fogs that fall through an air mass of below-freezing temperature and do not crystallize (i.e. supercooling), but turn into ice immediately upon contact with any object with a temperature below the freezing point (Jiang 1991).

Freezing rains: Rains that fall from a warm uplifted front through a colder air mass of below-freezing temperature, but which do not freeze (supercooling) before reaching the ground surface that is covered by an air layer at temperatures around the freezing point, but turn into ice immediately upon contact with any object with a temperature around the freezing point (Jiang 1991).

Growing forest eco-unit: A forest eco-unit dominated by *potential trees.

Kriging: A spatial interpolation technique, developed by Krige (1951), that calculates the interpolated value of a spatial variable as a linear combination of the values from several nearby observations. The weight of these observations depends on the degree of spatial *autocorrelation of the variable (Stein & Corsten 1991).

Light-demanding species: A plant species requiring high light intensities throughout its whole life.

Leptomorph rhizome (e.g. in *Indosassa shibataeoides*): A type of bamboo rhizome which is long and slender and has the following characteristics: a cylindrical or subcylindrical form, with a diameter usually less than that of the culms originating from it; internodes longer than broad, relatively uniform in length, symmetrical or nearly so, rarely solid, typically hollow, the usually narrow central lumen interrupted at each node by a diaphragm; nodes in some genera usually somewhat elevated or inflated, in others not; lateral buds in the dormant state boat-shaped, with a distally oriented apex (McClure 1966).

Mature forest eco-unit: A forest eco-unit dominated by trees that have reached their full height at a given site.

Mixed axis: See *plagiotropic mixed axis.

Montane zone: The upland slopes starting from an elevation that is 600 m higher than the foot of the mountain, and extending to the *subalpine zone if the latter is present. The lower limit is arbitrarily determined. However, according to Ellenberg's (1988) definition, the annual temperature at the lower limit of a montane zone is at least 3°C lower than at the foot of the mountain.

Orthotropy: Gravitational response which produces a vertical axis, hence orthotropic shoot with the complex of characters resulting from this response, i.e. radial symmetry and vertical orientation (cf. plagiotropy; Hallé *et al.* 1978).

Overstorey canopy trees: Trees that have reached their full height at a given site in a forest and can no longer be suppressed by surrounding trees (Peters 1992).

Pachymorph rhizome (e.g. in *Indocalamus longiauritus*): A type of rhizome that is short and thick and has the following characteristics: a subfusiform (rarely subspherical), usually more or less curved (rarely straight) shape, with a maximum thickness typically somewhat greater than that of the culm into which it is always transformed apically; internodes broader than long, asymmetrical (longer on the side that bears a bud), solid (apparently never hollow); nodes not elevated or inflated; lateral buds solitary, in the dormant state asymmetrically dome-shaped, with a subcircular margin and an intramarginal apex (McClure 1966).

Plagiotropy: Gravitational response which produces an oblique or horizontal axis, hence plagiotropic shoot with the complex of characters resulting from this response, i.e. dorsiventral symmetry and horizontal orientation (cf. *orthotropy; Hallé *et al.* 1978).

Plagiotropic mixed axis: A plagiotropic axis, the basal part of which becomes erected after leaf loss by secondary growth (see Troll's model under *architectural model) and forms a *trunk segment, its apical part remaining horizontal and forming a *branch segment; its basal part does not become orthotropic (no new leaf arrangement), only vertical secondarily (Hallé *et al.* 1978).

Potential tree: A young tree that is growing and has not reached its full height at a given site.

Reiteration: Development of shoots outside the sequence of meristem activation in the architectural model of a tree, as a specialized environmental response (Hallé *et al.* 1978).

Subtropics: A region between temperate region and tropics. In China, the subtropics are characterized by evergreen broadleaved forest as the zonal vegetation, a mean annual temperature between 15 and 20°C and a mean temperature in the coldest month above 0°C (Nature Zonation Committee 1959). The Chinese subtropical zone is equivalent to the warm-temperate zone in Troll and Paffen's (1980) climate classification.

Subalpine zone: High upland slopes immediately below the timberline (Webster's Dictionary 1981), where the climate is boreal. In the boreal climate in China, Kira's Warmth index lies between 15 and 55 °C · month, or annual potential evapotranspiration is between 350 and 550 mm (Fang & Yoda 1989); spruce and fir dominate the forest of the subalpine zone (Hou 1983).

Shade-tolerance (*sensu stricto*): The ability of a plant species to grow beneath an overstorey (Decker 1952). See *tree temperament.

Shade-tolerant species: A species whose seeds can germinate and its juveniles can grow beneath an overstorey for a certain period, though they may require higher light intensities to mature.

Storms: Winds with a velocity exceeding 17.2 m s⁻¹ (Meteorological Information Centre Beijing 1984).

Tree temperament: The character of a tree as shown by its growth-and-development reactions towards its environment during its life cycle (Oldeman & Van Dijk 1990). Also see *light-demanding and *shade-tolerant species.

Toposequence: A sequence of topographical positions, e.g. from valley to hill summit (Van Rompaey 1993).

Trunk: The main stem of a tree apart from its limbs and roots (Webster's Dictionary 1981). The axis that plays the main architectural role in a tree: which ensures the tree's foothold, its mechanical resistance, its extension growth in height through the successive forest storeys, while producing at its top new leaf-bearing *branches which profit from the best light conditions (Hallé & Oldeman 1970).

SOFTWARE USED

- EIS Ecological information system for China
© 1990 Laboratory of Quantitative Vegetation Ecology
Institute of Botany in Beijing, Chinese Academy of Sciences
- Lotus 1-2-3 Release 2.4 spreadsheet package
© 1992 Lotus Development Corporation
- NJSTAR 1.23 word processing package for Chinese
© 1991 Hong-po Ni
- Quattro.Pro® 5.0 spreadsheet package with graphics facilities
© 1992 Borland International
- SPSS R. 5.0.1 statistical package
© 1990 SPSS Inc.
- Surfer® Version 4 spatial interpolation package
© 1989 Golden software
- Thornth.For a programme for calculating Thornthwaite's
potential evapotranspiration
© 1989 Hsin-Shih Chang
- Wordperfect R. 5.1 word processing package
© 1991 Wordperfect Corporation

APPENDICES

Appendix 2.1. locations of 32 standard^a and 8 temporary (with superscripts) weather stations in the Chinese beech zone. Stations are presented in the order of occurrence from west to east.

Stations	Latitude (N)	Longitude (E)	Altitude (m, asl.)	Period recorded
Yuxi	28°39'	102°31'	1662	1953-1980
Zhaojue	28°00'	102°51'	2132	1956-1980
Leibo	28°16'	103°35'	1475	1954-1980
Guangxian	30°59'	103°40'	707	1954-1980
Zhaotong	27°20'	103°45'	1950	1951-1980
Wenshan	23°23'	104°15'	1246	1955-1980
Pingwu	32°25'	104°31'	877	1951-1980
Zhenxiong ¹	27°25'	104°51'	1667	
Wudu	33°54'	104°55'	1079	1954-1980
Guangnan	24°02'	105°02'	1250	1953-1980
Xingren	25°26'	105°11'	1379	1951-1980
Bijie	27°18'	105°14'	1511	1951-1980
Tianlin Laoshan ²	24°16'	106°14'	1600	1986-1990
Quiyang	26°35'	106°43'	1071	1951-1980
Tongzi	28°08'	106°50'	972	1951-1980
Daba For. Station ³	32°42'	106°55'	1450	1989-1992
Zunyi	27°42'	106°58'	844	1951-1980
Jinfoshan	28°57'	107°09'	1906	1956-1980
Meitan	27°46'	107°28'	792	1951-1980
Dushan	25°50'	107°33'	972	1951-1980
Kaili	26°36'	107°59'	720	1958-1980
Fupin	33°32'	107°59'	1088	1957-1980
Wanyuan	32°04'	108°02'	674	1952-1980
Leigongshan ⁴	26°40'	108°05'	830	
Fanjingshan ⁵	27°55'	108°45'	1200	
Zhenan	33°26'	109°09'	986	1958-1980
Longshan Bamianshan	28°54'	109°15'	1346	1971-1979
Longsheng Dananshan ⁶	25°58'	110°07'	1020	1985-1990
Lucongpo	30°47'	110°14'	1819	1957-1980
Wufeng	30°10'	110°37'	980	1958-1980
Xuefengshan	27°20'	110°25'	1405	1971-1980
Luanchuan	33°47'	111°38'	750	1965-1980
Nanyue	27°18'	112°42'	1266	1953-1980
Guidong Bamianshan ⁷	26°08'	113°57'	836	1971-1980
Jingongshan ⁸	26°38'	114°41'	848	
Lushan	29°35'	115°59'	1165	1955-1980
Qixianshan	27°57'	117°50'	1414	1955-1980
Huangshan	30°08'	118°09'	1840	1956-1980
Tianmushan	30°21'	119°25'	1497	1956-1980
Linhai Kuocangshan	28°49'	120°55'	1374	1956-1980

Data source: ^a, Met. Inf. Centre 1984 (for standard stations); ¹ and ⁷, Met. Inf. Centre Beijing, 1975; ² and ⁶, unpubl. data, Guangxi Agri. Coll.; ³, unpubl. data, Daba For. Station; ⁴, Gan & Mu 1989; ⁵, Huang 1982; ⁸, unpubl. data, Jingongshan Nat. Reserve.

Appendix 3.1. Important woody species with relative importance value greater than 5% in each of eight Chinese beech forest sites. The study sites are arranged from east to west.^a

Sites → Family	Important species ↓	ED ^b	shade-tolerance ^c	Jiulongshan	Huangshan	Miao'ershan	Tianpingshan	Fanjingshan	Kuankuoshui	Daba	Laoshan
Fagaceae	<i>Fagus haysiae</i> var. <i>pashanica</i>	D	T	-	-	-	-	-	-	Dom	-
	<i>F. engleriana</i>	D	T	-	Dom	-	-	-	-	Dom	-
	<i>F. lucida</i>	D	T	Dom	+	Dom	Dom	Dom	Dom	-	Subdom
	<i>Quercus stewartii</i>	D	L	-	Subdom ^d	-	-	-	-	-	-
	<i>Q. aliena</i> var. <i>acuterrata</i>	D	L	+	-	-	-	-	-	Subdom	-
	<i>Q. engleriana</i>	E	T	-	-	+	+	Subdom	-	-	-
	<i>Cyclobalanopsis multinervis</i>	E	T	Subdom	-	Subdom	Subdom	Subdom	-	-	-
	<i>C. stewartiana</i>	E	T	-	-	Subdom	Subdom	Subdom	-	-	+
	<i>C. glauca</i>	E	T	-	-	-	-	-	Dom	-	-
	<i>C. nidiolum</i>	E	T	+	-	+	+	+	+	+	+
	<i>Castanopsis lamoniellii</i>	E	T	-	-	Subdom	-	-	-	-	+
	<i>Castanopsis carlesii</i>	E	T	-	-	-	-	-	-	-	subdom ^d
Betulaceae	<i>Lithocarpus chrysocarpus</i>	E	T	-	-	-	-	-	Subdom	+	+
	<i>Lithocarpus hancei</i>	E	T	+	-	Subdom	+	-	-	-	-
	<i>Castanea seguinii</i>	D	M	-	Subdom	-	-	-	-	-	-
	<i>Carpinus cordata</i>	D	T	-	-	-	+	-	-	Subdom	-
	<i>Carpinus viminea</i>	D	T	Subdom	-	-	-	-	-	-	-
Magnoliaceae	<i>Carpinus fargesii</i>	D	T	-	Subdom	-	Subdom	-	-	-	-
	<i>Magnolia</i> spp.	D	L	Subdom ^d	Subdom	-	+	-	-	-	-
	<i>Manglietia</i> spp.	E	T	-	-	Underst.	-	-	+	-	Subdom
	<i>Liriodendron chinense</i>	D	L	Subdom ^d	-	4 ^d	+	4 ^d	-	-	-
	<i>Illicium</i> spp.	E	T	+	-	+	+	Underst.	+	-	+
Tiliaceae	<i>Tilia</i> spp.	D	T	Subdom	+	-	+	+	+	-	+
Rosaceae	<i>Prunus</i> spp.	D	L	+	Subdom	-	+	+	+	+	+
Lauraceae	<i>Sassafras</i> spp.	D	L	+	Subdom	+	+	+	Subdom ^d	+	+
	<i>Burretiodendron yunnanensis</i>	E	T	-	-	+	+	+	-	-	Subdom
	<i>Schinus</i> spp.	E	M	Subdom	-	+	+	+	+	-	Underst.
Theaceae	<i>Eurya</i> spp.	E	T	Underst.	+	+	+	+	Underst.	+	+
	<i>Camellia</i> spp.	E	T	Underst.	+	+	+	+	+	+	+
	<i>Rhododendron</i> spp.	D	L	+	+	+	+	+	+	+	+
Ericaceae	<i>Rhododendron</i> spp.	E	T	Underst.	+	Underst.	Underst.	Underst.	+	+	+

^a Dom = overstorey species with importance value (Iv) greater than 15%; Subdom = overstorey species with Iv of 5-14.9%; Underst. = understorey species with Iv of greater than 5%.

^b + = presence with Iv smaller than 5%; - = absence.

^c D = deciduous; E = evergreen.

^d L = light-demanding; M = intermediate; T = shade-tolerant.

^e species is not important or absent in the sample unit but is important or present in other stands in the same study site: based on Zhou (1965) for Huangshan, Wang *et al.* (1965) for Kuankuoshui, Chen and Tang (1982) for Jiulongshan, Huang (1982) for Fanjingshan, Wang *et al.* (1983) for Laoshan, and pers. comm. H.P. Chen for Miao'ershan.

Appendix 3.2. Estimated mean annual number of days on which the major climatic hazards occur in the study sites.^a

Sites	Code	Storm	Heavy rain	Freezing rain	Freezing fog	Snowfall	Thunder	Hail
Daba	D	22	2.5	28	43	38	43	1.8
Huangshan	HS	113	5	42	53	30	50	1.5
Tianpingshan	T1	33	5.4	58	63	38	55	3.3
Tianpingshan	T2	20	5.4	33	37	30	55	3.3
Jiulongshan	J	83	7	31	42	21	72	0.9
Kuankuoshui	K	24	3	37	33	22	58	2.3
Fanjingshan	F1	30	4.2	48	43	23	62	2.8
Fanjingshan	F2	24	4.2	39	35	21	62	2.8
Miao'ershan	M	35	5.5	48	50	14.5	58	1.4
Laoshan	L	21	2.2	13	12	5.5	71	1.3

^a Heavy rain here means diel rainfall over 50 mm. Code for each site is same as in Table 3.1 and Figure 3.1.

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Curriculum Vitae

Kun-Fang Cao was born on February 23, 1957 in Yanchen, Jiangsu Province, The people's Republic of China. He attended elementary, secondary and high school in his home town. He graduated from high school in July 1974. From 1975 to 1978, he worked in a rural brigade as an accountant and vice-head. In October 1978, he was enrolled in Nanjing (Nanking) Agricultural College (now University) and studied pomology at the Department of Horticulture. In July 1982, he graduated with a Bachelor's degree. Since August 1982 he has been working in the Institute of Botany in Beijing, Chinese Academy of Sciences. In 1985, he attended a six-month advanced intensive English language course at the Staff University of Chinese Academy of Sciences. In 1986, he worked for six months in the Bureau for International Cooperation, Chinese Academy of Sciences. Between June 1988 and September 1989, he studied in the former Department of Silviculture and Forest Ecology, Wageningen Agricultural University, The Netherlands. Since 1991, he has been assistant research professor at the Institute of Botany in Beijing. In March 1990, he was admitted to a doctoral program of the so-called 'sandwich' type at Wageningen Agricultural University. He is married and has one child.