Rob Peters

ECOLOGY OF BEECH FORESTS IN THE NORTHERN HEMISPHERE

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ECOLOGY OF BEECH FORESTS IN THE NORTHERN HEMISPHERE

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in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
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in het openbaar te verdedigen
op dinsdag 16 juni 1992
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Stellingen

1. In natuurlijke bossen van de gematigde streken zijn jaarringen in bomen een zeer belangrijk hulpmiddel bij de analyse van de bosdynamiek die heeft geleid tot het huidige bosbeeld.
(dit proefschrift)

2. Nederlandse beukenbossen op rijkere gronden zullen zich, zonder menselijk ingrijpen, verder ontwikkelen naar beuken-esdoornbossen.
(dit proefschrift)

3. In beuken-esdoornbossen wordt het aandeel van esdoorn in het kronendak in hoge mate bepaald door de frequentie van windworp of uitkap.
(dit proefschrift)

4. Effective research should not break observed fenomena into separate mechanisms or cause-effect relations, because it is unlikely that these can ever be reassembled into a functioning whole.
(R.H. Peters, 1991. A critique for ecology. Cambridge Univ. Press, p 146)

5. Complexiteit van ecosystemen is geen argument voor geringe voorspellende waarde van ecologische theorieën.

6. De universiteit zou de publikatie van wetenschappelijk onderzoek in de Engelse taal moeten stimuleren en ondersteunen door een taalcorrectie-service.

7. Ik vind dat een wetenschappelijke publikatie moet worden geschreven in de eerste persoon om duidelijk te maken wie voor welke uitspraak verantwoordelijkheid draagt.

8. Noord-Amerikanen zijn niet oppervlakkiger dan wij, en Aziaten zijn niet diepgrondelijker, zij gedragen zich alleen maar anders.

9. Alleen geestelijke vrijheid bestaat, alle andere zijn hersenspinsels.

Stellingen behorende bij het proefschrift "Ecology of beech forests in the Northern Hemisphere", door Rob Peters, 16 juni 1992.

dit werk is opgedragen aan mijn ouders

Preface

As a secondary school student, I became interested in the philosophy of the native Americans. They percieved the Earth as a Mother that nurtures us. On the other hand, they were well aware of being temporary guests that have a responsibility to leave the place intact for the ones to come after them. The Hau-de-no-sau-nee (Iroquois) always talked about the 'seventh generation', i.e. they felt responsible for at least seven generations after them. Their concept of a spiritual relation with the natural world interested me. So I looked for nature and found it in the forests, especially in the beech forests near my parents' home.

Forestry appealed to me because I could recognize something of the consideration of future generations. We plant and tend trees for our children or their children. Imagine a beautiful beech-wood chair, made from a tree that was tended by several generations. I concluded that my future work should be in the forests. Although I did not become a forest guard as initially intended, I found a way to satisfy my curiosity. I started to study forests. Then I focussed again on beech, but if my father had said to me: "Rob, go and study beech, so you will see something of the world", I would not have believed him. Nonetheless, this is exactly what I have done.

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This research project has been a great experience. I travelled to many places, and everywhere I encountered hospitality and friendliness. This research was possible because of the help I recieved, from lodging to fieldwork to discussion.

First of all, I thank you Prof. Oldeman: for your confidence and enthusiasm, for guidance and freedom, and for valuable discussions. Also Prof. Poulson played an important role in my study. Thank you for your help, advice and interesting discussions. Two persons accompanied me to many study sites, Cao Kunfang in China and Europe, Ohkubo 'Tatsu' in Japan, Korea and USA. Cao really spent much time in organizing our visits to Chinese beech forests which usually were in 'off limit' areas. Thank you Cao and Tatsu for your company and for sharing your ideas and enthusiasm.

Always the research started with visiting several beech forest areas before selecting study sites. Many persons guided me to the forest. Thank you for your guidance and for the interesting discussions in the forest, the best place to discuss forests:
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After selecting study sites, permission for carrying out the fieldwork was requested and always obtained from the responsible organisations. Thank you for you permission:
Michigan Department of Natural Resources for Warren Woods; Ohio Department of Natural Resources for Hueston Woods; Tall Timbers Research Station for Woodyard Hammock; The village of La Mojonera in Hidalgo, Mexico, for the beech forest of La Mojonera; Staatsbosbeheer for Speulderbos; City of Utrecht for Amelisweerd; Limburgs Landschap for Goedenraad; Direction Générale des Ressources Naturelles et de l'Environnement for Masblette; Büyükdüz Arastirma Orman in Karabük for Büyükdüz; Nagano Forest Service for Kayanodaira; Tochigi Forest Service for Takaharayama; Nanjiang Forest Service for Daba; Fanjing Shan Nature Reserve for Fanjing Shan; Miao'er Shan Nature Reserve for Miao'er Shan; and Longsheng Forest Service for Liluo.

Many persons helped me to make the fieldwork possible, for example by contacting responsible organisations, organizing my stay and transportation, or organizing assistance and guides. Thank you for your help:
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Wageningen
February 1992

Rob Peters

Contents

Chapter 1 - Introduction

1.1 BEECH

The beeches are a homogeneous group of 11 tree species growing in the Northern Hemisphere (Table 1.1). Beeches are deciduous trees with simple leaves and smooth pale bark. Two species are multi-stemmed with a little darker and rougher bark. The trees flower irregularly and their triangular nuts are edible. Hence, Roman poets called the tree *fagus*, i.e. "the glutton". In his *Species plantarum*, Linnaeus (1753) placed the beeches in the genus *Fagus*. Beech belongs to the *Fagaceae*, an important family in the Northern Hemisphere with many tree species that dominate forests. This is comparable to the important *Leguminosae* family in the tropics.

The ranges of beech cover large areas of eastern North America, Europe/western Asia and eastern Asia (Figure 1.1), and are found in a wide range of sites, from mountain slopes in the tropics to lowlands in the cool temperate zone, and from acid

Table 1.1
Species in the genus *Fagus*, their geographic range and their climatic range following Walter (1985).

species	geography	climate*
Fagus grandifolia Ehrhart eastern	U.S.A., Canada	V, VI
Fagus mexicana Martinez	Mexico	II.OB
Fagus sylvatica Linnaeus	Europe	VI, V-VI.OB
Fagus orientalis Lipsky	Turkey, Caucassus	V.OB
Fagus multinervis Nakai = F. engleriana	Ullungdo, S.Korea	VI
Fagus crenata Blume	Japan	VI, V-VI.OB, V.OB
Fagus japonica Maximowicz	Japan	VI, V.OB
Fagus hayatae Palibin ex Hayata	China, Taiwan	II.OB
Fagus engleriana Seemann	China	V.OB, V-II.OB
Fagus lucida Rehder et Wilson	China	V.OB, V-II.OB
Fagus longipetiolata Seemann	China, Vietnam	V.OB, V-II.OB
Fagus hayatae C.C. Yang spp pashanica	China (Sichuan)	V.OB
Fagus chienii Cheng	China (Sichuan)	V.OB

* Zonobiomes: II is tropical with summer rains, humido arid; V is warm-temperate (maritime), humid; VI is typical temperate with short period of frost (nemoral); OB is orobiome in mountainous environment; V-VI and V-II are transitional zones.

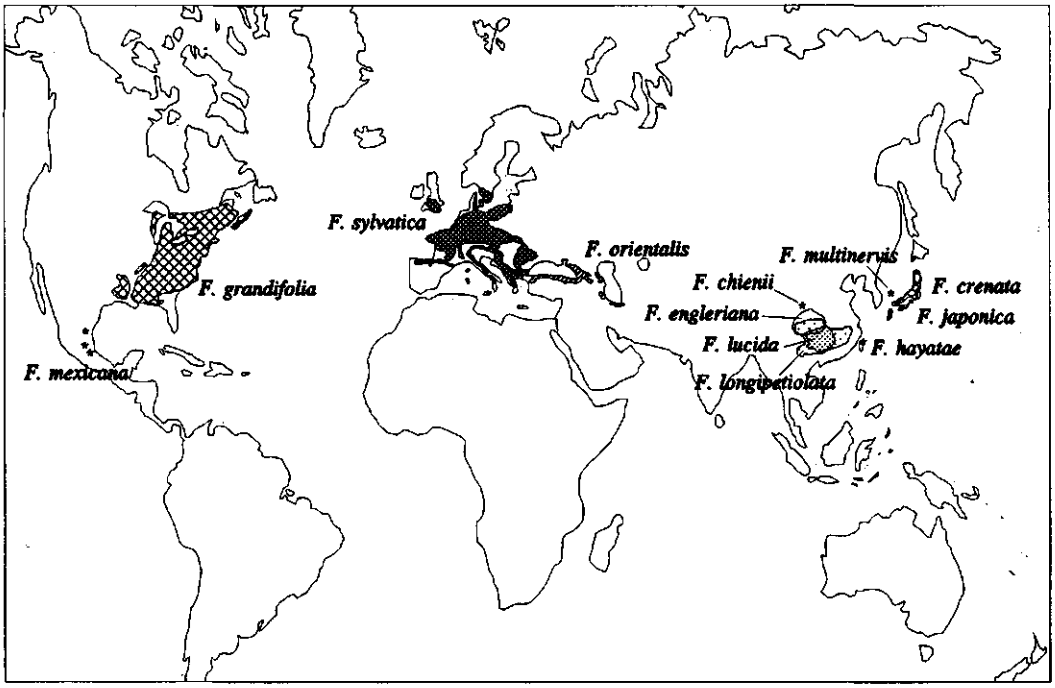


Figure 1.1
Ranges of the *Fagus* species.
Sources: Fagus grandifolia & Fagus mexicana (Little, 1971); Fagus sylvatica (Meusel et al., 1965); Fagus orientalis (Browicz & Zielinski, 1982); Fagus lucida, Fagus longipetiolata & Fagus engleriana (Tsien et al., 1975); Fagus hayatae (Zheng et al., 1985; Hsieh, 1989); Fagus chienii (Zheng et al., 1985); Fagus multinervis (Kim, 1988); Fagus crenata & Fagus japonica (Umehara et al., 1985).

podzol soil to neutral/alkaline rendzinas. The optimum for beech is on acidic and mesic loam soils. The ranges are limited by summer water deficits in continental and southern climates, and low winter temperatures and late spring frost in the north.

Beech forests are dominated by at least one *Fagus* species, which means that more than half of the canopy trees are beech (Figure 1.2). My study also considers forests where beech is an important codominant, i.e. belonging to the main canopy species. In the mesic areas of the temperate zone, beeches dominate old growth forest ecosystems. For example, in central European forests *Fagus sylvatica* achieves natural dominance in most parts of its wide physiological range, whereas others like *Quercus robur* and *Fraxinus excelsior* achieve dominance in wet, dry or nutrient poor extremes of their physiological ranges (Ellenberg, 1986). Likewise, *Fagus crenata* dominates the mesic sites in cool temperate Japan (Numata et al., 1975), and *Fagus* *grandifolia* is an important codominant tree in deciduous forest ecosystems of eastern North America (Braun, 1950).

In central European forestry, beech is the most widely used broad-leaved deciduous tree and the tree's silviculture is well studied (e.g. Hartig, 1851; Boer, 1857; Vaneslow, 1931; Mayer, 1984a; Lanier, 1986). Also studied is the silviculture of *Fagus grandifolia* in North America (Hamilton, 1955; Rushmore, 1961) and *Fagus crenata* in Japan (Kataoka, 1982; Maeda, 1988). Silvicultural practices were usually based on the knowledge of the ecology of beech trees and beech forests (Mayer, 1984a). Much of the knowledge on, for example, site requirement, growth, regeneration and shade tolerance can be found in old foresters' handbooks (Hartig, 1851; Boer, 1857).

To find out why beeches are such widespread successful trees, the purpose of my research was the study of general characteristics and local exceptions in beech species and beech forests. I tried to answer several questions:

1. Do these beech species, which occur in such varied sites, have something in common as forest organisms? What makes them different from codominant trees? Tree size and growth rate are parameters that show differences in growth strategies. For example, the relationship between height and stem diameter shows how trees invest energy in height growth as compared to stem-diameter growth. Because radial growth rate, tree height, stem diameter and crown projection are easily measured and compared, they were selected for the comparison of beeches within their own species, among different beech species and with other codominant tree species.
2. What are common characteristics of beech forests over the whole range? To find out which species could interact with beech during its lifespan, I compared species composition in beech forests on different sites. Tree-height distributions of tree populations were compared because they tell us whether or not a tree species remains dominant. The stage of development of a forest can be described by the abundance of forest patches dominated by different tree species and in different phases of development, i.e. forest architecture. Hence, I compared the architecture of different forests.
3. Are there common characteristics in the dynamics of beech forests? The relation between suppressed and released growth in trees, as well as release frequency, yields information about stability and change in the forest. Because this may explain codominance of tree species with certain light requirements, that need more or less frequent releases, I compared suppression and release in different sites.

Figure 1.2
Natural beech forests in Taiwan, *Fagus hayatae* (above), and in North America, *Fagus grandifolia* (below).

1.2 TAXONOMY

Nomenclature follows Fernald (1950) for U.S.A., Standley (1920-26) for Mexico, Tutin et al. (1964-80) for Europe, Davis (1965-88) for Turkey, Anonymous (1972-76) and Zheng (1983, 1985) for China, and Ohwi (1965) for Japan.

Phagos is Greek for the "glutton", but *fagus* was used by the Romans to denote the beech tree, referring to the edible nuts. During the Roman period, people differentiated between *silvae glandiferae*, forests where pigs were fattened upon acorns and beechnuts, and *silvae vulgaris pascue*, the normal pasture forests. In 1735 Linnaeus named the beech genus *Fagus* and in 1753 he named European beech *Fagus sylvatica*. In this study, I distinguish 11 *Fagus* species (Table 1.1). Contrary to Little (1965), *Fagus mexicana* is regarded as a species distinct from *Fagus grandifolia*. *Fagus moesiaca* in the Balkans is regarded as a subspecies of *Fagus sylvatica*. *Fagus engleriana* in China and *Fagus multinervis* in Korea are identical species (Ohkubo et al., 1988). In Sichuan, China, *Fagus pashanica* C.C. Yang is a subspecies of *Fagus hayatae*. *Fagus chienii* is doubted to be a valid species by Chang and Huang (1988), is rarely found, and may go extinct (Shen, pers. comm.).

1.3 RANGES

The ranges of the beech species vary from large to small (Figure 1.1). *Fagus sylvatica* and *Fagus crenata* occur in the lowland / colline zone of their northern range and in the montane zone in the south. *Fagus grandifolia* grows in the lowland / colline zone and the montane zone, throughout its range. *Fagus orientalis* and *Fagus japonica* occasionally grow at lower altitudes. The other beech species are restricted to montane zones. *Fagus grandifolia* has a wide range in eastern U.S.A. and southeastern Canada (Little, 1971). *Fagus mexicana* is restricted to the foggy mountains of tropical eastern Mexico where only a few isolated stands are known (Peters, in press). *Fagus sylvatica* has a wide range in Europe, and in central Europe it becomes the dominant forest tree species (Ellenberg, 1986). *Fagus orientalis* has a range from the Balkans, along the Black Sea, to Iran, with some relicts in southern Turkey. *Fagus crenata* has a wide range in Japan, and *Fagus japonica* is found less far to the north and on the lower side of *Fagus crenata's* range. *Fagus japonica* is typically restricted to areas with less than 50cm snowfall. *Fagus multinervis* (*Fagus engleriana*) grows on Ullungdo island in the Japan Sea (Kim et al., 1986; Kim, 1988). *Fagus hayatae* grows on some isolated mountains in northern Taiwan (Hsieh, 1989), and in Zhejiang and Sichuan, China. Chinese beeches grow in the montane zone, south of 34°N. *Fagus chienii* is only known from Pingwu county, Sichuan.

Fagus lucida, *Fagus longipetiolata* and *Fagus engleriana* have wider ranges. *Fagus longipetiolata* also grows in tropical northern Vietnam (Thái Van Trùng, 1978).

1.4 SOILS

In general, the ranges of beech species are not primarily determined by soil type. Beeches grow on a wide range of soil types, with an optimum in acidic and mesic loam soils.

Fagus sylvatica occurs over a wide range of mesic soils, with pH ranging from 3.5 to over 7, and humus from mull to mor (Le Tacon, 1981). In central Europe, this beech dominates the main central part of the moisture / nutrient range of forests (Ellenberg, 1979, 1986). Soil textures range from clay-loam to loamy sand. Water availability is important, especially if the summer precipitation is irregular or insufficient. Beech is neither found on soils with pseudogley, nor when reducing conditions are found within 20cm from the soil surface (Le Tacon, 1981). Beech can have an acidifying and podzolization effect on soil, and humus accumulates beneath these trees (Beyer et al., 1991).

Fagus grandifolia grows best on loamy soils with a high humus content and a pH of 4.1 to 6 (rarely over 7; Fowells, 1965). American beech grows on sand to clay-loam soils and is also sensitive to reduced soil moisture and flooding (Hamilton, 1955; Fowells, 1965). Soil moisture is important for survival of beech seedlings (Gleason, 1924). Also American beech has an acidifying effect on soil, and mineralization rate is lower under beech than under *Acer saccharum* (Boerner & Kozlowsky, 1989).

In Japan, *Fagus crenata* grows on wet-mesic to dry, loam or clay soils, with a pH of 3.7 to 6 (Saito, 1971; Hukushima, 1982). The soils are wetter and podzolized at higher altitudes (Maruyama, 1971). In Taiwan, *Fagus hayatae* grows on well drained, silty, clay soil with a pH of 3.2 to 4.2 (Hsieh, 1989). On Ullungdo, *Fagus multinervis* grows on well drained, mesic loam soils (Kim, 1988). Chinese beech forests are found on acid, sandy loam soils, with a pH from 4 to 6 (Wu, 1980; Hou, 1983), ranging from clay-loam to sandy-loam (Peters, pers. obs.).

1.5 CLIMATE

Beech species grow in temperate and tropical zones. Walter (1985) describes the zones where beech occurs as: mountain tropical with summer rains (orobiome II.OB); mountain, humid-warm temperate (orobiome V.OB); and typical temperate with a short period of frost (nemoral, zonobiome VI; Walter, 1985; Table 1.1). In the tropical and warm temperate zonobiomes, beech is restricted to the montane zone, with the exception of *Fagus grandifolia* in warm temperate southern U.S.A. (zonobiome V; Greller, 1989). The warm temperate zone is called the subtropical zone in Chinese research (Wu et al., 1980).

Moisture is important for *Fagus sylvatica* (van Schermbeek, 1898). Beech is absent where rain is insufficient (Becker, 1981), or where soil is too dry (Le Tacon, 1981; Ellenberg, 1986). Box (1981) gives a world terrestrial pattern of the annual moisture index, which is obtained by dividing average annual precipitation by average annual potential evapotranspiration (Thornthwaite, 1948). Some of the borders of the ranges for beech species (Figure 1.1) are related to a reduction in this annual moisture index, i.e. in North America to the west, in Europe to the south and southeast, and in China to the north. In the U.S.A., the western extension of beech is even more limited by drought in extreme years (Borchert, 1950). In tropical Mexico, beech is restricted to northeast facing slopes in the montane cloud forest zone (Peters, in press). In southern Europe, beech is restricted to the moist montane zone with low probabilities of drought (Thiébaut, 1984) and frequent fogs (Gutierrez, 1988). There, beech occurs at lower altitudes on northern slopes (northern Spain: Terradas, 1984; Etna, Sicily: Santocona, 1976; Balkans: Mayer, 1984b). In northwestern Spain, moist Atlantic winds are important (Hernández Bermejo & Sainz Ollero, 1978). The lower altitudinal limit of beech forests increases from north to south, e.g. from ca 350m above sea level in the north to 850m in the south of Yugoslavia (Mayer, 1984b). In the southeastern Balkans, *Fagus orientalis* occurs on warmer and dryer sites than *Fagus sylvatica* (Mayer, 1984b). Along the Black Sea coast in northern Turkey, *Fagus orientalis* occurs on northern slopes in the montane zone, and occasionally in lowland areas where humidity is high (north of Istanbul; Mayer & Aksoy, 1986). In China, beech occurs in the warm temperate zone which has no dry season, and which is influenced by Pacific monsoons (Hou, 1983). To the north and the west, the continental dry influence becomes stronger and beech is absent.

To the north and at higher altitudes, extreme temperatures are limiting. If summer temperatures are too low, beech has insufficient surplus production (Nomoto, 1964). For *Fagus crenata*, minimum winter temperatures (extremes < ca -30°C) also determine the northern extension (Sakai, 1975). *Fagus grandifolia* survives extremes of -42°C (Fowells, 1965), and *Fagus sylvatica*, -30°C (Walter & Breckle, 1986). *Fagus sylvatica* is sensitive to late spring frost (van Schermbeek, 1898; Becker, 1981) which causes seed production and seedling survival to fail (Watt, 1923; Burschel et al., 1964). Late spring frost may restrict beech in areas with sufficiently high summer temperatures and humidity. Factors which limit beech in Poland are minimum temperatures in winter, late spring frost, summer temperatures and duration of growing season (Slawiński, 1947). Near the eastern limit of beech in Poland, beech is found on nutrient rich soils in northern facing valleys (Matuszkiewicz, 1989). There, beech has strong growth and dominates forest communities, but is not expanding its range. Near the northern limit in Japan, *Fagus crenata* grows mainly on lower slopes, without preference of slope direction (Watanabe, 1987).

In North America, the length of the season that beeches retain their green leaves increases with decreasing latitude, i.e. from about 180 days in lowland southern Michigan (41°N) to 280 days in northern Florida (30°N) and 340 days in montane Hidalgo, Mexico (20°N; Peters, in press). In Europe, the length of the season that beeches retain their green leaves ranges from 131 days (56°N) to 150 days (46°N) in lowland central Europe (Lausi & Pignatti, 1973) and 168 days in northern Spain (41°N; Hernández & Sainz, 1978).

In general, the ranges of beech species are determined by rainfall and temperature. Summer water deficits limit beech in continental climates and in southern areas. Low winter temperature and late spring frost limit beech in northern areas. Species overlap largely in their moisture and temperature requirements, but they differ in their tolerance to drought and temperature extremes.

1.6 HISTORY

Fossil remains of *Fagus* are known from the middle Cretaceous (Takhtajan, 1969). *Fagus* and *Nothofagus* may have had a common ancestor in the Southern Hemisphere in Gondwanaland before continents separated (Poole, 1987). In eastern Asia, the most primitive and basic types of *Fagus* occur, whereas derived species occur in North America, Europe and western Asia (Takhtajan, 1969).

Gray (1846) described the analogy between the flora of Japan and that of the U.S.A. Since then, the relationships between the floras of the temperate zone in the Northern Hemisphere have been studied thoroughly (Hsü, 1983), especially the relationship between eastern Asia and eastern North America (e.g. Li, 1952;

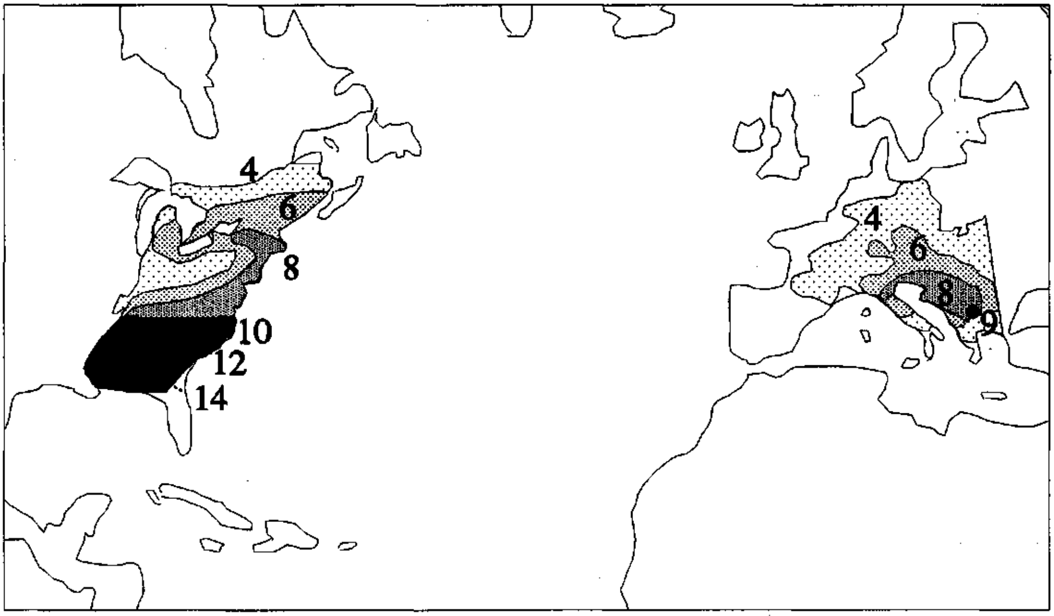


Figure 1.3
Migration of *Fagus sylvatica* in Europe and *Fagus grandifolia* in eastern U.S.A. after the last Glaciation (Huntley & Birks, 1983; Davis, 1981). Numbers indicate thousands of years B.P.. Areas in Europe indicate that more than 2% of total tree and shrub pollen is beech, and in North America the occurence of beech pollen or macrofossils.

Graham, 1972; Tiffney, 1985a). The relationship goes back to the early Tertiary when a mixed conifer / broad-leaved forest developed at high latitudes in Eurasia and North America (Hsü, 1983; Tallis, 1991). The Arcto-Tertiary Geoflora, which formed this forest, consisted of temperate plants with broad ecological tolerances (e.g. *Fagus*; Graham, 1972), and was not homogeneous (Tiffney, 1985a). In the Paleocene flora of Europe, *Fagaceae* and *Lauraceae* dominated (Takhtajan, 1969), as in the present Chinese *Fagus* forests (Wu et al., 1980). As temperatures dropped at high latitudes, tree species gradually migrated south (Chaney, 1940). The Arcto-Tertiary forest zone was fragmented by oceans and dry continental regions. Considering the age of currently common genera, most contact and migration took place before the late Eocene (Hsü, 1983), via the North Atlantic land bridge (Tiffney, 1985b).

During the Miocene, *Fagus* still occurred in the mixed broad-leaved and coniferous flora of Washington, Oregon and Nevada (Chaney, 1940; Robichaux & Taylor, 1977), but later beech became extinct in western North America. In the

Middle Miocene, temperate elements like *Fagus* first occurred in the vegetation of Veracruz in tropical Mexico (Graham, 1973). Miocene or Pliocene extension of the dry environment in continental North America prevented further contact. The *Fagus mexicana* forests, now growing in montane tropical Mexico, are relicts from the Tertiary forest. During Paleocene and Eocene, *Fagus* occurred in mixed conifer / broad-leaved forests of northern China and of montane eastern China (Hsü, 1983). From the Oligocene on, the climate in northern China became cooler and drier. During the Miocene, *Fagus* occurred in central and eastern China, where evergreen broad-leaved species also occurred (Hsü, 1983). In northern China, *Fagus* became extinct. In Japan, *Fagus* first occurred during the early Miocene (Tanai, 1972). Contact with Taiwan (*Fagus hayatae*) and Ullungdo (*Fagus engleriana/multinervis*) was possible due to lowering of the sea level during the Pleistocene.

In Europe and North America, *Fagus* retreated to the south during the Pliocene and Pleistocene. After the last Pleistocene Glaciation, *Fagus* spread north again (Figure 1.3), i.e. in Europe from the Balkans (Huntley & Birks, 1983), in North America from the southeast (Davis 1981; Bennett, 1985), and in Japan from coastal refugia south of 38°N latitude (Tsukada, 1982). In North America migration still continues (Davis, 1981), however in Europe 'natural' migration has been obscured by human interference which favors beech (Huntley & Birks, 1983).

1.7 SUMMARY

The objective of my study was to uncover and analyze general characteristics and local variations in beech trees and beech forests. In Chapter 2, I describe the study sites and the manner in which they were selected among old growth forests. My study sites were located along geographic gradients. Within study sites, the plots were selected far from traces of human impact.

In Chapter 3, I compare architecture, shade tolerance and radial growth of beeches and codominant tree species. The relation between the size parameters of tree height, stem diameter and crown projection yields information on the growth strategy of each tree species. To compare growth strategies, I analyzed size parameters among beech species and codominant species.

In Chapter 4, I analyze geographical trends in woody species composition and in forest architecture. Tree-height distributions of populations were compared because they show recruitment patterns and future dominance of a tree species. I described the stages of forest development by their forest architecture, i.e. the spatial position of components within a forest patch and the spatial position of different forest patches in different forest mosaics. Within each study site, I related tree populations and tree regeneration to forest architecture.

In Chapter 5, I use tree-ring chronologies to analyze forest dynamics. I obtained information on small-scale changes in the forest from the relation between suppressed and released growth in (shade-tolerant) trees, and the frequency of growth release. I studied the relation between growth strategy of trees, forest architecture and frequency of change in forests.

In Chapter 6, I propose a model which gives general rules underlying the ecological behavior of beeches in beech forests, and discuss the local exceptions to these rules. I also evaluate implications of the model for future forest development in relation to climatic change.

Chapter 2 - Study sites and data collection

2.1 STUDY SITE SELECTION

I selected sixteen study sites; four in eastern North America (AM), six in eastern Asia (AS) and six in Europe/western Asia (EU; Table 2.1, Figure 2.1). Beech forests with little human impact were available. The four study sites in the Netherlands and Belgium had a management record and were included to analyze the relation between soil type and beech. The study site in South Korea (AS3) showed traces of recent cuttings.

The study sites were selected to be representative of beech forests in different geographic areas, i.e. eastern North America, eastern Asia and Europe/western Asia (Table 2.1). In eastern North America and in eastern Asia, study sites were selected along a north-south gradient. In Europe/western Asia, one plot was in the southeastern part of the range and the others in the northwestern part. The forests were dominated by different *Fagus* species, and codominated by tree species typical for that region. In eastern North America, the study sites were located in mixed beech / sugar maple forest (AM1 & AM2), beech / magnolia forest (AM3) and beech / evergreen oak forest (AM4). In Japan, I selected a typical pure beech forest on the Japan Sea side (AS1) and a mixed beech forest on the Pacific side (AS2). The study site on Ullung Island (AS3) was in a pure beech forest. The Chinese study sites were in mixed beech / deciduous broad-leaved forest (AS4), pure beech beech forest with a dense evergreen tree understory (AS5) and mixed beech / evergreen broad-leaved forest (AS6). The European study sites were in pure beech forests (EU1 & EU4) and mixed beech / deciduous broad-leaved forests (EU2, EU3 & EU5). In Turkey, I selected a study site in mixed beech / coniferous forest (EU6).

The study sites had to be old growth forests with minimal human influences, a prerequisite for long-term natural development. I found no (in most) or little (in AM4) traces of cuttings or burnings in the study sites, although stumps or trunks decompose over time and are no longer evident, as are relics of non-timber historical human use. Hence, local sources of information and records of forestry services were used to avoid areas of post-human influences. The exception was in AS3 where many stumps were present. If traces of human impact were found or suspected then

Table 2.1
Location of study sites and relevant beech species.

Code	Name	Latitude	Longitude	*Fagus* species
AM1	Warren Woods (Michigan, U.S.A.)	41°50'N	86°40'W	*F. grandifolia*
AM2	Hueston Woods (Ohio, U.S.A.)	39°32'N	84°45'W	*F. grandifolia*
AM3	Woodyard Hammock (Florida, U.S.A.)	30°40'N	84°15'W	*F. grandifolia*
AM4	La Mojonera (Hildalgo, Mexico)	20°38'N	98°37'W	*F. mexicana*
AS1	Kayanodaira (Nagano, Japan)	36°50'N	138°33'E	*F. crenata*
AS2	Takaharayama (Tochigi, Japan)	36°53'N	139°48'E	*F. japonica*, *F. crenata*
AS3	Ullungdo (South Korea)	37°30'N	130°45'E	*F. multinervis*
AS4	Daba forest stat. (Sichuan, China)	32°42'N	106°55'E	*F. hayatae*, *F.engleriana*
AS5	Fanjing Shan (Guizhou, China)	27°55'N	108°45'E	*F. lucida*
AS6	Miao'er Shan (Guangxi, China)	25°50'N	110°40'E	*F. lucida*
EU1	Speulderbos (The Netherlands)	52°15'N	5°40'E	*F. sylvatica*
EU2	Amelisweerd (The Netherlands)	52°05'N	5°10'E	*F. sylvatica*
EU3	Goedenraad (The Netherlands)	50°50'N	5°50'E	*F. sylvatica*
EU4	Masblette (Belgium)	50°10'N	5°20'E	*F. sylvatica*
EU5	Fontainebleau (France) [illegible]	48°30'N	2°40'E	*F. sylvatica*
EU6	Büyükdüz (Turkey)	41°20'N	32°30'E	*F. orientalis*

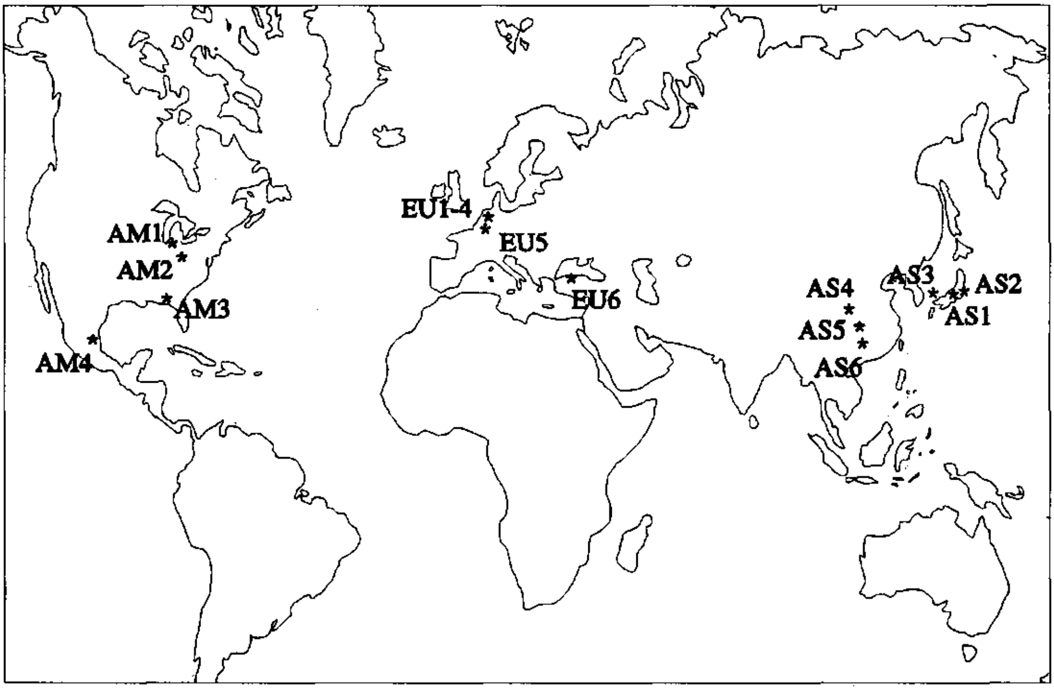


Figure 2.1
Location of the study sites.

plots were selected away from such sites, and away from roads and trails. In densely populated areas like eastern China and Japan, the sites were located on remote slopes in the mountain zone. However, remote location was not always a guarantee for little human impact, e.g. in Japan, forest people were living and working in the middle of forest areas during the summer and returned to their villages in winter (Umehara et al., 1985). Artificial fires may have reset forest development. For example, in the Daba forest station area (AS4) extensive fires occurred 150yr ago, and in the beech forests of Fanjing Shan (AS5) artificial fires have also probably occurred (Cao, pers. comm.). Also, in the Miao'er Shan nature reserve some cutting and burning was observed, but the study sites were located far from such sites. Furthermore, it should be noted that human influence may have long-term effects, e.g. after 600 years the effect of clear-cutting is still visible in the beech forest of Fontainebleau (Koop, 1989).

2.2 STUDY SITE CHARACTERISTICS

Nine Fagus species dominated the study sites (Table 2.1). The Mexican, Turkish, Chinese and Japanese sites were located in the montane zone with steep slopes (>10°, Table 2.2). The U.S.A., Korean and European sites were located in the lowland and submontane zones with gradual slopes (<10°), and with steeper slopes in EU3 and EU4. In general, the sites were on mesic moist, loam soils, with mull to moder type humus. Exceptions were the mesic-dry soils in AS1 and EU1 (sand soil), the mesic-wet soil in EU2 and the clay soil in EU3. Many of the soils could be classified as (Dystric) Cambisols, a large soil group in the FAO system (FAO, 1988; Table 2.3). The soils were stable, never shallow, and waterlogging did not occur, except in parts of AM1 and EU2 which were excluded from the plots.

The average annual temperature ranged from 5°C in AS1 to 20°C in AM3, and yearly precipitation ranged from 700mm in EU1/3 to 2550mm in AS5 (Table 2.4). The average monthly temperature of the coldest month should be -1°C or above for evergreen broad-leaved tree species to survive (Ohsawa, 1990) and this was true for the forests where these species codominate (AM3 & 4, AS5). The daily maximum temperatures in the growing season are important for assessing the probability of water deficit, but they were unavailable for many of the sites. In the montane zone, where the daily temperature range was expected to be largest, the summer precipitation was also largest (AM4, AS2 & 5). The warmest site with beech forest was located in lowland northern Florida (AM3), with an average annual temperature of 20°C and a summer precipitation of 950mm.

Table 2.2
Topography and soil characteristics of the study sites (? = unknown).

Site	Latitude	Topography			Soil			
	(°N)	Altitude (m)	Slope (°)	Aspect	Moisture	Stability	Texture[1]	Humus
AM1	42	180	0	-	mesic	±	SL,L	mull-moder
AM2	39	250	0	-	mesic	-	SiCL	mull
AM3	31	45	0	-	mesic	±	SL,L	mull
AM4	21	1850	20	W	mesic	-	?	?
AS1	37	1570	10	SW	mesic-dry	-	SL,L	moder
AS2	37	900	20	SE	mesic	-	SiL,L	mull
AS3	38	400	10	NW	?		?	?
AS4	33	1400	25	W&N	mesic	-	CL	moder
AS5	28	1800	30	SE-SW	mesic	-	SiL	moder
AS6	26	1600	30	SE-W	mesic	-	SL,L	mull-moder
EU1	52	50	0	-	mesic-dry	-	LS	moder-mor
EU2	52	5	0	-	wet-mesic	±	CL	mull
EU3	51	130	15	S	mesic	-	C	mull
EU4	50	350	20	S&N	mesic	-	L	moder
EU5	48	135	0	-	mesic	-	?	moder-mull
EU6	41	1450	15	NE	?	-	SL	?

1. Texture: S = sand; L = loam; Si = silt; C = clay.

Table 2.3
Local and FAO classification (1988) of soils in study sites (? = unknown).

Site	Local	FAO
AM1	(Aquic Arenic or Psammentic) Hapludalf	Haplic Luvisol (LVh)
AM2	Typic Hapludalf	Haplic Luvisol (LVh)
AM3	?	?
AM4	?	prob. Dystric Cambisol (CMd)
AS1	dry podzolic soil (Pd)	(Dystric) Cambisol
AS2	moderately moist brown forest soil (Bd)	Dystric Cambisol (CMd)
AS3	?	?
AS4	mountain brown earth	Haplic Acrisol (ACh)
AS5	mountain yellow-brown earth	Dystric Cambisol (CMd)
AS6	mountain yellow earth	Dystric Cambisol (CMd)
EU1	'holt' podzol soil	Cambic Podzol (PZc)
EU2	'polder' vague soil	Eutric Fluvisol(FLe)
EU3	'krijt' earth soil	Rendzic Leptosol (LPk)
EU4	sols bruns acides	Dystric (Eutric) Cambisol
EU5	sols bruns - sols podzolique	?
EU6	sandy loam soil	?

Table 2.4
Climatic data of the study sites.

Site	Temperature[1] (°C)			Precipitation[2] (mm)		Station (years)
	Av.yr.	Jan	Jul	Av.yr.	Apr-Sep	
AM1	9	-4	23	950	550	Benton Harbor (1970-87)[4]
AM2	12	-2	25	1500	850	Dayton (1951-80)[4]
AM3	20	11	27	1550	950	Tallahassee (1941-70)[4]
AM4	14	11	18[3]	2050	1750	Zacualtipán[5]
AS1	5	-8	17	1950	800	Nosawa Onsen (1926-60)[6]
AS2	9	-2	21	1900	1400	Ashio (1931-60)[6]
AS3	11	0	22	1500	700	Todong (1931-60)[7]
AS4	11	0	20	1500	?	Nanjiang (1960-83)[8]
AS5	9	-1	19	2550	1950	Fanjingshan (1967-78)[9]
AS6	11	1	19	2300	?	Miao'er Shan (2yr)[10]
EU1/3	9	3	19	700	350	De Bilt (1931-60)[11]
EU4	8	0	15	1100	?	St. Hubert (1959-70)[12]
EU5	10	2	19	700	350	Fontainebleau (1883-1970)[13]
EU6	7	-2	15	1200	500	Baklab./Büyük. (8yr)[14]

1. Temperatures are extrapolated from the nearest weather station values to values at the correct elevation by using a temperature decrease of 0.6°C per 100m increase.
2. Precipitation are the weather station values.
3. May (warmest month).
4. US Dept. Commerce, National Oceanic and Atmospheric Administration, Environmental Data Service.
5. After Puig (1976).
6. Annual Report of the Japan Meteorological Agency.
7. After Kim et al. (1986).
8. Nanjiang Meteoroligical Station, Sichuan.
9. After Huang et al. (1982).
10. Miao'er Shan Nature Reserve.
11. KNMI.
12. Thill et al. (1988).
13. City of Fontainebleau.
14. Karabuk forest station.

Table 2.5

Size, number of plots, number of increment cores (tree-of-present, released-growing potential tree, suppressed potential tree), and year of recording.

Site	Size (m^2)	Number of plots	Number of cores	Year	
AM1	80 x 30	2	34,17,7	1989	
AM2	70 x 30	2 (+1)	8,14,6	1989	
AM3	70 x 30	2	12, 2,7	1989	
AM4	50 x 30	2	6,10,2	1989, 1990	
AS1	40 x 10, 70 x 30	2, 1	24, 1,7	1986, 1990	
AS2	40 x 10, 30 x 10, 50 x 50	2, 1, 1	27,11,28	1986, 1990	
AS3	30 x 20	1	0	1990	
AS4	40 x 30, 50 x 10	1, 2	29,12,12	1991	
AS5	50 x 10, 30 x 10	5, 2	24, 3,1	1987	
AS6	50 x 20, 20 x 5	2, 2	0	1990	
EU1	50 x 50, 80 x 30	1, 1	7, 0,0	1988	
EU2	80 x 30, 60 x 30	1, 1	8, 7,14	1988	
EU3	50 x 50	1	7, 0,9	1988	
EU4	80 x 30, 50 x 30	1, 1	0	1988	
EU5	140 x 70	2	19,81	1984	data Koop (1989)
EU6	70 x 30, 60 x 30	1, 1	45,18,39	1991	

2.3 PLOT SELECTION

In each study site, I established at least two plots, with the exception of the small forest lot EU3. The plot size varied from 300 to 2400m², and was smaller on steep slopes (AS5) or ridges (AS6; Table 2.5). I selected the plots at each site in such a way that they included forest patches in different phases of development. The phases of development were distinguished by comparing the heights of dominant trees in each patch. I took care to select the plots away from traces of human impact and away from local wet areas to avoid unstable soils.

2.4 DATA COLLECTION

In the plots, I measured altitude, slope and aspect. The vegetation was recorded in three groups: A. trees taller than 5m; B. trees and shrubs between 0.5m and 5m tall; and C. trees and shrubs shorter than 0.5m and herbs (including Gramineae and ferns). The rationale for including group B was the regular presence of shrubs and medium-tall tree species less than 5m tall. I defined tall tree species below 0.5m as seedlings, and between 0.5m and 5m tall as saplings. I collected data for group A in the whole plot and for group B in a central belt of 1 or 2m wide, and data for group C in a central belt of 10m wide (Figure 2.2).

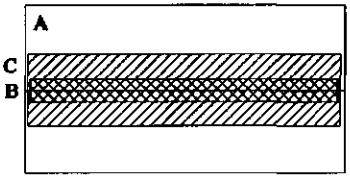


Figure 2.2
Example of a plot with sub-belts in three groups: A. trees taller than 5m; B. shrubs and trees between 0.5m and 5m tall; C. herbs, shrubs and trees under 0.5m tall.

With marked ropes and/or measuring tapes, I made a grid in the plots, and mapped the position of stem bases and vertical crown projection (cp) of trees and shrubs in groups A and B. From this map I calculated crown projections. I measured tree height (h) with a Haglöf clinometer (in m) for trees in group A and with a stick (in dm) for trees in group B. I measured stem diameters (in mm) with a π-tape at 0.5m height ($d_{0.5}$) and 1.3m height ($d_{1.3}$) for trees and shrubs in groups A and B. Crown densities in 20% classes were estimated visually for each tree. I used tree height, crown-projection map and profile sketches of individual trees to make profile diagrams of the plots. In group C, I recorded abundance of beech seedlings, and estimated percentage cover of important species, e.g. dwarf bamboo species in the Asiatic forests.

Within each plot, I took increment cores at 0.5m height from beech and codominant tall tree species. I distinguished three classes: trees in the forest canopy ('trees of the present'), trees in forest canopy gaps (released-growing 'potential trees'), and trees in the undergrowth (suppressed 'potential trees'; Chapter 3; Table 2.5). I took one core per tree, which is sufficient when relative growth rates are compared, and measured tree-ring width with a binocular microscope (in 0.01mm; Digitalpositiometer, Kutschenreiter, Wien).

For Fontainebleau (EU5), I could use the data from Koop (1989).

Chapter 3 - Size parameters and growth in beech trees

Among sites, I compared size parameters and radial growth of beech species, and within each study site I compared size parameters and radial growth of beech and codominant tree species. Size parameters were tree height, stem diameter and crown projection, and radial growth was measured in tree-ring chronologies.

3.1 INTRODUCTION

Architecture

The architecture of an object is its design and construction (Webster's New World Dictionary, 1988). In their analysis of tropical trees and forests, Hallé et al. (1978) define architecture as the "visible, morphological, expression of the genetic blueprint of organic growth and development". Oldeman (1990) stresses that in the study of forest, architecture concerns design and construction per hierarchical level. Examples of hierarchical organization levels are organisms, which are studied in this chapter, and eco-units and forest mosaics, which are studied in Chapter 4. Tree architecture explains much of the tree's strategy of light interception during succession (Horn, 1971).

The architecture of *Fagus sylvatica* is well studied (Thiébaut, 1982; Roloff, 1986; Thiébaut et al., 1990). *Fagus sylvatica* grows according to 'Troll's model' (see glossary), with the main characteristic of plagiotropic differentiation in all aerial axes (Hallé & Oldeman, 1970). Compared to orthotropic axes, the plagiotropic axes have flattened and highly organized leaf layers and so can intercept light over larger surfaces with less investment in biomass (Oldeman, 1989). On the other hand, orthotropic axes are better fit to growing upward quickly, and overtopping neighbor species. Plagiotropic axes, with flattened leaf layers, were also found in the other beech species (Peters, pers.obs.). *Fagus sylvatica* has a flexibility in forming short and long shoots, which depends on the tree's vitality and is a means of responding to environmental conditions (Roloff, 1986). Branching in *Fagus grandifolia* is practically identical to that in *Fagus sylvatica* (Roloff, 1989). The architecture of beech trees may be compared with legume trees, which occupy an equally important niche in the tropics of Africa and America (Rundel, 1989).

Table 3.1
Some architectural characteristics of genera found codominating the forest with beech.

	model[1]	shoot/branches	source
Quercus[2]	Rauh	orthotropic	Hallé et al. (1978)
Lithocarpus	Rauh	orthotropic	Hallé et al. (1978)
Castanopsis	Rauh	orthotropic	Cao (pers. comm.)
Pinus	Rauh	orthotropic	Hallé et al. (1978)
Picea	Rauh	orthotr. (little plagiotr.)	Edelin (1977)
Acer	Rauh/Scarrone	orthotr. (Scarrone: terminal flowering)	Hallé et al. (1978)
Abies	Massart	orthotr./plagiotr.	Edelin (1977)
Tsuga	Mangenot	plagiotr.(basis orthotr.)	Edelin (1977)
Carpinus	Troll	plagiotropic	Roloff (1989)

[1] See glossary.
[2] *Cyclobalanopsis* = *Quercus*

Legume trees also have a very flexible architecture, frequently showing Troll's model with plagiotropic axes (Oldeman, 1989).

Many of the genera codominating with beech have orthotropic axes (Table 3.1). They may have faster height growth and may be less successful than beech in intercepting light. Some of these genera, e.g. *Quercus* (Roloff, 1989), easily reiterate their architectural model, which gives them the ability to respond to environmental changes (Oldeman, 1974). The architectural models of *Fagus* and *Acer* are different (Table 3.1), but *Acer saccharum* occupies a successional niche that differs little from *Fagus grandifolia*. According to Horn (1971), *Fagus grandifolia* and *Acer saccharum* have the same successional status and are both monolayers, as opposed to the multilayers of *Quercus rubra* and *Acer rubrum*. For tree species, orthotropic vs plagiotropic axes, the ability to reiterate, and multilayers vs monolayers may explain differences in the size parameters of tree height, stem diameter and crown projection.

Size parameters

Tree height, stem diameter and crown projection are parameters of the tree's architecture. The ecological status of individual trees can be described by size parameters of stem and crown. Parameters like tree height, stem diameter and crown projection are measurable and comparable among regions and species. Clear allometric relationships exist among these parameters (e.g. Schober, 1972; Ogawa & Kira, 1977; LeGoff & Ottorini, 1979; Leersnijder, in press). These parameters are also an expression of a tree's growth strategy. To reach higher light levels, first a tree can invest relatively more energy in height growth than in stem diameter and crown growth. This tree will have a relatively high tree-height/stem-diameter (h/d) ratio and a relatively small crown projection. To occupy space first, a tree may invest relatively more energy in crown expansion and stem-diameter growth than in height growth. This tree will have a lower h/d ratio and a relatively large crown projection. The larger the intraspecific variation in the relationship between tree height, stem diameter and crown projection, the more flexible the growth strategy of the species.

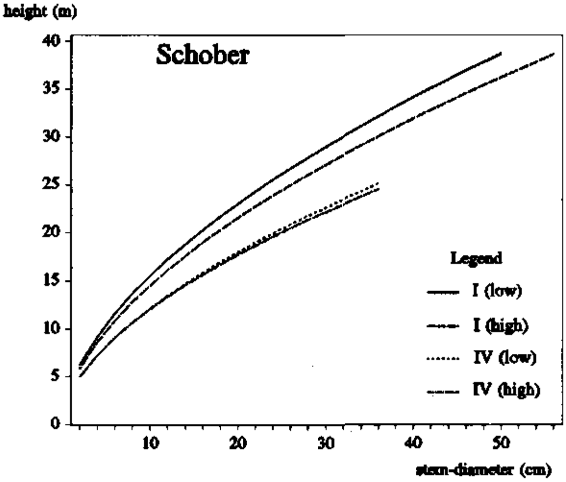


Figure 3.1
Tree height / stem diameter curves for low and high thinning intensities and for two site classes, one with good growth (I) and one with poor growth (IV). Based on yield table by Schober (1972).

The h/d ratio yields information about the tree's growth strategy, as well as the tree's physical flexibility and strength (Mayer, 1984a; Vogel, 1988). Putz et al. (1983) found for tropical trees that a lower h/d ratio favors uprooting over snapping. In tropical forests in Ivory Coast, snapped trees have a high h/d ratio and branch fall is most common in trees with lower h/d ratios (Vooren, 1986). Oldeman (1974, 1990) describes changes in the h/d ratio when the tree adapts its architecture to a changing environment. Early lowering of the h/d ratio during a tree's lifespan occurs with wide spacing among trees, e.g. in tropical trees (Oldeman, 1974) and in temperate conifers (Abetz, 1976; Mayer, 1984a; Bergel, 1990). Abetz (1976) found that on the average, the h/d ratio of trees decreases during their lifespan, and in even-aged stands the dominant trees have lower h/d ratios. For managed *Fagus sylvatica* forests, Schober (1972) shows that the h/d ratio is lowered by increased thinning intensity (Figure 3.1). He also found that slow-growing beech trees have lower h/d ratios than faster growing ones. Trees that grow under high light levels tend to have lower h/d ratios and trees with lower h/d ratios have lower probabilities of breaking. In my analysis of old growth forests, I used h/d ratios of beech trees to compare growth strategies of beech species with codominant species.

Phases in tree development

Oldeman (1974) distinguishes trees in different phases of architectural development, which are markers of forest development in the tropics. He recognizes three phases in the architectural development of a tree, i.e. 'tree-of-future', 'tree-of-present', and 'tree-of-past'. Trees-of-future (potential trees; Hallé et al., 1978) have not yet reached their maximum size and often still grow according to their growth model (cf. Hallé & Oldeman, 1970). Trees-of-present are in an enduring phase and build a complex architecture by reiterating their growth model in the crown (Hallé et al., 1978). Trees-of-past are degrading. Hallé et al. (1978) give further definitions: potential trees have a potential for future expansion within the forest mosaic; trees-of-present are dominant trees which codetermine forest architecture but without further capability for expansion; and trees-of-past are over-mature, decaying or damaged trees in the process of elimination from the forest. Because in the temperate zone trees soon form reiterations, the phase of prolific reiteration does not coincide with the phase of tree-of-present, which makes this architecture criterion useless. Although the type of expansion or growth may change from potential tree to tree-of-present, temperate trees continue to expand in size. Potential trees and trees-of-present can be seen as two phases in the growth of a tree. In potential trees the height growth is relatively more important and in trees-of-present the stem diameter and the crown extension growth become relatively more important. For example, in Slovakia, *Fagus sylvatica* trees have maximum height growth at an age between 25 and 130yr and maximum stem diameter growth around 45yr and between 140 and 190yr (Korpel', 1987). The transition between the two phases is gradual. To distinguish potential trees and trees-of-present, I set an empirical threshold at a certain height, which is species- and site-dependent. Tall tree species that have passed this height threshold are 'full grown' trees that can no longer be suppressed by other tall trees. I define the forest canopy as made up of the trees-of-present of tall tree species, and canopy gaps as the openings between the trees-of-present. Potential trees that are growing under high light levels are 'released-growing', whereas those growing in the shade are 'suppressed'.

Multi-stemmed vs single-stemmed

Two beech species have multi-stemmed growth forms under all conditions; *Fagus japonica* (Figure 3.2; Ohkubo et al., 1988; Peters & Ohkubo, 1990) and *Fagus engleriana* (= *Fagus multinervis*, Shen, pers. comm.; Kim et al., 1986; Peters, 1991). *Fagus japonica* grows on the Pacific side of Japan (31-40°N), on the warmer side of *Fagus crenata*'s range with typically little snow (<0.5m). *Fagus multinervis* grows on Ullung Island (37°N), South Korea, in the cool temperate zone with much snow (>1m). *Fagus engleriana* grows in the temperate montane zone of subtropical China (28-34°N). The multi-stemmed individuals are genets (genetic individuals; Harper, 1977), that form clusters of stems, each cluster several meters in diameter. *Fagus japonica* leaves from stems within the cluster are genetically similar (pers.comm. Ohkubo). At the root collar of the stems, especially on the outside of the clusters, sprouts are present and continuously forming. Each stem has a potential for separate existence (ramet, Harper, 1977), and may become over 20m tall.

Multi-stemmed beeches were especially successful in areas where the understory was dominated by dwarf bamboo. Through sprouts, multi-stemmed beeches evaded suppression by dwarf bamboo and extended their dominance (Peters & Ohkubo, 1990).

Botanically, trees are woody plants with acrotonic branching, and shrubs are woody plants with basitonic branching and shoots that grow up only for a few years (Troll, 1973; Braun, 1982). Multi-stemmed beeches are intermediate between shrubs and trees, with 'basitonic' branching and shoot growth which continues for a century.

The taller a tree becomes, the more light it needs to support its pre-existing biomass and achieve unit height growth (Raven, 1986). To ensure mechanical stability, the diameter of a stem should increase stronger than its height. Multi-stemmed plants have a more costly support skeleton and have higher whole plant light compensation points (Givnish, 1986). Tall multi-stemmed beeches contradict the ecophysiologically derived hypothesis that multi-stemmed plants are low in stature, whereas single-stemmed plants are tall (Givnish, 1984).

Multi-stemmed beeches resemble coppice in other beeches, with the difference that in coppice the sprouts become less vital and less numerous with increasing age of the tree. Coppiced beeches should be cut while young to enable sprouting. Coppice of *Fagus crenata* (Kamitani, 1986) or *Fagus sylvatica* (Mormiche, 1981) is only successful if the cutting cycle is shorter than 25 years. Dry Mediterranean or cool montane climate favor coppice of *Fagus sylvatica* (Mormiche, 1981; Mayer,

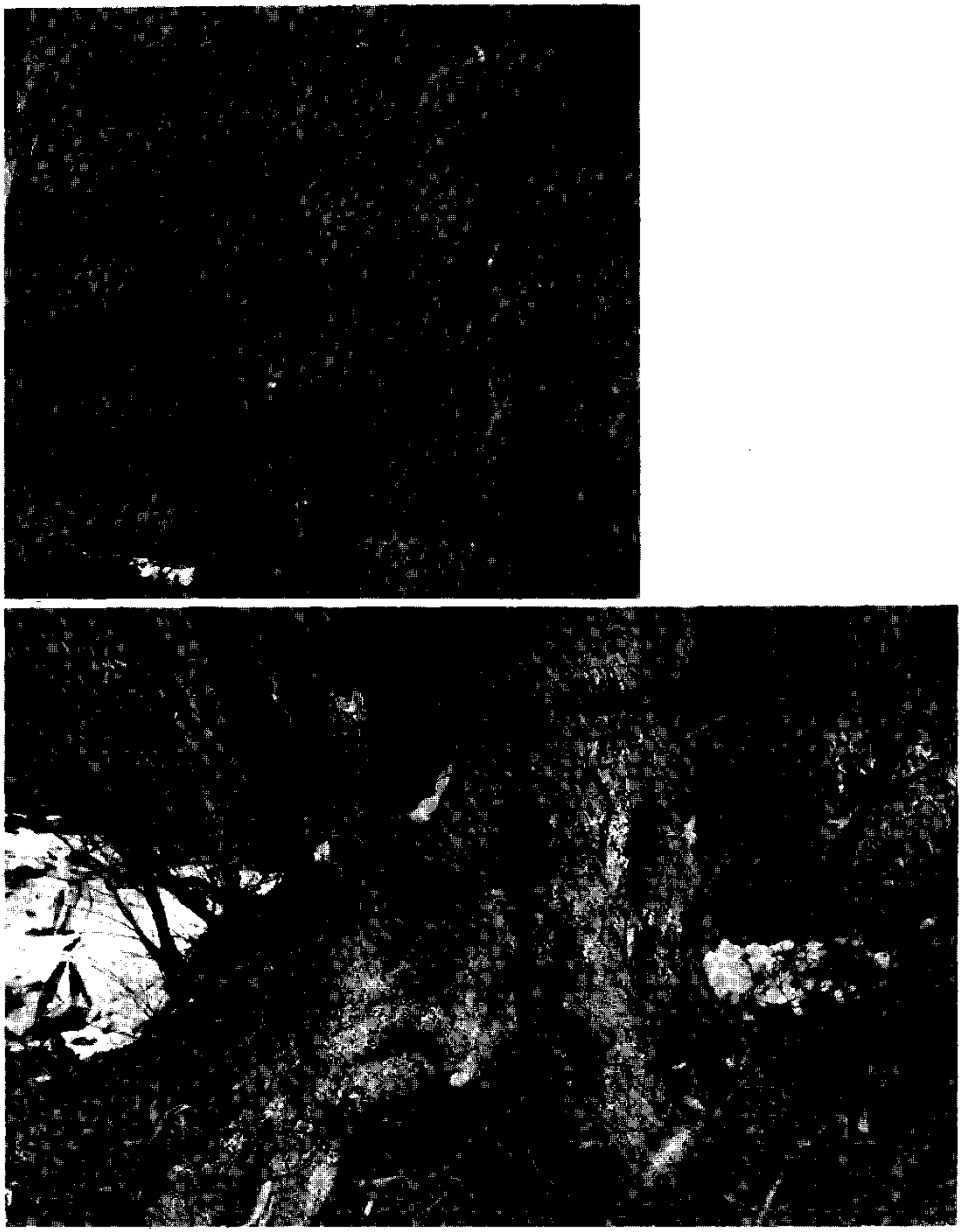


Figure 3.2
Multi-stemmed *Fagus japonica* (AS2). Above: cluster, tree height is about 20m and largest diameter is about 40cm. Below: sprouts.

1984a; Lanier, 1986). Natural sprouting in *Fagus sylvatica* occurs near the timberline in Central European mountains (Fanta, 1981). In *Fagus grandifolia*, natural root-sprouting is extensive near ridges in the Great Smoky Mountains ('beech gaps', pers.obs. Peters) and near the cool northern end of its range (Held, 1983), but is absent in the southern part of its range. Exposure and injury favor root-sprouting in *Fagus grandifolia* (Jones & Raynal, 1988). Whereas *Fagus japonica*, *Fagus engleriana* and *Fagus multinervis* are multi-stemmed under all conditions, *Fagus crenata*, *Fagus sylvatica* and *Fagus grandifolia* only become multi-stemmed under stress.

Stem-diameter growth

Tree photosynthesis, and in a complex way tree growth, is affected by light intensity, temperature, carbon dioxide supply, water supply, and nutrient supply (Kramer & Kozlowski, 1979). If nutrient supply, water-carrying capacity of the soil and carbon dioxide supply are sufficient, then the main environmental factors affecting tree growth are temperature, precipitation and light intensity. This condition of sufficient nutrient and water supply by the soil is met in the mesic soils where beech trees reach their greatest dominance.

The effect of changes in temperature and precipitation on tree-ring width is dependent on the site. In Solling, Germany, Makowka et al. (1991) found tree-ring width to correlate with temperature, and not with precipitation. Because the study site, Solling, is neither extremely cool nor dry, there is little effect of temperature and precipitation change on growth. In the submontane zone, Eckstein et al. (1984) found a positive correlation between tree-ring width in *Fagus sylvatica* and precipitation in the preceding autumn and during the growing season. Temperature was unimportant. Radial growth of beeches that have lower crown densities and smaller tree rings than their neighbors is less in dry years (Fischer & Rommel, 1989). Near the timberline, Müller (1981) demonstrated a correlation between temperature and tree-ring width in conifers. However, in Japan a shorter growing season, not temperature difference during the growing season, causes the annual photosynthetic surplus production of *Fagus crenata* to decrease with increase in altitude (Maruyama, 1977; Kakubari, 1977, 1987). In Spain, near the southern limit of *Fagus sylvatica*, tree-ring width decreases with altitude and tree rings are wider on warmer southern slopes than on cooler northern slopes (Terradas, 1984). In *Fagus sylvatica* and *Fagus crenata*, average tree-ring width is affected by site conditions, altitude and aspect. Year-to-year variation in tree-ring width is little affected by changes in temperature and precipitation, except on cool or dry sites.

The common year-to-year pattern in tree-ring width from many trees in a region may be identified as variance resulting from limiting macroclimatic factors (Fritts, 1976). In the study sites these were temperature and precipitation, and the resulting variance component was expected to be small. The differences among individuals within a stand may be attributed to variations in the life histories of individual trees (Fritts, 1976). The year-to-year variation may be ascribed to seed production, herbivory, small and temporary light changes (branch fall), and physical damages.

In eastern North American forests, tree-ring width may be determined less by climatic trends than by non-climatic trends, such as tree age, light level or growing space (Phipps, 1982). Exceptions are wet sites or sites with extremely shallow soils. On the other hand, Canham (1985, 1988, 1990) demonstrated a strong correlation between tree-ring width and light intensity in *Fagus grandifolia* and *Acer saccharum*. All except two of my study sites were located on mesic soils and distant from altitudinal extremes. Hence, I expected temperature and precipitation to have little effect on tree-ring width. The remaining environmental factor was light intensity. I compared tree-ring width with phase of tree development (tree-of-present, released-growing potential tree, suppressed potential tree), and I studied periodicity of suppression and released-growth in tree-ring chronologies of potential trees.

Biotic factors like pests and diseases and the physiological condition of the tree also affect tree growth. According to Koerber and Wickman (1970) the same climatic factors of low precipitations and high temperatures which are correlated with narrow tree rings (in certain areas) also favor the growth of insect populations, increasing defoliation, and consequently, further reduction in the width of tree rings. In managed even-aged conifer stands in the Netherlands, Luitjes (1975) found tree-ring width reduction after explosive developments of insect populations, i.e. *Diprion pini* on *Pinus sylvestris*, or *Cephalcia alpinia* on *Larix leptolepis*.

The physiological condition of the tree changes with increase in age and size. Often tree growth, and specifically tree-ring width, decreases with age or size and this trend can be recognized in tree rings from trees in open environments with little interaction among trees (Cook, 1987). In even-aged *Picea abies* stands, Gerecke (1991) found that tree-ring width decreases with age if trees are regularly released through thinning. If stand density remains high and thinning release is late, then after release by thinning, tree-ring width increases above that of regularly thinned stands. In *Fagus sylvatica*, age or size related decrease in tree-ring width is not described (cf. Kramer, 1982; Fischer & Rommel, 1989; Makowka et al., 1991). The forests I analyzed were all, except EU1 to 4 and AS3, old growth forests without (recent) cutting, and therefor age or size related growth trends were not expected.

In the measurement of tree-ring widths 'false annual rings' and 'missing rings' cause errors. 'False annual rings' are formed when, during the growing season, the wood density decreases and then suddenly increases due to temperature fluctuation. This occurs in, for example, spruce, fir and pine (Schweingruber, 1980) but are not reported in beech. 'Missing rings' occur in beech and are more frequent at 0m height than at 0.6m height (Turberville & Hough, 1939). Because increment cores were taken at 0.5m height, I assumed the error to be small.

In tree growth analyses, tree-height growth of released-growing trees is only dependent on environmental factors, whereas stem-diameter growth is secondary to tree-height growth, and will be reduced first when photosynthetic production is reduced. This is especially true in potential trees and less true in 'trees-of-present'. Kellomäki and Kanninen (1980) showed that for *Pinus sylvestris* in more shaded positions the ratio of height growth vs stem-diameter growth increases. Height growth in *Populus deltoides* is dependent on soil quality, whereas diameter is more related to crown volume, which is related to the ecological status of the tree (Berlyn, 1962). Schober (1972) demonstrated for *Fagus sylvatica* that when stand density increases, stem-diameter growth decreases while height growth remains constant. Just after thinning in managed *Fagus sylvatica* forests in France, tree crowns respond by expansion, whereas after the canopy closes again, with a lag of some six years, stem-diameter growth rate increases (Bouchon et al., 1989). Hence, in the analysis of tree height, stem diameter and crown projection relationships, I took stem diameter as the dependent variable.

Shade tolerance

Shade tolerance of *Fagus sylvatica* (Teissier du Cros et al., 1981), *Fagus grandifolia* (Fowells, 1965) and *Fagus crenata* (Nakashizuka & Numata, 1982b) is ecologically important. Establishment of *Fagus sylvatica* seedlings is best underneath 50% crown cover, and growth reduction becomes strong when crown cover increases over 75% (Burschel & Huss, 1964). Seedlings survive under reduced light conditions with reduced growth rates and adaptation of leaf morphology (Burschel & Schmaltz, 1965a,b), for example they survive 5yr in 2% of daylight (Watt, 1923). *Fagus sylvatica* saplings had increased height growth rates with increasing light levels of 10%, 35% and 100% daylight (Peters, unpublished). When light levels are increased *Fagus sylvatica* responds with increased growth (Mayer, 1984a). Like *Fagus sylvatica, Fagus grandifolia* responds to increased light levels with increased growth, and potential trees pass through alternating periods of suppression and released growth (Canham, 1990). *Fagus crenata* seedlings also survive in the understory of mature forests, but for only about 10 years (Nakashizuka & Numata, 1982b; Hara, 1987; Nakashizuka, 1987 & 1988), which is less than for *Fagus grandifolia*. In the analyzed beech forests, I checked the age of seedlings by counting bud scars. In these forests the other beech species also survived about 10 years in the understory, unless there was a cover of evergreen broad-leaved species.

Shade-tolerant plants have adaptations which enable their juveniles to survive in the shade (Grime, 1965; Hicks & Chabot, 1985; Oliver & Larson, 1990). Adaptation of shade leaves are important but also important is a longer growing season. With sufficient water supply, a longer growing season allows higher production rates per energy and nutrient investment in leaves. This is a possible explanation for the high density of beeches in all size classes in a Mexican beech forest (AM4), where the growing season is about 340 days (Peters, in press). Horn (1971, 1975) relates successional status to shade tolerance and shade tolerance to tree architecture. He suggests that late successional species are shade-tolerant and their monolayers have faster growth in the shade than multi-layers. In beech forests, differences on a finer scale are important, i.e. distinction of the relative tolerance of 'shade-tolerant' species that are monolayers by Horn's criterium, e.g. *Fagus grandifolia*, *Acer saccharum* and *Tsuga canadensis*. Often beech is more shade-tolerant than deciduous codominants, e.g. *Fagus grandifolia* vs *Acer saccharum*, *Fagus sylvatica* vs *Acer pseudoplatanus* or *Quercus robur*. On the other hand, beech is usually less shade-tolerant than evergreen codominants, e.g. *Fagus sylvatica* vs *Abies alba*, *Fagus orientalis* vs *Abies nordmanniana* and *Picea orientalis*, *Fagus lucida* vs *Castanopsis lamontii*, and *Fagus grandifolia* vs *Tsuga canadensis*.

Denslow (1980) defines shade-tolerant tree species as being 'small gap specialists', where small gaps are formed by single tree or branch fall. This is only partly true for *Fagus sylvatica*, *Fagus grandifolia* and *Fagus crenata*, which are not restricted to small gaps. The temperament of a tree may change during its lifecycle, for example a tree may change from being a 'struggler' to being a 'gambler' or vice versa when going from seedling to juvenile to mature phases (Oldeman & van Dijk, 1990). According to Oldeman (1990), most shade-tolerant trees need shade first and light later. Beeches seem to be flexible in this respect, as they may grow 'in light' all of their life, or they may alternate growth in shade and in light. In different sites I compared the successive intervals of suppression and released growth for each beech species.

3.2 OBJECTIVE OF STUDY

Beech species have wide geographic ranges. For example, *Fagus sylvatica* is found from 37°N to 60°N (Figure 1.1). Also, beech species are found in different climatic zones, from tropical montane zones (*Fagus mexicana*, *Fagus longipetiolata*), to warm temperate lowlands (*Fagus grandifolia*) and to cool temperate zones (*Fagus sylvatica*, *Fagus crenata*; Table 1.1). Beech is always a dominant tree and is found in the forest canopy. Although beeches are often able to survive a long time in the undergrowth, they are never restricted to the understory. Species that are codominant with beech vary, as they range from evergreen conifer to deciduous broad-leaved to evergreen broad-leaved species. For this reason, I expected large interspecific and intraspecific variations in the architecture and growth of beech trees.

My objective was to find out if the growth strategies of the beech species are the same and how different they are from codominant tree species. Among sites, I compared variations in growth strategies of beech species, and within each study site I compared growth strategies of beech and codominant tree species. I analyzed growth strategies by comparing tree size parameters and tree-ring chronologies. Size parameters were tree height, stem diameter and vertical crown projection, all of which were measurable and comparable over regions and species. I calculated the correlation between these size parameters. In the tree-ring chronologies of potential trees, I analyzed the duration of suppression and the alternation of suppression and released growth.

3.3 STUDY SITES AND METHODS

Study sites

Study sites are described in Chapter 2.2. In all sites, except EU1, the water and nutrient availability were sufficient for beech. The sites had mesic loam soils (Table 2.2). The sites were not located near the cool extreme of the beech range, thus growth was not influenced by fluctuations in temperature. Because the soils were not drought sensitive (except maybe EU1), nor were the sites temperature sensitive, tree-ring width was expected to be scarcely affected by temperature and precipitation. Hence, relative increase in tree-ring width could be compared. Altitude, slope and aspect, if not extreme, do not influence year-to-year change.

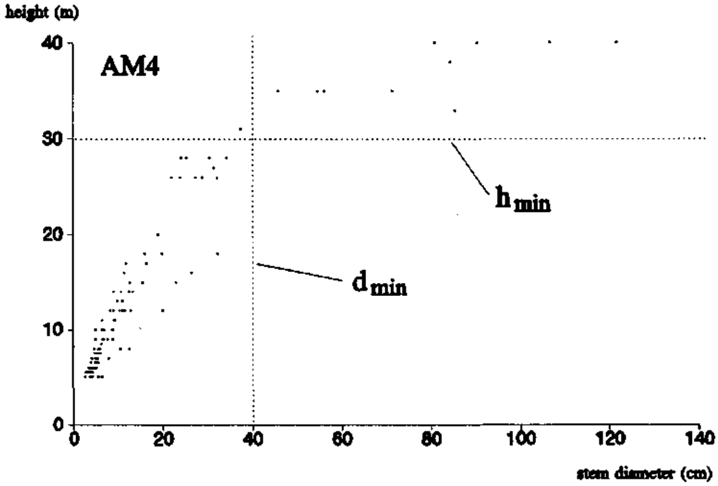


Figure 3.3
An example of a tree height / stem diameter scatter diagram with h_{min} and d_{min} thresholds for tree-of-present indicated (AM4).

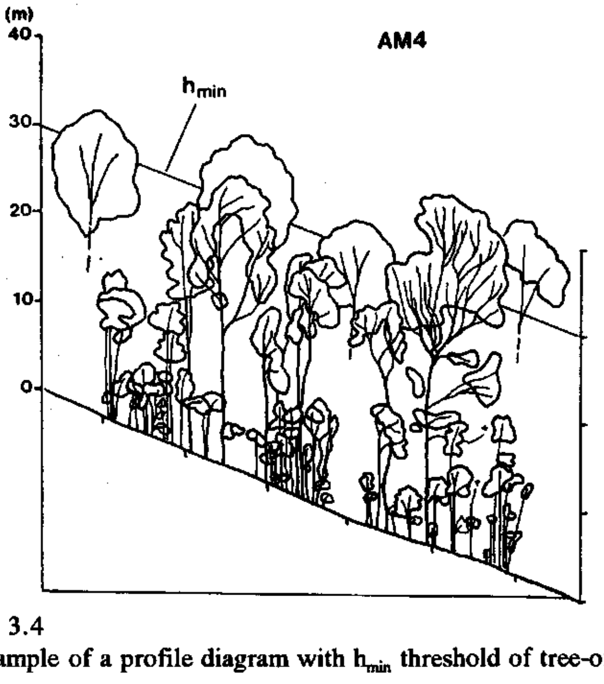


Figure 3.4
An example of a profile diagram with h_{min} threshold of tree-of-present (AM4).

Data collection

Methods of data collection are described in Chapter 2.4.

Size parameters

Analyzed tree size parameters for beech and codominant tree species were tree height (h), stem diameter at 0.5m height ($d_{0.5}$, all except AS2), stem diameter at 1.3m height ($d_{1.3}$, AS2), and vertical crown projection (cp). For each study site, I selected the thresholds for the minimum height (h_{min}) and minimum stem diameter (d_{min}) for trees-of-present, after comparing a h-d scatter diagram with the profile diagram (Figures 3.3, 3.4). The thresholds were rounded to the nearest multitude of 5. The h-d and h-cp-d relationships were fitted well by an exponential function, i.e. $d = \alpha * h^{\beta}$ and $d = \alpha * h^{\beta} * cp^{\tau}$, in which α, β and τ are empirical constants. I analyzed the relationships by non-linear regression and I used stem diameter as the dependent variable. I analyzed intraspecific and interspecific variation by comparing the coefficients of variation in the estimated curves, i.e. using the variance not explained by the regression curves. Among sites, I compared beech species, and within sites, beech and codominant species. Analyzed codominant species were *Acer saccharum* (AM1 & 2), *Magnolia grandiflora* (AM3), *Pinus glabra* (AM3), *Liquidambar styraciflua* (AM3), *Quercus ocoteaefolia* (AM4), *Castanopsis lamontii* (AS6), *Lithocarpus hancei* (AS6) and *Abies nordmanniana*(EU6).

Tree-ring chronologies

For each site, I analyzed the variation in the tree-ring chronologies for beech and codominant trees. I estimated the 'age-size trend' (Cook, 1987) by using 5yr moving averages. I selected a 5yr interval to preserve as much as possible the change in growth rates due to alternation of periods of suppression and released growth. 'Detrended tree-ring indices' were calculated by dividing raw tree-ring data by 5yr moving averages. For each site, I analyzed the variance in the detrended tree-ring indices following Fritts (1976), by calculating the variance components for total chronology of the site and for individual tree chronology, i.e. variation attributed to macroclimatic factors affecting all trees in one site and variation attributed to other factors affecting individual trees.

For different beech species, I compared the average tree-ring width of potential trees and trees-of-present. The average was calculated over whole cores for potential trees, and over the period of time after d_{min} for trees-of-present. For each site and species, I compared average tree-ring widths in the recent 5yr of suppressed trees with those of released-growing potential trees. Here, I selected an interval of 5yr to average out changes attributed to macroclimate, since during a 5yr interval I supposed the light environment to be fairly constant. Because light levels were not measured, the selected suppressed trees may still enjoy light flecks that favor higher growth rates. To obtain a measure for true suppressed growth, I selected the thresholds nearer to the average tree-ring width of suppressed than of released growing trees. Using selected thresholds between suppressed and released growth, I analyzed alternation of suppressed and released growth in cores from potential trees. Following Canham (1990), periods of suppression were intervals in which there were 4 or more years of growth below the threshold, during which there were no periods of 3 or more years of consecutive growth greater than this threshold. The most recent periods were not included in the analysis because they were not over yet. The oldest periods in the cores were only included if the cores started exactly at the tree center.

Table 3.2
Sizes ranges of *Fagus* trees-of-present. Bold numbers are the selected thresholds for tree height (h_{min}) and for stem diameter (d_{min}).

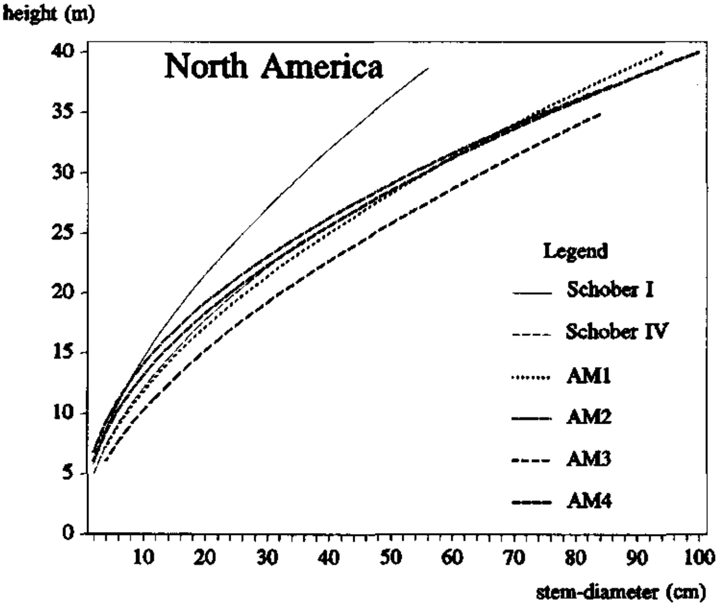
Species	Location	N[1]	Height h_{min}-h_{max} (m)	Diameter range (cm)	d_{min} (cm)
Fagus grandifolia	AM1	142	**30**-40	41-117	**40**
Fagus grandifolia	AM2	43	**30**-37	49-113	**40**
Fagus grandifolia	AM3	54	**25**-35	31- 97	**40**
Fagus mexicana	AM4	142	**30**-40	35-137	**40**
Fagus crenata	AS1	128	**20**-26	33-119	**40**
Fagus japonica	AS2	177	**20**-26	20- 63 [2]	**30**
Fagus multinervis	AS3 [3]	149	na	na	na
Fagus engleriana	AS4	17	**18**-24	20- 58	**30**
Fagus hayatae	AS4	58	**20**-27	20- 79	**30**
Fagus lucida	AS5	51	**20**-31	38-100	**40**
Fagus lucida	AS6	93	**15**-25	32- 95	**40**
Fagus sylvatica	EU1	68	**25**-34	45-101	**40**
Fagus sylvatica	EU2	18	**30**-41	53-139	**40**
Fagus sylvatica	EU3	36	**30**-42	45-152	**40**
Fagus sylvatica	EU4	68	**30**-38	37-103	**40**
Fagus sylvatica	EU5	96	**25**-38	20- 98	**40**
Fagus orientalis	EU6	117	**30**-37	34-100	**40**

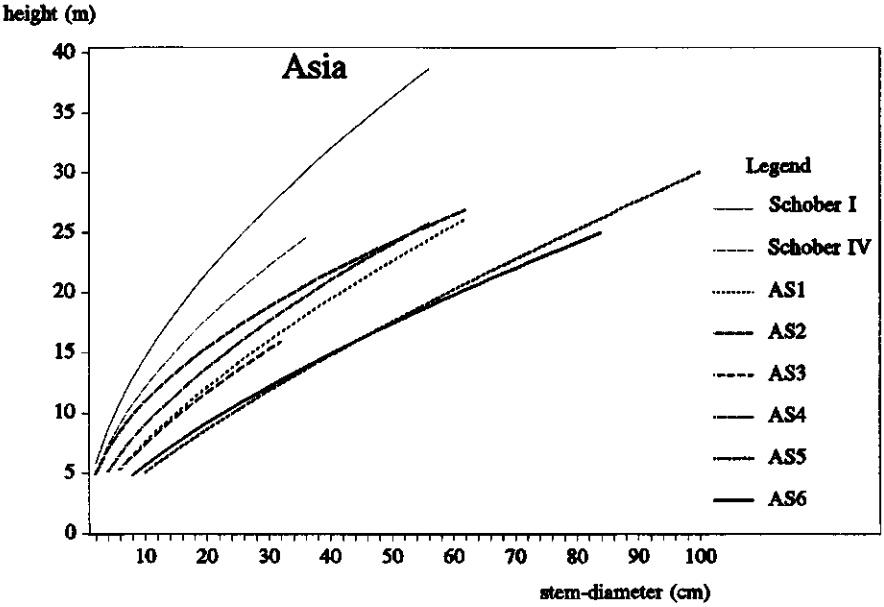
1. N is population of potential trees + trees-of-present.
2. Diameter at 1.3m.
3. Due to recent cutting, trees-of-present were absent, and values were not available (na).

3.4 RESULTS

Size parameters

The European and North American beech species reached tree heights of 35 to 40m, and the eastern Asiatic species grew 25 to 30m tall (Table 3.2). This difference could not be attributed to soil, as most analyzed forests were growing on mesic loam soils (Table 2.2). On dry sandy soil (EU1) *Fagus sylvatica* reached tree heights above 30m. The height difference also could not be attributed to difference in slope, as on steep slopes *Fagus sylvatica* (EU4) and *Fagus mexicana* (AM4) reached tree heights of 38m and 40m respectively. Maximum stem diameters ranged from about 100cm to 150cm, and were more dependent on site than on species (Table 3.2). Multi-stemmed beeches had smaller stem diameters, with maxima around 60cm.





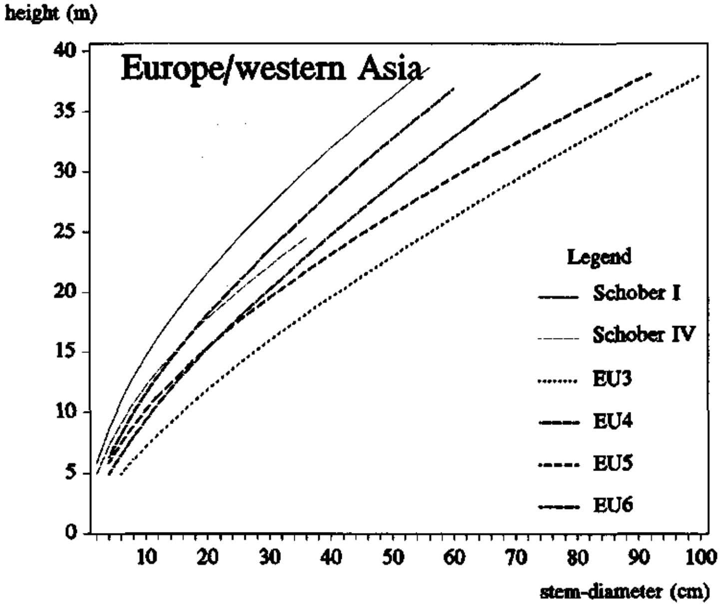
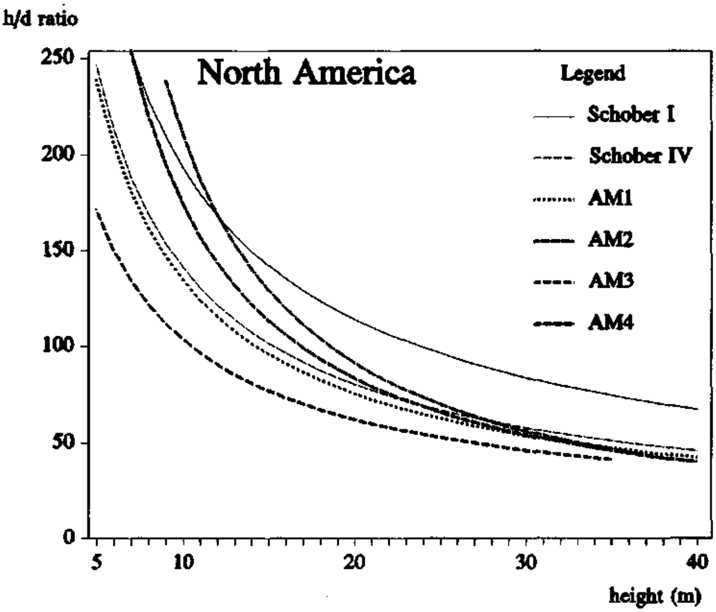
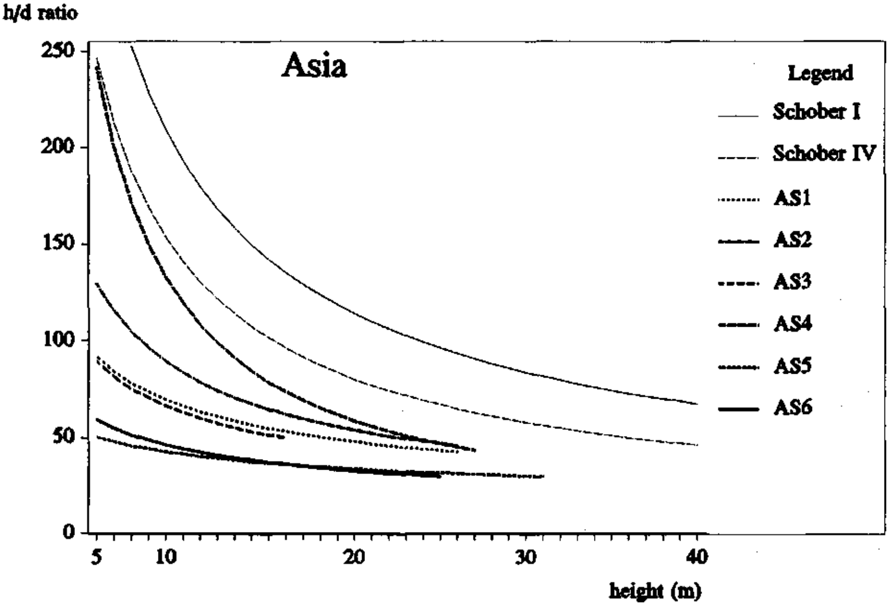


Figure 3.5
Height / stem diameter regression curves for beech: $d = \alpha * h^{\beta}$. For reference Schobers' curves for low thinning (Figure 3a) are given.


h/d ratio
250
200
150
100
50
0
North America
Legend
Schober I
Schober IV
AM1
AM2
AM3
AM4
5
10
20
30
40
height (m)


h/d ratio
250
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Asia
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AS2
AS3
AS4
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10
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40
height (m)

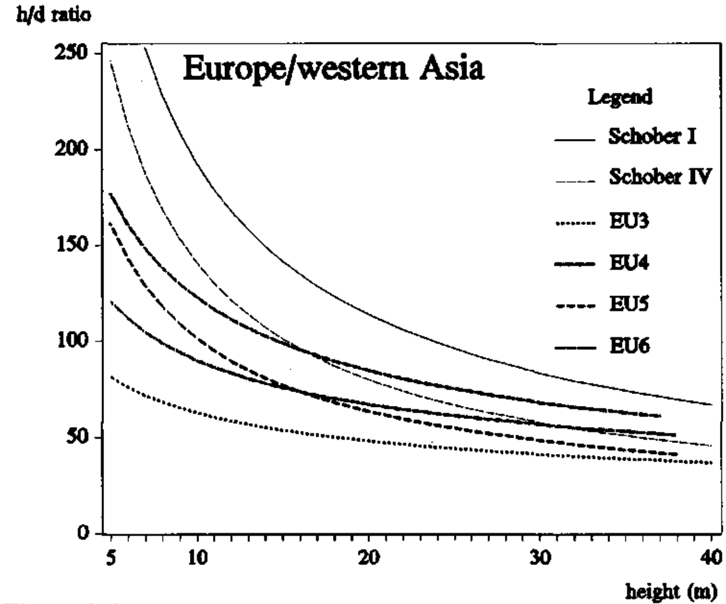

Figure 3.6
Tree height / stem diameter ratio curves for beech based on the regression curves, d = $\alpha * h^{\beta}$. The reference curves are calculated from Schober (1972).

For the different beech species, the estimated exponential regression curves for h-d and h-cp-d relationships showed good correlations, with correlation coefficients (R^2) above 70% and 80% respectively (Figure 3.5). However, the calculated coefficients of variation for the estimated curves were large, i.e. above 25% for estimation of d from h (Table 3.3), and above 20% for estimation of d from h and cp. Coefficients of variation were low for *Fagus lucida* in AS5 and for *Fagus sylvatica* in EU4. Maybe this resulted from both having few potential trees in the regression analysis, only 17% and 22% of all beech trees were potential trees in AS5 and EU4. Coefficient of variation was larger for multi-stemmed *Fagus japonica* and *Fagus engleriana*, than for their codominant *Fagus crenata* and *Fagus hayatae*. Regression curves with a high coefficient of variation have low predictability, and indicate a large within site variation among individuals of a species. Hence, the differences in h/d ratio development were interpreted as trends. In all sites, the h/d ratio decreased with increasing tree height, and trees-of-present had values between about 40 and 60 (Figure 3.6). The regression curves for h-d were lower for beech in forests where evergreen broad-leaved tree species codominated (AM3, AS5 & AS6), and they were lowest in Chinese beech forests (AS5 & AS6; Figure 3.5). Compared to the curves derived from Schober's (1972) yield tables of even-aged managed beech forests, all h-d curves were lower than the curves for yield class I (h=31.4m at age

Table 3.3
Coefficients of variation calculated from the deviation of estimated values from the height / stem-diameter regression curves, which is the variance not explained for by the regression curves. EU1 and EU2 are omitted because the correlation coefficient for the regression curves was low.

Site	Species		Coefficient of variance		Number of trees	
	beech	codominant				
AM1	*Fagus grandifolia*	*Acer saccharum*	34	41	142	164
AM2	*Fagus grandifolia*	*Acer saccharum*	33	35	43	73
AM3	*Fagus grandifolia*	*Magnolia grandiflora*	33	23	54	36
		Pinus glabra		23		12
		Liquidambar styraciflua		18		22
		Ilex opaca		21		36
		Ostrya virginiana		19		34
AM4	*Fagus mexicana*	*Quercus ocoteaefolia*	45	20	142	10
AS1	*Fagus crenata*		29		102	
AS2	*Fagus crenata*	*Fagus japonica*	26	39	17	178
AS3	*Fagus multinervis*		36		149	
AS4	*Fagus hayatae*	*Fagus engleriana*	45	57	58	17
AS5	*Fagus lucida*	*Cyclobalanopsis multinervis*	20	35	51	49
AS6	*Fagus lucida*	*Castanopsis lamontii*	39	36	93	30
EU3	*Fagus sylvatica*		31		36	
EU4	*Fagus sylvatica*		21		68	
EU5	*Fagus sylvatica*		37		96	
EU6	*Fagus orientalis*	*Abies nordmanniana*	35	30	117	115

100yr) and about equal or lower than those for yield class IV (h=19.2m at age 100yr). This suggested wider spacing among trees in the studied old growth forests and/or relatively poor sites. However, this was contradicted by the soil data.

The estimated exponential regression curves for h-d and h-cp-d relationships showed good correlations for all compared codominant species (R^2 above 75%), except for *Magnolia grandiflora* (R^2 47% and 66%). Compared with beech, the coefficients of variation were larger or about equal for *Acer saccharum* (AM1) and *Cyclobalanopsis multinervis* (AS5), about equal for *Castanopsis lamontii* (AS6) and *Abies nordmanniana*(EU6), and lower for *Magnolia grandiflora* (AM3), *Pinus glabra* (AM3), *Liquidambar styraciflua* (AM3) and *Quercus ocoteaefolia* (AM4). The coefficient for *Fagus lucida* might have been about equal to that of *Cyclobalanopsis multinervis* if more potential beech trees were present. Compared with beech, the

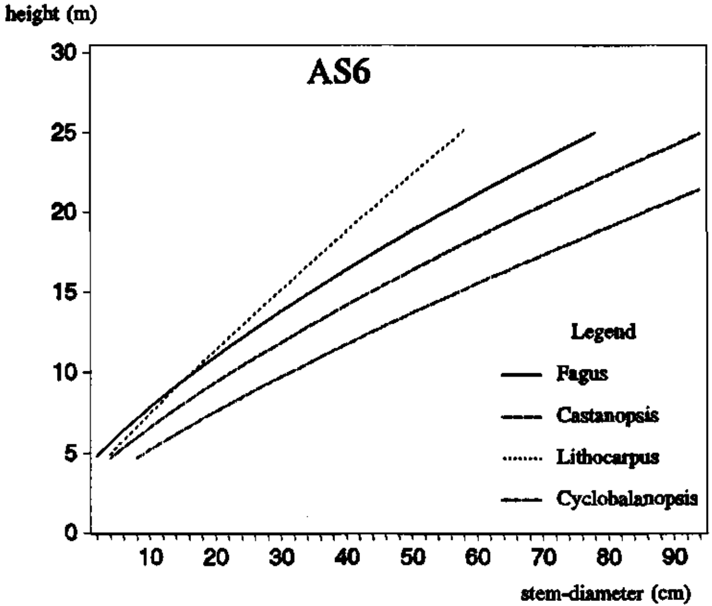

Figure 3.7
Example of the height / stem diameter regression curves for different species within one site (AS6): $d = \alpha * h^{\beta}$.

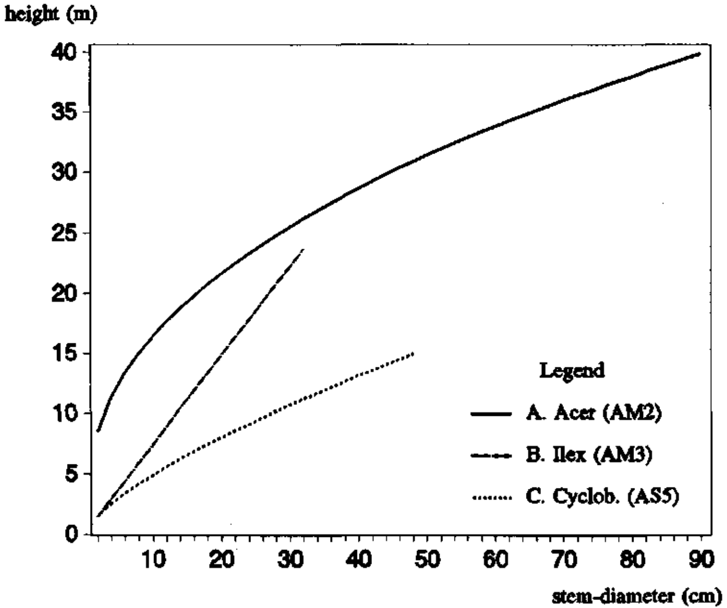

Figure 3.8
Examples of the three types of height / stem diameter regression curves.

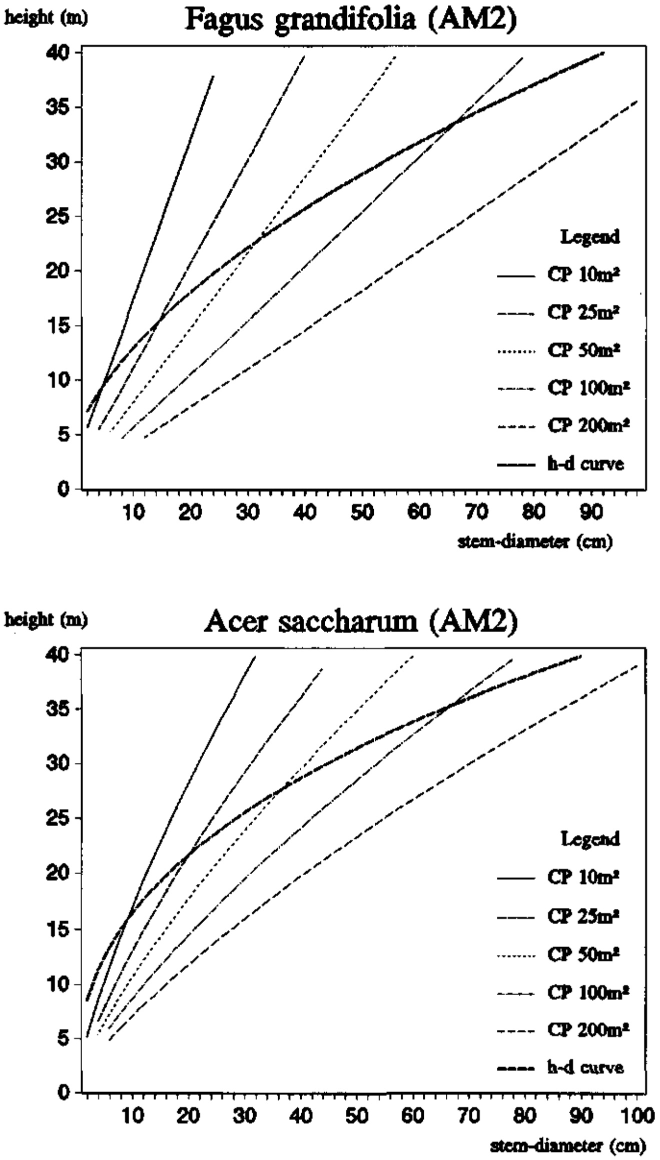

Figure 3.9
Two examples of height / crown projection / stem diameter regression curves in which crown projection is constant (AM2). For reference the height / stem diameter regression curve is drawn.

Table 3.4
Variance components of mean tree-ring indices in total chronology of the site (Total) and of tree-ring indices in chronologies of individual trees (Trees) in percentage, i.e. variation attributed to macroclimatic factor affecting all trees in one site and variation attributed to other factors affecting individual trees.

Site	Number of sample trees	Number of analyzed years	Variance components total (%)	trees (%)
AM1 mesic[1]	40	47	1	99
AM1 humid[1]	34	39	4	96
AM2	37	34	3	97
AM3	25	42	3	97
AM4	15	45	3	97
AS1	40	46	4	96
AS2	29	34	1	99
AS4	65	50	2	98
AS5	30	54	1	99
EU1	7	153	2	98
EU2	20	33	1	99
EU3	16	43	5	95
EU5 poor[2]	42	70	10	90
EU5 rich[2]	44	69	16	84
EU6	105	44	4	96

1. AM1 is split into a more mesic site and a more humid site.
2. EU5 is split into a more poor site and a more rich site.

estimated h-d curves were higher for *Acer saccharum* ($h < 30m$), *Liquidambar styraciflua*, *Pinus glabra* and *Lithocarpus hancei* (AS6), practically identical for *Magnolia grandiflora*, and lower for the others (e.g. AS6, Figure 3.7). In the h-d curves, I distinguished three types: A. exponential, B. straight with steep slope, C. straight with gradual slope (Figure 3.8). *Quercus ocoteaefolia* (AM4) and medium-tall *Ostrya virginiana* and *Ilex opaca* (AM3) had type B, *Lithocarpus hancei* (AS6) and *Fagus lucida* (few potential trees) and medium-tall *Illicium lanceolatum* (AS5) had type C, and the others had type A.

The h-cp-d regression curves for beech showed that crown projections were strongly related to tree-height, and for *Fagus grandifolia*, *Fagus mexicana* and *Fagus sylvatica* this was mainly so in taller trees (Figure 3.9). Compared to beech, codominant species crown projections were much smaller and were less related to height, e.g. *Quercus ocoteaefolia*, *Abies nordmanniana* and *Liquidambar styraciflua*.

Table 3.5
Average tree-ring width (mm) of trees-of-present (since d_{min} was reached) and potential trees (total cores).

		Trees-of-present	Potential trees
		avg ± SD (N)	avg ± SD (N)
AM1:	*Fagus grandifolia*	1.7 ±0.60 (21)	1.1 ±0.48 (27)
	Acer saccharum	1.3 ±0.40 (13)	1.2 ±0.53 (10)
AM2:	*Fagus grandifolia*	1.7 ±0.44 (6)	1.4 ±0.49 (12)
	Acer saccharum	1.6 ±0.63 (4)	1.5 ±0.60 (14)
AM3:	*Fagus grandifolia*	2.5 ±1.02 (6)	1.2 ±0.25 (8)
	Magnolia grandiflora	1.5 ±0.16 (5)	1.5 ±0 (1)
	Pinus glabra	3.4 ±0,08 (2)	-
AM4:	*Fagus mexicana*	2.6 ±0.92 (5)	1.1 ±0.61 (17)
AS1:	*Fagus crenata*	1.2 ±0.51 (20)	0.7 ±0.29 (18)
AS2:	*Fagus crenata*	2.4 ±0.71 (8)	0.7 ±0 (1)
	Fagus japonica	1.2 ±0.58 (18)	0.9 ±0.38 (41)
AS4:	*Fagus hayatae*	1.8 ±0.48 (15)	1.0 ±0.36 (24)
	Fagus engleriana	1.1 ±0.44 (3)	1.2 ±0.64 (10)
AS5:	*Fagus lucida*	1.3 ±0.46 (22)	1.1 ±0.27 (6)
EU1:	*Fagus sylvatica*	1.2 ±0.32 (7)	-
EU2:	*Fagus sylvatica*	2.0 ±0.62 (7)	1.2 ±0.66 (17)
EU3:	*Fagus sylvatica*	2.2 ±0.53 (7)	1.0 ±0.35 (8)
EU6:	*Fagus orientalis*	1.4 ±0.61 (23)	1.0 ±0.48 (32)
	Abies nordmanniana	2.1 ±0.72 (16)	1.0 ±0.45 (28)

Tree-ring chronologies

In the tree-ring chronologies, I found no directional, ascending or descending, age-size trend. The analysis of variance in the tree-ring chronologies showed that 16% or less could be attributed to common trends of macroclimatic factors of temperature and precipitation (Table 3.4).

The between-site variation in tree-ring widths was larger among trees-of-present than among potential trees (Table 3.5). In *Fagus grandifolia* and *Fagus crenata* trees-of-present, average tree-ring widths were wider in warm sites than in cooler sites. There was a clear difference between tree-ring widths during the most recent 5yr in suppressed and in released-growing potential trees (Table 3.6). In the analyzed beech species a growth response to release was still possible after more than 40yr of suppression (Table 3.7). Several potential trees spent in total over 100yr in continuous suppressed state. For codominant *Acer saccharum* (AM2) and *Abies nordmanniana* (EU6) the maximum continuous and total suppression never lasted

Table 3.6
Average tree-ring width of most recent 5yr in suppressed and released-growing potential trees, and the selected threshold for suppressed vs released-growth.

Threshold		Released-growing		Suppressed		
		avg ± SD (mm)	(N)	avg ± SD (mm)	(N)	(mm)
AM1:	*Fagus grandifolia*	2.2 ±0.87	(17)	0.8 ±0.61	(10)	1.0
	Acer saccharum	1.8 ±1.07	(6)	0.7 ±0.57	(4)	1.0
AM2:	*Fagus grandifolia*	1.6 ±0.40	(4)	0.8 ±0.50	(8)	1.0
	Acer saccharum	2.2 ±1.00	(10)	0.9 ±0.46	(4)	1.0
AM3:	*Fagus grandifolia*	1.4 ±0.47	(2)	1.3 ±0.60	(6)	-
	Magnolia grandiflora	-		0.5 ±	(1)	-
AM4:	*Fagus mexicana*	1.4 ±1.03	(10)	0.5 ±0.36	(2)	0.8
AS1:	*Fagus crenata*	0.5 ±0	(1)	0.2 ±0.09	(7)	0.35
AS2:	*Fagus crenata*	0.4 ±0	(1)	-		-
	Fagus japonica	1.2 ±0.82	(10)	0.5 ±0.32	(28)	0.7
AS4:	*Fagus hayatae*	1.3 ±1.00	(6)	0.9 ±0.84	(9)	1.0
	Fagus engleriana	1.8 ±1.10	(6)	0.5 ±0.22	(3)	0.7
AS5:	*Fagus lucida*	1.3 ±1.13	(3)	0.6 ±0	(1)	-
EU2:	*Fagus sylvatica*	2.3 ±0.43	(4)	0.8 ±0.52	(12)	-
EU3:	*Fagus sylvatica*	-		0.4 ±0.10	(8)	-
EU6:	*Fagus orientalis*	0.9 ±0.81	(8)	0.3 ±0.52	(22)	0.5
	Abies nordmanniana	0.4 ±0.37	(10)	0.3 ±0.19	(17)	0.35

more than 60yr. Beech trees experienced on the average about 2.5 periods of suppression (Table 3.7).

3.5 DISCUSSION

All beeches were tree species, and they grew up to be dominating trees in the forests where they were found. Although *Fagus japonica*, *Fagus engleriana* and *Fagus multinervis* had a multi-stem architecture throughout their range, their stems became more than 20m tall and 60cm in diameter. The other beech species were single-stemmed. Compared to the North American and European beeches, the eastern Asiatic beeches were smaller in stature but so were the codominant tree species. The intraspecific variation in the h-d relationship was great within each site.

Table 3.7
Maximum continuous (Cmax) and maximum total (Tmax) years of suppression for individual trees, and average number of suppressed periods per tree.

Site	Species	Suppression Cmax	Tmax	Avg. number suppressed periods
AM1	*Fagus grandifolia*	121	209	2.6
	Acer saccharum	45	50	1.9
AM2	*Fagus grandifolia*	31	48	2.4
	Acer saccharum	48	56	1.8
AM4	*Fagus mexicana*	89	105	2.5
AS1	*Fagus crenata*	41	104	3.4
AS2	*Fagus japonica*	66	74	2.3
AS4	*Fagus hayatae*	73	73	1.5
	Fagus engleriana	40	52	1.7
EU6	*Fagus orientalis*	67	87	2.5
	Abies nordmanniana	49	49	1.8

Light intensity was the most important abiotic factor influencing tree-ring width in the analyzed beech trees (Tables 3.5 & 3.6). Because environmental factors like light strongly influence the variation in tree-ring width I did not find age-size related trends. Analysis of variance showed that common trends, as induced by the macroclimatic factors of temperature and precipitation, were unimportant. In all analyzed beech species, potential trees could grow in the shade. The tree rings of these suppressed potential beeches were smaller than those of released-growing ones, although not significantly. Canham (1990) found significant differences because his suppressed and released-growing classes were more distinct than mine. The beeches could respond to release, even after more than 40yr of suppression. Often, potential trees underwent an alternation between periods of suppression and released growth. Thus, beech trees need more than one gap to reach the forest canopy (cf. Runkle, 1990).

Different beech species and codominant species had different growth strategies. The ecological implication of the exponential h-d curve (type A, Figure 3.8) is that in the first phase of a tree's lifecycle, investment is more on height growth (definition of potential tree) and in the later phase more on diameter growth (definition of tree-of-present). However, this was more evident in the h-d scatter diagram (Figure 3.3) than in the regression curves (Figure 3.5). In some codominant species this initial emphasis on height growth was large compared to beech, and usually they were less shade-tolerant than beech, e.g. *Acer saccharum* in AM1, *Liquidambar* and *Pinus* in AM3. A linear h-d relationship (type B, C) suggests that the tree species never reaches tree-of-present status, and this was found in medium-tall tree species in the understory, *Ilex opaca* and *Ostrya virginiana* in AM3 and *Illicium lanceolatum* in AS5. These medium-tall tree species may need long lasting gaps to reach tree-of-present status. *Quercus ocoteaefolia* in AM4 showed a linear h-d relationship. The oaks could reach the canopy but did not expand, probably due to the presence of shading beech crowns. Of course, the steepness of the slope of the curve is also influenced by the spacing among trees as shown by low curves for *Fagus lucida* in AS5 & 6 and wide spacing among the dominant beeches.

The coefficient of variation of h-d is small if trees grow up continuously to reach the canopy. The coefficient is large if trees can respond to environmental changes, e.g. if increased light levels will result in an increase in height growth which is relatively stronger than the increase in diameter growth. This is shown by the fact that, compared to beech, in *Acer saccharum*, variation was larger but so was the difference in height growth in shade vs light (Canham, 1988). In a similar way, I expected multi-stemmed *Fagus japonica* and *Fagus engleriana* to respond with stronger growth rate increases to improved light levels than *Fagus crenata* and *Fagus hayatae* since the multi-stemmed beeches had larger variations in h-d ratios.

Species codominant with beech in the analyzed beech forests could be separated into a less shade-tolerant deciduous broad-leaved species group and a more shade-tolerant evergreen broad-leaved species group (perhaps except *Magnolia grandiflora* in AM3). Compared to their codominant species, beech species had stronger lateral crown expansion. With plagiotropic axes beeches can show stronger lateral crown expansion than their codominants with orthotropic axes. In general, the tree-height growth, relative to stem-diameter growth, was low in beech species compared to the deciduous codominant species, and high compared to the evergreen codominant species. In the understory of the less shade-tolerant deciduous broad-leaved species, beech species can survive and optimize light interception using their plagiotropic axes (Oldeman, 1989). When growing among the more shade-tolerant evergreen broad-leaved species, beech species have to and appear to invest relatively more energy in height growth because they cannot survive in the dark undergrowth of the evergreen trees.

The h-d relationship, the regression curve and the coefficient of variation were valid measures to compare growth strategies among tree species. Beech species have the same growth strategies. They are flexible in adjusting the investment in height growth vs stem-diameter growth. Whether adjustment is made depends on the codominants. Codominants are usually less flexible, and either invest relatively more in height growth when more light-demanding or less when more shade-tolerant.

Chapter 4 - Species composition and forest architecture in beech forests

In this chapter, I analyze geographical trends in woody species composition and eco-unit architecture. Within each site, I compare tree populations and tree regeneration and relate them to forest architecture.

4.1 INTRODUCTION

The same genera of plants are found in the beech forests of eastern Asia, eastern North America, and, to a lesser extent, Europe. This similarity is thought to be the result of continuous distribution during the early Tertiary (Hsü, 1983; Tiffney, 1985). Still, there is a large variation in species composition of beech forests on each continent today. Even tree species codominant with beech vary essentially from coniferous to deciduous broad-leaved to evergreen broad-leaved (Table 4.1). These forests can be studied and compared from the point of view of their organization, i.e. their architecture and structure (Rollet, 1978). Forest architectural analysis focuses on the 'morphology' of forests, and structural analysis focuses on the mathematical relations within populations, e.g. distribution of tree heights within species (Rollet, 1978).

Tree populations

Analysis of size distributions yields much information on the ecology of a population of trees. Tree sizes, and especially tree height, can be related to phases of development (Chapter 3.1). Because of mortality among potential trees, in order to remain dominant it is important for a tree species that its population contains more small than large individuals. Size distribution reveals how a species succeeds or fails in remaining dominant. Tree species that have distinct growth strategies will have different size distributions leading to the same degree of dominance. In *Fagus grandifolia / Acer saccharum* forests, Poulson and Platt (1989) found that sugar maple had initially high densities and high mortality in small-sized individuals, whereas *Liriodendron tulipifera* had relatively low densities and low mortality in small-sized individuals. In both species the same number of successful trees remained. After clear-cut in New England hardwoods, *Quercus rubra* had low

Table 4.1
Tall tree species codominating with beech.

1. Beech & evergreen coniferous

Fagus grandifolia	*Tsuga canadensis* (Eastern N.America)
Fagus crenata	*Abies homolepis* (Japan)
Fagus orientalis	*Abies nordmanniana, Picea orientalis* (Turkey)
Fagus sylvatica	*Abies alba, Picea abies* (Europe)
	[illegible]

2. Beech & deciduous broad-leaved

Fagus grandifolia	*Acer saccharum* (Eastern N.America)
Fagus sylvatica	*Quercus petraea, Quercus robur* (Europe)
Fagus sylvatica	*Acer pseudoplatanus* (Europe)
Fagus hayatae	*Fagus engleriana, Quercus aliena* (China)

3. Beech & evergreen broad-leaved

Fagus grandifolia	*Magnolia grandiflora, Quercus spp.* (East. N.Am.)
Fagus mexicana	*Quercus ocoteaefolia* (Mexico)
Fagus lucida	*Cyclobalanopsis multinervis, Castanopsi lamontii, Lithocarpus hancei, Manglietia chienii* (China)
F. longipetiolata	*Cyclobalanopsis sp., Castanopsis sp.* (China)

densities compared to *Betula lenta* and *Acer rubrum*, but with good height growth, oak dominates the stand after 30yr (Oliver, 1978).

In general, within a population of trees the size distribution will yield a reverse J-shaped curve. For tropical trees, Bongers et al. (1988) describe three types of stem-diameter distribution types for tree species with good reproduction: I. continuous recruitment, II. discontinuous recruitment, III. sparse recruitment. However, often the reproduction of trees is discontinuous (strugglers: Oldeman & van Dijk, 1990), e.g. beech and oak have irregularly, years of abundant seed production and years of little or no seeds. Recruitment into sapling from seedling size classes may occur at longer intervals, e.g. favored by temporary higher light levels. Hence, one would expect discontinuous recruitment into the forest canopy. In analysis of tree populations in temperate forests, sapling densities are important as they show the success of recruitment, whereas seedling densities greatly fluctuate. Because stem-diameter growth depends on stand characteristics like the distance between individuals (Chapter 3), tree-height distributions give more information on the distribution of trees in different phases of development.

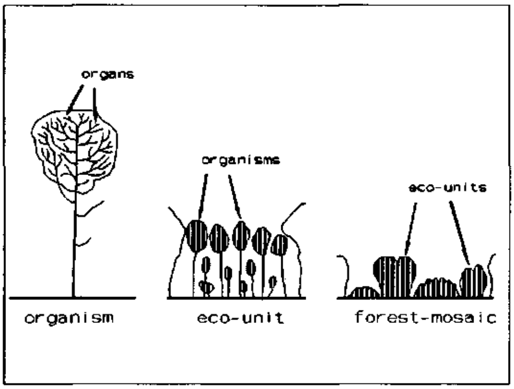

Figure 4.1
Hierarchical levels in forest ecosystems: the architecture of an organism is built by organs; of an eco-unit by organisms; of a forest mosaic by eco-units (figure inspired by Oldeman, 1983, 1990).

Forest architecture

Since the work of Vanselow (1931) and Watt (1947) in temperate forests and Aubréville (1938) in tropical forests it has become increasingly appreciated that forest communities are mosaics of patches in different phases of development (e.g. for beech forests in Europe and Japan: Lemée, 1978; Mayer & Neumann, 1981; Koop & Hilgen, 1987; Koop, 1989; Nakashizuka & Numata, 1982a; Hara, 1983). Describing forest patches, Oldeman (1990) defines the term 'forest eco-unit' as "every surface on which at one moment in time a vegetation development has begun, of which the architecture, eco-physiological functioning and species composition are ordained by one set of trees until the end". I interpreted this forest eco-unit as a forest patch that is dominated by a set of trees in one phase of tree development (Figure 4.1). Oldeman (1990) distinguishes four phases of eco-unit development, i.e. innovation, aggradation, biostasis and degradation. In the innovation phase, tree seeds germinate and seedlings establish themselves (cf. reorganization phase, Bormann & Likens, 1979). The aggradation phase is dominated by released-growing potential trees, and vertical growth is still important. The biostatic phase is dominated by trees-of-present, and crown expansion is important (Chapter 3.1). In the degradation phase the tallest trees are senescent. For practical reasons, the first three phases can be defined by height, but this is site- and species-dependent. I defined the forest canopy as the biostatic phases of tall tree species eco-units, and I defined the canopy gaps to be the innovation and aggradation phases of tall tree species eco-units, and the medium-tall tree species and shrub species eco-unit types.

Different types of eco-units were distinguished next to each other, not underneath each other. Abiotic gradients, especially light, can be continuous across the limits of the individual eco-units. Canham et al. (1990) show how maximum light levels move further to the north side of the gap with increasing latitude. I did not regard eco-units as discrete entities, but rather as abstractions, by which forest architecture and development could be described. Within a forest ecosystem the eco-unit types in different developmental phases form a 'forest mosaic' (Figure 4.1, Oldeman, 1990).

Within each eco-unit in biostatic phase of development, trees- and shrubs-of-present (full-grown trees and shrubs) form structural ensembles at different heights (Hallé et al., 1978). Some aggrading eco-units with a canopy dominated by tall tree species already have a structural ensemble below formed by shrubs-of-present or medium-tall trees-of-present (Lescure, 1978). According to Oldeman (1990), the structural ensembles are the main entities determining forest architecture since they determine the growing space for potential trees in the understory or in-between. Thus, for comparison of architecture in different forest types, I focused on structural ensembles of biostatic eco-units.

Developmental phases were recognized by the tallest trees in the eco-unit and only released-growing potential trees dominated aggrading eco-units. Furthermore, most height growth is in released-growing potential trees (cf. Canham, 1988). Because yield tables are calculated for trees that are never suppressed, I could use yield tables to estimate the approximate time spent in each phase of eco-unit development. In Chapter 3, the empirical minimum height for trees-of-present (h_{min}) was about 3/4 of the maximum tree-height for the species (Table 3.2). The yield tables for *Fagus sylvatica* by Schober (1972) show that, regardless of site or treatment, at an age of about 90yr this h_{min} is reached. Released-growing beech seedlings take about 5yr to grow taller than 0.5m (where I set the seedling threshold) and the 'maximum' age for *Fagus sylvatica* is 200 to 400yr. In the canopies of old growth beech forests, I found few or no trees 'standing dead'. Hence, I estimated the time interval for phases of eco-unit development in natural *Fagus sylvatica* forest to be about 5yr for innovation, about 90yr for aggradation, 100 to 300yr for biostasis and zero to a few decades for degradation. In Japanese *Fagus crenata* forest, trees spent about 120yr in potential tree phase and 100 to 200yr in tree-of-present phase (Peters et al., in press). Part of the potential tree phase is spent in suppression, thus not dominating an eco-unit. In addition to increasing time intervals, the sizes of the dominant trees in each phase increase toward the biostasis. Hence, I expected that total areas occupied by each phase would range from small in innovation to large in biostasis.

To understand recruitment of a species, its size distribution must be considered in the context of forest architecture. I analyzed the abundance of released-growing potential trees by calculating the area covered by tree eco-units in aggradation phase, which were dominated by the released-growing potential trees. I analyzed the abundance of suppressed potential trees by calculating the area they covered underneath the biostatic phase. The presence of juveniles underneath canopy trees was used by Horn (1975) to predict tree by tree replacement probabilities for each species combination.

4.2 OBJECTIVE OF STUDY

Beech species have wide ranges and are found in different climatic zones (Table 1.1, Figure 1.1). In the study sites all beech species were shade-tolerant and light intensity was the main abiotic factor influencing stem-diameter growth (Chapter 3). The growth strategy followed by the beeches depended on the codominant tree species, and was different with deciduous or evergreen broad-leaved tree species (Chapter 3). Variation in forest types where beech species dominate is evident and my purpose in this chapter is to analyze whether geographic trends can be recognized in species composition, population structure and forest architecture.

To detect geographic trends, I compared beech forests in eastern Asia, North America and Europe/western Asia, as well as northern and southern beech forests on these continents. As the distinction of evergreen and deciduous codominants was important, I also analyzed tree species compositions. I compared tree-height distributions of all trees, beech species and codominant species among sites, to detect recruitment strategies. Next, I investigated forest architectural trends at eco-unit and forest mosaic scales.

4.3 STUDY SITES AND METHODS

Study sites

Study sites are described in Chapter 2.2.

Data collection

Methods of data collection are described in Chapter 2.4.

Woody species composition

For the northern and southern beech forests of eastern North America, Europe and eastern Asia, I used literature to enumerate tree species in all genera. From data for each study site, I calculated ratios of the number of tree to shrub species, and of evergreen broad-leaved to deciduous broad-leaved species.

Tree populations

In each site, I used 1m height classes to plot the cumulative distributions of tree heights (h) for all trees taller than 5m, for beech and for the main codominant tree species. For different sites, I compared the number of beech seedlings ($h < 0.5m$) and saplings ($0.5m \leq h < 5m$) in the understory and in canopy gaps where vegetation is as high as or lower than these seedlings or saplings.

For trees-of-present, I used the tree-ring chronologies to calculate how many years had passed since each tree reached the threshold stem diameter for trees-of-present (d_{min}, Table 3.2). Thus, I made an estimation of year of recruitment into the forest canopy.

Eco-units and forest mosaics

In the biostatic tall tree eco-units within each study site, I estimated heights and cover densities of 'structural ensembles' formed by trees- and shrubs-of-present. Tall tree species formed a structural ensemble if they were trees-of-present, i.e. if they were taller than h_{min} (Table 3.2). I set empirical thresholds for medium-tall tree species and for shrub species, at 2/3 and ½ of their maximum height, but measured total cover for dwarf bamboo. In the crown projection maps, I indicated biostatic eco-units and trees- and shrubs-of-present (Figure 4.2), and used these crown projection maps to estimate cover density for each structural ensemble.

I analyzed eco-unit distribution in eight study sites; AM1, AM2, AM3, AM4, EU6, AS1, AS2 and AS5. I distinguished eco-units by their tallest and dominant species. An eco-unit could be dominated by trees, shrubs, or even herbs or ferns.

For tree-type eco-units, I used the developmental phases of dominant tree species to distinguish the four phases of eco-unit development. In innovation phases the 'dominant' trees were seedlings with a height of less than 50cm. Aggradation phases were dominated by potential trees, and had a height between 50cm and h_{min}, the threshold for trees-of-present. Biostatic phases were dominated by trees-of-present, and had a height above h_{min}. In degradation phases the tallest trees were senescent. I set a threshold for senescent trees at a crown density of less than 10%, or a density of less than 50% and more than half of the crown area dead. In the crown projection maps, I indicated the eco-unit types and the four phases of development in tree-type eco-units, and measured the total cover of each.

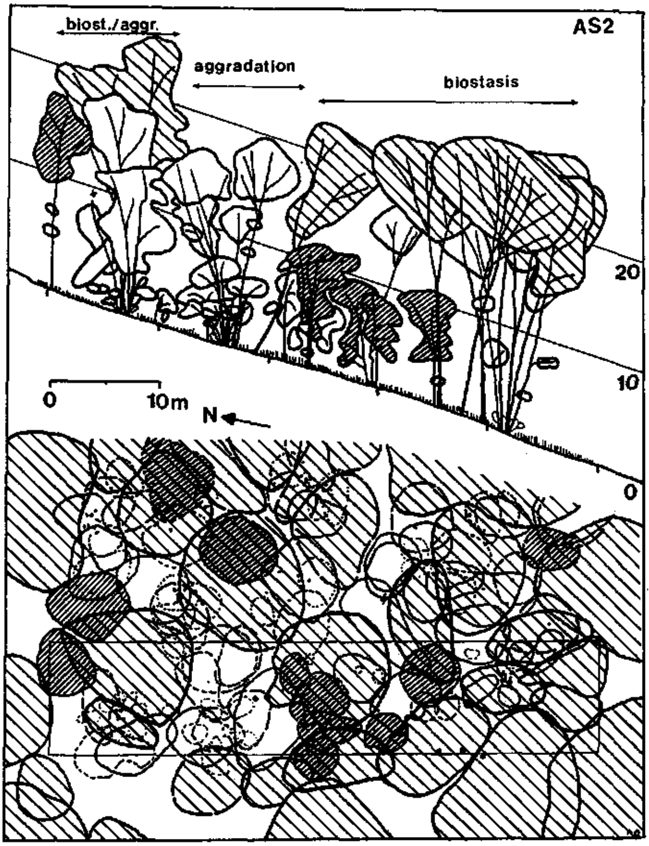

Figure 4.2

Example of a crown projection map and a profile diagram where biostasis and trees-of-present (hatched) are indicated. Tall trees-of-present are *Fagus japonica*, *Fagus crenata* and *Acer nikoense*. Medium-tall trees-of-present are mainly *Carpinus cordata*, *Styrax japonicum* and *Meliosma meriantha*.

To evaluate the importance of potential trees in the understory of biostatic eco-units, I measured the area covered by potential trees underneath the crown projection of each tree-of-present. I distinguished four height classes of potential trees, i.e. 5-10m, 10-15m, 15-20m, ≥20m.

Table 4.3
Percentages of deciduous plants and shrubs among all woody plants.

Site	N	Deciduous (%)	Shrub (%)	Source[1]
AM1	30	100	33	Cain (1935)
AM2	22	100	22	Runkle (1984)
AM3	34	82	18	Platt (unpubl.)
AM4	18	61	22	
AS1	25	92	52	Nakashizuka & Numata (1982a)
AS2	38	89	32	
AS3	14	100	14	Kim et al. (1986)
AS4	27	85	37	
AS5	41	49	51	
AS6	34	29	29	
EU1	5	80	40	
EU2	12	100	25	
EU3	16	100	44	
EU4	4	100	0	
EU5	5	100	20	Lemée (1978)
EU6	10[2]	50	20	Aksoy (1978)

1. Data from this study unless other source mentioned.
2. Including five conifer species.

4.4 RESULTS

Woody species composition

Eastern North America, eastern Asia and Europe have many tree genera in common, the first two richer in genera (Table 4.2). Important codominants are in the *Fagaceae*, *Aceraceae* (north) and *Magnoliaceae* (south). In the south many evergreen broad-leaved tree species become important. The ratio between evergreen and deciduous broad-leaved species increased toward the southern sites, and was highest in the southern sites in China (Table 4.3). I did not find geographic trends in the ratio of trees to shrubs (Table 4.3).

Tree population

For beech, I distinguished three types of height distribution (Figure 4.3). Type 1 had many potential trees and the distribution showed a 'dip' just below canopy-height (AM1, AM4, AS2). Type 2 had a more equal distribution over all height classes with a slight dip in mid-heights (AM3, AS4, EU6). AM2 was like type 2, but had low densities below 10m height. Type 3 had few individuals below the canopy (AS1, AS5, AS6). In each site, the height distributions for all the trees together belonged to the same types as the beech populations, with the exception of AS5 and AS6, where distribution type 1 was found for all trees together. The main codominant tree species had the same distribution types as beech with two exceptions. In AS6 *Fagus lucida* belonged to type 3 and *Castanopsis lamontii* to type 2. And in AS2, *Fagus japonica* belonged to type 1 and *Fagus crenata* to type 3.

As most beech seedlings die within one year, the density of seedlings fluctuated among the sites depending on the time interval since the last seed year, e.g. high in AM1 with a recent seed year. Beech saplings were few ($<1/100m^2$) or absent in sites where dwarf bamboo was dense (AS1 & 2) or with many evergreen broad-leaved tree species (AS5 & 6). Beech sapling densities of 1 to $20/100m^2$ showed success of recruitment in the eight other sites, where saplings were frequent both in the understory and in the open. Saplings of codominant tree species were frequent for *Acer saccharum* (AM1, 2), *Pinus glabra* (AM3), and *Castanopsis lamontii*, *Lithocarpus hancei* and *Manglietia chungii* (AS6). There were few saplings of codominant *Magnolia grandiflora* (AM3), *Liquidambar styraciflua* (AM3), *Quercus ocoteaefolia* (AM4) and *Cyclobalanopsis multinervis* (AS5, AS6).

Table 4.2

Number of tree species in different genera that are present in beech forests. Especially in China, species may have been omitted because the central part was excluded.

		N.America		Eur.	China		Japan
Family	Genus	N[1]	S[2]	all[3]	N[4]	S[5]	all[6]
Pinaceae	*Pinus*	-	2	1	2	-	-
	Picea	-	-	1	-	-	-
	Abies	-	-	1	1	-	3
	Tsuga	1	-	-	-	-	2
	Cathaya	-	-	-	1	1	-
Taxaceae	*Taxus*	-	-	1	-	-	-
Magnoliaceae	*Magnolia*	1	2	-	2	-	1
	Manglietia	-	-	-	-	2	-
	Liriodendron	1	1	-	1	1	-
	Michelia	-	-	-	-	1	-
	Parakmeria	-	-	-	-	1	-
Illiciaceae	*Illicium*	-	-	-	-	3	-
Lauraceae	*Sassafras*	1	-	-	-	1	-
	Pseudosassafras	-	-	-	-	1	-
	Lindera	-	-	-	-	1	-
	Persea	-	1	-	-	-	-
	Litsea	-	-	-	-	1	-
	Neolitsea	-	-	-	-	3	1
	Cinnamomum	-	-	-	-	1	-
	Machilus	-	-	-	-	3	-
	Beilschmiedia	-	-	-	-	1	-
Cercidiphyllac.	*Cercidiphyllum*	-	-	-	-	1	1
Hamamelidaceae	*Liquidambar*	-	1	-	-	1	-
Betulaceae	*Betula*	1	-	1	1	1	1
	Carpinus	1	1	1	2	-	4
	Ostrya	1	1	-	-	-	-
Fagaceae	*Fagus*	1	1	1	3	2	2
	Quercus	4	10	3	1	-	4
	Cyclobalanopsis	-	-	-	3	2	-
	Castanea	1	-	1	1	-	-
	Castanopsis	-	-	-	-	5	-
	Lithocarpus	-	-	-	-	5	-
Elaeocarpaceae	*Elaeocarpus*	-	-	-	-	2	-
Tiliaceae	*Tilia*	1	-	2	2	-	1

Table 4.2 (cont.)

		N. America		Eur.	China		Japan
Family	Genus	N[1]	S[2]	all[3]	N[4]	S[5]	all[6]
Theaceae	*Camellia*	-	-	-	-	2	-
	Stewartia	-	-	-	1	-	2
	Ternstoemia	-	-	-	-	1	-
	Adinandra	-	-	-	-	3	-
	Eurya	-	-	-	-	4	-
	Cleyera	-	-	-	-	2	-
	Schima	-	-	-	-	1	-
Flacourtiaceae	*Idesia*	-	-	-	-	1	-
Ulmaceae	*Ulmus*	2	1	1	-	-	1
	Celtis	1	-	-	-	-	-
	Zelkova	-	-	-	-	-	1
Clethraceae	*Clethra*	-	-	-	-	1	1
Moraceae	*Morus*	-	1	-	-	-	-
Ericaceae	*Vaccinium*	-	1	-	-	-	-
	Oxydendrum	-	1	-	-	-	-
	Rhododendron	-	-	-	-	1	-
Cyrillaceae	*Cyrilla*	-	1	-	-	-	-
Symplocaceae	*Symplocos*	-	1	-	-	3	-
Styracaceae	*Styrax*	-	-	-	2	2	2
	Pterostyrax	-	-	-	1	1	-
	Halesia	-	2	-	-	1	-
	Rehderodendron	-	-	-	-	1	-
Saxifragaceae	*Itea*	-	-	-	-	1	-
Rosaceae	*Prunus*	2	2	1	1	2	2
	Sorbus	-	-	1	1	-	3
	Amelanchier	1	-	-	-	-	-
	Photinia	-	-	-	1	1	-
	Eriobotrya	-	-	-	-	1	-
Leguminoseae	*Cercis*	-	1	-	-	-	-
	Cladrastis	-	-	-	1	-	-
	Albizia	-	-	-	-	1	-
Erythroxylaceae	*Erythroxylum*	-	-	-	-	1	-
Nyssaceae	*Nyssa*	1	1	-	1	1	-
Cornaceae	*Cornus*	1	1	-	1	-	2
Aquifoliaceae	*Ilex*	-	1	1	1	6	2
Euphorbiaceae	*Sapium*	-	-	-	-	-	1
	Daphniphyllium	-	-	-	-	2	-
Aceraceae	*Acer*	2	2	4	4	3	9
Sabiaceae	*Meliosma*	-	-	-	2	3	1
Anacardiaceae	*Rhus*	-	-	-	-	1	1

Table 4.2 (cont.)

Family	Genus	N.America N[1]	N.America S[2]	Eur. all[3]	China N[4]	China S[5]	Japan all[6]
Juglandaceae	*Juglans*	2	1	-	1	-	-
	Carya	3	4	-	-	-	-
	Platycarya	-	-	-	1	-	-
Rutaceae	*Phellodendron*	-	-	-	-	-	1
Araliaceae	*Aralia*	-	1	-	-	-	-
	Kalopanax	-	-	-	1	-	1
	Acanthopanax	-	-	-	-	1	1
	Dendropanax	-	-	-	-	2	-
Oleaceae	*Fraxinus*	2	1	1	2	-	2
	Osmanthus	-	1	-	-	1	-
Acanthaceae	*Prismatomeris*	-	-	-	-	1	-

1. North America northern range: Cain (1935), Williams (1936), Braun (1950).
2. North America, southern range: Braun (1950), Platt & Schwartz (1990).
3. Europe: Mayer (1984b), Ellenberg (1986).
4. China, northern range: Chen et al. (1965), Gan et al. (1986), Cao (pers. comm.), data AS4.
5. China, southern range: Wang (1984), Wang & Li (1986), Anonymus (1982), Wu et al. (1987).
6. Japan: Sasaki (1970).

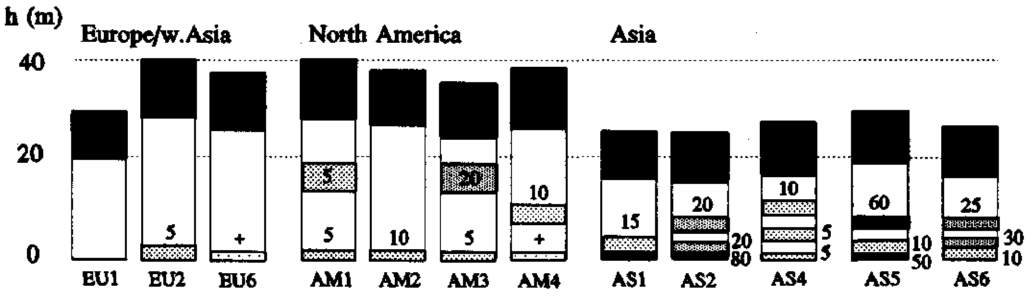

Figure 4.4
Vertical arrangement of structural ensembles in tree type eco-units in biostatic phase; tall tree, medium-tall tree, shrub and dwarf bamboo species. Shading and numbers indicate density (%) of structural ensembles. Potential trees do not belong to structural ensembles and are omitted, but they may have high densities, e.g. in AM1 and AM2.

The estimated time since recruitment into the forest canopy showed that beech and codominant trees could spend over 100yr, sometimes over 200yr, in the forest canopy (Table 4.4). In AM1, AS4 and EU6 fewer trees stay longer in the canopy. In AS1 and AS5, I found peaks in the 50 to 100yr period since recruitment, hence during that period relatively many entered the canopy. In AM1, *Acer saccharum* seemed to have entered the forest canopy before beech. In the other sites data were not sufficient to distinguish trends.

Table 4.4

Number of individuals in the canopy that are in different classes of time intervals that passed since d_{min} was reached.

time (yr)		0	.	.	.	.	50	.	.	.	.	100	.	.	.	150		.	.	.		200+
site	sp[1]																					
AM1	FG	4	2	2	1	-	1	2	2	2	2	2	1	2	-	1	-	-	-	1	-	1
	AS	-	-	-	1	1	-	1	-	-	-	1	1	1	1	1	-	1	2	1	-	1
AM3	FG	-	1	-	1	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1
	MG	-	-	-	-	-	-	-	1	1	1	1	1	-	-	-	-	-	1	-	-	
	PG	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
AS1	FC	1	3	6	4	7	4	9	16	5	5	3	1	2	2	-	1	2	1	-	-	3
AS2	FJ	1	1	1	1	-	2	1	3	2	1	-	2	1	1	-	-	-	-	-	-	1
	FC	-	-	1	-	2	1	2	-	1	-	1	-	-	-	-	-	-	-	-	-	
AS4	FH	4	4	1	1	-	1	-	2	-	1	2	1	-	2	-	-	-	-	-	-	
	FE	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	QA	-	1	-	3	1	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	
AS5	FL	-	1	-	2	-	-	-	3	1	2	2	2	-	2	-	2	-	1	-	1	3
EU6	FO	4	3	4	1	-	2	5	-	4	-	1	-	-	-	-	-	-	-	-	-	1
	AB	2	2	1	2	-	1	1	2	1	1	-	1	-	-	-	-	-	1	-	-	1

1. Species:

FG = *Fagus grandifolia*	AS = *Acer saccharum*
MG = *Magnolia grandiflora*	PG = *Pinus glabra*
FC = *Fagus crenata*	FJ = *Fagus japonica*
FH = *Fagus hayatae*	FE = *Fagus engleriana*
QA = *Quercus aliena*	FL = *Fagus lucida*
FO = *Fagus orientalis*	AB = *Abies nordmanniana*

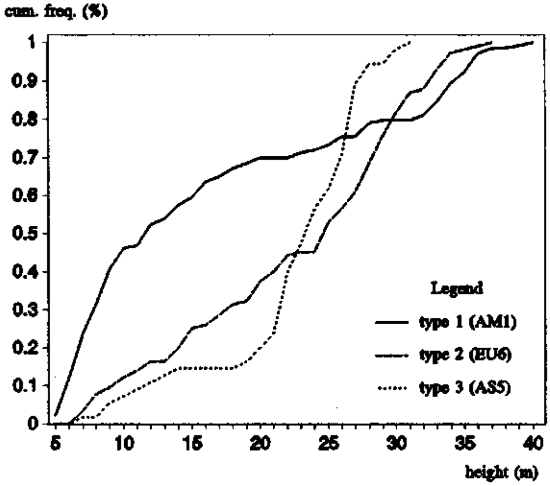

Figure 4.3
Examples of three cumulative tree height distribution types: 1. with a dip below canopy height; 2. with a slight dip in mid-heights; 3. with few individuals below canopy.

Table 4.5
Eco-unit types and phases of tall tree species eco-unit development. Medium-tall tree, shrub and dwarf bamboo types of eco-units were not split into different phases of development.

Site	Area	Eco-unit type						
		tall tree			medium-	shrub	dwarf	
						tall		bamboo
	(ha)	innovation	aggradation	biostatic	degradation	tree		
		%	%	%	%	%	%	%
AM1	0.48	8	27	65	0	0	+	0
AM2	0.48	4	25	71	0	0	+	0
AM3	1.42	11	16	67	+	6	0	0
AM4	0.3	4	22	71	1	0	2	0
AS1	1.56	+	13	58	3	0	8	18
AS2	0.25	+	13	74	0	9	+	4
AS5	0.38	3	1	75	0	18	2	1
EU6	0.84	9	28	63	0	0	0	0

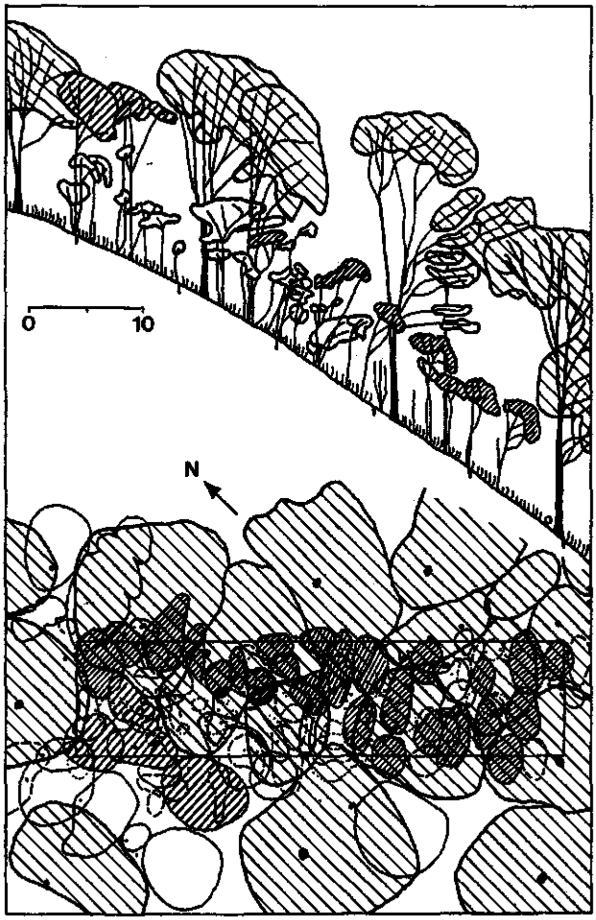

Figure 4.5
Example of a forest (AS5) with three structural ensembles: 1. tall tree species (20-30m tall, *Fagus lucida* and *Quercus engleriana*); 2. medium-tall tree species (10-15m tall, *Illicium lanceolatum*, *Schima sinensis* and *Cyclobalanopsis multinervis*); 3. dwarf bamboo species (1-2m tall, *Sinarundinaria chungii*). In canopy gaps medium-tall trees may grow over 15m tall.

Eco-units and the forest mosaic

Eco-unit architecture differed from site to site (Figure 4.4). From the European to the North American to the eastern Asiatic sites, the number and density of structural ensembles increased (Figure 4.5). Unique to the eastern Asiatic beech forests was the dense structural ensemble formed by dwarf bamboos.

In five study sites, tall tree-type eco-units covered more than 94% of the surface (Table 4.5). In the other three sites, medium-tall tree-type eco-units covered 9% of AS2 and 18% of AS5, and shrubs and dwarf bamboo types of eco-units covered 26% of AS1 (Figure 4.6). For tall tree-type eco-units, innovation, aggradation and biostatic phases covered about 5%, 20% and 70% respectively, as I expected considering increasing tree sizes and approximate times spent in each phase. Degradation phases were unimportant, except for AS1 where unusually many beeches died standing. Innovation phases were rare in AS1 and 2 where dwarf bamboo was dense (Figure 4.4). Aggradation phases were rare in AS5 where medium-tall trees and dwarf bamboo were dense in the understory (Figure 4.5).

In all sites, potential beech trees taller than 5m were found underneath trees-of-present, although densities varied from high (AS1 & AM4) to low (AS5; Table 4.6). In AM1 and AM2, potential *Acer saccharum* trees covered a larger area than beech trees. In AS5 many medium-tall evergreen broad-leaved trees were present underneath canopy beech trees where they formed a structural ensemble, however they could also grow taller in canopy gaps.

Table 4.6

Percent of area underneath trees-of-present covered by potential trees. Per site Fagus and other trees-of-present together are 100%.

	site	AM1		AM2		AM3		AM4		EU6		AS5		AS1
trees-of-present[1]		F	O	F	O	F	O	F	O	F	O	F	O	F
	N	26	13	10	22	14	38	22	7	28	50	19	3	40
potential trees	height (m)	%	%	%	%	%	%	%	%	%	%	%	%	%
Fagus	20-30	3	5	2	6	2	9	6	2	6	6	-	-	-
	15-20	1	0	0	3	2	1	10	1	2	3	5	0	24
	10-15	3	2	2	3	1	2	9	+	3	3	0	1	9
	5-10	3	4	0	0	+	1	14	1	1	+	0	0	5
Others	20-30	+	1	3	12	3	3	1	1	3	2	-	-	-
	15-20	5	3	3	4	1	2	0	0	4	+	0	0	0
	10-15	12	1	0	2	0	1	3	0	4	2	8	4	0
	5-10	5	1	+	1	0	+	+	0	1	0	50	0	4
Without pot.tr.		40	9	29	29	39	33	43	9	35	25	22	10	58
Total per site		74	26	40	60	48	52	86	14	59	41	85	15	100

1. F = *Fagus*; O = others: in AM1 & AM2 mainly *Acer saccharum*, in AM3 mainly *Magnolia grandiflora*, in AM4 *Quercus ocoteaefolia*, in EU6 *Abies nordmanniana*, in AS5 mainly *Cyclobalanopsis multinervis* (< 10m much *Illicium lanceolatum*).

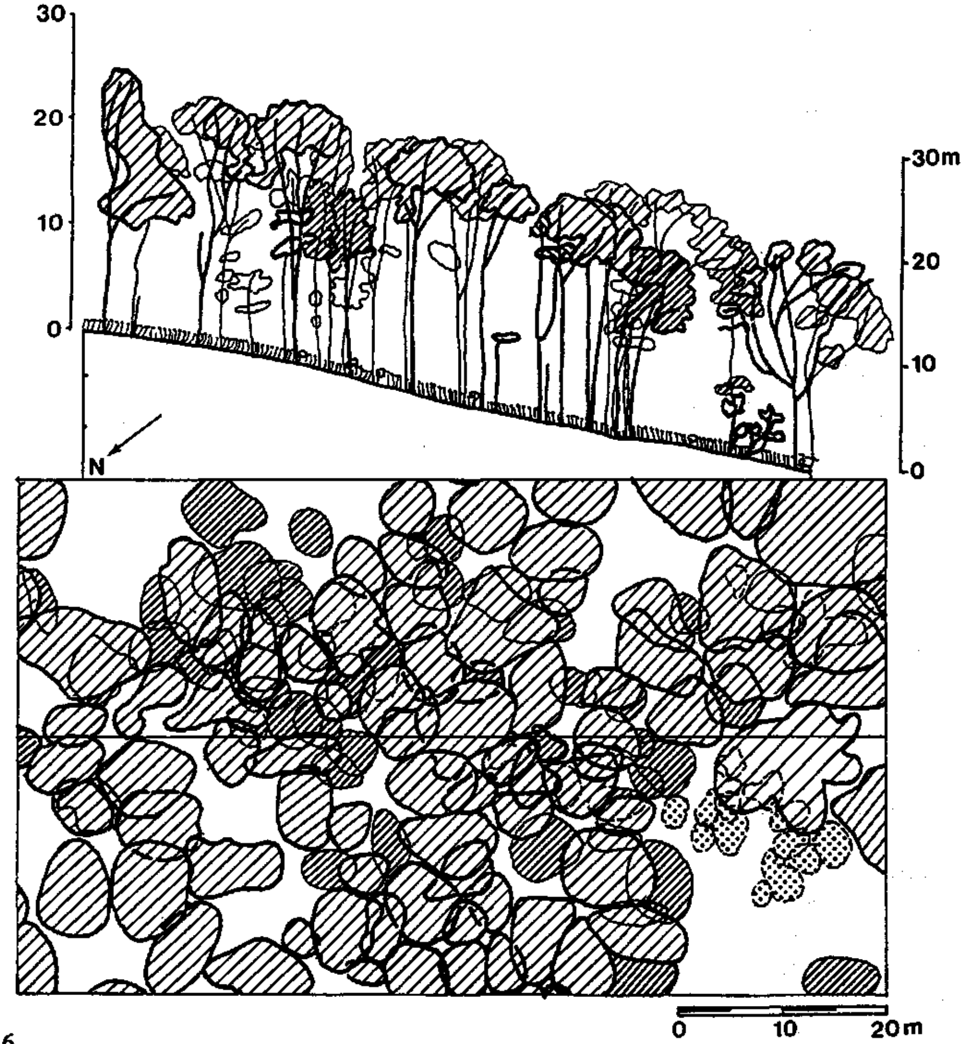

Figure 4.6
Example of a forest with different types of eco-units and their phases of development (AS1). Tree type eco-units are shaded, dark shaded if in aggrading phase and light shaded if in biostatic phase. Shrub type eco-units are stipulated and dwarf bamboo eco-units are white.

4.5 DISCUSSION

Height distributions were different for trees in different sites (Figure 4.3). Height growth rates change with light levels and with age, e.g. released-growing potential trees have larger height growth rates than trees-of-present. Hence, height class distributions do not parallel age distributions (cf. Oliver, 1978). An increase in number of trees per class with increasing height is the result of larger trees having lower height growth rates. The 'dip' below canopy height in type 1 height distributions probably covered the height classes where trees were rarely suppressed and had strong height growth and a high probability of reaching the forest canopy. Likewise, the 'dip' in type 2 may be the result of continuing good height growth rates and reduced mortality rates in smaller sized trees. When the distribution over the lower height classes becomes more equal, I expect lower mortality rates. In type 3, the evergreen broad-leaved trees and dwarf bamboo cast too much shade for shorter beech to survive. In type 3 forests, AS1, AS5 and AS6, few beech seedlings and saplings were found. Thus, in type 3 forests I expect that the forest architecture, including lower structural ensembles, must change drastically to allow establishment of beech. In fact, near the plots of AS6, beech dominated the regeneration in clear-cut areas that probably were grazed for some time. In AS5 and AS6 artificial fires have occurred, but their extent is unknown and certainly small in AS6. In both sites however, fires that changed the forest architecture may have favored establishment of beech. In contrast, in type 1 and 2 forests I expect that beech and codominant tree species can reach the forest canopy without very large changes in the forest architecture.

The estimated time since recruitment into the forest canopy (Table 4.4) yields information on the dynamics of the forest. With time, the probability of damage increases for a tree, and consequently the probability of heart-rot. I assumed that the physical strength of trees-of-present decreases with time, whereas with increasing crown size and tree height the necessary strength to withstand wind force increases. The height distributions showed a decrease towards larger height classes. When recruitment is regular, I expect the number of trees to decrease with increase of time since recruitment, first slowly, later more quickly. This pattern was visible in AM1, AS2, AS4 and EU6, where I found height distribution type 1 and 2 with probably a regular recruitment.

The distribution of tree eco-unit phases of development (Table 4.5) was as expected considering increasing tree sizes and approximate time spent in each phase. An exception was AS5, where the evergreen broad-leaved component was important and dominated 18% of the plots. Another exception was AS1, where the height

Figure 4.7
Canopy gap in *Fagus crenata* forest (AS1) dominated by dwarf bamboo, *Sasa senanensis*, 1.5 to 2m tall.

distribution was type 3, few beech saplings were present, most trees recruited in the canopy 50 to 100yr before, and shrubs and dwarf bamboo dominated in 26% of the plots. Shrub and small tree species form a sparse structural ensemble under beech, but after a tree fall they expand and become dense (Hara, 1983). Sometimes shrubs form a stable community and inhibit regeneration of trees for several decades, for example *Viburnum lentago* in hardwood regions of eastern U.S.A. (Niering & Egler, 1955) or *Rhododendron ponticum* in *Fagus orientalis* forests of northern Turkey (pers. obs.). In AS5, dwarf bamboo was also dense, but dominated canopy gaps and mainly on steep slopes. In Japan there are many records of dwarf bamboos dominating the undergrowth, limiting regeneration of tree species and becoming dominant in canopy gaps (Figure 4.7; Yoshioka, 1939; Nakashizuka & Numata, 1982a; Nakashizuka, 1987; Maeda, 1988; Tanaka, 1988; Peters, Ohkubo & Nakashizuka, in prep.). In a similar way, dwarf bamboo inhibits regeneration of *Nothofagus* in the Chilean Andes (Veblen, 1982, 1989), and *Pteridium aquilinum* inhibits regeneration of *Fagus sylvatica* in Europe (Watt, 1923; Koop & Hilgen, 1987). All merely postpone establishment of forest. Bamboo is known for synchronous flowering and consequent death once in 50 to 100 years (Numata, 1970; Janzen, 1976; Dwivedi, 1988). In Chile, heavy snow kills dwarf bamboo in

Table 4.7
Characteristics of architecture and woody components of study sites and their classification following Wolfe (1979).

Site	Main codom.[1]		Woody sp		Beech populations			Forest mosaic		Forest type Wolfe (1979)
	d/e	s/l	decid. (%)	shrub (%)	height distrib. type[2]	saplings present	recruitm. into canopy	nr. of structural ensembles	non-tree eco-units	
AM1	d	l	100	33	1	+	regular	3	-	simple broadleaved decid.
AM2	d	l	100	22	(2)	+	.	2	-	mixed broadleaved decid.
AM3	e	l	82	18	2	+	(regular)	3	-	notophyll. broadl. evergr.
AM4	(e)	=	61	22	1	+	.	3	-	microphyll. broadl. evergr.
AS1	(d)	l	92	52	3	-	peaked	3	+	mixed coniferous
AS2	d	l	89	32	1	-	regular	4	-	mixed mesophytic
AS3	d	l	100	14	.	+	.	.	.	mixed mesophytic
AS4	d	l	85	37	2	+	regular	4	.	mixed mesophytic
AS5	e	s	49	51	3	-	peaked	4	+	mixed coniferous
AS6	e	s	29	29	3	-	.	4	.	mixed coniferous
EU1	(d)	l	80	40	.	+	.	1	.	mixed coniferous
EU2	d	l	100	25	.	+	.	2	.	mixed coniferous
EU3	d	l	100	44	.	+	.	2	.	mixed coniferous
EU4	d	l	100	0	.	.	.	.	.	
EU5	d	l	100	20	.	.	.	.	.	mixed coniferous
EU6	e	s	50	20	2	+	regular	2	-	mixed coniferous

1. d/e = deciduous vs evergreen; s/l = more shade tolerant vs more light demanding than beech.
2. see 4.4 Results

canopy-gaps and allows regeneration of *Nothofagus* (Veblen, 1982). In Europe, bracken eventually dies of old age (Page, 1976; Watt, 1976).

Structural ensembles were more numerous in eastern Asia, and more dense when evergreen broad-leaved species were involved. In AS5 and AS6 the wide spacing of tall trees probably helped the establishment of the dense evergreen structural ensemble. The nutrient-poor and relatively dry forest EU1 had only 1 structural ensemble. Terborgh (1985) describes how distribution of gaps among the trees-of-present and latitude determine light distribution and structural ensembles underneath the canopy. This latitudinal effect was not evident among my sites because the shapes of the dominant trees, beeches, did not change with latitude, and the second structural ensembles did not increase in height with decreasing latitude (cf. Terborgh, 1985). Instead, among my sites the formation of structural ensembles was dependent on species composition and soil moisture / nutrient content.

Horn (1975) uses the relative abundance of juveniles of different species underneath the forest canopy to predict successional replacement. I found it difficult to determine a direct tree-by-tree relation between suppressed potential trees and trees-of-present, because often potential trees were at the edges of two crown projections. Then the area occupied by the potential tree was divided among the two trees-of-present. Thus, I predict that parts of several trees replace one tree rather than having a one-for-one replacement. Underneath the biostatic phase, 50% of the space was without juveniles. This left space for invasion after tree fall by more light demanding species. In a 15yr old tornado gap in AM1, I found that most of the potential beeches and maples were 30 to 60yr old and had been there before the tornado. However, some 15yr old *Liriodendron* were also present and had about the same height as the beeches and maples. Tree species have different mortality and growth rates in the potential phase, resulting in different types of size distribution. Hence, the method of evaluating space occupied by potential trees underneath the biostatic phases should be combined with knowledge about their survival in shade and growth rates in gaps. Then an assessment can be made of probability of future presence in the canopy of shade-tolerant species. This cannot be done for light demanding species that germinate after gap formation.

Other abiotic factors than temperature and precipitation determined structure and architecture in the beech forests. For mesic sites in Asia, Wolfe (1979) uses only temperature parameters to predict the potential forest type. In his classification, AM3 & AM4 should be evergreen broad-leaved forest, and AS1 and EU1 to EU6 should be mixed coniferous (Table 4.7) but they are not. Rather, all nine sites have high proportions of deciduous broad-leaved trees and shrubs. According to Wolfe (1979), high proportions of deciduous broad-leaved trees and shrubs are characteristic of secondary successions. Hence, I concluded that Wolfe's expected successional transition to forest types that 'belong' in these study sites was not just slow, but rather was interrupted by abiotic disturbances like wind or fire impacts.

I found clear north / south trends in species composition, but not in the population structure nor the forest architecture. Species composition is more related to abiotic factors such as temperature, precipitation and soil nutrient, but population structure and forest architecture seem to be more related to random abiotic factors such as wind impacts.

Chapter 5 - Beech forest: Dynamics

Tree-ring chronologies and beech forest development

In this chapter, I used tree-ring chronologies to analyze forest dynamics. I analyzed the relation between growth strategy of trees, forest architecture, and frequency of change in forests.

5.1 INTRODUCTION

Old growth beech forests on different continents and in different climate zones were heterogeneous in their architecture (Chapter 4). Part of the heterogeneity results from the differences in codominant species and their temperaments (Chapter 3). Also, the beech forests were interacting with their environment. The old growth forests analyzed are the outcome of such interactions during at least the past 100 to 300yr. The importance of considering long time intervals is clear from the old growth *Fagus sylvatica* forest of Fontainebleau, where after 600yr the effect of a clear-cut is still visible in the age distribution (Koop, 1989). Forest architecture is the result of forest dynamics and in its turn strongly influences future dynamics. In the course of time, forest architecture changes, and consequently growing space and resource availability change. Neighboring trees are affected, and they may show a change in growth rate. Beech trees and several of their codominants are known to respond to change in light intensities with a change in tree-ring width (Canham, 1985, 1990; Bouchon et al., 1989; Chapter 3). Hence, I used tree-ring chronologies to analyze tree responses and to infer past changes in forest architecture.

Abiotic factors determine processes that influence beech forest development. Temperature, precipitation, soil moisture and soil nutrients are 'constant factors' that vary within certain ranges and are more or less predictable. Over the long-term however, the ranges of the climatic factors change, and year-to-year climatic changes may have strong effects in forest development, e.g. the occurrence of a moist summer after a seed year favors seedling establishment in a usually dry undergrowth. In many coniferous forest ecosystems, fire is a predictable 'interval factor'. For example, fire recurrence interval is less than 10yr in *Pinus palustris* forest in southeastern USA (Christensen, 1988) or more than 100yr in *Pinus contorta* forest in Yellowstone National Park (Peet, 1988).

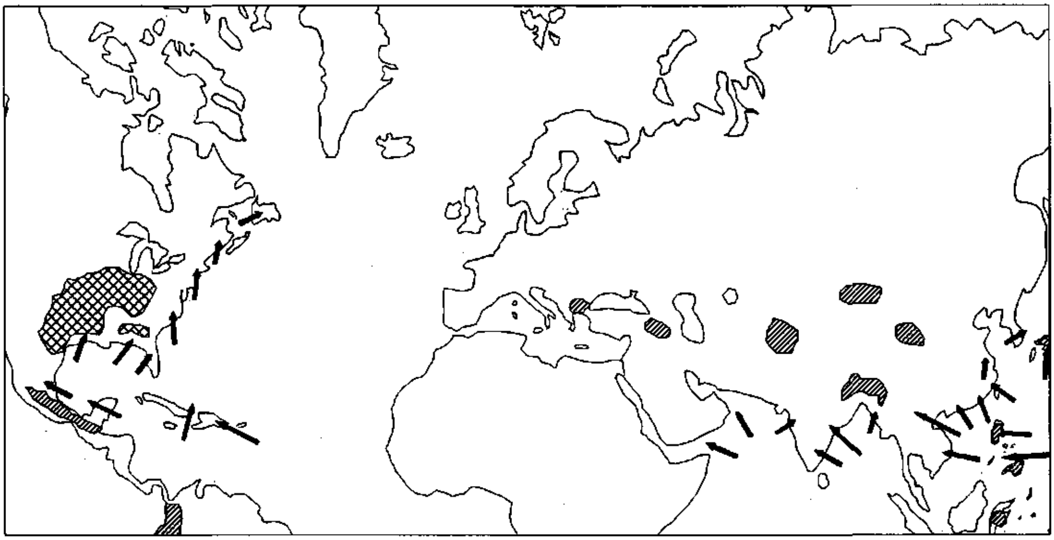

Figure 5.1
Regions of the Northern Hemisphere most likely to be affected by cyclonic storms (arrows), tornados (cross hatched) and earthquakes (hatched; Strahler & Strahler, 1984). The incidence of these abiotic factors is only shown within potentially forested regions.

Cyclonic storms, tornados, glaze storms, earthquakes and volcanic eruptions are examples of long-term 'interval factors' that cannot be predicted (White, 1979; Oliver & Larson, 1990; Figure 5.1). Cyclonic storms are important in the lowland coastal zone of North America and East Asia (Arakawa, 1969; van der Leeden & Troise, 1974), and may affect beech forest located there (Platt, pers. comm.). At higher altitude the pressure drops, the cyclone force becomes less, and fewer tree falls result. Tornados are important in North American beech forest, and they cause tree fall over a continuous area. The impact of tornados ranges from several trees, e.g. Warren Woods (this study), to many hectares, e.g. Tionesta in Allegheny National Forest (pers. obs.). Glaze storms in beech / maple forests affected whole forests and caused more branch fall than tree fall (Downs, 1938; De Steven et al., 1991). Earthquakes and volcanic eruptions may rarely affect beech forest, e.g. in Japan.

Increasingly, the long-term 'interval factors' are regarded as being essential to community development. For example, Henry and Swan (1974) analyzed 300yr of development in a mixed forest in New Hampshire, and found that a fire and a hurricane were the main mediators of change. A gradient of minor to major 'catastrophic' events caused by these 'interval factors' adds temporal variation as an extra axis of community pattern (White, 1979). The other axes of community pattern are the constant abiotic factors which change continuously across the landscape (cf. coenocline; Whittaker, 1975). Recognizing these 'interval factors' as turning points in forest development on eco-unit scale, Oldeman (1990) introduced the abstract term 'zero event'. Henceforth, I will call each of these events by its particular name, e.g. fire impact, wind impact.

The abiotic interval factors have in common that they change the forest architecture by changing the growing space for trees and the availability of light, water and nutrients. The scale of change in forest architecture ranges from branch fall to complete annihilation of the architecture by massive downburst storms. In old growth beech forest, the most common interval factor changing forest architecture is wind impact (Brewer & Merritt, 1978; Bormann & Likens, 1979; Runkle, 1985; Koop 1989). In Japanese *Fagus crenata* forest the most common scale of wind impact is single tree fall with regular frequency, and often trees die standing (Nakashizuka, 1984; Yamamoto, 1987). Also in Slovak old growth *Fagus sylvatica* forest, multiple tree falls are rare (Korpel', 1982). In the *Fagus crenata* forest of Kayanodaira (AS1), a 1982 typhoon caused tree fall of only 3% in tree number and 7% in basal area (Watanabe et al., 1985). In the old growth *Fagus sylvatica* forest of Fontainebleau (EU5), two storms in 1967 caused about eight times as many tree falls as the yearly average (Faille et al., 1984). Fire in beech forest is rarely recorded, but may be important on the dryer sites of the range (Henry & Swan, 1974). In a beech / magnolia forest in Georgia, U.S.A., a ground fire that spread from a neighboring pine forest swept through the forest (Blaisdell et al., 1974). Although fire is common in the hemlock-pine-hardwood forest of northeastern U.S.A., in areas with recent fire history beech is absent (Pyne, 1982).

Wind impacts cause branch and tree fall and so change forest architecture and availability patterns of space, light and nutrients. On wet soils, wind-throw probability increases with duration of storm, whereas on mesic or dry soils strong gusts determine wind-throw probability (Hütte, 1968). Hence, in the study sites maximum wind speeds and pressure are important for evaluating the possible impact of wind (Wieringa & Rijkoort, 1983). A low h/d ratio favors uprooting or branch-fall over snapping in tropical trees (Putz et al., 1983; Vooren, 1986). Faille et al. (1984) found that during storms with strong gusts in Fontainebleau, *Fagus sylvatica* trees mainly are uprooted, whereas during weaker storms snapping off is more common. In the Netherlands, during the January storm of 1990, *Fagus sylvatica* and *Quercus robur* trees usually snapped off at rotten spots (Borgesius & de Vries, 1991). The ratios among crown size (mass), tree height (momentum) and stem diameter (stiffness) are important for tree stability (Vogel, 1988). Tree stability is also influenced by the rootsystem (anchorage) and soil characteristics, i.e. shallow vs deep, mesic vs wet. Waterlogging may occur in beech forests at the wet end of their range which increases the risk of uprooting, e.g. in *Fagus crenata* forest in Japan (Yamamoto, 1989) and in the *Fagus grandifolia* / *Acer saccharum* forest of Warren Woods (AM1) wet areas had more uprootings than snap-offs (Poulson & Peters, in prep.). Forest architecture is also important, and forests with an open architecture are more susceptible to wind impact (Foster, 1988; Borgesius & de Vries, 1991). This is not so for forest edges exposed to open farmland (Brewer & Merritt, 1978).

Wind-impact variables are magnitude, frequency, size and dispersion (Pickett and White, 1985). Magnitude and size determine time needed for recovery and length of period of released growth after release. Frequency determines interval between major releases and duration of suppression.

Tree-ring width chronologies from shade-tolerant trees yield information about wind-impact variables. Intervals between wind-throw have been calculated using size/age distribution in a south Appalachian forest (Lorimer, 1980), from dating stumps and fallen logs in pine / northern hardwood forest (Henry & Swan, 1974) or from releases in living trees (Glitzenstein et al., 1986; Payette et al., 1991). Using tree-ring chronologies for the last 100 years, I calculated the per tree per year probability that a 'major release' occurs. Evaluating year to year changes, I compared alternation of suppression and released growth. Short periods of suppression indicate frequent change in forest architecture by tree or branch fall, resulting in higher light intensities in the understory. Short periods of released growth indicate that the past changes in the forest architecture were small (branch fall vs tree fall) and/or that gaps are quickly filled in by growth of surrounding taller trees.

5.2 OBJECTIVE OF STUDY

All beech species analyzed were shade tolerant and light intensity was the main abiotic factor influencing stem-diameter growth (Chapter 3). The growth strategy of beech species codominating with deciduous broad-leaved tree species was different from the growth strategy of beeches with evergreen broad-leaved species (Chapter 3). Tree-height distributions were site dependent (Chapter 4). The architecture of beech forests changed from site-to-site, but showed a geographic trend, being most complex in East Asia (Chapter 4). Forest architecture is the result of abiotic events and (mainly) the response of trees to those events. In the present chapter, I combine the growth strategies (Chapter 3) and the forest architecture (Chapter 4) and relate them to changes in tree-ring width over time. My purpose is to find common characteristics in the dynamics of beech forests.

Tree-ring chronologies are well suited to analyzing changes in time. The main exogenous factors influencing tree-ring width were light intensity and growing space (Chapter 3), which depend on forest architecture. To evaluate frequency and intensity of changes in architecture, I studied the alternation of suppressed and released growth. For a 100yr time interval, I compared the probabilities of major releases occurring in each site.

5.3 STUDY SITES AND METHODS

Study sites

Study sites are described in Chapter 2.2.

Data collection

Methods of data collection are described in Chapter 2.4.

Tree rings

Following the method of Chapter 3, I distinguished the periods of suppressed and released growth in the tree-ring chronologies. To analyze frequency and intensity of change in light levels, I compared frequency distributions of suppressed and released-growth period lengths in each site (AM1, AM2, AM4, AS1, AS2, AS4, EU6).

I assumed that large increases in tree-ring width were related to large changes in the forest architecture due to 'major releases' which strongly increased light levels and growing space for trees. To define a threshold for a major release, I divided the average tree-ring width of 5yr by the average tree-ring width of the preceding 5yr. A 5yr interval averaged out the effect of year-to-year variation. Calculations of this measure indicated that a threshold of 2x to 2½x increases yields about one release event per tree every 100yr. These thresholds were selected because 100yr was of the same size order as turnover times calculated for both temperate and tropical forests (see Nakashizuka, 1984; Jans et al., in prep). Turnover times indicate the average interval between two gap formations on one site, and for temperate deciduous forests they are estimated to range from about 50 to 300yr (Runkle, 1982; Nakashizuka, 1984). In each tree-ring chronology, for the most recent 100yr interval, I calculated the per tree probability that a major release occurred and averaged this across all cores for each site, excluding EU1 to EU4 because these were too much influenced by management. I compared averages for all trees and for beech trees alone. In two sites (AM1, AS1), I analyzed changes in time of these probabilities by comparing averages for three successive 50yr intervals.

5.4 RESULTS

With the exception of AM1, more than 70% of the periods of suppression were shorter than 20yr (Table 5.1, Figure 5.2), suggesting frequent change in forest architecture and light intensities. With the exception of EU6, more than 65% of the periods of 'released growth' were shorter than 20 years (Table 5.1, Figure 5.2),

Table 5.1
Percentages of periods of suppressed and released growth that were shorter than 20 years.

Site	Species	Number trees	Suppressed ≤20yr (%)	Released ≤20yr (%)
AM1	*Fagus grandifolia*	27	54	80
	Acer saccharum	11	63	77
AM2	*Fagus grandifolia*	10	75	82
	Acer saccharum	13	80	79
AM4	*Fagus mexicana*	17	79	82
AS1	*Fagus crenata*	19	76	67
AS2	*Fagus japonica*	40	84	82
AS4	*Fagus hayatae*	23	71	69
	Fagus engleriana	10	92	73
EU6	*Fagus orientalis*	23	81	50
	Abies nordmanniana	17	100	30

Table 5.2
Per tree per year probability that a major release occurs.

Site	No. of sample trees	Probability 2x[1] (%)	2½x[1] (%)	
AM1	80	2.2	1.3	
AM2	36	2.5	1.6	
AM3	25	2.6	1.4	
AM4	23	3.0	1.8	
AS1	59	1.4	0.7	
AS2	85	2.4	1.6	
AS3	18	1.6	1.3	
AS4	73	1.2	0.6	
AS5	30	1.5	0.6	
AS6	12	1.7	0.6	
EU5	100	2.0	1.3	(data Koop, 1989)
EU6	105	1.1	0.5	

1. Tree-ring width increase threshold.

suggesting that the changes in architecture were small and/or that the neighboring taller trees responded quicker and closed the light gap. This meant that the growth conditions for potential trees changed regularly.

The 'major release' analysis showed two groups of sites which had different ranges of per tree per year probabilities of release, i.e. higher probabilities in AM1 to 4, AS2 and EU5, and lower ones in AS1, AS4 to 6, and EU6 (Table 5.2). The analysis clearly revealed the known major releases in three sites, i.e. 1975 tornado in AM1 (Figure 5.3), 1984 hurricane in AM3, 1967 windstorm in EU5. The successive 50yr intervals showed different probabilities, though not statistically significant, that tended to decrease during the most recent 50yr (Table 5.3).

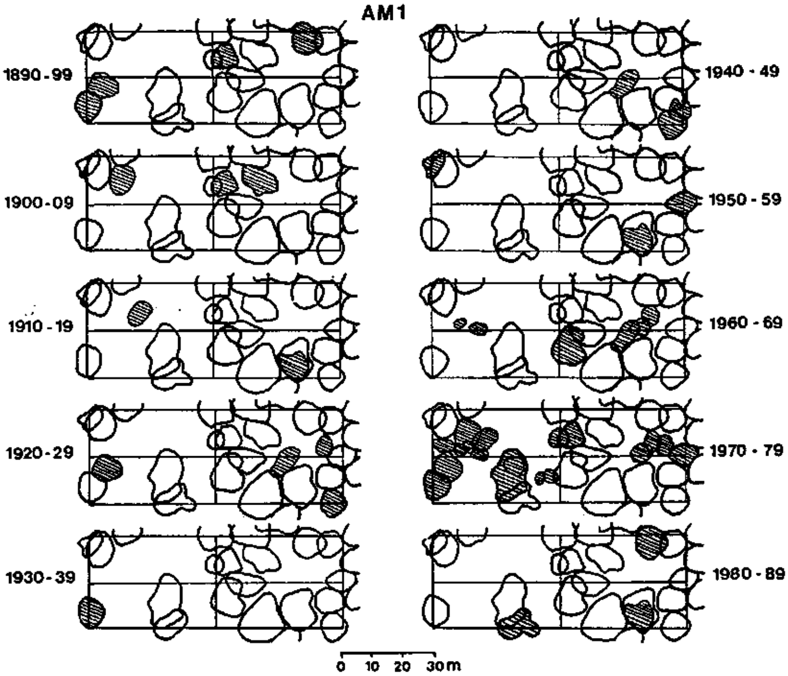

Figure 5.3
Crown projection maps with for 10yr interval the sample trees that had a major releases indicated (AM1). In all maps trees-of-present are indicated, and potential trees only in a map if they had a major release.

Table 5.3
Time trends in per tree per year probability that a major release occurs in a low- and a high-probability site.

Site	Time interval	No. of sample trees	Probability 2x[1] (%)	2½x[1] (%)
AS1	1941-1990	59	1.4	0.7
	1891-1940	48	1.5	0.8
	1841-1890	36	1.8	1.0
AM1	1940-1989	78	2.1	1.4
	1890-1939	50	2.8	1.3
	1840-1889	19	2.9	1.5

1. Tree-ring width increase threshold.

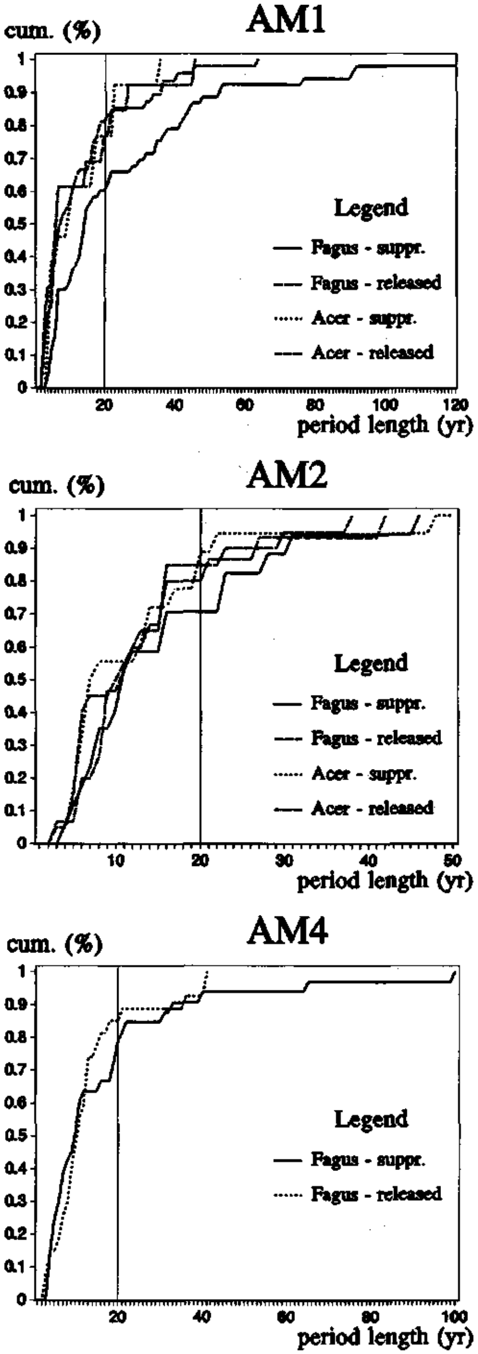

Figure 5.2
Cumulative distribution of periods of suppression and released growth.

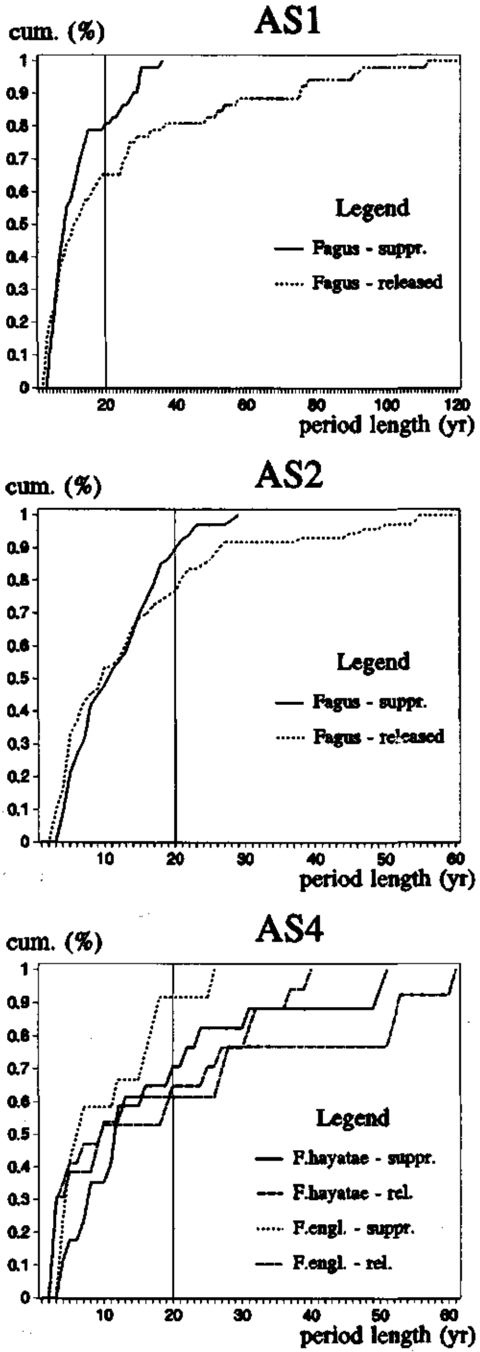

Figure 5.2 (cont.)

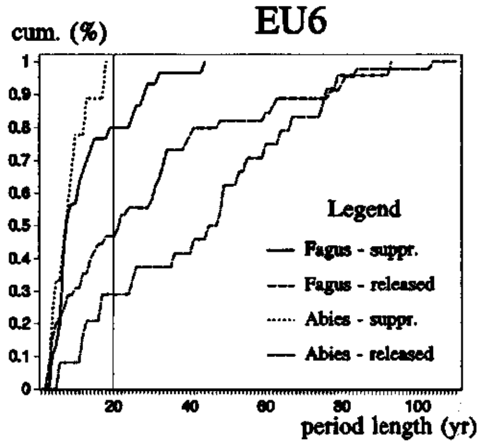

Figure 5.2 (cont.)

5.5 DISCUSSION

For all the study sites the common natural agent causing changes in architecture is windstorms. The probability of tree fall may be increased by site factors, but in the plots that I selected the soils were stable, deep, and not wet. Steep slopes might positively influence tree fall, but again, soils were stable and deep, and trees reached heights similar to those on more gradual slopes. The probability of damage-induced physical weakness increases with time, and was in my estimation wind-impact rather than site-related. Heart-rot is usually caused by wounds that expose the sapwood to decay fungi (Kopinga, 1978; Manion & Zabel, 1979; Highley & Kirk, 1979). Hence, I concluded that wind was the most important agent changing the forest architecture by affecting trees-of-present. In addition, the probability of a tree-of-present to be windthrown increased with time.

Abiotic factors like windstorms that recur over long-term intervals, could be recognized in tree-ring chronologies. Macroclimatic factors caused little of the year-to-year variation in the tree-ring chronologies. I attributed the periodical (≥5yr) variation in the tree-ring chronologies to change in light level and in growing space for each tree. The 'major releases' were reflections of real changes in the forest architecture. Thus, major releases were indicators of long-term changes and the

Table 5.4
Characteristics of woody components, forest architecture and growth of trees.

Site	Main codom.[1]		Beech populations			Forest Mosaic		Percentage of periods $\leq$20yr		Major release
	d/e	s/l	height distib. type	saplings presence	recruitm. into the canopy	nr. of structural ensembles	non-tree eco-units	suppressed	released growth	per tree per year probab. (%)
AM1	d	l	1	+	regular	3	-	55	79	1.3
AM2	d	l	2	+	.	2	-	78	81	1.6
AM3	e	l	2	+	(regular)	3	-	.	.	1.4
AM4	(e)	=	1	+	.	3	-	79	82	1.8
AS1	(d)	l	3	-	peaked	3	+	76	67	0.7
AS2	d	l	1	-	regular	4	-	84	82	1.6
AS3	d	l	.	+	.	.	.	.	.	1.3
AS4	d	l	2	+	regular	4	.	64	58	0.6
AS5	e	s	3	-	peaked	4	+	.	.	0.6
AS6	e	s	3	-	.	4	.	.	.	0.6
EU1	(d)	l	.	+	.	1	.	.	.	.
EU2	d	l	.	+	.	2	.	.	.	.
EU3	d	l	.	+	.	2	.	.	.	.
EU4	d	l	.	.	.	.	.	.	.	.
EU5	d	l	.	.	.	.	.	.	.	1.3
EU6	e	s	2	+	regular	2	-	86	43	0.5

1. d/e = deciduous vs evergreen, if codominant rare in brackets; s/l = more shade-tolerant vs more light-demanding than beech.
Dot indicates not available.

calculated per tree per year probabilities were their indices. I expected the calculated indices to have some bias, because only 'survivor' trees were sampled (Fox, 1989). Because of different lengths in the tree-ring chronologies, the number of cores that could be compared decreased when going back in time. Back in time a larger proportion of the remaining cores was from trees that eventually reached the canopy, and presumably had been released more often than the trees that died before reaching the canopy. The decrease in per tree per year probability of major release toward the most recent 50yr interval (Table 5.3) may have resulted from this bias. Of course an alternative hypothesis is that the frequency of major releases actually changed in successive intervals. I do not expect any biases to affect comparison among sites. The relative difference in probabilities among the sites, with different 'major release' thresholds (2 or 2½), showed that frequency and intensity of releasing factors varied among sites.

The time interval of 100yr that I used to calculate probabilities was likely not long enough for all sites to include the very rare major storms which resulted in large-scale architectural change that affected all remaining trees. Such a year was included in site EU5, where in 1967 a strong storm affected 70% of the sample trees. This did not happen in AM1, where in 1975 a very localized tornado occurred, making 3 small multiple tree gaps in an area of about 20 ha. Hence, a problem will occur when using probabilities for explaining present composition of forest canopy which is determined 100 to 300yr ago with the establishment of juveniles, and growth and survival of potential trees (cf. Clark, 1990).

The beech forests with low vs high per tree per year probabilities for major releases had biologically different codominants. In the high probability sites, beech had codominant species that were less shade-tolerant (Table 5.4). So these codominants need higher light levels and more frequent and larger releases to become trees-of-present (Poulson and Platt, 1989, in prep.). In AM4, the high release probability may have favored beech over the more shade-tolerant evergreen *Quercus ocoteaefolia*. In EU5 the only codominant present was the more light-demanding *Quercus robur*, which cannot survive under beech. In the low probability sites, beech had codominant species that were evergreen and more shade-tolerant (Table 5.4). Thus, these codominants can grow under lower light levels and need fewer releases. In AS1 and AS4, low frequency of major releases may have favored beech over more light-demanding codominant species, resulting in almost pure beech forests. Similarly, monospecific dominance in tropical rain forests occurs on undisturbed sites with a shade-tolerant dominant (Hart, 1990). In AS5 and AS6, the low frequency of major releases favored evergreen broad-leaved species over beech, which had few potential trees (distribution type 3, Figure 4.3). The low-release probability sites AS1 and AS5, had peaks of recruitment into the canopy, which indicates that these sites may have had single major releases and peaks in establishment of saplings. This is demonstrated for AS1 by Nakashizuka and Numata (1982a), who suggest one major release of all saplings by simultaneous flowering and death of dwarf bamboo. In AS5 and AS6 a complete change of forest architecture seems necessary for beech to establish. Similarly, Veblen (1985, 1989) found that disruption of dwarf bamboo dominance was necessary for *Nothofagus* to become established. Thus, in Chilean *Nothofagus* forests *Nothofagus* seedlings can establish themselves only after landslides, volcanic ash or flood deposition, or extensive blowdowns, whereas shade-tolerant evergreen broad-leaved trees become established underneath *Nothofagus*.

The observations support the 'intermediate disturbance' hypothesis, which proposes that intermediate frequency, size and intensity of disturbance leads to highest species diversity (Connell, 1978). Higher per tree per year probability of major release in beech / maple forests leads to higher frequencies of tree species which codominate with beech in AM2 compared to in AM1. A similar relation is found in beech forest in New Zealand where *Nothofagus fusca* is favored over the more shade-tolerant *Nothofagus menziesii* if frequency and scale of disturbances increase (Stewart et al., 1991). As predicted by Connell (1978), some low release probability sites (AS1, EU6) had only one or two dominant tree species. Likewise, in other low release probability sites (AS5, AS6) species abundance seemed to be reduced favoring evergreen over deciduous broad-leaved tree species, contrary to Wolf's predicted potential forest type (Table 4.7). These sites developed towards dominance by species that were most shade-tolerant and had, relative to stem diameter, slow height-growth rates (cf. Hart, 1990). Release probabilities do not explain differences among sites with essentially different species compositions.

The generally short duration of periods of suppressed and of released growth implied frequent small-scale changes in forest architecture. Sites with low probability of major releases had longer periods of released growth, whereas suppressed periods were not different for high vs low probability sites (Table 5.4). Compared to AM2, AM1 had, on the average, longer periods of suppression, which may explain dominance of beech over sugar maple. In the beech / fir forest of EU6 periods of released-growth were on the average longest, which suggests a more open forest architecture (due to fir canopy architecture). Comparison of duration of periods of suppressed and released growth did not allow distinction among sites, partly because extreme sites like AS5 and AS6 lacked potential trees.

The per tree per year probability of major release was a valid indicator of the forest dynamics. This probability made an explanation of the relative dominance of beech possible.

Chapter 6 - Conclusions

6.1 OVERVIEW

Beech species, and especially species like *Fagus grandifolia* and *Fagus longipetiolata* with their large geographic range (Figure 1.1), are tolerant to a large range of mesic climates and soils. Of course this is necessary for any tree species occupying a large geographic range however it does not explain the specific ecological success of beeches.

All analyzed beeches were shade-tolerant tree species. As potential trees, beeches could survive long periods of suppression, and they usually passed through alternating phases of suppressed and released growth before reaching the forest canopy. In the northern and central ranges, the beeches were the most shade-tolerant species among deciduous broad-leaved codominants. Toward the southern ranges, the beeches were less shade-tolerant than the increasingly abundant evergreen broad-leaved codominants. To the north and at higher altitudes in the central ranges, codominant conifers were more shade-tolerant than beech. The same beech species could be found growing in different ranges with deciduous and/or evergreen codominants, e.g. *Fagus grandifolia* in North America or *Fagus lucida* in China.

Beeches had flexible growth strategies, usually more so than codominant species. Beech trees grow according to 'Troll's model' (Glossary), with the main characteristic of plagiotropic differentiation in all aerial axes. Many of the codominant species have orthotropic axes. With the exception of *Acer saccharum* and *Cyclobalanopsis multinervis*, beeches had more variable h-d relationships than any codominant analyzed. Beeches had relatively lower h/d ratios than deciduous broad-leaved codominants and higher h/d ratios than most evergreen broad-leaved codominants. A lower h/d ratio indicates that the tree invests relatively less energy in height growth and more in diameter growth. This agrees with the hypothesis that beech has to grow up first in order to survive among evergreen broad-leaved trees that have denser crowns casting deeper shade. Beech can remain behind and expand more horizontally when growing among fast-growing deciduous broad-leaved trees that have more open crowns. In general, crown projections of beeches were larger than those of codominants.

Fagus japonica and *Fagus engleriana/multinervis* were multi-stemmed throughout their range. The multi-stemmed beeches form clusters of stems. Each stem has a potential for separate existence and may become 25m tall. In other beech species the multi-stem form only occurs under stress, e.g. cold stress at high latitude or altitude. Multi-stemmed beeches had more flexible growth strategies than codominant single-stemmed beeches.

Populations of beech usually had the same tree-height distribution as codominant trees. An exception was Miao'er Shan in China (AS6), where codominant evergreen broad-leaved species like *Castanopsis lamontii* had juveniles but *Fagus lucida* did not. Absence of beech juveniles was determined by the abundance of evergreen broad-leaved codominant tree species or by the density of shrub and dwarf bamboo layers.

The architecture of beech forests was most simple in some European beech forests and became increasingly complex in Asiatic beech forests. This difference was mainly due to presence of dwarf bamboo and evergreen tree or shrub species in Asiatic beech forest. The Asiatic beech forests were richest in woody species and had the highest ratio of evergreen vs deciduous broad-leaved trees. Eco-units dominated by tall tree species prevailed in beech forest mosaics, and their development phases of innovation, aggradation, biostasis and degradation covered about 5%, 20%, 70% and 0% of the area respectively. The remaining 5% of the area was dominated by shrubs or medium-tall trees. Exceptions occurred in sites where medium-tall tree species or shrub and dwarf bamboo species successfully dominated eco-units, and beech juveniles could not establish themselves.

In beech forests diversity was maintained by wind impact that changed the forest architecture, and thus changed light supply and growing space. Wind impact caused releases from suppression in potential trees. There was a relationship between per tree per year probability of major release and the codominance by other tree species. High probabilities of major release in areas where deciduous broad-leaved tree species could occur favored these tree species over beech. Low probabilities of major release in areas where evergreen broad-leaved tree species could occur favored these tree species over beech. Of course in the low probability areas, major releases may occur on a large scale but with such long intervals between major releases that my method missed them.

In most beech forests, beeches were regularly recruited into sapling size classes and the forest canopy. The balance between beech and codominants like maple depended on frequencies of wind impacts, higher frequencies favoring more light-demanding species. In many Asiatic beech forests however, other woody species inhibited regular recruitment of beech. These inhibiting species were evergreen broad-leaved tree species in the more southern ranges, and shrub and dwarf bamboo species in the more northern ranges. In these forests, large changes in the forest architecture are necessary for beech to establish itself. Dwarf bamboo gives such opportunity by gregarious flowering and death. It is unclear to me what exogenous factors may cause large changes. Windstorms affect trees but not dwarf bamboos. However, there are a few records of artificial fires or clear-cuttings in the Chinese study sites and their impacts should not be underestimated offhand. Both in China and Japan I found that beeches where among the first to establish themselves after clear-cut. For tree species like beech, one such event every two or three centuries may be sufficient for successful regeneration, and peaks in canopy recruitment indeed point that way.

6.2 PERSPECTIVES

Climates are naturally changing; forests adjust and also change. Forests may be quite stable if climatic changes occurring within the lifespans of trees are tolerated by those trees (e.g. Koop, 1989). Long-term climatic changes like those after the last Glaciation cause tree populations to migrate. Tree-species composition of forests may change because tree species migrate at different rates by fast or slow diaspore dispersal (Huntley & Birks, 1983; Davis, 1989; Tallis, 1991), have different tolerances of climate and soil, and differ in their capability to adjust (e.g. to day length, Jesler & Kramer, 1939).

Due to increase in atmospheric CO_2 and other gases, the climates are predicted to change more rapidly than before (Bolin et al., 1986; Graham et al., 1990). The climatic change may be too fast for species to follow, thus we may end up with forests where species intolerant of the new climate have disappeared and tolerant species have not yet arrived (Fabian, 1991). 'General circulation models' predict global mean surface warming and mean precipitation increase, but for the temperate zone accurate forecasts cannot be given (Andrasko, 1990). For beech to profit, higher temperatures should be accompanied by higher precipitation levels during the growing season, e.g. like the climates of *Fagus grandifolia* in Florida and *Fagus longipetiolata* in southern China. I expect that other beech species may grow in similar climates. For example, in the Paleocene flora of Europe, beech was found together with *Lauraceae* (Takhtajan, 1969), a combination now found in the montane zone of subtropical China. If cool temperate climates become warmer temperate climates with abundant summer rain then codominant deciduous broad-leaved tree species in beech forests might be replaced by evergreen broad-leaved tree species. However, if such a change were not accompanied by an increased wind-impact frequency, beech could not maintain its dominance in these forests.

6.3 CONCLUSIONS

The species in the genus *Fagus* form an ecologically homogeneous group of tree species that are successfully dominating or codominating the forest ecosystems where they occur. Shade tolerance and flexible growth strategies form the basis for the success of beech. This is an adaptation to long-term forest dynamics, due to wind impacts. Beeches have a wide tolerance for macroclimate and soil as long as these are sufficiently humid, however the extent of their dominance is determined by the frequency of wind impacts.

Summary

Beech forests are dominated or codominated by at least one *Fagus* species. The beeches are a homogeneous group of 11 deciduous tree species growing in the Northern Hemisphere (Figure 1.1). They often dominate forest ecosystems throughout their ranges. The optimum for beech is on acidic and mesic loam soils. The ranges are limited by summer water deficits in continental and southern climates, and low winter temperatures and late spring frost in the north.

The purpose of my research was to find out why beeches are such widespread successful trees. I tried to answer several questions:

1. Do these beech species have something in common as forest organisms? What makes them different from codominant trees? In Chapter 3, I selected radial growth and size parameters for such comparisons among trees. Size parameters were tree height, stem diameter and crown projection.
2. What are common characteristics of beech forests over the whole range? In Chapter 4, I analyzed geographical trends in woody species composition and forest architecture. Within each site, I compared tree-height distribution and tree regeneration and related them to forest architecture.
3. Are there common characteristics in the dynamics of beech forests? The relation between suppressed and released growth in trees, as well as release frequency, yields information about stability and change in the forest. In Chapter 5, I compared suppression and release in tree-ring chronologies of trees in different study sites. The per tree number of major releases was counted over one century. For each study site, I used this parameter to calculate the per year per tree probability of a major release.

In Chapter 2, I described the 16 study sites (Figure 2.1, Table 2.1) which were representative of beech forests in different geographic areas. They were selected in sites with minimal human influences. In each study site, I selected at least two plots. The plots included different phases of forest development and were between 300 and 2400m^2 in size. Tree height and stem diameter were measured in trees taller than 5m, and in a subplot, trees between 0.5m and 5m were measured. Their stem position and crown projection were mapped. Among plants lower than 0.5m, I recorded abundance of beech seedlings and estimated percentage cover of important plant species. Increment cores were taken from trees growing in the forest canopy, in canopy gaps and in the understory.

Generally, beeches are more shade-tolerant than their deciduous broad-leaved codominants and less shade-tolerant than their evergreen broad-leaved codominants. During its lifecycle a beech tree can pass several periods of suppression (Table 3.7). Compared with beech, height/stem-diameter ratios were relatively higher in deciduous and lower in evergreen broad-leaved codominants. With the exception of *Acer saccharum* and *Cyclobalanopsis multinervis*, beeches had more variable height / stem-diameter relationships than any codominant analyzed (Table 3.3). Beech had a more flexible growth strategy than codominant tree species.

The architecture of beech forests was most simple in some European beech forests and became increasingly complex in eastern Asiatic beech forests (Chapter 4). The eastern Asiatic beech forests were richest in woody species and had the highest ratio of evergreen vs deciduous broad-leaved tree species. In each study site, the forest canopy covered about 70% of the area and potential trees dominated in the canopy gaps. Exceptions were some Asiatic sites where medium-tall tree species or shrub and dwarf bamboo species dominated in the canopy gaps, and beech seedlings could not establish themselves. Beech juveniles were also absent from Chinese study sites where evergreen broad-leaved trees were abundant in the understory. The beech forests are very different in architecture and species composition.

There was a relationship between per year per tree probability of major release and the codominance of other tree species (Chapter 5). High probabilities of major release in the study sites where deciduous broad-leaved tree species could occur, favored these tree species over beech. Low probabilities of major release in the study sites where evergreen broad-leaved tree species could occur, favored these tree species over beech. In the study sites with evergreen broad-leaved trees, codominance of beech is probably maintained through infrequent and large-scale major releases. The interval between changes in the forest architecture, and consequently light levels in the forest, is important in determining the dominance of beech.

The *Fagus* species form an ecologically homogeneous group of tree species that are successfully dominating or codominating the forest ecosystems where they occur. Shade tolerance and flexible growth strategies form the basis for the success of beech. Beeches have a wide tolerance for macroclimate and soil as long as these are sufficiently humid, however the extent of their dominance is determined by the frequency of wind impacts.

Samenvatting

Beukenbossen worden gedomineerd door één of meer *Fagus*-soorten. De beuken vormen een homogene groep van 11 zomergroene boomsoorten op het Noordelijk Halfrond (Figuur 1.1). De beuken domineren vaak de bosecosystemen waarin ze voorkomen. Het optimum voor beuk ligt op matig zure leembodems met een goede vochthuishouding. In zuidelijke streken wordt het natuurlijke verspreidingsgebied bepaald door watertekort gedurende de zomermaanden, in noordelijke streken door lage wintertemperaturen en late voorjaarsvorst.

Het doel van mijn onderzoek was verklaringen te vinden voor het feit dat beuken wijdverspreid voorkomen en bosecosystemen domineren. Verschillende vragen wilde ik hier beantwoorden:
1. Wat hebben beukensoorten gemeen en wat onderscheidt hen van andere codominante boomsoorten? In hoofdstuk 3 heb ik diameter groei en grootte van bomen gebruikt voor een dergelijke vergelijking. Grootte van bomen werd bestudeerd aan de hand van de parameters boomhoogte, stamdiameter en kroonprojectie.
2. Wat zijn de gemeenschappelijke karakteristieken van beukenbossen? In hoofdstuk 4 onderzocht ik de relatie tussen het geografische voorkomen, de soortensamenstelling en de bosarchitectuur. Per studieobject bestudeerde ik verder de relatie tussen boomhoogteverdeling, verjonging en bosarchitectuur.
3. Zijn er gemeenschappelijke karakteristieken in de dynamiek van beukenbossen? Beuken kunnen een groot deel van hun leven in de schaduw van het kronendak groeien voordat ze door het ontstaan van een gat in het kronendak worden vrijgesteld. De afwisseling van periodes van onderdrukte en vrije groei van individuele bomen, alsmede de frequentie van vrijstellingen, geven inzicht in stabiliteit en verandering in het bos. In hoofdstuk 5 gebruikte ik daarom met behulp van een aanwasboor verkregen jaarringseries voor de vergelijking van de duur van periodes van onderdrukking en vrije groei van bomen in de verschillende studieobjecten. Per boom werd geteld hoe vaak een grote vrijstelling plaatsvond gedurende een periode van 100 jaar. Hieruit kon per studieobject de kans per jaar en per boom op een vrijstelling worden bepaald.

De 16 studieobjecten waren geselecteerd in gebieden met minimale menselijke invloeden (Figuur 2a, Tabel 2a). Ze waren representatief voor beukenbossen in verschillende geografische streken. Per studieobject werden tenminste twee proefvlakken, met afmetingen van 300 tot 2400m^2, gekozen. De proefvlakken waren kleiner op ruggen en steile hellingen. De proefvlakken bevatten stukken bos in verschillende fasen van bosontwikkeling. Boomhoogte en stamdiameter werden gemeten van alle bomen hoger dan 5m, en in een gedeelte van het proefvlak eveneens van alle bomen tussen 0.5 en 5m. Stampositie en kroonprojectie werden gekarteerd. In een gedeelte van het proefvlak werden in de vegetatie lager dan 0.5m de beukenkiemplanten geteld en de bedekkingsgraad van belangrijke plantensoorten geschat. Boorkernen werden verzameld van bomen in het kronendak, in kronendakgaten en in de ondergroei.

In het algemeen verdragen beuken meer schaduw dan zomergroene en minder schaduw dan altijdgroene codominante bomen. Een beuk kan gedurende zijn leven afwisselend onderdrukt worden en vrij groeien (Tabel 3.7). In vergelijking met de beuk waren hoogte/diameter verhoudingen hoger voor zomergroene en lager voor altijdgroene codominante bomen. Dus in vergelijking met zomergroene boomsoorten investeerde de beuk relatief minder in hoogte- dan in diametergroei, en andersom in vergelijking met altijdgroene boomsoorten. Met uitzondering van *Acer saccharum* en *Cyclobalanopsis multinervis*, vertoonden beuken meer variatie in de hoogte / diameter relaties dan de geanalyseerde codominante boomsoorten (Tabel 3.3). Dus wat betreft relatieve investering in hoogte- of diametergroei was er een grotere flexibiliteit in de groeistrategie van de beuk dan in die van de meeste codominante boomsoorten.

De architectuur van beukenbossen is eenvoudigst in Europa en het meest complex in Oost-Azië (Figuur 4.4). De Aziatische beukenbossen waren het rijkst aan houtige plantensoorten en hadden het hoogste aandeel aan altijdgroene versus zomergroene loofboomsoorten. In de meeste studieobjecten bedekte het kronendak 70% van het oppervlak en domineerden er boomsoorten in de kronendakgaten (Tabel 4.5). Uitzonderingen vormden sommige Aziatische bossen waar kleine boomsoorten, struiken of dwergbamboes de kronendakgaten domineerden, en beuken zich niet konden vestigen. Beukenverjonging was ook zeldzaam in die Chinese beukenbossen waar altijdgroene loofbomen domineerden in de ondergroei. De beukenbossen zijn heel verschillend wat betreft hun bosarchitectuur en soortensamenstelling. Toch domineert overal de beuk.

In bossen waar zomergroene loofbomen voorkwamen, bevoordeelde een grote kans op vrijstelling per jaar en per boom de zomergroene loofbomen boven de beuk (Tabel 5.4). In bossen waar altijdgroene loofbomen voorkwamen, bevoordeelde een kleine kans op vrijstelling de altijdgroene loofbomen boven de beuk. In deze studieobjecten met altijdgroene loofbomen kan beuk zich waarschijnlijk handhaven als codominant via zeldzame maar grootschalige afbraak van de bosarchitectuur. Dus het interval tussen en de mate van radicaliteit van veranderingen in de bosarchitectuur, en daarmee het lichtklimaat in het bos, spelen een beslissende rol in de bepaling van de mate van dominantie door beuk.

De *Fagus*-soorten vormen een ecologisch homogene groep van bomen die succesvol (co)domineren in de bossen waar ze voorkomen. Schaduw-tolerantie en een flexibele groeistrategie vormen de basis voor het succes van de beuk. Beuken hebben een grote tolerantie voor macroklimaat en bodem zolang er voldoende vocht beschikbaar is. De mate van dominantie van de beuk wordt echter bepaald door de frequentie en intensiteit waarmee veranderingen in de bosarchitectuur optreden.

Glossary

In case no authors are mentioned, definitions are specific for the present book.

Aggradation phase: A phase in eco-unit development that follows the innovation phase or a release from suppression, a forest patch dominated by released-growing potential trees.

Architectural tree model: Generalized growth program which determines successive architectural phases of a tree (Hallé et al., 1978). Examples of definitions (Hallé et al., 1978):

> ***Mangenot's model*** (*Tsuga*): Axes are mixed, the apical meristem producing initially a basal vertical part, followed by a distal horizontal part, often associated with a change from spiral to distichous phyllotaxis, and from small to large leaves. Indefinite superposition of such axes at the level of transition builds the architecture of the tree, with the trunk made up of successive proximal vertical parts, the branches of horizontal distal parts.
> ***Massart's model*** (*Abies*): 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 arrangment or symmetry, but never by apposition.
> ***Rauh's model*** (*Pinus*, *Picea*, *Quercus*): A monopodial trunk which grows rhythmically and so develops tiers of branches, the branches themselves morphogenetically identical with the trunk. Flowers are always lateral.
> ***Scarrone's model*** (*Acer* spp.): 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*** (*Fagus*, *Carpinus*): Axes are all plagiotropic with continual superposition; main-line axes contribute part trunk, part branch, the proximal part becoming erected, most often secondarily 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 erected portion.

Architecture: design and construction of an object (Webster's New World Dictionary, 1988).

Beech forest: Forest where at least one of the 11 *Fagus* species dominates the forest canopy or is main codominant.

Biostatic phase: A generally long-lived phase in eco-unit development that follows an aggradation phase; a forest patch dominated by trees-of-present.

Canopy gap: The openings between trees-of-present of tall tree species (cf. dynamic phase, Oldeman, 1978).

Degradation phase: A phase in eco-unit development that follows the biostatic phase; tallest trees are senescent.

Eco-unit: A vegetation patch that is dominated by either trees, shrubs, or herbs in one phase of development. Tree type, shrub type, dwarf bamboo type and herb type eco-units are dominated by tree species, shrub species, dwarf bamboo species or herb species respectively. Eco-units in different phases of development exist next to each other as a horizontal mosaic, not vertically below each other.

Forest canopy: Consists of trees-of-present of tall tree species (cf. homeostatic phase, Oldeman, 1978).

Forest eco-unit: A forest patch that is dominated by a set of trees in one phase of tree development. Tall tree type and medium-tall tree type eco-units are dominated by tall tree species and medium-tall tree species respectively.

Forest mosaic: a forest ecosystem with different kinds of eco-units, each in different phases of development.

Innovation phase: A phase in eco-unit development, occurs in a canopy gap when tree seeds germinate and seedlings establish themselves.

Potential tree: A tree in a development phase in which height growth is more important than stem-diameter and crown-extension growth. Transition from potential tree to tree-of-present phases is gradual, but in each site an empirical height-threshold can be set.

Released growth: For potential trees, growth under high light levels.

Suppressed growth: For potential trees, growth under low light levels.

Tree-of-past: A tree in a development phase that follows a potential tree of tree-of-present phase, and in which the tree is senescent.

Tree-of-present: A tree in a development phase that follows the potential tree phase, and in which stem-diameter and crown-extension growth are more important than height growth. Transition from potential tree to tree-of-present phases is gradual, but in each site an empirical height-threshold can be set.

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Curriculum vitae

Rob Peters werd geboren op 18 november 1959 te Sint Michielsgestel. Na het behalen van het diploma Atheneum-B aan het Sint Janslyceum begon hij in 1978 aan de studie bosbouw van de Landbouwhogeschool te Wageningen. Na het behalen van het kandidaatsdiploma in 1982 werd gedurende 11 maanden in Japan een praktijkstage en een studie van Japanse berken- en beukenbossen gedaan. De doctoraalstudie omvatte de vakken Boshuishoudkunde, Bosteelt & Bosoecologie en Plantkunde. Gedurende deze tijd verrichtte hij onderzoek naar de history van het landgoed Biljoen, de ecologie van Japanse beukenbossen en de cellulaire reactie van iepenhout op verwondingen. In 1985 werd het doctoraalexamen behaald. Daarna werd met behulp van een Japanse studiebeurs in Japan een onderzoek verricht dat vooruitliep op dit onderzoek. In 1987 kon hij via een uitwisselings overeenkomst van het Ministerie van Onderwijs en Wetenschappen met de Chinese Academie van Wetenschappen voor 5 maanden onderzoek verrichten in de Chinese beukenbossen. Vanaf 1988 werd dit onderzoek gedaan bij de vakgroep Bosbouw van de Landbouwuniversiteit. Gedurende 9 maanden in 1989/90 was hij gastonderzoeker in de Universiteit van Illinois in Chicago, van waaruit de Amerikaanse beuken werden bestudeerd.