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Monospecific and mixed stands of *Fagus* and *Nothofagus* species in the temperate zones of the world

– Christoph Leuschner, Göttingen –

Abstract

The majority of the 13 *Fagus* and 16 temperate *Nothofagus* species form pure stands (or dominate mixed forests) in part of their distribution ranges. This phenomenon, which distinguishes the beeches and southern beeches from most other temperate tree genera, is examined using examples of pure and mixed forests from all five continents where temperate forests occur. Pure stands are formed under optimal climatic conditions, i.e. high moisture in the growing season and sufficiently high summer temperatures. The often high competitive strength of these ~30 species primarily bases on specific morphological and physiological traits and is not the consequence of forest management or unnaturally high ungulate browsing which can suppress competing tree species and reduce tree diversity.

1. Introduction

Despite low species numbers, the genus *Fagus* in the Fagaceae contains one of the most important group of trees in the northern hemispheric temperate forests because this genus dominates large tracts of forest in East Asia, western Eurasia and eastern North America, and has considerable importance for forestry. The more species-rich genus *Nothofagus* (Fagaceae, recently placed in an own family, Nothofagaceae) plays a similar role in the temperate forests of the southern hemisphere, particularly in Chile, Argentina, New Zealand and, locally, in Australia. One characteristic of the two genera is that the species often form pure stands, or at least achieve high cover values in the canopy. This may distinguish the beeches and southern beeches from other temperate genera such as *Acer, Tilia* or *Quercus* where monospecific stands are rare or absent.

This short review compiles information on the occurrence of monospecific and mixed forests of the more widespread eight *Fagus* species and compares the results with relevant data from the temperate *Nothofagus* species of the southern hemisphere.

2. Diversity of beeches and southern beeches

Based on morphological and molecular evidence, 13 *Fagus* species are distinguished worldwide (Table 1), of which three (*F. bijiensis, F. tientaiensis* and *F. brevipetiolata*) are only known from each one or very few locations in China and were assumed by HUANG et al. (1999) and DENK (2003) to belong to *F. longipetiolata*. Thus, 10 *Fagus* species are broadly accepted, three in Japan (*F. crenata, F. japonica, F. okamotoi*), five in China, Taiwan and Korea (*F. engleriana, F. lucida, F. longipetiolata, F, hayatae, F. chienii*), one in Europe and western Eurasia (*F. sylvatica*) and one in North America (*F. grandifolia*). More widespread are only seven species, while *F. okamotoi, F. chienii* and *F. hayatae* are known from each one to six locations only. *F. chienii* may be extinct (GUO & WERGER 2010). Table 1 gives rough

Table 1: Species and important subspecies of the genus *Fagus* according to the classification by SHEN (1992). *F. orientalis* is now considered a subspecies of *F. sylvatica* (DENK 2003), and *F. bijiensis, F. tientaiensis* and *F. brevipetiolata* were included within *F. longipetiolata* by HUANG et al. (1999) and DENK (2003).

Species	Distribution	Approx. range size
Single-stemmed beeches (Subgenus FAGUS)		
A Sections FAGUS and GRANDIFOLIA		
North America and Western Eurasia		
F. sylvatica L.	Central, Western & South-eastern Europe	~ 910,000 km^2
F. orientalis Lipsky	N Iran, Caucasus, Turkey, E Bulgaria, E Greece	~ 400,000 km^2
F. grandifolia Ehrh.	Eastern North America	~ 1.5 Mio km^2
F. grandifolia subsp. *mexicana* (Martínez) A.E. Murray	NE Mexico	1.5 km^2
East Asia		
F. longipetiolata Seemen	Central & south-eastern China, northern Vietnam	~ 2 Mio. km^2
F. brevipetiolata Hu	Sichuan to Yunnan	few locations
F. tientaiensis T.N. Liou	Zhejiang (E China)	one location south of Shanghai
F. bijiensis C.F. Wei & Y.T. Chang	Guizhou (S China)	one location in Guizhou
B Section LUCIDA		
F. lucida Rehder & Wilson	South-eastern China	~ 1 Mio. km^2
F. hayatae Palibin	South-eastern China, Taiwan	six locations
F. chienii Cheng	Sichuan (C China)	one location in Sichuan
F. crenata Blume	Japan (mostly Japan Sea side)	~ 100,000 km^2
Multi-stemmed beeches (subgenus ENGLERIANA)		
F. engleriana Seemen	Central (Sichuan) & eastern China	~ 500,000 km^2
F. japonica Maximowicz	Japan (Pacific Coast side)	~ 50,000 km^2
F. okamotoi Shen	Japan, central Honshu	very locally

estimates of the distribution range sizes of these 7 species. It must be kept in mind that these range size figures are partly misleading because many *Fagus* species have a discontinuous distribution area. For example, the Chinese beeches occur only at higher elevations in the mountains, as does *F. sylvatica* in the southern and southeastern parts of its range. Two important subspecies have to mentioned, (1) *F. sylvatica* ssp. *orientalis* (Oriental beech), which was long considered a separate species (*F. orientalis* Lipsky) (DENK et al. 2002), and *F. grandifolia* ssp. *mexicana*, which occurs very locally in montane forests in NE Mexico as on outpost of the continuous distribution range of American beech (RODRIGUEZ-RAMIREZ et al. 2013).

The genus *Nothofagus* has recently been split into four genera (Fucospora, Lophozonia, Trisyngyne, Nothofagus; HEENAN & SMISSEN 2013) comprising about 35 recent species (HILL & DETTMANN 1996), of which about 19 species occur in a tropical or tropical-montane climate on New Guinea and New Caledonia (and surrounding islands). The other 16 species (plus one important natural hybrid) are distributed in the cool to warm temperate zone of the southern hemisphere and are of prime interest here. Nine species (plus the hybrid) are found in southern South America (Chile and Argentina), three in Australia, and four species (of which one is split into two ecologically different variants) in New Zealand (Table 2). For convenience, I will use the genus name *Nothofagus* throughout the paper instead of the new genus names.

Table 2: The 18 extra-tropical taxa of the former genus *Nothofagus* in New Zealand, Australia, Chile, and Argentina.

	New genus	Distribution	Leaf size class[2]
Evergreen taxa			
N. moorei	Lophozonia	AUS	large
N. cunninghamii	Lophozonia	AUS	small
N. solandri var. *solandri*	Fucospora	NZ	small
N. solandri var. *cliffortioides*	Fucospora	NZ	small
N. menziesii	Lophozonia	NZ	medium
N. fusca	Fucospora	NZ	medium
N. truncata	Fucospora	NZ	medium
N. dombeyi	Nothofagus	C/A	small
N. nitida	Nothofagus	C/A	medium
N. betuloides	Nothofagus	C/A	small
Summergreen taxa			
N. gunnii	Fucospora	AUS	medium
N. obliqua	Lophozonia	C/A	large
N. pumilio	Nothofagus	C/A	medium
N. antarctica	Nothofagus	C/A	small
N. alpina	Lophozonia	C/A	large
N. alessandri	Fucospora	C/A	large
N. glauca	Lophozonia	C/A	large
N. leoni[1]	Lophozonia	C/A	large

[1] = hybrid *N. obliqua* x *N. glauca*; [2] small (< 2cm), medium (2-4 cm), large (> 4 cm)

3. Beech distribution and climate

All 13 *Fagus* species are deciduous and have mesomorphic and relatively large leaves (about 5 to 10 cm long). From an ecological point of view, the leaf morphology is remarkably similar across the *Fagus* species in Asia, Europe and North America, despite distinct differences in the climatic spaces in which these *Fagus* species are occurring (Fig.1). The analysis of climate stations at the northern (or upper) and the southern (or lower) distribution limits of the more widespread *Fagus* species shows that *F. sylvatica* tolerates relatively cold as well as relatively dry climates compared to the other species (FANG & LECHOWICZ 2006). This is also true for its subspecies *F. s.* ssp. *orientalis* which, however, extends more into regions with a more continental climate than ssp. *sylvatica* (Fig. 2). In contrast, the North American *F. grandifolia* extends much more into warmer subtropical climates than the other species, e.g. in northern Florida, Texas and also in NE Mexico. On the other hand, American beech is also relatively tolerant of cold winters at its northern range limit. This is also true for *F. crenata*, but this main Japanese species seems to be much more dependent on a sufficiently humid climate than *F. sylvatica, F. orientalis* and *F. grandifolia*. The other Japanese species,

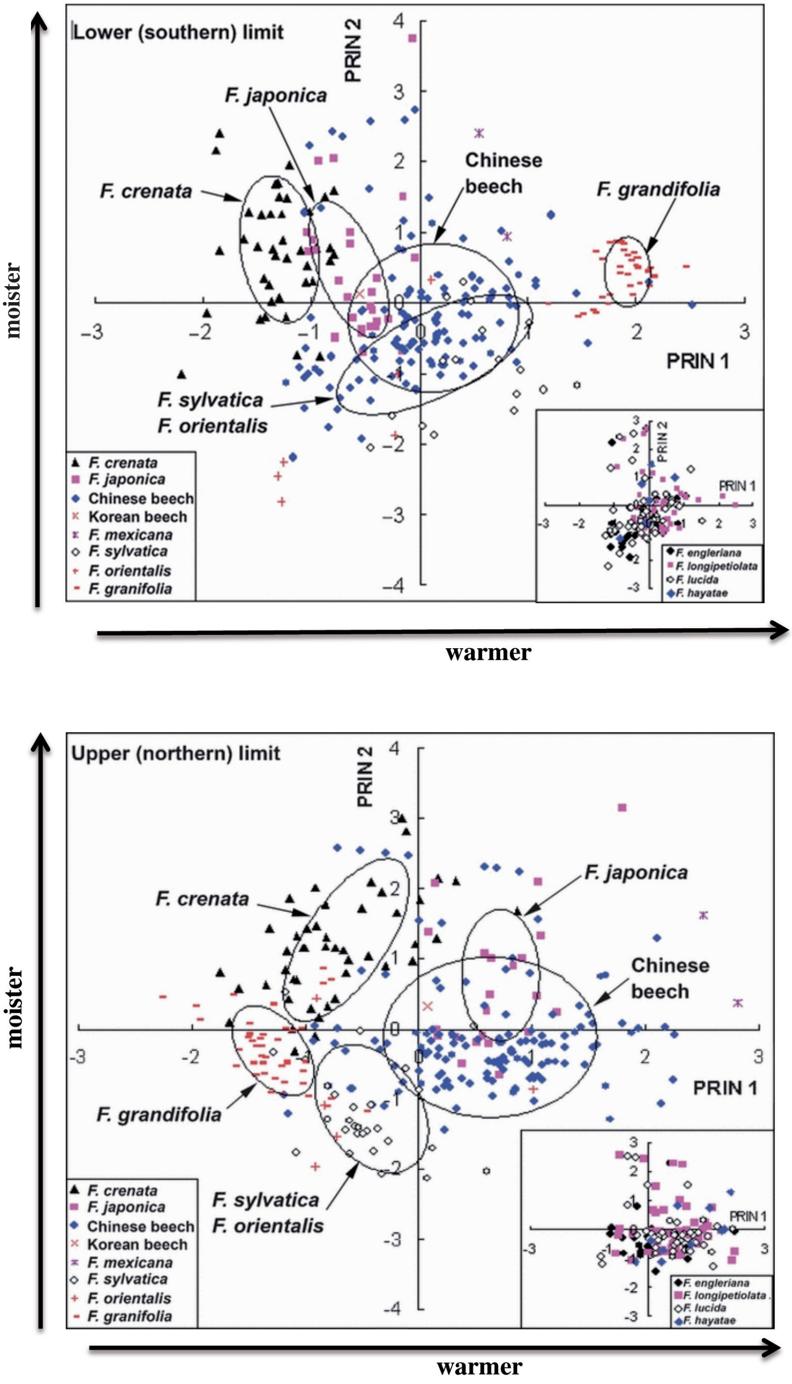


Fig. 1: Climatic spaces of *Fagus sylvatica* (incl. ssp. *orientalis*), *F. grandifolia*, *F. crenata*, *F. japonica* and the four more widespread Chinese beeches at the southern (or lower) and the northern (or upper) distribution limits according to Principal Components Analyses of FANG & LECHOWICZ (2006).

F. japonica, which is restricted to the Pacific side of Japan, is less cold-tolerant than *F. crenata*, but apparently similarly dependent on moisture. Finally, the four main Chinese beeches can be characterized as occupying intermediate positions in the climate spaces derived by FANG & LECHOWICZ (2006) with relatively low cold tolerance at their northern (upper) and also southern (lower) distribution limits, and relatively high moisture and heat demand. The temperature spaces plotted by PETERS (1997) also indicate that *F. sylvatica* is the most oceanic species of the beeches (lowest annual temperature variation), while *F. orientalis, F. crenata* and in particular *F. grandifolia* tolerate much larger thermal fluctuation, the latter also much higher summer warmth (Fig. 2). Somewhat surprising from the Central European perspective is that *F. sylvatica* seems to withstand higher drought intensity than the other *Fagus* species (Fig. 1), given its oceanic distribution range. However, the results of the PCA must be interpreted as a ranking among the *Fagus* species only, and this comparison does not tell us much about drought sensitivity in absolute terms.

Leaf size is much more variable among the 16 temperate *Nothofagus* species ranging from about 1 cm (e.g. in *N. solandri*) to more than 8 cm (e.g. in *N. alpina*). While small leaves (typically <2 cm long) are mostly occurring in the evergreen species (an exception is the small-leaved deciduous *N. antarctica*), the deciduous species mostly possess medium- to large-sized leaves (Table 2). With respect to leaf size and phenology, the rare *N. alessandri* and *N. glauca*, followed by the somewhat more widespread *N. alpina* and *N. obliqua* (in its variety *macrocarpa*), are the species resembling most the northern hemispheric beeches (cf. RAMIREZ et al. 1997).

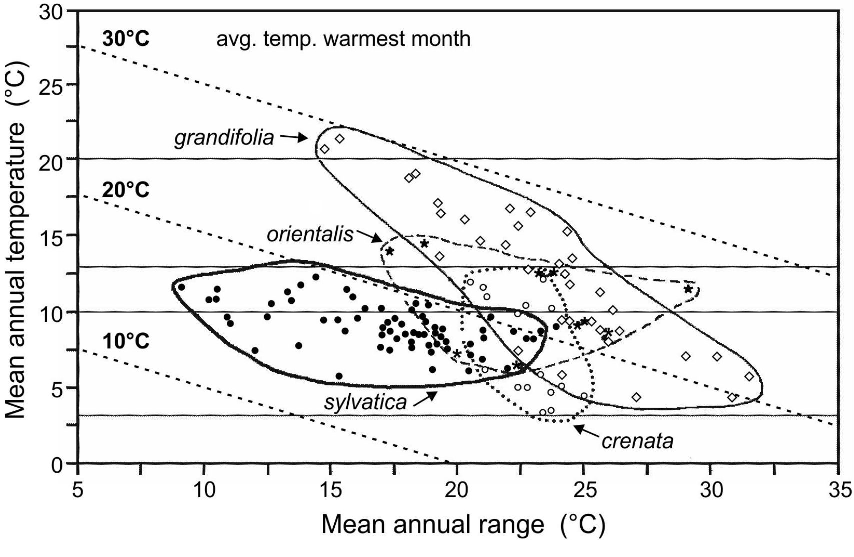


Fig. 2: Mean annual temperature and difference between mean temperature of coldest and warmest month (annual range) for selected stands of *Fagus sylvatica, F. crenata, F. grandifolia* and *F. sylvatica* ssp. *orientalis* according to PETERS (1997).

Nine of the 16 temperate *Nothofagus* species (and both variants of *N. solandri*) are evergreen, seven (plus the hybrid *L. leoni*) are deciduous. It is important to note that all but one of the deciduous species are occurring in South America; the Tasmanian species *Nothofagus gunnii* is the only deciduous southern beech in Oceania. This is mainly a consequence of the colder winter temperatures in inland Patagonia (and in montane Tasmania) as compared to

New Zealand and mainland Australia, where leaf shedding in winter does not represent an advantage over evergreen foliage.

4. The occurrence of monospecific and mixed stands of *Fagus* and *Nothofagus* in the northern and southern hemispheres

The available descriptions of forest vegetation on the five continents with temperate forests (North America, Europe, Asia, South America, Oceania) reveal that many of the more widespread *Fagus* and *Nothofagus* species are forming monospecific stands under certain conditions. Monospecific stands are formed irrespective of the species richness of the woody flora of the continent, or whether the species is deciduous or evergreen, or forms large or small leaves. Table 3 lists each eight deciduous and evergreen beech and southern beech species, for which the occurrence of extended monospecific forests (or at least stands with more than 80 % canopy cover) is known. Four examples of monospecific stands are shown as stand profiles in Figs. 3a – d, i.e. for *F. orientalis* (northern Turkey) and *F. sylvatica* (eastern Slovakia).

The Japanese *F. crenata* dominates many montane broad-leaved forests on the Japanese Sea-side of Honshu (KAKUBARI 1991, MASAMUNE 1960, MIYAWAKI 1980-1989, MIYAWAKI 1984, YAMAMOTO 1989), while for the more locally distributed *F. hayatae*, pure stands have been described for the montane belt of Taiwan (PETERS 1997). The more widespread Chinese beeches (*F. lucida, F. longipetiolata, F. engleriana*) dominate at places the montane forests in the north-western part of their distribution ranges in the subtropical mountains of China (GUO & WERGER 2010, WANG 1961). *F. orientalis* dominates many beech forests in the montane belt of the Pontic Mountains in northern Turkey (MAYER & AKSOY 1986), in the Caucasus (e.g. WALTER 1974, TSEPLYAEV 1961) and in the Elburz of northern Iran (MATAJI & GILKALAEI 2006, SAGHEB-TALEBI & SCHÜTZ 2002, KNAPP 2005, ZOHARY 1981).

Table 3: *Fagus* or *Nothofagus* species that form pure forests or forests with high dominance (>80 % canopy cover) of that species in the temperate or subtropical zones of the earth. Species-poor stands occur also in the mountains of SE China where *F. lucida, F. longipetiolata* and *F. engleriana* occur at higher elevations in the middle and northern parts of their distribution ranges as dominants (GUO & WERGER 2010).

Deciduous trees

- *Fagus sylvatica*, Central Europe: on acid soils (Luzulo-Fagenion)
- *Fagus orientalis*, northern Turkey, Caucasus, northern Iran in montane belt
- *Fagus crenata*, NW Japan in montane belt
- *Fagus hayatae*, northern Taiwan in montane belt
- *Nothofagus pumilio*, southern Patagonia
- *Nothofagus glauca*, central Chile
- *Nothofagus alessandri*, central Chile
- *Nothofagus gunnii,* Tasmania, in montane belt

Evergreen trees

- *Nothofagus betuloides*, southern Patagonia
- *Nothofagus dombeyi*, southern Chile
- *Nothofagus solandri* var. *cliffortioides*, NZ, in montane belt
- *Nothofagus menziesii*, NZ, in montane belt
- *Nothofagus fusca*, NZ, in lower montane belt
- *Nothofagus solandri* var. *solandri*, NZ, mostly lowland
- *Nothofagus moorei*, eastern Australia
- *Nothofagus cunninghamii*, Tasmania, in montane belt

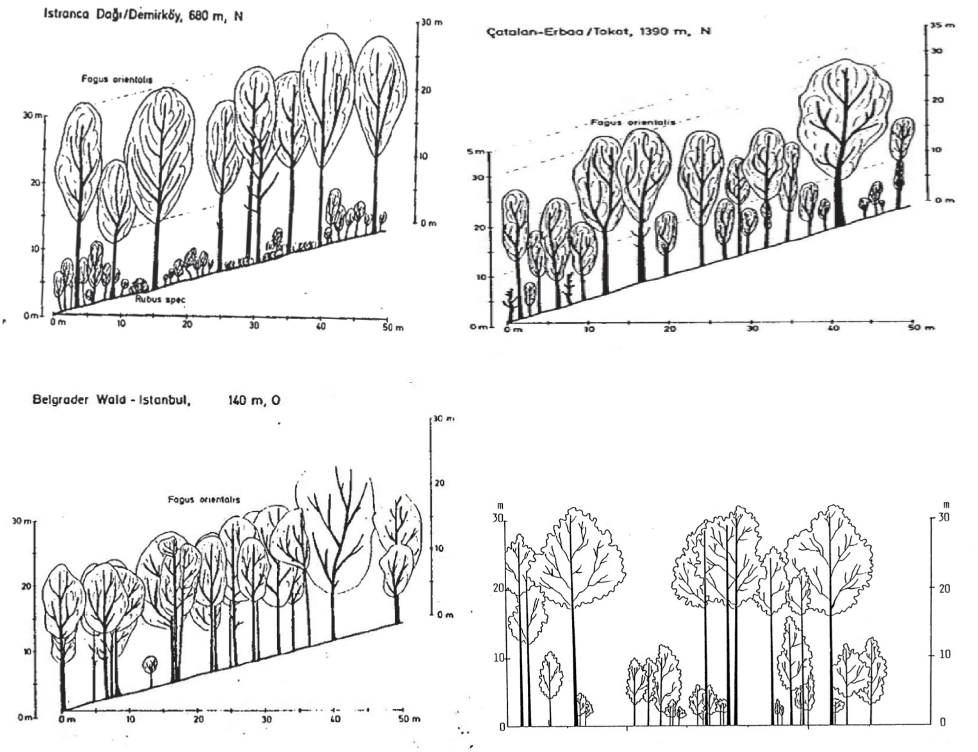
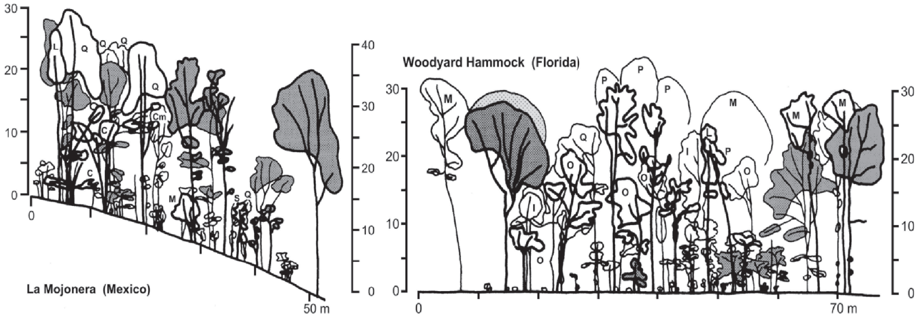


Fig. 3: Monospecific forests of *Fagus orientalis* at three locations in the north of Turkey (after MAYER & AKSOY 1986) (upper row and lower row: left) and monospecific *F. sylvatica* virgin forest in eastern Slovakia (Kyjov; KORPEL 1995) (lower row: right).

Monospecific beech forests are conspicuous in large parts of the distribution range of *F. sylvatica* in Europe. *Fagus* dominance is particularly pronounced on strongly to slightly acidic soils (e.g. in the Luzulo- and Galio-Fagenion suballiances in Central Europe), but is also found in many beech forests on base-richer soils. Here, species such as *Acer pseudoplatanus*, *Fraxinus excelsior* and *Acer platanoides* often contribute with 5 to 20 % to canopy cover (ELLENBERG & LEUSCHNER 2010). The comprehensive data base in OBERDORFER (1992) for beech forests in southern Germany indicates that acid-soil beech forests (Luzulo-Fagetum) on average consist of only 2 tree species per relevé with clear dominance of *Fagus* over large areas (LEUSCHNER 1999).

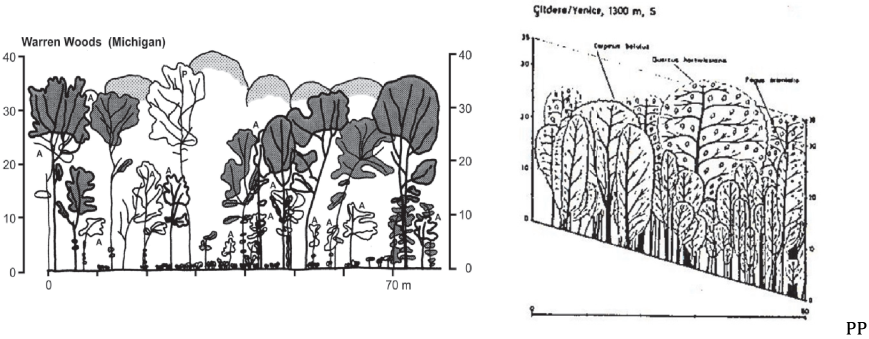
Age-class forest management with preference given to beech has certainly contributed to this *Fagus* dominance in various regions of Europe. However, *Fagus sylvatica* does form extended monospecific stands also in regions where management has never occurred as in the large beech virgin forest reserve Uholka in the Ukrainian Carpathians (on ca. 80 km^2, BRÄNDLI & DOWHANYTSCH 2003), and in virgin forests in the Romanian and Slovakian Carpathians (e.g. Semenic, Kyjov and Havesova National Parks, KORPEL 1995, TURCU & STETCA 2006). To explain this dominance, it has been proposed that high browsing pressure by ungulates is contributing to the dominance of *F. sylvatica* in Central Europe because many other broad-leaved tree species (such as *Acer*, *Fraxinus* or *Quercus*) are typically damaged to a larger extent than *Fagus* (e.g. SCHULZE et al. 2014). This effect likely has reduced the abundance of *Acer* and *Fraxinus* in some stands on richer soil, but it cannot explain beech domi-

Fig. 4: Examples of broad-leaved mixed forests with *Fagus* species in the temperate and subtropical zone.



(a) Subtropical *Fagus-Quercus* cloud forest with *Fagus grandifolia* ssp. *mexicana* near La Mojonera at 1950 a.s.l. in northeastern Mexico. Shaded: *Fagus*, C: *Cleyera theaeoides*, Cm: *Clethra macrophylla*, L: *Liquidambar styraciflua*, M: *Magnolia schiedeana*, Q: *Quercus ocotaeifolia* (after PETERS 1997).

(b) Subtropical *Fagus-Magnolia* mixed forest with *Fagus grandifolia* at Woodyard Hammock, northern Florida (45 m a.s.l.). Shaded: *Fagus*. M: *Magnolia grandiflora*, I: *Ilex opaca*, L: *Liquidambar styraciflua*, O: *Ostrya virginiana*, P: *Pinus glabra*, Q: *Quercus* spp. (after PETERS 1997).



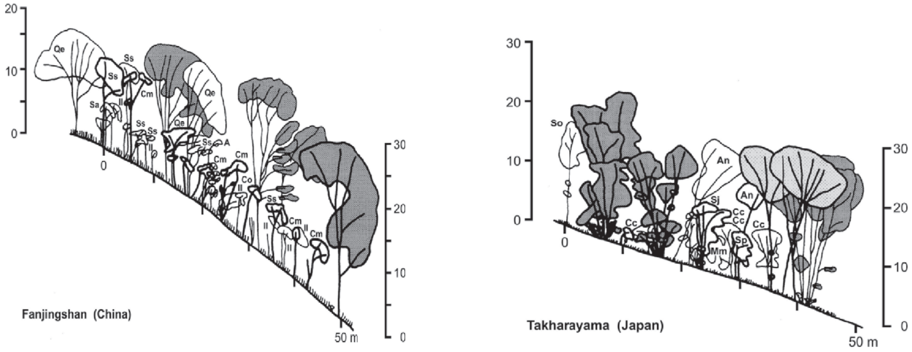
(c) Temperate *Fagus-Acer* mixed forest with *Fagus grandifolia* at Warren Woods, Michigan 180 m a.s.l.). Shaded: *Fagus*, A: *Acer saccharum: Prunus grayana* (after PETERS 1997).

(d) Mixed *Fagus*-broadleaf tree forest with *Fagus orientalis, Quercus hartwegiana* and *Carpinus betulus* in NW Turkey at the transition from humid (beech-dominated) to semi-humid climate (after MAYER & AKSOY 1986).

nance on the widespread soils with lower base richness where these potential competitors of *F. sylvatica* do not grow. That high browsing pressure is a main cause of the existence of pure *Fagus* or *Nothofagus* forests around the world, is unlikely given that monodominant forests occur on all five continents with temperate climate, where the ungulate faunas and browsing intensities are largely different. Moreover, pure stands of *Fagus* species also are present in remote forest regions (e.g. in the Carpathians of eastern Europe or the southern Andes) where large predators such as brown bear, wolf, lynx or mountain lion are still present which may keep ungulate populations in check.

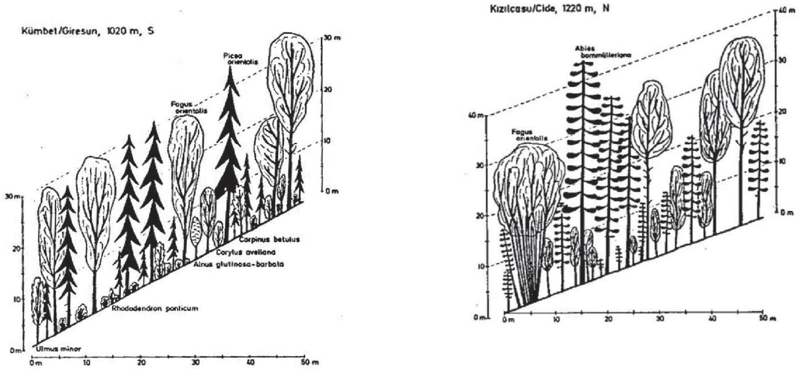
Similar to *Fagus*, most of the deciduous or evergreen *Nothofagus* species of South America, Australia and New Zealand are known to form nearly monospecific stands in certain areas

Fig. 4 (continued)



(e) Montane mixed forest of *Fagus lucida* with various broadleaved deciduous tree species in subtropical southeastern China (Fanjng Shan, 1800 m a.s.l.). Shaded: *Fagus lucida*. A: *Acer* sp., Cm: *Cyclobalanopsis multinervis*, Co: *Cyclobalanopsis oxyodon*, Il: *Illicium lanceolatum*, Qe: *Quercus engleriana*, Sa: *Syplocos anomala*, Ss: *Schima sinensis* (after PETERS 1997).

(f) Temperate mixed *Fagus crenata – Fagus japonica* forest in Takaharayama, central Japan (900 m a.s.l.). Light shaded: *Fagus crenata*, dark shaded: *Fagus japonica*. An: *Acer nikoense*, Cc: *Carpinus cordata*, Mm: *Meliosma myriantha*, Sj: *Sapium japonicum*, So: *Styrax obassia*, Sp: *Stewartia pseudo-cammellia* (after PETERS 1997).



(g) Mixed *Fagus orientalis*-conifer forest at montane elevation (1020 m a.s.l.) in northern Turkey. At the upper limit of *Fagus* dominance in the Pontic Mountains, *Fagus* mixes often with *Abies bornmuelleriana* and *Picea orientalis*. Dense layers of *Rhododendron ponticum* are frequently present. After MAYER & AKSOY 1986.

(h) Mixed *Fagus orientalis-Abies bornmuelleriana* forest at montane elevation (1220 m) in northern Turkey. After MAYER & AKSOY (1986).

of their distribution range. Monospecific stands of great extension are formed in particular by the deciduous species *N. pumilio* in southern Patagonia and the evergreen *N. menziesii* in the montane belt on the western slopes of New Zealand's Southern Alps (OGDEN et al. 1996, VEBLEN et al. 1996). Remarkably, pure stands are also characteristic for the rare *Nothofagus* species *N. alessandri* and *A. glauca* in southern-central Chile which only exist in several small but mostly monospecific stands (DONOSO 1996). An exception seems to be *F. grandifolia*, which in most cases does not form larger monospecific stands in eastern North America, but generally mixes with other deciduous (in the north; *Acer*, *Fraxinus, Liriodendron* etc.) or evergreen trees (in the south; *Magnolia, Quercus, Liquidambar* etc.) (BRAUN 1950, CAIN

Table 4: Major forest types in North America, western Eurasia and East Asia with contribution of *Fagus* species (according to PETERS 1997, MAYER & AKSOY 1986, ELLENBERG & LEUSCHNER 2010, HORVATH et al. 1974, WANG 1961, MIYAWAKI 1980-1989 and other sources).

North America – lowland/colline/submontane		
Fagus-Acer forest	*Fagus grandifolia./Acer saccharum* (domin.) with *Fraxinus, Liriodendron, Tilia* species	South of Great Lakes
Tsuga-Pinus-northern hardwoods	*Tsuga canad./Pinus strobus/Fagus grandifolia/ Acer saccharum/Tilia americana*	Transition to boreal zone, Minnesota – Atlant. Coast
Fagus-Magnolia forest	*Fagus grandifolia./Liquidambar/ Quercus* species/*Magnolia*	Gulf of Mexico (Florida – Texas)
North America - montane		
Mixed Mesophytic Forest	Fagus *grandifolia/Liriodendron/ Acer saccharum/Tilia* spp./*Aesculus oct.*	Appalachians
Fagus-Quercus cloud forest	*Fagus grandifolia* subsp. *mexicana*/ *Liquidambar*/evergreen *Quercus* species/*Magnolia*	NE Mexico
Western Eurasia – lowland/colline/submontane		
Acidic beech forests	pure *F. sylvatica*	C & West Europe
Base-rich beech forests	*F. sylvatica* (dominant) with *Acer pseudoplatanus/ A. platanoides./Fraxinus excelsior*	C & Southeast Europe
Western Eurasia – montane/subalpine		
Montane beech-fir forests	*F. sylvatica/Abies alba/Picea abies*, often with *Acer pseudoplatananus*	C & Southeast Europe
Montane beech-fir forests	*F. orientalis/Abies nordmanniana-/Abies bornmuelleriana/Picea orientalis*	North Turkey, Caucasus
Montane beech forests	*F. orientalis* (dominant) with *Acer velutinum + pseudoplatanum, Tilia* species etc.	N Iran, Caucasus, North Turkey
East Asia – lowland/colline/submontane		
Beech-fir forests	*Fagus crenata/Abies sachaliensis*	N Japan (Hokkaido)
East Asia – montane/subalpine		
Montane beech forests	*F. crenata* (domin.) with *Acer mono/ Fraxinus sieboldiana, Tilia + Quercus* spp.	NW side of Japan
Montane mixed beech forests	*F. crenata + F. japonica* (dominant) with *Carpinus/Acer/Quercus/Tilia* and conifers	Pacific side of Japan
Montane beech-evergreen broadleaved forests	*F. lucida* or *F. longipetiolata* with many laurel forest species *(Castanopsis* etc.*)*	Mountains in SE China
Montane/subalp. beech-mixed deciduous forests	*F. lucida* or *F. engleriana* or *F. hayatae* with *Quercus/Castanea/Acer/Betula* etc.	Mountains in central and S China
Montane beech forests	pure *F. hayatae*	N Taiwan
Montane beech-maple forests	*F. engleriana* (domin.) with *Acer* species, *Prunus takeshimensis, Tilia insularis*	Ulreung-do Island, Korea

1935, WHITE 1987). High proportions of beech have only been found in certain extrazonal habitats, e.g. damp ravines (MONK 1967). The exact causes of the absence of pure stands in *F. grandifolia* are not fully understood. In the north of its distribution range, *Acer saccharum* is a highly competitive species, but it is not known why *Acer pseudoplatanus, Acer mono* or other European and Japanese *Acer* species do not reach similarly high shares in mixture with beech as is observed for *A. saccharum*.

Not only *F. grandifolia* but most other *Fagus* and *Nothofagus* species are also forming mixed forests with either deciduous or evergreen broad-leaved trees. For the *Fagus* species, this is visible in Table 4 which contains a list of major forest types in North America, western Eurasia and East Asia with contribution of beech. This compilation shows that most *Fagus* species tend to form monospecific or at least species-poor stands in the optimum range of climatic conditions, i.e. climates with sufficient summer moisture and warmth, while they mix with various more drought-tolerant broad-leaved trees towards drier climates, and with conifers towards colder climates (PETERS 1997). In many regions, highest beech dominance is achieved in the lower montane to montane belt of the mountains with sufficient summer moisture but still favourable thermal conditions. The monodominant *F. sylvatica* virgin forests in the Carpathians are a good example of this optimum range of beech occurrence (STANDOVAR & KENDERES 2003).

Table 5: Aboveground live biomass of pure and mixed temperate forests in the northern and southern hemisphere, either with dominance of *Fagus* or *Nothofagus* species or with contribution of these genera. Managed (MAN) or natural (NAT) forests.

Forest type	**Location**	**M/N**	**Mg ha^{-1}**	**Authors**
Pure forests or with high dominance of Fagus/Nothofagus				
Fagus sylvatica	Germany (mean)	MAN	ca. 290	BURSCHEL et al. 1993
Fagus sylvatica	Central Europe, 22 stands	MAN	310 ±59	RADEMACHER et al. 2009
Fagus crenata	Japan, 10 montane stands	NAT	340-435	KAKUBARI 1991
Nothofagus pumilio	Tierra del Fuego	NAT	432, 284, 265	FRANGI & RICHTER[1]
Nothofagus pumilio	Tierra del Fuego	NAT	382	WEBER 1999
Nothofagus truncata	New Zealand	NAT	273, 299, 327	in OGDEN et al 1996
Nothofagus solandri	New Zealand	NAT	273, 285	in OGDEN et al. 1996
Mixed forests with contribution of Fagus				
Mixed *F. grandifolia* forests	Eastern US, 3 old-growth forests	NAT	330, 250, 247	LICHSTEIN et al. 2009
Broad-l. mixed forests	N America, 21 natural forests	NAT	276 ±68	LICHSTEIN et al. 2009
Broad-l. mixed forests	Eastern US, 6 natural forests	NAT	258 ±38	BROWN et al. 1997

[1] in VEBLEN et al. 1996

5. Some functional consequences of mixtures: biomass and productivity in pure and mixed forests

The co-occurrence of monospecific and mixed forests with participation of *Fagus* and *Nothofagus* species in the temperate zones of the world raises the question whether the mixed forests are more productive than the pure forests, as has been postulated by various authors (e.g. MORIN et al. 2011, VILÀ et al. 2007, ZHANG et al. 2012, MORIN et al. 2013). Data on aboveground live biomass of pure and mixed temperate forests with contribution of *Fagus* or *Nothofagus* species are compiled in Table 5. Except for the data from *F. sylvatica*, the values refer to unmanaged natural forests. The figures range between 250 and 430 Mg d.m. ha^{-1} with relatively low values in the north American mixed forests (mostly <280 Mg ha^{-1}) and in the species-poor *N. solandri* forests in New Zealand, and highest values in the pure *N. pumilio* forests of southern South America and the species-poor *F. crenata* forests in Japan. The species-richer forests had rather smaller, than higher, biomasses compared to the pure stands. The productivity data in Table 6 show considerable variation in ANPP (5.2 – 12.5 Mg ha^{-1} yr^{-1}) but do not indicate that species-richer temperate forests, as are present in North America, are more productive than the monospecific *F. sylvatica* and *F. crenata* forests in Europe and Japan.

Table 6: Aboveground net primary productivity of pure (or very species-poor) *Fagus* forests in Japan and Central Europe in comparison to broad-leaved mixed forests with higher tree diversity in eastern North America

Forest type	**Region**	**ANPP (Mg ha^{-1} yr^{-1})**	**Source**
Fagus crenata forests	Japan (montane), 4 stand	5.2 – 8.1	KAKUBARI 1977, 1991
Fagus sylvatica forests	C Europe (lowland-montane), ca. 10 stands	7.7 – 12.5	ELLENBERG & LEUSCHNER 2010
Temperate deciduous hardwoods	N America & Europe (mean)	8.8 ± 3.0	REICH & BOLSTAD 2001

6. Conclusions

Competitive superiority over most of the co-occurring tree species seems to be a characteristic of *Fagus* and *Nothofagus* species which, in many mixed stands, may eventually lead to dominance. Among the traits underlying the competitive strength of *Fagus* species are a high shade tolerance of seedlings, immature and even adult trees, the generation of deep below-canopy shade, and a high morphological and physiological plasticity. The phenomenon of *Fagus* or *Nothofagus* dominance seems not be related to the influence of forest management or unnaturally high browsing pressure, but mainly a consequence of species- or genus-specific traits. To prevent the beeches from becoming dominant, the presence of species with similar shade tolerance and shading capability as in *Fagus* seems to be necessary; an example *is Acer saccharum* in eastern North America. Beech reaches dominance probably easier in species-poor tree floras as in Europe, but *Fagus* can also dominate at places where a rich tree flora is present as in China or Japan. In the temperate *Nothofagus* species, the factors leading to dominance may differ in part from those for *Fagus* because many southern beeches are more light-demanding than the *Fagus* species (VEBLEN et al. 1996).

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Author address:

Prof. Dr. Christoph Leuschner, Albrecht-v.-Haller-Institut für Pflanzenwissenschaften, Abt. f. Ökologie und Ökosystemforschung, Untere Karspüle 2, D-37073 Göttingen

E-Mail: cleusch@gwdg.de

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