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Structure and dynamics of a mature tree stand in submontane alluvial forest of *Carici ramotae-Fraxinetum* in the Sudety Mts foothills (Lower Silesia, Poland)

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Abstract: The structure and dynamics of a submontane alluvial forest, with structural attributes of old-growth, in the Sudety Mts, Central Europe were examined. Stand structure was measured in circular sampling plots, and the distribution of gaps in belt transects. Past dynamic was reconstructed on the basis of analysis of events of release from suppression by inspection of growth pattern. The age distribution of canopy trees was also surveyed. The stand was dominated by ashes (*Fraxinus excelsior*) aged 77–151 years, which created the upper layer, whereas the lower layer was dominated by dense hazel (*Corylus avellana*) shrubs. The analysed stand was developed in site which was used as a grassland in first quarter of XIX century, but its history include several fine-scale disturbances when canopy trees were established. Recent dynamic was related to low intensity gap formation. The light conditions at the forest floor were good, and the average percentage of PPFD was 13%. Seedlings of ash and sycamore (*Acer pseudoplatanus*) were abundant throughout the stand. However, continuous browsing by game prevented growth of seedlings; in the sapling layer sycamore had disappeared and the number of ash saplings was strongly reduced. Regeneration was dominated by hazel of vegetative origin both in gaps and under the canopy.

Additional key words: Acer pseudoplatanus, browsing, canopy gaps, Corylus avellana, dendroecology, Fraxinus excelsior, forest dynamics, natural regeneration

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Introduction

Alluvial forests of temperate Europe are communities rich in plant and animal species, with high structural diversity, and also have an important function in carbon gain and protection of water resources. For these reasons high priority is given to these habitats for nature conservation as well as environmental protection. However, floodplains along rivers have been severely altered through the centuries, and many have lost their riparian forest (Brinson and Verhoeven 1999; Klimo and Hager 2001). Today, conservation and restoration of remnants of these forests are among the main focuses of European forestry (Anonymous 2006, Armbuster et al. 2006), requiring knowledge about the natural processes and structures of this communities.

The ecology of the alluvial forests in valleys of large rivers, where periodic floods are the major driving factor of ecological processes, has been intensively studied and is quite well understood (e.g. Carbiener and Schnitzer 1990, Trémolières et al. 1998, Armbuster 2006). Knowledge about the ecology of other types of riparian forest in Europe is relatively scarce, mostly due to the small number of areas left to spontaneous development where natural processes can be observed (Pawlaczyk 2004, Janik et al. 2008).

In the submontane and lower mountain zones of the eastern part of Central Europe alluvial forests are represented by ash-alder woods *Carici remotae-Fraxinetum* Koch 1926 (Neuhäuslova and Káňa 1999, Matuszkiewicz 2008). In the European system "Natura 2000", these forests are considered as a priority habitat requiring special attention. The most informative data about their ecology come from long-term observations performed in strict reserves (Kenders et al. 2008). Unfortunately similar data on submontane ash-alder woods are not available (Pawlaczyk 2004). In such situations the results of recent observations of forest structure could by supported by reconstructive studies (Foster et al. 1996).

The aims of this study were to examine the structure and recent dynamics of a mature stand with old-growth attributes, representing a priority European habitat, and to reconstruct its past dynamics using a dendroecological approach.

Materials and methods

Study site

The study was performed in the Kaczawy Mts (Sudety massif, Lower Silesia, Poland) in the southern part of the "Buki Sudeckie" reserve (50°56'25"N, 16°01'13" E), which is managed by the administration of the State Forest, Jawor District. The average altitude of this area is 420–440 m asl. The average annual temperature is 7.0°C (July 16.1°C, January –2.6°C); average annual precipitation is 801 mm, with a maximum in July–August; the average length of growing season is 200–220 days.

The mature stand (around 15 ha) was located in the lower part of a gentle slope, in the fork of two streams (Fig. 1). The site was additionally wetted by small springs that form a sloping wetland. The land relief meant that the site was not flooded, but the soil was saturated. According to the Braun Blanquet approach the plant community was classified as *Carici remotae-Fraxinetum* (Koch 1926) ash-alder wood of springs and rivers (Berdowski 2000). Dominant forest floor species in the summer were *Senecio fuchsii*



Fig. 1. Distribution of sampling plots and stripe transects in the studied site

and *Stachys sylvatica* (Berdowski 2000). The habitat was classified as sub-type 44.31 of priority habitat alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Natura 2000 code 91E0). The investigated stand bordered on a beech forest (*Dentario enneaphyllidis-Fagetum* Oberd. 1953), an artificial spruce plantation and arable land.

The detailed history of the management of the stand before 1950 was unknown, due to historical and political changes in this area. In the middle of eighteen century (map from 1748) the study site had been a part of large forest complex, however map from 1824 revealed that the study site was converted into meadows or pastures (Fig. 1). Subsequent maps (since 1888) again have shown this site as forested areas. In this patch, after II WW only limited, compulsory felling had been performed, most recently between 1988 to 1993, when around 6 m³ of timber was removed per hectare (administration of State Forest, Jawor District – personal communication). The site has been a non-intervention forest reserve since 1993.

Nowadays, across the whole Jawor district (146.4 km²) the density of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) is high: 26 red deer/1000 ha and 178 roe deer/1000 ha (Wrocław Regional Directorate of State Forests – personal communication, data for 2008). There is also a population of mouflon (*Ovis ammon*) at 8.8 individuals/1000 ha, however these most probably do not penetrate the reserve. The density of game in the period before 1945 was much lower (Wrocław Regional Directorate of State Forests – personal communication, lower (Wrocław Regional Directorate of State Forests – personal communication).

Methods

Eight sampling plots were established in the central part of the stand in a 100×100 m grid. Each plot consisted of two circular, concentric sampling areas. In the large plots (500 m²) the diameter at breast

height of all standing trees with a diameter higher than or equal to 7 cm was measured. The number of fallen logs and stumps were recorded, and the percentage cover of forest floor vegetation was visually assessed. The height all living trees was measured in the small, inner plots (250 m²). Three sub-plots were established in each sampling plot, each 25 m², located 5 m in the direction of 0, 120 and 240 degrees from the plot centre. The height of all saplings (individuals taller than 0.5 m and with diameter below 7 cm) was measured in these sub-plots, along with the number of seedlings (individuals shorter than 50 cm), and the number of seedlings and saplings damaged by browsing. The aggregate height of saplings was calculated as an efficient measure both size and density of saplings (Fei et all 2006).

Light was measured at 0.5 m above ground level in the centre of all 500 m² plots and in each sub-plot using hemispherical photographs (32 photographs in total). The photographs were analysed using Win-Scanopy 2003b software by Regent Instruments Inc. The results were expressed as the relative photosynthetic photon flux density under canopies (% PPFD).

Gaps were sampled in three stripe transects (two 20 \times 200 m and one 20 \times 224 m) according to the protocol described by Runkle (1992). The size of gaps was measured according to the Brokaw's (1982) method, assuming a minimal gap size of 15 m². We also assume that all gaps caused by trees logging, what could be indicated by lack of tree trunks and presence of stumps, were created before 1993 (year of reserve establishing). The gaps caused by trees uprooting or breaking, where trees trunk was presented, were established since 1993. The state of the vegetation inside gaps was described, we also measured the diameter of fallen trees in the vicinity of sampling areas.

Among ashes (Fraxinus excelsior) growing on sampling plots individuals representing whole range of diameter size were chosen. They were cored at 1.3 m above the ground for age determination and radial growth analysis. If ashes in desired diameter class were absent on sampling plots we would take individuals nearest to sampling plots. The cores were obtained from 27 trees with a diameter between 11 and 77.5 cm; one core was taken per tree. The cores were dried, mounted, and sanded, then they were scanned and tree rings were measured using CooRecorder and CdDendro software with an accuracy of almost 0.01 mm. The age of trees was estimated on the basis of the number of tree ring plus 10 years (the time necessary to reach 1.3 cm of height, according to observations of growth of unbrowsed saplings). Cores were examined for periods of suppression and release according to boundary - line release criteria proposed by Black and Abrams (2003). The percentage of trees released from suppression was grouped in decades and considered as evidence of past disturbance (Lorimer 1985, Black and Abrams 2003). Consideration of 10-years moving average ring width value excluded the first and last 10 years of the dendrochronologies from computation of percentages, which thus spanned the period from the 1880s to the 1990s.

Field measurements and tree cores were taken in 2006 and 2007.

Results

Study plots description

The forest floor vegetation covered on average of 46% of the studied plots, varying between 15 to 80%. Stumps of cut trees were present on almost all sampling plots. The mean density of stumps was 37 N/ha, varying from 0 to 60 N/ha. Fallen logs were counted on three plots, which gave average density of 15 N/ha.

The average percentage of PPFD at the level of the forest floor vegetation was 13% (standard deviation S.D. 3.4%). We found a statistically significant correlation between the cover of forest floor vegetation in summer and light conditions (r = 0.86, p = 0.006).

Stand structure

The average density of living trees was 492 N/ha (S.D. 153); the average stand volume 526 m³/ha (S.D. 141); the mean sum of basal area was 39.4 (S.D. 8.4 m²/ha). The diameter distribution of living trees had the form of a rotated sigmoid (Fig. 2).

The mixed stand was dominated by ash (*Fraxinus* excelsior), which accounted for more than half of its volume (Table 1). Sycamore (*Acer pseudoplatanus*) comprised nearly one third of stand volume. These two tree species were found in each plot, along with hazel (*Corylus avellana*). Other species present included lime (*Tilia platyphyllos*), oak (*Quercus robur*), beech (*Fagus sylvatica*), aspen (*Populus tremuloides*) and wych elm (*Ulmus glabra*) (Table 1). Three to six species were found per plot.



Fig. 2. Diameter distribution of all trees

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Characteristics	Species												Course
	FE	AP	QR	FS	TP	CA	PT	UG	App	SA	СМ	DM	- Sum
stem volume [m³/ha]	305.9	139.7	27.1	16.7	27.6	4.3	4.1	0.5	0	0	0	0	525.9
%	58.2	26.6	5.2	3.2	5.3	0.8	0.8	0.1	0	0	0	0	100
basal area [m²/ha]	22.84	11.19	2.03	1.18	0.95	0.82	0.29	0.06	0	0	0	0	39.37
%	58.0	28.4	5.2	3.0	2.4	2.1	0.7	0.2	0	0	0	0	100
stem density [N/ha]	165	90	20	12.5	35	165	2	3	0	0	0	0	492.5
%	33.5	18.3	4.1	2.5	7.1	33.5	0.5	0.5	0	0	0	0	100
sum of height of saplings [m/ha]	480.8	0	0	168.3	125	2584.9	0	32.5	0	0	222.7	20	3634.3
%	13.2	0	0	4.6	3.4	71.1	0	0.9	0	0	6.1	0.6	100
saplings density [N/ha]	1283	0	0	83	17	1917	0	100	0	0	133	17	3549.9
%	36.2	0	0	2.3	0.5	54.0	0	2.8	0	0	0.04	0	100
seedlings density [N/ha]	23433	10666	133	316	16	266	0	800	233	33	266	0	36166.5
%	64.8	29.5	0.4	0.9	0	0.7	0	2.2	0.6	0.1	0.7	0	100

Table 1. The stand structure by species. Species codes: FE – Fraxinus excelsior, AP – Acer pseudoplatanus, QR – Quercus robur, FS – Fagus sylvatica, TP – Tilia platyphyllos, CA – Corylus avellana, PT – Populus tremula, UG – Ulmus glabra, App – Acer platanoides, SA – Sorbus aucuparia, CM – Crataegus monogyna, DM – Daphne meserum

Ashes were absent from the 22–27 cm diameter class. There was also a lack of small diameter sycamores (Fig. 3), whereas limes were usually in the lower classes of diameter; hazels (not shown) were the most numerous species in the lowest diameter distribution class.

The upper tree layer consisted predominantly of ash (maximum height 38 m) and sycamore (maximum height 39 m). The lower layer consisted mainly of hazel, with a small admixture of lime and ash. The majority of the volume was associated with trees from the upper layer (trees taller than 25 m), whereas the volume of the lower layer, was almost negligible (Fig. 4).

The age of ashes varied from 77 to 151 years. In some cases, trees of similar ages differed in diameter by more than 30 cm (Fig. 5). The observed releases from suppression were mainly major and not syn-



Fig. 3. Diameter distribution of *Tilia platyphyllos* (TP), Acer pseudoplatanus (AP) and Fraxinus excelsior (FE)



Fig. 4. Height structure of the tree stand and volume distribution among height classes

Fig. 5. Age and diameter distribution of cored Fraxinus excelsior

Fig. 6. The percentage of trees established every year (black bars) and the percentage of trees with release events in decades (grey bars). The upper panel shows the number of sampled cores

chronous; less than 25% of trees per decade showed evidence of past major disturbances (Fig. 6).

The density of dead, standing trees varied from 0 to 140 N/ha. These were usually relatively small hazels, and thus their contribution to volume was negligible. The density of large (above 50 cm in diameter) dead, standing trees was 5 N/ha, consisting of ashes and sycamores.

The diameter of fallen trees varied from 29 to 58 cm (average 42 cm); these were exclusively ashes. They were broken (58%) or uprooted (42%) due to wind damage.

Regeneration

Seedlings were found in all plots with an average density of 36 167 N/ha (S.D. 29 227 N/ha). The average participation of one-year seedlings at each sampling point was 1.9 % with a maximum of 11.8 %. The most abundant were seedlings of ash, then sycamore and wych elm. The participation of seedlings of beech, hazel, hawthorn (*Crataegus monogyna*), maple (*Acer platanoides*), oak, rowan (*Sorbus aucuparia*) and lime was below 1% each, giving a total of 3.5%. All lime seedlings were one year old; in the case of oaks the participation of one-year seedlings was 12.5%, in maple 5%, and in ash 0.5%. Seedlings of other species were older than one year.

The percentages of browsed seedlings were: wych elm (75%), ash (15%), beech (12%), sycamore (6%), and hawthorn (6%). In the case of sycamores and ashes, browsing was strongly related to seedling height: individuals smaller than 15–20 cm were virtually unbrowsed, whereas all taller individuals were injured.

There were no statistically significant correlations between seedling density and light conditions.

Saplings were present on 83% of all (24) sub-plots, but they were mainly hazel saplings. Saplings of other

Fig. 7. Distribution of gap size (white bars) and cumulative gap areas in each size class (grey bars)

tree species (ash, beech, lime and elm) occurred in only two sampling areas on 6 sub-plots, comprising 25% of all sub-plots; the lack of sycamore saplings should be noted. The average sapling density was 3550 N/ha, the average aggregate height was 3634 m/ha. Hazel saplings clearly dominated, both in aggregate height and density.

The impact of browsing was especially high in the case of ash and wytch elm –84% and 83% of their living saplings were browsed, respectively. Beech saplings (60%) were also browsed. No browsing was evident in the other species.

Gap structure

We found 21 gaps in the transects. The area covered by gaps was 10.5%, and the area of individual gaps varied from 15 to 153 m². Small gaps, up to 30 m², were the most frequent, however the largest area was covered by large gaps (Fig. 7). The number of gaps created spontaneously during the last 13 years amounted to 38% of the total; in three other cases (14%) the gaps were created initially by tree cutting, and were extended as a result of windfall. The total area of gaps created exclusively by wind activity and natural tree death was 502 m², whereas the sizes of gaps created by previous forest management was 614 m². The area of gaps created spontaneously over the last 13 years was 3.9% of the investigated area, and the rate of gap creation was 0.3% per year. The median sizes of natural and man-made gaps were 57 and 46 m², respectively, with no significant difference between them (Mann-Whitney U test, U=39.00, p=0.929). In most cases (95%) gaps were filled by hazel, and in one case ash saplings were present.

Discussion

The volume of the analysed stand was relatively high: it was equivalent to the volume of a primeval ash-alder stand in Białowieża Forest, which was calculated as 500 m³ (Faliński and Pawlaczyk 1995). A higher stand volume was found in near-natural floodplain forest Fraxino pannonicae-Ulmetum (Janik et al. 2008) where volume fluctuated over time from 591 to 547 m³/ha with a tree density of 186-203N/ha. In the latter forest the high stand volume was related to the presence of old, large oaks which had been promoted by past management and contemporary they are disappearing from stand (Janik et al. 2008). The basal area was higher than that in alluvial forests dominated by ash (community Querco-Ulmetum minoris) in a flooded part of the Rhine valley, where the sum of the basal area was $32.3 \text{ m}^2/\text{ha}$ with a tree density of 734.9 N/ha (Trémolières et al. 1998). The high stand volume in this study was the result of site productivity: ashes and sycamores reached almost the maximal height for these species, however the diameter of ashes was not as large (Marigo et al. 2000, Jaworski 2004). The density of large living trees with a diameter above 70 cm in the study site was lower (7 per hectare) than in an ash, alder and spruce mixed forest in Białowieża, a primeval forest with a density of 18 large trees per hectare (Nilsson et al. 2003). The smaller number of large ashes in this study was related to their recent natural mortality: the heartwood of practically all ashes with a diameter above 70 cm was decayed, and many of them had broken branches or hollows. According to Faliński (1986) ashes aged 250-400 years are not rare and individual trees may live longer than 400 years in the Białowieża primeval forest. On the other hand Emborg et al. (2000) stated that in the Suserup Skov forest reserve in Denmark ash typically degenerates at age 130 years and only a few individuals grow larger than 80 cm in diameter.

In XIX century, ash and sycamore were not considered as valuable for forest management in Silesia (Nyrek 1992, Wilczkiewicz 1992), thus we assumed that the stand has developed as a result of spontaneous succession in abandoned grassland. As could be revealed from the age analysis the oldest tree was established in 1856, however there are not any data about vegetation structure from the period of 32 years, between 1824, when study site remained a grassland and the year of the establishment of the oldest trees. Thus, we do not know if there were any other pioneer trees established before observed stand. Age of trees revealed that the current stand does not consist of only one cohort established immediately after abandonment of the grassland. It was stated that the establishment of trees lasted through 75 years. Such age differentiation is much greater than that observed in an ash-sycamore stand which had developed after large clear-cutting of beech forest (Holeksa and Paruel 1992). Possible explanations of such extension can be related to factors, which could

locally hamper the succession (eg. competition of grassland vegetation) or/and to some disturbances (eg. browsing by cattle, wild boar activities, cutting down of trees). Another possible explanation of reconstructed stand dynamics is an earlier colonization by light demanding pioneer tress (e.g. alder), overgrown later on by the ashes or/and cut down gradually by human. Such activity generated gaps in canopy, which is reflected in observed frequency of trees revealed growth release events. In fact, the frequency and spatial extension of past disturbances in canopy layer and subsequent tree recruitment reveals pattern similar to typical gap-phase stand dynamic. According to the authors knowledge, there have not been any long-term studies performed in similar site conditions, which could give credence for some of mentioned above explanations.

Our results concerning age-diameter relationships confirm that retrieving the age structure from diameter distribution could lead to serious misinterpretation, also the diameter distribution could not be unambiguous indicator of past stand dynamics. For example rotated sigmoid diameter distribution, like observed in this study, could be attributed both for even-aged forest (Sakio 1997) developed after large-scale disturbance, as well as for balanced multi-cohort old growth stand (Rubin et al. 2006, Westphal et al. 2006) with fine-scale disturbances driven by gap dynamics.

Recently (since 1993), stand dynamics have been related to the death of single trees. The density of dead standing trees larger than 50 cm in diameter was 14 per hectare in ash, alder and spruce mixed forest in Białowieża primeval forest (Nilsson et al. 2003) whereas in this study there were only 5 such trees per hectare. This was relatively high, given that the dead trees have accumulated over only 14 years. Trees were also felled or broken by the wind, which often resulted in creation of gaps in the canopy layer. The distribution of gap sizes generally correspond with the typical course where small-sized gaps are more frequent than large-sized gaps (Yamamoto 2000). An exception was the group of largest gaps, which were more numerous than mid-sized gaps, although two of the three largest gaps were the aftermath of previous forest management. Generally, the gap percentage and gap size were in the lower part of the range found in different natural temperate forests, according to the data presented by Yamamoto (2000) and Kenderes et al. (2008). Other studies showed a high density of trees uprooted on wet, unstable ground in an Carici remotae-Fraxinetum stand (Faliński and Falińska 1965), the uprooting was correlated with the dynamics of spring (Pawlaczyk 2004); unfortunately these result were not quantified. In this study the rate of gap creation was rather small, comparable to those observed in stable beech forests (Kenderes et al. 2008).

Gaps were predominantly filled by hazel, as a result of rapid spread of hazel sprouts that were growing at gap peripheries. The long offshoots with large leaves filled gaps and efficiently impeded establishment of other tree species by shading young individuals. The phenomenon of filling entire gaps by hazel was reported by Bobiec (2002) in an oak-lime-hornbeam forest in the Białowieża primaeval forest. Similar rapid overgrowth of gap by sprouts of wytch elm was observed in a deciduous forest in Denmark (Emborg et al. 2000); however in the long term such elms could be topped by beech (Emborg et al. 2000). In the analysed stand beech was the most shade-tolerant species, but in riparian forest it occurred sporadically in admixtures, because of its very low tolerance to soil inundation (Glenz et al. 2006). Thus it is unrealistic to predict similar overgrowth by beech as a major process of further stand dynamics.

In spite of the unavailability of gaps for natural regeneration of canopy tree the density of ash and sycamore seedlings were relatively high. The average seedling density corresponded to the density of seedlings and saplings (individuals <1.5 m in height) in a flooded hardwood floodplain forest of the upper Rhine (Deiller et al. 2003), and was almost two times higher than seedling density under the canopy of mature maple-ash forest (Holeksa and Parusel 1992). This was the result of favourable light conditions under canopies in study site. Data presented by Emborg (1998) showed that a PPFD around of 10-12% (the most common value in the analysed stand) occurred only in the degradation or innovation phase in mixed beech-ash forest, whereas in other phases the PPFD was much lower. Other studies confirm low light attenuation by the canopy of ash trees; in pure ash forest the light level at the forest floor was 15–20%, and in mixed ash-alder alluvial forest it was 10-15% (Faliński and Pawlaczyk, 1995). Seedlings of ashes and maples are moderately shade tolerant (Jaworski 2004, Janse-Ten Klooster 2007, Petritan et al. 2007) and therefore were distributed across the study site without obvious relation to the light intensity. According to the model proposed by Petritan et al. (2007), the mortality ratio of ash and sycamore saplings is small in light conditions similar to those in our (lower than 13% for ashes and 8% for sycamores). However, it is known that ash and sycamore are among the most commonly browsed species (Faliński and Pawlaczyk 1995; Modry et al. 2004) and it has been reported that continuous browsing could permanently prevent ash and sycamore regeneration (Faliński and Pawlaczyk 1995; Boratyński and Filipiak 1999). Monitoring of natural regeneration in elm-ash floodplain forest in the Czech Republic (Čermák and Mrkva 2006) revealed that browsing was the primary cause of the reduction in number and average height of natural regeneration. The reduction of density of natural regeneration was 45% for ash and 84% for sycamore over a four-year period (Čermák and Mrkva 2006). Seedlings mortality was high in the analysed stand due to strong pressure from ungulates; sycamore saplings were absent, the number of ash saplings was dramatically reduced and recruitment was dominated by hazel, mainly of vegetative origin.

Conclusions

- 1. The stand with attributes of structural old-growth was developed on previously agricultural areas, however no more than 180 year after agriculture abandonment, any evidence of previous land use were not visible during field work, thus without analysis of historical maps such origin was undetectable.
- The age structure was diverse, but the relationship between trees diameter and age was weak: trees in almost the same diameter class could differ about 40 years in age. Such differentiation without age analysis was also undetectable.
- 3. Recent stand dynamics was gap driven, however the size of gaps was rather small, also frequency of gaps creation was low, it is quite surprising because it could be expected that on moist soil the level of trees uprooting could be high.
- 4. The basic factor altering recent stand regeneration is browsing by game: it eliminates sycamore and strongly diminish ash regeneration.

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References

- Anonymus 2006. European forest types Categories and types for sustainable forest management reporting and policy. European Environment Agency. Technical report No 9.
- Armbruster J., Muley-Fritze A., Pfarr U., Rhodius R., Siepmann-Schinker D., Sittler B., Späth V., Trémolières M., Rennenberg H., Kreuzwieser J. 2006. FOWARA Forested Water Retention Areas. Guideline for decision makers, forest managers and land owners. The FOWARA-project;

Chair of Tree Physiology, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

- Berdowski W. 2000. Rezerwat przyrody "Buki Sudeckie" w Górach Kaczawskich oraz jego walory botaniczne. Przyroda Sudetów Zachodnich 3: 3–10.
- Black B.A., Abrams M.D. 2003. Use of boundary line growth patterns as a basis for dendroecological release criteria. Ecological Applications 13: 1733–1749.
- Bobiec A. 2002. Living stands and dead wood in the Białowieża forest: suggestions for restoration management. Forest Ecology and Management. 165: 125–140.
- Boratyński A., Filipiak M. 1999. Zarys ekologii jawora. In: Bugała W. (ed.) Klony Acer campestre L., A. platanoides, A. pseudoplatanus L. Bogucki Wydawnictwo Naukowe, Poznań, pp. 275–327.
- Brinson M.M., Verhoeven J. 1999. Riparian forests. In: Maintaining biodiversity in forest ecosystems. Hunter M.L. (ed.). Cambridge University Press, Cambridge, pp. 255–299.
- Brokaw N.V.L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14: 158–160.
- Carbiener R., Schnitzler A. 1990. Evolution of major pattern models and processes of alluvial forest of the Rhine in the rift valley (France/Germany). Vegetatio 88: 115–129.
- Čermák P., Mrkva R. 2006. Effects of game on the condition and development of natural regeneration in the Vrapač National Nature Reserve (Litovelské Pomoraví). Journal of Forest Science 52: 329–336.
- Deiller A.F., Walter J.M.N., Trémolières M. 2003. Regeneration strategies in a temperate hardwood floodplain forest of the Upper Rhiene: sexual versus vegetative reproduction of woody species. Forest Ecology and Management 180: 215–225.
- Emborg J. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 106: 83–95.
- Emborg J., Christensen M., Heilmann-Clausen J. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 126: 173–189.
- Faliński J.B. 1986. Vegetation dynamics in temperate lowland primeval forest. Kulver, Dordrecht.
- Faliński J.B., Falińska K. 1965. Szata roślinna rezerwatu krajobrazowego "Źródła rzeki Wałszy" (Wzniesienia Górowskie). Materiały Zakładu Fitosocjologii Stosowanej Uniwersytetu Warszawskiego 7: 1–83.

- Faliński J.B., Pawlaczyk P. 1995. Zarys Ekologii. In: Jesion wyniosły (*Fraxinus excelsior*). Bugała W. (ed.). Sorus, Poznań–Kórnik, pp. 217–305.
- Fei S.L., Gould P.J., Steiner K.C., Finley J.C. 2006. Aggregate height – A composite measure of stand density for tree seedling populations. Forest Ecology and Management 1–3: 336–341.
- Foster D.R., Orwig D.A., McLachlan J.S. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trees 11: 419–424.
- Glenz C., Schlaepfer R., Iorgulescu I., Kienast F. 2006. Flooding tolerance of Central European tree and shrub species. Forest Ecology and Management 235: 1–13.
- Holeksa J., Parusel J. B. 1992. Struktura lasu jaworowo-jesionowego w reglu dolnym na północnym stoku Wielkiej Czantorii (Beskid Śląski). Parki Narodowe i Rezerwaty Przyrody 11: 17–27.
- Janik D., Adam D., Vrska T., Hort L., Unar P., Kral K., Samonil P., Horal D. 2008. Tree layer dynamics of the Cahov-Soutok near-natural floodplain forest after 33 years (1973–2006). European Journal of Forest Research 127: 337–345.
- Jaworski A. 2004. Podstawy przyrostowe i ekologiczne odnawiania oraz pielęgnacji drzewostanów. PWRiL, Warszawa.
- Janse-ten Klooster S.H., Thomas E.J.P., Sterck F.J. 2007. Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. Journal of Ecology 95: 1250–1260.
- Kenderes K., Mihók B., Standovár T. 2008. Thirty years of gap dynamics in a central European beech forest reserve. Forestry 81: 111–123.
- Klimo E., Hager H. 2001. The Floodplain Forests in Europe. Brill Academic Publishers.
- Lorimer C.G. 1985. Methodological considerations in the analysis of forest disturbance history. Canadian Journal of Forest Research 15: 200–213.
- Matuszkiewicz J.M. 2008. Zespoły leśne Polski. PWN, Warszawa.
- Marigo G., Peltier J-P., Girel J., Pautou G.. 2000. Success in the demographic expansion of *Fraxinus excelsior* L. Trees 15: 1–13.
- Modry M., Hubeny D., Rejsek K. 2004. Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. Forest Ecology and Management 188: 185–195.
- Neuhäuslova Z., Káňa K. 1999. Mokřadní a pobřežní křoviny a lesy. In: Míchal I., Petřiček V. (eds) Peče o chránená území II. Lesní společenstva. Praha, pp. 279–321.
- Nilsson S.G., Niklasson M., Hedin J., Aronsson G., Gutowski J.M., Linder P., Ljungberg H., Mikusiński G., Ranius T. 2003. Erratum to: "Densities of large living and dead trees in old-growth tem-

perate and boreal forests". Forest Ecology and Management 178: 355–370.

- Nyrek A. 1992. Kultura użytkowania gruntów uprawnych, lasów i wód na Śląsku od XV do XX wieku. Acta Universitas Wratislaviensis, Historia 97, Wrocław.
- Pawlaczyk P. 2004. Podgórski łęg jesionowy. In: Poradniki ochrony siedlisk i gatunków Natura 2000 podręcznik metodyczny. Herbich J (ed.) Lasy i bory. Vol. 5. Ministerstwo Środowiska ul. Wawelska 52/54, 00-922 Warszawa, pp. 227–232.
- Petritan A.M., Lüpke B. von, Petritan I.C. 2007. Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. Forestry 80: 397–412.
- Rubin B.D., Manion P.D., Faber-Langendoen D. 2006. Diameter distributions and structural sustainability in forests. Forest Ecology and Management 222: 427–438.

- Runkle J.R. 1992. Guidelines and sample protocol for sampling forest gaps. General Technical Report PNW-GTR-283. Portland.
- Sakio H. 1997. Effects of natural disturbance on the regeneration of riparian forests in a Chichibu Mountains, central Japan. Plant Ecology 132: 181–195.
- Trémolières M., Sánchez-Pérez J.M., Schnitzler A., Schmitt D. 1998. Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest. Plant Ecology 135: 59–78.
- Westphal C., Tremer N., Oheimb G. von, Hansen J., Gadow K., Härdtle W. 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? Forest Ecology and Management 223: 75–83.
- Wilczkiewicz M. 1992. Rys historyczny gospodarki w lasach sudeckich. Sylwan 136 (6): 49–53.
- Yamamoto S.-I. 2000. Forest gap dynamic and tree regeneration. Journal of Forest Research 5: 223–229.