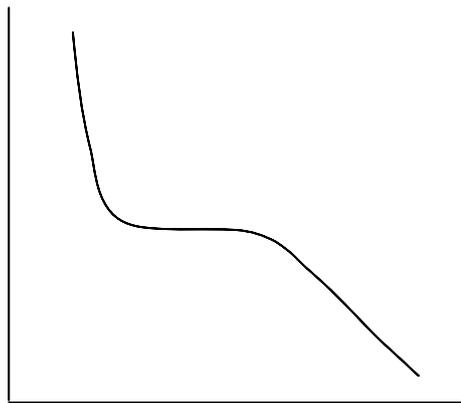




Age structure and diameter distribution in a southern Swedish beech dominated landscape



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Abstract

Tree ages and tree diameters were investigated in an 800 ha south Swedish beech dominated landscape with old-growth associated conservational values. Ca. 1200 trees from 53 sites with beech present were used in the analysis. At landscape level, the tree diameter distribution revealed a rotated sigmoid pattern without logarithmic transformation, well in accordance with existing models of size structure and suggesting that the forest is under a small-scale disturbance regime. The age distribution at the landscape scale was irregular with prominent peaks and absent recruitment periods, suggesting occurrence of disturbances. The analysis of age over diameter showed that there was a low age-diameter correlation. Age distribution revealed existence of three cohorts that originated in the periods 1720-1760, 1850-1900 and 1930-1950 between which low recruitment of regeneration occurred. Forest utilisation is suggested to be a major reason for the irregular age structure and the different cohorts' history.

Introduction

One of the commonly used and well-studied variables in forest ecological studies is the frequency distribution of diameter classes (Zhang 2001; Goodburn & Lorimer 1999; Goff & West 1975; Leak 2002). This variable is relatively easy to measure in field, analyse and model. The diameter structure of trees is often used as a proxy of age, based on the assumption that young trees are small and old trees are large. A diameter distribution has become an important attribute for the management and conservation of biodiversity in forests (McElhinny et al. 2005). One of the most widespread axioms in forest ecology is the inverse-J shaped diameter distribution of natural forests that is usually translated into an all aged age structure even in cases when the curves are irregular or have prominent peaks (Leak 1996; Lorimer 1980; Oliver & Larson 1990; White & Pickett 1985). The concept behind the inverse-J model is that a dynamic association of many small stands, or 'patches' (gap dynamics, shifting-mosaic) of different age and structure created by small annual disturbances produces an all aged forest with a constant decrease in number of individuals in age classes (Bobiec et al. 2000; Emborg et al. 2000; Zhang 2001). The inverse J-shape has been shown to hold also for large forest tracts of forest not necessarily virgin as simple compilation of stands of different age or species (Goff & West 1975). At smaller scale of a stand where canopy recruitment process of gap-filling is more pronounced, Goff and West (1975) found a logarithmic rotated sigmoid diameter distribution reflecting dynamic interactions between canopy and under-story and suggested this as an ecologically more reasonable model for uneven-aged stands. The rotated sigmoid diameter distribution often found in natural forests is characteristic for its more or less pronounced horizontal trend at the mid-section of an inverse-J curve (Goff & West 1975; Lorimer 1980; Piovesan et al. 2005; Leak 2002). Leak (1996) however, argued that such pattern may be a result of a past disturbance such as cuttings.

Age and diameter structure of old-growth temperate European beech forests has not been studied until the recent years (Nilsson et al. 2003; Piovesan et al. 2005; Rozas & Prieto 2000; Wolf et al. 2004). Diameter distributions observed in these forests conformed generally to common model of an old-growth forest, exhibiting inverse-J shape distribution of a diameter at the breast height [DBH] (Piovesan et al. 2005; von Oheimb et al. 2005; Pontailier et al. 1997; Rozas & Prieto 2000). The presented DBH distributions however, were not usually tested at smaller scale or critically analysed in terms of diameter-age correlation. Pontailier *et al.* (1997) for example, in the study from Fontainebleau forest observed inverse-J shape of DBH of mature beech trees but noted that at smaller scale (0,25 ha) such pattern was not maintained, which indicates that scale and intensity of sampling may influence the diameter distribution. Age structures of the investigated areas did not conform well to the same inverse-J shape model, revealing discontinuous or irregular patterns (Piovesan et al. 2005; Rozas & Prieto 2000; Rozas 2003).

In this study I attempt to characterise age and DBH distributions and structural attributes of an 800 ha beech dominated forest in southern Sweden (Figure 1). In the late 1980s high conservational values were discovered in the area which is now being protected as one of the largest semi-natural deciduous forests in southern Sweden. Earlier studies and inventories have revealed numerous stands with high conservation values connected to old-growth features (Fahlvik 1999; Fritz & Larsson 1996; Karlsson 1996; Niklasson 2002). In this forest was found a large number of red-listed species connected to very old trees, indicating long continuity of natural or semi-natural conditions (Nilsson 2001). Specifically I address the following question: How do the diameter structure and age structure of the studied landscape

conform to the common theories of old growth forest? My approach in this study is based on structural and dendroecological analysis of long-term recruitment patterns in a large number of plots. To achieve answers I have studied age structure, recruitment of tree species, diameter structure and species composition with use of dendroecological techniques.

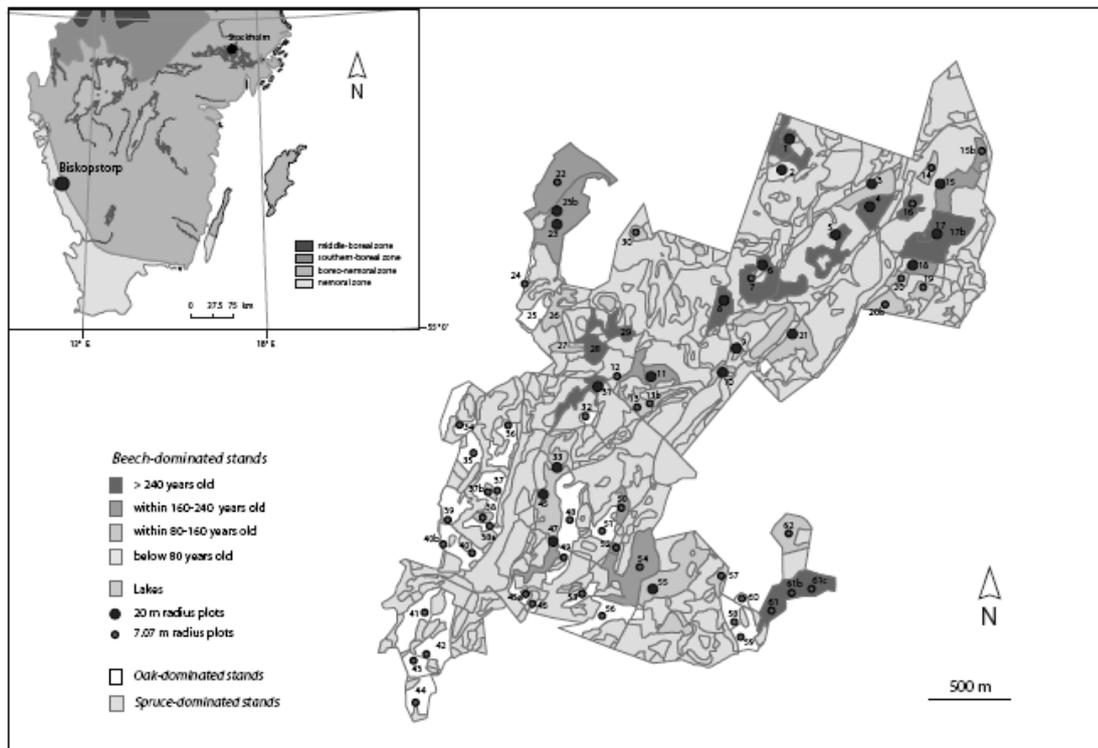


Figure 1. Map of the studied landscape with numbers and locations of set plots.

Material & Methods

Study area

The Biskopstorp forest is located in south west Sweden, 10 km north of Halmstad (56° 48'N; 12° 52'E), Halland county (Figure 1). The climate of the region is temperate and heavily influenced by proximity of the ocean. This results in generally moderate weather with mean temperatures of January and July being -2°C and 16°C, respectively. Yearly precipitation is 1000 mm/year. Dominant soil type is podzol with mor humus, developed on gneiss bedrock (Fredén 2002). The area lays at the northern limit of European temperate deciduous forest within nemoral zone (Ahti et al. 1968).

The forest of Biskopstorp has a total area of 812 ha (Bengtsson 1999). The landscape is characteristic of its diverse topography, rich in hills up to 100 m, steep ravines, and rocky outcrops and many small streams and lakes. Among previously managed spruce stands, planted around 1930, there are old natural and semi-natural stands of beech, oak and alder. The long term history based on pollen and charcoal analysis indicated gradual increase of *Fagus sylvatica* since A.D. 1000 followed by decline of oaks, birch and hazel (Karlsson 1996; Björkman 2000). Deciduous stands with beech, oak and birch cover over 50% of the total forest area. Forest management was carried out until 1990, mainly in the spruce stands. All the oldest and most valuable beech and oak stands are protected in total of 33 key-habitat reserves.

Field sampling

In 64 mixed deciduous stands a total of 73 circular plots were established, 21 plots with a radius of 20 m and corresponding area of 0.1257 ha and 52 plots with a radius of 7.07 m and corresponding area of 0.0157 ha. One big plot and up to three small plots were set up in each stand selected. Number of small plots within a stand was dependent on stand size and variation in stand structure, with larger and more structurally diverse stands, receiving more small plots than “more homogeneous” stands. Centres of the plots were chosen subjectively to represent most homogeneous parts of the stands and to avoid stand borders, clear-cuts and canopy gaps larger than 0.05 ha (Niklasson et al. 2005). Out of 21 big plots, 12 plots were originally set up as a part of another study (Fritz 2004; Martinsson 2004). GPS units (Garmin GPS E-trex and Magellan GPS 320) were used to locate and find centre points already set up and newly established plots. The plots’ centre points were marked with a metal stick and coloured plastic straw.

From the plot centres I recorded angular (in grades, from direction to the North) and linear distances to each tree, stump, snag or log with a measuring tape and compass. Trees above 2 m height were mapped and classified as living, dying, or dead. For living, dying or dead trees and snags diameter was measured at 1.37 m. Diameter was measured at both ends in case of logs. Dead logs longer than 1m and larger than 10 cm in diameter were measured. Species of each tree, stump, snag or log was identified. Snag was defined here as a dead broken or snapped tree whereas dead standing tree was defined as not snapped. All living trees larger than 2 m were cored with Haglöf increment borer at lowest possible point, usually at 30-40

Table 1. Number and distribution of samples by plot type.

	cores	wedges	total
20 m – plots	1003	185	1188
7.07 m – plots	250	41	291
out of the plot	19	51	70
total	1272	277	1549

cm above ground. Only cores with pith present or pith estimated to be located within 20 mm from the oldest present ring of the sample were accepted for further analyses. From stumps, logs and snags full or partial cross-sections were taken by chainsaw. From the 53 plots with beech present 1199 trees were aged by using cores or cross-sections (Table 1).

Tree ring analyses

All cores were mounted on wooden sticks, dried and polished to a smooth surface with a belt sander up to a 400 grid paper. Cross-section samples were glued if they were broken or too small. For samples from healthy (not rotten) trees where piths were missed I applied a graphical method to estimate pith location. Dead samples were cross-dated with the pointer year method (Stokes & Smiley 1968). The method is based on the identification of temporal pattern in appearance of pointer years, which are defined as years with the most replicated negative growth anomalies in the dataset studied. The following years had conspicuous narrow rings and were the most useful as pointers: 1869, 1890, 1911, 1925, 1956, 1960, and 1974.

Results

Age structure

The shape of age distribution did not conform to the model inverse-J curve. The age structure of *Fagus sylvatica* pooled from all the plots with beech present (n=53) showed discontinuous pattern with prominent peaks of regeneration pulses and periods of either low or absent recruitment (Figure 2). Clear depressions in regeneration occurred in the periods: 1770-1850, 1920's and 1970's. The age distribution was subjectively divided by three age thresholds to define each of the regeneration pulses as cohorts (<87, 87-175 and 175-300 years) (Figure 2). The cohorts significantly differed from each other in respect to mean diameters. The oldest cohort had the highest mean diameter and the most narrow diameter range. The middle age cohort had trees with the largest diameters observed (Table 2).

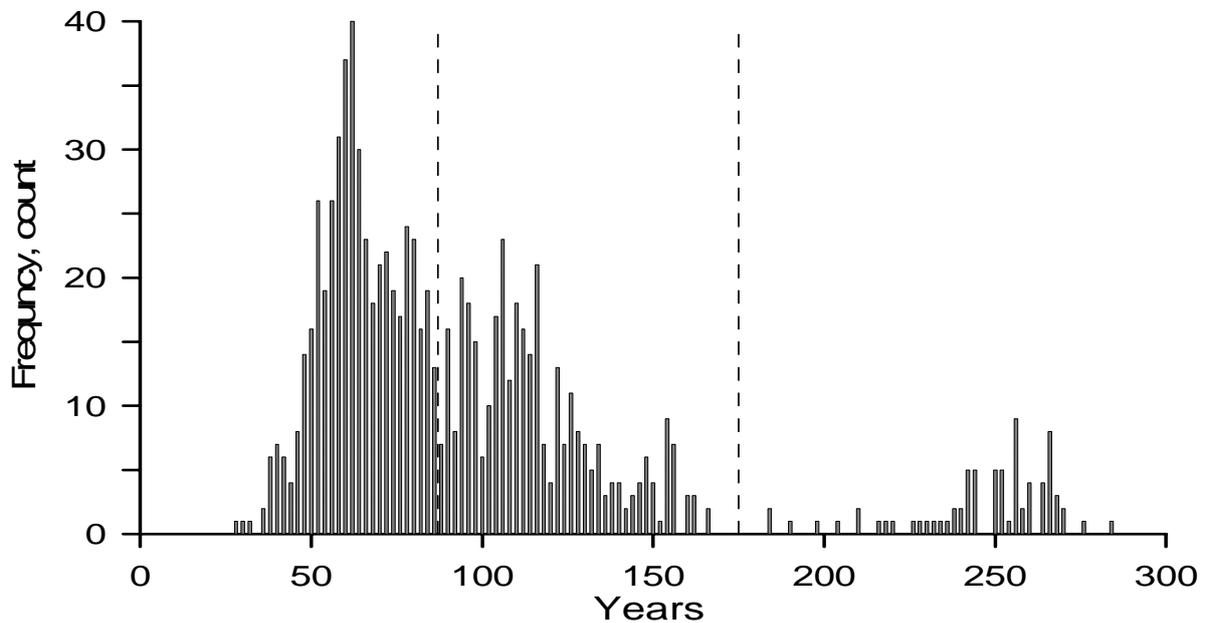


Figure 2. Age structure of *Fagus sylvatica* pooled from all the plots with beech present (n=53), subjectively divided by age thresholds to define three cohorts (<87, 87-175 and 175-300 years).

Table 2. Statistics based on DBH [cm] of each subjectively established cohorts.

	Young cohort	Middle cohort	Old cohort
Valid N	495,00	341,00	75,00
Mean	14,77	31,10	51,20
Range	65,00	88,00	58,00
Median	11,00	30,00	51,00
Std.Dev.	10,84	15,76	9,24
Minimum	3,00	3,00	20,00
Maximum	68,00	91,00	78,00
Frequency	40,00	13,00	7,00
Variance	117,48	248,41	85,38
Sum	7313,38	10605,52	3840,10
Mode	5,00	24,00	50,00
Standard	0,49	0,85	1,07
Skewness	1,25	0,83	-0,19
Kurtosis	1,87	1,00	1,32

At plot scale, age distribution varied considerably across plots, reflecting presence of one or several age cohorts. Few plots showed continuous beech regeneration over last 150 years. Out of all big plots, the five plots (no. 1, 4, 5, 6, and 8) had beech populations composed of two cohorts, separated by over 100 year period with no recruitment (Appendix 1). The oldest stands expressed by maximal age of trees on the plot were: 1 (265 years), 4 (265), 5 (265), 6 (254), 8 (284), 17 (260) and 29 (264). Stands 5, 8 and 29 showed the highest basal area weighted mean age: 245, 250 and 255 years respectively (Table 3 and Appendix 1). The oldest beech was 284 years old, found in stand 8. The majority of beech trees in the landscape belonged to the 1940-1950 years class (Figure 2).

Table 3. Basic statistics of the 20m radius plots.

Plot	SD DBH	SD Age	Maximum Age	Density	Number of species	Basal area <i>Fagus</i>	Total basal area	Deadwood density > 40 cm in diameter
1	18.66	87.03	264	469.48	4	32.11	35.00	15.92
2	8.30	6.92	73	557.01	4	22.48	28.93	0.00
3	14.02	11.79	85	807.93	2	37.07	37.07	0.00
4	17.59	87.67	264	119.36	4	20.82	20.92	47.75
5	10.60	41.43	264	119.36	1	21.41	21.41	47.75
6	20.95	87.55	254	214.85	3	19.30	19.48	47.75
8	20.63	103.98	283	509.27	3	20.33	20.33	71.62
9	15.58	22.87	128	485.40	6	33.14	37.16	7.96
10	11.76	20.36	114	459.43	10	9.18	29.39	9.99
11	14.65	18.16	158	294.42	1	30.10	30.10	0.00
15	26.03	26.88	147	159.15	3	25.22	47.00	0.00
17	12.92	40.75	259	318.29	6	16.10	18.92	0.00
18	10.95	15.33	164	230.76	3	23.17	23.17	0.00
21	16.00	22.82	136	541.10	5	20.52	27.17	7.96
23	11.48	29.71	160	433.65	4	20.81	25.47	0.00
23b	17.44	41.54	165	340.48	2	20.58	25.30	0.00
31	17.54	31.39	218	437.65	3	27.46	34.11	31.83
33	8.52	16.66	104	366.04	4	9.67	15.67	0.00
45	12.04	31.56	152	1066.28	6	23.03	34.19	7.96
47	9.36	22.83	132	954.88	5	24.49	33.45	7.96
55	26.66	35.74	154	278.51	2	20.80	22.31	15.92

Diameter distribution

At landscape level, diameter distribution pooled from all the plots with beech present (n=53) revealed a rotated-sigmoid pattern without logarithmic transformation which holds a characteristic feature of horizontal trend in the mid-DBH range (Figure 3). The diameter distribution fitted well a negative exponential function (R-squared =0.92) (Figure 3). The correlation between age and diameter was low, $R^2=0.52$ (Figure 4).

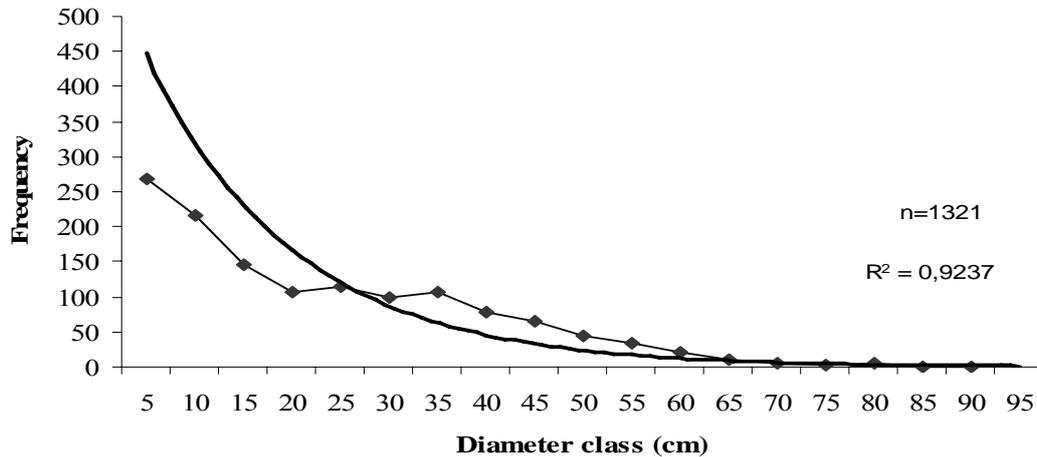


Figure 3. Diameter distribution of *Fagus sylvatica* pooled from all the plots with beech present (n=53).

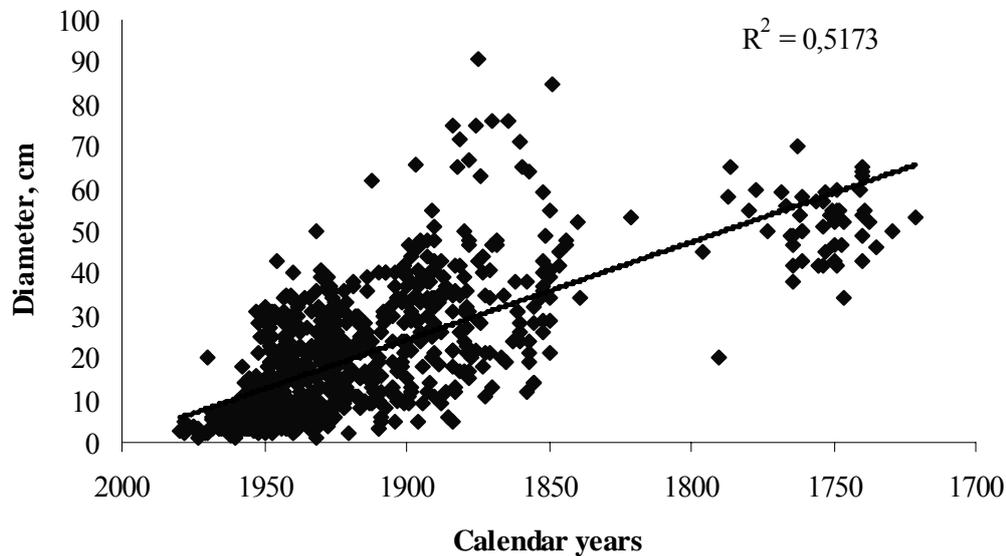


Figure 4. Relationship between age and diameter (n=817).

Structural characteristics

Current species composition

The two tree species *Fagus sylvatica* and *Quercus* spp. account for 89% of the total stem density. *Fagus sylvatica* was found in 59 plots dominating the landscape in terms of both stem density (57% of total) and basal area (60% of total). *Quercus robur* was present in 44 plots (10 – 20m radius and 34 – 7.07m radius) and occupied roughly 31% of the total density and ca. 30% of total basal area. Several large, 250-500 years old individual oaks were found outside the plots, probably remnants from periods of more open forest conditions. *Betula pendula* was present in 18 plots (12 – 20m radius and 6 – 7.07m radius) with a relative density 3% of total, but with smaller relative dominance (1.6% of total basal area). *Pinus sylvestris* was found in 18 plots (3 – 20m and 15 – 7.07m) with 4.08% stem density share and occupied ca 7% of total basal area. *Picea abies* relative dominance was less than 1% but in terms of stem density was similar to birch component (3.3% of total stem density). Norway spruce was present in 16 plots (12 – 20m and 4 – 7.07m). *Sorbus aucuparia*, *Acer platanoides* and *Frangula alnus* were of minor importance occurring mainly in the under-story layer. The existence of the pioneer species *Populus tremula* was recorded in plot 45, but individuals of this species were observed also in plot 18. In four stands I recorded also a few living and several dead individuals of *Juniperus communis*, Its occurrence is connected with open, exposed and rocky patches where several large, over 3 m high individuals were found. *Tilia cordata* and *Ulmus glabra*, were observed in few stands, exclusively on the rocky ravines, the former regenerating through vegetative sprouts. *Fraxinus excelsior*, *Prunus padus*, *Acer pseudoplatanus* and *Corylus avellana* were observed in small numbers.

Live tree structure: density, basal area, volume based on 20m plots

Mean density of living trees is 565 ind.ha⁻¹ (range 119 – 1337), 506 ind.ha⁻¹ (89.59%) for stems DBH≤40 cm and 62 ind.ha⁻¹ (11.06 %) for stems DBH>40 cm (Table 4). Trees larger than 70 cm were found in plots 15, 21, 31 and 55. The density of large trees with DBH>70 cm is ca. 4 ind.ha⁻¹ (range 0 – 24) which stands for 0.7% of the living trees. Trees with DBH in 1-10 cm class represents 41.75 %, while individuals with DBH in 10-40 class represents 53.77% of the living trees. In two plots there were no individuals with DBH≤10 cm. The lowest density was found in plots nr 5 and 4 with 119 and 143 ind.ha⁻¹ respectively. In both plots most of the trees were in the class with DBH>40 cm. The highest density was found in the plots nr 47 and 45, 1337 and 1225 ind.ha⁻¹ respectively. In both plots most of the trees were in DBH≤40 cm class. Basal area of the living trees ranged from 16-48 m².ha⁻¹ with the mean value 28 m².ha⁻¹. Most of the basal area is represented by the trees in 30>DBH≤40 cm class (26,6%). Ca. 53% of the basal area belongs to the trees with DBH≤40 cm and ca. 47% to DBH>40 cm. Ca. 2% of the total basal area is due to the trees with DBH≤10 cm. The mean volume of living trees was 202 m³.ha⁻¹, varying from 53 to 364 m³.ha⁻¹ (Table 4)

Dead trees and CWD structure: density, basal area, volume

Snags

Mean density of snags is 26 ind.ha⁻¹ (range 0-150 ind.ha⁻¹). There were no snags in the plots 2, 9, 11, 15, 17, 23b, 45 and 55 (Table 4). The highest density of snags was recorded on the plots 3, and 47, with 150 and 72 ind.ha⁻¹ respectively. All of the snags in plot 3 belong to the DBH ≤10 cm class while snags in the plot 47 are more evenly distributed among DBH classes. As much as 72.1% of the snags belong to the DBH≤40 cm class and 27.9% to the DBH>40 cm class. The highest density have snags in the DBH≤10 cm class, representing 46.0% of total number of snags. On average there is 1 ind.ha⁻¹ with DBH>70 cm (2.9%) and 5

ind.ha⁻¹ with DBH>50 cm. Out of all standing trunks (living trees, snags, dead standing trees) snags represents 4.2%. If basal area is considered instead of snags number, 13.1% of total snags basal area is due to snags in the DBH≤40 cm class, and 86.85% due to snags in DBH>40 cm class. Large snags with DBH>70 cm stand for 28.7% of total basal area. Mean basal area of snags is 2.4 m².ha⁻¹ ranging from 0-11 m².ha⁻¹. Most of the snags were *Fagus sylvatica* (77.46%) and *Betula pendula* (10.98%). The mean volume of snags was 8.9 m³.ha⁻¹ ranging from 0 to 72 m³.ha⁻¹.

Dead standing

The mean density of dead standing trees was 31 ind.ha⁻¹ (range 0-223 ind.ha⁻¹). The highest density was found in plot 47 - 223 ind.ha⁻¹ and smallest in plot 17 - 8 ind.ha⁻¹. Only 8 ind.ha⁻¹ standing dead trees with DBH>40 cm were found. Of all dead standing trees most (69.1%) were in the DBH≤10 cm class. Out of all standing trunks (living trees, snags, dead standing trees) dead standing trees represent 5.0%. Mean basal area of dead standing trees is 0.4 m².ha⁻¹ (range 0.0-4.2 m².ha⁻¹). Dead standing trees in the DBH≤40 cm class represents 84.6% and trees in the DBH>40 cm class 16% of dead standing trees basal area. The mean volume of dead standing trees was 0.05 m³.ha⁻¹ varying from 0 to 0.5 m³.ha⁻¹ (Table 4).

Table 4. Structural variables of the 20 m radius plots.

Plot	N		G		V	Biomass	Dead wood volume				N					
	total	>10cm	total	>10cm			Total	CWD	Stumps	Snags	?40	>40		Total		
	n/ha	n/ha	m2/ha	m2/ha	m3/ha	Mg/ha	m3/ha	m3/ha	m3/ha	m3/ha	n/ha	n/ha	n/ha	n/ha	n/ha	n/ha
1	525	342	35	34	364	260	9	0	4	4	8	64	8	8	16	72
2	645	533	29	28	124	145	7	1	6	0	0	0	0	0	0	0
3	808	419	37	36	281	267	28	26	2	0	150	0	0	0	150	0
4	135	127	21	21	189	179	3	3	0	0	8	103	24	24	32	127
5	119	119	21	21	189	185	7	3	4	0	0	72	24	24	24	95
6	255	119	19	19	157	162	14	8	5	0	0	16	32	16	32	32
8	525	159	20	20	182	167	21	15	2	4	24	95	32	40	56	135
9	613	414	37	37	273	283	43	21	1	21	0	0	0	8	0	8
10	939	380	29	28	135	217	25	10	11	4	10	0	10	0	20	0
11	294	247	30	30	263	238	13	0	13	0	0	56	0	0	0	56
15	470	414	48	47	311	384	5	2	3	0	0	88	0	0	0	88
17	406	318	19	19	110	135	67	7	3	58	0	56	0	0	0	56
18	231	231	23	23	266	179	89	9	7	73	8	32	0	0	8	32
21	700	374	27	26	166	203	6	2	4	0	16	48	0	8	16	56
23	545	421	25	25	194	180	23	21	2	0	37	50	0	0	37	50
23b	384	236	25	25	180	195	7	1	6	0	0	61	0	0	0	61
31	573	446	34	34	270	263	4	0	3	0	40	127	16	16	56	143
33	756	470	16	15	53	93	119	111	8	0	32	64	0	0	32	64
45	1225	501	34	33	154	243	14	7	7	0	0	111	0	8	0	119
47	1337	859	33	31	122	208	56	31	0	25	64	151	8	0	72	151
55	294	143	22	22	265	192	11	5	6	0	0	32	0	16	0	48
Mean	561	346	28	27	202	209	27	13	5	9	19	58	7	8	26	66
SD	324	178	8	8	78	62	31	24	3	20	35	43	11	11	36	48

Dead logs/laying dead wood

Mean density of logs is 67 ind.ha⁻¹ (range 0-159 ind.ha⁻¹). Logs with diam \leq 40 represents 88.1% (mean 59 ind.ha⁻¹, range 0-159) and with diam $>$ 40 11.9% (mean 8 ind.ha⁻¹, range 0-40) of total number of logs. Only 0.6% of the total logs number is due to trunks larger than 70 cm. The majority (52.7%) of logs belong to the 10<diam \leq 20 cm class (Table 4). Distribution of logs among decay classes showed that 38.5% of logs belong to decay class 5 and 25% to decay class 4 (Table 4).

Stumps

Mean density of stumps is 296 ind.ha⁻¹ (range 16-1057 ind.ha⁻¹). Distribution of stumps among decay classes showed that majority of them belongs to classes 4 (24.9%) and 5 (36.2%). Most of the stumps were *Fagus sylvatica* (73.71%) and *Picea abies* (17.3%) (Table 4).

Discussion

Age structure

The age analysis, in contrast to the size distribution, revealed that the studied forest is composed of three age cohorts, which are different in terms of development history (Figure 2). The oldest trees reach almost 300 years in age which is near the upper limit reported for the species. The distinct early cohort regenerated between 1720 and 1750 over seemingly a large area. There are many indications that these trees are a result of human activities rather than natural disturbances. Although hurricanes are fairly common in the area, they occur predominantly in winter when deciduous trees are much less susceptible. A striking example was given by the hurricane the 8th of January 2005 when about 25% of the Norway spruce monocultures in the reserve were overthrown. In the *Fagus* stands only occasional trees were broken which was observed also in the Fontainebleau forest after the storms in 1996 (Pontailier et al. 1997). Uprootings are extremely rare in *Fagus* stands. Soil mounds after uprootings may remain for centuries (Falinski 1978) but very few can be found in Biskopstorp (Churski pers. obs.). Historical evidence of large-scale felling operations in the early 1700s in the area has been found although the precise locations of these remain unresolved (Anon 1998). Some indications of landscape opening in the 1700s are found also in pollen diagrams, where around the 1700s the amount of grass pollen increased and rapid decrease of *Fagus* was found (Björkman 1996; Karlsson 1996; Björkman 2000). This period of extensive forest utilisation probably created strong regeneration pulse, visible on the present age structure as old cohort. After that event the recruitment slowed down creating distinct 100 years long flat trend of the cumulative regeneration curve (Figure 5). Periods of low or absent recruitment may indicate suppression by an external factor (eg. grazing) or filled regeneration space (Eriksson & Jakobsson 1999), i.e. when there is no available space for new saplings to recruit successfully. The lack of regeneration in the 1760-1840 period is difficult to interpret. Rozas (2003) in a study from lowland forest in Northern Spain argued intense grazing pressure inhibited establishment of beech regeneration whereas beech recruitment was continuous in periods of forest protection against grazing. If this is the case in Biskopstorp combination of grazing and filled regeneration space may have inhibited stronger regeneration pulses. Periods of rapid recruitment (steep cumulative curve) indicate availability of space for new saplings to establish and recruit (Figure 5). As long as sufficient number of seed trees are present, the slope ("steepness") of the cumulative curve may indicate the degree to which a stand is

opened up/disturbed and available for regeneration in combination with disturbance intensity (degree of removal of canopy trees). In the Biskopstorp forest next disturbance that changed conditions to become suitable for successful regeneration and recruitment took place in the 1850s which is indicated by steeper cumulative beech curve and by appearance of two light demanding species: pine and birch, which is an evidence of more open conditions (Figure 5). For the next 100 years the cumulative beech curve is constantly steep, probably indicating moderate disturbances. The next disturbance that created regeneration pulse took place in 1920s-1940s (Figure 5 and Figure 2). After that fast recruitment was followed by constantly decreasing regeneration rate. I interpret the disturbance as the onset of shelterwood management system which at this time was substituting old grazing and small scale forest use.

Diameter structure

Considering the great economic importance of the European beech and the dominating role it has in many of Europe's forested ecosystems, studies of size and age attributes are surprisingly rare (Piovesan et al. 2005; Pontailler et al. 1997; Rozas & Prieto 2000; Rozas 2003; Rozas 2004; Wolf et al. 2004). Inverse-J shape diameter distribution as a generally accepted model of diameter structure for shade tolerant species such as beech suggest small scale disturbance commonly described as gap-phase dynamics (White & Pickett 1985). Detail description of natural dynamics and structure in beech dominated forest in Denmark was presented by Emborg et al. (2000) and Emborg (1998). The mosaic-cycle concept was applied to describe structural dynamic of this near natural deciduous forest, indicating that it is approaching the shifting mosaic steady state within a relatively small area. The diameter distribution of beech conformed to the negative exponential model. The average patch size was in the Danish study of beech forest ca. 0,08 ha, ranging from 0,01 to 0,2 ha (Emborg et al. 2000) and in the Fontainebleau forest 0,0175 ha (Pontailler et al. 1997). Since the plot size in this study is 0,12 ha it is theoretically possible that on average a plot should cover more than one patch of a natural forest. Managed forests are composed of much bigger homogeneous patches usually arranged geometrically. Often number of developmental phases is lower than in natural stands lacking usually old-growth stage (Bobiec 1998). In this landscape, the

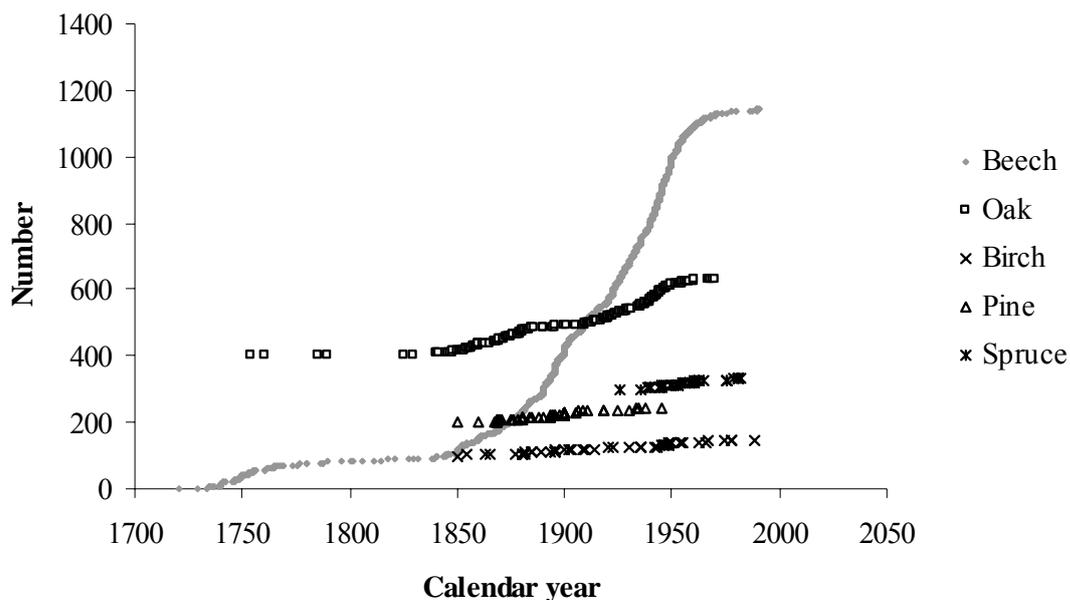


Figure 5. Cumulative age distribution for all aged trees by species. Y-axis is valid only for beech.

inverse J-shape DBH distribution is rather built up by the compilation of one- or two-aged stands regenerated in different time periods, which is in agreement with common conception that inverse-J shape size distribution forests may occur if many stands of different age are analysed together or if several species are grouped together (Goff & West 1975; Lorimer 1980). Since the inverse J-shape curve is usually interpreted as a situation where small-scale (gap) dynamics drive the succession with trees in all ages (sizes) at a small scale, this must imply that for the studied landscape, the disturbance regime has been operating at a larger scale than the studied plots (0,12 ha). This calls for careful interpretation of tree size distributions, in particular should the scale be more involved in this.

Age-diameter correlation

In the studied landscape demographic parameters are badly approximated using DBH (Figure 4). The main cause for the low fit is the great plasticity in diameter growth. A large number of trees in the older groups especially have grown very slowly, with 250 years old trees not more than 78 cm at breast height, while in other stands the same size could be reached in less than half the time (Figure 4). Similar results have been found in other parts of the *Fagus sylvatica* distribution range. For example, in a recently discovered old growth beech stands in central Apennines (Piovesan et al. 2005), an analysis of size distribution in 5-cm DBH classes, gave a good fit to the inverse-J model. Age at breast height varied between 131 and 501 years and was not significantly correlated with DBH. Another study from Spain showed the shape of diameter distributions of two Cantabrian beech populations were also inverse-J type but corresponded to the uneven-aged population structure composed of two well differentiated cohorts. This indicated distinct pulses of regeneration separated by over 100 years period of absent recruitment (Rozas & Prieto 2000). Moreover, despite a park-like structure with sparsely growing old, large trees and grass, probably caused by grazing, one of the studied by Rozas & Prieto (2000) populations showed similar size distribution to the population with no evidences of grazing. In the Biskopstorp forest the five (no. 1, 4, 5, 6, 8) oldest stands hold very similar to the Cantabrian forest park-like composition and demographic structure, composed of two well differentiated cohorts, separated by over 100 period of low recruitment (Appendix, Figure 2). This may be a result of different stand development history between the oldest cohort and two other cohorts. Low age-diameter correlation may also be a result of different mortality rates between trees from the same cohort. After the initial disturbance trees are starting to regenerate and continue until the regeneration space is filled, which may take several years in case of shade tolerant species (Oliver & Larson 1990). As a result there is an actual difference in age and size of the trees coming from the same cohort. Trees that regenerate shortly after the disturbance face most favourable conditions and are growing fast, reaching large dimensions. Subsequently as they advance in age the growth slows down and they become more susceptible to mechanical damages, diseases and pests which increase mortality rates in these diameter classes. These trees rarely reach maximum age limit for the species. Trees that regenerate in longer time after the disturbance ('regeneration tail') face less favourable conditions mainly due to competition from already established saplings, and as a result are growing very slow. The survival of these trees depends on canopy openings that allow them to enter upper canopy layer. Consequently these trees often attain high age but have relatively small dimensions. In the Biskopstorp forest the old cohort visible on the age distribution is probably composed of trees that were recruiting in the 'regeneration tail' long after the initial disturbance. They were probably suppressed and also escaped cuttings, because of low quality and size. Accordingly diameter range of these trees is placed within the diameter range of the middle age cohort, which explains smooth diameter distribution (Figure 3 and Figure 4). In the same time they are the most important for biodiversity management, since most of the red-listed species are found on the oldest trees. Therefore, this

study indicates that using diameter for substitution of age seems problematic for European beech and may in fact be misleading. Analysis of diameter structure should be revised by age analysis of appropriate amount of samples. According to Lorimer (1980) it is possible to study dynamic processes of a forest analysing diameter curves if the correlation between age and diameter is fairly good – R-squared = 0.9. Since the diameter variation in old age classes may be substantial and since diameters in each age class have a tendency to be normally distributed, inverse-J tree size curve can theoretically reflect other conditions than old growth (Lorimer 1980). One is an example of an old, even-aged over-story of a shade tolerant species (e.g. beech) with uneven-aged under-story of the same species developing underneath. Such pattern might be a result of a disturbance such as shelter wood management, common for beech forest in Europe (Agestam et al. 2003; Gemmel et al. 1996; Gemmel et al. 1996). It is therefore desirable to test age-diameter correlation prior to subsequent analysis.

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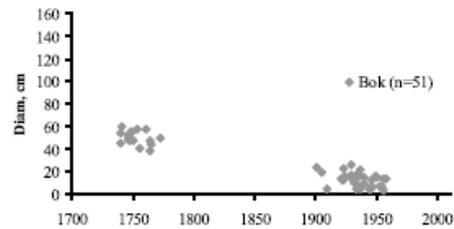
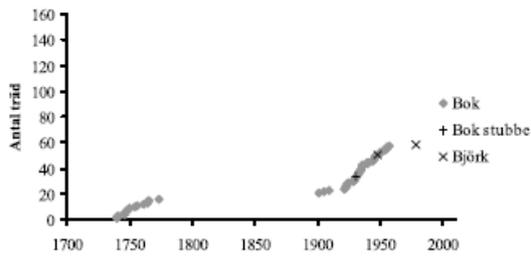
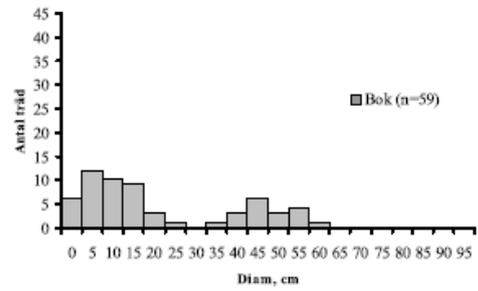
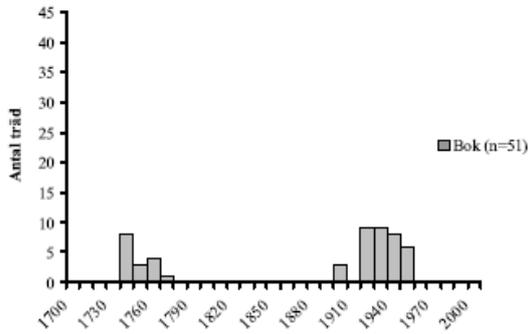
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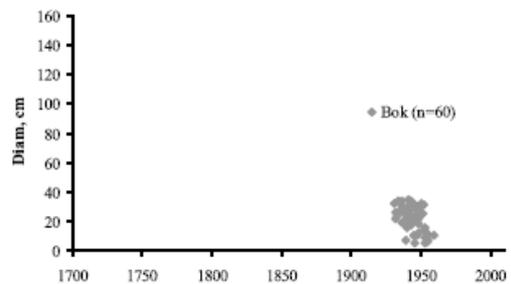
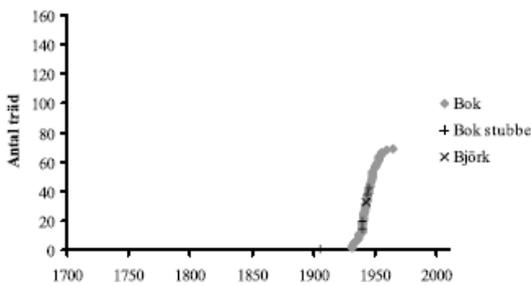
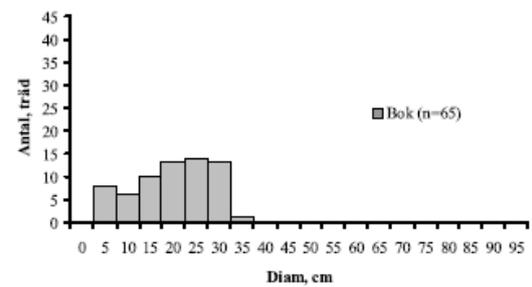
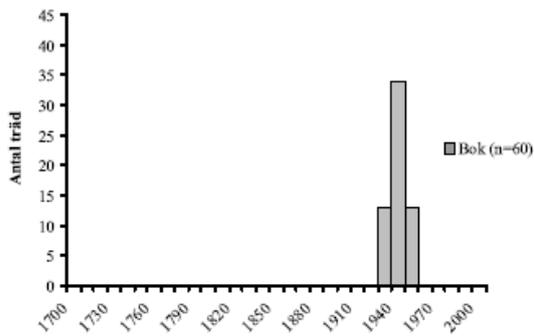
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Appendix 1. Tree ages and diameters in the 20m plots.

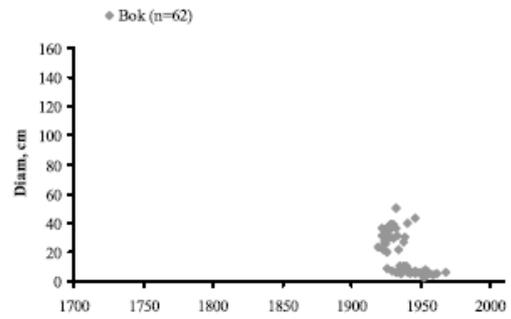
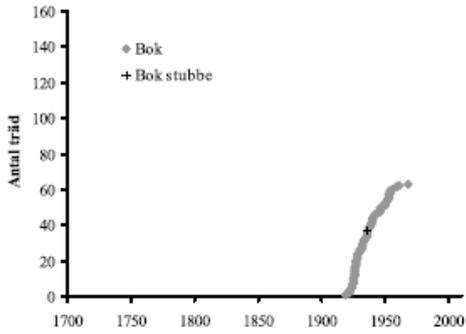
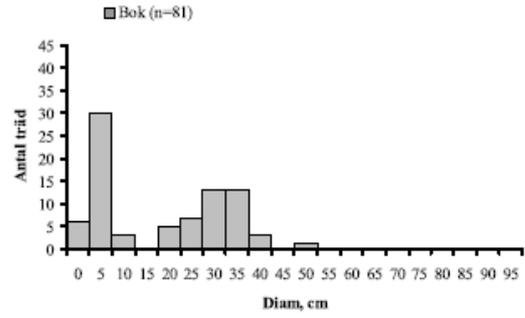
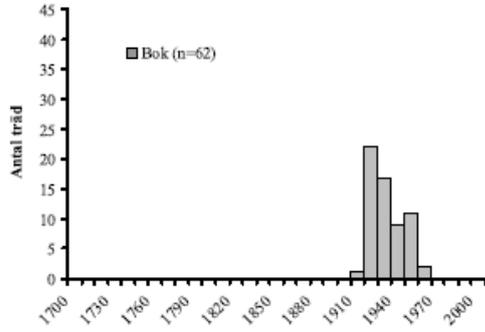
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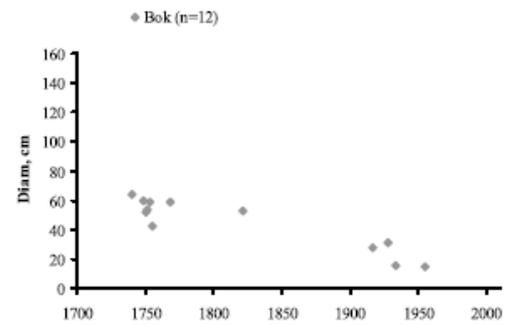
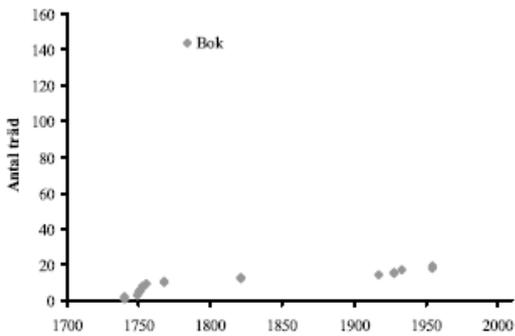
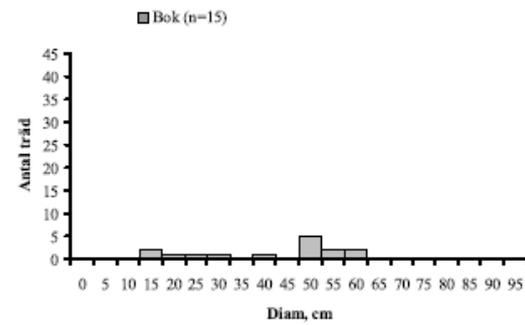
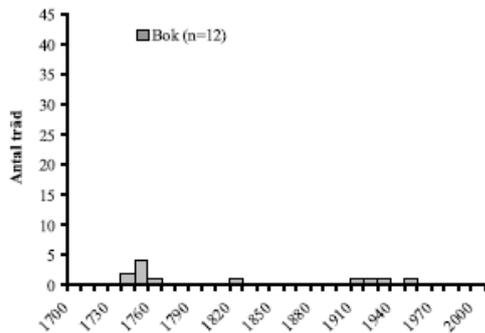
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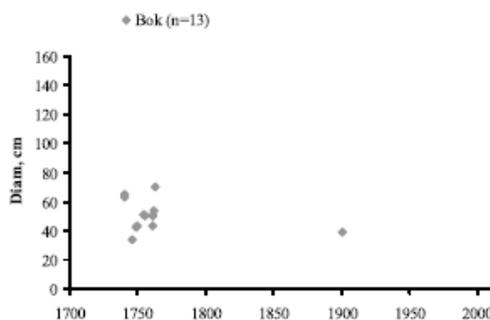
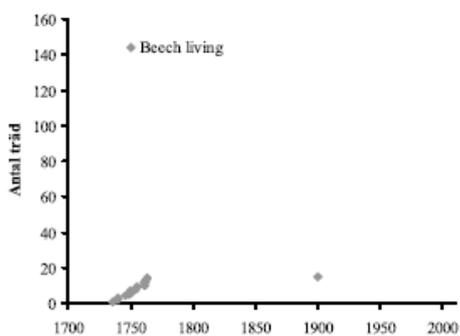
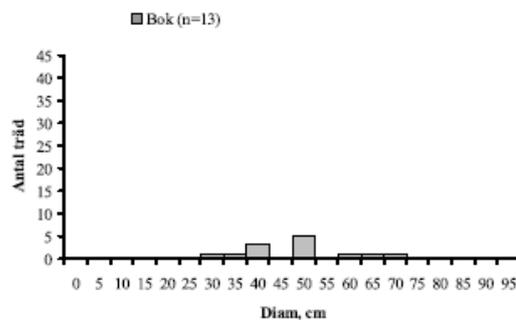
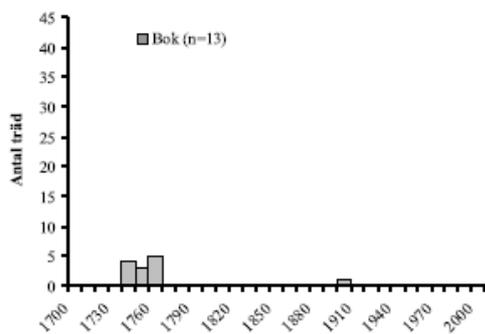
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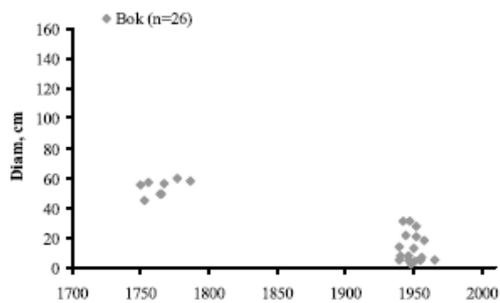
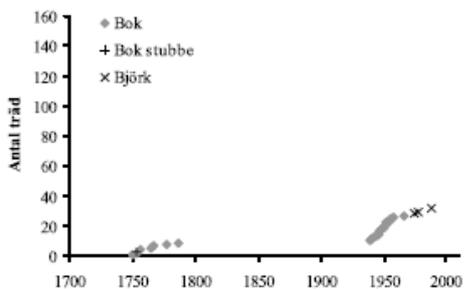
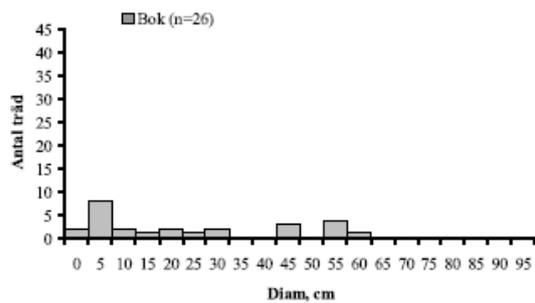
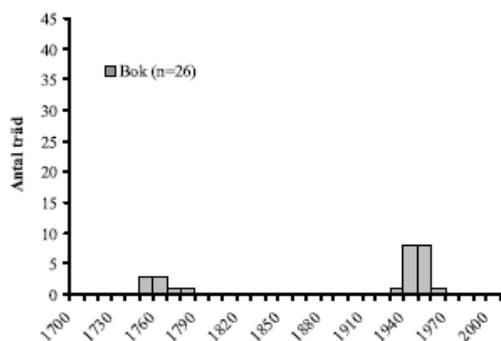
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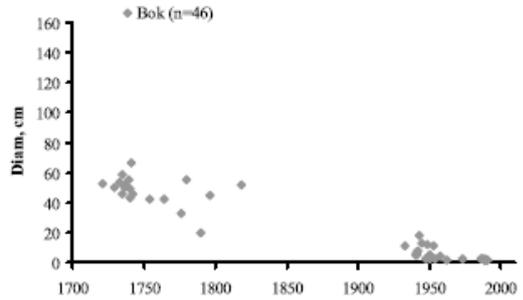
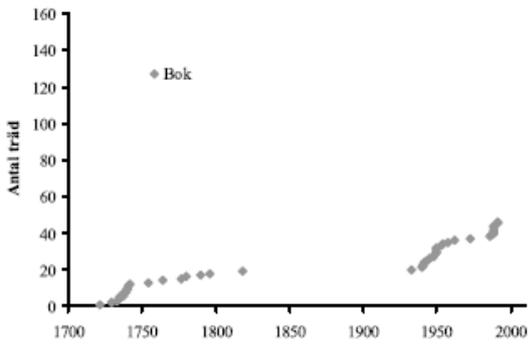
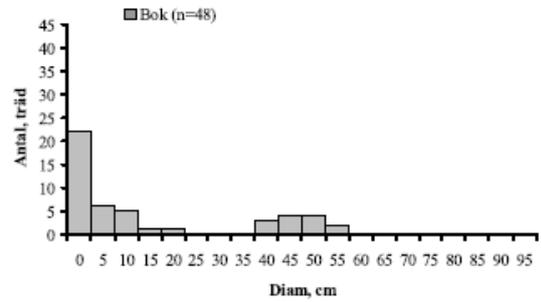
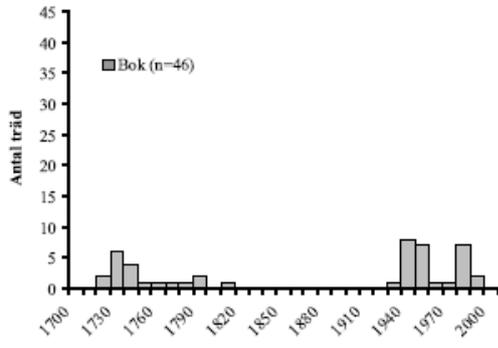
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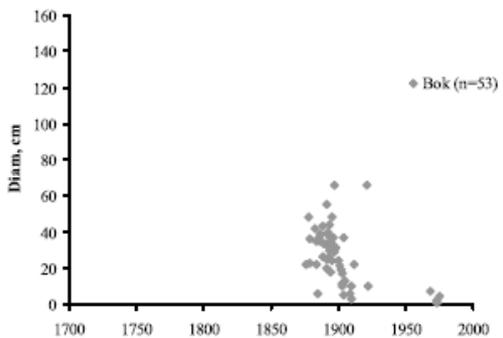
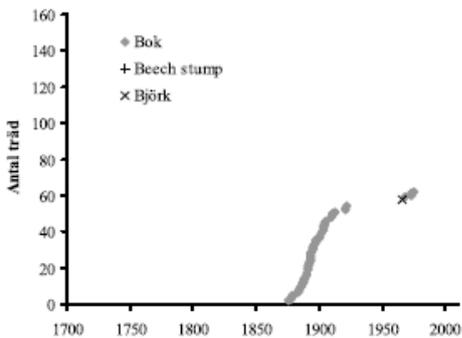
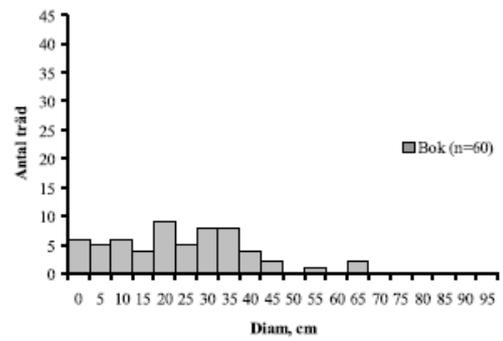
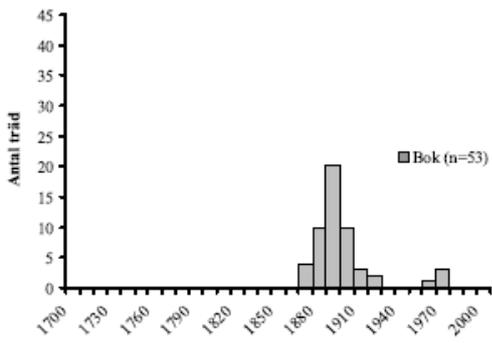
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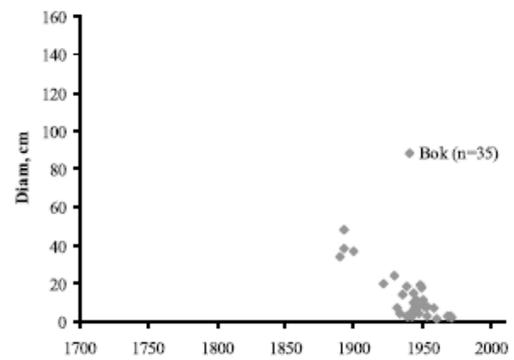
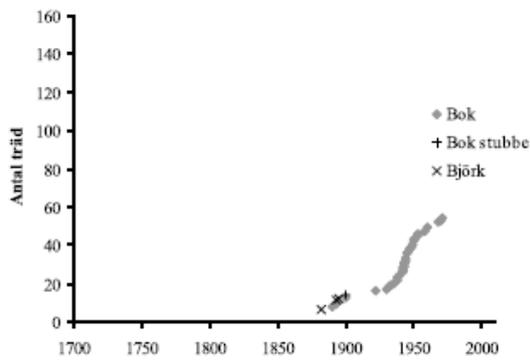
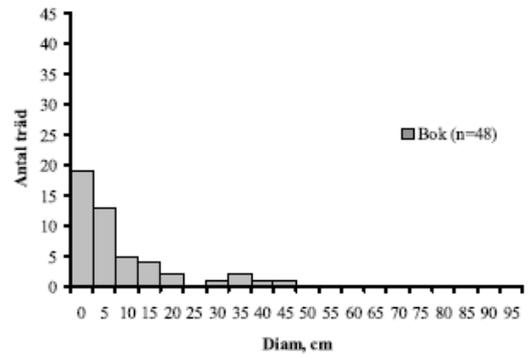
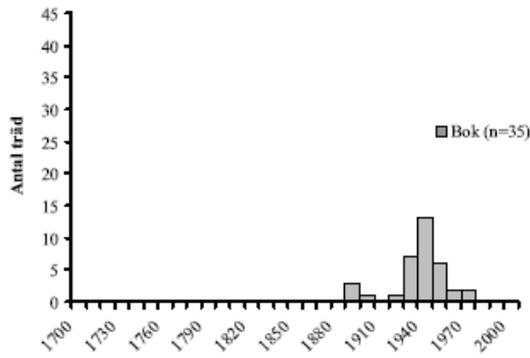
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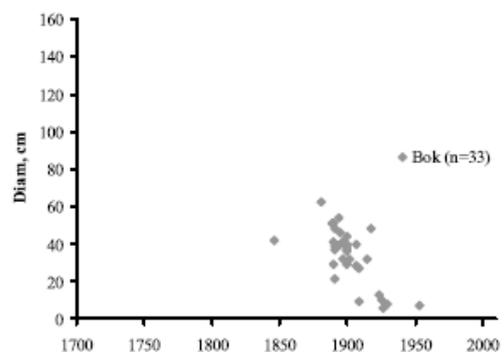
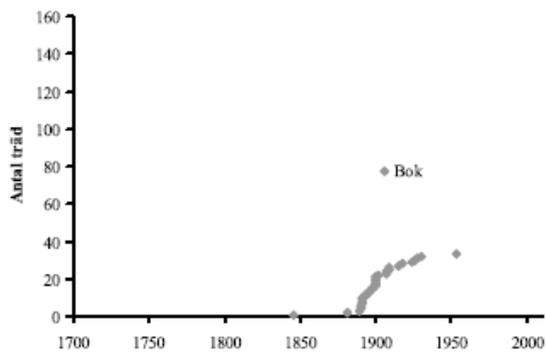
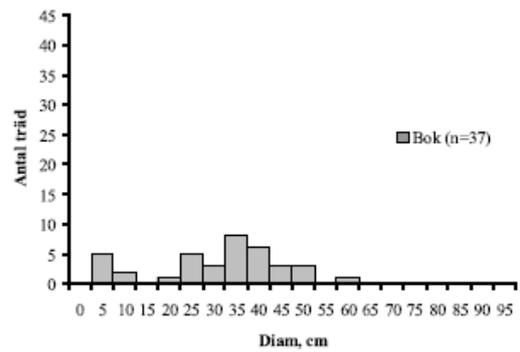
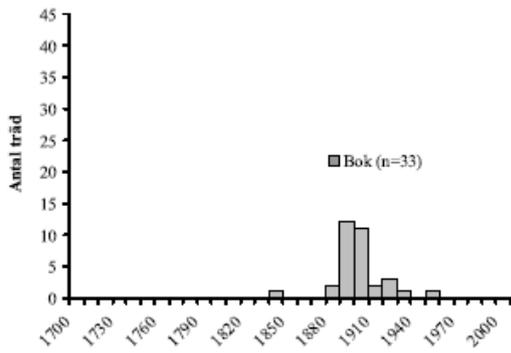
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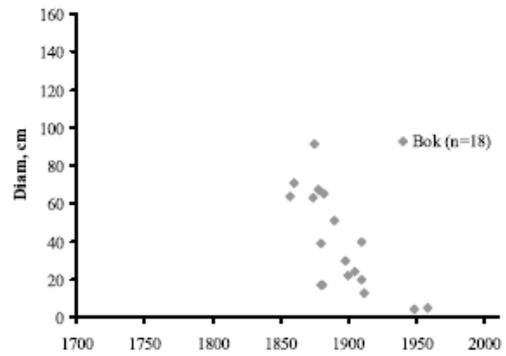
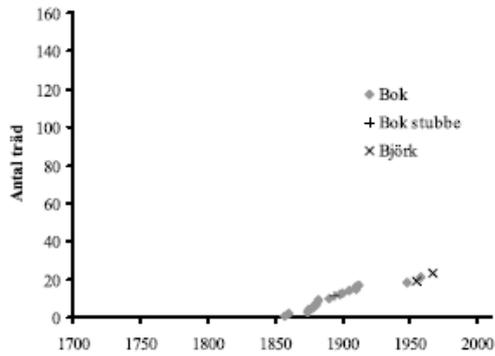
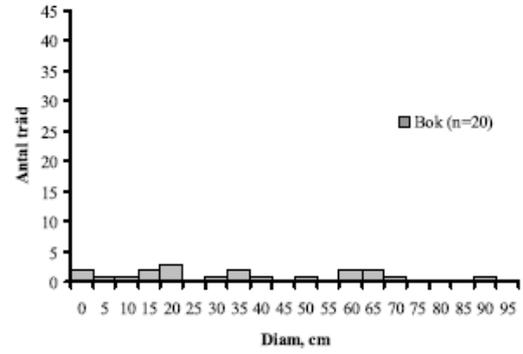
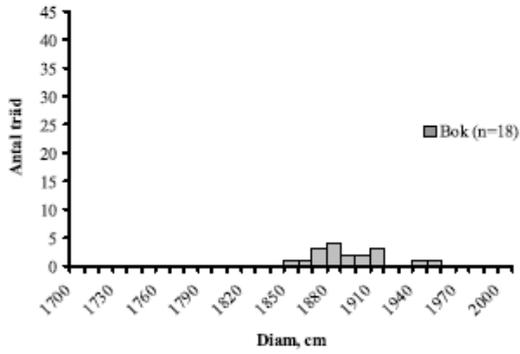
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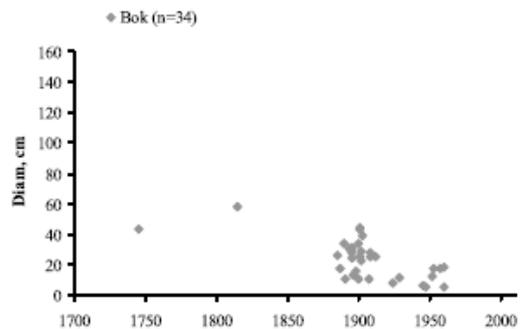
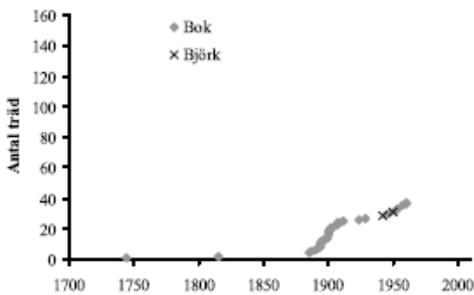
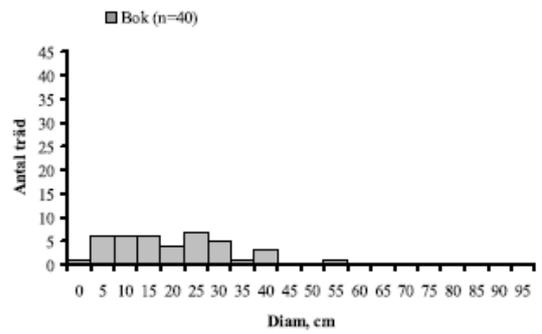
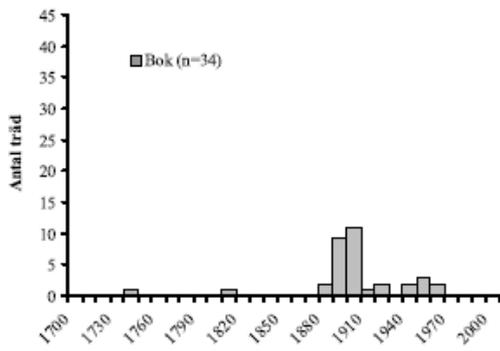
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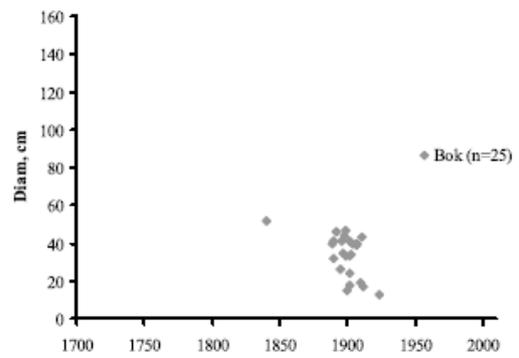
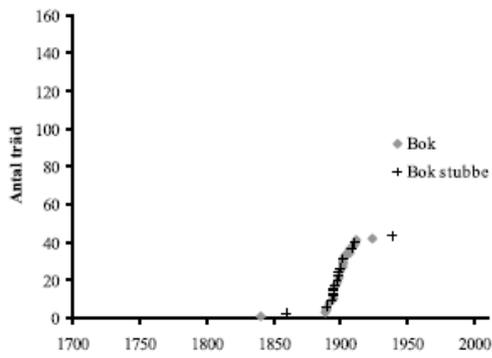
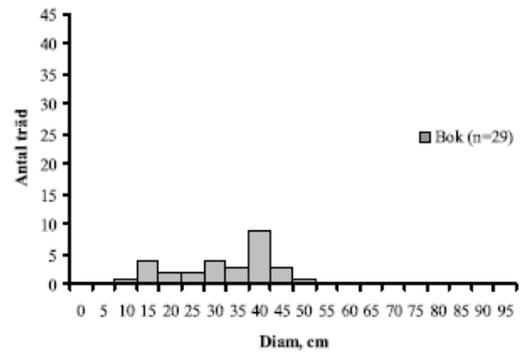
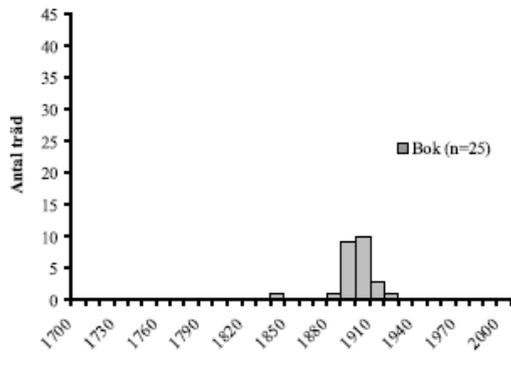
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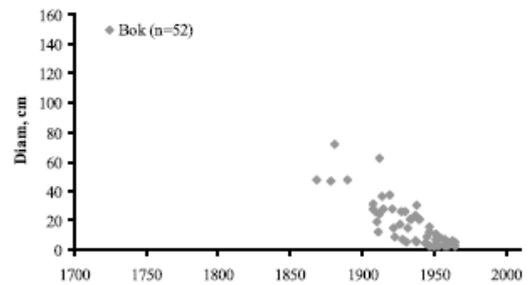
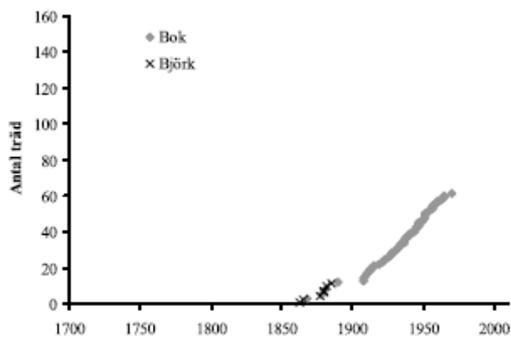
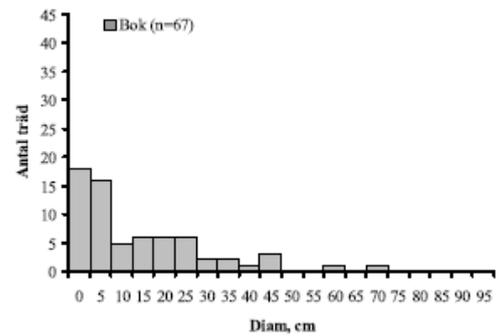
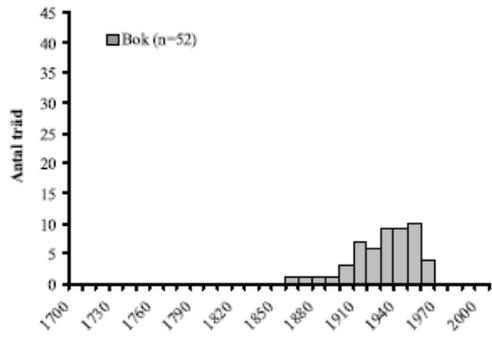
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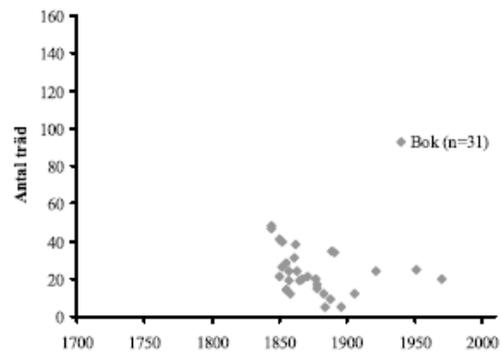
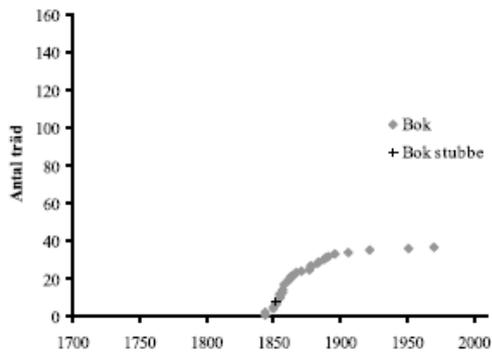
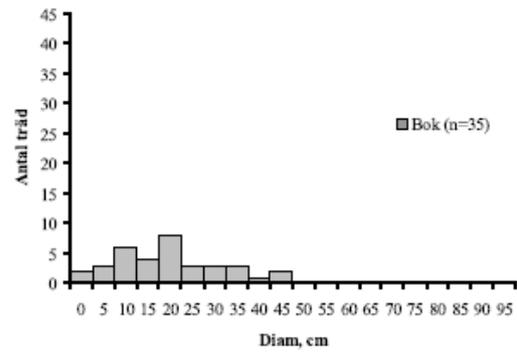
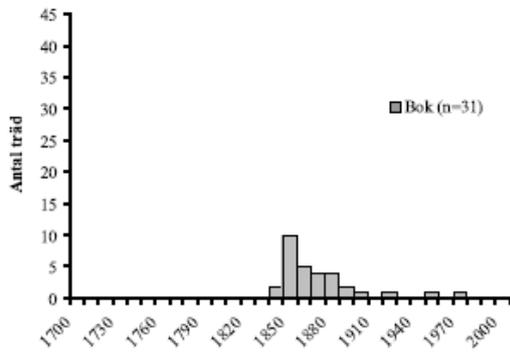


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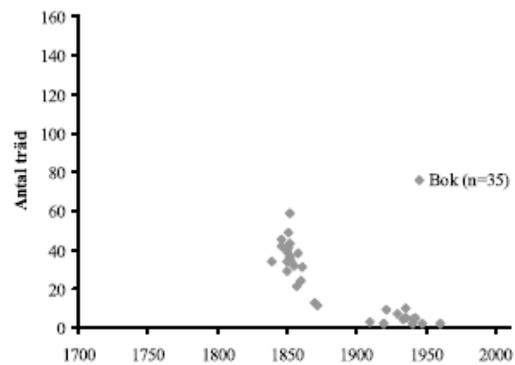
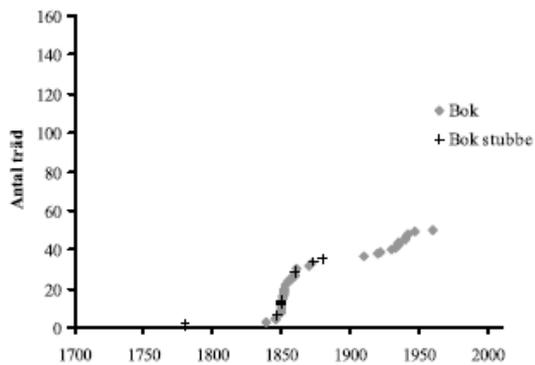
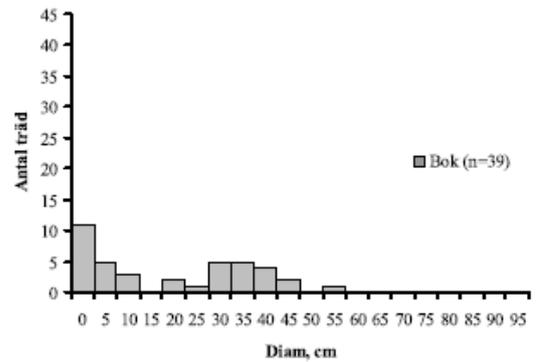
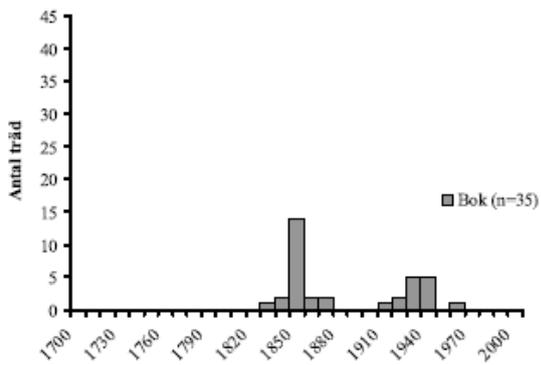


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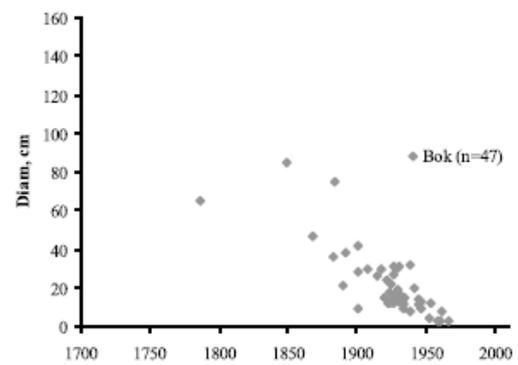
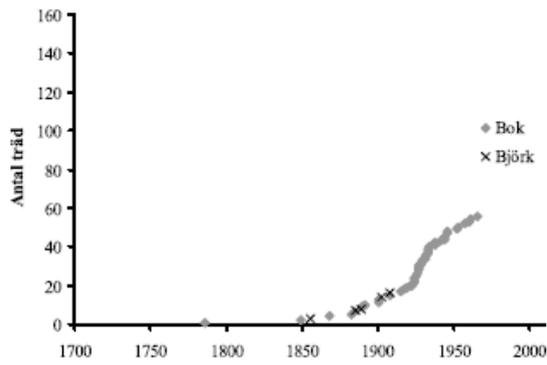
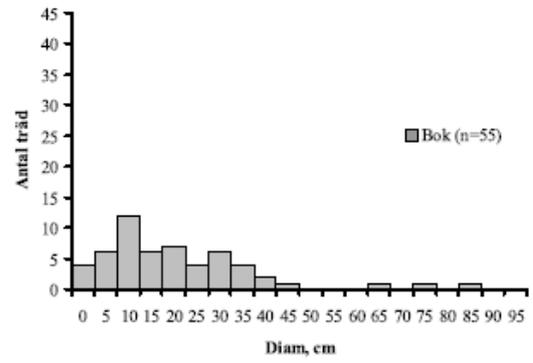
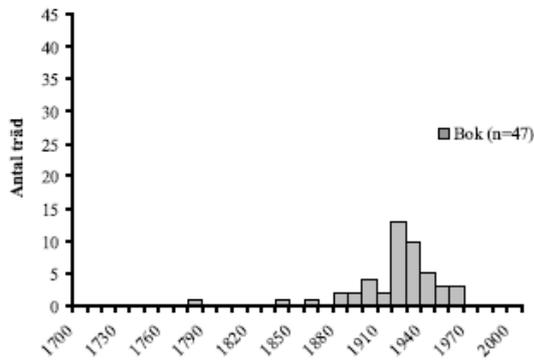




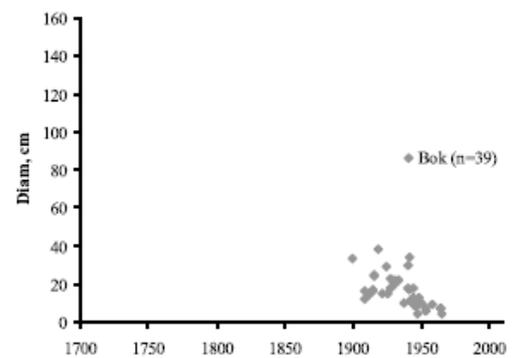
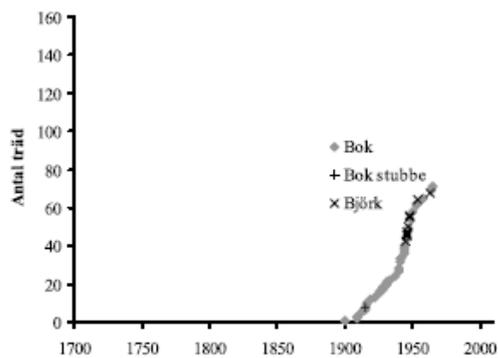
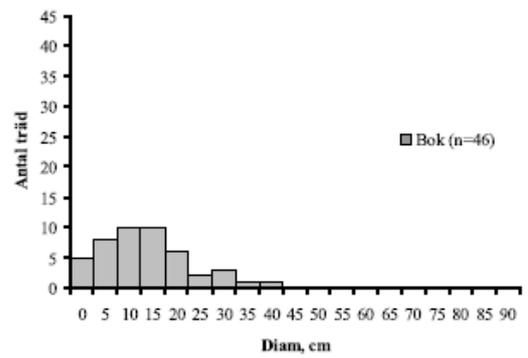
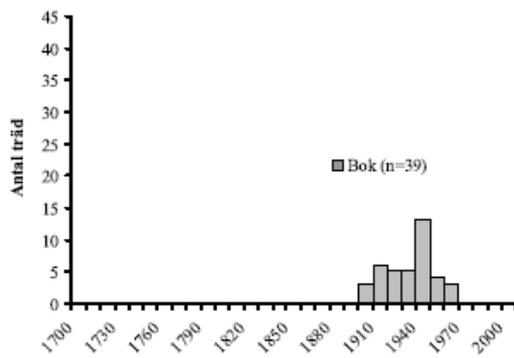
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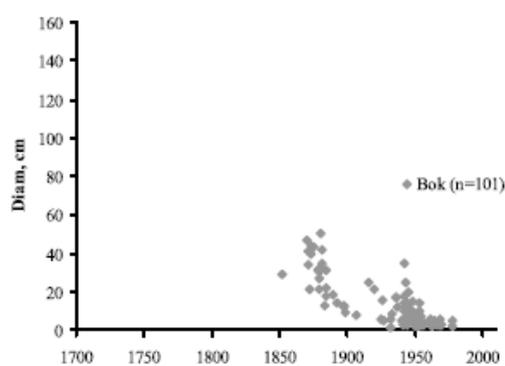
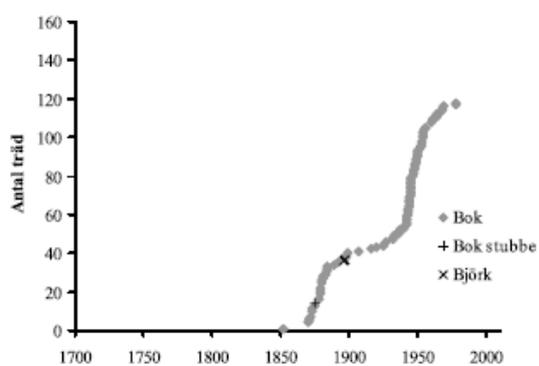
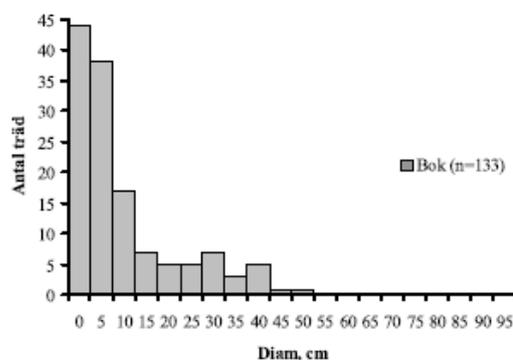
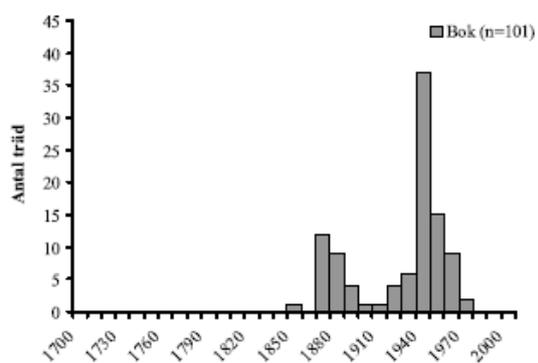
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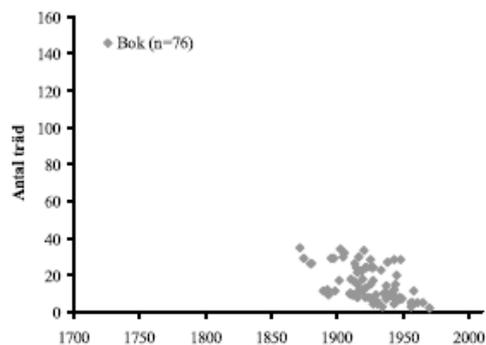
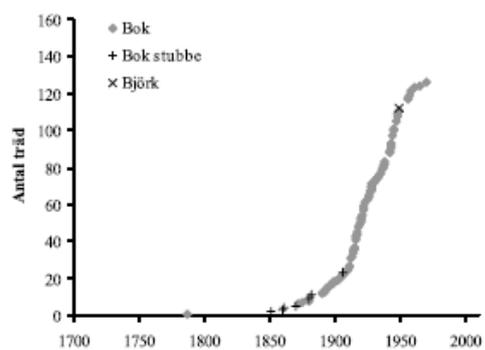
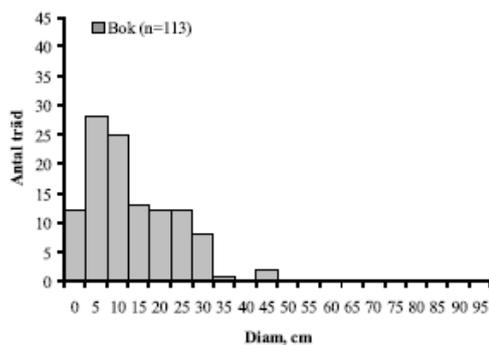
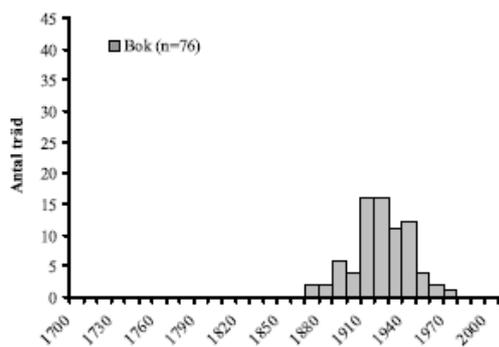
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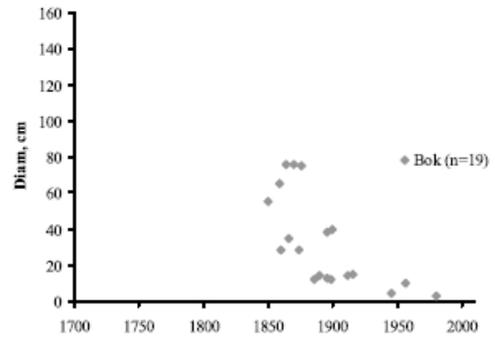
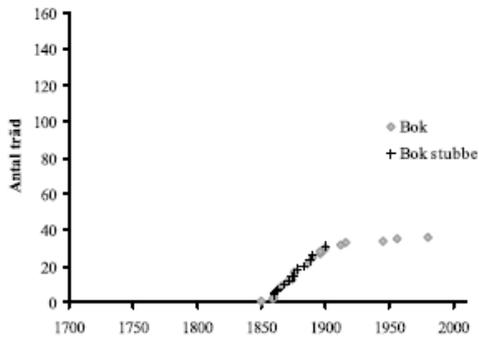
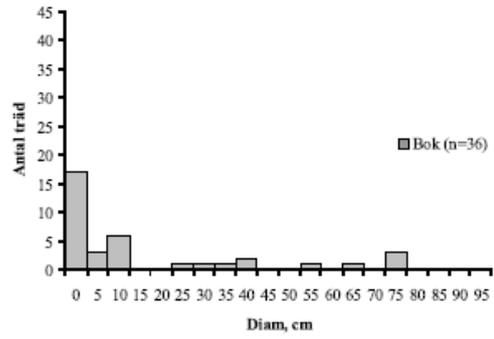
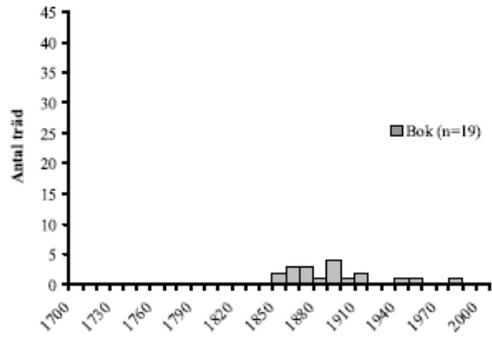


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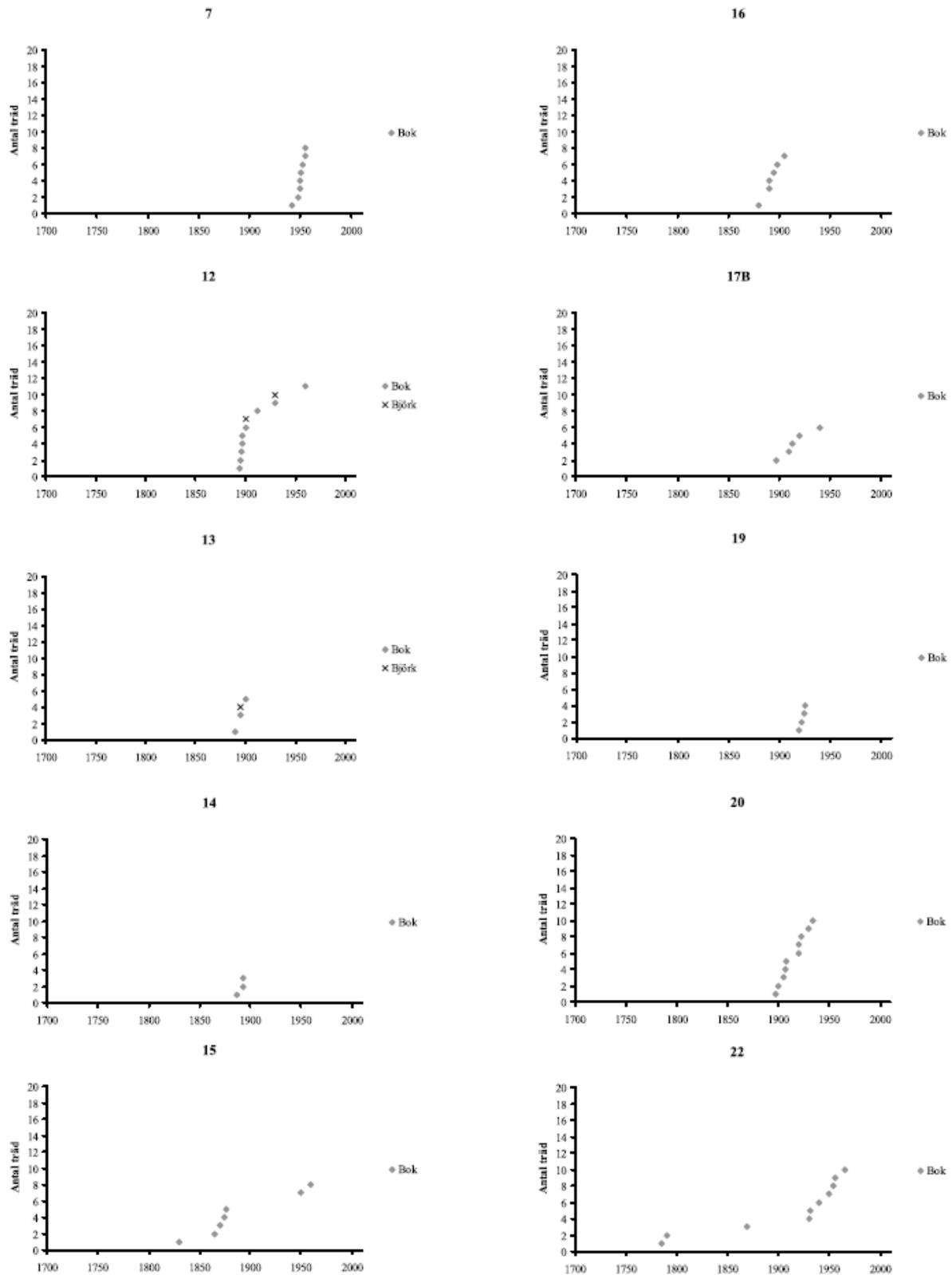


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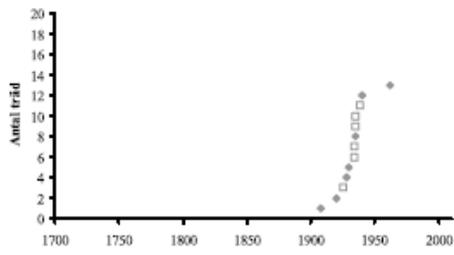




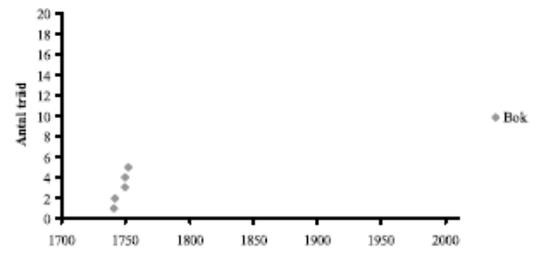
Appendix 2. Tree ages in the 7.07m radius plots.



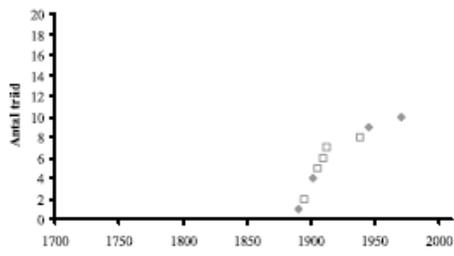
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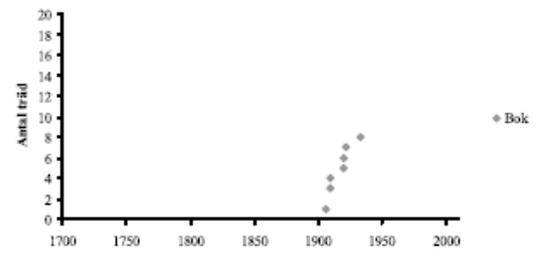
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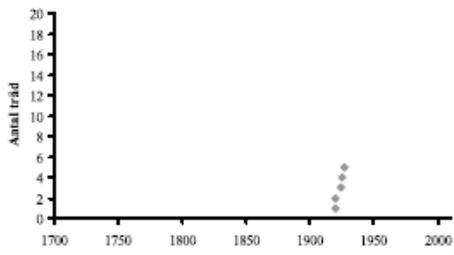
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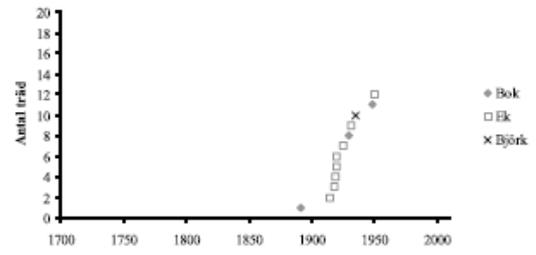
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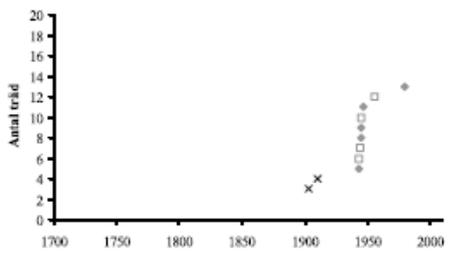
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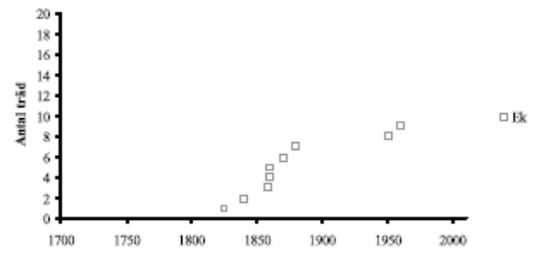
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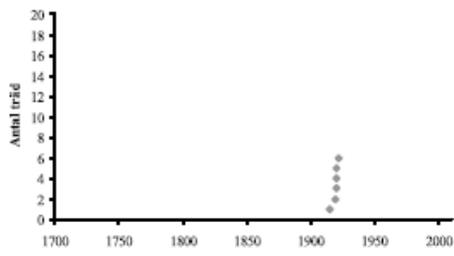
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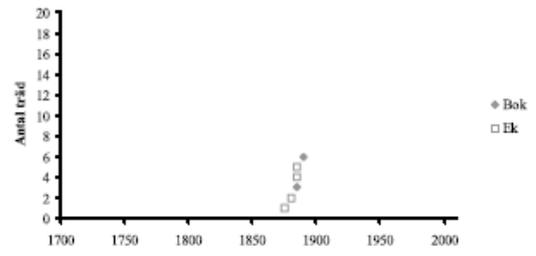
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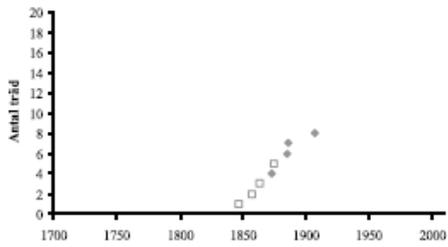
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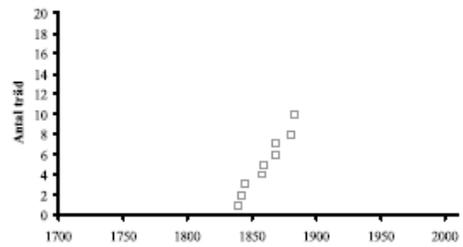
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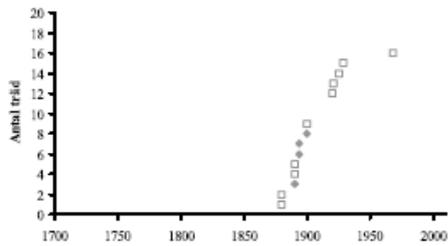
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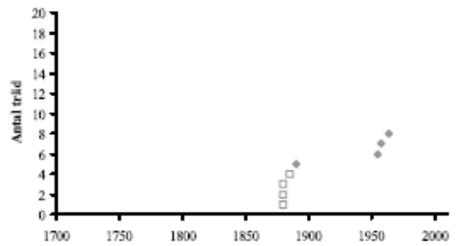
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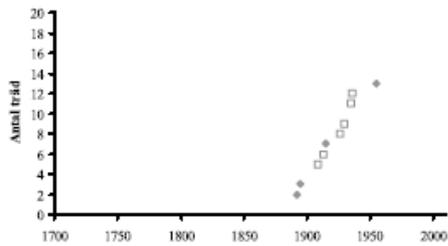
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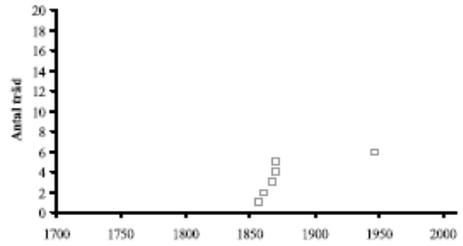
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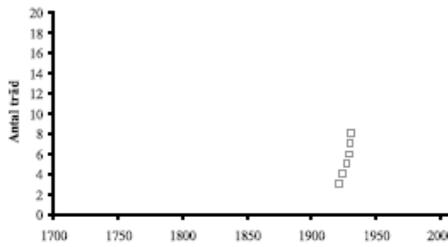
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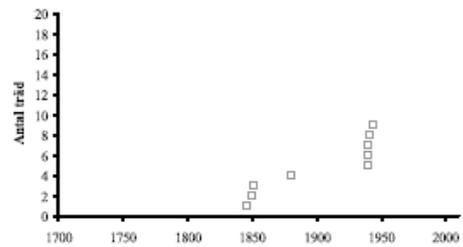
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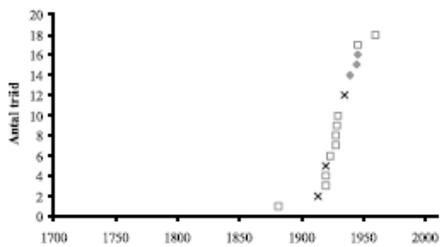
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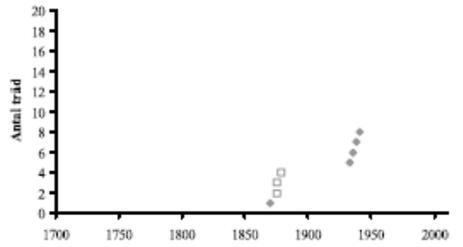
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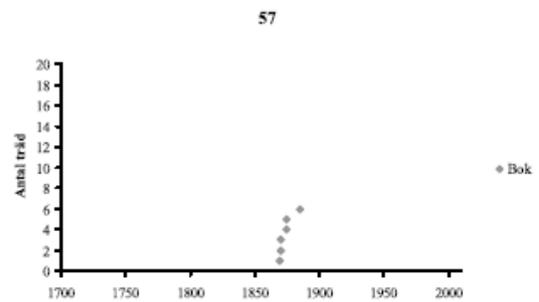
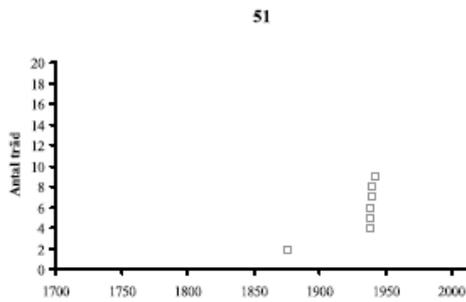
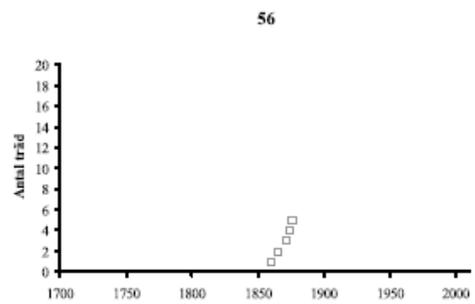
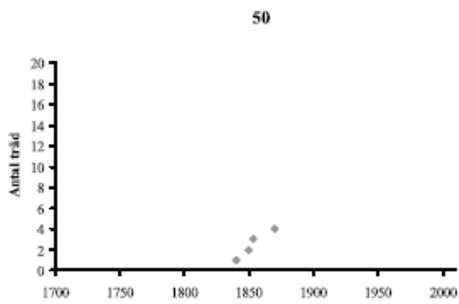
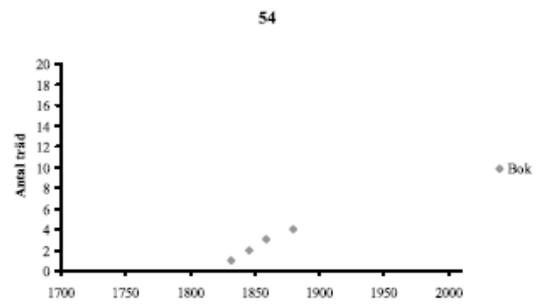
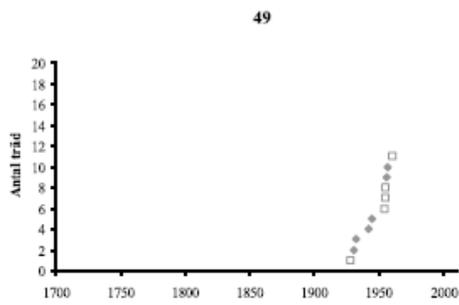
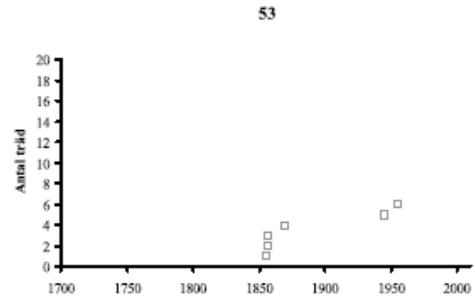
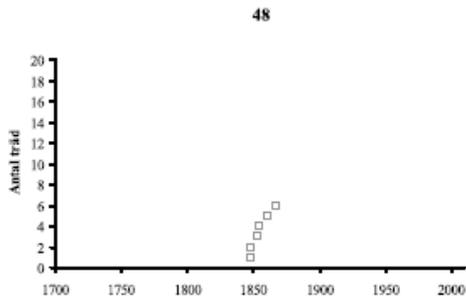
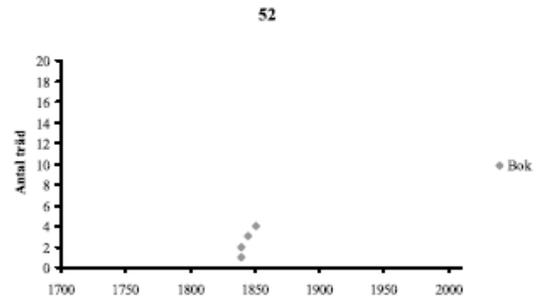
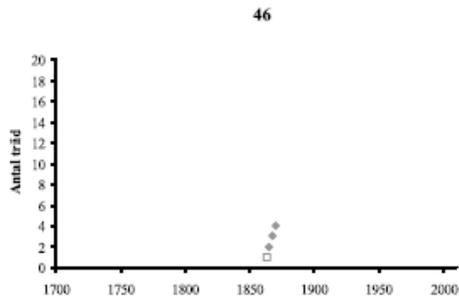


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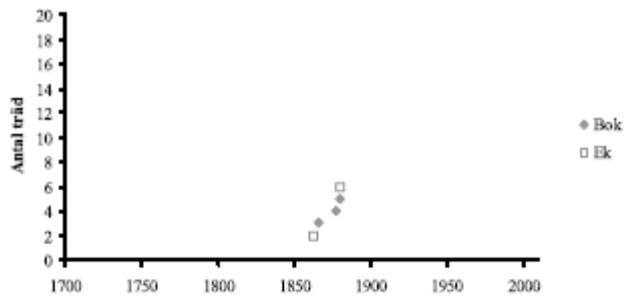


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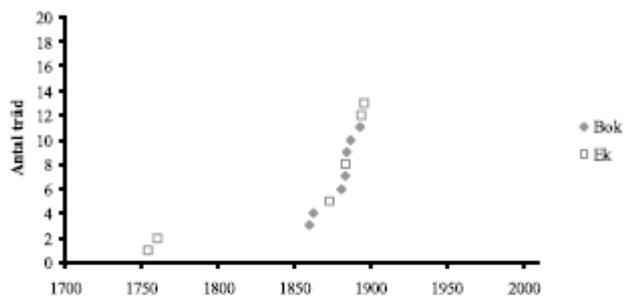




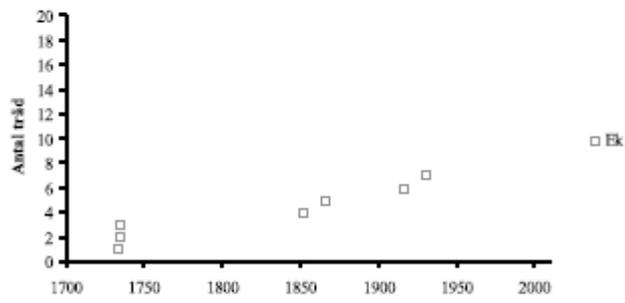
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