

DENDROCHRONOLOGICAL ANALYSIS OF SUBFOSSIL *FRAXINUS* FROM THE MIDDLE AND LATE HOLOCENE PERIOD IN LITHUANIA

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ABSTRACT

Dendrochronological investigations on subfossil European ash (*Fraxinus excelsior* L.) wood found in two bogs of Western Lithuania are presented. Radiocarbon dating has revealed that *Fraxinus* grew in the Middle and Late Holocene, from approximately 4700 BC to 1500 BC. It is proposed that the growth of *Fraxinus* at these bogs was limited by differing hydrological regimes. Rising soil water levels induced a long decline in radial growth followed by a sharp reduction (up to 51%) in ring widths before the trees died. Until now, forest history in Lithuania was mostly based on results from palynological studies. This research demonstrates the potential of using dendrochronology to extend the distribution record of *Fraxinus* in the Baltic region during different periods of the Holocene.

Keywords: *Fraxinus*, ash, dendrochronology, Holocene, subfossil, bog, radiocarbon.

ZUSAMMENFASSUNG

Vorgelegt wurde ein dendrochronologisches Gutachten über subfossiles Holz von Gemeinen Eschen (*Fraxinus excelsior* L.) aus zwei Mooren im westlichen Teil Litauens. Die Radiokohlenstoff-Datierung dieses Holzes ergab, dass die *Fraxinus* im Mittel- und Spätmittelalter des Holozän wuchsen, etwa 4700–1500 vor Christi. Das Wachsen der analysierten *Fraxinus* aus diesen Mooren wurde von verschiedenen hydrologischen Bedingungen beschränkt. Das Ansteigen des Boden-Wasserspiegels veranlasste langfristigen geringen Zuwachstrend. Danach folgte plötzliche Reduktion der Jahresringe (bis 51%), und so den Untergang der Bäume verursachte. Bis zur gegenwärtigen Zeit ist die Geschichte der Wälder Litauens beinahe nur auf palynologischen Forschungen begründet. Diese Forschung demonstriert das Potential der Dendrochronologie, lässt vervollständigen das bisherige Wissen über das Verbreiten von *Fraxinus* im Baltischen Gebiet während verschiedener Perioden des Holozän.

Schlüsselwörter: *Fraxinus*, Esche, Dendrochronologie, Holozän, subfossil, Moor, Radiokohlenstoff.

INTRODUCTION

Dendrochronological measurements from subfossil wood preserved in bogs have been widely used for the reconstruction of climate and ecological conditions during the Holocene (Baillie 1982; Fritts 1991; Eronen *et al.* 2003). The greatest numbers of millennium-length chronologies used for the reconstruction of environmental conditions in Western Europe have been compiled using oak (*Quercus* spp.) wood excavated from river sediments and bogs (Schmidt 1973; Leuschner and Delorme 1988; Brown and Baillie 1992; Leuschner *et al.* 2002; Leuschner and Sass-Klaassen 2003). In

contrast, *Fraxinus* wood was only investigated in the rare situation where it was mixed with oak wood (Baillie 1982; Leuschner *et al.* 2002). However, Sass-Klaassen *et al.* (2003) have confirmed that the tree-ring series of *Fraxinus* are suitable for dendrochronological analysis.

Pollen analysis in bogs and lakes (Kabailienė 2006) has shown that *Fraxinus* trees grew between 8000 and 2870 BC and spread widely throughout Lithuania in the Late Atlantic period (4500–3000 BC). The prevalence of *Fraxinus* during the Holocene in Western Europe was determined by the long-term (centennial and millennial) climate changes and human impact in the last millennium

(Davis *et al.* 2003). The anthropogenic impact on forests and woodlands is mainly responsible for the decrease of area occupied by broadleaf trees as a consequence of conversion to arable lands, building activity, and hardwood timber trade to Western Europe (Wazny 2002; Haneca *et al.* 2005; Kabailienė 2006). *Fraxinus* prefers fertile alkaline soils (Wardle 1961). To date, *Fraxinus* forests occupy about 2.5% of the total forest area in Lithuania and are mostly located on wet humus and carbonaceous soils of Central Lithuania.

Dendrochronological investigations on subfossil wood in Lithuania are mostly based on *Pinus* and *Quercus* wood from bogs and river deposits (Bitvinskas *et al.* 1978; Pukienė 1997; Pukienė 2003). Until now, *Fraxinus* wood from bogs in Lithuania had not been investigated using dendrochronological methods. The aim of this study was to assess the potential of the tree rings from subfossil *Fraxinus* found in bogs to document forest history in Lithuania during the Holocene.

SITE DESCRIPTION

Investigations were carried out in two bogs in the Žemaičiai Uplands in Western Lithuania (Figure 1). This region is distinguished by higher amounts of annual precipitation (738 mm, whereas the average in Lithuania is 683 mm over the 1924–2008), milder winters (the temperature for the coldest month, January, is -4.3°C , whereas the average in Lithuania is -5.7°C), and cooler summers (the temperature of the warmest month, July, is $+16.8^{\circ}\text{C}$, whereas the average in Lithuania is $+17.3^{\circ}\text{C}$). The Kegai low bog (a bog rich in minerals with drainage from a surrounding area to the center) is situated near the Kegai village in the Telšiai Administrative District of Lithuania ($55^{\circ}50'\text{N}$, $22^{\circ}17'\text{E}$). The bog has a rectangular shape approximately 40×70 m in size. The thickness of the peat layer is up to 3 m. The bog is overgrown by young trees and shrubs, such as *Salix*, *Alnus*, *Betula*, and *Populus*. Research was carried out expecting to find wood of *Quercus* for dendrochronological studies. During the investigation, 78 stem disks of wood were collected.



Figure 1. Location of the Bubėnai and Kegai study sites in Lithuania.

The Bubėnai high bog (an ombrotrophic peat bog that depends solely upon precipitation for moisture and nutrients) is located in the Plungė Administrative District of Lithuania and is approximately 25 km west from the Kegai bog ($55^{\circ}48'\text{N}$, $21^{\circ}53'\text{E}$). The bog has an irregular shape with an approximate size of 1.5×2 km; the depth of the peat layer is 5–7 m.

METHODS

The tree species present were identified using microscopic anatomic analysis (Schweingruber 1990).

Because long-term ring-width chronologies don't exist for *Fraxinus* in Lithuania, radiocarbon dates provided an initial timeframe for dating the samples. Seven *Fraxinus* samples (five from the Kegai bog and two from the Bubėnai bog), three *Quercus* samples, and one *Alnus* sample (both from the Kegai bog) were radiocarbon dated. The *Quercus* and *Alnus* wood was dated to better understand the history of bog formation. This work was accomplished at the Environmental Research Center of Vytautas Magnus University using a "Quantulus LSC 1220" high precision Liquid Scintillation Counter (Wallac OY, Turku, Finland). The chemical preparation of samples was performed at the Institute of Geology and Geography (Vilnius). Radiocarbon dates were calibrated using the CALPAL program (Weninger *et al.* 2003) with the INTCAL98 tree-ring calibration curve (Stuiver *et al.* 1998).

Tree-ring widths of each wood sample were measured along at least two radii to the nearest 0.01 mm using a LINTAB tree-ring measuring table and the TSAP 3.14 computer program (F. Rinn Engineering Office and Distribution, Heidelberg). Series obtained from several radii of each sample were crossdated by visual comparison (Eckstein 1987) of ring-width graphs and were checked statistically using TSAP to produce a mean series for each sample. According to the radiocarbon dates, the mean series were then crossdated among each other to obtain the floating curves. For this purpose, common statistics used in dendrochronological dating were applied, such as coefficient of similarity (glk) (Eckstein and Bauch 1969), correlation coefficient (r), and standard t-value (Baillie and Pilcher 1973). Common statistics applied in dendrochronology, such as mean sensitivity, standard deviation, and 1st-order autocorrelation, were calculated for each sample curve. The values of mean sensitivity are divided into three classes: low sensitivity (compliant series <0.15), medium sensitivity (0.16–0.29), and high sensitivity >0.30 (Till 1987). Frequencies of the cycles expressed in the tree-ring series of *Fraxinus* were assessed using a single series Fourier (Spectral) Analysis (Bloomfield 1976). For this purpose Statistica 6.0 (StatSoft, Inc. www.statsoft.com) was applied.

RESULTS

Species Identification

Six tree genera among the wood samples from the Kegai bog were identified: *Alnus* (48 samples), *Fraxinus* (11 samples), *Betula* (9 samples), *Acer* (7 samples), *Quercus* (3 samples), and *Pinus* (1 sample). *Fraxinus* wood was identified among three samples from the Bubėnai bog.

Radiocarbon Dating

The radiocarbon dates of seven *Fraxinus* samples from both bogs are presented in Table 1. The conventional radiocarbon ages for *Fraxinus* range from 5753 ± 34 to 3240 ± 45 BP. The calibrated dates indicate that *Fraxinus* from the oldest period grew approximately between 4700–

4600 BC. The other trees (Keu2, Keu3, and Keu27) grew later by at least one millennium (Figure 2). *Fraxinus* from the youngest period grew approximately between 1600–1500 BC (sample Keu43). The conventional radiocarbon ages of three *Quercus* wood samples range from 4599 ± 47 to 3892 ± 120 BP. Calibrated dates demonstrate that *Quercus* lived approximately between 3400 and 2300 BC. The dated *Alnus* grew much earlier—in the Late Boreal period (conventional age 7453 ± 79 BP and calibrated date 6320 ± 60 BC).

Dendrochronological Analysis, Crossdating, and Mean Curves

Ten out of the 11 *Fraxinus* samples from the Kegai bog and two of the three samples from the Bubėnai bog were suitable for dendrochronological analysis. Because of poor preservation, two *Fraxinus* samples were not measured.

The investigation shows that the ages of individual *Fraxinus* trees range from 59 to 238 rings (Table 1) with waney edge missing in all samples. The ring widths among *Fraxinus* samples vary from 0.44 to 0.78 mm. The radial growth of *Fraxinus* is characterized by low, medium, or high mean sensitivity (0.13–0.32). The standard deviation of tree-ring series ranges from 0.15 to 0.29, and autocorrelation from 0.46 to 0.85.

The crossdating of 12 *Fraxinus* series derived for each sample enabled six tentative floating mean curves to be constructed spanning 98 to 246 years, each including one to four samples. They are radiocarbon dated (Figure 2) to 4688–4576 BC (Keu1 and Keu54), 3540–3295 BC (Keu2, Keu3 and Keu27), 2829–2730 BC (Buu5), 2209–2112 BC (Keu36), 2030–1913 BC (Buu1), and 1573–1471 BC (Keu43, Keu49, Keu50 and Keu52). The similarity between the tree-ring series used for the construction of the floating mean curves is usually very high; coefficient of similarity varies from the lowest (66%) to the highest (82%), and t-value_{BP} from 6.6 to 15.7 (Figure 3).

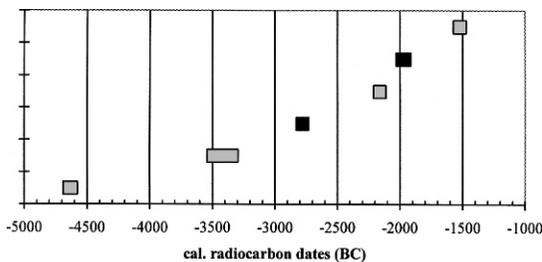
Abrupt growth depressions occurring every 40–60 years are common for three of the *Fraxinus* curves (Figure 4 curve B, series C and Figure 5 series B) dated to 3540–3295, 2209–2112 and

Table 1. Results of radiocarbon dating and characteristics of tree-ring series of subfossil *Fraxinus* samples found in the Kegai and Bubénaï bogs.

Sample	Radiocarbon Lab. No	C ¹⁴ Age (BP)	CalAge, p-68% (BC)	CalAge, p-95% (BC)	Span	Average Ring Width (mm)	Mean Sensitivity	Standard Deviation	1 st Order Auto-correlation
Keu1	Vs-1322	5753 ± 34	4610 ± 60	4730–4490	113	0.49	0.17	0.17	0.64
Keu2	Vs-1323	4590 ± 32	3340 ± 140	3620–3060	238	0.78	0.18	0.21	0.60
Keu3	Vs-1324	4593 ± 54	3320 ± 150	3620–3020	227	0.60	0.14	0.17	0.79
Keu27					235	0.73	0.15	0.21	0.75
Keu36	VDU-175	3753 ± 51	2160 ± 90	2340–1980	98	0.55	0.17	0.19	0.71
Keu43	Vs-1587	3240 ± 45	1520 ± 70	1660–1380	100	0.49	0.19	0.16	0.62
Keu49					87	0.60	0.28	0.21	0.51
Keu50					59	0.64	0.26	0.20	0.46
Keu52					86	0.52	0.24	0.16	0.46
Keu54					69	0.44	0.13	0.15	0.85
Buu1	Vs-1584	3610 ± 45	1970 ± 70	2110–1830	118	0.56	0.32	0.29	0.54
Buu5	Vs-1581	4210 ± 45	2780 ± 80	2940–2620	100	0.62	0.17	0.17	0.66

2030–1913 BC, respectively. Spectral analysis confirms the presence of 19, 29, 33, 41, 49, 58, 61, 82 and 98-year cyclic components among the patterns of these curves. No visible depressions are present among three curves dated to 4688–4576, 2829–2730 and 1573–1471 BC, respectively (Figure 4 curve A, series D and Figure 5 series A). Spectral analysis reveals the presence of shorter cycles for these series: 2, 4, 5, 6, 7, 8, 11, 12, 14, 15, 19, 22, 28, 29, 34, 37, 43, 44 and 56-year cyclic components.

A long growth decline is typical of four curves of *Fraxinus*: 4688–4576, 3540–3295, 2209–2112 and 1573–1471 BC (Figure 4 curves A, B, C and D). The trees in the 4688–4576, 3540–3295 and 2209–2112 BC chronologies have a sharp growth reduction before death, *i.e.* 39, 51, and 17% reductions, respectively, during the last five years in comparison to the five preceding years (Figure 4 curves A, B, and C).

**Figure 2.** Radiocarbon-dated floating curves of *Fraxinus* from the Kegai (gray pattern) and Bubénaï (black pattern) bogs.

DISCUSSION

Growth of *Fraxinus*

Fraxinus prefers fertile, moist, but well-drained sites. It is a common tree in waterlogged habitats, but the growth is usually poor (Wardle 1961). In northern habitats, *Fraxinus* is intolerant to winter colds, whereas in the Mediterranean region its prevalence is limited by hot summers (Wardle 1961). In Great Britain, *Fraxinus* is judged to be highly sensitive to summer rainfall (Wardle 1961). This is in agreement with the Tardif and Bergeron (1993) investigations in Canada, where a strong influence of climate factors in the year before the growth and current vegetation period was found. The studies demonstrated that *Fraxinus* growth in waterlogged sites is negatively affected by high discharge and longer duration of floods (Tardif and Bergeron 1993). Wardle (1961) has shown that *Fraxinus* is intolerant to water shortages in waterlogged sites where the roots are unable to penetrate deeply. This is in accordance with results obtained by Dufour and Piégay (2008) while investigating growth and regeneration of *Fraxinus* in floodplain forests.

The *Fraxinus* trees investigated in this study grew on peat soil. At present, peat bogs are not the typical sites for broadleaf species in Europe. Therefore, it is impossible to study the growth of modern *Fraxinus* in bogs. Baillie (1982) hypothesized that such atypical vegetation on bogs in the past may indicate drier geological periods.

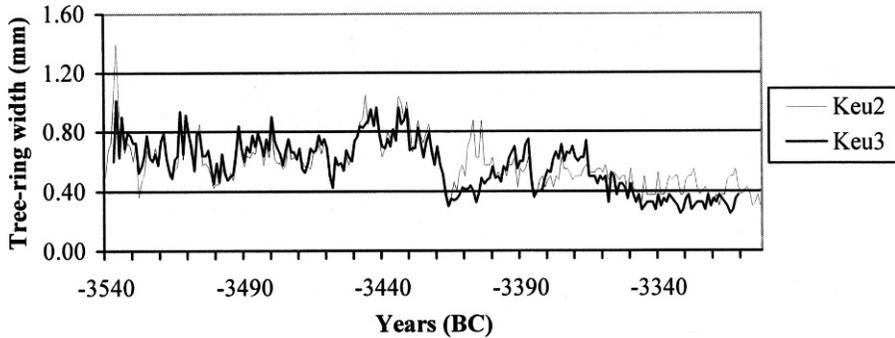


Figure 3. Tree-ring series Keu2 and Keu3 radiocarbon dated to ca. 3540–3303 BC and possibly originated from the same tree.

The radial growth of living broadleaf trees is poorly investigated in Lithuania. This is mainly a consequence of the prevalence of coniferous forests in Lithuania (57% of the total area) and the higher importance of coniferous wood in forest economy. Therefore, the number of published results on tree rings of broadleaf trees in Lithuania is limited (Bitvinskis *et al.* 1978; Pukienė 2003; Pukienė 2004).

The narrow tree rings (on average 0.58 mm/year) are typical for the *Fraxinus* trees investigated in this study (Table 1). They indicate poor growing conditions connected to a high water table of the bog. The average tree-ring widths of living *Fraxinus* trees in Lithuania are 2.08 mm (Karpavičius and Vitas 2006; personal observations). However, narrower tree rings (on average 1.44 mm) are common for *Fraxinus* growing in poor sites near bogs (personal observations). This contrasts with the results obtained by Dufour and Piegay (2008), who found larger rings in *Fraxinus* at sites near bogs.

The average mean sensitivity (Table 1) for subfossil *Fraxinus* trees (0.20) is similar to that observed for living *Fraxinus* and *Quercus* trees—0.21 and 0.23, respectively (Karpavičius and Vitas 2006; personal observations). The mean sensitivity for subfossil *Quercus* found in river sandy deposits is 0.24 (personal observations).

The standard deviation of subfossil *Fraxinus* was found to be 0.19, whereas for living *Fraxinus* and *Quercus* it is 0.99 and 0.68 respectively (Karpavičius and Vitas 2006, personal observations). The standard deviation of subfossil *Quercus* was similar to modern, at 0.70 (personal observations). The standard deviation indicates variation

in tree rings and increases along with tree-ring widths.

The autocorrelation for subfossil *Fraxinus* series is 0.64. It is smaller (statistically significant at $p = 0.04$) in comparison to living trees (0.73) (Karpavičius and Vitas 2006; personal observations). A similar autocorrelation (0.70) is typical for subfossil *Quercus* (personal observations). This indicates the unfavorable growth conditions and weaker overall trend in the growth patterns of *Fraxinus* in comparison to living trees. This is in agreement with the Pukienė (1997) investigations on subfossil *Pinus* carried out in an oligotrophic bog, where most trees did not demonstrate a downward trend related to increasing tree age.

Subfossil *Fraxinus* trees are usually older than living trees. The oldest age of subfossil *Fraxinus* reaches 238 years with outermost rings missing on all samples, whereas the average age of living trees is 76 years (Karpavičius and Vitas 2006). Dendrochronological investigation on subfossil *Quercus* wood in Lithuania has revealed that the oldest sample found in a bog contained 417 rings (personal observations). Comparatively old trees (on average, 155 tree rings) also predominate among subfossil *Quercus* from Smurgainiai river sediments, Western Belarus (personal observations). Dendrochronological crossdating of *Fraxinus* samples investigated in this study has revealed a high similarity among tree-ring patterns. Therefore, it may be supposed that a portion of the samples belongs to the same tree. For example, a high similarity between Keu2 and Keu3 dated to 3540–3303 BC (glk 0.80 and $t\text{-value}_{BP}$ 18.2) suggests that these samples originated from the same tree (Baillie 1982) (Figure 3).

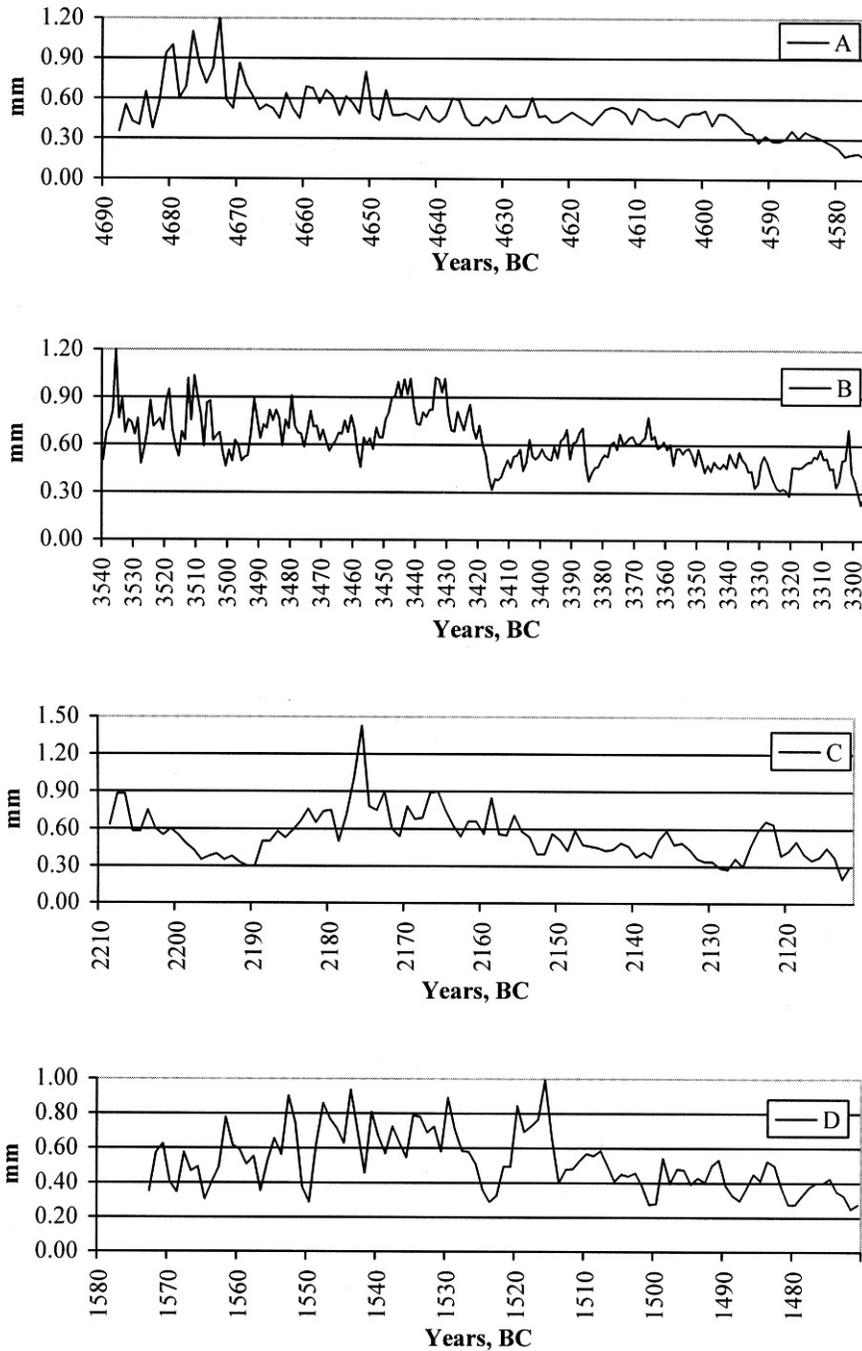


Figure 4. Floating tree-ring curves of *Fraxinus* from the Kegai bog: A—mean curve (two trees) radiocarbon dated to ca. 4688–4576 BC, B—mean curve (three trees) dated to ca. 3540–3295 BC, C—series (one tree) dated to ca. 2209–2112 BC, D—mean curve (four trees) dated to ca. 1573–1471 BC.

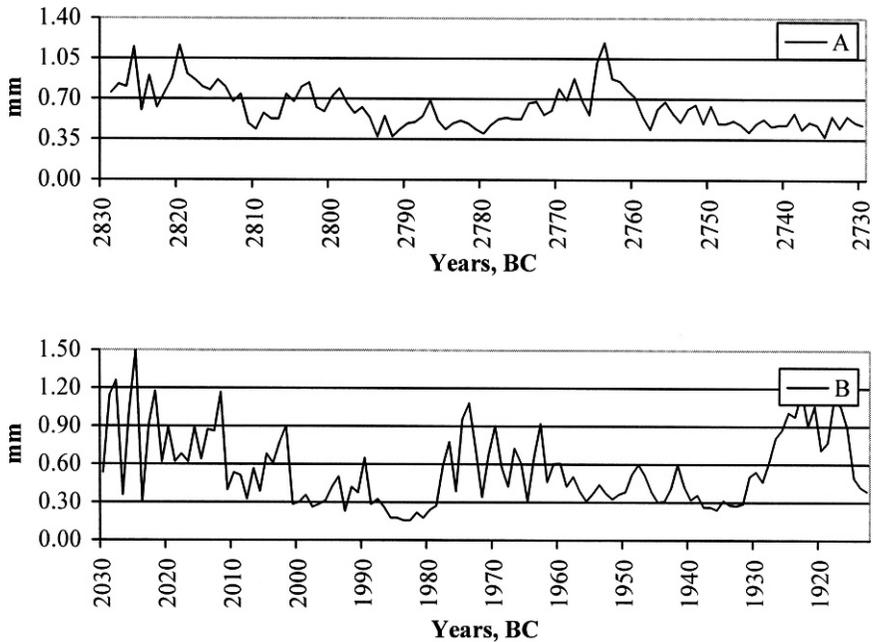


Figure 5. Floating tree-ring series of *Fraxinus* from the Bubėnai bog: A—series (one tree) radiocarbon dated to ca. 2829–2730 BC, B—series (one tree) dated to ca. 2030–1913 BC.

Fraxinus Distribution

The history of flora in Lithuania during the Holocene has been mainly reconstructed from palynological data (Kabailienė 1990; Kabailienė 2006). *Fraxinus* pollen was found in sediments dated to 8000 BC (with the maximum quantity observed in the Atlantic period from 4700–3000 BC). The prevalence of vegetation and forest species during the Holocene fluctuated depending on the long-term climate changes and anthropogenic activity (Kabailienė 1990). Dates based on palynological investigations are only approximate because disturbance may mix pollen into deeper layers of sediments, and the quantitative reconstruction of the prevalence of species is complicated because different plants produce unequal quantities of pollen during the flowering period (Kabailienė 2006).

Radiocarbon dating confirms that in the initial stages of the bog (Late Boreal period), it was overgrown by *Alnus* (approximately 6300 BC). This is in accordance with studies on bog history in Western Europe (Leuschner and Sass-Klaassen 2003). *Fraxinus* trees grew in the Late Atlantic and Sub-Boreal periods (approximately 4700–1500 BC). *Quercus* trees also grew in the bog

in the Late Atlantic and Sub-Boreal periods—approximately 4700–1500 BC and 3400–2300 BC, respectively. The Sub-Boreal period (3000–1000 BC) is characterized by a flourishing of coniferous and broadleaved species (*Pinus*, *Betula*, *Picea*, *Alnus*) in Lithuania (Kabailienė 2006). Therefore, *Fraxinus* wood dated to the Sub-Boreal period extends the available palynological information on the forest history in the Baltic region.

Occurrence of *Fraxinus* in Prehistoric Times

Investigation of pile-dwelling settlements from the Stone Age confirms that *Fraxinus* was a common tree in prehistoric times. For example, investigations at the Žemaitiškės-2 pile-dwelling settlement (Eastern Lithuania) have shown that *Fraxinus* posts predominate in wooden constructions (57%) (Pukienė 2004). Samples were radiocarbon dated to 4850–2500 BC. Because there are no forests with *Fraxinus* in this region of Lithuania at present, it might be supposed that *Fraxinus* was more widely distributed in prehistoric times in comparison to the present time (Pukienė 2004). These findings are in agreement

with investigations on prehistoric settlements in Slovenia (Čufar *et al.* 2005), where *Fraxinus* samples were dated to 3200–2500 BC. Our study on *Fraxinus* sub-fossil trees confirms that ash trees were quite common in the territory of Lithuania from approximately 4700 to 1500 BC.

Growth Depressions and Death

The growth depressions among three tree-ring curves of *Fraxinus* occurred with a periodicity of 40–60 years and lasted from several to ten or more years as illustrated in Figure 4 (B and C) and Figure 5 (B). Spectral analysis confirms the presence of longer cycles (from 19 to 98 years) in their growth patterns. Leuschner *et al.* (2002) has attributed growth depressions in *Quercus* to the rise of soil water, a finding that was confirmed by other investigations (Sass-Klaassen and Hanraets 2006). A sharp reduction of the growth before death in three tree-ring mean curves indicates a constant worsening of the growth conditions connected to the bog hydrological regime caused by a rise in the water level (Figure 4 A, B and C).

The depth of soil water in bogs is controlled by the precipitation and temperature regime (Mannerkoski 1991). Increased precipitation and rise of soil water causes a physiological response of trees typical to the anoxic environment by altering a variety of physical, chemical and biological processes, *i.e.* shortage of oxygen, accumulation of CO₂, increased solubility of mineral substances, reduction of Fe and Mn, anaerobic decomposition and formation of toxic compounds (Ponnamperuma 1984; Gambrell *et al.* 1991; Kozłowski 1997). The growth inhibition of trees is triggered by reduction in the rate of photosynthesis, lowering of the concentration of adenosine triphosphate, decreased absorption of nutrients, reduction of mycorrhizae, injury by toxic compounds, and shifts in hormone relations (Kozłowski 1997).

There are no visible persistent depressions in growth among the oldest (4688–4576 BC) and youngest (1573–1471 BC) mean curves of *Fraxinus* (Figure 4, A, D). The oldest samples are also characterized by narrower tree rings, smaller

variations in ring-width patterns, and higher autocorrelation (Table 1) that indicate a pronounced downward trend, and shorter cyclic components (from 2 to 56-year length). The different radial growth patterns of the oldest and youngest *Fraxinus* may be explained by (i) less contrast in climatic conditions in these periods or (ii) differences in site conditions. The second assumption is based on comprehensive studies of bog oaks in Western Europe. It was established there are two groups of trees: some were rooted on a mineral soil and overgrown by peat, whereas others rooted directly on a peat soil (Leuschner *et al.* 1987). A visible downward trend (Figure 4, A, B, C, D) confirms that trees probably grew on mineral soil (Vitas and Erlickytė 2007). On the other hand, the lifespan of the oldest *Fraxinus* coincides with an intensive formation of bogs in Lithuania (Kabailienė 2006) triggered by a humid Atlantic climate. Therefore, trees in this period probably grew on a thin peat layer and were later overgrown by an accumulation of peat. Because the roots of investigated *Fraxinus* were rotten, comprehensive soil examinations are missing and the number of samples is small. Therefore it is impossible to answer several questions related to the growth of trees, such as (i) did they grow on raised bog peat or on the fen peat? (ii) did the trees grow on a slope of the bog and did they accidentally fallen into the bog?

The lifetime of *Fraxinus* in the Kegai and Bubėnai bogs (Figure 5), especially during 4688–4576, 3540–3295, and 2829–2730 BC, corresponds to the phases of bog oak prevalence in Western Europe (Spurk *et al.* 2002; Leuschner and Sass-Klaassen 2003). This indicates that investigated *Fraxinus* were under the control of large-scale climate changes, involving wide areas of Europe and that *Fraxinus* seems to be sensitive to the same climate extremes (cooling and increased humidity) as *Quercus*. Results of the study are preliminary as they are limited by a small number of samples, and therefore, future investigations are needed. The current study extends our knowledge on the growth of *Fraxinus* in the Holocene pointing to greater age of the ancient trees and perhaps a wider distribution in different periods of the Holocene than has been established using palynological data.

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