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Dendroecological differences between *Taxus baccata* males and females in comparison with monoecious *Abies alba*

Received: 28 March 2011; Accepted: 24 May 2011

Abstract: *Taxus baccata* L. is a rare and endangered dioecious species in Europe. Species of this mating system are considered to be the most vulnerable to extinction. It is believed that one reason for this state may be the uneven reproductive effort and different habitat requirements of the two sexes. Silver fir and European yew have very similar ecological requirements, but fir is a monoecious species. The aim of this study was to compare the growth rate and the effect of precipitation and temperature on the annual tree-ring width of silver fir and both sexes of European yew. The study site was the Knyazhdvir reserve in western Ukraine, located near the limit of the geographical range of both species. Knyazhdvir reserve is the site of one of the last yew populations in Europe with a large number of individuals (about 15,000 individuals above 1.3 m height) growing alongside fir. Wood samples were taken from 15 male and 15 female specimens of *T. baccata* and from 15 specimens of *A. alba* and were subjected to a standard dendrochronological procedure. The results showed high positive correlation between the temperatures in February and March and the tree-ring width in the studied species and genders. The response of annual tree-ring width to the examined climatic factors was relatively similar in yew and fir. However slight differences were found between males and females of *T. baccata*. The growth rate decreased more rapidly in females compared to males, probably following sexual maturation. Precipitation in April had a positive effect on firs and female yews, but not on male yews. This confirms earlier reports of the requirement of female specimens of dioecious species for a higher humidity than male individuals.

Additional key words: reproductive effort, dendrochronology, European yew, silver fir

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Introduction

Since the dawn of history the European yew has been excessively exploited by humans (Thomas and Polwart 2003), leading to a significant reduction in the area covered by this species. As a result, yew is now an endangered species and woodlands dominated by *Taxus* have received priority habitat status under Annex I of the EU Habitats Directive.

Very little is known about *T. baccata* ecology. Despite the protection of this species, natural regeneration has only been observed in a few places. In the short term this situation may lead to the extinction of many valuable populations (Ruprecht et al. 2010). The main reasons for the low regeneration success of this species are considered to be the negative impact of animals (Myserud and Østbye 2004; Farris and Filigheddu 2008; Perrin et al. 2006), excessive shad-

ing (Iszkuło and Bortyński 2006; Dhar et al. 2008), and the interaction between shading and low temperatures (Iszkuło 2010). The yew is a dioecious species. Due to the small number of individuals in most populations, an important factor that may affect the reproductive success of yew could be the differences in the ecological requirements of female and male individuals (Iszkuło et al. 2009). Several studies have shown that species with a dioecious mating system are more likely to become extinct than others (Heilbuth 2000; Vamosi and Vamosi 2005).

One of the reasons for this phenomenon could be the greater reproductive effort incurred by females, which produce not only flowers, but also seeds with arils. Reproductive effort may directly affect the growth and development of vegetative organs (Leigh et al. 2006, Zunzunegui et al. 2006). In most cases females grow more slowly than males (Obeso 2002, Leigh et al. 2006). Moreover, female plants are usually more demanding with regards site fertility and moisture (Freeman et al. 1976, Iglesias and Bell 1989, Bertiller et al. 2002). Female yews were found to have smaller diameter and height compared to males. In addition, the percentage of females in comparison with males was positively correlated with precipitation (Iszkuło et al. 2009). This was confirmed by dendrochronological studies, indicating a slightly greater correlation of the tree-ring width of females with precipitation compared to males (Cedro and Iszkuło 2011). A reduction in the growth rate of females compared to males following sexual maturity has also been shown (Cedro and Iszkuło 2011).

No studies have been performed for the species with different mating system, growing in the same area. Moreover, differences between sexes of dioecious tree with respect to the monoecious could be more distinctive. In our opinion, silver fir is an appropriate species for the comparison with the yew, although it has a monoecious mating system. These two species have similar requirements for light, temperature and moisture (Ellenberg et al. 1991; Brzeziecki and Kienast 1994). The aim of this study was to compare the growth rate and effect of precipitation and temperature on the tree-ring width of both European yew males and females in comparison with silver fir.

Materials and methods

The studied population is located in the Knyazhdvir reserve in western Ukraine, at longitude 24°50'W and latitude 48°30'N. It is one of the largest populations of yew in Europe (Thomas and Polwart 2003). An additional advantage of this population for this study is the successful natural regeneration of yews and firs (Iszkuło et al. 2005) and its location at the limit of its geographical range (Jalas and Suominen 1973), which should emphasize the differences between species

and the two sexes. It is situated in the foothills of the Outer Eastern Carpathians (Konracki 1989), on north-facing slopes above the river Prut, at an elevation of 320–460 m a.s.l. The slopes are composed of Neogene sandstones covered with Pleistocene deposits, mostly loams and/or sandy-clays. These are undercut by the river, with several water-bearing horizons being exposed. The steepness and permanent waterlogging of the slopes result in landslides. Brown or slightly acid brown soils that are frequently leached and permanently humid predominate within the nature reserve (Boratyński et al. 2001). *Taxus baccata* is common in the second layer of the stand.

15 wood samples of silver fir and 30 from yew (15 females and 15 males) were collected using a Pressler borer at 1.3 m height. Trees were selected according to dendrochronological methodology (Schweingruber 1988), i.e. dominant trees growing in the close of neighbourhood were selected to avoid differences in environmental conditions.

The presence of micro- and mega-strobili and seeds or remains of arils was used to determine the sex of each sampled individual.

The samples were scanned at 1200 dpi and a ring-width analysis was conducted using a WinDendro image analysing system. Following this analysis, a computerized measurement system (WinDENDRO™ Ver. 2008d) was used to measure individual ring widths to the nearest 0.001 mm. Signal homogeneity was subsequently verified using the COFECHA software (Holmes 1994).

Chronologies were made separately for male and female trees of *Taxus baccata* and for *A. alba*: one non-detrended raw-data series, and one detrended residual series. The non-detrended raw-data chronologies were used to test the differences in growth between *A. alba* and *T. baccata* male and female trees. The analysis of climatic influence on tree growth was based on detrended data. After crossdating, individual path measurements were standardized using the computer program Arstan (Holmes 1994). A two-stage detrending method was used, in which the data were first detrended using a negative exponential curve or a linear trend, and later in the second step using a cubic-smoothing spline with a 50% frequency cutoff to remove any remaining inherent age or growth trends (Holmes 1994). Dendroclimatological analyses used meteorological data collected from 1950 to 2007 by the weather station in Chernivtsi 48° 18'N, 25°55'E, 246 m a.s.l. located 80 km SEE from the study population. The average annual temperature was 8.1°C while the average rainfall was 655 mm (Fig. 1).

To test for climatic effects on both male and female trees, bootstrapped correlation functions (Guiot 1991) were computed using the software DENDROCLIM2002 (Biondi and Waikul 2004). In each case,

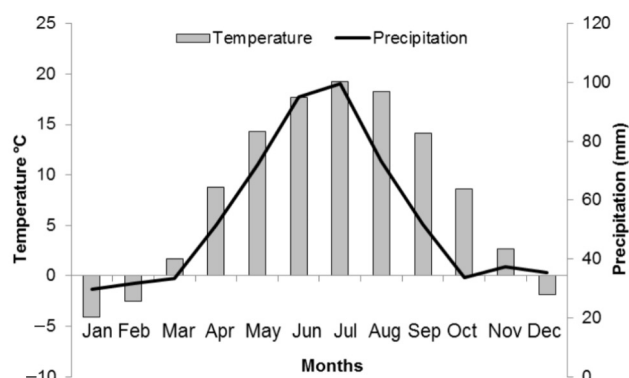


Fig. 1. Average monthly temperature and average sum of monthly precipitation at Chernivtsi meteorological station (1950–2007)

the residual chronology was used as the independent variable.

Statistical analyses (Tukey-Kramer Test) were conducted using JMP 8.0 software (SAS Institute).

Results

The average diameter at 1.3 m of the fir was 64.6 cm. Males were thicker (14.2 cm) than females (13.7 cm), but differences were significant only between fir and both sexes (Tukey-Kramer test). The average annual tree-ring width of the fir (2.92 mm) was almost four times wider than that of the yew (males 0.740 mm and females 0.715 mm) (Figs. 2A, 3). The sampled firs

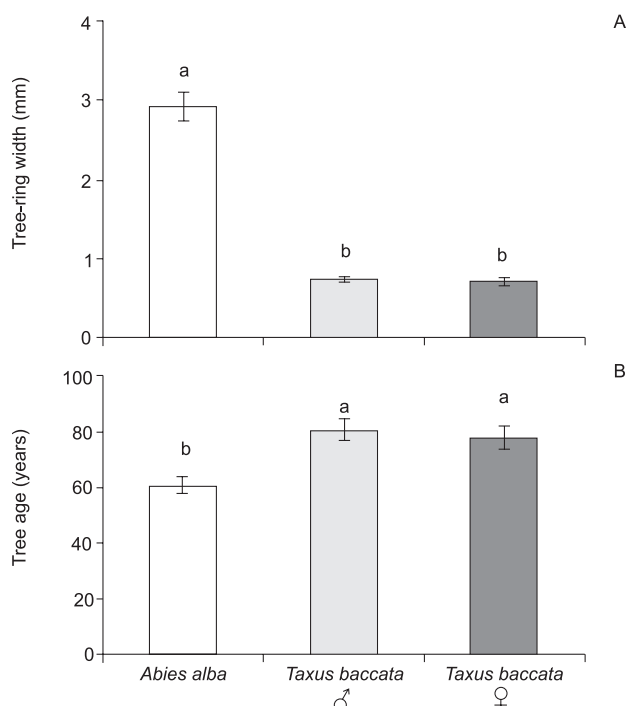


Fig. 2. Average tree-ring width (A) and age (B) of *Abies alba* and *Taxus baccata* male and female trees in Knyazhdvir reserve. Different letters mean significant differences between female and male and west and east slopes ($P=0.05$, Tukey-Kramer test)

were also about 10 years younger than the yews. Although male yews had a slightly wider tree-ring width and were about 3 years older than females, the differences were not statistically significant (Fig. 2B).

The cumulative tree-ring growth rate was also much higher in the fir than in the yew (Fig. 3A). At the age of 30 years the growth rate of female yews was reduced compared to the males. This trend continued until the end of the analysed period (Fig. 3b). However, when comparing the average tree-ring width of females and males in different years these relationships were not as clear. In some periods the tree-ring width of the females was wider than that of the males.

The course of the annual increment in tree-ring width was very convergent for both species and both sexes in *T. baccata*. This indicates the influence of the same environmental factors (mainly climate) on tree-ring width variation (Fig. 4).

Temperature had a greater influence on tree-ring width than precipitation in the case of yews and firs. There was a surprising negative correlation between temperature in the previous July and September and tree-ring formation in both species and male and female trees of yew (Fig. 5a). As expected, there was a

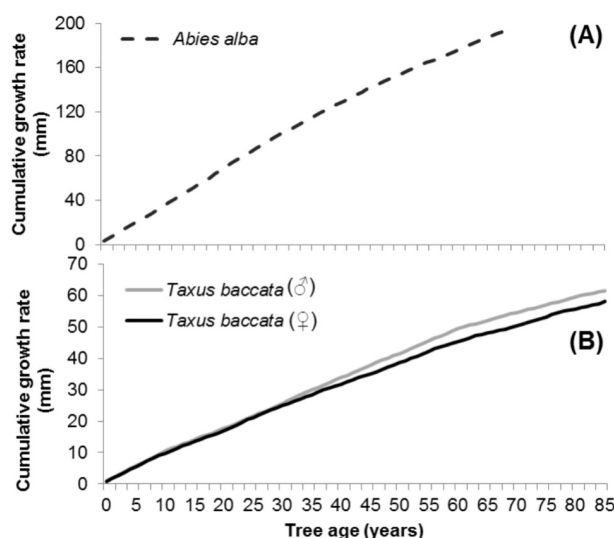


Fig. 3. Relationship between cumulative tree-ring width and tree age of *Abies alba* (A) and *Taxus baccata* males and females (B)

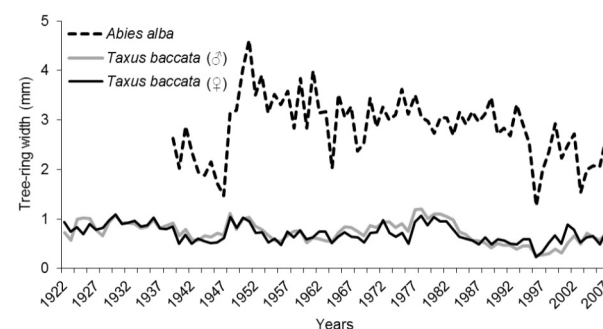


Fig. 4. Similarity of tree-ring width and age of *Abies alba* and *Taxus baccata* males and females

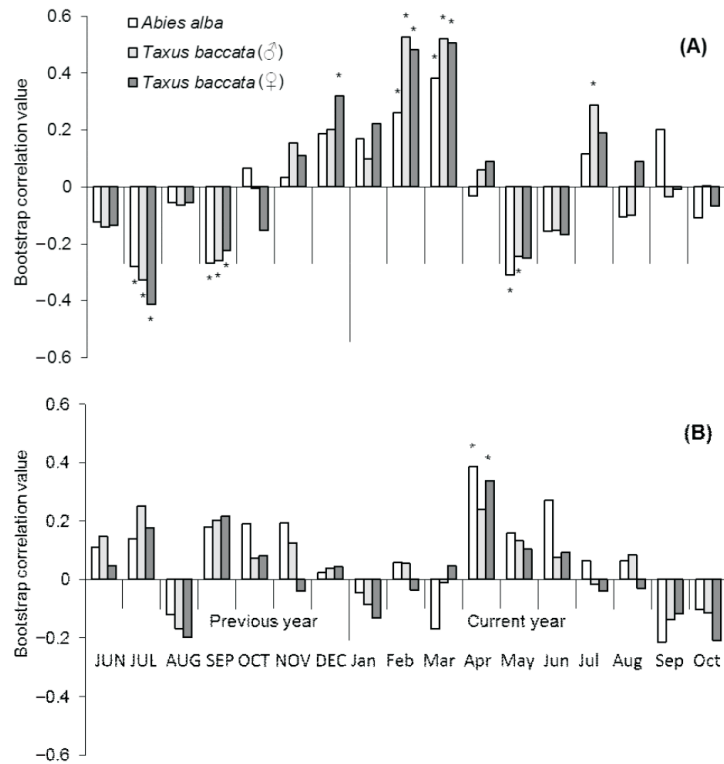


Fig. 5. Bootstrap correlation values for the previous-year and current-year monthly mean temperature (A) and sum of monthly precipitation (B). Asterisks indicate a significant relationship ($p < 0.05$)

high positive correlation between the temperatures in February and March and the tree-ring width in the studied species and genders. In addition, there was a positive correlation between the tree-ring width and the temperature in December in females. The temperature in May was negatively correlated with the tree-ring width of firs and males of *T. baccata*. A positive correlation was found between the temperature in July and the annual tree-ring width of *T. baccata* males (Fig. 5a).

In the case of precipitation only the sum of average rainfall in April had a significant positive impact on *Abies alba* and females of *T. baccata* (Fig. 5b).

Discussion

Yew and fir occupy very similar ecological requirements and grow in similar communities. However, silver fir trees have much potential growth (height and diameter) than the European yew (Brzeziecki and Kienast 1994). In addition, yew grows in the second layer of the forest (Thomas and Polwart 2003). Therefore, firs were expected to show a higher growth rate than yews.

The high positive correlation between the tree-ring width of *T. baccata* and *A. alba* and the winter–spring temperature confirms earlier studies (Cedro and Iszkuło 2011; Feliksik 1990; Manetti and Cutini 2006; Koprowski and Glawenda 2007; Lebourgeois 2007; Feliksik and Wilczyński 2009; Bijak 2010). The

higher positive correlation between tree-ring width and winter temperatures may indicate a slightly greater sensitivity of yew to low winter temperatures compared to fir. However, the similar response of the annual increments to precipitation and temperature should be noted, confirming the high ecological similarity of European yew and silver fir. Yew and fir are located in the same or very similar ranks in different ecological systems defining habitat requirements (Ellenberg et al. 1991; Brzeziecki and Kienast 1994; Zarzycki et al. 2002). Given the relatively small differences in the reactions to climate between the yew and fir, it was particularly interesting to compare the male and female yews.

As observed in other dioecious species (Bañuelos and Obeso 2004; Montesinos et al. 2006) the tree-ring width of *Taxus baccata* females in Knyazhdvir reserve was lower than that of males. The differentiation in tree-ring width between males and females probably began when the yew trees reached sexual maturity, possibly because of the assumed greater reproductive effort of females in comparison with males (Cedro and Iszkuło 2011). The reduced growth of vegetative organs is linked to the shift from vegetative growth to sexual reproduction (Morris 1951; Powell 1977; Koenig and Knops 1998). The growth rate of females and males equalized after the period of differentiation. This confirms the hypothesis that for the dominance of males over females in dioecious species is responsible the initial period of sexual maturity and

abundant production of seed cones (Iszkuło and Boratyński 2011). Equalization of the reproductive effort may be associated with more abundant strobilus production in males than in females, similarly as in *J. communis* (Ward 2007).

There was a negative correlation between temperatures in July and September in the year prior to the formation of the annual tree rings and their width. Similar results were observed in several silver fir populations in Poland (Feliksik 1990; Bijak 2010), in the Alps, and in Mediterranean areas (Carrer et al. 2010) as well as in yew populations (Cedro and Iszkuło 2011). In the case of *A. alba* this was explained by the negative impact of drought and high temperature (Feliksik 1990). There is another possible interpretation of this phenomenon. Summer is the period of seed maturation and simultaneous formation of generative buds in *A. alba* (Hejnowicz 1975) and in both sexes in *T. baccata* (Bugala 1975). It is possible that trees only form large numbers of generative buds and later flowers and cones at high temperatures, which thus result in increased reproductive effort. High seed production in the previous year may limit tree-ring growth in the current year (Cedro and Iszkuło 2011). The abundant production of seeds and cones had a negative impact on current year of *Abies balsamea* tree-ring width (Morris 1951) and height (Morris 1951; Powell 1977).

However, according to a recent study in Poland, only female individuals of yew react negatively to August temperatures (Cedro and Iszkuło 2011). This difference in the gender response may be due to climatic differences. The average temperature at Chernivtsi meteorological station (the study area) was about 1.3°C higher in July, 0.8°C higher in August and 0.7°C higher in September than at Kórnik in central Poland (Fig. 1; Cedro and Iszkuło 2011). This suggests a different response of the two sexes depending on the specific climatic conditions, especially in areas at the limit of the geographical range.

In the case of precipitation only the average sum of rainfall in April was positively correlated with the annual tree-ring width of fir and female yew. The lack of a statistically significant relation with males may indicate that females are slightly more demanding with regards water. Similar results were obtained for other yew populations (Cedro and Iszkuło 2011). These results confirm previous studies concluded that female specimens of dioecious species are more demanding with respect to moisture than males (Freeman et al. 1976; Ward et al. 2002). It was found, that number of *T. baccata* females decreases at the sites with less precipitation (Iszkuło et al. 2009). In opposite, male individuals dominate on higher and drier microsites (Freeman et al. 1976; Faliński 1998). Such a situation also makes transport of pollen grains over longer distances possible for males (Obeso 2002).

Conclusions

Silver fir and European yew tree-ring width responded similarly to temperature and precipitation. Comparison of dioecious and monoecious species confirmed that male and female individuals of dioecious *T. baccata* respond to climatic factors in a different way. This study provides indirect evidence of differences in the habitat requirements of the two sexes.

Acknowledgments

This study was supported by the Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland. I thank Dr. Dmytro Yakushenko for help during the fieldwork.

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