

DO FEMALES DIFFER FROM MALES OF EUROPEAN YEW (*TAXUS BACCATA* L.) IN DENDROCHRONOLOGICAL ANALYSIS?

ANNA CEDRO¹ and GRZEGORZ ISZKUŁO^{2,3*}

¹Climatology and Marine Meteorology Department, Szczecin University, Szczecin, ul. Wąska 13, 71-415 Szczecin, Poland

²Institute of Dendrology, Polish Academy of Sciences, ul. Parkowa 5, 62-035 Kórnik, Poland

³University of Zielona Góra, Department of Biology, Prof. Z. Szafrana 1, 65-516 Zielona Góra, Poland

ABSTRACT

Female and male plants often differ in reproductive effort and habitat requirements. The aim of this study was to analyze these differences between the sexes and the effect of climate on tree-ring width in European yew (*Taxus baccata*). The study was conducted in five yew populations in western Poland. Wood samples were taken from 196 trees (98 females and 98 males) and subjected to the standard procedure of dendrochronological dating. Mean tree-ring width was significantly higher in males since about the beginning of sexual maturity. No such relationship was observed in the youngest population, which is the most distant from the current geographic limit for this species. In most of the analyzed populations, width of tree rings in female individuals, in contrast to males, was negatively correlated with high temperatures in August and September in the year prior to the formation of the tree ring, and correlated positively with precipitation in June and July in the current year. The differentiation of tree-ring width between males and females likely began when the yew trees reached sexual maturity, probably because of the assumed greater reproductive effort of females in comparison with males. The lack of difference in the youngest population may result from a short time since the beginning of sexual maturity or from a milder climate in that region. Different reactions of the two sexes to climate indicate that this may affect the range and viability of populations at the limits of the range.

Keywords: Dendroclimatology, dioecy, tree-ring width, resource allocation, yew, Poland.

INTRODUCTION

Only 6% of all species of the world's flora are dioecious (Givnish 1980). In many parts of the world, however, the contribution of dioecious plants is much greater than 6% and often exceeds 25% (Ward *et al.* 2002; Krishnan and Ramesh 2005). At the same time, many studies show that dioecious plants are more likely to become extinct than other mating systems (Heilbuth 2000; Vamosi and Vamosi 2005). One of the major reasons why dioecious plants are more vulnerable to increased mortality, apart from the decreasing numbers of seed-bearing individuals, is an assumption of the greater reproductive effort of one sex (de Jong and van der Meijden 2004; Iszkulo *et al.* 2009). 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 in regard to site fertility and moisture (Freeman *et al.* 1976; Iglesias and Bell 1989; Bertiller *et al.* 2002).

One very important factor that influences greater allocation of females is seasonal scale of resource investment. Males have maximum reproductive effort at the time of flower production. Later on, males do not invest resources in reproduction. Females, however, have the main reproductive effort from the time when ovules are pollinated, because ripening of fruit is more costly than flowering (Obeso 2002; Montesinos *et al.* 2006). Costs of reproduction are often divided into direct costs (incurred at the time of the reproduction process) and indirect costs (connected with delayed or demographic costs of reproduction)

*Corresponding author: iszkulo@man.poznan.pl

(Newell 1991; Nicotra 1999). Indirect costs of reproduction are interpreted as the demographic consequences of resource investment in the reproductive process (Obeso 2002). These indirect costs are often subdivided into short (reduced growth or reproduction in the subsequent season) and long-term costs (Newell 1991; Ashman 1992; Obeso 2002). Detection of indirect reproductive costs in the short term might be difficult owing to physiological compensation mechanisms (Obeso and Retuerto 2002). Long-term cumulative variables such as tree-ring width are often used as a proxy of vegetative investment in woody plants (Obeso 1997; Silvertown and Dodd 1999). Differences between males and females in yew are typical for dioecious plants. Males of yew are taller and of larger diameter. The sex structure of the population changes with tree age and there are fewer female individuals (Iszkulo *et al.* 2009). Simultaneously, percentage of females in comparison to males increased with increasing sum of precipitation. This may indicate that female individuals require more moisture (Iszkulo *et al.* 2009).

Progress in dendrochronological methods enables analysis of the effect of sex growth dynamics and plant reaction to climate. Research on a population of *Juniperus thurifera* (Montesinos *et al.* 2006) and seven populations of *Rhamnus alpinus* (Obeso *et al.* 1998) showed that tree-ring growth after sexual maturity has been reached is reduced in both sexes. Furthermore, females experience a significantly stronger growth reduction than males, which indicates a lower vegetative allocation in females. In addition, growth is positively correlated with precipitation in the previous winter and spring in male trees, but only with precipitation in the previous spring in females of *Juniperus thurifera* (Montesinos *et al.* 2006). The tree-ring growth of female trees of *Rhamnus alpinus* differs significantly from that of males in periods with low annual precipitation, which could exacerbate the costs of reproduction (Banuelos *et al.* 2004). Also, in *Austrocedrus chilensis*, at the majority of studied sites, mean tree-ring width was greater in males. No difference in the reaction of this plant to climatic factors was observed, however (Rovere *et al.* 2003). In the

available literature on European yews, no studies of this type have been found. Tree-ring width measurements in yew from NW Poland, conducted without reference to sex, revealed a decisive influence of temperature in winter months and of precipitation in summer on cambial activity and tree-ring formation (Cedro 2004, 2005).

Research on the effect of sex on radial growth dynamics has been conducted in only a few dioecious species, including a single population of *Juniperus thurifera* (Banuelos *et al.* 2004; Montesinos *et al.* 2006), and thus research of this type is needed. Also supporting a need for this type of research is the observed direction of global climatic change, which can adversely affect dioecious species. Populations located near the limits of the species range, and threatened plants in particular, can be at greater risk of extinction if one sex is more sensitive to changing environmental factors (Iszkulo *et al.* 2009).

We formulated and tested the following hypotheses in this study: (1) mean tree-ring width is smaller in female individuals than in males; (2) differences between the sexes in tree-ring width appear after they reach sexual maturity; (3) males and females react differently to climatic factors.

MATERIAL AND METHODS

European yew (*Taxus baccata*) trees from five populations of western Poland were studied (Figure 1, Table 1). The southernmost sites are located on northeastern slopes of the Bardzkie Mountains, in the Cisowa Góra (population 1) and Cisy (population 2) nature reserves, and on the Bolków-Wałbrzych foothills in the Przełomy Książa reserve near Książ (population 3). Central Poland is represented by yews growing in the Kórnik Arboretum (population 4), and the northern part of the country by the Cisy Rokickie reserve near Rokita (population 5). In total, wood samples were taken from 196 adult trees (age between 48 and 168 years at 1.3 m height), comprising 98 females and 98 males. The presence of micro- and mega-strobili and seeds or remains of arils was used to determine the sex of every individual. Tree-ring widths were measured twice from the pith towards the bark, to the nearest



Figure 1. Location of the populations studied marked with filled circles. Range of European yew is marked in grey (after Jalas and Suominen 1973). Meteorological stations are marked with filled triangles.

0.01 mm using Dendrometer software (*Dendrometer 1.0* (2000) developed by B. Mindur, Kraków, Poland).

The samples were collected with a Pressler borer at breast height; when possible, each tree was sampled twice ($n = 310$). Also, we measured trunk circumference at breast height. We measured a total of 28,408 tree rings. In addition, we recorded presence of very narrow rings and very wide rings, or tree rings identified by different anatomical characteristics, traumatic zone, compression wood, false and missing ring or density fluctuation.

The time series were analyzed with the TRRAD module of the TREE RINGS package (Krawczyk 1995; Krawczyk and Krąpiec 1995) and visual crossdating was done by DendroGraph software (Walanus 2001). Following that, if statistical indicators were high (linear correlation

coefficient k , values of Student- t test, and Gleichläufigkeit GI , *i.e.* a measure of the year-to-year agreement between the interval trends of two series) (Eckstein 1969), then results of the measurements of both samples from the given tree were averaged to obtain its growth curve. Subsequently, classical dendrochronological techniques (crossdating—the procedure of matching variations in ring width among several tree-ring series, which allows the identification of the exact year in which each tree ring was formed) (Kaennel and Schweingruber 1995) were used to compile a local chronology, which underwent quality control using COFECHA software (DPL package; Holmes 1983, 1994). Seventy-five female and 80 male trees were exactly dated and then used to build chronologies. We made two sets of separate chronologies for male and female trees, one that averaged unmodified ring-width series and one that averaged the detrended and indexed growth series.

For analysis of cumulative ring width, we used only the samples with juvenile wood or visible pith, or the number of tree rings to the pith was reliably assessed (on the basis of their pattern). The second chronology was indexed by double detrending method and negative exponential curve, ARSTAN module of the DPL package (Holmes 1983, 1994) to highlight annual variability in tree-ring width and to eliminate long-term trends (*e.g.* a centennial trend). The compiled chronology (residual chronology) served as a tool for dendroclimatological analysis of response functions.

The climate *vs.* tree-ring width relationship was explored along with the response-function analysis (Fritts and Xiangding 1986; Cook and Kairiukstis 1992). The response function was calculated with the DPL software package (RE-

Table 1. Characteristics of analyzed *Taxus baccata* populations.

| No. | Population | No. of Samples | Region | Altitude (m a.s.l.) | Geographic Coordinates | |
|-----|-------------|----------------|------------------|---------------------|------------------------|---------|
| 1 | Cisowa Góra | 22♀, 21♂ | Bardzkie Mts. | 395–550 | 50°55'N | 16°69'E |
| 2 | Cisy | 19♀, 22♂ | Bardzkie Mts. | 370–480 | 50°54'N | 16°73'E |
| 3 | Książ | 17♀, 16♂ | Wałbrzyskie Mts. | 353–433 | 50°50'N | 16°17'E |
| 4 | Kórnik | 20♀, 20♂ | Września Plateau | 75 | 52°25'N | 17°06'E |
| 5 | Rokita | 20♀, 19♂ | Goleniów Plateau | 25 | 53°57'N | 14°28'E |

Table 2. Climatic characteristics from meteorological stations. T = air temperature; P = precipitation.

| Met. Station | Annual T _{mean} (°C) | Monthly T _{min.} (°C) | Monthly T _{max.} (°C) | Growing Period (days) | Annual P (mm) | Monthly P _{min.} (mm) | Monthly P _{max.} (mm) | Snow Cover (days) |
|--------------|----------------------------------|-----------------------------------|-----------------------------------|--------------------------|------------------|-----------------------------------|-----------------------------------|----------------------|
| Kłodzko | 7.4 | -2.2 (Jan) | 16.7 (Jul) | 200–210 | 599 | 22 (Jan) | 97 (Jul) | 80–100 |
| Kórnik | 8.3 | -1.7 (Jan) | 18.5 (Jul) | 220 | 544 | 31 (Feb) | 73 (Jul) | 40–50 |
| Szczecin | 8.6 | -0.5 (Jan) | 17.9 (Jul) | 225 | 534 | 31 (Feb) | 69 (Jul) | 40–50 |

SPO module; Holmes 1983, 1994) with mean monthly air temperature and monthly total precipitation as independent variables. Effects of climatic factors on tree-ring width sequence were studied with the response function analysis for 16-month-long periods (from June of the previous year to September of the current year).

Analysis of variance was used to study the relationships between populations and sex in analyzed populations. The analyses were conducted using JMP software (SAS Institute Inc.).

Dendroclimatological analyses used meteorological data collected from 1948 to 2005 at several sites: the weather station of the Institute of Meteorology and Water Management in Szczecin, located 41 km SSW of population 5; a station in Kłodzko, located 10 km S of populations 1 and 2 and 50 km SE of population 3; and the station of the Institute of Dendrology, Polish Academy of Sciences, located in the Kórnik Arboretum, very close to population 4 (Table 2).

RESULTS

Differences in Tree-Ring Width between Males and Females

Analysis of variance showed a significant effect of the analyzed populations and sexes on tree-ring width (Table 3). Therefore, analyzed populations and sexes had different growth rate.

Table 3. Significance of effects of population and sex on tree-ring width in European yew.

| Source of Variation | df | F | p |
|---------------------|----|-------|---------|
| Population | 4 | 58.19 | <0.0001 |
| Sex | 1 | 11.59 | 0.0009 |
| Population × sex | 4 | 1.79 | 0.1347 |

(ANOVA, N = 155)

Lack of interaction between sex and populations (Table 3) means that differences between sexes have a similar tendency and male yews had higher average ring widths than females (Table 4). The age at which sex-based differentiation in growth began varied from site to site (Figure 2). At population 1, females experienced lower growth rates than males after the age of 10 years. In population 2, the growth difference became visible after age 15, and in population 4 the division did not occur until age 30 (Figure 2). The poor condition of the cores near the pith and juvenile wood from population 3 prevented accurate age determination and therefore they were not included in this analysis.

Dendroclimatological Analysis

Temperature in winter, from December of the previous year through March of the current year, correlates positively with male and female growth (Table 5). Temperatures of August and September of the previous year and June of the current year affect tree-ring width for females (statistically significant level for $p \leq 0.05$ in August: population 2 and 3, $r = -0.14$; population 4, $r = -0.26$; in September: population 2, $r = -0.14$, population 4, $r = -0.24$, population 5, $r = -0.19$). In those months, negative values of regression coefficients prevail, which means that a decrease in temperature is accompanied by increased cambial activity. Average June and July precipitation correlates well with increased growth of females (statistically significant level for $p \leq 0.05$, in June: population 2, $r = 0.17$; population 3, $r = 0.18$; population 5, $r = 0.22$). Additionally, in males August temperatures have an effect (positive regression), whereas for precipitation, statistically significant values are more numerous only in October of the year preceding growth (Table 5).

Table 4. Statistical data of measured and non-indexed chronologies.

| Population | Sex | No. of Years | Time Span | No. of Samples | Mean Ring Width (mm) | Std. Deviation | RESIDUAL CHRONOLOGY | | | | |
|-----------------|-----|--------------|-----------|----------------|----------------------|----------------|---------------------|--------|------------------|----------------|-------|
| | | | | | | | Mean Sensitivity | Median | Mean Sensitivity | Std. Deviation | |
| Cisowa Góra (1) | ♀ | 173 | 1835–2007 | 14 | 0.58 | 0.46 | 0.34 | 0.98 | 0.25 | 0.22 | 0.02 |
| | ♂ | 218 | 1790–2007 | 14 | 0.65 | 0.51 | 0.32 | 0.99 | 0.26 | 0.22 | -0.09 |
| Cisy (2) | ♀ | 168 | 1840–2007 | 15 | 0.48 | 0.29 | 0.30 | 0.99 | 0.23 | 0.21 | 0.01 |
| | ♂ | 171 | 1837–2007 | 20 | 0.60 | 0.37 | 0.30 | 1.02 | 0.25 | 0.21 | 0.01 |
| Książ (3) | ♀ | 205 | 1803–2007 | 10 | 0.43 | 0.35 | 0.31 | 0.98 | 0.27 | 0.24 | 0.02 |
| | ♂ | 190 | 1818–2007 | 10 | 0.51 | 0.32 | 0.31 | 1.00 | 0.24 | 0.20 | -0.15 |
| Kórnik (4) | ♀ | 148 | 1858–2005 | 18 | 0.88 | 0.51 | 0.32 | 1.00 | 0.25 | 0.22 | 0.02 |
| | ♂ | 105 | 1901–2005 | 19 | 1.44 | 0.72 | 0.33 | 0.99 | 0.33 | 0.27 | -0.08 |
| Rokita (5) | ♀ | 49 | 1959–2007 | 18 | 1.02 | 0.50 | 0.39 | 1.01 | 0.31 | 0.28 | 0.19 |
| | ♂ | 51 | 1957–2007 | 17 | 1.06 | 0.50 | 0.39 | 1.07 | 0.28 | 0.24 | -0.02 |

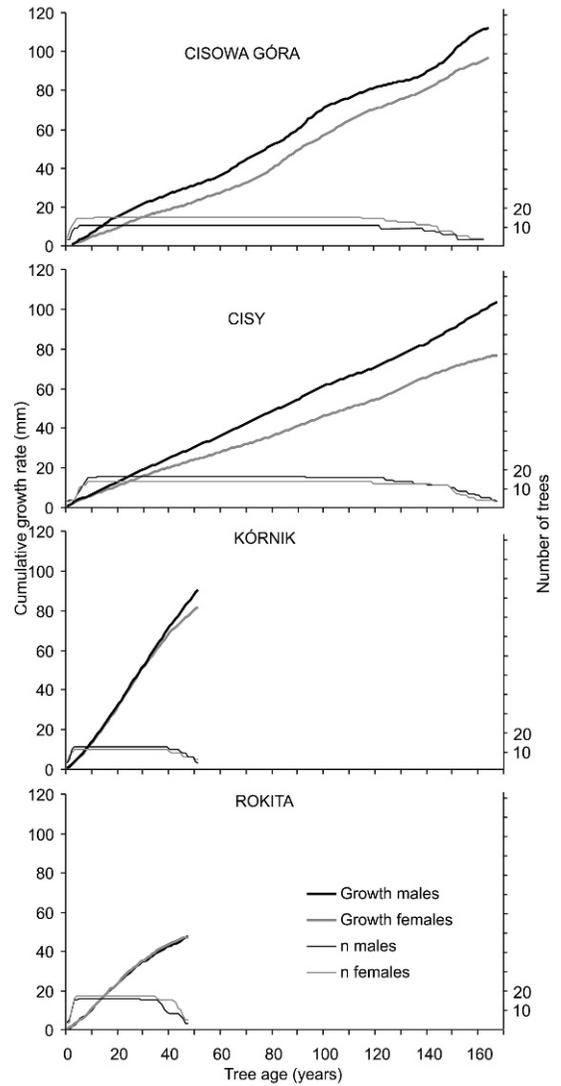


Figure 2. Relationship between cumulative ring width and tree age of males and females of European yew (using only the samples with juvenile wood or visible pith). In population 3 the analysis was impossible because internal wood decay in most trees did not permit reliable age estimation.

DISCUSSION

In all the analyzed populations, mean ring width of yew was smaller in female individuals than in males. This was associated with a decrease in tree-ring width observed from about 10 years in population 1, from 15 years in population 2, and from 30 years in population 4. The decrease in tree-ring width is most often associated with

Table 5. Regression coefficients of response function analysis for temperature, precipitation and tree-ring width. When three or more populations are significantly correlated (in bold $p \leq 0.05$) in a month, the column is marked in black (negative) or grey (positive).

| No. of Population | N | Months of Previous Year | | | | | | | Months of Current Year | | | | | | | | |
|--------------------------------|----|-------------------------|--------------|--------------|--------------|-------------|-------------|--------------|------------------------|-------------|-------------|--------------|--------------|--------------|-------------|-------------|--------------|
| | | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep |
| Temperature – females | | | | | | | | | | | | | | | | | |
| 1 | 14 | -0.07 | 0.04 | 0.03 | 0.06 | 0.08 | 0.05 | 0.08 | 0.06 | 0.23 | 0.18 | 0.08 | -0.07 | 0.17 | 0.11 | 0.19 | 0.04 |
| 2 | 15 | -0.08 | -0.02 | -0.14 | -0.14 | -0.11 | -0.02 | -0.01 | 0.20 | 0.30 | 0.33 | -0.08 | -0.01 | -0.22 | 0.10 | 0.11 | 0.15 |
| 3 | 10 | 0.00 | 0.01 | -0.14 | -0.01 | -0.06 | 0.04 | 0.00 | 0.21 | 0.40 | 0.36 | -0.02 | -0.03 | -0.17 | 0.19 | 0.08 | 0.17 |
| 4 | 18 | 0.14 | 0.04 | -0.26 | -0.24 | -0.06 | 0.05 | 0.12 | 0.37 | 0.25 | 0.10 | -0.08 | -0.07 | -0.23 | -0.03 | 0.06 | 0.10 |
| 5 | 18 | -0.18 | 0.16 | 0.32 | -0.19 | -0.07 | 0.05 | 0.13 | 0.02 | 0.09 | 0.18 | -0.33 | -0.27 | -0.19 | -0.11 | 0.11 | -0.11 |
| Temperature – males | | | | | | | | | | | | | | | | | |
| 1 | 14 | 0.01 | -0.08 | 0.14 | -0.05 | -0.05 | 0.03 | 0.09 | 0.08 | 0.14 | 0.06 | 0.07 | -0.03 | -0.03 | 0.31 | 0.26 | -0.05 |
| 2 | 20 | -0.01 | 0.05 | -0.10 | -0.01 | -0.08 | 0.02 | -0.03 | 0.18 | 0.35 | 0.34 | -0.11 | -0.07 | -0.14 | 0.00 | 0.19 | 0.03 |
| 3 | 10 | 0.02 | -0.09 | -0.11 | -0.01 | -0.10 | 0.05 | 0.11 | 0.16 | 0.34 | 0.26 | 0.00 | -0.16 | -0.09 | 0.22 | 0.19 | 0.19 |
| 4 | 19 | 0.14 | -0.05 | -0.17 | -0.14 | -0.05 | -0.12 | 0.24 | 0.16 | 0.31 | 0.25 | -0.30 | -0.08 | -0.18 | -0.10 | 0.05 | -0.25 |
| 5 | 17 | -0.18 | 0.03 | 0.15 | -0.07 | 0.04 | 0.03 | 0.07 | -0.12 | 0.09 | 0.00 | -0.19 | -0.13 | -0.15 | -0.04 | 0.17 | -0.06 |
| Precipitation – females | | | | | | | | | | | | | | | | | |
| 1 | 14 | 0.03 | 0.12 | 0.05 | 0.05 | 0.08 | -0.14 | 0.01 | 0.00 | 0.05 | -0.09 | 0.03 | -0.04 | 0.01 | 0.19 | 0.05 | 0.11 |
| 2 | 15 | -0.03 | -0.11 | 0.19 | 0.00 | 0.04 | 0.04 | -0.06 | -0.02 | -0.07 | -0.01 | -0.09 | -0.11 | 0.17 | 0.09 | -0.06 | 0.05 |
| 3 | 10 | 0.13 | -0.18 | 0.01 | -0.09 | -0.07 | 0.15 | 0.00 | -0.04 | -0.02 | 0.00 | 0.12 | 0.09 | 0.18 | 0.19 | 0.11 | 0.03 |
| 4 | 18 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 | -0.02 |
| 5 | 18 | 0.02 | -0.11 | -0.06 | 0.13 | 0.05 | 0.10 | 0.16 | 0.20 | 0.16 | 0.05 | 0.03 | 0.11 | 0.22 | 0.14 | -0.09 | -0.18 |
| Precipitation – males | | | | | | | | | | | | | | | | | |
| 1 | 14 | -0.07 | 0.23 | 0.14 | 0.06 | 0.17 | -0.02 | -0.05 | -0.10 | -0.04 | -0.05 | 0.06 | 0.03 | -0.06 | 0.35 | 0.14 | 0.14 |
| 2 | 20 | -0.08 | -0.05 | 0.19 | 0.04 | 0.22 | -0.12 | -0.18 | 0.16 | -0.05 | 0.00 | -0.02 | -0.14 | 0.06 | 0.12 | -0.02 | 0.13 |
| 3 | 10 | 0.00 | -0.16 | 0.06 | -0.02 | 0.04 | 0.00 | 0.09 | -0.11 | 0.09 | 0.01 | 0.11 | -0.05 | 0.04 | 0.16 | 0.10 | -0.02 |
| 4 | 19 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | 0.05 | -0.01 | -0.01 | -0.01 | -0.01 | -0.01 | -0.01 | -0.01 | -0.01 | -0.01 |
| 5 | 17 | -0.01 | -0.01 | 0.04 | -0.05 | -0.04 | 0.12 | 0.19 | 0.06 | 0.23 | 0.01 | -0.03 | 0.11 | 0.31 | 0.07 | -0.13 | -0.15 |

reaching sexual maturity in the population (Banauelos and Obeso 2004; Montesinos *et al.* 2006), which is linked with a shift from vegetative growth to sexual reproduction (Koenig and Knops 1998). Similar trade-off between the reproductive and the vegetative functions was found only in the insect-pollinated species Alpine buckthorn (*Rhamnus alpinus*) (Banauelos and Obeso 2004) and in one population of wind-pollinated Spanish juniper (*Juniperus thurifera*) (Montesinos *et al.* 2006).

The larger size of males can be linked with the survival strategy of the species. Larger male trees have a greater potential for pollen dispersal over longer distances (Freeman *et al.* 1976; Obeso 2002; Montesinos *et al.* 2006). Despite this, in European yew a greater pollen production associated with larger size and larger number of males in

the population does not insure population persistence (Iszkulo *et al.* 2009). European yew is an endangered species, distributed in a restricted area with a relatively high density of trees (Iszkulo *et al.* 2005; Iszkulo and Boratynski 2006; Dhar *et al.* 2008). Most likely, higher male growth rates caused female trees to lose in competition for light, nutrients, and access to water and could contribute to risk of extinction for yew (Iszkulo *et al.* 2009). This may be a factor increasing the risk of extinction of dioecious species.

The lack of differences between sexes in tree-ring width in population number 5 may be because of the young age of the population. They have probably reached sexual maturity recently and the differences have not yet developed. Maturity for yew is variable, and it may be reached at different

times in different populations. According to White (1998) maturity is reached between 30 and 60 years for yews growing in different sites. Because we know only age at the breast diameter (1.3 m), we have to add to this age the number of years needed to reach 1.3 m. The mean age of reaching breast height is known only for population 4, and it is estimated at thirteen years (Iszkulo and Boratynski 2005). This means that the differences in tree-ring width between sexes start to be observed in population 4 at the age of 40 to 45 years. It is possible that in the other populations this age does not have such great variations (between 10 and 30 years), because the rate of tree-ring growth is much lower in montane populations (1 and 2), and the age of reaching breast height can be much higher there than in population 4.

Age of population 5 is over 50, but, as seen below, it is possible that it reached sexual maturity recently. Another explanation for the lack of differences in tree-ring growth between the sexes can, however, be suggested. In population 5, a decrease in growth rate is noticeable, which can be connected with reaching sexual maturity. This population is located relatively far from limits of the species range and grows in more favorable climatic conditions than the other populations. It has been proven that unfavorable conditions have a negative effect, chiefly on females in seabuckthorns (*Hippophaë rhamnoides*) (Li *et al.* 2007). On the other hand, research on fifteen populations of Chilean cedar *Austrocedrus chilensis* showed that only seven populations exhibited tree rings that were significantly wider in males than in females; in three populations tree rings were narrower in males, whereas in five populations no significant difference was detected. This may indicate that in optimal conditions (*i.e.* at the center of the species range) the dynamics of tree-ring growth can be similar in both sexes.

Reproduction and vegetative growth often compete for the same resources (Koenig and Knops 1998). Differences in sexes in tree-ring width reaction to climate can be interpreted in connection with vegetative investment in woody plants (Obeso 1997; Silvertown and Dodd 1999). In most of studied European yew populations, females positively react to precipitation in June and July. This is

the period of intensive tree-ring growth in European yew. At that time, males are in the post-flowering stage, while in females the development and maturation of seeds takes place. Thus the resources are used not only for vegetative growth but also for the development of seeds and arils. That is probably why females react more positively to precipitation in those months. Nevertheless, growth of Spanish juniper males correlated positively with precipitation from the current winter and spring, and female growth was positively correlated only with current spring precipitation (Montesinos *et al.* 2006). Montesinos *et al.* (2006) interpreted this climatic response to mean that females do not use current winter precipitation for current vegetative growth but rather that they allocate resources for subsequent cone maturation, and only surplus resources from current spring precipitation are used for current growth. Our results support the general rule that female plants are usually more demanding with respect to moisture than male plants (Freeman *et al.* 1976; Iglesias and Bell 1989; Bertiller *et al.* 2002). Females of boxelder (*Acer negundo*) exhibited higher growth rates with increasing precipitation and soil water availability (Ward *et al.* 2002). Moreover, in grayleaf willow (*Salix glauca*), annual shoot growth for females was greatest in mesic habitats and females had lower drought tolerance than males during years of extreme aridity (Dudley 2006; Dudley and Galen 2007). It was shown that the number of females decreases at the sites with less precipitation in the 25 studied yew populations (Iszkulo *et al.* 2009).

High temperatures in August and September of the previous year affected female growth negatively in most of the studied populations. This is the period of seed maturation and simultaneous formation of generative buds in both sexes (Bugala 1978). It is possible that only at high temperatures do large numbers of yew seeds mature, which causes an increased reproductive effort. High seed production in the preceding year can limit tree-ring growth in the current year. It has been demonstrated that abundant production of seeds decreases radial growth (Nicotra 1999). The negative effect of June temperatures in the preceding year on tree-ring growth in the current year is probably linked with

the correlation of low temperature with high precipitation in an intermediate climate (between oceanic and continental), because at the same time a positive influence of precipitation on tree-ring width was observed in yews. In the only two studies known to us in which this kind of relationship was analysed (Rovere *et al.* 2003; Montesinos *et al.* 2006), correlations between annual tree-ring growth and temperature (and precipitation in Rovere *et al.* 2003) did not differ between male and female trees.

CONCLUSIONS

The results presented here show that the higher tree-ring width in males compared with females probably emerged when the yew trees reached sexual maturity. This phenomenon probably occurs because of the assumed greater reproductive effort of females in comparison with males. The lack of difference in the youngest population may result from a very recent beginning of sexual maturity or from a milder climate in that region. In most of the analyzed populations, width of tree rings in female individuals, in contrast with males, was negatively correlated with high temperatures in August and September in the year prior to the formation of the tree ring, and correlated positively with precipitation in June and July in the current year. Different reactions of the two sexes to climate indicate that this may affect the range and viability of populations at the limits of the range.

ACKNOWLEDGMENTS

This study was supported by the Polish Ministry of Science and Higher Education, from the research fund in 2008–2010 (grant number N306 424234). We thank Mr. Tomasz Szeszycki (forest district manager) and Marek Kmiciek for their kindness and help in our fieldwork. We are grateful to Elisabeth Dawn Miller for language correction of the final version of the manuscript.

REFERENCES CITED

- Ashman, T., 1992. Indirect costs of seed production within and between seasons in a gynodioecious species. *Oecologia* 92: 266–272.
- Banuelos, M., and J. Obeso, 2004. Resource allocation in the dioecious shrub *Rhamnus alpinus*: The hidden costs of reproduction. *Evolutionary Ecology Research* 6:397–413.
- Banuelos, M., M. Sierra, and J. Obeso, 2004. Sex, secondary compounds and asymmetry. Effects on plant-herbivore interaction in a dioecious shrub. *Acta Oecologica-International Journal of Ecology* 25:151–157.
- Bertiller, M., C. Sain, and A. Carrera, 2002. Effect of fine-scale spatial variation of soil nitrogen on the performance of the sexes of *Poa ligularis* in patchy ecosystems of Northern Patagonia. *International Journal of Plant Sciences* 163: 419–425.
- Bugała, W., 1978. Systematics and variability. In *The Yew-Taxus baccata L.*, edited by S. Białobok, pp. 18–38. Department of the National Centre for Scientific and Technical, and Economics Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.
- Cedro, A., 2004. Wpływ warunków klimatycznych na kształtowanie się przyrostów radialnych cisa pospolitego (*Taxus baccata L.*) w Rezerwacie Cisy Staropolskie w Wierchlesie. In *Rekonstrukcja i prognoza zmian środowiska przyrodniczego w badaniach geograficznych*, edited by M. Błaszkie-wicz, and P. Gierszewski 200:47–57. *Prace Geograficzne*.
- Cedro, A., 2005. Czynniki wpływające na szerokość przyrostów rocznych cisa (*Taxus baccata L.*) ze stanowisk Pomorza Zachodniego, edited by J. Gierjatowicz, and C. Koźmiński, pp. 8–13. *Hydrograficzne i meteorologiczne aspekty badań wybrzeża Bałtyku i wybranych obszarów Polski*. Oficyna In Plus, Szczecin.
- Cook, E., and A. Kairiukstis, 1992. *Methods of Dendrochronology*. Kluwer Academic Publishers, Dordrecht, Boston, London.
- Dhar, A., H. Ruprecht, and H. Vacik, 2008. Population viability risk management (PVRM) for in situ management of endangered tree species—A case study on a *Taxus baccata L.* population. *Forest Ecology and Management* 255: 2835–2845.
- Dudley, L., 2006. Ecological correlates of secondary sexual dimorphism in *Salix glauca* (Salicaceae). *American Journal of Botany* 93:1775–1783.
- Dudley, L., and C. Galen, 2007. Stage-dependent patterns of drought tolerance and gas exchange vary between sexes in the alpine willow, *Salix glauca*. *Oecologia* 153:1–9.
- Eckstein, D., 1969. *Entwicklung und Anwendung der Dendrochronologie zur Altersbestimmung der Sredrung Haithrobu*. Ph.D. dissertation, University Hamburg.
- Freeman, D., L. Klikoff, and K. Harper, 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193:597–599.
- Fritts, H., and W. Xiangding, 1986. A comparison between response-function analysis and other regression techniques. *Tree-Ring Bulletin* 46:31–46.
- Givnish, T., 1980. Ecological constraints on the evolution of breeding systems in seed plants: Dioecy and dispersal in gymnosperms. *Evolution* 34:959–972.
- Heilbuth, J., 2000. Lower species richness in dioecious clades. *American Naturalist* 156:221–241.

- Holmes, R., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43: 69–78.
- Holmes, R., 1994. *Dendrochronology Program Library. Users Manual*. University of Arizona, Tucson.
- Iglesias, M., and G. Bell, 1989. The small-scale spatial distribution of male and female plants. *Oecologia* 80:229–235.
- Iszkulo, G., and A. Boratynski, 2005. Different age and spatial structure of two spontaneous subpopulations of *Taxus baccata* as a result of various intensity of colonization process. *Flora* 200:195–206.
- Iszkulo, G., and A. Boratynski, 2006. Analysis of the relationship between photosynthetic photon flux density and natural *Taxus baccata* seedlings occurrence. *Acta Oecologica-International Journal of Ecology* 29:78–84.
- Iszkulo, G., A. Boratynski, Y. Didukh, K. Romaschenko, and N. Pryazhko, 2005. Changes of population structure of *Taxus baccata* L. during 25 years in protected area (Carpathians, western Ukraine). *Polish Journal of Ecology* 53:13–23.
- Iszkulo, G., A. Jasinska, M. Giertych, and A. Boratynski, 2009. Do secondary sexual dimorphism and female intolerance to drought influence the sex ratio and extinction risk of *Taxus baccata*? *Plant Ecology* 200:229–240.
- de Jong, T., and E. van der Meijden, 2004. Sex ratio of some long-lived dioecious plants in a sand dune area. *Plant Biology* 6:616–620.
- Kaennel, M., and F. Schweingruber, 1995. Multilingual Glossary of Dendrochronology. WSL FNP, Haupt.
- Koenig, W., and J. Knops, 1998. Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226.
- Krawczyk, A., 1995. Program komputerowy TREE RINGS [Computer software TREE RINGS]. Kraków.
- Krawczyk, A., and M. Krąpiec, 1995. Dendrochronologiczna baza danych. [Dendrochronological data base.]. In *Materiały II Krajowej Konferencji: Komputerowe wspomaganie badań naukowych [Proceedings of the Polish Conference on Computer Assistance to Scientific Research]*. Wrocław.
- Krishnan, R., and B. Ramesh, 2005. Endemism and sexual systems in the evergreen tree flora of the Western Ghats, India. *Diversity and Distributions* 11:559–565.
- Leigh, A., M. Cosgrove, and A. Nicotra, 2006. Reproductive allocation in a gender dimorphic shrub: Anomalous female investment in *Gynatrix pulchella*? *Journal of Ecology* 94: 1261–1271.
- Li, C., G. Xu, R. Zang, H. Korpelainen, and F. Berninger, 2007. Sex-related differences in leaf morphological and physiological responses in *Hippophae rhamnoides* along an altitudinal gradient. *Tree Physiology* 27:399–406.
- Montesinos, D., M. De Luis, M. Verdu, J. Raventos, and P. Garcia-Fayos, 2006. When, how and how much: Gender-specific resource-use strategies in the dioecious tree *Juniperus thurifera*. *Annals of Botany* 98:885–889.
- Newell, E., 1991. Direct and delayed costs of reproduction in *Aesculus californica*. *Journal of Ecology* 79:365–378.
- Nicotra, A., 1999. Reproductive allocation and the long-term costs of reproduction in *Siparuna grandiflora*, a dioecious neotropical shrub. *Journal of Ecology* 87:138–149.
- Obeso, J., 1997. Costs of reproduction in *Ilex aquifolium*: Effects at tree, branch and leaf levels. *Journal of Ecology* 85: 159–166.
- Obeso, J., 2002. The costs of reproduction in plants. *New Phytologist* 155:321–348.
- Obeso, J., M. Alvarez-Santullano, and R. Retuerto, 1998. Sex ratios, size distributions, and sexual dimorphism in the dioecious tree *Ilex aquifolium* (Aquifoliaceae). *American Journal of Botany* 85:1602–1608.
- Obeso, J., and R. Retuerto, 2002. Sexual dimorphism in holly *Ilex aquifolium*: Cost of reproduction, sexual selection or physiological differentiation? *Revista Chilena De Historia Natural* 75:67–77.
- Rovere, A., M. Aizen, and T. Kitzberger, 2003. Growth and climatic response of male and female trees of *Austrocedrus chilensis*, a dioecious conifer from the temperate forests of southern South America. *Ecoscience* 10:195–203.
- Silvertown, J., and M. Dodd, 1999. The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). *The American Naturalist* 29:321–332.
- Vamosi, J., and S. Vamosi, 2005. Present day risk of extinction may exacerbate the lower species richness of dioecious clades. *Diversity and Distributions* 11:25–32.
- Walanus, A., 2001. DendroGraph—program druku krzywych grubości słoju przyrostów rocznych. Instrukcja obsługi programu DendroGraph [DendroGraph—a software for plotting tree ring width curves. DendroGraph Software User's Manual]. Kraków.
- Ward, J., T. Dawson, and J. Ehleringer, 2002. Responses of *Acer negundo* genders to interannual differences in water availability determined from carbon isotope ratios of tree ring cellulose. *Tree Physiology* 22:339–346.
- White, J. E. J., 1998. *Estimating the Age of Large and Veteran Trees in Britain*. Forestry Commission Information Note 012. HMSO/Forestry Commission, London, UK.
- Zunzunegui, M., M. Diaz Barradas, A. Clavijo, L. Cansino, F. Lhout, and F. Novo, 2006. Ecophysiology, growth timing and reproductive effort of three sexual forms of *Corema album* (Empetraceae). *Plant Ecology* 183:35–46.

Received 16 June 2009; accepted 30 July 2010.