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Irregular Shelterwood Cuttings Promote Viability of European Yew Population Growing in a Managed Forest: A Case Study from the Starohorské Mountains, Slovakia

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Abstract: The increasing probability of *Taxus baccata* (L.) decline given climate change brings forth many uncertainties for conservation management decisions. In this article, the authors present the effects of applying regeneration cuttings since the year 2000 on the viability of the understory yew population. By collecting data from a stand located at the centre of the largest population of European yew in Slovakia, containing approximately 160,000 individuals, and analysing tree-ring records from 38 sampled trees, the improved performance of yews, including stem growth, seed production, and number of regenerated individuals, was revealed. Thinning the canopy by removing 15% of the growing stock volume per decade, combined with the subsequent irregular shelterwood cuttings, was assessed as a useful strategy. Moreover, lower radial growth of females compared to males, but simultaneously their similar response to climate, suggests a possible trade-off between reproduction and growth. Release cuttings of up to 30% of the standing volume in the vicinity of the female trees, executed in the rainy summers following warmer winters, and consistent elimination of deer browsing, can further enhance the positive effects of applied cuts on yew viability. Overall, the suggested active measures could be considered as an effective option to preserve the unique biodiversity of calcareous beech-dominated forests in Central Europe.

Keywords: yew regeneration; growth rate; dioecy; temperate forests; dendroecology

1. Introduction

European yew is a previously common evergreen gymnosperm tree species which has disappeared from many areas, primarily due to direct human activities connected with the devastation of its natural habitats and its overexploitation. This has increased public concern and led to direct conservation actions, resulting in its individual protection, as well as the establishment of yew protected areas. Changes in climate, together with the slow growth, delayed reproduction, and extraordinary long life cycle of yew (*Taxus baccata* L.), brings up many challenges for forest management operations aimed at maintaining suitable ecological conditions for yew in forest stands. Because of distinctive habitat fragmentation and the shrinking [1] and patchy distribution of suitable habitat conditions, given its restriction to calcareous soil and poor dispersal ability [2], climate change is likely to increase the probability of yew decline.

The largest threat to yew maintenance in forest stands is their decreased growth, and related to this pattern, the high rates of adults' auto-reduction and extensive absence of regeneration [3].

Deliberate cessation of silvicultural interventions can result in an increase in canopy density, with the lack of yew regeneration as a consequence [4]. Other reasons for unsuccessful natural regeneration include the competition of other tree species [5] and browsing and bark-stripping by ungulates [6], which could become a fatal threat to yews in the initial phases of their development [7,8]. Studies on the management of yew populations by silvicultural treatments, aimed at maintaining and potentially improving the status of this species, are scant [4,9–11], as are the investigations into the relationship between regeneration and parent trees [12]. Release cuttings were confirmed to have a positive effect on fruit production in tree species [12]. A careful selective cutting also relieves competition pressure from neighbouring trees. As observed earlier, the removal of 18–20% of the standing volume consequently reduces inter-species competition and increases the average height of yew trees [9]. Intense disturbances and sudden exposition of yew trees to direct sunlight may have a strong negative effect on their growth [13], but silvicultural measures could help mitigate the effects by improving the stability of stand structures and reducing the risk of large-scale extinction.

The use of regeneration cuttings is primarily aimed at promoting the reproduction of yew trees, and also offers the opportunity to compare growth pattern responses and to test resource allocation between vegetative growth and sex-related investment into the production of pollen, fruits, and seeds [14]. Dioecy is an evolutionary strategy focused on maximizing reproductive success, and is costly—especially when combined with the production of extraordinarily heavy fruits and seed crops, aimed at attracting many seed dispersers [15,16]. "Normal" masting sensu Kelly [17] refers to mast fruiting, which is the production of large seed crops, where individuals are assumed to switch resources away from vegetative growth or reserves toward seed production, while still producing some seeds in other years [18]. This production of large amounts of seeds is assumed to deplete the trees' internal carbon reserves [19]. Yew therefore represents an interesting opportunity to study intra-species differences in carbon allocation to growth and reproduction processes. Scientific findings on gender-based differences in growth are relatively consistent. In optimum environmental conditions, males have higher growth rates and are larger than females [14,20]. Sex-related differences in growth—if not impaired by stressful environmental conditions [21]—are a result of higher reproductive costs for females after they have reached sexual maturity [22]. Nevertheless, it was observed that female trees growing at the microsite level in more productive, favourable, and wetter sites are able to outperform males [23].

Still, little is known on the long-term influence of reproduction on growth and changes in tree-ring widths [16,22]. Under higher reproductive demands, tree-ring widths may potentially be used to record the reproductive costs of growth in dioecious species. Inter-annual variations in climate that drive the radial growth of trees also modulate the process of reproduction. Possible differences in growth rates between males and females in a particular year could also be attributed to sex-related differences in responses to climate. In temperate forests, sex-specific sensitivity of tree growth to climate has rarely been studied, and research provides inconsistent results. For example, young Spanish juniper females (*Juniperus thurifera* L.) were found to be more sensitive to water stress during summer than the male trees [24]. Higher female sensitivity to low temperature and low rainfall was also confirmed for common juniper (*Juniperus communis* subsp. *Communis* L.) [22]. Contrary to this, there are also observations showing no significant differences in growth and response to climate variability between female and male trees [25].

Populations of European yew are currently reported to be increasing [26]. Their expansion is likely the result of a combination of conservation actions and changes in forest management systems. The need for active management intervention to relieve the stress on young and old yew trees is becoming obvious. The general goal of our study was to assess the effectiveness of irregularly cutting shelterwood with the specific aim of improving the growth and regeneration processes of the European yew population growing in actively managed forests. Besides the regeneration of the dominant tree species (beech), the localization of shelterwood cuts took into consideration the existence of yew throughout the stand, resulting in irregular spatial arrangement of regeneration groups. We focused on one case study area in Slovakia and analyzed stand structure, yew natural regeneration, and tree-ring records. To improve the active management strategy, the evaluation was performed considering the possible effects of current climate change affecting the viability of yew.

In the study, we hypothesised that:

i The intensity of small-scale shelterwood cuttings influences the seed production and growth processes of mature yew trees.
ii The density of naturally regenerated yew is related to the size and radial growth rate of the parent trees.
iii Reproduction (masting) reduces the diameter increment, and therefore sex-related differences in radial growth should be expected.
iv Different life strategies of male and female trees are likely to result in gender-specific sensitivity to variation in climate.

2. Materials and Methods

2.1. Study Area

The study area of Pavelcovo is at an altitude range of 400–825 m a.s.l. and has 6000 to 7000 yew individuals, and belongs to the Starohorské Mountains, where the largest and most concentrated population of European yew in Slovakia, with 160,000 individuals, is present ([6,27,28], Figure S1). The selected managed forest stand (48°46′14.88″ N; 19°07′10.33″ E) represents a limestone beech forest (*Fagetum dealpinum*) in which yew trees exhibit the top growth performance. It is located in the research demonstration facility Pro Silva "Šípovo", established in 2008 to preserve and improve the yew population status, covering an area of 119 hectares. Annual precipitation is 840 mm and the mean annual temperature is 8.0 °C. The total area of the stand is 15.41 ha, has a slope of 35% with a prevailing south-eastern aspect, and the growing stock reaches 284 m^3 per hectare (Table S1). The stand was established by seeding after a clear-cut in 1880–1890 [29], but historical records provide no information on the origin and survival of yew in the stand. In the past, limited thinning of the canopy was completed in the stand, resulting in decreasing the vitality of the yew population. Based on the research results from the Pavelcovo yew reserve (which has a common border with the subject forest stand [9,11]), crown thinning with positive selection in the overstory, with an intensity of 15% per decade, was proposed as a measure to maintain light availability, to increase crown volume and surface area, and thus stimulate yew growth and fructification. In 2000, the first interventions were aimed at stand regeneration with an irregular shelterwood cut with a planned regeneration period of 30 years, 1–2 interventions per decade, and intensity from 20 to 30% (Figure S2). Besides the beech stand regeneration, the intervention took into consideration the creation of favourable conditions for the maintenance of yew. Therefore, some of the regeneration groups were placed into parts of the stand with the presence of adult yews that existed in an irregular distribution of regeneration groups across the stand. Middle- and lower-layer beech stems around yew trees remained intentionally untouched, in order to protect them from sudden exposure to direct sunlight. If the middle and lower layer was absent, several canopy stems surrounding yew trees were excluded from the cutting. Regeneration cuttings resulted in successful fructification, but due to heavy browsing of yew juveniles by deer, no seedlings with lateral branches—which yew forms at the age of 4–5 years—were recorded during the subsequent field survey in 2011 [30]. In 2008, a fence 18 m × 20 m was built in the stand to study the dynamics of yew natural regeneration protected from browsing, and PVC nets were applied to stems of older yews as a protection against bark-stripping.

In the investigated sites, European beech (*Fagus sylvatica* L.) was the dominant tree species, reaching a proportion of 50% as calculated from stem density. The most abundant admixed tree species were sycamore maple (*Acer pseudoplatanus* L., 13%), Norway spruce (*Picea abies* (L.) Karst., 13%), and European yew (*Taxus baccata* L., 12%). The proportions of the other tree species did not exceed 5%: *Acer platanoides* (L.) (5%), *Fraxinus excelsior* (L.) (3%), *Abies alba* (Mill.) (2%), *Sorbus torminalis* (L.)

Crantz (1%), and *Pinus sylvestris* (L.) (1%). Stand structure as described by using diameter and height distributions according to tree species shows that beech is represented in all diameter classes and it occupies the entire vertical profile (Figure 1). The majority of admixed spruce and maple is concentrated in the middle and upper tree layer, whereas yew is found almost exclusively in the lower tree layer.

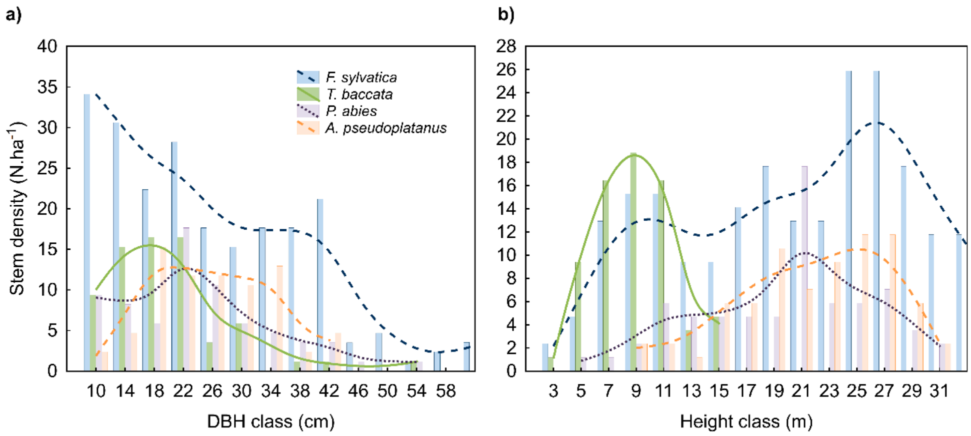

Figure 1. (**a**) Diameter and (**b**) height distributions of four tree species of the studied forest stand. DBH: diameter at breast height.

2.2. Sampling Design and Measurements

The stand was surveyed in autumn 2015. Starting near the upper border of the stand, we walked along the contour line (isohypse) and marked a point every 40 m. If a mature yew with diameter at breast height (DBH) ≥15 cm was present in a distance less than 3 m, a circular sampling plot of 500 m^2 with the yew in the centre—hereafter called the "central stem"—was established. After reaching the stand border, we moved 40 m down the slope and walked again following the isohypse. Using this pattern, we covered the entire stand area and established 30 research plots in total. For central stems, we selected mature yews with DBH ≥15 cm to ensure that they are of reproductive age and have a sufficient number of tree-rings for further dendroecological study. For each sampling plot, we recorded altitude, aspect, slope, intervention type, and additional characteristics such as position within the slope. Intervention type included three categories: no intervention, moderate intervention, and heavy intervention. For the no intervention category, we classified the plots with no visible stumps and no shelterwood cuts in the vicinity of the plot. Plots after the first regeneration cut (seeding cutting) in the plot and in the plot's neighbourhood were assigned to the moderate intervention category. The heavy intervention category was characterised by having an executed first regeneration cut (seeding cutting) in the plot, as well as an already finished shelterwood cut (final cutting), with no canopy trees in the plot's surroundings. On the plots, the positions of all living trees with DBH ≥8 cm, snags, and stumps were recorded by FieldMap (IFER—Monitoring and Mapping Solutions, Ltd., Jílové u Prahy, Czech Republic, http://www.fieldmap.cz). For every standing tree, the following characteristics were recorded: tree species, DBH, height, height of the crown base, four perpendicular crown radii (x_1–x_4), and in the case of yew, the sex. For central stems of yew, we calculated additional crown characteristics (C_L—crown length, C_R—crown ratio, C_{PA}—crown projection area, C_V—crown volume, and C_{SA}—crown surface area) following the formulae in Table S2 [31]. For the stumps, we recorded tree species, diameter at the top, height, and degree of decomposition. In the 12 plots that belonged to the moderate intervention category (six plots with a male and six plots with a female central tree), natural regeneration of yew was registered on circular subplots within a 3-m radius. In the height category of <10 cm, we recorded the total density of yew seedlings. For individuals taller than 10 cm, we registered the height and the last three height increments.

For the dendrochronological analysis, we collected increment cores from all 30 central stems and 8 additional mature yews located on sampling plots, for a total of 38 cored yew stems. Two cores in perpendicular directions were extracted from each tree at 1.3 m above ground, with the aim of avoiding reaction wood. Cores were mounted on wooden bars, dried, and sanded [32]. Samples were scanned using the Epson Expression 10,000 XL scanner, and ring widths were measured to the nearest 0.001 mm using the WinDENDRO™ software (Regent Instruments Inc., Québec, Canada). Individual ring-width series were carefully cross-dated [33] and checked for missing rings and other cross-dating errors with the COFECHA software (Richard L. Holmes, Tuscon, AZ, USA) [34].

2.3. Climate Records

A time series of selected climate variables were completed for mean monthly temperatures and precipitation sums, covering the period from 1901 to 2014. Mean monthly observations of updated CRU TS3.23 (0.5° × 0.5° grid interpolated points) available at the KNMI Climate Explorer [35] were used. Course CRU TS3.23 data were employed without corrections [36]. Climate diagrams with mean monthly precipitation sums (mm) and temperatures (°C) over the period of 1901–2014 and 1991–2014 for the study area are illustrated in Figure S3.

2.4. Data Analysis

To evaluate the relationship between the growth parameters of parent yew trees and the amount of naturally regenerated individuals, we used simple linear regression. The differences in the number of seedlings between male and female trees, as well as the mean tree characteristics of adult female and male adult yews, were evaluated by *t*-test. To test whether high resource availability (as expressed by higher radial growth rate) is positively related to seed production in 2014 and subsequent natural regeneration, we evaluated the relationship between growth rates during three consecutive years (2013–2015) and the number of newly regenerated seedlings under mother trees in 2015. To detect differences in growth rates between males and females in a particular year as attributed to sex-related differences in response to climate, we used temperature and precipitation data of the current (2014) and the previous (2013) growing season to interpret the results. Normalised monthly mean temperature and precipitation values for each month of the selected years (2013 and 2014) were used. Temperature and precipitation anomalies were calculated as deviations from the long-term mean (1901–2014) and expressed in standard deviation (SD). Normalised values exceeding the ±1 SD were interpreted as warm or cold, or dry or wet months. Values exceeding ±2 SD were interpreted as extremely warm or cold, or extremely dry or wet [37].

To compare inter-annual differences in radial growth between males and females, individual tree-ring width (TRW) series were combined to develop raw and residual site chronologies. Bi-weight robust mean was used for computing mean chronologies. Basic descriptive statistics [38] were calculated for the common interval for each chronology, either from the raw tree-ring width series (TRW, SD, mean sensitivity of series (MSs), and first-order autocorrelation coefficient (AC_1)) or residual chronologies (mean between trees correlation RBT and expressed population signal, EPS). MSs measures the relative year-to-year variation, and AC_1 reflects the way in which the previous year's growth influences the current year's growth [38]. RBT is a measure of the between-tree signal, and is the average correlation between tree cores [39]. In addition, the calculation of EPS was to assure that the chronologies correctly portray the hypothetical perfect chronology [40]. In order to identify climate factors controlling tree growth, correlations between residual chronology (residual ring-width index values) and mean monthly weather characteristics were computed for the period of 1901–2015. The correlations were performed in 16-month windows, from the previous May to the current September. Climate factors that showed statistically significant correlations with residual index values were used to examine the sex-related climate response of yew trees. The similarity of climate–growth relationships between sexes was assessed by testing the differences between the correlation coefficients and by linear regression of sex-specific correlation coefficient values.

Mean values of the raw chronologies were additionally computed in a 5-year moving window to evaluate trends in yew growth, according to the three intervention types: no, moderate, and heavy intervention. The impact of silvicultural intervention on the radial growth of yew stems was analysed using the boundary line method [41]. The boundary line is a regression function describing the relationship between prior growth (PG) and percentage growth change (PGC) values. All registered PGCs were scaled relative to the boundary line. If a value of scaled PGC was 20% below the boundary line, no release was detected.

3. Results

3.1. Yew Tree Characteristics

Diameter and height distribution of yew stems were significantly left-skewed, with most stems growing in the 10–30 cm diameter class and 5–11 m height class. The largest observed yew stem had a diameter of 52.7 cm, and the highest stem was 16 m high. The stem density of yews (DBH $\geq$ 8 cm) was 71 trees per hectare, with an average DBH and height of 22.8 cm and 10.7 m, respectively (Table 1). Although the analysed yew females were slightly older and larger than the males (with the exception of crown ratio), no significant differences were registered between the female and male yews (Table 1).

Table 1. Description of the sampled European yew trees.

Single Tree Characteristics (*n* = 38 Trees)					**Female**	**Male**
		Min	**Mean ± SD**	**Max**	**Mean ± SD**	**Mean ± SD**
Diameter	DBH (cm)	11.9	22.8 ± 8.14	52.7	23.5 ± 7.9	22.6 ± 8.38
Height	h (m)	7.0	10.7 ± 2.5	16.0	11.0 ± 2.3	10.3 ± 1.68
Stem basal area	g (m^2)	0.01	0.05 ± 0.04	0.22	0.05 ± 0.04	0.05 ± 0.04
Stem volume	v (m^3)	0.03	0.21 ± 0.19	0.96	0.23 ± 0.18	0.20 ± 0.20
Crown length	C_L (m)	5.1	8.3 ± 2.1	13.0	8.1 ± 2.3	7.4 ± 1.76
Crown ratio	C_R	0.56	0.73 ± 0.07	0.81	0.76 ± 0.07 *	0.70 ± 0.06
Crown projection area	C_{PA} (m^2)	10.2	22.0 ± 12.6	49.2	22.4 ± 13.2	21.7 ± 13.1
Crown volume	C_V (m^3)	17.3	62.8 ± 47.9	168.8	66.0 ± 41.5	59.6 ± 57.5
Crown surface area	C_{SA} (m^2)	30.6	70.2 ± 34.0	140.5	75.7 ± 27.7	64.8 ± 41.4
Age	(years)	62	94 ± 13	118	103 ± 12	95 ± 14

Note: * marks significant differences between female and male individuals at $p < 0.05$.

3.2. Yew Natural Regeneration

The mean yew natural regeneration density in the sample plots reached 12,500 ha^{-1}, and the greatest density of 11,800 ha^{-1} was found in the height category of $\leq$10 cm. Seedlings between 10.1 cm and 20 cm tall were very rare (690 ha^{-1}), and yew regeneration higher than 20 cm did not occur at all in the sample plots (Figure 2).

The sex ratio of the 38 evaluated trees (two individuals without determination) was male-biased, with a value of 1.188, meaning that 47.2% of the yews were females. The mean number of seedlings under female trees, calculated per crown projection area, was 2.38. Crown projection area was slightly higher in the group of female trees (Table 1). This difference was most likely age- and size-related. Selected female trees (n = 6) had slightly older age and larger size compared to male trees (n = 6). A certain amount of yew seedlings were also detected under male trees at 0.72 per crown projection area. The difference in the number of seedlings between male and female trees was not significant.

In forest stands, yew trees usually develop rounded or pyramidal irregularly-shaped crowns with multiple branches spreading. According to crown ratio values (C_R) (Table 1), living crowns of yews represented, on average, nearly 75% of the tree height, with no crown shorter than 56%. From selected crown parameters, only crown length (C_L) was significantly correlated ($p < 0.05$) with the number of seedlings corresponding to a mother female tree (R_{CL} = 0.88). All size-related characteristics of mother trees (DBH, height, basal area, and volume) were significantly and positively correlated with the number of corresponding seedlings, with the highest correlation coefficient provided for tree volume ($R_V = 0.91$).

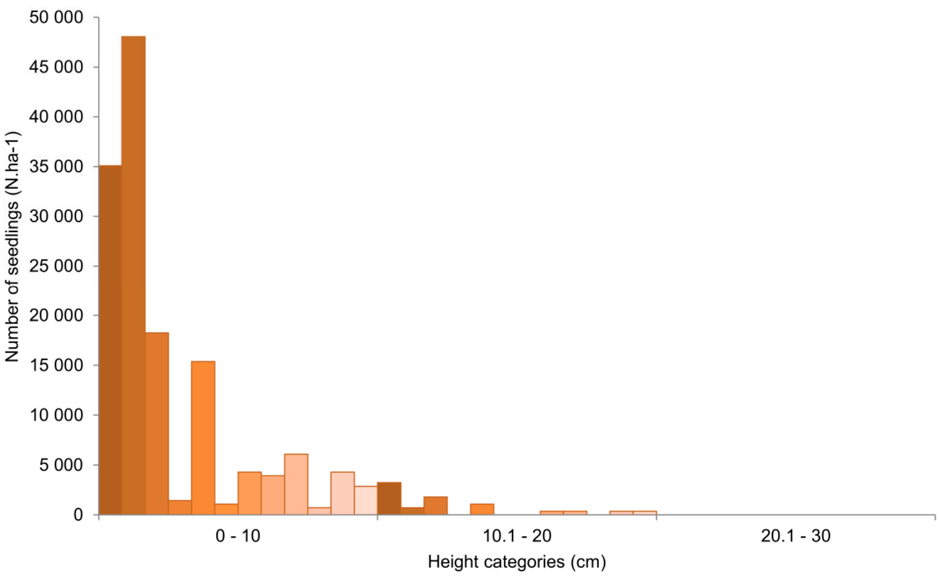

Figure 2. Density of yew natural regeneration according to height categories. Vertical bars represent individual sampling plots.

3.3. Growth–Climate Relationship and Patterns of Yew Radial Growth

In the study area, radial growth of yew trees was temperature- and precipitation-sensitive. Climate sensitivity of male and female individuals was almost identical, with no significant differences between the correlations of monthly climatic variables and ring-width residuals (Table 2, Figure S4). The growth of yew was positively affected by higher precipitation during the summer (June–August) and September, and by temperature during the previous spring and early summer (May–June), and during the winter and early spring (December–March). On the other hand, higher temperatures in the current spring and early summer (May–June) resulted in decreased radial growth.

Table 2. Climate response and basic statistics of yew tree-ring series and residual chronology (common time span 1935–2015).

			Female	Male	All
Raw series		Time span	1898–2015	1901–2015	1898–2015
		Number of sampled trees—Nt	18	20	38
		Mean series length—MSL	97	94	96
		Mean tree-ring width (mm)—TRW	0.94	1	0.97
		Standard deviation—SD	0.46	0.6	0.53
		Mean sensitivity of individual series—MSs	0.23	0.25	0.24
		First-order autocorrelation coefficient—AC_1	0.75	0.77	0.76
Residual chronology		Between trees correlation—RBT	0.38	0.45	0.44
		Expressed population signal—EPS	0.91	0.94	0.96
Climate response	TMP	May–June—mj	0.26	0.18	0.22
		November–March—ndJFM	0.48	0.37	0.39
		May–June—MJ	−0.2	−0.19	−0.21
	PRE	June–August—JJA	0.26	0.34	0.37
		September–S	0.22	0.23	0.19

TMP—mean monthly temperature sums, PRE—monthly precipitation sums, statistically significant correlations of ring-width residual indices with monthly and seasonal TMP and PRE values: mj, ndJFM, MJ, JJA, and S; capital letters refer to months of the current year, small letters to months of the previous year. Note: no statistically significant differences between females and males in response to climate.

Deviations of temperature and precipitation from the long-term normal in the years 2013 and 2014 are illustrated in Figure 3. Long-term mean monthly temperature and precipitation sums over the period of 1901 to 2014 are shown in the climate diagrams (Figure S3). In 2013, weather conditions were characterized by an extremely wet winter, an extremely warm summer, and a dry July. This resulted in a pronounced decrease in the radial increment of yew trees, regardless of sex. On the contrary, in 2014, an extremely warm winter and early spring (January–March), and an extremely wet July and August, had a positive effect on yew growth, resulting in above-average radial growth and significantly higher growth rates of males compared to females (Figure 6 and Figure S5). Differences were detected in radial growth between male and female individuals in 2014, as well as between the analysed years of 2013 and 2014 for both males and females, were significant ($p < 0.01$).

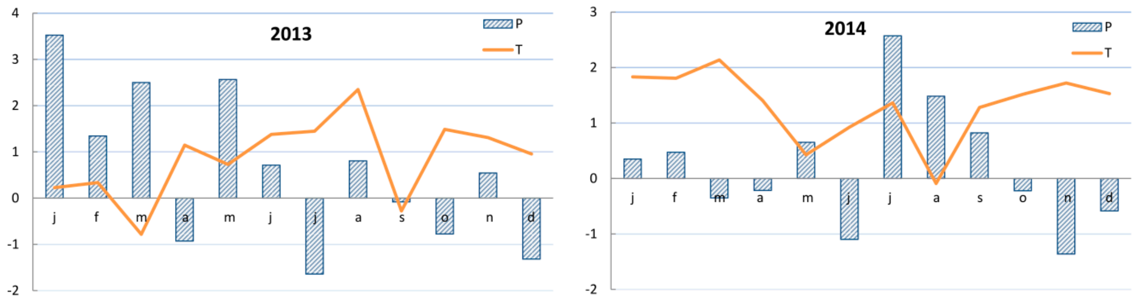

Figure 3. Temperature and precipitation anomalies standardised with respect to the 1901–2014 mean and expressed in standard deviation units, where P is the monthly precipitation sum, and T is the mean monthly temperature).

The year 2014 was reported as a heavy seed (masting) year for yew in the studied locality, most likely due to the weather in the previous year. The majority of seedlings recorded in the vicinity of yew trees that germinated in 2015 likely originated from the seed crop in 2014. In the period of 2013 to 2015, annual growth rates of mother trees were positively associated with the density of yew seedlings, and therefore, seed crop (Figure 4). In the year prior to seed formation (Figure 4a), we found the strongest relationship between radial growth and seedling density. In 2014, in the season of seed formation, the relationship was distinctively weaker (Figure 4b); however, it was restored again in the following year (Figure 4c).

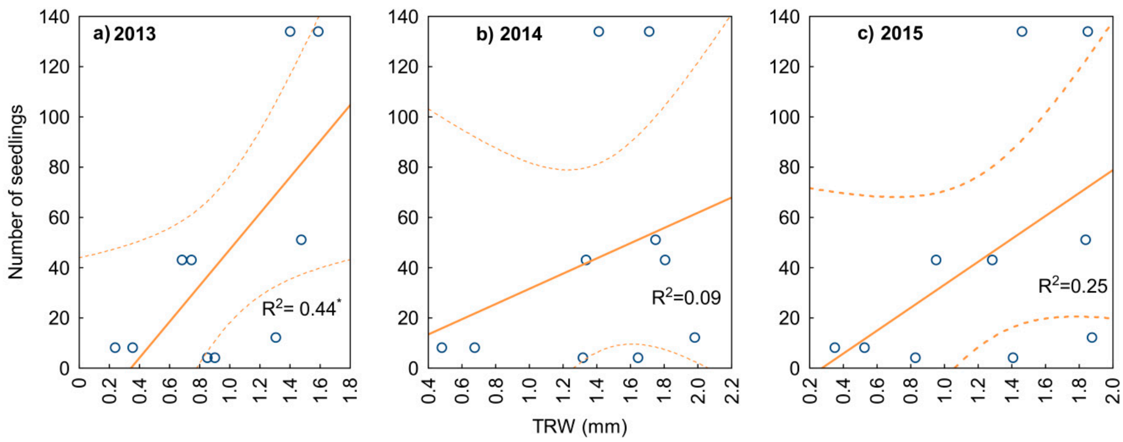

Figure 4. Relationship between density of yew seedlings and radial increment of mother trees in (**a**) the year prior to seed formation; (**b**) the year of seed formation; and (**c**) the year after seed formation.

At the stand level, a significant increase in the tree-ring width of yews was observed after the beginning of stand regeneration via shelterwood cutting in 2000, for both males and females (Figure 5).

Moreover, in this period, a significant difference in the radial growth of females and males was recorded for the first time (Figure 6). It is therefore possible to align detected growth differences with higher fructification in females.

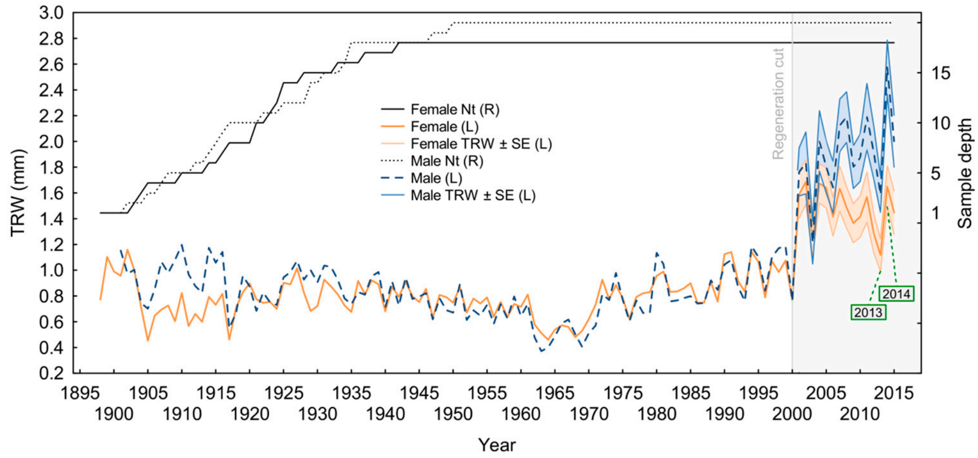

Figure 5. Differences in radial growth between male and female yew individuals. For the period of 2000 to 2015, values of TRW ± SE (standard error of raw mean chronology) are shown. TRW: tree-ring width, Nt: number of trees, R: right y-axis, L: left y-axis.

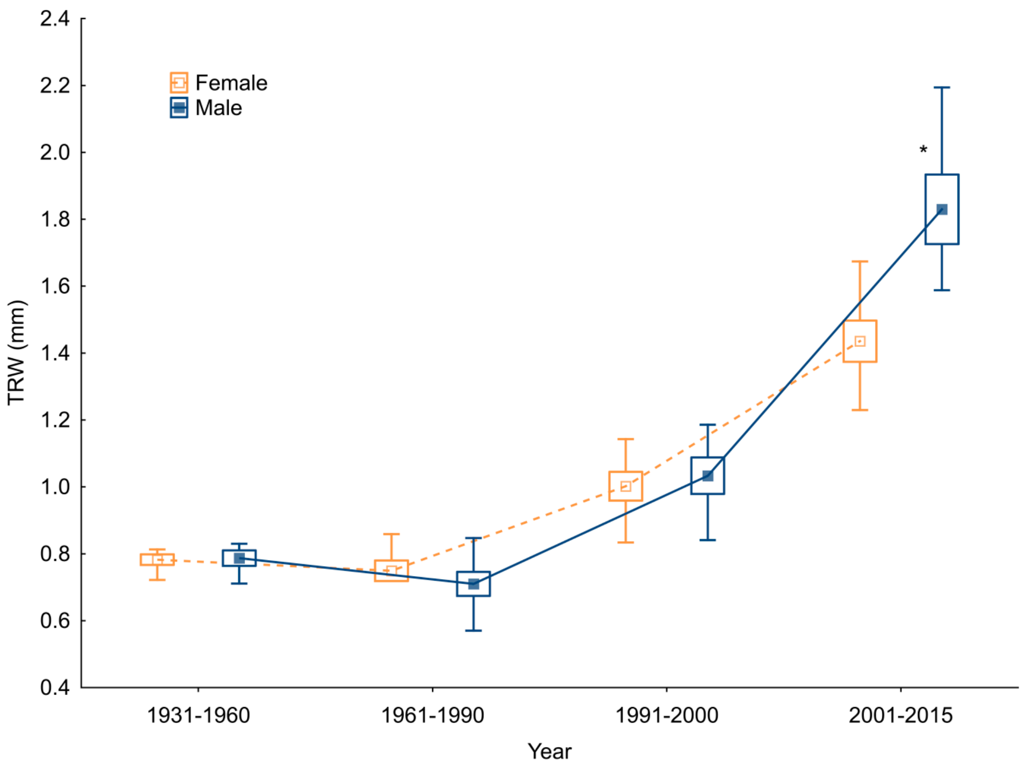

Figure 6. Comparison of mean periodic radial increments according to sex. Boxes represent standard deviations and whiskers range of TRW values; * denotes a significant difference between male and female yews.

In general, radial growth of yews first gradually decreased and reached a minimum in the 1960s and 1970s. Following the 1970s, radial growth first slightly increased and then markedly since 2000 (Figure 7). After 2000, we observed clearly different patterns of radial growth, according to the type of intervention (Figure 7 and Figure S6). Yews growing in sample plots classified as heavy intervention revealed permanent improvement of radial growth lasting up to the time of sampling in 2015 (Figure 7a). Trees in the moderate intervention plots also revealed enhanced growth, but the reaction to the release of crown space, visible in the tree-ring series persisted for about seven years (Figure 7b). The trees with no intervention revealed no enhancement of radial growth, which remained below average for the whole study period (Figure 7c). Average growth corresponded to a mean growth rate of 0.97 mm (Table 2).

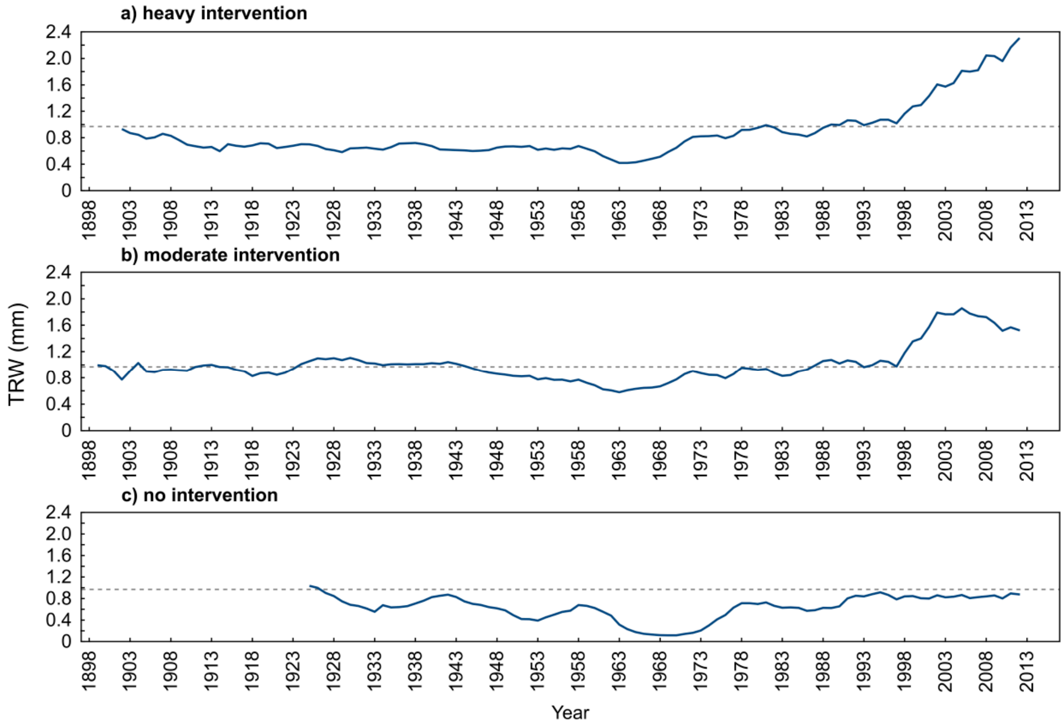

Figure 7. Tree-ring width (TRW) chronologies of sampled yews according to intervention type (**a**—heavy, **b**—moderate, and **c**—no intervention). Chronologies are expressed as five-year moving average values (solid line); the dashed line indicates the mean growth rate of all sampled yew trees.

4. Discussion

In the studied forest stand, light was one of the most important limiting factors for yew growth. Whenever access to light was provided, yew responded with accelerated growth, with corresponding central trees showing releases from suppression. Improved light conditions resulted in higher growth rates of both male and female yews, and in significant differences in radial growth between female and male individuals after the beginning of regeneration cuttings. Lower radial growth rates of female yews were likely the result of their higher reproductive costs, indicating a possible trade-off between reproduction and growth. The size and growth rate of mother trees positively affected the amount of newly regenerated seedlings. Their amount probably also depended indirectly on the intra-annual weather variation during the current and previous growing season. No statistical differences in the radial growth response to climate variability between female and male trees were detected.

4.1. Stand Structure

Our study showed that with limited or no stand tending, beech and maple formed dense canopy closure in the stand overstory and growth performance of yew trees remained rather poor and below the mean growth rate. In the study, sampled yew trees were growing on limestone bedrock covered by fresh soil, in the middle and upper parts of the southeast-southwest exposed slopes. As already shown [42], dense stands with a canopy closure of 2.2 to 3.8, and less suitable site conditions—especially north-facing slopes—did not provide an environment favourable for yew growth and reproduction. In such conditions, yew was reported to experience high mortality rates, even among adult trees (e.g., the National Nature Reserve Horný Harmanec). Canopy closure below 1.6 was confirmed to markedly improve yew growth performance, and yew showed good potential for regeneration processes under canopy closure of 1.6 to 1.7.

In temperate forests, the weak competitive abilities of yew restrict its distribution to habitats with the absence of faster-growing tree species [5,43]. To maintain healthy populations, yew trees require the reduction of canopy density and light competition [3]. Continuous selective thinning with a removal of 30% of the stocking volume was recommended to reduce the competition of beech [4,44]. Most likely due to the cuttings, the Danish population of yew increased from no more than 200 individuals in 1925 to above 2000 in 1998; regular selective cuttings of large beech trees have been applied since the area was protected in 1993 [45]. In comparison to the "do nothing" strategy in natural reserves, the probability of yew survival was reported to increase by 75 to 95% when using the alternative conservation strategy combining selective thinning, protection measures, and game control with public relation activities [10]. Our results showed that with under-designed irregular shelterwood cuttings, the increase in yew growth as a response to a removal of 15 to 20% of growing stock, persisted for about seven to eight years after the first intervention in 2000. This time interval likely corresponds to the closing of canopy gaps after the selective cutting of trees from the overstory.

4.2. Yew Natural Regeneration

In our study, improved light conditions caused higher fructification rates in adult females since the beginning of regeneration cut. The high number of established seedlings in the vicinity of adult yew trees indicated good conditions for their initial development. Similar results regarding the yew regeneration density were observed in populations in Poland and Austria [46,47]. On the other hand, some studies from Western Europe (Denmark, England, and Ireland) reported very poor natural regeneration of yew, reaching less than 2000 individuals per hectare [45,48,49]. Nevertheless, having some specific problems which are unknown in Central Europe (e.g., yew seed herbivory by rodents) means that these regions are not directly comparable. Similar to the results of Svenning and Magård [45], our results showed that growth of yew, its regeneration, cone production, and seedling recruitment were favoured by an open canopy. In a study from Poland [50], the most favourable development of five-year-old yew saplings planted under the canopy of older forest stands occurred at 30% canopy openness, whereas an insufficient amount of light resulted in a low height increment and an extended period of direct competition of yews with herbaceous species. Another study also revealed that the biomass of seedlings was highest under a light intensity of 30% out of the four levels of light intensity tested [51]. In our stand, a recent study [42] confirmed a rather low average level of relative light (below 20% of full solar radiation) was required. The main limitation of successful regeneration was that seedlings 10.1 to 20 cm tall were very rare, and taller seedlings and saplings did not occur under any adult yew individual. The Starohorská yew population was assigned to the category with the most damaged stems by wild ungulates, which in Slovakia involves bark-stripping mostly by red deer [52]. Wherever the game had access, every individual tree was damaged. Based on previous studies in the area, browsing pressure in the stand was enormous, and even lethal to natural regeneration. Established new seedlings were almost completely grazed by the wild game [30]. As a study from Germany confirmed [7], the presence of predators such as bears may positively influence the occurrence and dispersion of yew due to deer elimination and endozoochoric seed dispersion to new areas. Despite the increasing density of predators reported in Slovakia since the 1970s [53], the ungulate density has been increasing as well [54]. Our results, along with those of Iszkuło et al. [55], indicate that yew requires protection against animals for successful development. Browsing by game and insufficient light conditions were the most critical limiting factors not only to the growth of adults, but also to the natural regeneration of yew in the selected study area [8,9].

4.3. Regeneration in Relation to Mother Trees

In general, a yew seedling is usually two-to-eight cm tall at the end of its first season, with subsequent annual growth of often less than 2.5 cm [43]. Our results showed that the number of such seedlings was associated with the size of the mother trees. In contrast to the crown characteristics, stem parameters—namely stem volume—were confirmed as better predictors of the number of regenerated individuals. This is likely due to the use of the usual crown parameters that were not specific enough to capture the variable and irregularly-shaped crowns of understory yews. In this case, a future study would be needed to find some more specific variables suitable for characterizing yew crowns.

In Eastern Europe, reproduction of yew starts at the age of 70 to 120 years, and good seed crops occur every two to three years because of ceased fruit production in temperate, closed-canopy, mixed beech forests, and less optimal site conditions [56]. We showed that variation in the number of seedlings and the seed production was strongly correlated with resource availability. Based on the positive relationship between release cuttings and seed crop [57], higher resource availability—in our case expressed by higher radial growth rates—was related to higher seed production. Increasing the amount of light was likely to directly favour growth of yew—a species very sensitive to variations in solar radiation. The higher the growth rate, the more carbon resources could be allocated to reproduction and fruiting in a particular year, as documented by the positive relationship between radial growth rate and the number of regenerated seedlings in the vicinity of mother trees.

We also recorded a certain number of seedlings under male central stems. This could be consistent with the foraging behaviour of avian seed dispersers that preferentially select nearby male yew trees for the protection provided by their tree canopy. In a study from Spain, it was shown that microhabitats under target yew trees—both females and males—received 98.8% of dispersed seeds, 80% of which were under yew females, despite quantitative differences in total seed densities between sites and years [58]. The spatial arrangement of yew trees was important to seed dispersal processes. The variation in seed and seedling density across the landscape was spatially restricted, and was more a reflection of the differences in yew proportion among the sites [59–61].

A recent study from Ireland confirmed that the density and canopy cover of yew adults were negatively related to the recruitment of yew juveniles [49]. This is in line with some other studies suggesting that adult yew trees may have inhibited the establishment of new regeneration underneath them [12,62,63]. However, results of a study from the Central Apennines, Italy [1] showed that regarding the spatial scale, this relationship was more complex. Considering the landscape scale, yew regeneration was positively related to the basal area of yew. Nevertheless, at stand, a high density of yew trees can become the factor limiting yew regeneration. In this case, more suitable conditions for yew regeneration represented yews scattered across the stand, or just an increasing distance from dense yew patches. Similarly, management operations concentrated on regeneration around the edges of yew woodlands were suggested as a suitable way to preserve yew stands [49]. In our study, the majority of yew seedlings regenerated in the vicinity of adult yews, confirming the low dispersal ability of yew seeds. A limited number of seeds were able to escape from mother trees, which points to the necessity of adjusting ecological conditions in the vicinity of mother trees to become favourable for yew recruitment.

4.4. Sex-Related Patterns of Radial Growth and Climate Sensitivity

The results of this study showed the positive effect of regeneration cuttings on yew radial growth, and a significant difference in growth between male and female yews following the cuttings. In our case, increased radial growth was likely related to cutting operations, based on releases identified in later life stages rather than on species-specific yew auto-ecology or climate change. Before beginning of the regeneration cuttings, female and male individuals displayed similar growth rates. Following the start of regeneration cuttings, significant sex-related differences in growth variability appeared. Better growth performance of the males could be attributed to the reproductive process, where the males invest less carbon resources than females. Besides flowering and pollination, in the case of males, females continue to invest during the whole growing season into seed and fruit production and their subsequent dispersal [16]. In temperate forests, the reproduction cycle for a yew female lasts about six months, beginning with pollination in April and finishing with seed dispersion in September. The formation of flower buds is accomplished during the second half of the summer in the previous vegetation season [43]. The reproductive effort of males is much lower, confined to late summer of the previous season for flower bud formation and ending with pollination in April of the current season. The higher resource investment of females [22] could be the cause of growth differences recorded in our study site since 2000. Variation in the number of seedlings was strongly correlated with resource availability. In the study, females switched resources to seed production to produce seed crops, leading to a lower correlation between number of seedlings and growth rate in the year of seed formation and in the subsequent year. Costly seed production shows the favouring of reproduction at the expense of growth in female trees [14]. It is therefore possible that there is a trade-off between reproduction and growth [64], which, as expected, is particularly obvious in dioecious plants due to sexual dimorphism resulting from gender-specific functional traits of individuals. In other tree species, a negative relationship between fruit production and radial growth was shown (e.g., in beech) [65,66]. On the contrary, radial growth in the year of seed formation and the year after did not differ between trees with low and high seed crops for rowan [67].

However, carbon resources are not the only factor that controls the reproduction process in plants [19]. Inter-annual environmental variability is another main driver [68]. Unfortunately, no time series records on annual seed production were available to compare the long-term variability in seed production with fluctuations in climate variables. For reproduction, variations in precipitation and water availability seem to be more influential than temperature [18,24]. A study on oaks in California [69] showed that the response of reproduction (in terms of acorn production) to annual weather conditions was inversed to that of growth (radial increment). This seems to confirm growth and reproduction could be independent of each other, and negative relationships suggesting trade-offs could be determined by correlated environmental factors rather than being causal [69,70]. For example, higher precipitation amounts stimulating radial growth in early spring could inhibit flowering and anemophilous pollen dispersion of males, finally resulting in decreased seed production in females. Likewise, water deficits in the vegetation period inhibiting radial growth could favour flower buds' formation in the end of the growing season [19].

As shown in our results, there might be a lagged relationship between seed production and climate, which is responsible for the production of larger seed crops of yew following the drought season. Apparent drought-induced reduction in aboveground net primary production is often the result of shifts in carbon allocation toward fruit production triggered by warm and dry weather in the previous summer [71]. In European beech, a trade-off between growth and reproduction in years with heavy seed production could have been responsible for the observed lagged correlations between growth and water availability in the previous growing season [72].

In temperate forest zones, climate is generally less influential on the growth of trees than in arctic or semi-arid regions, resulting in a rather lower correlation with climate variables [32]. With respect to higher RBT, EPS, and MSs values of tree-ring chronologies, moderate climate–growth relationships in the study could be partly attributed to the source of climate data used. In fact, *Fagetum dealpinum* represents a particular niche in the ecology of European yew, where the climate only moderately modulates the growth of trees, where a mixed, rather than strong temperature in high elevations or precipitation in the lowlands, climate signal is expected. However, calcareous bedrock on often steep slopes could represent a water-limited environment that influences the growth of yew.

Our results showed that sensitivity of tree-ring variability to climate did not appear to be sex-dependent. In a study from Western Poland, unlike the male trees, the growth of European yew female trees was negatively correlated with temperature during the previous year, and positively with precipitation in the current year [73]. However, in our study, no significant differences in response to climate were found between the sexes. We assume that the lacking difference in sex-specific response of radial growth to climate was due to the relatively short time since the vivid regeneration of females was induced by cuttings, which did not allow the different climate sensitivity to become apparent.

Sex-specific life histories can bias the sex ratio in dioecious species, and therefore the resource heterogeneity in terms of varying light intensity [74]. In this study, the yew population in a secondary managed forest of relatively young age of about 90 to 120 years had an equally biased sex ratio. In the later life stage or eventually in old-growth forests, sex-differing growth traits, stem diameters, sex ratios, stem densities, and even spatial distribution patterns could be expected [75]. This should eventually result in sex-specific differences in growth sensitivity to climate variability. On the contrary, in the future, in an environment that is less water-limited, the differences in climate responsivity may remain uniform.

5. Conclusions and Conservation Management Strategy Suggestions

Preserving tree species threatened by climate change remains a great challenge for forest management decision-making. To assure the long-term existence of yew, the presence of old-growth beech forests with incorporated yew patches appears to be important [1]. Admitting that yew requires stable ecological conditions for its existence, increasing frequency and intensity of large-scale disturbances under climate change present a serious issue to the long-term growth of yew. In recent decades, not only coniferous, but also more stable deciduous forest stands have been heavily damaged. For example, in Slovakia, 44% of the salvage felling volume was made up of deciduous forest stands, damaged by the large storm Žofia in 2014.

Another issue is the enhanced tree growth, higher standing stocks of trees, and density of forest stands in relation to changes in climate, nitrogen deposition, and forest land management. As suggested in some studies [76,77], the forest canopies have grown denser across much of Europe over recent decades. On the other hand, a study by Pretzsch et al. [78] showed that accelerated growth resulted in faster ageing, whereas the maximum tree density did not change. Nevertheless, in regions where an actual increase in forest canopy density was observed, the actions to balance ecological conditions in favour of successful yew growth would be appropriate. Overall, stand competition might determine how European yew will cope with a changing climate. Our results indicate that local populations of European yew might decrease in areas with forest succession, leading to the dominance of faster growing shade-tolerant tree species. We found that continuous crown thinning—overstory thinning (positive selection) with an intensity of 15% applied once per decade, respectively once every seven to eight years, with consequent irregular shelterwood cutting with the intensity of 15 to 20% in the recovery phase of the stand—could form the basis of a conservation management strategy for maintaining the viability of yew. Since European yew is a sensitive species with a narrow ecological range, without such management interventions its chances of extinction may dramatically increase in many areas within its range [2].

Nevertheless, higher growth rates and investment in regeneration could lead to higher susceptibility of yew trees to environmental stress, such as extreme drought episodes. Due to the higher energy costs, females in later life stages may be shorter in height and smaller in diameter and subsequently exhibit higher mortality rates under stress conditions [64], resulting in male-biased sex ratios [12]. Accordingly, our findings suggest that females under increased density of the surrounding stand would have a higher mortality risk than males because of reduced growth that would eventually lead to carbon starvation. This may be a factor in increasing the risk of extinction of dioecious species [73]. Males can likely maintain themselves better than females, which emphasises the importance of making silvicultural treatments for females a priority. Adjusting the thinning and release cuttings to higher intensities—up to 30% of growing stock removal, thus keeping canopy closure at the values favourable to yew growth below 1.6—could be recommended for the female trees and their surroundings. Such interventions could possibly favour subsequent natural regeneration, allowing seeds to germinate and seedlings to grow outside the crown of mother trees. Either reduced access to light in the understory or open habitats along with frosts are the direct reasons for the high mortality of newly germinated seedlings, while light conditions at 30% of full solar radiation are optimal for seedling growth [51].

However, the suggested conservation measures can succeed only with consistent elimination of browsing and bark-stripping by deer. Ungulates are significantly involved in the reduction of adult yew trees in the understory. The unequivocal effect of fencing in the protection of natural yew recruitment surveyed during the eight years was clearly confirmed. Yew recruitment age categories above five years old were present only inside the fenced area.

Rainy summers, early autumns, and warm winters enhance the radial growth of yew, which could direct the timing of regeneration cuttings to seasons following such climatic conditions to support the effect of the release cut. Still, further studies on sex-related differences in response to climate and extreme events may allow the improvement of designed conservation and management actions regarding the viability of yew trees under climate change.

Overall, we found that release cuttings increased the performance of the rare and mostly understory tree species *T. baccata* in terms of stem growth and seed production. Such measures could counteract the ongoing decrease in the growth performance and increase the viability of populations, so as to preserve the unique biodiversity of calcareous beech-dominated forests. Continuous thinning and cutting operations seem to be an effective conservation management approach to ensure the persistence of rare tree species growing in the understory, if their existence is inhibited by forest succession of faster growing and shade tolerant trees.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/8/289/s1. Figure S1, Location of the study area, Pavelcovo (PAV, Starohorské Mts.) in Slovakia, Figure S2, Stem volume cuttings removed from the stand calculated per hectare for all tree species other than yew, Figure S3, Climate diagram with mean monthly precipitation sums (mm) and temperatures (°C) over the periods of 1901–2014 and 1991–2014 in the study area Pavelcovo, Figure S4, Strong linear relationship between correlation coefficient values illustrating uniform (no sex–specific) response of residual ring width indexes to variations in climate, Figure S5, Mean tree-ring width (TRW) values between years and sex of yew trees in 2013 and 2014, Figure S6, Chronology of yew trees showing releases, Table S1, Description of the investigated sites, Table S2, Abbreviations, symbols, and formulae of tree crown variables.

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