Mariana Kýpeťová, Łukasz Walas, Peter Jaloviar, Grzegorz Iszkuło

Influence of herbivory pressure on the growth rate and needle morphology of *Taxus baccata* L. juveniles

Abstract: Damage by herbivore grazing negatively influences the development of subsequent forest generations. Little is known about the long-term impacts of grazing and interactions between grazing and light conditions on sapling growth after the cessation of herbivory impact. In this study, *Taxus baccata* saplings were grown over a period of four years in artificial shading at 2, 8, 30 and 100% of full sunlight (described as initial light). These saplings were planted in fenced and unfenced plots in a mixed forest in Poland. After six years with no protection from grazing, deer pressure was eliminated by fencing. In this study, we analysed sapling growth and needle morphology five years after deer suppression. Overall, grazing had a negative significant impact on the growth rate and needle morphology of *T. baccata* saplings. Saplings damaged by herbivores had a height increment approximately one-third that of non-grazed saplings. The grazed yew saplings had a lower needle area and length and a higher specific leaf area (SLA) than non-grazed saplings. Initial and current light conditions did not influence tree growth rates and needle morphology. However, we found positive correlations between sapling height and both leaf area and leaf length and a negative correlation between sapling height and SLA. Browsed yews also had a greater tendency to form polycormic (multi-stemmed) individuals. Lower growth rates, smaller needles and polycormic stems indicate a strategy of "escaping" herbivory pressure even five years after elimination of deer pressure.

Keywords: *Taxus baccata* L., herbivory grazing, regeneration, sapling growth

Addresses: M. Kýpeťová, Faculty of Forestry, Technical University, 960 53 Zvolen, Slovakia,
e-mail: mariana.kypetova@tuzvo.sk
Ł. Walas, Institute of Dendrology, Polish Academy of Sciences, 62-035 Kórnik, Poland,
e-mail: lukaswalas@wp.pl
P. Jaloviar, Faculty of Forestry, Technical University, 960 53 Zvolen, Slovakia,
e-mail: peter.jaloviar@tuzvo.sk
G. Iszkuło, Institute of Dendrology, Polish Academy of Sciences, 62-035 Kórnik, Poland and Faculty of
Biological Science, University of Zielona Gora, 65-516 Zielona Gora, Poland,
e-mail: iszkulo@man.poznan.pl

Introduction

Browsing by herbivores is one of the most limiting factors of natural and artificial regeneration in central European forests (Kamler et al., 2010). Wild ungulates are a natural part of forest ecosystems, and young trees are a normal part of their diet (Kupferschmid et al., 2013). However, browsing by mammalian herbivores can cause considerable damage to woody plants of ecological and silvicultural significance (Duncan et al., 1998). Therefore, many studies have evaluated the effect of grazing on the growth of various tree species (e.g. Kupferschmid et al., 2013; Tanentzap et al., 2012; Heuze et al., 2005; Vila et al., 2003). Deer browsing and bark stripping markedly limit normal tree growth and development in three main ways: browsing on seedlings, browsing on terminal shoots or browsing on lateral shoots. According to this, we can distinguish the structural changes of trees in terms of wood density, height growth or foliage density (Gill & Beardall, 2001). During the early stages of forest regeneration, foresters deal with the issue of deer browsing to ensure the protection and regeneration of target tree species. Hereby, they have to choose appropriate methods to reduce herbivore damage, e.g. mechanical or chemical protection (Kamler et al., 2010). The damage caused by deer browsing can be severe and markedly influence the survival and growth of endangered species. *Taxus baccata* L. is one of these endangered rare species and is currently conserved by different regimes of protection (Thomas & Polwart, 2003; Schirone et al., 2010; Vessella et al., 2013; Vessella et al., 2015). Therefore, certain woodland communities containing *Taxus baccata* have received priority habitat status (EU Habitat Directive 92/43/EEC), but climatic changes may further enhance the decline of this species (Garbarino et al., 2015; Thomas & Garcia-Marti, 2015; Vessella et al., 2015). Because of these threats, a number of yew conservation and restoration programs have been launched in many European regions (Farris et al., 2012; Katsavou & Ganatsas, 2012; Peragón et al., 2015), including Poland (Niemczyk et al., 2015). The result of these projects is the enrichment of tree species composition of Polish state forests with planted yew and the realisation of active management with a partial conservation regime in order to maintain this valuable tree species (Magnuszewski, 2015). Despite the high toxicity of plant organs of *Taxus*, the species is highly browsed by deer (Svenning & Magård, 1999; García et al., 2000; Mysterud & Østbye, 2004; Perrin et al., 2006).

So far, the studies regarding the influence of deer pressure focused primarily on the survival of tree regeneration (e.g., Mysterud & Østbye, 2004; Farris & Filigheddu, 2008) and the changes in tree species composition resulting from animals grazing preferences (Augustine & McNaughton, 1998; Gill & Beardall, 2001). However, few studies have considered the effects on the growth and physiology of seedlings and saplings after the elimination of herbivore pressure. Cessation of herbivore pressure may occur as a consequence of fencing, or after the regeneration has outgrown the reach of ungulates and became unavailable for herbivory (Zamora et al., 2001).

Besides grazing, excessive shading is the next problem for the successful growth yew regeneration (Iszkuło & Boratyński 2006; Dhar et al., 2008, Perrin & Mitchell, 2013; Devaney et al., 2015). In natural populations, a large number of seedlings are observed to die in a short time after germination (Hulme, 1996; Svenning & Magård, 1999; Thomas & Polwart, 2003). One of the most important reasons is the insufficient light intensity at the forest floor (Niemczyk et al., 2015; Dhar et al., 2007). Therefore, there is a need to reduce excessive shading to actively promote the growth of natural regeneration. The reaction of yew saplings to changes of light conditions (e.g. by the reduction of canopy in natural populations) has not been analysed in detail yet. Nevertheless, the current results confirm the negative influence of full light exposure on growth and development of yew regeneration (Perrin & Mitchell, 2013; Iszkuło et al., 2014).

In general, light significantly affects survival, growth and development of plants, which reflects in their adaptation to light conditions. Leaves morphology is particularly sensitive to light intensity. The needles in shady conditions are longer, have larger surface and specific leaf area (Wyka et al., 2008; Devaney et al., 2015). However, Devaney et al. (2015) found that the height of *T. baccata* individuals is much more important for needle morphology of saplings than light intensity. The main objective of this paper is to evaluate growth and recovery of *T. baccata* saplings after elimination of herbivory and the interaction between growth recovery and light intensity.

We tested the following hypotheses: (i) previous herbivory pressure has a negative influence on the growth rate and needle morphology of *Taxus baccata*, (ii) initial and current light conditions affect the further growth and development of yew saplings, (iii) needle morphology is more correlated with sapling height than with light intensity.

Material and methods

Study site

The studied population of *Taxus baccata* is located in a mixed forest with dominant protective function in the Babki Forest District, Poland (geographic coordinates: N 52°16'43'', E 17°04'23'', 95 m a.s.l.). The area has an average annual precipitation of 544 mm and an

average annual temperature of 8.3°C, measured at the Kórnik meteorological station located four kilometres from study site (Cedro & Iszkuło, 2011). The soil type is brown earth soil with sandy loam. In the experimental area, the forest stand is dominated by larch (*Larix decidua* Mill.) and oak (*Quercus robur* L.) and forms two canopy layers. The upper layer represents larch, the lower layer represents oak. Larch density is 86 trees per hectare, with mean height of 35.6 m (± 0.393 SE) and mean diameter of 53.6 cm (± 1.87 SE). Oak density is 199 trees per hectare, with mean height of 26.4 m (± 0.298 SE) and mean diameter of 26.1 cm (± 0.554 SE) (for details, see Iszkuło et al., 2014).

Establishment of study plots

The population of *Taxus baccata* was established from the artificial regeneration. The history of seed and seedling treatments in the experiment is presented in Table 1. Prior to planting in the forest, the seedlings of *T. baccata* were grown in an artificially shaded outdoor garden in Kórnik under four different light rates of 2%, 8%, 30% and 100% of full solar radiation ("initial light variant", Iszkuło et al., 2014). In 2006, four-year-old saplings were planted in a 3 × 3 m spacing at three sample plots (blocks of 24 × 24 m), each divided into fenced and unfenced part ("treatment"). We used 16 saplings from each initial light variant resulting in a total of 384 analysed saplings (16 saplings × 4 initial light variants × 2 treatments × 3 blocks). From 2006 to 2011, all unfenced yew saplings were intensively grazed (see Iszkuło et al., 2014, for details). In 2011, the mean (± standard error) height of grazed saplings was 27.23 cm (± 1.65), and the mean height of un-grazed saplings was 71.47 cm (± 2.88). The highest mortality was noted in the first year of planting (2006) and for the particular light variants in fenced treatment it reached 46% (2% of full sunlight), 33% (8% of full sunlight), 6% (30% of full sunlight) and 0% (full sunlight), with the overall average of 21%. In the unfenced variant, the respective mortality rates were 58%, 29%, 15% and 8%, with the overall average of 27%. The mortality

Table 1. History of *Taxus baccata* seed and seedling treatments in the experiment

Treatments	Year
Collecting seeds from 10 parent individuals in the Malinówka (SE Poland) nature reserve	2000
Seed stratification and storage (according to Suszka 1985)	2000–2002
Growth in the nursery in the Kórnik Arboretum	2002–2003
Growth in artificial shading at 2, 8, 30 and 100% full sunlight	2003–2006
Growth in the forest in fenced and unfenced plots (see Iszkuło et al. 2014	2006–2011
Growth in the forest only in fenced plots (fencing unfenced plots - this study)	2011–2016

by 2011 was lower in the fenced treatment (35% in total) than in the unfenced treatment (45% in total) (see Iszkuło et al., 2014 for details).

Measurement of parameters

At the end of growing season in 2011, all plots without protection against herbivory were fenced in order to eliminate the herbivory damage. In June 2016, we measured the actual height of every *T. baccata* sapling and the five annual height increments of growing seasons 2011–2015 to an accuracy of 1 cm at the bud whorls along the main (highest) axis of the sapling (Fig. 2). Simultaneously to height measurements, we evaluated the survival and recovery of all *Taxus baccata* saplings. For each sapling, we counted the number of produced stems higher than half of the height of the particular sapling. In addition to the vertical growth of saplings, the horizontal growth was recorded by measuring crown diameter in two perpendicular directions. In the analysis, we used the mean crown diameter.

In addition, we measured the length of the lateral increment in order to calculate the light factor (Honowski light factor), presenting the ratio of the length of the longest side shoot and the terminal shoot in the particular year. Honowski light factor describes the relationship between light of actual forest stand and current growth of yew saplings. Light factor was used to describe the crown morphology and habit of saplings, which is indirect indicator of light conditions in the understorey. A value below 1.2 indicates a large increase of the terminal shoot, often resulting in a well-formed crown and a healthy young tree. In contrast, a value above 2.0 indicates a reduction in tree height and thus a rather limited suppressed tree (Kupferschmid et al., 2013, Fabijanowski et al. 1974).

Light intensity (PPFD) was measured by a quantum light sensor (Spectrum Inc.) in June 2016 at the time of full foliage of the canopy layer. It was important to observe the principles of measurement under

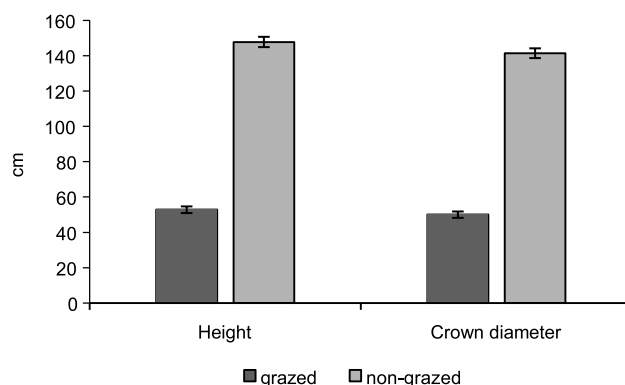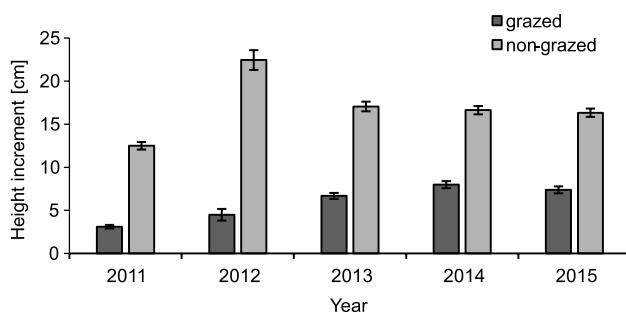Fig. 1 Means of height and crown diameter (± standard error) of grazed and non-grazed *Taxus* saplings

Fig. 2 Mean value (± standard error) of height increment in 2011–2015 of non-grazed and previously grazed saplings of *T. baccata*

standard overcast conditions (cloudy day), to ensure reliable data of relative radiation. Two measurements were recorded in perpendicular directions at the height of each yew sapling and the mean value was considered as a characteristic of the light conditions at this stand. At the time of PPFD measurement, light in an open area with the use of a light sensor was recorded. Relative PPFD (RPPFD) was calculated as the ratio of mean PPFD in the plots in the forest to the PPFD in the open area at the same time.

For the analysis of yew needle morphology, we used 20 needles from whorl formed in growing season 2015. Needles were collected from a south-oriented lateral shoot. The needle samples were chosen to cover all types of initial light (2, 8, 30 a 100% of RPPFD) and include the widest possible range of the light condition in the forest. In total, there were 48 samples, specifically 2 treatments × 4 types of initial light × 6 light classes in the forest stand (class to 5, 5–7, 7–9, 9–11, 11–13, above 13% of RPPFD) = 48 samples. Fresh needles were measured and analysed using WinSeedle (Regent Instrument Inc.). From the WinSeedle output file we used means of needle length (mm), needle width (mm) and needle area (mm^2). For analysis of morphological parameters, we used the mean values of these 20 needles. Subsequently, the needles were dried at 60°C for 3 days and weighed to calculate specific leaf area (SLA), which is the ratio of total projection area to dry mass.

Data analysis

The multivariate approach (MANOVA, O'Brien & Kaiser 1985) to repeated measures was used to analyse the yearly increment of saplings. Percent data (light intensity) were transformed with an arcsine function, which normalised distributions in order to satisfy the assumptions of MANOVA. Between MANOVA subjects, the T-test was used. Within MANOVA subjects, T-test, Wilks' Lambda, Pillai's Trace and Hotelling-Lawley Trace were also examined and allowed consistent interpretations in all cases. Mixed model analysis of covariance (ANCOVA)

was used to compare grazing, RPPFD (as a covariant) and height, crown diameter, needle area, length, width, SLA, and Honowski light factor of *T. baccata* saplings. Statistical model included: 1) random variables: block, block nested in grazing and 2) constant variables: grazing, relative variations. All data were analysed using JMP Pro 12.0 (SAS Institute Inc.).

Results

The total number of *Taxus baccata* saplings in 2016 was 341, which represents around 0% of mortality, compared with year 2011 (342 saplings).

Light intensity in experimental plots varied approximately between 3 and 16% of RPPFD, with a mean value of 8.24% of RPPFD (± 0.099 SE). Extreme values of light intensity fluctuated between particular plots, but the differences between plots were not significant (ANOVA, F=1.653 P=0.1453, N= 64 samples per plot = 384 per experiment.). Preliminary analysis found that initial light level had no significant effects and thus this variable is not considered further.

Growth parameters

There was a significant influence of grazing on height and crown parameters (Fig. 1), but the influence of RPPFD was not significant (Table 2). The non-grazed saplings reached the mean height 147.77 cm (± 2.912 SE) and grazed saplings 52.81 cm (± 1.880 SE). Non-grazed saplings had also larger dimension of crown with the mean crown diameter of 141.40 cm (± 2.768 SE) in contrast with grazed saplings with the mean value 50.0 cm (± 1.803 SE).

There was no significant influence of RPPFD on height increment of yew saplings (Table 3). The growth rate of *T. baccata* saplings was mainly influenced by grazing and changed over time (Table 3). Saplings had higher height increments in the fenced subplots. Mean height increment during the period 2011–2015 for grazed *T. baccata* saplings was 5.92 cm (± 0.266 SE), while non-grazed saplings showed an increment of 16.92 cm per year (± 0.379 SE). Until 2014 there was a general trend for the height increments of grazed saplings to increase over time (Fig. 2). However, the height increment in 2015 was similar to that in 2014, which indicates equal growth

Table 2. Mixed model analysis of covariance (ANCOVA) used to compare grazing, RPPFD (as a covariant) and height, crown diameter of *T. baccata* saplings

Feature	Variables	DF	F Ratio	P
Height	Grazing	1	744.71	<.0001
	RPPFD	1	0.0201	0.8875
Crown diameter	Grazing	1	734..34	<.0001
	RPPFD	1	0.0039	0.9501

Table 3. Repeated Measures Analysis of *T. baccata* yearly increment (years 2011–2015) against time effect and grazing, with RPPFD as a covariant

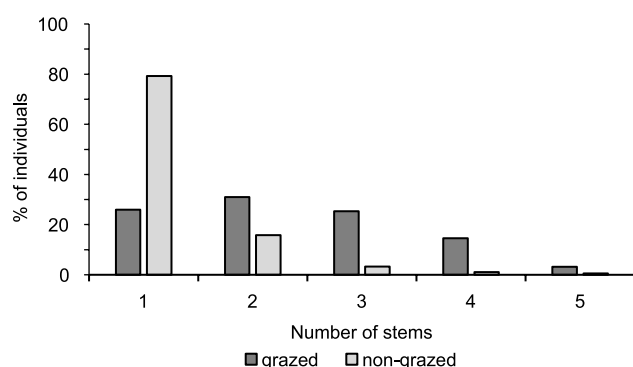| Variables	F Value	DF	Prob>F
Between subjects			
Grazing	1.3330	1	<0.0001
RPPFD	0.0039	1	0.2506
Within subjects			
Time	0.1101	4	<0.0001
Time × Grazing	0.1891	4	<0.0001
Time × RPPFD	0.0232	4	0.1032

Fig. 3 Differences between number of saplings forming side shoots in grazed and non-grazed *T. baccata* saplings

in previously grazed saplings (Fig. 2). Contrary to the height increment, sapling habitus expressed by Honowski light factor was not influenced neither by grazing nor by RPPFD.

In addition, the herbivory pressure on young yew saplings became evident by the formation of polycormic (multi-stemmed) individuals. The occurrence of one main stem was dominant in non-grazed saplings (79.23%) but not in grazed saplings (25.94%), which tended to polycormicy as a reaction to grazing (Fig. 3).

Needle morphology

Grazing history had significant influence on the morphology of *T. baccata* needles, while RPPFD had not significant effect on any of the analysed parameters

Table 4. Mixed model analysis of covariance (ANCOVA) used to compare grazing, RPPFD (as a covariant) and needle area, length, width, SLA, and Honowski light factor of *T. baccata* saplings

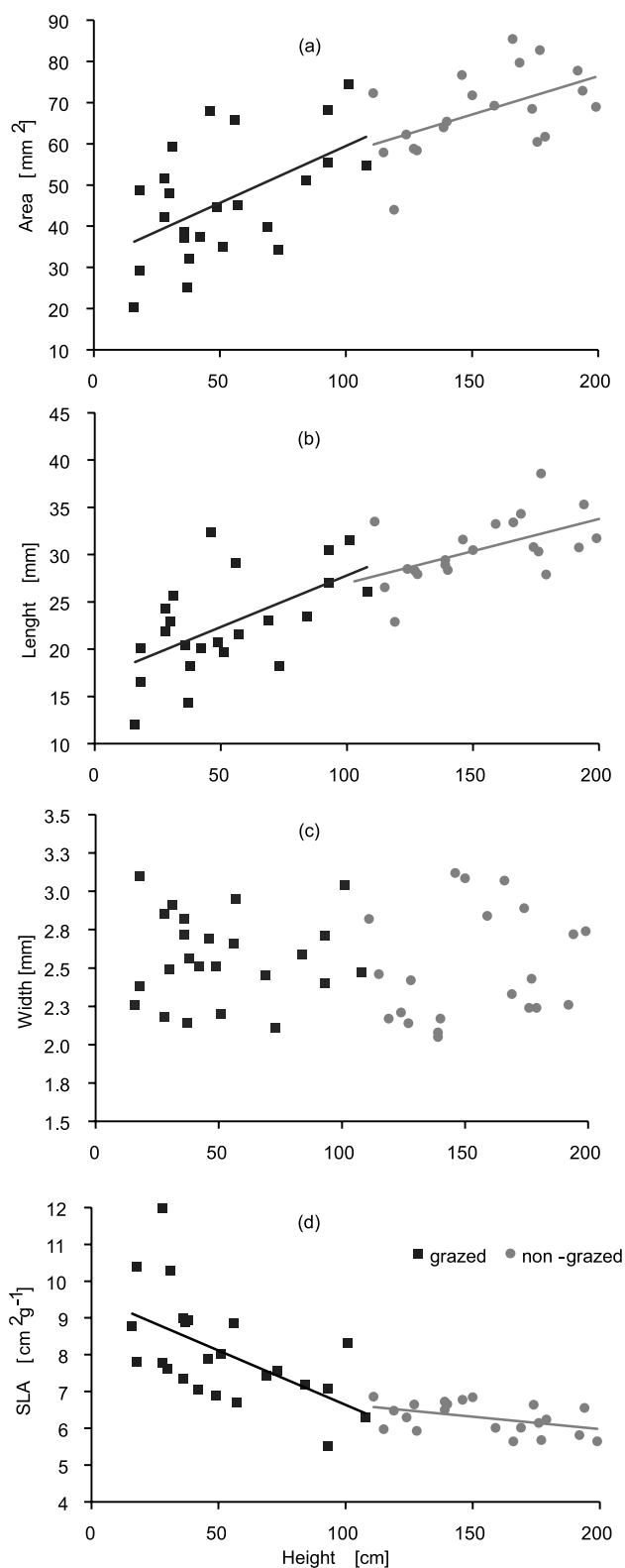|	Source	DF	F Ratio	P
Area	Grazing	1	40.626	0.0230
	RPPFD	1	1.1592	0.2881
Length	Grazing	1	64.1953	0.0124
	RPPFD	1	1.1994	0.2805
Width	Grazing	1	0.2459	0.6690
	RPPFD	1	1.4562	0.2342
SLA	Grazing	1	28.4606	0.0370
	RPPFD	1	0.0309	0.8613
Light factor	Grazing	1	0.0809	0.8033
	RPPFD	1	0.0121	0.9129

Fig. 4 Relationship between height of *T. baccata* saplings and needle **area**: (a) grazed: $R^2 = 0.287$, p = 0.007, non-grazed: $R^2 = 0.275$ p = 0.0148, **length** (b) grazed: $R^2 = 0.337$, p = 0.0029, non-grazed $R^2 = 0.2978$ p = 0.0105, **width** (c) grazed: $R^2 = 0.0001$, p = 0.8972, non-grazed: $R^2 = 0.0425$, p = 0.3701, **SLA** (d) grazed: $R^2 = 0.331$, p = 0,0033, non-grazed $R^2 = 0.199$ p = 0.0429

Table 5. Mean (± standard error) values of SLA, Honowski light factor, needle area, length and width of *T. baccata* saplings

	SLA (cm²g⁻¹)	Light factor (cm.cm⁻¹)	Area (mm²)	Length (mm)	Width (mm)
Grazed	8.07 ±0.289	2.16 ±0.322	46.09 ±2.906	22.51 ±1.057	2.57 ±0.058
Non-grazed	6.56 ±0.198	2.01 ±0.671	63.41 ±2.663	29.41 ±0.936	2.48 ±0.070

(Table 4). Non-grazed needles had a greater projection area, length and lower SLA compared to needles from grazed *Taxus* saplings (Table 5).

The height of *T. baccata* saplings was positively correlated with needle area and length (Figs. 4a, b) and negatively correlated with SLA (Fig. 4d). Needle width was not correlated with sapling height (Fig. 4c).

Discussion

Our investigations have shown that previous grazing (six years) was the most important factor affecting the growth rate and morphology of yew needles. Our results therefore confirmed the first hypothesis that herbivory pressure has a significant negative influence on growth of yew juveniles and parameters of needle morphology. Contrary to grazing, light conditions in the analysed plots had no significant influence on further growth and development of yew saplings.

Grazing

Mortality

Despite the previous heavy herbivory damage on plots unfenced until 2011 (Iszkuło et al., 2014), there was negligible mortality of yew juveniles in the monitored growing seasons. Grazing is a significant cause of mortality of youngest seedlings, however, with increasing age, the negative influence of grazing diminishes (Harmer, 2001). Most deciduous tree species of temperate zones are able to survive long-lasting herbivory attacks if they survive the first critical vegetative season (Ammer et al., 2010). Conifers usually have higher mortality rates in the subsequent growing years because of their poorer regeneration abilities. *Taxus baccata*, growing on favourable sites, has high regeneration abilities, which makes it an exception among conifers (Thomas & Polwart, 2003). However, its dioiceous character makes it vulnerable in forest stands with varied climatic conditions (Garbarino et al., 2015; Vessella et al., 2015).

Growth

Height growth of yew saplings was significantly affected by previous grazing, and saplings damaged by herbivores had more than three times lower height and more than twice slower height increment values in the fourth and fifth year after fencing than saplings protected from herbivory. Browsing frequently damages the most palatable parts of saplings, i.e. leading shoots, buds and upper leaves that are the most actively growing and nutritious parts, thereby physically reducing juvenile height (Gill & Beardall, 2001; Bergquist et al., 2003). It should be noted that increases in height growth of grazed saplings were observed for the first four years, but in the fifth year after eliminating grazing pressure, tree growth was similar (Fig. 2). Stagnation of height growth is generally the most frequent evident consequence of intensive herbivory in young forest stands (Harmer, 2001; Ammer et al., 2010). Due to the influence of height increment on the current height of individuals (Uzoh & Oliver, 2008), we recorded lower absolute values of height increment for previously grazed (lower) yew saplings than for non-grazed saplings. Even after four vegetative seasons without herbivory damage, the previously grazed saplings did not reach the mean yearly height increment of the non-grazed ones. This indicates that browsed saplings suffer an impairment in height growth and are not able to catch up with non-browsed ones. There are three main mechanisms to reduce the impacts of herbivory: escape, defence or tolerance (Boege & Marquis, 2005). In our study, limited height and reduced leaf area of grazed saplings might be a measure of escape or avoidance, resulting in a reduced likelihood to be grazed by herbivores or decreased attractiveness (Milchunas & Noy-Meir, 2002). Another response of grazed *Taxus baccata* juveniles was the formation of more than one stems. Once the damage has occurred, the negative impacts of herbivory can be reduced through tolerance, which means the ability of recovery and maintaining a healthy condition (Boege & Marquis, 2005). The production of higher number of shoots or sprouts is a mechanism by which some conifers may react and recover after disturbance in the sapling stage (Del Tredici, 2001). Most of grazed *T. baccata* saplings (74%) in the studied area had more than one stem, in comparison, nearly 80% of un-grazed trees monocormic (Fig. 3). In a similar study, previous herbivory damage had a considerable impact on Sitka spruce (*Picea sitchensis*) sapling morphology, because damaged spruces had significantly lower height, tree span, and leader shoot width and length compared to undamaged trees (Duncan et al., 1998). Wallgren et al. (2014) found that grazing may require Scots pines (*Pinus sylvestris*) to allocate more resources into the compensation of the removed tissues, such as forming new buds, and less into height and diameter growth. Similar results has been found by Rasmussen et al. (2003) in case of growth allocation changes of *Abies nordmanniana* L.

European yew develops lateral buds at irregular intervals, they are frequent along the stem, which explains why *T. baccata* can withstand pruning the main trunk (Thomas & Polwart, 2003). In addition, *Taxus baccata* has a tendency to form multiple stems (Thomas & Polwart, 2003), but it seems that in undisturbed populations, most individuals are monocormic, this was the case in the Knyazhdvir Nature Reserve (Ukraine), where the percentage of one-stemmed individuals ranged between 74 and 87% (Iszkuło et al., 2005), similar to the percentage of one-stemmed, un-grazed saplings in our study.

Needle morphology

Grazing had also a negative impact on the needle morphology of studied yews. The non-grazed yew saplings had a greater surface area and needle length than the grazed yew saplings. According to Kartusch & Richter (1984), the morphological changes of *T. baccata* needles are probably the result of water transport impairment to the tree body through the cutting of the stems, because stem cutting causes a form of xeromorphic needles with reduced leaf area, a thicker cuticle and smaller inner cells. This might characterise an escape mechanism from grazing, in particular due to the small leaf size and the high leaf dry matter content, however, in our study, the SLA of juvenile yew needles increased under herbivore pressure and was higher in grazed than in non-grazed saplings. This finding is in agreement which the observation of other authors who confirmed that grazing tolerance can be expressed as high specific leaf area (SLA) and low leaf toughness, which increase shoot regrowth ability and selectivity by herbivores (Zheng et al., 2010).

Light intensity

Growth

We found no effect of light conditions on *T. baccata* growth rates, confirming earlier findings by Iszkuło (2014) who transferred saplings from different to similar light conditions. Mean light intensity dropped from 13.95% (± 0.1807 SE) in 2011 (Iszkuło et al., 2014) to 8.24% (± 0.099 SE) in 2016, but still there was no significant influence of light on yew growth, although light demand increases with increasing age (Iszkuło & Boratyński, 2006). According to Iszkuło & Boratyński (2006), the ecological light optimum of *Taxus baccata* is 2–7% of full sun, but the physiological light optimum is much higher (Iszkuło, 2010). Forest ecosystems with natural occurrence of *T. baccata* in Europe are often beech-dominated (Linares 2013), as a consequence, they have a low light intensity in the understorey. However, the results under controlled light conditions (2, 8, 30 and 100% of full sun) indicated optimum growth at 8 and 30% of full sun (Iszkuło, 2010). In our studied forest stand, relative radiation ranges between 3 and 16% of RPPFD, which can be a small range for the observation of growth reactions to light. Height growth of *Taxus* was significantly influenced by light environment in several studies (Iszkuło 2010; Perrin & Mitchell, 2013; Devaney et al., 2015; Peragón et al., 2015), however, these works have been performed in broader intervals of light intensity. Additionally, yew juveniles grow under light-demanding tree species (oak, larch) that lose their leaves each year. The general statement is that shade-tolerant and evergreen species begin to grow very early in spring, before the deciduous tree species leaf out, and finish their growth after the defoliation of the deciduous trees (Gill et al., 1998; Walters & Reich, 1999). Average annual height increases in the years 2011–2015 in non-grazed saplings was about 17 cm. In other studies, mean height growth rates were much lower (Perrin & Mitchell, 2013; Niemczyk et al., 2015; Peragón et al., 2015). This indicates that the light conditions in the experiment were sufficient for optimum growth. All analysed *Taxus* juveniles had values of the Honowski light factor higher than 2, suggesting a flat, wide and umbrella-shaped crown, which is an indicator of suppressed saplings in the understorey (Kupferschmid et al., 2013). Williams et al. (1999) confirmed that the tendency of tree crowns to horizontal growth is mainly a result of low light conditions and a characteristic feature of shade-tolerant species. Horizontal growth at the expense of height growth may explain the ability to survive for many years under shaded conditions (Messier et al., 1999).

Needle morphology

As in the case of growth, there was no effect of RPPFD on needle morphology. This finding is surprising because these calculated leaf traits are common predictors of light intensity (Fabjanowski et al., 1974; Zheng et al., 2010), our results therefore indicate that these methods are not suitable to evaluate light conditions of *T. baccata* stands in small a range of light intensity (between 3 and 16% of full sunlight). Another reason for the lack of correlation could be the distribution of sample points within this range and also the sampling method and sample size.

However, the needle length and area were positively and SLA negatively correlated with yew height (Fig.4). These results correspond with the findings of other studies in conifers (e.g. Steele et al., 1989; Lilles et al., 2014). Greater needle size in higher plants is often explained with a transition from shade to sun leaves (Steele et al., 1989) or preparation for reproduction (Thomas, 2011). Indeed, we could not observe sexual determinants of saplings in yew individuals in the analysed plots.

Conclusions

Herbivory pressure has a negative effect on the growth and needle morphology of *Taxus* juveniles. Six years of grazing influenced height growth, needle parameters and number of stems, and these impacts markedly affected the development in the subsequent five years, irrespective of herbivory elimination. Height reduction, polycormicy, and needle size reduction indicate a persisting species strategy as a result of escaping from grazing. The effect of light conditions in the range of 3–16% on needle morphology was not significant. A good growth of non-grazed *T. baccata* saplings in the experiment shows appropriate light conditions ranging from 3 to 16% of full light. We also confirmed the correlation between needle size and individual sapling height.

Acknowledgments

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