ABSTRACT: The aim of the study was an examination of the thesis, that canopy tree genera (species) can have positive or negative influence on the germination of seeds and growth of seedlings and saplings of *Taxus baccata*. The species population spontaneously formed in the Kórnik Arboretum (W Poland) during last decades was the field of investigations. All yew individuals (including seedlings) were positioned and measured on two plots (area 1900 and 2000 m²) permanently marked in the field. The crown ranges of canopy trees and tree-like yews were measured and projected on the maps. The numbers of seedlings, saplings and tree-like yews under canopies of particular tree genera were compared. The seeds of *T. baccata* germinated under canopies of all species, most abundantly under the canopy of *Pseudotsuga* and *Abies*, but also under mother trees. Seedlings older than 2 years were also most numerous under the canopy of coniferous trees, while the saplings under the canopy of broadleaved trees. The greatest numbers of tree-like individuals were found under *Tilia* and *Carpinus* species.

KEY WORDS: Taxus, allelopathy, species co-occurrence, regeneration ecology, conifers

1. INTRODUCTION

*Taxus baccata* L. is a shade-tolerant tree (Dolukhanov 1959, Browicz and Gostyńska-Jakuszewska 1969, Pučalski and Prusinkiewicz 1975, Ellenberg 1988, Ellenberg et al. 1991, Zarzycki et al. 2002). It enters the broadleaved forest, in central Europe mostly from *Querco-Fagetea* class (Ellenberg 1988, Matuszkiewicz 2002, Zarzycki et al. 2002). The species is moderately calciphilous and occurs first of all on the limestone rocks, rendzinas and on the soils containing CaCO₃ (Ellenberg et al. 1991, Zarzycki et al. 2002). Its phytocenotic optimum is in associations from alliance of *Cephalentero-Fagion* (Ellenberg 1988, Ellenberg et al. 1991, Matuszkiewicz 2002). Outside calcium-containing substrata, as for example in the Central-European Lowland, *T. baccata* occurs in the oak-hornbeam forests of *Carpinion betuli* and in the mixed forests of *Querco roborit-petraeae* alliances. All these are forests with well developed tree layer, composed of several species of trees. The yew forms the second layer under the canopy of the large and high trees,
mostly from genera Quercus, Tilia, Acer, Carpinus, Picea and Abies (Paczoski 1928, Sokolowski 1970, Stypiński et al. 1984, Jahn 1991, Thomas and Polwart 2003). The regeneration of Taxus baccata in the natural conditions takes place under the canopy of various tree species and is rather rarely observed. The seedlings are frequently injured by pests or even completely destroyed by herbivores (Mańska et al. 1968, Findo and Stefancik 1988, Hulme 1996, Boratyński et al. 1997, Iszkuló 2001, Thomas and Polwart 2003). In the majority of nature reserves in Poland established for yew protection, the seedlings of the species disappear in their first 2–3 years. A numerous population of Taxus baccata was formed spontaneously during last decades in the Kórnik Arboretum in West Poland (Wróblewski 1928, Chylarecki 1958, Giertych 2000, Iszkuló and Boratyński 2004). The yew colonized the new area under the canopy of several taxa of trees. The success of yew seedling recruitment can be recognized actually in the occurrence of a number of their tree-like individuals under crown projections of particular trees. The aim of the present study is the analysis of interaction between particular genera of canopy trees and success of spontaneous regeneration and seedling recruitment of yew.

2. STUDY AREA

The study was carried out in West Poland, in the Kórnik Arboretum (17°06'E, 52°15'N, altitude 75 m) on two plots. The Arboretum was established in XIX century. Presently is administrated by the Institute of Dendrology and covers an area of about 40 ha. The soils of Arboretum are of podzolic or gley-podzolic type, developed from shallow deposits, with pH_{H_2O} 4.6–6.2 in humus horizon and 6.6–8.5 at the depth of 100–110 cm (Kowalski and Prusinquiewicz 1959). The area of Arboretum is protected against herbivores, which strongly influence the yew regeneration (Paczoski 1928, Findo and Stefancik 1988, Hulme 1996, Köpp and Chung 1997, Boratyński et al. 1997, Iszkuló 2001).

The population of Taxus baccata developed spontaneously in several parts of the Arboretum during last decades from a dozen or so mother trees, planted about 150–180 years ago (Chylarecki 1958, Giertych 2000, Iszkuló and Boratyński 2004). The climate of Kórnik area is characterized by average precipitation less than 500 mm per year and mean monthly temperatures typical for Wielkopolska Lowland region in West Poland (Chylarecki and Filipiak 1987). The soil and climate conditions of the Kórnik area resemble stands of the species in lowland broad-leaved forests (Myczkowski 1961, Król 1973, Matuszkiewicz et al. 1995).

3. MATERIAL AND METHODS

The yew is an ornithochoric/barochoric species. Their seeds in the Kórnik Arboretum are distributed mostly by Turdidae and Sitta europaea (Bartkowiak 1970, 1978, Bartkowiak and Zieliński 1973, Giertych 2000), or they drop down under crowns of mother trees (Iszkuló and Boratyński 2004). The plots (covering area of 1900 and 2000 m²) where the observations were conducted are at an average distance of about 100 m from approximately a dozen of potential mother trees (Iszkuló and Boratyński 2004). Only one mother tree of Taxus baccata older than about 60 years was found in the corner of one of the plots examined. The seeds were probably dispersed on the whole area, but mostly under crown projections of almost all tree species or in small gaps between them. The present day distribution of tree-like yews is a result of seeds dispersal and interaction between seedlings and the influence of canopy trees. The final result of the complex interaction was measured by the number of the yew trees and/or seedlings under crowns of particular tree genera.

The study was conducted on two permanently marked plots. The plots were divided into large squares of 10 m × 10 m, and then into small squares of 1 × 1 m. Trees of all species and all specimens of T. baccata were precisely positioned and measured. The map of spatial structure was prepared on that basis with the crown projections of all canopy trees. The final result of the complex interaction was measured by the number of the yew trees and/or seedlings under crowns of particular tree genera.

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European yew interaction with canopy trees

Fig. 1A. Distribution of *Taxus baccata* individuals under canopy of coniferous and broadleaved trees in the Kórnik Arboretum – plot 1 with great number of tree-like yews.
The number of tree-like yews under the crown projections of the particular canopy tree species was a result of the influence of the latter on the germination, seedling recruitment and the growth of yew. The numbers of tree-like *T. baccata* individuals under crown projection of every canopy tree were determined in July – August of 2000 in the field studies and then verified on the maps. The cartographic method was used to show the projections of all canopy tree crowns and the tree-like yew individuals distribution and Corel software was used in the spatial analysis.

The density of seedlings was calculated as a ratio of total number of seedlings found under canopy of trees from particular genera and summarized the total area of their crown projections. The seedlings found under canopies of two trees were counted two times. The canopy tree genera represented by less than 3 individuals were excluded from analyses.

4. RESULTS

The 99 canopy trees were found (Table 1) on both analyzed plots. The stands were formed mostly by three layers of canopy trees, with crown projections frequently overlapping (Fig. 1AB). The tree-like yews formed the lowest forest layer. The seedlings of the species occurred mostly under the canopy of stand forming trees. Only exceptionally they were found outside the crown projections (Fig. 1AB).

The greatest numbers of *Taxus baccata* seedlings up to 6 cm high were found under the canopy of *Pseudotsuga menziesii* and *Abies* species. Quite great seedling densities were also observed under the canopy of *Taxus baccata*, *Picea* (mostly *P. abies*), *Pinus sylvestris* and *Fraxinus* (mostly *F. excelsior*) (Fig. 2A). The greatest survival rate during first 3–4 years was characteristic of the seedlings of *Taxus baccata* under the canopy of *Pseudotsu-
European yew interaction with canopy trees

Table 1. Canopy tree genera of the analysed populations of *Taxus baccata* in the Kórnik Arboretum. No of individuals on both plots observed (total area of 3900 m²); H – average height ± standard deviation; D1.3 – average trunk diameter at height of 1.3 m above ground level ± standard deviation.

<table>
<thead>
<tr>
<th>No</th>
<th>Tree genus</th>
<th>No of individuals</th>
<th>Average dimensions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>H [m] D1.3 [cm]</td>
</tr>
<tr>
<td>1</td>
<td><em>Pseudotsuga</em></td>
<td>16</td>
<td>18.9±0.8 21.5±1.2</td>
</tr>
<tr>
<td>2</td>
<td><em>Abies</em></td>
<td>12</td>
<td>16.4±0.6 19.4±1.1</td>
</tr>
<tr>
<td>3</td>
<td><em>Picea</em></td>
<td>16</td>
<td>16.1±2.7 24.9±5.8</td>
</tr>
<tr>
<td>4</td>
<td><em>Pinus</em></td>
<td>4</td>
<td>28.8±1.3 101.5±10.5</td>
</tr>
<tr>
<td>5</td>
<td><em>Larix</em></td>
<td>9</td>
<td>27.1±0.9 49.8±3.0</td>
</tr>
<tr>
<td>6</td>
<td><em>Fraxinus</em></td>
<td>3</td>
<td>30.4±1.6 27.5±8.3</td>
</tr>
<tr>
<td>7</td>
<td><em>Tilia</em></td>
<td>9</td>
<td>22.8±1.4 70.4±15.0</td>
</tr>
<tr>
<td>8</td>
<td><em>Quercus</em></td>
<td>3</td>
<td>26.3±2.7 34.8±4.4</td>
</tr>
<tr>
<td>9</td>
<td><em>Carpinus</em></td>
<td>14</td>
<td>16.4±1.8 28.3±4.1</td>
</tr>
<tr>
<td>10</td>
<td><em>Acer</em></td>
<td>9</td>
<td>28.1±1.8 45.3±8.0</td>
</tr>
<tr>
<td>11</td>
<td>Remaining</td>
<td>(Betula, Corylus, Fagus, Sorbus)</td>
<td>4</td>
</tr>
<tr>
<td>Sum</td>
<td></td>
<td></td>
<td>99</td>
</tr>
</tbody>
</table>

Fig. 2. The relation of co-occurrence of *Taxus baccata* with genera of canopy trees: A – seedlings to 6.0 cm tall; B – seedlings 6.1–25.0 cm tall; C – saplings 25.1–100.0 cm tall; D – tree-like individuals 100.1 cm tall and more (average number of yew individuals per 1 m²).

Fig. 3. Mean numbers of seedlings, saplings and tree-like individuals of *Taxus baccata* under canopy of coniferous, broadleaved deciduous trees and under yew canopy (average number of yew individuals per 1 m²) on both plots (total area of 3900 m²).

*menziesii* and *Abies* species, as the greatest numbers of seedlings of the height of 6–25 cm were found in the shade of trees of these two genera (Fig. 2B).

The saplings 25–100 tall were very rare. Their most frequent occurrence was found under the canopy of *Pseudotsuga menziesii*, *Acer*, and *Fraxinus* species (Fig. 2C). Only few tree-like yews were found, however, under the canopy of *Pseudotsuga* and *Abies* (Fig. 2D). The greatest numbers of *T. baccata* individuals higher than 1 m were found under limes and hornbeams. Generally, the seedlings occurred more frequently under canopies of coniferous rather than broadleaved trees, but the proportions have drastically changed for saplings and tree-like individuals (Fig. 3).
The Taxus baccata seeds are dispersed by birds and/or drop down directly under the crown of mother tree. The consequence of that should be the great number of seedlings under the mother tree crowns. The youngest seedlings were observed in such a situation, but most of them did not survive more than 1–2 years (Fig. 2B). It is comparable with observations from many places in the species range (Gieruszyński 1961, Ostrowski 1968, Pridnya 1984, 2002, Köpp 1991, Hulme 1996, Boratyński et al. 1997, Köpp and Chung 1997, Seidling 1999, Saniga 2000, Iszkuło 2001).

The results of our investigation confirm the possibility of germination of the seeds of Taxus baccata under the canopy of mother trees. Nevertheless, the number of seedlings under the canopy of Pseudotsuga menziesii and Abies species was much larger, than under Taxus baccata mother trees. The differences were even larger in the seedling class of 6–25 cm high (Fig. 2A and B). The main reason for the different numbers of seedlings under canopies of particular genera were preferences of birds, and probably the heights of trees and their vertical projection of the crown (Bartkowiak 1970; Bartkowiak and Zieliński 1973, Król et al. 1980; Król 1986; Giertych 2000). The other possible reason was the influence of canopy trees on seed germination, which, however, should be verified in a special study.

Generally, the changes of the number of yew individuals under canopy trees of particular genera were different. Some of them had the large number of young seedlings under crown projections, but saplings (25–100 cm high) occurred more frequently under the canopy of trees representing genera with considerable small numbers of seedlings (compare Fig. 2A and 2C). It suggests, that some of the tree genera had a negative influence on the seedling survival rate and growth. It could be determined by emission of the growth inhibitors in root system areas, also by different, specific for particular genera, area of leaves and litter decomposition rates, as well as the competition for nutrients and water (Massey 1925; Bode 1958; Vandermast et al. 2002).

The seedlings were more numerous under the canopy of coniferous trees than under deciduous ones. Nevertheless, survival rate under the canopy of broadleaved trees was higher than under coniferous, and the saplings were already more numerous under them (Fig. 3). The Picea abies and Larix species were exceptions of that.

The small number of youngest seedlings of Taxus baccata under deciduous broadleaved trees could indicate the negative influence of autumn litter fall on the seedlings survival rate. However, the seedlings that have overcome this difficulty, had better conditions to growth. It can be explained by possible early spring photosynthetic activity of yew seedlings, which can reduce the lack of the light during the growing season, when the canopy trees are leaved (Iszkuło and Boratyński 2004), as it was described for other shade-tolerating species (Gill et al. 1988). It also confirmed the seed-seedling conflict, recognized among several woody species in N America (Schupp 1995).

Some of seeds have been dispersed, and consequently germinated outside the crowns of trees, where the light conditions were much better. The slow growth of yew seedlings (Gieruszyński 1961; Voliotis 1986; Garcia et al. 2000) and their poor performance in competition with seedlings of other tree species and first of all with the herbs are other possible reasons for considerably small number of seedlings and saplings in such condition (Iszkuło and Boratyński 2004).

Our results present the contemporary state of canopy tree distribution. The state from about 40 or more years ago is not known. Nevertheless, most of Taxus baccata seedlings was found under the canopy trees, and only a small number of them outside (Fig. 1AB).

T. baccata is said to emit the allelopathic substances, which diminished the seeds germination and eliminated the seedlings (Thomas and Polwart 2003) in their first growth stages, similarly as it took place under canopies of Juglans regia (Massey 1925; Bode 1958), Castanea dentata (Vandermast et al. 2002) and Taxus brevifolia. The last species inhibit seed germination and seedlings’ growth (Del Moral and Cates 1971). The possibility of growth of young generation of T. baccata under the canopy of old trees of the species was also
limited (Del Moral and Cates 1971; Pelliser and Souto 1999). It was also reported from many nature reserves established for yew protection in Poland, where the concentration of yew trees is high (Gieruszyński 1961, Myczkowski 1961, Ostrowski 1968, Kościely and Król 1970, Jackowski 1972, Boratyński et al. 1997). The negative influence of old individuals of Taxus baccata has not been observed in sparse mother population, as lately described in Denmark (Svenning and Magård 1999), however, the regeneration there has not been disturbed by herbivores. The regeneration of T. baccata in the natural state is normally strongly reduced by herbivores (Findo and Stefancik 1988, Hulme 1996, Boratyński et al. 1997, Garcia et al. 2000, Iszkuło 2001). The protection against the deer in the Kórnik Arboretum eliminated this influence.

The spontaneously formed subpopulations of Taxus baccata in the Kórnik Arboretum are at an average distance of 100 m or more from the potential mother trees. The tree-like yews on the analysed plots are of ornithochoric origin. Thus, the mother trees did not exist on the plots at the moment of population formation (Iszkuło and Boratyński 2004). The present day young regeneration on the plots is under very strong influence of the tree-like yews. The inhibition of germination has not been observed, but the number of saplings (individuals 25–100 cm high) was significantly greater outside the tree-like yew canopy or they grew on the border of yew crowns’ range. In the latter case the saplings survived from the seedlings, which began to grow 5–8 years before (Iszkuło and Boratyński 2004), outside the crowns of yews.

6. CONCLUSION

The spontaneous population of Taxus baccata was formed in some distance from the old yew-trees. The most successfully growing individuals are of ornithochoric origin and this type of seed dispersal is the typical regeneration strategy of T. baccata. The regeneration of T. baccata was most successful under the canopies of Tilia cordata, Carpinus betulus and coniferous trees, as Pinus sylvestris, Picea abies and Larix decidua.

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