Response of *Taxus baccata* to environmental factors

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ABSTRACT

The survival, growth and reproductive success of *Taxus baccata* is strongly affected by the environmental conditions under which it grows. Knowledge of how it responds to different factors is important in conservation management of this rare and endangered species. This chapter summarizes the known responses of *T. baccata* to environmental variables and represents a synthesis and update of the review by THOMAS & POLWART (2003).

Key words: *Taxus baccata*, light, temperature, precipitation, drought, tree-rings, fire, wind, pollution, climate change.

RESUM

La supervivència, el creixement i l'èxit reproductiu de *Taxus baccata* es veuen afectats per les condicions mediambientals en les que es desenvolupa. El coneixement de com respon a factors diferents és important en la gestió per a la conservació d'aquesta espècie rara i amenaçada. Aquest capítol resumeix les respostes conegudes de *T. baccata* a variables mediambientals i representa una síntesi i actualització de la revisió elaborada per THOMAS & POLWART (2003).

Paraules clau: anells d'arbre, canvi climàtic, contaminació, incendis, precipitació, sequera, *Taxus baccata*, temperatura, vent.

RESUMEN

El éxito en la supervivencia, crecimiento y reproducción de *Taxus baccata* está fuertemente condicionado por las condiciones ambientales bajo las que crece. Conocer como responde a los diferentes factores ambientales es importante en el manejo y conservación de esta especie rara y amenazada. Este capítulo resume las respuestas conocidas de *T. baccata* a las variables ambientales y representa una síntesis y actualización de la revisión de THOMAS & POLWART (2003).

Palabras clave: anillos de árbol, cambio climático, contaminación, incendios, precipitación, sequía, *Taxus baccata*, temperatura, viento.

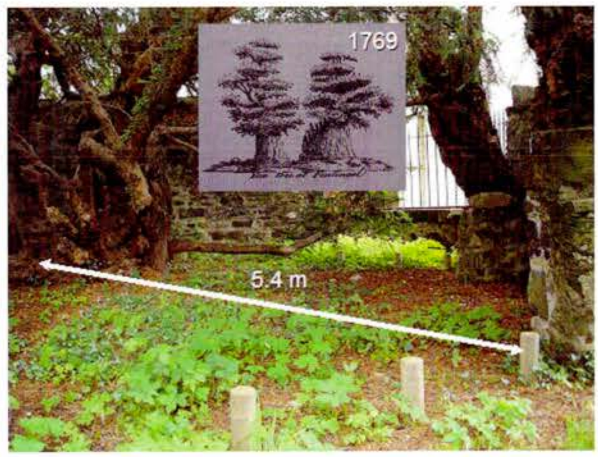

Figure 1. The Fortingall Yew (above) in the churchyard of the village of Fortingall, at the foot of Glen Lyon, Perthshire, Scotland. The tree is now reduced to two living portions seen inside the walls on either side of the picture. However, the remains of the old trunk can be found in the soil, indicated by the lines of posts between the living fragments, making a circle 5.4 m in diameter. The inset picture is a woodcut from 1769 showing that the tree was once a single individual. It is suggested that this tree is now 5,000 years old but, of course, there is no certain method of dating what is left.

The Ankerwycke Yew at Runnymede (below) on the north shore of the River Thames to the west of London, England. It is estimated that this tree is 2,500 years old, and was a venerable tree in 1215 when King John signed Magna Carta under its canopy, the basis for English common law and constitutional documents such as the Constitution of the USA.

INTRODUCTION

Taxus baccata (yew) is slow growing (20-30 cm height gain per year), slow to reach maturity (c. 70 years) and shade-tolerant but able to withstand full sun. This mode of growth has been confirmed by the recent modelling work of WUNDER *et al.* (2008). Slope is rarely limiting and it will grow on almost any soil. Although it favours calcareous soils in northern Europe, growth is best on deep, moist sandy loams and well-drained clays, and worst on dry, rocky and sandy soils. *Taxus baccata* is affected by very few fungal diseases and is even fairly resistant (though by no means immune) to *Armillaria* spp. There are, however, signs that it may prove increasingly sensitive to the fast-changing species of *Phytophthora* (e.g. LANE *et al.*, 2004; DENMAN *et al.*, 2005).

The oldest trees in Europe are almost certainly several millennia old (Figure 1), helped by having a strong decay-resistant wood. The largest in Britain – the Fortingall Yew in Perthshire, Scotland – at 5.4 m diameter is reputed to be 5,000 years old. If this is true it rivals the oldest known trees in the world – the bristlecone pines (*Pinus aristata*) in western USA.

All these factors together indicate that *T. baccata* follows a stress-tolerant life strategy, maintaining itself in the wild by individual trees enduring stresses and living for a long-time. The importance of enduring stresses is highlighted by the suggestion of SVENNING & SKOV (2005) that the current distribution of yew around Europe and (although probably to a lesser extent) on the local scale is governed more by environmental factors than human history of planting and clearing. In this case, the sensitivity of yew to different environmental factors has important implications for its long-term conservation.

DISTRIBUTION AND ENVIRONMENTAL FACTORS

Taxus baccata is classified as European Temperate and grows best in oceanic climates with relatively mild winters, abundant rainfall and high humidity. Consequently, the largest and purest populations are in the British Isles (Figure 2), Poland to Romania and the Caucasus Mountains where the climate is moderated by the Black and Caspian Seas. Outside of these optimum areas, yew extends northwards to c. 63° in Norway and Sweden (eventually limited by low temperatures), eastwards to Estonia and the Baltic countries (limited here by the severe continental climate), and southwards to Greece, northern Spain, Portugal and into Algeria (increasingly limited here by drought, high temperatures and low humidity). It is absent from the most continental climatic regions of Europe including northern and south-eastern Russia, and also Crete, the Faeroes and Iceland.

Figure 2

Two almost pure yew woodlands. Above a woodland in Silverdale, Lancashire, England dominated almost exclusively by yew with scattered *Sorbus aria* that survive by being taller than the yew. Below another almost pure stand of yew at Reenadinna Yew Wood in Killarney National Park, Co. Kerry, Ireland. These woodlands are exceptional in being so dominated by yew. Away from these special areas, towards the extremes of its range in Europe, yew tends to become a decreasing component of woodlands until at the southern extreme end of its range it is restricted to being a scarce understory tree.

Table 1 Height above sea level at which *Taxus baccata* is found. Data are from Thomas & Polwart (2003).

Metres above sea level	Geographical region
0- 470	British Isles
600-1.400	Alps
1.400-1.650	Pyrenees
up to 1.700	Sardinia
up to 1.800	Macedonia
1.600-1.950	Southern Spain
up to 2.000	Greece
up to 2.500	NW Africa

Near these climatic extremes, yew becomes restricted to moist niches. Thus, the altitude at which yew will grow generally increases towards the south (Table 1). In mountainous areas of Europe, the angle of slope is generally not important but aspect plays a crucial role in where *T. baccata* will grow. In southern mountains yew tends to grow on the shaded north-western or north-eastern slopes, particularly under tree cover, where there is an oceanic-like microclimate. In northern mountains, yew still tends to grow on northern slopes even though these are colder; the reason seems to be that the later start to the growing season allows the tree to avoid spring frosts that would otherwise damage sensitive new tissue. In mild, oceanic climates, such as in England, *T. baccata* tends to grow on the drier southern and eastern slopes since here it avoids waterlogging, the prevailing westerly winds and the cold northern exposure.

In addition to the broad macroclimate effect of altitude, yew is also strongly affected by microclimate, particularly near the extremes of its southern range. Here it tends to prosper in humid, sheltered microsites such as those found near wetlands and under the canopy of trees or in rock crevices, deep valleys and in the lee of rocks.

INDIVIDUAL ENVIRONMENTAL FACTORS

Light

Taxus baccata is the most shade tolerant tree in Europe (even surviving below its own formidable shade: Iszkuło *et al.*, 2005). It is even capable of producing viable seeds in <5% sunlight. But even under optimum oceanic conditions, regeneration within mature *Taxus* stands is comparatively rare and it establishes best in more open conditions. This leads to a shifting mosaic of trees over time where new saplings are more likely in the gaps between older trees.

Even though seedlings can grow in <0,5-5% full sunlight (e.g. Iszkuło *et al.*, 2007), growth is better with increasing light. Growth is generally fastest, however, under a certain amount of residual shade. This is due to the more favourable microclimate under shade (especially in eastern Europe and possibly further south) and the reduced levels of competition from other vegetation that yew would face in fully open conditions (Iszkuło & Boratyński, 2006). Indeed, in more continental climates, yew may grow well in open conditions only when it is on a fertile, moist soil and so has a competitive advantage. Even on optimum sites, growth to adult size is slow and may take as long as 75 years and its maintenance in woodlands may only be possible due to the extreme longevity of individual trees and its tolerance of shade.

Temperature

Taxus baccata is intolerant of severe and prolonged frost, but leaves and buds can resist damage in northern Europe down to −21 to −35 °C. In the Austrian Alps, exposure to −21 °C for three hours has resulted in 10–15% frost damage to leaves and −23 °C in 100% damage (Pisek *et al.*, 1967). In Britain, damage starts at −13,4 °C in midwinter (Melzack & Watts, 1982) whereas by March this had risen to −9,6 °C in the hardiest provenance (south England) and −1,9 °C in the most susceptible (north-east England) as the yews become more physiologically active with increasing temperatures and so gradually lose their frost resistance. The greater susceptibility to spring frosts in northern England may be due to the yew responding to the shorter growing season by preparing for growth earlier in the spring. Sensitivity to frost in early spring is undoubtedly a crucial limiting factor in the northerly oceanic distribution in Europe of this species but probably less so in the south.

Resistance to high temperatures is comparatively high but can be problematic. Lange (1961) found the LT^{50} for a 30 minutes exposure was reached at 51 °C, and that a 30 minute exposure to 48-50 °C damaged needles. However, under hot still conditions, such temperatures are readily reached on leaf and bark surfaces, especially in the south of its range. The potential susceptibility of yew to high temperatures is indicated by the recommendation in the UK that plastic tree shelters should not be used for yew as overheating can occur, despite the shelters being suitable for most other tree species. This further highlights the potential need of yew for partial shade.

The optimum temperature range for photosynthesis is between 14–25 °C; higher than in other species of gymnosperm. During the summer, photosynthesis will continue between a maximum of 38-41 °C and a minimum of −3 to −5 °C, a remarkably wide range compared to most European trees. In winter, photosynthesis is possible down to −8 °C so, providing water is available, some sugar production is possible to offset respiratory costs from autumn to spring when any tree canopy above is likely to be leafless and light intensities are higher. This may help explain why yew rarely grows under a canopy of other evergreens despite being very shade tolerant.

Although photosynthesis is possible under a wide range of light and temperature conditions, yew is nevertheless a shade-tolerant tree and is sensitive to sudden change in light and exposure to the sun. Yew needles live for 4-8 years although photosynthesis declines in older needles (WYKA *et al.*, 2008) by 50% in 7-year-old needles. Since the needles live for so long it can take around eight years for a yew canopy to convert from having shade leaves to one having sun leaves. The consequence of this is that sudden removal of other trees around a yew tree can lead to extensive damage or even death. This should be borne in mind when considering opening up a canopy to increase the regeneration of yew, and explains the suggestion of DHAR *et al.* (2008) that stands containing yew should be thinned by no more than 30% at any one time.

Moisture

The best performance of *Taxus baccata* is seen under high rainfall. In England 80% of *T. baccata* woodlands occur in areas of maximum rainfall (>1000 mm year^{-1}). Yew can also tolerate temporary flooding but is susceptible to long-term waterlogging. This is demonstrated by the ability of yew to grow on a wide range of soils, including well-drained calcareous peat but not on sites where the water table is at or near the surface. High humidity is normally a requirement for the best growth of yew although in Bavaria around 50% of needles can be killed in a year by fungal attack due to high humidity (HUBERT RÖSSNER, personal communication).

At the other end of the moisture scale, *T. baccata* is very tolerant of drought. BRZEZIECKI & KIENAST (1994) ranked yew as 2 on a 1–5 scale where 1 is very drought tolerant. There are two reasons behind this tolerance. Firstly, the stomata on the leaves react rapidly to internal water deficits, quickly and effectively reducing water loss when the tree is stressed. Secondly, the tracheids in the xylem are very narrow with a mean diameter is 18,4μm, the narrowest of any European tree. These narrow tracheids are detrimental to a degree since they impart a great deal of friction to the water column in each tracheid, slowing the water flow. But, more importantly, this friction helps to give cohesion to the water columns so when a tree is under great evapotranspiratory stress, and extreme negative pressures develop in the tracheids, there is less likely to be irreversible cavitation and the tracheids will remain water filled and so be able to function when water becomes more available (see THOMAS, 2000 for more details). These narrow tracheids are reflected in the high density of yew wood; pine (*Pinus*) wood is typically 510 kg m^{-3}, oak (*Quercus*) 720 kg m^{-3}, while yew is normally 640-800 kg m^{-3}.

Conditions for growth

Tree ring growth in yew responds mainly to precipitation (particularly rainfall in February to July in England, moving to a month earlier in the Balkans), and also to temperature in late autumn (October) and late winter (January to March). The effect of precipitation is understandable given the oceanic preference of yew, and the response to temperature appears primarily related to the length of the growing season; a milder spring and autumn extending the season. Conversely, high summer temperatures (particularly in June) tend to inhibit growth, presumably due to heat stress but most likely due to lower humidity and lower soil moisture (THOMAS & PACKHAM, 2007). Thus mild/wet winters combined with cool summers provide ideal growing conditions.

Care is needed in interpreting past growing conditions from the tree rings of yew, partly due to the large number of 'missing' rings (which normally means rings that are very narrow and often incomplete and so easily missed) and partly, as in most trees, due to the great reduction in ring-width with age of the tree. In England, ring widths of 0.13–2.54 mm are normal in younger yew trees, falling to as little as 0,051 mm in older trees or 20 rings mm^{-1}.

Wind

Wind is important in determining the distribution of yew as indicated by the extensive wind-shaping in exposed areas. Although yew needles show excellent stomatal control, they cannot resist high transpiration rates (LEUTHOLD, 1980; ZOLLER, 1981) and can be killed by prolonged dehydration. This is a particular problem in areas with colder winters where ice particles blown by the wind abrade the waxy cuticle from needle surfaces, hastening desiccation. At the ends of its range, the value of tree cover is not just in maintaining humidity but also the protection provided from exposed conditions.

Fire

Several features of yew help it evade fire. Núñez-Regueira *et al.* (1997) found its branches (< 8 cm diameter complete with leaves, collected in the mountainous zone of north-west Spain) to be average in calorific value and flammability amongst 12 tree species tested (all the others being angiosperms). This suggests that the non-resinous *T. baccata* has low flammability compared to most gymnosperms. Moreover, since in the south it tends to grow in mixed woodlands, which overall have a very low flammability; yew can often completely evade fire. Having said this, in areas with more a Mediterranean climate, dominated by flammable shrubs, yew can readily meet fire. In these situations, the thin bark gives little protection and yew is readily killed.

Nutrition and pollution

It has been reported that, compared to other gymnosperms, *T. baccata* leaves have a high N, P, K, Mn, Zn, B and Mo content as well as low Al, Si and Fe content. Compared to angiosperm trees (*Quercus robur, Fagus sylvatica, Castanea sativa, Acer pseudoplatanus* and *Sorbus aucuparia*) growing in north-west Spain, yew branches (< 8 cm diameter plus leaves) had high levels of Cd (up to 40 ppm), Zn (41 ppm), and Mn (up to 3074 ppm) (Núñez-Regueira *et al.*, 1997) but with little signs of ill-health. It is also known that the roots of *T. baccata* have arbuscular mycorrhiza [endomycorrhiza] associations. This is unusual given that 90% of northern temperate trees are ectomycorrhizal (Thomas, 2000) but may give yew a competitive advantage under increasingly polluted conditions. Atmospheric nitrogen pollution has increased from a natural background level of deposition of around 1 kg ha^{-1} y^{-1} to upward of 7 kg ha^{-1} y^{-1} and into many tens or even hundreds of kg per hectare per year (Thomas & Packham, 2007). Much of this N pollution is in non-organic forms. Arbuscular mycorrhizas have better access to non-organic sources of N and P (Ashmore, 1997) and so yew may have better access to this extra nitrogen than plants with ectomycorrhizas.

Taxus baccata is tolerant of air pollution with a high resistance to SO_2, though concentrations higher than 50 mg m^{-3} have damaged needles, and acid fog treatment of pH 2,5 increases needle damage relative to pH 3,5–5,5. *T. baccata* is more tolerant of smoke from copper foundries, heavy metals and hydrogen fluoride than *Pinus* or *Abies* species. Indeed, yew needles have been used as a bioindicator of heavy metal emissions in Germany. *Taxus baccata* is sensitive to air-borne salt spray.

Climate Change

Hättenschwiler & Körner (2000) and Hättenschwiler (2001) exposed seedlings of six major European temperate forest tree species, including *T. baccata*, to elevated levels of carbon dioxide at 500 and 660 ppm CO_2 in the understorey of an old-growth forest in Switzerland. Seedlings were exposed to a known light intensity ranging from 0,8% to 4,8% of full sun. Biomass production in the deep-shade tolerant yew increased by 37% under elevated CO_2 in low light microsites but was not significantly different among CO_2 treatments in high light microsites. Thus, yew trees are likely to be at an advantage at higher carbon dioxide concentrations but may lose their advantage in only slightly higher light levels which still represent shaded conditions. Thus, as CO_2 concentration rises, germination, recruitment and survival of yew is likely to improve in deep shade conditions such as under a dense tree canopy.

On the negative side, higher temperature and lower rainfall (compounded by higher evaporation and lower humidity) may reduce growth and survival, particularly of older trees. There is a need for ecological modelling to investigate the overall affect of these opposing factors before a firm conclusion can be made on the overall effect of climate change of *T. baccata*.

Biotic factors

Although strictly speaking these are not environmental factors they are sufficiently linked to the response of *T. baccata* to its environment that they need to be considered.

A potential problem for yew is that being dioecious, pollination may fail if the population becomes sufficiently fragmented that females receive insufficient pollen. Although pollen can travel long distances – many thousands of km in the high atmosphere - the question is whether pollen reaches a tree in high enough amounts to ensure complete pollination. Anecdotal evidence suggests that adequate pollination can occur over a number of kilometres but pollen distribution is, of course, tied in with population fragmentation, topography and wind patterns and may not always be sufficient to maximise seed production. Certainly in the common juniper (*Juniperus communis*) poor pollination is a distinct problem in fragmented populations throughout Europe (THOMAS *et al.*, 2007) and is likely to be so in *T. baccata*.

A compounding factor is that of sex ratios in yew. Published information suggests that the percentage of female trees increases from about 45% in the UK to around 70% in the Sierra Nevada Mountains of Spain. This may be an artefact due to poor recording or analysis, and is worthy of further investigation. If this variation proves to be true, it would be useful to know the cause; if it is due to increasing temperature or reduced rainfall or humidity in the south, this has important implications for climate change.

The time taken for yew trees to reach sexual maturity (i.e. when they first start producing viable seeds) is slow by the standards of most other European trees: around 30-35 years in open trees an up to 70-120 years in dense stands. This raises questions as to whether environmental changes induced by climate change will happen too quickly for a stress tolerant, slow-growing trees such as yew to respond.

Despite its poisonous properties, yew is very susceptible to browsing and bark stripping by rabbits, hares, deer and domestic animals (e.g. DHAR *et al.*, 2006). However, yew is tolerant of repeated pruning of the foliage (as demonstrated by its use in topiary) and is usually able to continue growth even under severe browsing pressure (although repeated very heavy grazing to ground level can kill yew). Successful regeneration of *T. baccata* is often best below shrubs (especially those that are thorny and/or have fleshy fruits). These shrubs maintain a suitably moist microclimate, give protection from herbivores and, as identified by GARCÍA *et al.* (see GARCÍA *et al.*, 2000, 2007 and MARTINEZ *et al.*, 2008) in the Sierra Nevada Mountains, the fleshy fruits attract birds that defecate or drop *T. baccata* seeds into the shade below.

CONCLUSION

It is clear that *Taxus baccata* has a stress-tolerant life strategy and is successful by being long-lived and surviving disturbances. This may make it vulnerable to rapid anthropogenic changes in environmental conditions. Yew is favoured by high rainfall and humidity, mild, wet winters and cool summers – an oceanic rather than a continental climate. Having said this, yew is drought tolerant and very shade tolerant and so can find suitably conditions outside of its main range by finding shelter below the canopy of trees and in other microniches. Its ability to photosynthesise at low temperatures aids this process by allowing growth at the 'shoulder seasons' of spring and autumn while the canopy above is leafless.

Yew also benefits from the wind protection provided by other trees but this does leave it vulnerable to sudden removal of shade by inappropriate management or major disturbances such as wind storms. Fire can also be a problem for trees growing in flammable areas but in most moist forests the flammability of the community is sufficiently low to protect yew trees from meeting fire. Pollution is potentially damaging to a long-lived stress-enduring species but yew does seem fairly resistant to pollutants and high levels of inorganic nitrogen may prove beneficial via the arbuscular mycorrhizas found on the yew. Climate change is still an unknown quantity. Yew can tolerate fairly high temperatures, and higher carbon dioxide levels may benefit the yew but associated lower rainfall, lower humidity and abnormally high temperatures may prove detrimental. Most importantly, the predicted changes may just be too fast to cope with for a long-lived tree such as yew.

It is clear that *T. baccata* is rare and endangered throughout Europe showing widespread population decline and increasing fragmentation (GARCÍA *et al.*, 2005). As DHAR *et al.* (2008) suggest, "It is evident that maintaining the population of yew... will require intensive management to prevent its extinction." Population Viability Risk Management (PVRM) analyses by DHAR *et al.* (2008) in Austria suggest that fencing and game control to reduce grazing pressure along with selective thinning and some harvesting to increase light under the canopy is the best option for conservation management of *Taxus baccata*.

Given that this tree is so unique in Europe we should be making every effort to understand how environmental factors affect the yew now and in the face of climate change.

BIBLIOGRAPHY

ASHMORE, M. 1997. Plants and pollution. In: *Plant Ecology* (Second edition) (CRAWLEY, M.J., ed.), pp. 568-581. Blackwell Science, Oxford.

BRZEZIECKI, B. & KIENAST, F. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management* 69: 167–187

DENMAN, S.; KIRK, S.A.; BRASIER, C.M. & WEBBER, J.F. 2005. In vitro leaf inoculation studies as an indication of tree foliage susceptibility to *Phytophthora ramorum* in the UK. *Plant Pathology* 54: 512–521

DHAR, A.; RUPRECHT, H.; KLUMPP, R. & VACIK, H. 2006. Stand structure and natural regeneration of English yew (*Taxus baccata* L.) at Stiwollgraben in Austria. *Dendrobiolog* 56: 19–26

DHAR, A.; RUPRECHT, H. & VACIK, H. 2008. Population viability risk assessment (PVRM) for in situ management of endangered species – A case study on a *Taxus baccata* L. population. *Forest Ecology and Management* 255: 2835-2845

GARCÍA, D.; MARTINEZ, I. & OBESO, J.R. 2007. Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate. *Basic and Applied Ecology* 8: 533-543

GARCÍA, D.; QUEVEDO, M.; OBESO, J.R. & ABAJO, A. 2005. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). *Forest Ecology and Management* 208: 29–43.

GARCÍA, D.; ZAMORA, R.; HÓDAR, J.A.; GÓMEZ, J.M. & CASTRO, J. 2000. Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biological Conservation* 95: 31–38

HÄTTENSCHWILER, S. 2001. Tree seedling growth in natural deep shade: functional traits related to interspecific variation in response to elevated CO_2. *Oecologia* 129: 31–42

HÄTTENSCHWILER, S. & KÖRNER, C. 2000. Tree seedling responses to in situ CO2-enrichment differ among species and depend on understorey light availability. *Global Change Biology* 6: 213–226

ISZKUŁO, G. & BORATYŃSKI, A. 2006. Analysis of the relationship between photosynthetic photon flux density and natural *Taxus baccata* seedlings occurrence. *Acta Oecologica* 29: 78–84

ISZKUŁO, G.; BORATYŃSKI, A.; DIDUKH, Y.; ROMASCHENKO, K. & PRYAZHKO, N. 2005. Changes of population structure of *Taxus baccata* L. during 25 years in protected area (Carpathians, western Ukraine) *Polish Journal of Ecology* 53: 13-23

ISZKUŁO, G.; LEWANDOWSKI, A.; JASINSKA, A.K. & DERING, M. 2007. Light limitation of growth in 10-year-old seedlings of *Taxus baccata* L. (European yew). *Polish Journal of Ecology* 55: 827-831

LANE, C.R.; BEALES, P.A.; HUGHES, K.J.D.; TOMLINSON, J.A.; INMAN, A.J. & WARWICK, K. 2004 First report of ramorum dieback (*Phytophthora ramorum*) on container-grown English yew (*Taxus baccata*) in England. *Plant Pathology* 53: 522

LANGE, O.L. 1961. Die Hitzeresistenz einheimischer immerund wintergrüner Pflanzen im Jahreslauf. *Planta* 56: 666-683

LEUTHOLD, C. 1980. Die ökologische und pflanzensoziologische Stellung der Eibe (*Taxus baccata*) in der Schweiz. Veröffentlichungen des Geobotansichen Institutes der eidg. Technol. Hochschule Stiftung Rübel (Zürich), *Heft* 67: 217 S.

MARTINEZ, I.; GARCÍA, D. & OBESO, J.R. 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience* 15: 189-199

MELZACK, R.N. & WATTS, D. 1982. Cold hardiness in the yew (*Taxus baccata* L.) in Britain. *Journal of Biogeography* 9: 231–241

NÚÑEZ-REGUEIRA, L.; RODRÍGUEZ AÑÓN, J.A. & PROUPÍN CASTIÑEIRAS, J. 1997. Calorific values and flammability of forest species in Galicia. Continental high mountainous and humid Atlantic zones. *Bioresource Technology* 61: 111–119

PISEK, A.; LARCHER, W. & UNTERHOLZNER, R. 1967. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier- und Frostschadensbereiche der Blätter. *Flora* 157: 239–264

SVENNING, J.-C. & SKOV, F. (2005). The relative roles of environment and history as controls of tree species composition and richness in Europe. *Journal of Biogeography* 32: 1019–1033

THOMAS, P.A. 2000. *Trees: Their Natural History*. Cambridge University Press, Cambridge

THOMAS, P.A.; EL-BARGHATHI, M. & POLWART, A. 2007. Biological flora of the British Isles. *Juniperus communis* L. *Journal of Ecology* 95: 1404–1440

THOMAS, P.A. & PACKHAM, J.R. 2007. *Ecology of Woodlands and Forests*. Cambridge University Press, Cambridge

THOMAS, P.A. & POLWART, A. 2003. Biological flora of the British Isles. *Taxus baccata* L. *Journal of Ecology* 91: 489-524

WUNDER, J.; BRZEZIECKI, B.; ŻYBURA, H.; REINEKING, B.; BIGLER, C. & BUGMANN, H. 2008. Growth-mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. *Oikos* 117: 815-828

WYKA, T.; ROBAKOWSKI, P. & ŻYTKOWIAK, R. 2008. Leaf age as a factor in anatomical and physiological acclimative responses of *Taxus baccata* L. needles to contrasting irradiance environments. *Photosynthesis Research* 95: 87-99

ZOLLER, H. 1981. *Gymnospermae (Taxaceae)*. In: Illustrierte Flora von Mitteleuropa. Band 1/Teil 2. *Gymnospermae, Angiospermae, Monocotyledoneae*-1. (CONERT, H.J.; HAMANN, U.; SCHULTZE-MOTEL, W. & WAGENITZ, G., eds.), pp. 126–134. Verlag Paul Parey, Berlin/Hamburg.