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Taxus baccata L.

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Taxus baccata is a native evergreen non-resinous gymnosperm tree up to 20(–28) m, often with multiple trunks and spreading, rounded or pyramidal canopy. Capable of producing leafy branches from old branches and trunks, and sometimes from stools. Root system shallow with extensive horizontal roots, often above ground on calcareous substrates. Bark reddish-brown, thin, scaly. Branches long, not whorled. Twigs green and irregularly alternate; buds very small, bud scales dark-brown, rounded, imbricate and closely appressed. Leaves, spirally attached but on lateral shoots twisted more or less into two ranks, can live for up to 8 years; 1–3(−4.5) cm long and 2–3 mm wide, parallel-sided, shortly stalked, mucronate, dark glossy green above, paler and yellowish beneath with two pale stomatiferous stripes; midrib prominent on both sides, margins recurved, tapering to a petiole-like base. Normally dioecious, rarely monoecious; reproductive structures green, borne in leaf axils near the end of the previous summer's growth. Male parts in small cones (simple strobili; Mundry & Mundry 2001) 2–3 mm diameter, made up of 6–14 stalked peltate microsporophylls each with 4–9 pollen-sacs; strobili in clusters of up to 20–30 near branch ends. Female structures (ovuliferous brachyblasts *sensu* Stützel & Röwekamp 1999) 1.5–2.0 mm long, solitary or in pairs in leaf axils on underside of shoots, not forming cones, consisting of several imbricate scales, the uppermost fertile, bearing a single ovule. Seed ovoid, smooth and shiny, brown-yellow, 6–7 × 5 mm at maturity, with a tough seed coat, partly surrounded by a fleshy red aril typically 9 × 7 mm which falls with the seed at maturity, the 'fruit' ripening in the first year.

More than 70 varieties and cultivars are recognized (Vidaković 1991; Welch & Haddow 1993; Cope 1998) including the columnar Irish yew (cv Fastigiata Loudon) originating on the flank of Cuilcagh Mountain in Co. Fermanagh, N. Ireland, first found in 1780 (Elwes & Henry 1906; Nelson 1981).

Taxus is a genus of around seven closely related species scattered through the northern temperate region. There is some indication from morphological and chemical characteristics that the different species are sufficiently closely related that they constitute geographical variations of *T. baccata* (Hess *et al.* 1967 cited in Voliotis 1986; Burns & Honkala 1990; Dempsey & Hook 2000). Indeed, the heartwood constituents of *T. baccata*, *T. brevifolia*, *T. cuspidata* and *T. floridana* have been found to be almost indistinguishable chemically (Erdtman & Tsuno 1969). Most species contain the alkaloid taxol and although Dempsey & Hook (2000) found wide variation in morphological characteristics and chemical features (paclitaxel content) between varieties of *T. baccata* they found no sufficiently distinctive interspecific differences of taxonomic value between different species. They thus question the correct identification of plant material used in many pharmacological studies.

Taxus baccata has a stress-tolerant life strategy *sensu* Grime (1979), being slow growing, slow to reach maturity (*c.* 70 years), long-lived (> 1000 years), shade-tolerant but can withstand full sun; it can grow on a wide range of soils and produces strong decay-resistant wood (Lilpop 1931; Brzeziecki & Kienast 1994). It forms dense stands in oceanic climates but increasingly becomes an isolated understorey tree in more continental climates.

This evergreen poisonous tree is local in Britain but may form nearly pure woodlands on chalk and limestone in England.

I. Geographical and altitudinal distribution

In Britain, *Taxus baccata* woodlands are almost wholly confined to the chalk of the South Downs and, to a lesser extent, the North Downs in south-east England especially along the sides and bottom of dry valleys and on scarp slopes (Tittensor 1980; Rodwell 1991). There are also examples on the Magnesian Limestone of County Durham in the north-east, the Carboniferous Limestone around Morecambe Bay in the west and on the limestones of south-west Ireland, especially the Killarney woodlands (Kelly 1981). Further small, natural-seeming stands of yew are found in Ireland on limestone outcrops at Lough Derg, north Co. Tipperary, Cahir Park, south Co. Tipperary and Garryland Wood, south-east Co. Galway (McEvoy 1943).

Individual yew trees are more widespread, occurring naturally in woods and on cliffs, including sea cliffs,

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*Abbreviated references are used for many standard works: see *Journal of Ecology* (1975), **63**, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and, where different, Stace (1997).

especially on neutral to alkaline soils. They are notable on the limestone of the Peak District at the southern end of the Pennines, at Borrowdale, on Conzie Scar near Kendal (Elwes & Henry 1906) and widely distributed in the west and north of Ireland (Webb 1977). Apparently native *T. baccata* individuals are also known from Perth and Argyll (56° N) on to the Inner Hebrides and Orkney although whether yew is native to Scotland has been debated (Dickson 1994). The natural distribution is clouded by the extensive planting of yew trees, especially in churchyards, and it is virtually impossible to separate native and alien records; however, the occurrences mapped in Fig. 1 give the best information available.

Taxus baccata extends northwards to *c.* 63° N in Norway and Sweden (Vidaković 1991), eastwards to Estonia, Poland, to the Caspian Sea and Turkey, and southwards to Greece (including the islands of Euboea, Thasos and Samothraki; Voliotis 1986), northern Spain (Peñalba 1994), Portugal and into Algeria (Vidaković 1991). Large populations are found in the Ukraine, Poland, Hungary, Slovakia, Romania and the Caucasus Mountains (Bugala 1978). It is absent from the most continental climatic regions of Europe and also northern, south-eastern divisions of Russia, Crete, Faeroes and Iceland, and is almost extinct in the Azores. The distributions of *Taxus* species, including *T. baccata*, are given in Fig. 2.

In the British Isles, *T. baccata* grows from sea level to 425 m in England and Wales and to 470 m on Purple Mountain, Kerry (Alt. range Br. Pl.). In the north of its range, including Britain, *T. baccata* grows only at fairly low altitudes whereas in the south it is primarily a montane tree growing only on higher mountains in the Mediterranean region, although in the Caucasus Mountains it grows from sea-level to 2050 m. Maximum altitudes: south Slovakia, 660–1000 m; Alps, 1100–1400 m; Iran, 1400 m; Turkey, 1400–1900 m; Pyrenees, 1400–1650 m; southern Spain, 1600–1900 m; Carpathians, 1660 m; Sardinia, 1700 m; Macedonia, 1800 m; central

Fig. 1 (a) The distribution of *Taxus baccata* in Britain. Native: (○) pre-1950, (●) 1950 onwards; introduced: (×) pre-1950, (+) 1950 onwards. Each symbol represents at least one record in a 10-km square of the National Grid. Mapped by Henry Arnold, Biological Records Centre, using Alan Morton's DMAP program, mainly from records made by members of the Botanical Society of the British Isles.

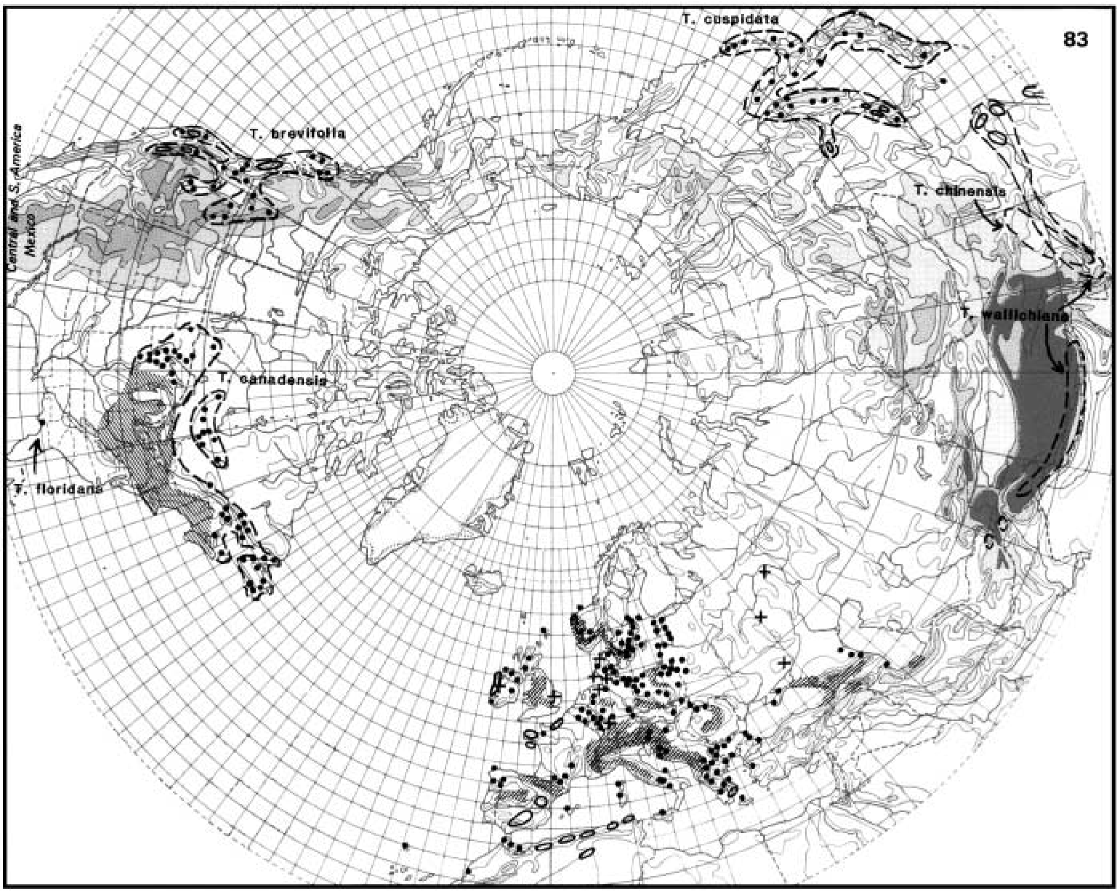


Fig. 2 The circumpolar distribution of *Taxus baccata* and other *Taxus* species from Hultén & Fries (1986). + indicates interglacial records; ● indicates isolated occurrences; hatched areas indicate regions of common or fairly common occurrence. Broken lines outline the distribution of *Taxus* species other than *T. baccata*. Reprinted with permission.

Greece, 1950 m; northern Africa, 2000–2500 m, and Caucasus Mountains, 2050 m (Elwes & Henry 1906; Bugala 1978; Król 1978; Melzack 1979; Voliotis 1986; Hartzell 1991; Vidaković 1991; Schweingruber 1993).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Taxus baccata grows best in the high humidity of mild oceanic climates. In England it thrives particularly in areas with relatively mild winters, abundant rainfall, high humidity and where mist frequency is greater than average, as in the coastlands of Hampshire and Sussex and lowland parts of the Lake District (Tittensor 1980; Melzack & Watts 1982b). Conversely, severe winter cold or strong cold drying winds in the spring appear to restrict yew growth on exposed sites in the UK (Voliotis 1986).

Taxus baccata sensu stricto is classified as European Temperate by Preston & Hill (1997). In mainland Europe, the ecological barriers limiting distribution are low temperatures in the north, severe continental climate of the Baltic countries and Poland in the east, long droughts in Turkey to the south-east, and drought and high temperatures in north Africa (Kamppa 1926; Król 1978; Środoń 1978). Near these climatic extremes, *T. baccata* becomes more restricted to moist niches, such as near marshes and bogs on the Baltic coast (Król 1978), rock crevices, or as an understorey tree gaining protection from low humidity and frosts (Sokolowski 1921; Hoffmann 1958; Faegri 1960; Tittensor 1980; Peñalba 1994; Saniga 2000). In mountainous areas of Europe, yew tends to grow on the shaded north-western or north-eastern slopes, where under deciduous or mixed stands there is an oceanic-like climate (Markiewicz 1978; Schweingruber 1993).

Taxus baccata woods on the South Downs occur on slopes of almost any aspect but primarily linked to south, east and, to a lesser extent, west slopes where there is high insolation and wind-exposure (Watt 1926; Williamson 1978). Slope is rarely limiting; stands of yew occur on moderate to very steep slopes (Rodwell 1991) and, further north, cliffs are a common habitat (Pigott 1969). On the western South Downs, 80% of yew woodlands were investigated by Tittensor (1980) and found to be between 90 and 250 m altitude, 62% on steep slopes, 57% along the main ridge and 90% on chalk. Moreover, 80% of the woods occur in the area of maximum rainfall (> 1000 mm year^{-1}).

(B) SUBSTRATUM

Stands of yew are typically associated with limestone slopes carrying shallow dry rendzinas (Rodwell 1991). Soils are normally grey rendzinas of the Upton series, thin, often rich in downwashed flints and poor in earthworms. Yew grows equally well on thin, warm chalk soils, limestone pavement and fen peat (Williamson 1978). In south-west Ireland, yew grows on Carboniferous Limestone pavement with a soil pH in the hollows of 6.8 ± 0.11 (SE) (Kelly 1981). Along valley bottoms, *T. baccata* woodland may extend on to somewhat deeper and moister soils.

Although the majority of natural stands in Europe grow on calcareous soils, yew will also grow on almost any soil, including siliceous soils derived from igneous and sedimentary rocks (Elwes & Henry 1906; Watt 1926; Webb 1977; Król 1978; Kelly 1981; Vidaković 1991). Thus in south-east England, yew grows on the chalk of the North and the South Downs, the Weald Clay and the sandstones of the Lower Greensand and the Central Weald. In the west and north of Ireland, individual trees occur on rocky terrain, siliceous as well as limestone, and in Killarney woods, individuals are found on Devonian sandstone (Kelly 1981). Voliotis (1986) states that *T. baccata* is favoured by slightly calcareous soil in northern Europe and siliceous soils in southern Europe. Watt (1924, 1934a,b) noted that yew is a successful pioneer on highly calcareous, exposed sites of the South Downs, but on more acidic plateau soils *T. baccata* is a scarce but local feature with low constancy and frequency values. Across Europe, best yew growth (in terms of rates of growth and largest dimensions) is seen on deep, moist sandy loams and well-drained clays, and worst on dry, rocky and sandy soils where it occurs as scattered and stunted individuals (Webb 1977; Bugala 1978).

Yew generally is absent from wet soils, such as wet acidic peat and wet clay (Król 1978; Williamson 1978; Ellenberg 1988), although it does grow well upon calcareous fen peat, and indeed is a significant species in the wood peat accumulations of the East Anglian fens (Godw. Hist.). Even here, however, it is susceptible to poor drainage.

Substratum conditions are known to be altered by *T. baccata*. Howard *et al*. (1998) compared soil physicochemical conditions under oak (*Quercus*) and yew trees growing on the same soils. Under yew, the humic acids were more oxidized; ash content was less under yew (55.6%) than under oak (73.8%); a greater total C, N and Ca was found under yew (23.7%, 1.3% and 2.1%, respectively) than under oak (13.1%, 0.8% and 1.1%), attributed to the absence of large earthworms under yew. Soil pH was not, however, significantly affected by tree species.

III. Communities

In Britain, *T. baccata* forms a remarkably species-poor woodland with yew as the only constant species, typically forming a closed, very dense canopy (W13 in the National Vegetation Classification; Rodwell 1991). The woodland forms 'sometimes quite extensive stretches of striking floristic poverty and uniformity' especially on the warm and sunny south-facing slopes over shallow limestone soils (Rodwell 1991). Yew thrives better than any other tree on steep calcareous slopes and so few other trees occur; when they do it is usually as scattered individuals, notably *Sorbus aria*, but also *Fraxinus excelsior* and widely scattered individuals of *Fagus sylvatica*, *Acer pseudoplatanus* or *Quercus robur*. Shrubs are rare except in gaps and edges of stands, seldom form a true shrub layer, and are usually restricted to poor specimens of *Sambucus nigra* and very occasional *Ilex aquifolium* or *Crataegus monogyna*. *Buxus sempervirens* is a rare associate. The field layer is, as would be expected, extremely sparse usually consisting of patchy herbs with extensive bare ground. The most frequently encountered species are *Mercurialis perennis* with very occasional *Arum maculatum*, *Brachypodium sylvaticum*, *Fragaria vesca*, *Glechoma hederacea*, *Hedera helix*, *Rubus fruticosus* agg., *Urtica dioica* and *Viola* spp. (Rodwell 1991). This is caused not just by shade but by the intense root competition in soils which are often already dry. Bryophytes are equally poorly developed in the UK, in striking contrast to the Killarney yew woods (see below).

Rodwell (1991) recognizes two subcommunities. The *Sorbus aria* subcommunity (W13a) contains this tree as a fairly frequent associate in the canopy, at about 2–3 trees ha^{-1}, and even more rarely, *Fraxinus excelsior*, *Fagus sylvatica*, *Quercus robur* or *Acer pseudoplatanus*. In Co. Durham, Hulme (1996) also found *Corylus avellana* and *Ulmus glabra* in all four yew woodlands visited. *Sambucus nigra* is the usual shrub although in a few stands in the south-east, notably Box Hill, Surrey, *Buxus sempervirens* can be locally important and can grow up to form a dense shrub layer or even part of the canopy. A field layer is usually absent or at most very sparse – scattered bryophytes, bare soil and litter. In the *Mercurialis perennis* subcommunity (W13b), yew dominates with very infrequent *Sorbus aria* and *Fraxinus*. The canopy tends to be more open, allowing a more frequent and somewhat denser growth of *Sambucus* beneath, sometimes with sparse *Ligustrum vulgare*, *Euonymus europaea*, *Cornus sanguinea* and *Clematis vitalba* or *Tamus communis*. The field layer is a little less sparse than in the *Sorbus aria* subcommunity (although most of the ground is still bare) with *Mercurialis perennis* as a patchily abundant constant component of the field layer, sometimes with *Atropa belladonna*, *Brachypodium sylvaticum*, *Fragaria vesca*, *Inula conyza*, *Iris foetidissima*, *Rubus* spp., *Urtica dioica* and *Viola* spp.

Yew saplings are also a component of the *Crataegus monogyna–Hedera helix* scrub (W21). Young yew trees are found in the *Brachypodium sylvaticum* subcommunity but is a more major component of the *Viburnum* *lantana* subcommunity confined to free-draining calcareous soils, and best represented on the chalk of the south-east. *Taxus baccata* and *Sorbus aria* are the most frequent trees. Yew is associated with *C. monogyna* on deeper, moister soils on gentle, sheltered slopes but especially with *Juniperus communis* bushes on shallower, drier soils on steeper and more exposed sites where yew has a high constancy (Watt 1934a; Rodwell 1991). This reflects the need of yew for nurse plants in establishing new trees and leads to seral development.

The juniper sere starts with juniper establishing (in windier areas than *Crataegus*) which is invaded by yew, leading to a yew scrub with associated *Cornus sanguinea*, *Prunus spinosa*, *Rubus fruticosus*, *C. monogyna*, *Ilex aquifolium* and *Sambucus nigra* (Watt 1924, 1926, 1934a). Owing to its extreme tolerance of shade and the dense shade it creates, yew eventually outcompetes other species and develops progressively into pure yew woodland, often with the dead woody remains of the former juniper scrub beneath. There can be occasional *I. aquifolium* and rare straggling *C. monogyna* and *Prunus spinosa*, with an occasional *Sorbus aria* above the yew canopy, as at the head of Kingley Vale, Sussex. The *Sorbus* initially survives by outgrowing the yew in earlier years to persist as emergents or invaders of gaps. But as they die they are not replaced and the canopy of yew fuses into a virtually continuous layer (Watt 1926). The association of juniper and yew is not solely found in the south-east; Larson *et al.* (2000) records the two species growing together on the sea cliffs of the Great Orme and the Little Orme of northern Wales in 1997.

The hawthorn sere is similar, although *C. monogyna* is less good at providing protection for yew seedlings from grazers, even when mixed with *Prunus spinosa*. Moreover, on the deeper, moister soils where *Juniperus* is replaced, other trees, notably *Fraxinus excelsior*, increase in importance as invaders, leading to a more species-rich scrub. Hulme (1996) shows data which suggest a *Crataegus/Fraxinus* successional sequence in Co. Durham yew woods, with yew eventually killing out the scrub elements.

Although yew is capable of invading grassland (Williamson 1978), either juniper or hawthorn appears essential for its regeneration (Watt 1926, 1934a; Williamson 1978). This association between yew and shrubs has been interpreted as a requirement for establishing yew to have shade and/or protection from browsing vertebrate herbivores (Watt 1926; Williamson 1978). As such, juniper may be the more favoured nurse plant because it grows on soils more suitable for the domination of yew but also because juniper provides a better defence against herbivores. Hulme (1997) and García *et al.* (2000) point out that scrub will attract seed-dispersing birds and so increase yew seed deposition while, conversely, attracting high seed predation from rodents under the shelter of scrub. Nevertheless, dispersal appears to direct seeds to microhabitats most suitable for seedling survival, identified by García *et al.* (2000) as a favourably moist and nutrient-rich microclimate (especially in the face of summer drought), protected from large herbivores.

Tittensor (1980) working on the South Downs found that twice as many Recent as Ancient Woodlands contained yew, and that yew regeneration was far more common in Recent woods. Those Ancient Woodlands containing yew had few canopy yew and none with yew as a dominant species. Combining this with the estimated young age of woodland yews, she and others (e.g. Watt 1926; Williamson 1978) point out that the South Downs yew woods largely result from the abandonment of land during the last two centuries as a result of the Napoleonic wars, agricultural neglect in the 1920s and myxomatosis. Similar expansion in Irish yew woodlands has been seen following a cessation in grazing or human disturbance (Watts 1984; Mitchell 1988; O'Connell *et al.* 1988) although some, such as the Reenadinna Wood at Killarney, are estimated to have developed 3000–5000 years ago (Mitchell 1990b). Tittensor (1980) also suggests that because many of the woodlands straddle parish boundaries, old marker trees (which may be centuries or even millennia old) may have been the seed parents and the cause of yew woodland development which is not seen in other areas of abandonment.

Yew is extremely shade tolerant; nevertheless regeneration within mature yew woodland is rare in Britain and across Europe (Król 1978). The replacement of individual trees depends entirely on the development of a shrubby sere in gaps left by dead yews but primarily around the edge of existing woodland (Watt 1926; Williamson 1978). Regeneration to adult size may take as long as 75 years and the maintenance of yew woodlands is possible only owing to extreme longevity of individual trees and yew's tolerance of shade (Watt 1926; Tittensor 1980). Newbould (1960) concludes that yew woods are single generation stands 'moving' across the landscape by edge regeneration. If shrubs fail to develop densely enough, rabbits may prevent regeneration and the woodland degenerates by a failure to recolonize gaps formed by the death of old yews, leaving individual relict trees until eventually they die leading to 'abandonment of the area' (Watt 1926). Scrub can reform and the cycle would begin again with slow yew recolonization. Newbould (1960) suggests that yew woods may be considered as a type of secondary seral scrub that will progress to a 'woodland community as yet unknown' once the life-span of its component yews is reached.

Individual trees are also found much further north as a natural part of stands of *Fraxinus excelsior–Acer campestre–Mercurialis perennis* (W8) woodland on Carboniferous Limestone in Wales, Derbyshire, the Pennines and around Morecambe Bay (Rodwell 1991). Here the yew may form part of the canopy, a distinct lower tier to the canopy as in Matlock Dale in Derbyshire, or exist as scattered saplings or isolated specimens on cliffs as in Dove Dale Wood, Derbyshire (Pigott 1969). Although Rodwell (1991) considers these northern examples as part of the mixed deciduous woodland of W8, Hall *et al.* (2001) report that it is now common practice that they be included within the yew woodlands proper (W13).

Yew establishment is hindered and saplings often die or show poor growth with few leaves when beneath the shade of beech. In this way, beech may prevent the succession to yew. Yew does better on drier, more exposed conditions and this may explain why yew dominates here but beech is the dominant on the deeper soils of *Fagus–Mercurialis* woodland (W12). The circumstances under which yew develops from being an occasional component of woodland to becoming the dominant species remain poorly understood.

Yew is an occasional and sometimes prominent associate in various kinds of deciduous woodlands, most notably those in the Fagion alliance, especially the three kinds of beech woodland, *Fagus sylvatica–Mercurialis perennis* (W12), *Fagus sylvatica–Rubus fruticosus* (W14) and *Fagus sylvatica–Deschampsia flexuosa* (W15) woodlands. Here it forms part of a subcanopy of shade-tolerant trees being especially prominent in areas such as the New Forest and the chalk of south-east England. In *Fagus–Mercurialis* woodland, the *T. baccata* subcommunity (W12c) is found predominantly on south-facing steep calcareous slopes of the North Downs and some gaps in the Chilterns, with high exposure to wind and sun. Here *T. baccata* is a constant and it can be abundant as a lower tier of saplings beneath the *Fagus* or sometimes even break through into the canopy. It seems likely that in these woodlands, as in W13, *T. baccata* establishes in *Juniperus*-dominated scrub and the invasion of *F. sylvatica* is hampered by the shallow, impoverished soils of these steep, sun-baked slopes. Sometimes *T. baccata* occurs with *Sorbus aria*, although *Fraxinus excelsior* or *Buxus sempervirens* can be scarce companions but with little *Crataegus monogyna* or *Corylus avellana*. The field layer is usually a sparse mixture of *Mercurialis perennis* and *Rubus fruticosus* with a number of other species at low frequency. Thus there is a transition between W12c and *T. baccata* woodland proper (W13).

On the low base-status moist brown earths of the *Fagus–Rubus* woodland (W14), such as occasionally in the New Forest and sometimes in Surrey and Sussex, much more rarely in the Chilterns, and on the very base-poor, infertile soils of the *Fagus-Deschampsia* woodlands (W15) in the southern lowlands, the undertier of *Ilex aquifolium* can be sporadically accompanied by scattered individuals of *T. baccata*, which may reach high enough to break almost through the canopy. These fall within Corine Code 9120/Palaearctic Habitat Classification 41.12 – Atlantic acidophilous beech forests (Quercinion robori-petraeae or Ilici Fagenion) (Interpretation Manual of European Union Habitats 1999). In a similar way, *T. baccata* can also be found in *Quercus–Pteridium–Rubus* woodlands (W10) on base-poor brown earths as a patchy lower tier beneath the oak, as in some New Forest stands.

As noted above, *T. baccata* woodlands are found in close association with grasslands and scrub which reflect grazing relaxation over the south-eastern chalk. Thus, yew stands can be found in mosaics and zonations with a complete sequence of vegetation types from close-cropped turf of *Festuca ovina–Avenula pratensis* (CG2), other swards dominated by coarse grasses to various kinds of *Crataegus monogyna–Hedera helix* scrub (W21).

Taxus baccata woodland (W13) is synonymous with the yew-woods of Tansley & Rankin (1911), Watt (1926), Tansley, Br. Isl. and Ratcliffe (1977) and in Europe is classified as Corine Code 91J0 and Palaearctic Habitat Code 42.A71 (Interpretation Manual of European Union Habitats 1999).

In south-west Ireland, the Killarney woodlands contain extensive stands of yew dominating on bare Carboniferous Limestone pavement areas, and classified as facies of *Taxus baccata* of the Association Corylo × Fraxinetum (Order Fagetalia, Class Querco-Fagetea) (Ir. Pfl.) and also belong within Corine Code 8240 and Palaearctic Habitat Classification 62.3 (Interpretation Manual of European Union Habitats 1999). On more broken rocky terrain the shorter yew trees on the limestone outcrops are intermingled with taller *Quercus* (largely *Q. petraea*) in the intervening soil-filled hollows (Kelly 1981). Little grows under the yew canopy although *Corylus avellana* or *Ilex aquifolium* become frequent locally and *Corylus* can replace yew as the dominant. The field layer is sparse, the most constant species being *Brachypodium sylvaticum*, *Fragaria vesca*, *Oxalis acetosella*, *Potentilla sterilis* and *Sanicula europaea*. Unlike the yew woodlands of southern England, here there is a very dense moss cover, primarily *Thamnium alopecurum* with *Eurhynchium striatum* and *Thuidium tamariscinum* (Kelly 1981).

There is no direct equivalent of these species-poor mature stands in continental Europe. Delelis-Dusollier & Géhu (1972) and others put samples of fairly species-rich yew scrub from south-east England into a Roso-Sorbetum ariae which they took as the British equivalent to the Taxo-Prunetum mahalebis, a community found on chalk cliffs along the Seine. British yew woodland is best considered as part of the Fagion alliance in the Querco-Fagetea (see Kelly 1981; above), alongside the *Fagus–Mercurialis* woodland and the European communities such as the Taxo-Fagetum (e.g. Król 1978; Rodwell 1991; Saniga 2000).

From Portugal to the Crimea in the east, constrained by the need for a humid climate, *T. baccata* is usually a minor component of climax deciduous, coniferous or mixed woods (Tittensor 1980). For example, in northern Spain yew grows only as isolated individuals within the beech forest (Peñalba 1994); in central and eastern Europe yew is an understorey component of beech, or mixed forests of beech and conifers (e.g. Sokolowski 1921; Hoffmann 1958; Saniga 2000). Yew occurs in all ecological regions of Cephalanthero-Taxetum on shell-limestone or chalk (Król 1978). These communities are intermediate between Melico-Fagetum and Seslerio-Taxetum with the occurrence of *Fraxinus excelsior* and *Tilia cordata*. The community Seslerio-Taxetum is used to distinguish stands with yew from those with beech (Seslerio-Fagetum) – Moor 1952 cited in Król (1978). In the mountainous regions of Czechoslovakia, yew grows in fir and beech forests, and at lower elevations it is part of the oak and hornbeam forests (Futak *et al.* 1966). In Poland, yews grow amongst beeches on podsolic soils (Melico-Fagetum) and in a calcium-rich ash and alder carr (Circaeo-Alnetum) (Bojarska & Plitcha 1968, cited in Król 1978). Also in Poland, yew is found in Querco-Carpinetum medio-europaeum stands and with alder on fen soils (Carici elongatae-Alnetum).

Outside of Britain, *T. baccata* appears to form single-species stands only in the oceanic climates of the Crimea and Caucasus Mountains on a small scale (Pridnya 1984). Król (1978) records that, in the Caucasus, stands of pure yew or where yew dominates can be up to 10 ha with trees up to 32.5 m in height. These grade into forests formed by *Fagus sylvatica*, *Carpinus* spp., *Fraxinus excelsior*, *Acer platanoides*, *A. campestre*, *A. pictum*, *Ulmus elliptica* and *Fagus orientalis* mixed with *Abies nordmaniana* and *Picea orientalis*, with an understorey of *Buxus sempervirens* (Bugala 1978; Pridnya 1984). Purer yew woodlands are apparently being invaded by beech and ash. The islands of Corsica and Sardinia also have very local woodlands dominated by *T. baccata*, often with *Ilex aquifolium* and *Buxus sempervirens* (in Corsica), *Sorbus aria* and *Mercurialis perennis* (classified as Corine Code 9580 and Palaearctic Habitat Classification 42.A72 and 42.A73 in the Interpretation Manual of European Union Habitats 1999). These are thought to represent a senescent phase of the original beech or beech-fir wood. Similar *T. baccata* relicts, sometimes of small isolated formations, exist in the north and centre of Portugal.

IV. Response to biotic factors

Despite its poisonous properties, yew is very susceptible to browsing and bark stripping by rabbits, hares, deer and domestic animals such as sheep and sometimes even cattle (Elwes & Henry 1906; Watt 1926; Kelly 1975, 1981; Mitchell 1988, 1990a; Haeggström 1990; Sarmaja-Korjonen *et al.* 1991). Indeed, Kelly (1975) describes *T. baccata* as one of the most grazing-sensitive trees in the Irish Killarney woodlands. Despite this, yew is tolerant of repeated pruning (as demonstrated by its use in topiary) and is able to continue growth under severe browsing pressure (Tittensor 1980). Tabbush & White (1996) suggest that the swelling of many yew boles, with burr-like convoluted grain beneath, is probably the result of prolonged exposure to browsing. Welch & Haddow (1993) state that a feature of the whole genus is the almost total inability to develop fresh leader growth following damage; however, new leaders have been seen to form from buds just below the damaged tips 1–2 years after simulated browsing (Philip Perrin, pers. comm.). In the Burren of western Ireland, individual yew trees are restricted to prostrate dense shrubs, some fitting into solution hollows in the limestone pavement, primarily as a result of goat grazing; if the grazing is removed by exclosures, new vertical shoots produce rapid upwards growth. Trees can be killed by being scored by deer antlers, as has been observed in Killarney woodlands (Larner 1977), caused by Japanese sika deer (*Cervus nippon*).

Rabbit and deer grazing of seedlings and seed predation by rodents are known to be a major factor in lack of recruitment (Watt 1926; Williamson 1978; Kelly 1981; Mitchell 1988; Haeggström 1990; Hulme 1996; Hulme & Borelli 1999; Saniga 2000). The decline of yew in Denmark is attributed to widespread deforestation and selective felling followed by poor regeneration due to grazing (Svenning & Magård 1999). García *et al.* (2000) found that yew regenerated mostly under fleshy-fruited shrubs in the Sierra Nevada mountains of Spain (dominated by *Juniperus communis*, *J. sabina*, *Berberis hispanica* and *Rosa* spp.). The estimated density of the yew in the study plot was 288 individuals ha^{-1}, more than 90% being juveniles (seedlings 82% and saplings 9%), which were mostly located under shrubs. This is dense regeneration, even by UK standards (see Hulme 1996). Saplings suffered serious herbivore damage when unprotected by shrubs. The high density of fleshy-fruited shrubs appears to be the key by (i) attracting frugivorous birds with a consequent accumulation of voided yew seeds beneath, (ii) maintaining a favourably moist and nutrient-rich microclimate (especially in the face of summer drought), and (iii) protecting against herbivores by the woody parts being relatively unpalatable with imbricate and often thorny branching. The shade-tolerant nature of the yew, of course, allows it to grow well in the heavy shade of the shrubs. In the stands studied, ungulates attacked 31.1% of marked juvenile yews. Damaged plants lost an average of 23 ± 3.6% (SE, $n = 31$) of their shoots to ungulates, damage reaching 67.7% in some individuals. Repeated herbivory was positively correlated with damage intensity which was negatively correlated with height and age. The risk of being grazed and the damage caused declined with increase in shrub cover and height.

Yew is shade tolerant even under dense shade (Lilpop 1931; Król 1978; Brzeziecki & Kienast 1994). However, yew establishment is hindered and saplings often die or show poor growth with few leaves when beneath the shade of beech (Czartoryski 1978; Król 1978; Pridnya 1984). In Slovakia, Saniga (2000) found that even though yew is very shade tolerant, a reduction in surrounding timber (dominated by *Fagus sylvatica* and *Picea abies*) by 18–20% volume improved the height growth of yew whereas a reduction in volume by 7–8% resulted in no growth above the control plots. He also found that with a good growth of *Rubus* sp., etc., on clear-cut sites, or with successful regeneration of beech, the conditions for the germination, survival and growth of yew were less favourable. Pridnya (1984) mentions that in the Caucasus broadleaf trees do not permit yew trees to grow because of their thick crowns which 'offer mechanical interference'. In contrast, in areas with more continental climates, other trees (or rocky outcrops) protect against extremes of dryness or temperature, and yew is thus restricted to an understorey tree as in eastern Europe (Sokolowski 1921).

V. Response to environment

(A) GREGARIOUSNESS

In optimum oceanic climates, *T. baccata* is gregarious, forming pure often even-aged stands with measured densities in Denmark of 1388 individuals ha^{-1}, including 513 adults (≥ 30 mm diameter) (Svenning & Magård 1999). On the edges of yew stands at Kingley Vale, Sussex, where *T. baccata* is invading scrub, Williamson (1978) has described 'families' of yews where around four trees grow up through each juniper nurse plant, each some distance away from the next family; 'The families may consist of one fat member, average girth 5 feet [1.5 m], two medium-sized, 3 feet [0.9 m], and one skinny member with as little as 2 inches girth [5 cm]'. Outside these stands, *T. baccata* is common as isolated trees on a wide range of soils. This is especially so in northern Britain and continental Europe where yew occurs mostly singly or as groups in the undergrowth. Extensive planting in the British Isles has led to the widespread occurrence of single or small groups of trees in gardens, towns and especially churchyards. Indeed in north-west Wales, yew is the commonest churchyard tree, constituting 33% of all trees (Denne 1987).

(B) PERFORMANCE IN VARIOUS HABITATS

Although, as noted above, saplings may do poorly or die under a canopy of beech, evidence suggests that once established yew can continue growing slowly in dense shade. Saplings can persist and grow very slowly for very many years before breaking through the beech canopy (Rodwell 1991). In Denmark, yew woodlands on glacial sand and clay have increased rapidly in radius at ≤ 3 m year^{-1} into beech forest (Svenning & Magård 1999). Nevertheless, growth of yew is slow compared to most other trees even under optimum conditions and after eliminating potential competitors. Consequently, even the oldest individuals do not attain considerable height. Height growth of 20–30 cm per year in the open is normal, trees reaching 4.5 m after 20 years. In Killarney woodlands, yew has a low canopy 6–14 m in height (Kelly 1981). There is a high energy investment in defensive mechanisms which increase resistance of wood against fungi and insect attacks.

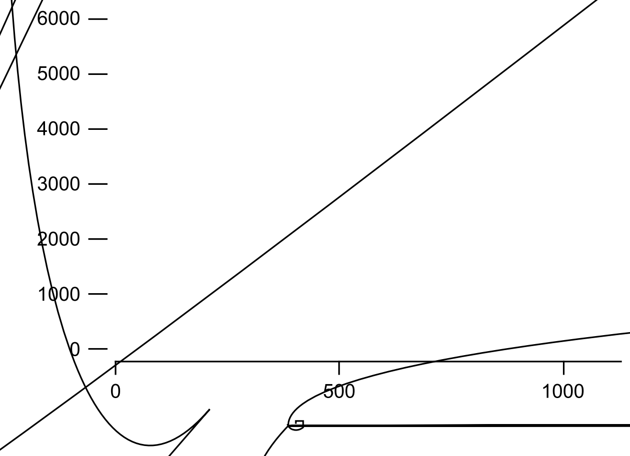
Melzack (1979) found evidence of a geographical variation in yew growth in England with southern trees having the most vigorous shoots (in terms of leaf number) and the smallest leaves compared to those in the north-east. There was also a suggestion that trees in the south are bigger than those in the north-east. Watt (1926) pointed out that grazing can drastically affect net growth rates; under high grazing pressure from rabbits on the South Downs, he found one small yew just 18 cm high with approximately 55 growth rings.

Hulme (1996) shows that Castle Eden and Hawthorn Denes woodlands in Co. Durham have a truncated age-distribution – very few young trees – suggesting that over time there is declining recruitment but relatively constant mortality. This is consistent with the hypothesis that regeneration declines progressively as yew woodlands develop (Watt 1924, 1926). An important factor appears to be low levels of seedling recruitment (Williamson 1978; Kelly 1981; Hulme 1996). Hulme (1996) found 0–208 seedlings ha^{-1} in his Co. Durham woodlands. He suggests that this was partly because of high seed predation by small mammals (especially high beneath the shade of shrubs) but argues that lack of suitable microsites beneath scrub vegetation is an increasingly limiting factor in older yew woodlands as the scrub is progressively killed out.

Under a continental climate, growth is somewhat reduced as yew becomes more of an understorey tree. Many authors consider that in eastern Europe, yew grows better in shade, especially when young (e.g. Maly 1930). Traczyk (1953) suggested that yew will tolerate open conditions in such a continental climate providing it is on a fertile, moist soil.

Williamson's (1978) general figure for rates of trunk growth, as measured by width of annual rings, of 0.9–1.2 mm appears to be generally applicable in the British Isles. However, annual ring width has been found to vary from as little as 0.095 mm (a yew growing on thin peat and subsequently preserved in a bog of Co. Laois, Ireland; Adams 1905) to 3 mm or more on favourable soils (see Table 1). From empirical data, White (1998) suggests that maturity (judged by the cross-sectional area of successive rings reducing over time to reach a constant) is reached in 30 years for yews growing inside woodland, 40 years on poor ground or with some exposure, 55 years in churchyards and 60 years on an average garden or parkland site.

The rate of ring-width growth also depends on the age of the tree. As seen in Table 1, ring width slows dramatically once the yew reaches maturity, as it does in most trees. Newbould (1960) found ring widths of 0.13–2.54 mm in younger trees, falling to 0.051 mm in older trees. White (1998) gives a method for calculating the age of different species of tree from diameter based on empirical knowledge of how annual ring-width changes over time. White's data give an average ring-width for the first juvenile phase of growth (where ring width is approximately constant as diameter of the tree



increases) of 3 mm year^{-1} for the first 30–60 years (least on most favourable sites), producing the rates of growth in Fig. 3. However, Tabbush & White (1996) found ring-widths on the dry, infertile soils of Kingley Vale, Sussex, to average 2.5 mm over the first 30 years, suggesting a slower rate of growth on these poor soils (see Fig. 3, curve b) compared to richer soils (curve a). Moreover, as trees enter senescence, with reduction in canopy size, growth rates will reduce still further. Meredith produced an empirical age-diameter relationship for yew using data from trees throughout the British Isles (data cited in Milner 1992; see Fig. 3, curve d).

Based primarily on measurements of ring widths and repeat measurements of old trees and trees of known planting date, Tabbush (1997) produced the following empirical formula for English churchyard yews (see Fig. 3, curve c):

Tree age = Girth (in cm)^2/310

The data used extend to trees around 1000 years of age although, not unexpectedly, the scatter of points around the line (not shown in Fig. 3) increased with girth; overall, the curve accounts for 56.9% of the variation.

Moir (1999) used empirical measurements of yew growth from 12 trees growing at Hampton Court, London, on sand and gravel river terraces to produce a linear regression: age (in years) = 17.8 + 1.08 × girth (in cm); see Fig. 3. However, there is considerable variation between the age of a tree and its mean ring width or girth measurement. Again, Moir noted a great variation in growth rates such that trees in an avenue planted probably between 1890 and 1900 varied from 30 to 80 cm in diameter. The fairly high growth rates found here were attributed by Moir to the warmth created by the London conurbation.

Figure 3 shows the great variability between estimates of growth rates, dependent upon soil and other environmental factors. There is also a great deal of scatter around each line (not shown), suggesting very different growth rates even within the same site. Thus, a number of authors suggest that the girth has only limited use in estimating the age of a yew tree (e.g. Denne 1987; Moir 1999) and should be interpreted with reference to soil type, history of the canopy, exposure, etc.

Why is growth rate within one site variable? White (1998) points out that the yew is unusual in that it can return to juvenile rates of growth at almost any stage, perhaps stimulated by extra nutrition from branch layering and vigorous regeneration after catastrophic damage. Supporting this, a study of ring widths in a 335-year-old yew at Alice Holt Lodge, Surrey (T. Hindson pers. comm.) showed two distinct peaks of ring widths over 2.0 mm with the tree still producing rings over 1.0 mm wide after 300 years.

As is usually the case, growth rates (whether from direct measurements of ring widths or inferred from external measurements of the tree) also appear to vary according to where measurements are made on the trunk. The measurements by Lowe (1897) in Table 1 on trees 0.3 m in diameter and 75 years old were made at 3 feet (0.91 m) above ground level while the much larger average ring widths of Henslow (1889) were made 'near the ground' on trees 0.6 m diameter and 54 years old. Indeed, a number of records given by Lowe (1897) show initially much faster rates of growth near or at ground level but growth at ground level may appear then to stop or slow dramatically producing an 'inverted' tree shape. For example, the Ormiston Yew in Scotland in 1834 was 3.88 m in girth at ground level and 5.38 m at 1.5 m above.

Yews are renowned for an unusually wide trunk in old trees; the rotting trunk of the Fortingall yew on Tayside, Perth, traced at ground level, is approximately 5.4 m in diameter (Chetan & Brueton 1994) and the largest intact trunk is listed by Mitchell *et al.* (1990), at Defynnoc Church, Powys, as 3.42 m diameter. Such large size has led to speculation about their extreme age (e.g. Lowe 1897; Brzeziecki & Kienast 1994; Tabbush & White 1996) – including a suggestion that the Fortingall Yew in Perthshire is between 1500 and 5000 years old (Christison 1897; Renwick 1913; Cornish 1946; Chetan & Brueton 1994; Dickson 1994; Hartzell 1995). Watt (1926) suggested that the yews of Kingley Vale were up to 1000 years old, but others (e.g. Lowe 1897; Newbould 1960; Williamson 1978; Tittensor 1980) have suggested 500 years to be a more accurate estimate. Thus many authors, including Tansley (Tansley, Br. Isl.), have concluded that 'the age of old yews is often considerably overestimated'.

The growth rates given above point to the antiquity of yews but the great variation makes it difficult to estimate accurately the age of any one individual. Certainly, ring counts of 400–500 are not uncommon (e.g. Bowman 1837; Bebber & Corona 1986; Parsapajouh *et al.* 1986). Ring counts cannot generally be used to date older trees reliably since these are invariably hollow; Mitchell (1972) stated that all yews over 4.5 m in girth are very likely to be hollow. Moreover, yew is renowned for missing or, at least, very narrow (and thus easily missed) rings. Lowe (1897) reported on a tree in Kew Museum that had 250 rings on one side and just 50 on the other. To help accurate counting, Moir (1999) points out that very narrow rings are usually more easily seen on the lobes/flutes common in yew trunks. Tabbush & White (1996) conclude that 'the age of the oldest trees cannot be determined with certainty, but we can be confident that they are in excess of 2000 years old'.

There are other pitfalls in estimating age. As with other tree species, old senescent trees can produce new stems from remains of the former large trunk and appear as young trees. Grazing may also keep a tree artificially small. The yew, however, is also renowned for the apparent production of large trees from the fusing of several trunks. Lowe (1897) and Williamson (1978) give many instances of trunks with two or more centres surrounded by their own concentric growth. Williamson (1978) described a felled yew 37 cm in diameter which contained seven centres ranging from 21 to 53 cm in circumference, each 46 years old. Several possible causes for several centres have been considered. This may arise from a coalescence of several individuals ('aggregates of individuals' Lowe 1897) either from dense new shoots from around the base of a dying trunk which become welded togther, or from a circle of seedlings, for example, around a juniper, which eventually coalesced. Chetan & Brueton (1994) argue that the latter is unlikely because such coalescence would normally result in male and female branches growing on the same tree which is not usually observed. Either way, yew is particularly prone to fuse with other stems and surround objects such as stones. Several centres may also result from the inclusion of branches into a trunk or, in very old trees, from the coalescence of roots originating at the bases of branches and growing down through the hollow centre of the tree (Tabbush & White 1996).

Lowe (1897) argued that the fusing of multiple stems/roots would make an individual appear much older than it really is. However, overall growth rate of the new trunk when young is unlikely to be much greater than a single tree of the same size. Indeed, Tabbush & White (1996) argue using rough calculations that the coalescing of seedlings would actually make little difference to age estimates. Providing the original circle of trees was not much larger than 1 m in diameter, the error in subsequent age determination of the resulting 'tree' would be minor.

(C) EFFECT OF FROST, DROUGHT, ETC

Taxus baccata is intolerant of severe and prolonged frost (Godw. Hist.; Brzeziecki & Kienast 1994; Skorupski & Luxton 1998) and icy winds (Bugala 1978). Elwes & Henry (1906) give examples of yew being damaged or killed by frosts during the severe winter of 1837–8 in the west of Scotland, and the death of many young shoots on trees at Burton-on-Trent in the winter of 1859–60. Till (1956) reported that needles from trees in southern Sweden showed a maximum winter resistance of −33 °C to −35 °C. Vegetative buds of the same trees showed a maximum resistance of −23 °C to −26 °C, whereas male reproductive buds were damaged below

−21 °C to −23 °C. From the Austrian Alps, Pisek *et al.* (1967) reported that exposure to −21 °C for three hours resulted in 10–15% frost damage to needles and −23 °C resulted in 100% damage. Maximum tolerance to frost occurs in mid-winter (January), declining rapidly in early spring (Melzack & Watts 1982b; Brzeziecki & Kienast 1994) when tissue is vulnerable to severe frost conditions. In Britain, Melzack & Watts (1982b) found that, in midwinter, damage started at −13.4 °C 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). They suggested that this may explain the scarcity of native yew stands in the north-east. Sensitivity to frost in early spring is undoubtedly the crucial limiting factor in the northerly oceanic distribution in Europe of this species. *Taxus* × *media* is more resistant to low temperature in Poland than *T. baccata*, as also is its other parent, *T. cuspidata* (Bugala 1978).

The heat resistance of *T. baccata* (LT_{50}, 30 min exposure) has two peaks, one in summer and one (the higher) in winter of 51 °C (Lange 1961).

Taxus baccata is tolerant of drought (Hättenschwiler & Körner 2000). Brzeziecki & Kienast (1994) rank *T. baccata* as 2 in a 1–5 scale where 1 is very tolerant of drought. The effects of drought are seen as needles older than 2 years turning yellow from their base upwards before falling (Strouts & Winter 1994). Experiments using double saw cuts to increase hydraulic resistance of the stem in 'older male' yews (Kartusch & Richter 1984) resulted in new needles above the cuts having more xeromorphic characteristics: reduced leaf area, thicker cuticle and a decreased number of stomata per unit area. A previous study (Richter 1974) had shown that these morphological changes were related to consistent differences (of up to1.5 MPa) in water potential between the treated and control shoots with the treated shoot frequently reaching a water potential of around −2.0 MPa. Parker (1971) observed an unusual lipid layer surrounding the tonoplast of the photosynthetic cells of several conifers, including *T. baccata*, which appeared to be related to drought resistance.

Watt (1924, 1926) surmised that wind is important in determining the distribution of yew on the South Downs as indicated by the extensive wind-shaping, the general limitation of the yew-woods to the valleys, and 'from the greater and more rapid extension along sheltered slopes and to leeward of existing communities' (Watt 1926). He also suggested that the real value of junipers is not just protection from grazing but the protection provided from exposed conditions. Certainly, at Kingley Vale, Sussex, salt winds from the sea (5 km away) turn exposed yew foliage brown-red, and trees on exposed slopes lean away from the south-west, the prevailing wind direction (Williamson 1978). *Taxus baccata* is sensitive to air-borne salt spray (Lemer 2001) and immersion in salt water (Buschbom 1968), winter shoots being 100% damaged by a short immersion in 23% NaCl or 23% $CaCl_2$.

Owing to its thin bark, *T. baccata* is intolerant of fire (Hartzell 1995). 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.

VI. Structure and physiology

(A) MORPHOLOGY

Taxus baccata is slow-growing, reaching 20(−28) m with a spreading, rounded or pyramidal canopy. The trunk is frequently very fluted and asymmetrical, and often with multiple stems. Branches are long, not whorled. Twigs are green and irregularly alternate. Even 4-year-old branches have parts still with an intact epidermis under which are live cork cells rich in chloroplasts (Hejnowicz 1978). Buds are very small, bud scales dark-brown, rounded, imbricate and closely appressed to the bud. When the bud opens, the bud scales unfold and remain at the base of the growing shoot, and on older branches persist as dry brownish scales. Lateral buds develop at irregular intervals, many of which remain dormant; epicormic buds are thus frequent along the upper sides of branches or on the stem which explains why *T. baccata*, unusually for gymnosperms, can withstand pruning back to the main trunk (Elwes & Henry 1906) and can produce leafy branches from old branches and trunks, and sometimes from stools. Yew occasionally produces burrs around the epicormic buds. The largest recorded is probably that seen by Howard (1944) from the Caucasus 'measuring more than seven feet [2.1 m] in length and more than four feet [1.2 m] in depth, and weighing nearly a ton'. The bark is reddish-brown, thin, scaly with a rough and irregular outer surface due to exfoliation of the subereous layers as thin flat flakes. It is odourless and with a slightly bitter and astringent taste. The outer bark has a single periderm with 10–15 layers of phellem cells, the layers formed by alternating rows of thin- and thick-walled cells. The periderm does not have lenticels (Hejnowicz 1978). The phloem contains tangential bands of axial parenchyma with abundant calcium oxalate crystals embedded in the cell walls. Crystals of calcium oxalate are also in the phloem fibres (Hejnowicz 1978). Sieve cells are 150–200 μm in length. Di Sapio *et al.* (1997) give further details of phloem cell structure.

The wood of *T. baccata* lacks axial parenchyma (Hejnowicz 1978; Bell & Hemsley 2000) and resin canals although traumatic resin canals are formed when injured (Hejnowicz 1978). Woodpeckers (Picidae) are known to inflict damage on yew trees in Switzerland, resulting in traumatic xylem and phloem (Kučera 1972). The reddish heartwood is distinct from the pale sapwood. The early/late wood transition within each annual ring is gradual. The wood is hard, heavy and flexible, with a high density of 640 kg m^{-3} (Brzeziecki & Kienast 1994) to 700–800 kg m^{-3} (Schweingruber 1993). This is especially high for a gymnosperm, as dense as beech and even oak. The wood is described as one of the most durable of temperate trees (Eaton & Hale 1993). The tracheids have uniseriate pits and prominent spiral thickening; the latter may explain the great elasticity of yew-wood and its consequent use in bow making (Sporne 1974). The wood has a lower cellulose to lignin ratio (1.13), and an ash content (0.3%) which is 2–3 times lower than *Pseudotsuga menziesii* and *Picea abies* (Kučera 1998 cited in Lyubenova & Nedelchev 2001).

Narrow tracheid diameter makes for low permeability of gases – Eaton & Hale (1993) present data that show it is one of the least permeable softwoods ($< 18.1 \times 10^{-6}$ darcys). Not surprisingly, Redding (1971) classified yew as resistant to impregnation by creosote, requiring long treatment times and even then difficult to achieve better than 3–6 mm penetration. Retention of creosote was 336 kg m^{-3}, comparable to ash but much more than oak (56 kg m^{-3}) which was referred to as extremely resistant and virtually untreatable.

Like *Fagus sylvatica*, *T. baccata* has an extensive horizontal root system with a thick-felted mat of fine roots ramifying through the soil near the surface (Rodwell 1991). In some areas, notably on Carboniferous Limestone pavements in south-west Ireland, the roots of yew spread out over the rock surface and penetrate deeply into the fissures (Kelly 1981). On chalk, a similar situation can arise with the roots spreading over and penetrating into the surface of otherwise bare rock.

The needles are spirally attached but on lateral shoots are twisted more or less into two ranks; 1–3 (–4.5) cm long and 2–3 mm wide with (in England) a mean of 28 needles per shoot produced each year (Melzack 1979). They live for 4–8 years before falling (Bugala 1978; Szaniawski 1978). The lower epidermis and petiole have calcium oxalate crystals embedded in the cuticle. Four different long-chain esters have been isolated from the cuticular wax (Jetter *et al.* 2002). Stomata are found on the underside of leaves only, within two pale stomatiferous stripes but they are not arranged in lines within the stripes (Di Sapio *et al.* 1997). Stomata are sunken with elevated subsidiary cells. Stomatal density has been counted as 59 mm^{-2} (Di Sapio *et al.* 1997), 82–119 mm^{-2} (in 25 varieties of yew; 92 mm^{-2} in *T. baccata* proper; Dempsey & Hook 2000), and 115 mm^{-2} (Salisbury 1927). The petiole has no stomata.

Pollen grains are spherical, sometimes rounded-triangular, without air sacs and with no visible pore or furrow (Vidaković 1991). Size ranges from 22 to 30 µm (West 1962; Hejnowicz 1978; Moore *et al.* 1991).

(B) MYCORRHIZA

Taxus has only endomycorrhizas (Levisohn 1954; Strullu 1978, 1991). Harley (1959) summarized the description of Pratt (1926), and Harley & Harley (1987) cite 13 references in their checklist. Successful beneficial inoculation with *Glomus mosseae* has been achieved by Gianinazzi *et al.* (1995). Sainz *et al.* (2000) have shown that there is a significant improvement in nursery stock growth of *T. baccata* after inoculation with either *Acaulospora scrobiculata* or *Glomus deserticola*. They also showed that neither of the latter endosymbionts protect the seedlings from infection by the root pathogen *Phytophthora cinnamomi*.

(C) PERENNATION: REPRODUCTION

Taxus baccata is a long-lived phanerophyte. Old trees may show vegetative reproduction by branches touching the ground and producing adventitious roots (Suszka 1978), which can survive independently upon the demise of the main trunk. *Taxus baccata* will also sprout from the stump. Elwes & Henry (1906) record that yew never produces root suckers. Davis (1965) refers to large *T. baccata* trunks being built up of 'coalescing suckers' on steep slopes; however, Tabbush & White (1996) suggest that such new shoots match the description of Watt (1926) of the 'pioneer' seedlings or epicormic shoots fusing into one trunk. Fallen yew trees will continue to grow as long as some of the root plate is intact, with lateral branches becoming new leaders.

Taxus baccata can be propagated artificially through cuttings, seed, grafting or layering (Hartzell 1991). Experiments in Germany, where about 50% of all cuttings developed roots, have shown that clonal differences for rooting ability are high with 71.2% of the total variance explained by clone differences. No differences were found in the rooting ability between female and male clones by Schneck (1996) but Nandi *et al.* (1996) found that auxin treatment of cuttings induced higher rooting success in male trees (55%) compared to female (15%). The use of plastic tree shelters is not recommended for *T. baccata* as failures can occur owing to overheating.

(D) CHROMOSOMES

$2n = 24$ (Dark 1932; Sax & Sax 1933; Lövkvist 1963, cited in Moore 1982). One chromosome has a terminal or subterminal attachment point, one is distinctly heterobrachial, while the others are more or less isobrachial (Sax & Sax 1933). Details of the meiotic stages of *T. baccata* are given by Dark (1932). Polyploids are not reported.

(E) PHYSIOLOGICAL DATA

(i) Light

Taxus baccata is shade tolerant (Bugala 1978; Ellenberg 1988; Brzeziecki & Kienast 1994) but it also establishes and grows faster in open conditions (Watt 1926; Król

1978; Mitchell 1988; Vidaković 1991; Svenning & Magård 1999). It can survive its own formidable shade and family groups of trees are a common feature of young yew woods (Watt 1926). It also will 'flower' and fruit in heavy shade (Bugala 1978). In North America, natural seedlings develop beneath other trees but grow more rapidly and are denser in number in the open (USDA 1948).

Mitchell (1998) compared sun grown and shade grown *Taxus brevifolia* with sun grown *T. baccata*. Above a PPFD (Photosynthetic Photon Flux Density) of 400 µmol m^{-2} s^{-1}, both species had a similar maximum photosynthetic rate (4 µmol CO_2 m^{-2} s^{-1} and 3 µmol CO_2 m^{-2} s^{-1}, respectively), both indicative of shade tolerant plants. Although both are shade tolerant, Mitchell (1998) found that *T. baccata* appeared to be better adapted to grow in full sunlight.

Taxus baccata can assimilate CO_2 down to 2–3 klux (*c.* PPFD of 75 µmol m^{-2} s^{-1}) (Pisek & Rehner 1958). The light compensation point varies from 175 lux in summer to 3.2 klux in February (Pavletic & Lieth 1958). Pisek *et al.* (1969) showed that the maximum summer rate of photosynthesis at 10 klux (*c.* PPFD of 300 µmol m^{-2} s^{-1}) in *T. baccata* from the Austrian Alps is 7 mg CO_2 gDW^{-1} h^{-1} whereas the maximum winter rate is 5.5 mg CO_2 gDW^{-1} h^{-1}. The optimum temperature range (90% of maximum or greater) they found was 14–25 °C. This optimum temperature for photosynthesis is higher than in other species of conifer. Summer temperature minimum for photosynthesis is −3 to −5 °C (Pisek *et al.* 1967) and winter minimum is −8 °C. The summer temperature maximum for photosynthesis is 38–41 °C (Pisek *et al.* 1968, 1969). A review (in English) of these data is given by Pisek & Larcher (1973).

Photosynthetic ability of *T. baccata* leaves declines with age, to 50% in 7-year-old needles compared to young needles (Szaniawski 1978).

(ii) Water relations

In his comparison of *T. brevifolia* and *T. baccata* (see above), Mitchell (1998) found no difference in stomatal conductance at a PPFD of 200 µmol m^{-2} s^{-1}, but *T. baccata* showed significantly lower conductances at PPFD's of 400 and 900 µmol m^{-2} s^{-1} (stomatal conductances of 0.017 and 0.024 mol m^{-2} s^{-1} vs. 0.053 and 0.073 mol m^{-2} s^{-1} for *T. brevifolia*). He found no difference in stomatal density but there was a significantly higher number per leaf (4684 vs. 1604) as the leaf of *T. baccata* is larger.

Moir (1999) examined tree ring widths from yews at Hampton Court growing on sand and gravel and found that precipitation (particularly in the months February to July) had a positive effect on growth. Increased ring width was also positively related to late winter temperatures (January and February) and late autumn (October) temperatures, probably indicative of an extended growing season. High summer temperatures (particularly June) appeared to inhibit growth. Moir (1999) concluded that mild/wet winters combined with cool summers provide ideal growing conditions for yew, and that hot dry summers adversely affect yew growth. The yew chronology cross-matched well with those of *Pinus*, *Fagus*, *Castanea*, *Carya*, and to a lesser extent *Quercus*. In the Balkans, Lyubenova *et al.* (2001) found that 93% of ring width variation could be attributed to January–June precipitation of the current year and October–December precipitation of the previous year.

(iii) Temperature

Ring width and maximal densities of rings in northern Iran have been correlated to February and March temperatures (Parsapajouh *et al.* 1986). Optimum temperature for meiosis in pollen mother cells is between 1 °C and 10 °C (Chira 1964). Temperatures above or below this, if lasting for several days, have a negative effect on meiosis causing partial or complete sterility (Vidaković 1991).

(iv) Nutrition

Fiedler *et al.* (1986) and Allen (1989) report that, compared to other conifers, *T. baccata* leaves have a high N, P, K, Mn, Zn, B and Mo content as well as low Al, Si and Fe content. With increasing needle age, the N, P, K, Mg and Mo content decreases (Fiedler *et al.* 1986). They also found that the content of Cu, Mn, Zn, Mo, Al and Si depends on the substrate; for example on acid silicate sites, old needles have very high Mn (up to 1.5%), Zn and Al levels. Nemec (1951) reported that, in Slovakia, the genus *Taxus* has high requirements with regard to mineral nutrition particularly for K, P and Ca.

Sun grown *T. baccata* leaves had a significantly higher nitrogen content (1.89% N and 0.22 mg N cm^{-2}) compared to *T. brevifolia* leaves (1.21% N and 0.16 mg N cm^{-2}) (Mitchell 1998).

Compared to angiosperm trees (*Quercus robur*, *Fagus sylvatica*, *Castanea sativa*, *Acer pseudoplatanus* and *Sorbus aucuparia*) growing in north-west Spain, *T. baccata* branches (< 8 cm diameter plus leaves) had high levels of Cd (up to 40 p.p.m.), Zn (41 p.p.m.), and Mn (up to 3074 p.p.m.) (Núñez-Regueira *et al.* 1997).

Several authors have investigated the composition of *T. baccata* arils. Herrera (1987) found arils (with seed) from Spain were typically 764 mg fresh weight (10.9 mm length × 10.3 mm width – larger than the average, see introduction), with a dry pulp of 158.7 mg. Percentage moisture of the aril and seed together was 66.3% while Suszka (1978) found that fresh seed in Poland had 31.1% moisture, and Hegnauer (1962, cited in Bartkowiak 1978) measured the aril alone to have 80% moisture. The dry pulp consists of 0.2% lipids, 2.3% protein, 2.6% fibre, 93.5% non-structural carbohydrate and 1.4% ash (Herrera 1987). The following mineral contents were also found (in g kg^{-1}): Ca, 0.2; Mg, 0.1; P, 0.4; K, 6.0; Na, 0.2, and (in mg kg^{-1}) Fe, 25;

Mn, 1; Zn, 5; Cu, 1. Energy content has been variously measured: dry aril pulp, 3.88 kcal g^{-1} (Hulme 1997); ripe arils 5.07 kcal g^{-1}; embryo and cotyledons 8.41 kcal g^{-1} (Smal & Fairley 1980b).

(v) Other aspects

Taxus baccata is tolerant of air pollution (Mez 1963) with a high resistance to SO_2 (Białobok 1978), though concentrations higher than 50 mg m^{-3} damaged needles. Szaniawski (1978) reviewed the literature and commented that *T. baccata* is more tolerant of smoke from copper foundries and to hydrogen fluoride than *Pinus* or *Abies* species. Emissions of heavy metals in Germany have been effectively monitored using *T. baccata* needles as a bioindicator (Höllwarth 1984). Barker & Ashenden (1993) showed that acid fog treatment of pH 2.5 significantly increased *T. baccata* needle damage relative to pH 3.5–5.5.

Hättenschwiler & Körner (2000) and Hättenschwiler (2001) exposed seedlings of six major European temperate forest tree species, including *T. baccata*, to elevated levels of 500 p.p.m. CO_2 and 660 p.p.m. CO_2 in the understorey of an old-growth forest in Switzerland. Seedlings were exposed to a known quantum flux density (QFD) ranging from 0.36 to 2.16 mol m^{-2} day^{-1} (0.8% to 4.8% of full sun). Biomass production in the deep-shade tolerant species (*Fagus sylvatica* and *T. baccata*) increased by 73% and 37%, respectively, under elevated CO_2 in low light microsites but was not significantly different among CO_2 treatments in high light microsites. Thus, these two species 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. As CO_2 concentration rises, germination, recruitment and survival of these two species in deep shade conditions are likely to improve.

(F) BIOCHEMICAL DATA

All parts of the tree except the aril contain the alkaloid taxin (Vidaković 1991).

There is a very large literature on several biochemistry aspects, particularly on the anticancer properties of the taxanes. A short account is given here.

An overview of the history, chemistry, supply, biology and clinical aspects is given in Suffness (1995). Originally extracted from the bark of the Pacific yew (*T. brevifolia*), taxol (paclitaxel) can now be synthesized from a taxol congener (10-deacetylbaccatin III) which can be extracted at approximately 10 times the quantity per unit weight from the leaves of *T. baccata* and other *Taxus* species than from *T. brevifolia* bark (Denis 1988). Thus the final taxol is 'semisynthesized' from the taxane core (Nicolaou *et al*. 1996). Taxol has also been synthesized *de novo* (Nicolaou *et al*. 1996). Taxotere (docetaxel) is a semisynthetic taxane also derived from 10-deacetylbaccatin III from the needles of *T. baccata* (Vaishampayan *et al*. 1999). A very large number of taxanes and their derivatives have been isolated from yew trees including *T. baccata* (Parmar *et al*. 1999). Guéritte (2001) has reviewed recent developments in taxoid chemistry and also has given the structure of these taxoids, as have the other papers cited in this paragraph.

Vesela *et al*. (1999) found the highest concentration for all taxanes examined in *T. baccata* in Czechoslovakia to be in October and the lowest in January. Hook *et al*. (1999) examined French and Irish trees of *T. baccata* and concluded that there was not a consistent maximum annual peak of taxoids as it appeared to vary with location, variety and taxoid type. The taxane content of the needles, stems and clippings of 92 cultivars (mostly *T. baccata*) obtained from nurseries in the USA is reported by Elsohly *et al*. (1997). The taxane content of the leaves, stems and clippings in the studied cultivars ranged from 0.0135–0.1471% (w/w), 0.0055–0.0462% and 0.0121–0.1183%, respectively. 10-deacetylbaccatin III and taxol were the most abundant.

Taxol compounds are unusual in their anticancer effect in that they bind to microtubulin in the cells. By stabilizing the microtubules, mitosis is inhibited (Altmann 2001; He *et al*. 2001; Miglietta *et al*. 2002). Taxol compounds are used to treat a variety of cancers, including breast, lung and ovary carcinomas. Taxotere is particularly effective in the treatment of breast cancer (Jennewein & Croteau 2001). Both Aventis Pharma (Taxotere) (Aventis Pharma Ltd. 2002) and Bristol-Myers Squibb (Taxol) (Mead Johnson Oncology Products 2000) produce very well informed leaflets for the practitioner and the patient.

Tissue culture of *Taxus* species is now an alternative source for taxoid production (e.g. Jaziri *et al*. 1996). However, cultures based on *T. baccata* varieties generally showed weak biological activity in the tubulin test compared to *T. media* varieties (Parc *et al*. 2002). Tissue culture of *T. baccata* is being used in an attempt to increase taxane production either by purification of important synthetic pathway enzymes, e.g. geranylgeranyl diphosphate synthase (Laskaris *et al*. 2000), or by isolation of biosynthetic genes (Walker & Croteau 2001).

The seeds and foliage of *T. baccata* are rich in toxic alkaloids (Miller 1980), all parts being poisonous apart from the aril. They contain taxin(e), a complex mixture of alkaloids that is rapidly absorbed from the digestive tract and interferes with the action of the heart (Cooper & Johnson 1984). All parts apart from the arils contain a cyanogenic glycoside–taxiphyllin (Cooper & Johnson 1984; Barnea *et al*. 1993), but the poisonous properties of yew are primarily due to the alkaloid taxine (Clarke *et al*. 1981). A review of the toxic properties of these alkaloids in *T. baccata* has been given by Wilson *et al*. (2001), where they concluded that the chief action of the taxines in humans and other mammals is on cardiac myocytes with resultant heart failure and death. Shanker *et al*. (2002) have also implicated toxic effects involving the liver.

Erdemoglu & Sener (2001) found that ethanol extracts of heartwood of yew collected in Turkey exhibited a significant activity against some gram-negative bacteria but not against gram-positive bacteria. It also showed antifungal properties against five species of fungi of medical importance.

Seed oils and seed storage proteins of *T. baccata* have been analysed and described by Wolff *et al*. (1996) and Allona *et al*. (1994), respectively.

VII. Phenology

'Flower' buds form in the second half of the summer. They open the following spring (February/March in western Europe and into April in the east and north) and are thus one of the earliest British trees to flower with *Ulmus* and *Corylus*. In western Europe, Richard (1985) found that yew strobili open 100 days after mean daily temperatures fall below 10 °C in autumn. Fertilization occurs 6–8 weeks after pollination (Hejnowicz 1978; Pennell & Bell 1986). 'Fruits' ripen and seeds are shed primarily in August to October in mainland Europe and north-eastern USA (USDA 1974; Bugala 1978) extending into November in Russia (Sukachev 1928; Wyman 1947) and southern Ireland (Smal & Fairley 1980b).

VIII. Reproductive and seed characters

(A) REPRODUCTIVE BIOLOGY

Pollination anemophilous although honeybees have been observed collecting pollen. When fully mature, the nucellus secretes a sugary fluid which accumulates as a drop at the orifice of the micropyle (Hejnowicz 1978). This pollination drop serves to trap wind-borne pollen. Subsequent reabsorption of the drop draws the pollen down to the surface of the nucellus where it germinates (Ruguzov *et al*. 1992). The male gametes are non-motile. Seeds mature within 1 year.

Svenning & Magård (1999) observed that production of reproductive organs increased strongly with tree diameter in Denmark and also with canopy openness. In adult trees, 62% of female trees and 29% of males produced reproductive organs in the open, while in shade, 19% of females and 10% of males produced them. Watt (1926) noted that yew does not produce 'fruit' under a closed beech canopy.

Taxus baccata is dioecious. Sex ratios have been found to vary from 44% female in Kingley Vale, Sussex (Williamson 1978), and 47.8% female on an island in Loch Lomond, Scotland (Pilkington *et al*. 1994), to 67% female in the Caucasus Mountains (Pridnya 1984) and 70% female in the Sierra Nevada Mountains of Spain (García *et al*. 2000). Change in sex of an individual tree is possible. The Irish Yew (*T. baccata* Fastigiata) is derived from cuttings from a female tree transplanted into Florence Court, Co. Fermanagh, Ireland; in 1927, however, male Irish yews were discovered in Sussex (Hartzell 1991). Bowman (1837) remarked on a 60-year-old tree in Shropshire (almost 7 m in girth) which had one female branch on an otherwise male tree. As in this case, such examples are normally of a single branch carrying reproductive structures of a different sex from the rest of the tree. However, Elwes & Henry (1906) reported on a tree near Stuttgart that bore male and female structures irregularly over the whole tree, each on separate twigs. Very occasionally both sexes may be found on the same branch. In the Caucasus Mountains, Pridnya (1984) found 1% of trees to be bisexual.

Megaspore development is discussed by Cecchi *et al*. (1991). Seeds are filled with an oily white fat-rich endosperm (Suszka 1978). When the aril is ripe, the embryo is immature and minute, barely 1.2–1.5 mm long in a seed 5 mm long (Heit 1969; Hejnowicz 1978).

(B) HYBRIDS

The Japanese yew, *T. cuspidata* Siebold & Zuccarini, hybridizes freely with *T. baccata* to produce a variable hybrid *Taxus* × *media* Rehder. The cross was first made by T.D. Hatfield at Hunnewell Pinetum, Massachusetts, around 1900. A chemotaxonomical study of the genus, based on the concentration of six neutral taxanes in its needles, showed some separation of the species *T. baccata*, *T. cuspidata* and *T.* × *media*, but did not indicate an intermediate position for *T.* × *media*, but rather a heterosis effect for the hybrid (van Rozendaal *et al*. 1999).

(C) SEED PRODUCTION AND DISPERSAL

Seed production starts at 30–35 years old (USDA 1948; Vidaković 1991) in single trees and open stands, and at 70–120 years old in dense eastern European stands (Brzeziecki & Kienast 1994; Lyubenova & Nedelchev 2001). In Britain, prolific 'fruit' is produced in most years (Fuller 1982; Snow & Snow 1988) although in less optimal eastern European areas good seed crops occur every 2–3 years (Brzeziecki & Kienast 1994). In the Killarney yew woodland, the number of part and complete 'fruits' falling was estimated at 2.6 and 6.2 million ha^{-1} in the two years, respectively, beginning autumn 1975 (Smal & Fairley 1980b). This corresponds to 96.4 and 308.3 kg ha^{-1} with a total energy content of 0.56 and 1.87 M kcal ha^{-1}, respectively. The authors estimated that birds removed 35.1% and 43.3% of the weight of arils, in each of the two years. Smal & Fairley (1980b) should be consulted for a breakdown of these figures into different 'fruit' categories.

The average fresh weight of *T. baccata* seeds has been reported as 57 mg ($n = 20$), Lichfield, Staffordshire; 64 mg ($n = 50$), Keele University, Staffordshire; 64 mg ($n = 140$), Box Hill, Surrey; 69.9 mg, Durham (Hulme & Borelli 1999). Melzack & Watts (1982a) found the average seed weight from six stations throughout England to be 56.5 mg. They also found that seeds from the south and west of Britain, with a more oceanic climate, were significantly heavier than seeds from drier more central and eastern sources. Thus weights ranged from 69.5 ± 7.3 mg (SD, $n = 30$) for Butser Hill, south Sussex to 44.9 ± 6.6 mg ($n = 30$) from Overton Hall, Derbyshire. Also there was some evidence (but not significant) that seed weight increased from the south at Butser Hill to the north at Yew Barrow, Cumbria (60.7 ± 7.1 mg, $n = 30$).

A similar trend in average seed weights appears across continental Europe, from the oceanic west (77 mg in the Netherlands (Detz & Kemperman 1968) and 69.9 mg on the Iberian peninsula (Herrera 1987)) to the continental climate of Poland (43–59 mg; Suszka 1978; Brzeziecki & Kienast 1994). This raises the question of why seed in Britain is, on average, lighter than in western continental Europe. Seed from *T. baccata* grown in the USA range from 59 to 76 mg (Heit 1969; USDA 1974).

The main agent of seed dispersal is birds which consume the aril and seed, and disgorge the seeds or pass them in their faeces (Bartkowiak 1978; Fuller 1982; Snow & Snow 1988; Hulme 1996). Most birds excrete the seed although Ridley (1930, cited in Bartkowiak 1978) found that the mistle thrush (*Turdus viscivorus*) eats large quantities of the 'fruit' and sometime later they 'spit out a red mass of partly digested pulp with brown yew seeds'. Up to 23 seeds were found in one spit.

Bartkowiak (1978) proposed that the birds that eat yew 'fruit' are limited to those that can swallow such a big seed, and indeed the 'fruit' is eaten primarily by the thrushes (especially the blackbird *Turdus merula*, mistle thrush *T. viscivorus*, song thrush *T. philomelos*, fieldfare *T. pilaris*, redwing *T. iliacus* and ring ouzel *T. torquatus*), starling (*Sturnus vulgaris*), waxwing (*Bombycilla garrulus*) and jay (*Garrulus glandarius*) (Creutz 1952; Bartkowiak 1970, 1978; Snow & Snow 1988; García *et al*. 2000). However, Bartkowiak (1970) also reports that in the Kórnik Arboretum, Poland, seedlings are found at the root collar of trees (and from cracks in trunks and even walls) resulting from seeds stored up to 50–70 m away from the parent tree by the nuthatch (*Sitta europaea*).

Vogler (1904) attributed the abundance of yew on cliffs in Switzerland (especially on rock ledges used as bird roosts) partly to the seeds spread by birds that can travel long distances. This leads to the occurrence of isolated yews on cliffs remote from other yew populations. This interpretation may not always be true because isolated trees can be remnants of previously extensive woodland.

In Oxford, Barnea *et al*. (1993) found that blackbirds and starlings spent a comparatively short-time visiting yew trees (an average of 1.3 ± 0.6 min (SE, $n = 12$)) and ate 4.3 ± 2.8 ($n = 15$) 'fruits' on each visit, compared to visits to hawthorn of 3.0 ± 2.4 min ($n = 26$) and a meal size of 5.7 ± 4.4 ($n = 34$) 'fruits'. Unlike the other fruits tested (holly, ivy and hawthorn) which contained cyanogenic glycosides only in the fleshy part of the fruit, yew was found to have these only in the seed coat and not the aril (no species tested had them in the seed itself). Poisons in the fleshy parts are often explained (e.g. Sorensen 1984) as an adaptation to prevent birds consuming too many seeds at once, which, with the short visit time, will ensure better seed dispersal as only few seeds will be deposited at one site at one time. However, visit time and meal size are smaller for yew than hawthorn, despite the lack of poisons in the aril, so other factors must limit feeding apart from toxins in the food. It seems rather that the toxins in the seedcoat are to prevent eating of the seed itself by wood pigeons and crows (see section IX). Small meal size may also explain why so many yew seeds are left on the tree to fall beneath the canopy.

Bartkowiak (1978) in reviewing the European literature found a number of records of squirrels dispersing yew seeds by eating the aril and seed, and regurgitating the seed. In the Andalusian highlands, Hulme (1997) found that two species of ant, *Cataglyphis velox* (Sants.) and *Aphaenogaster iberica* (Em.), were responsible for the removal of a few percent of seeds from traps on the ground: they consumed the aril but not the seed and so contributed to small-scale redistribution of seeds. Seeds taken from the ground by rodents are hoarded and may germinate. However, Hulme & Borelli (1999) found that shrubs act as sinks for the accumulation of bird-dispersed seeds (preferential deposition), provide a suitable microclimate, and protection from large herbivores but also harbour high rodent pressure on seeds (indeed a large number of empty seed cases are common under yew in the UK).

(D) VIABILITY OF SEEDS: GERMINATION

Seed viability can be high, approaching 100% (USDA 1948) but germination rates of 50–70% are more normal (USDA 1974) although Heit (1969) achieved 95% germination over a 3-year period. The viability of *T. baccata* seeds can be maintained artificially for up to 4 years by storing in damp sand or peat at 'low temperatures' (USDA 1974). Yew seed can also be stored for 5–6 years by drying at room temp to *c.* 10% moisture content and then storing at 1–2 °C (Heit 1968, 1969) or even lower at −3 °C (Suszka 1985).

Yew seed rarely germinates the first year. Most germination is in the second or even the third year (Melzack 1979; Melzack & Watts 1982a), but seed can remain viable for up to 4 years (Suszka 1978).

The strong but variable dormancy is attributed to the small immature embryo present when the seed is mature. Certainly, the seed coat is not impermeable to water, artificial scarification with sulphuric acid does not enhance germination, and neither alternating temperatures nor short periods (20–30 days) of moist prechilling increase germination (although Williamson (1978) suggests that frost is necessary to break down the seed case and overcome dormancy). Various authors (e.g. Heit 1968 and ISTA 1966) have stated that

2–9 months of pre-chilling at low temperatures (typically 3–5 °C) is needed prior to germination. Suszka (1985), however, maintained that a cold-only stratification by itself does not appreciably promote germination even after 4 years of treatment, though the seeds remain viable. Indeed, Suszka (1985), and a number of researchers before him (e.g. Mitiska 1954; Heit 1968, 1969), found that a warm moist period (e.g. 15–20 °C for 90–210 days) before chilling (e.g. 60–120 days at 2–5 °C) is essential. Suszka (1985) found using Polish seed that under such treatment the small embryos almost doubled in length and changed from white to green during the initial warm phase. Suszka (1985) also recommends that a fluctuating temperature in the pre-chilling warm period is essential for high subsequent germination. Such a treatment appears to simulate seed in the soil passing through a summer and winter, thus explaining why most seeds germinate in the second year.

Page-Degivry & Garello (1973), working with *T. baccata* Fastigiata, found that embryo dormancy was eliminated when cultured *in vitro* in a liquid nutrient medium. They found no morphological development; rather germination was produced by a leaching of water-soluble germination inhibitors. However, distilled water alone did not remove dormancy; this was achieved only when sucrose was added to the medium and was further enhanced by the addition of Ca or K ions.

Natural germination of *T. baccata* is improved if the seeds have passed through the digestive tract of birds (USDA 1948; Suszka 1978). Indeed, Williamson (1978) planted 600 seeds in mouse-proof cages at Kingley Vale, Sussex, and obtained just 2% germination. However, treatments with hot water or sulphuric acid to break down the seed coat do not result in higher germination (Suszka 1978). Heit (1969) surmised that it was not the bird's digestive juices that helped germination, but the removal of the aril which is beneficial: he found that in pot trials there was less decay of seeds if the aril was removed, resulting in 4–6% germination with arils compared to 27–28% without.

Once dormancy is broken, a temperature range of 13–16 °C has been found optimal for maximum germination, which gives higher germination than 20 °C (Suszka 1978). However, alternating temperatures speed germination: ideal night/day temperatures have been variously recommended as 20/30 °C (ISTA 1966), 10/20 °C in Belgium (Devillez 1978) and 3/20 °C for Polish seeds (Suszka 1978). Germination is not stimulated by light. Vogler (1904) suggests that yew can germinate and grow on fully exposed bare rock as long as water is not limiting, which explains why yew is frequently found in cliff environments in Europe.

Melzack & Watts (1982a) found that seeds from the oceanic west of England were larger than those from the drier east. However, in laboratory trials there was no significant relationship between seed weight and germination rate or seed weight and seedling weight two months after germination. The only suggestion of the effect of seed weight is that the lightest seed from Overton Hall, Derbyshire (averaging 44.9 mg), produced the most erratic germination pattern over time with two peaks of germination.

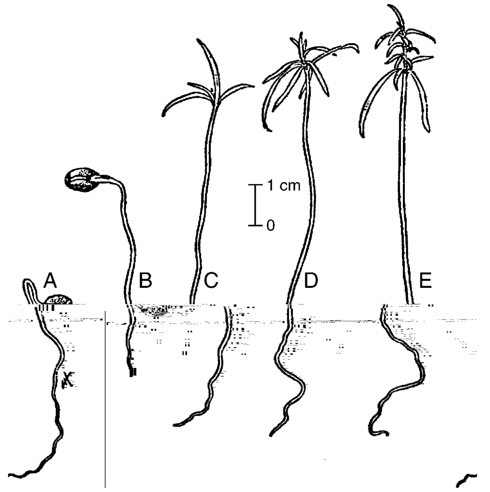


Fig. 4 Germination and seedling development of *Taxus baccata* (a) at 1 day, (b) 8 days, (c) 12 days, (d) 22 days, and (e) 39 days. Reproduced with permission from USDA (1948).

(E) SEEDLING MORPHOLOGY

Germination is epigeal. Seeds have two cotyledons with rounded apices, up to 2 cm long with stomata bands above (Vidaković 1991). Three to four opposite pairs of leaves are produced above the cotyledons, followed on vigorous plants by a few alternate leaves around the terminal bud. By end of first season, the seedling is usually 2–8 cm high. A strong tap root with a few laterals develops in the first year (Elwes & Henry 1906). Subsequent growth for the next 4–5 years is slow, often less than 2.5 cm annually. Seedling development is shown in Fig. 4.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

(i) Mammalia

Despite popular opinion and the views of early writers (e.g. Tansley & Rankin 1911), yew is not invariably toxic to larger mammals (Clarke *et al.* 1981). Herbivory of leaves, twigs and bark is recorded by a range of mammals. The trees are generally susceptible to browsing by roe deer (*Capreolus capreolus*) (Tittensor 1980) and in south-west Finland can be thus 'jeopardized' (Klötzli 1965). In Norway, roe deer grazing on yew in winter was highest when bilberry (*Vaccinium myrtillus*) was in low density or snow covered. Observations suggest that roe deer may be the main factor affecting yew survival in areas where other preferred feeding plants are not available (Mysterud & Ostbye 1995). Dickson (1994) records fallow deer (*Dama vulgaris*) feeding on yew in Scotland but Dietz *et al*. (1994) record yew poisoning of fallow deer in Denmark. Deer have also been noted as causing a persistent problem by browsing on *Taxus* species in nurseries in north-east USA (Lemieux *et al*. 2000).

Hares and rabbits appear to browse *T. baccata* regularly without harm (Lowe 1897; Watt 1926; Williamson 1978). Grey squirrels (*Sciurus carolinensis*) will also browse on bark and twigs (Tittensor 1980) and eat arils (although the seed are later regurgitated; Bartkowiak 1978). Williamson (1978) comments on seeing foxes (*Vulpes vulpes*) and badgers (*Meles meles*) eating arils from the ground in Kingley Vale, Sussex, the former probably regurgitating the seed, the badger crunching the whole 'fruit' up. Bartkowiak (1978) records large quantities of seeds and undigested arils in badger faeces. He also mentions martens (*Martes martes*) eating *T. baccata* 'fruit' in the Caucasus.

Wild Barbary macaques (*Macaca sylvanus*) in Morocco forage for *T. baccata* 'fruit' (Mehlman 1988).

Small mammals also play a part in the herbivory of yew, especially of the seeds (Tittensor 1980; Hulme & Borelli 1999). Rates of yew seed predation may be very high particularly during the fruiting period of yew when it is the main diet of the rodents (> 60% of seed fall predated in Co. Durham; Hulme 1996). Yew woods support higher densities of rodents (principally wood mouse *Apodemus sylvaticus* and bank vole *Clethrionomys glareolus*) than comparable deciduous woodlands (Smal & Fairley 1980a). Watt (1924, 1926) and Williamson (1978) point out that although plenty of seeds were found in gaps between and under yews on the Sussex Downs, the vast majority had been opened and eaten by small mammals (or birds, presumed to be tits). In Durham woodlands, Hulme & Borelli (1999) found that rodents foraged more beneath the cover of shrubs (*c*. 60% removal of seeds and 'fruit') than in open areas (38% removal). They identified *Apodemus sylvaticus* and *Clethrionomys glareolus* as being principal seed consumers using selective exclosures. Unidentified vertebrate seed predators (probably birds, rabbits and/or squirrels) also appeared to be significant seed removers in three of the five woodlands examined. Rates of removal differed among the three tree species studied, increasing in the order *Fraxinus excelsior* < *T. baccata* < *Ulmus glabra*, but were not related to seed mass or seed density. The larger seeds of yew benefited little from seed burial whereas, by comparison, encounter of the smaller *Ulmus* seeds fell by almost two-thirds. Hulme & Borelli conclude that the opportunity to escape seed predation via burial or reduced seed density is limited, and that while seed predators may influence regeneration of small-seeded *Ulmus*, it probably plays a lesser role in the dynamics of *T. baccata* and *Fraxinus*.

A similar study done by Hulme (1997) in the Andalusian highlands, south-east Spain showed losses of 87% of seeds over three day periods. Rodents, primarily *Apodemus sylvaticus*, were the main post-dispersal removers of 73% of seeds. A greater proportion of bare seed (56.8%) was removed compared to intact 'fruit' (aril and seed) (49.5%), and indeed on a 'number of occasions' rodents removed the toxic seeds and left the empty energy-rich arils behind.

Domestic animals such as goats and sheep are recorded as grazing on quantities of yew with impunity in Britain (Lowe 1897; Watt 1926; Williamson 1978; Oliver 1998) yet in only small amounts in Finland (Björkman 1958; Haeggström 1990). Indeed, yew has been directly implicated in the death of lambs in the Netherlands (Smit 1992).

Cattle and especially horses can suffer quick and fatal effects from eating yew twigs or bark (Lowe 1897; Watt 1926; Knowles 1949; Williamson 1978; Kite *et al*. 2000) and will therefore produce comparatively little browsing damage. Cattle have been observed by Haeggström (1990) not to eat *T. baccata* in wooded meadows in south-west Finland. However, yew has been used as an animal fodder in continental Europe (Williamson 1978) and in Asia (USDA 1948), and cattle, sheep (Lowe 1897) and horses (Lowe 1897; Elwes & Henry 1906; Stählin 1944 cited in Haeggström 1990) appear to build an immunity to yew if regularly fed small quantities. In the mountains of Hanover and Hesse in Germany the peasants fed their cattle with branches of yew during the winter, beginning with small quantities and gradually increasing the amount (Williamson 1978). Small quantities and habitual access seems to be the key because there are many records of cattle freely browsing in pastures with yews (but with plenty of other fodder available) which suffer no ill-effects (Lowe 1897). Animals let into fields with yew in winter have been recorded as dying presumably because yew was the only green food readily available. Access to cut branches has led to many domestic animal deaths. Foliage is reputed to be even more poisonous when wilted or dried (Elwes & Henry 1906; Williamson 1978) but according to Cooper & Johnson (1984) they are 'as toxic as the fresh plant'.

The lethal dose of *T. baccata* leaves is given by Völker 1950 (cited in Clarke *et al*. 1981) as 100–250 g for sheep, 500 g for cattle, 100–200 g for horses and pigs, and 30 g for a dog. Cornevin (1892, cited in Clarke *et al*. 1981) gives oral lethal doses (in grams of leaves per kg of animal) as: donkey and mule, 1.6; horse, 2; pigs, 3; domestic dog, 8; sheep and cattle, 10; goat, 12; rabbit, 20. The greater resistance of the ruminant is probably due to the dilution of the ingested yew with the contents of the rumen (Clarke *et al*. 1981). Panter *et al*. (1993) found an estimated dose of 0.36–0.70 g kg^{-1} of *T. baccata* clippings killed 35 cattle in western USA; this is much less than the 10 g kg^{-1} quoted above, but was a one-off exposure to wilted foliage.

Yew is poisonous to humans, causing heart failure (Clarke *et al*. 1981; Von der Werth & Murphy 1994; Willaert *et al*. 2002). Wine from hip-flasks made of yew wood was said by Pliny to poison travellers (Woods & Calnan 1976) and 'miliary eruptions' were reported from sleeping under the tree (Piffard 1881). Various authors report skin irritation and dermatitis caused by yew wood (Senear 1933; Long 1938; Wahl *et al*. 1992). Krenzelok *et al*. (1998) investigated 11 197 records of yew poisoning (from all *Taxus* species) in humans (96.4% in children less than 12 years old) and found no deaths. Van Ingen *et al*. (1992) reported that to their knowledge only 10 authenticated cases of fatal human poisoning by *T. baccata* have been recorded in the scientific literature in the previous 31 years, and these were all deliberate. Fifty to one hundred grams of chopped leaves is considered fatal to adults. However, adults and children of the Upper Valley of the Serchio River of Central Italy, who have a traditional diet of wild collected food, regularly eat *T. baccata* arils as a snack but often with the seeds as well (which Lowe (1897) says are almond flavoured). Pieroni (1999) suggests that the seeds are voided before they can be broken down to liberate the toxic alkaloids.

(ii) Aves

Many birds are known from yew woodland (see Williamson & Williamson 1973; Batten 1976; Williamson 1978). Snow & Snow (1988) record 18 species of birds, one third of them in the thrush family, that eat yew arils. Song thrushes (*Turdus philomelos*) and mistle thrushes (*T. viscivorus*) are the main seed takers in southern England (Hartley 1954; Williamson 1978). In autumn and winter large groups of thrushes feed on yew arils. In late summer, flocks of mistle thrushes descend on some yews and defend the aril crop which may not be eaten until late in winter (Fuller 1982). In October large flocks of redwings (*Turdus musicus*) and fieldfares (*T. pilaris*) join the thrushes until mid winter when aril stocks are depleted (Tittensor 1980). Williamson (1978) records seeing fieldfares remove up to 30 'fruits' at one time. After mid winter, blackbirds (*Turdus merula*) are the commonest thrushes. Arils are also taken by ring ouzel (*T. torquatus*), robin (*Erithacus rubecula*), blackcap (*Sylvia atricapilla*), starling (*Sturnus vulgaris*), nuthatch (*Sitta europaea*) and pheasant (*Phasianus colchicus*) (Heymer 1966; Bartkowiak 1978; Bugala 1978; Tittensor 1980; Barnea *et al*. 1993; García *et al*. 2000). Starlings eat 'fruit' in Britain and Saxony (Heymer 1966) but do not seem to in eastern Europe (Hungary, Slovakia) (Szijj 1957; Havlin & Folk 1965). In the Andalusian highlands, Hulme (1997) found that most seeds were taken from the ground (and eaten) by small rodents but approximately an extra 14% of seeds were removed when animals larger than rodents had access; this was attributed in part to birds, particularly chaffinches (*Fringilla coelebs*).

The greenfinch (*Carduelis chloris*) is the main seed predator, but seeds are also eaten by great tit (*Parus major*), bullfinch (*Pyrrhula pyrrhula*), hawfinch (*Coccothraustes coccothraustes*), nuthatch, green woodpecker (*Picus viridis*) and great spotted woodpecker (*Dendrocopos major*), and occasionally by blue tit (*Parus caeruleus*) and marsh tit (*P. palustris*) (Tittensor 1980; Snow & Snow 1988). Greenfinches, however, undoubtedly destroy a small fraction of the yew crop compared to that taken by the main seed dispersers (Snow & Snow 1988). Greenfinches mandibulate the 'fruit' until the aril falls, then strip off the brown seed coat (which contains cyanogenic glycosides; Barnea et al. 1993) before eating the rest of the seed. Barnea et al. (1993) therefore suggest that the poison is concentrated in the seed coat which explains why woodpigeon (*Columba palumbus*) and some of the larger crows (which grind the whole seed in the crop) do not eat the 'fruit'. Tits on the whole hold the seeds in their feet and hammer them open with their beak. Nuthatch and woodpeckers take the seed to a neighbouring tree, wedge it in a crack and open it. Nuthatches rub the aril off on the tree bark before wedging the seed into the bark. Chaffinches feed on the fragments of endosperms dropped by greenfinches (Snow & Snow 1988).

Lowe (1897) states that birds of all kinds are poisoned by eating yew leaves. Pheasants are noted as being prone to this (Tegetmeier 1896; Jordan 1964) and Williamson (1978) records that pheasants around Kingley Vale, Sussex, that live their lives within the yew trees, tend to be smaller than average and 'are not particularly tasty to eat'. Poisoning by yew leaves is known in domestic poultry (Orr 1952).

(iii) Reptilia

Young individuals of two Mediterranean tortoises (*Testudo hermanni boettgeri* and *T. marginata*) have died after ingesting dried yew branches (Wiechert *et al*. 2000).

(iv) Acarina

The yew big bud mite (*Cecidophyopsis psilaspis* Nalepa: Eriophyidae) is considered a serious pest of yew in northern and central Europe. Feeding the mites results in abnormal elongation and swelling of bud scales, leading to extensive and chronic bud mortality throughout the canopy and an irregular branching pattern, producing an asymmetrical crown (Duncan *et al*. 1997). Skorupski & Luxton (1998) list 199 species of mesostigmatid mites from 19 Orders sampled from *T. baccata* in England and Wales. These are mostly free-living predators although many ectoparasitic forms are known and some may consume carrion or microbial tissue. It is unlikely that any of the species are strictly confined to *T. baccata*. There is a distinct difference in species associated with 'solitary yews' (39 species found solely within the environment of solitary yews) and those in stands ('forest yews', 25 species of mites). The most frequently represented Orders were Parasitidae, Laelapidae and Zerconidae. The most widespread species were *Pergamasus crassipes*, *Proctolaelaps pygmaeus*, *Veigaia nemorensis* and *V. planicola*. The most frequent species (appearing in > 20% of samples) were

Veigaia nemorensis, *V. planicola*, *Uropoda minima*, *Paragamasus lapponicus*, *Proctolaelaps pygmaeus*, and *Cosmolaelaps claviger*.

False spider mite *Pentamerismus taxi* (Haller) (Tenuipalpidae) has been found at the base of yew needles, being originally described from yews in Switzerland (and also recorded on the southern coast of the Crimea, see Siwecki 1978); it has also been reported from *T. baccata* in California (Pritchard & Baker 1951). Also, *P. morishitai* n. sp. has been reported on *T. baccata* in California (Pritchard & Baker 1951). *Epitrimerus gemmicola* Nalepa (Eriophyidae) has been recorded on yew by Kapuściński (1947). *Oligonychus ununguis* (Jacobi) (Tetranychidae) has also been recorded from *T. baccata* (Phytophagous Insect Database).

(v) Insecta

Insects records for *T. baccata* are shown in Table 2. Daniewski *et al*. (1998) comments on the wood not being readily attacked by woodworm, and the needles by very few insects. They attribute this to the very strong antifeedant effect exhibited by the storage pests *Tribolium confusum*, *Trogoderma granarium* and *Sitophilus granarius* to 10-deacetylbaccatin III and V from *T. baccata*.

The scale insect *Parthenolecanium pomeranicum* is damaging to the foliage, and the excreted honeydew is colonized by sooty moulds (Strouts & Winter 1994). Dennis (1964) mentioned chemical control of yew scale (*Eulecanium pomeranicum*) which parasitizes yew growing in hedges. Although many species of the Miridae (Homoptera) have been recorded on conifers, none has so far been reported on any *Taxus* species (Lattin 1998).

Larvae of the fruit tree tortrix *Ditula angustiorana* and of *Hedya pruniana*, which can girdle and kill individual shoots (the last normally found on *Prunus* spp. and other Rosaceous trees), were found on yew in Kent (Ferguson 1995).

The yellow gall midge *Taxomyia taxi* causes the artichoke gall, a formation of dense needle clusters; widespread, probably wherever yew grows in Britain. The galls persist for several years (Redfern 1975; Strouts & Winter 1994). It can inhibit shoot growth and weaken trees, and has been described by Skuhravá (1965, cited in Siwecki 1978) as 'the most dangerous parasite of *T. baccata* in Europe'.

The black vine weevil *Otiorhynchus sulcatus* is widespread in western Europe (Kapuściński 1947; Strouts & Winter 1994; Pehl & Wulf 2002). It girdles stems and thus damages buds, young shoots and leaves; larvae also eat bark from yew roots. Doss *et al*. (1997) record that taxoids from *T. baccata* act as pyrethroid insecticide synergists against *O. sulcatus*. *Taxus baccata* releases volatile compounds that attract the weevil (van Tol *et al*. 2000) – in dual-choice olfactometer experiments, chambers containing yew sprigs attracted 88% of released weevils ($n = 40$). Sapwood of yew has been found in culture experiments to be susceptible to attack by larvae of the house longhorned beetle (*Hylotrupes bajulus* L., Coleoptera: Cerambycidae) and death watch beetle (*Anobium punctatum* Deg., Coleoptera: Anobiidae) by Dominik (1965, cited in Siwecki 1978).

(B) PLANT PARASITES AND EPIPHYTES

Caruso *et al*. (2000a,b) isolated six genera of actinomycetes primarily (and unusually) from inside fresh wood samples of *T. baccata* grown in central-northern Italy: *Actinomadura*, *Actinoplanes*, *Kitasatospora*, *Micromonospora*, *Nocardioforme* and *Streptomyces*. Smith (1942) noted the bacterial swelling caused by *Agrobacterium tumefaciens* E.F. Smith & Town. on yew roots.

Table 3 lists the fungi and Myxomycota directly associated with *T. baccata*. Nomenclature follows the British Mycological Society Fungal Records Database (BMSFRD; see Table 3). The BMSFRD includes 258 species of fungi and slime moulds recorded on *T. baccata* itself or on soil beneath, compared to 2200+ species for *Fagus* and *Quercus*. A number of authors (e.g. Pehl & Wulf 2002) report that *T. baccata* is affected by few serious fungal diseases.

Of the slime moulds (Myxomycota), *Licea perexigua* (Liceales) is recorded as being particularly associated with the bark of *Taxus* and *Juniperus* spp.

(i) Mastigomycotina

Phytophthora cinnamomi Rands (Oomycota, Pythiales) causes damping off in seedlings (Hepting 1971).

(ii) Zygomycotina

A *Mucor* sp. (Mucorales) has been recorded from inside wood, twigs and leaves samples of *T. baccata* in central-northern Italy (Caruso *et al*. 2000a).

(iii) Ascomycotina

Lewandowski *et al*. (1995) report that poor natural regeneration in Poland is due to a hostile microbiological soil environment including the pathogenic fungi *Nectria radicicola* Gerlach & Nilsson (Hypocreales) that kills *T. baccata* seedlings. Peace (1962) regarded *Dothiora taxicola* as the most dangerous pathogen affecting needles and shoots.

(iv) Basidiomycotina

The most common decay fungus of heartwood is 'chicken of the woods', *Laetiporus sulphureus* (Strouts & Winter 1994). *Suillus tridentinus* is common beneath yew trees. Heartwood of yew is not attacked by the dry rot fungus, *Serpula lacrymans* (Wulfren) J. Schröt (Boletales) (Eaton & Hale 1993).

Table 2 Insects recorded from *Taxus baccata* in Britain and continental Europe

Species classification	Source	Ecological notes
HEMIPTERA		
Coccidae		
Aonidiella taxus Leonardi	Johnson & Lyon (1991)	Pest of leaves on the Iberian peninsula
Chloropulvinaria floccifera (Westwood)	PIDB*	Recorded in Holland and Italy; introduced to Britain: adult and larval feeding from [illegible]
[= *Pulvinaria floccifera* (Westwood)]	Kapuściński (1947)	

Table 3 Fungi and slime moulds directly associated with *Taxus baccata*. Data taken from (1) the British Mycological Society Fungal Records Database (BMSFRD; http://194.131.255.3/bmspages/index.htm), (2) European data from de Vries & Kuyper (1990), (3) Caruso *et al.* (2000a), (4) Strobel & Hess (1997), (5) Ridley (1994), (6) Lewandowski *et al.* (1995), (7) Hepting (1971), (8) Kapuściński (1947), (9) Peace (1962), (10) Siwecki (1978) and (11) Strobel *et al.* (1996)

FUNGI		
Mastigomycotina		
Phytophthora cinnamomi Rands (Oomycota, Pythiales)	Damping off	7
Zygomycotina		
Mucor Fresen. sp. (Mucorales)	Wood/twigs/leaves	3
Ascomycotina		
Anthostomella formosa Kirschst. var. *taxi* (Grove) S.M. Francis (Xylariales)	Dead leaves/twigs	1
Bisporella citrina (Batsch) Korf & S.E. Carp. (Leotiales)	Dead wood	1
Botryosphaeria ribis Grossenb. & Duggar (Dothideales)	Leaves/shoots	7, 8, 9
Buellia punctata (Hoffm.) A. Massal. (Lecanorales)	Bark	1
Chaenothecopsis caespitosa (W. Phillips) D. Hawksw. (Caliciales)	Wood	1
Chaetomium Kunze sp. (Sordariales)	Saprophyte	5
Diaporthe occulta (Fuckel) Nitschke (Diaporthales)	Leaves/shoots	7, 8, 9
Dothiora taxicola (Peck) M.E. Barr [= *Sphaerulina taxi* (Cke) Mass] (Dothideales)	Leaves	1
Farlowiella carmichaeliana (Berk.) Sacc. (Dothideales)	Dead wood	1
Guignardia philoprina (Berk. & M.A. Curtis) Aa (Dothideales)	Dead leaves	1
Hamatocanthoscypha laricionis (Velen.) Svrcek (Leotiales)	Leaves	1
Hyaloscypha hyalina (Pers.) Boud. (Leotiales)	Wood	2
Kretzschmaria deusta (Hoffm.) P.M.D. Martin (Xylariales)	Dead wood	1
Lophodermium abietis Rostr. (Rhytismatales)	Leaves/shoots	7, 8, 9
Nectria cinnabarina (Tode) Fr. (Hypocreales)	Wood	2
Nectria coccinea (Pers.) Fr. (Hypocreales)	Wood	2
Nectria fuckeliana C. Booth (Hypocreales)	Damping off	6
Nectria radicicola Gerlach & Nilsson (Hypocreales)	Seedlings	6
Trichomerium grandisporum Speg. (Dothideales)	Leaves	1
Xylaria hypoxylon (L.) Grev. (Xylariales)	Dead wood	1
Basidiomycotina		
Amylostereum laevigatum (Fr.) Boidin (Stereales)	Bark/wood	1, 2
Antrodia albida (Fr.) Donk (Polyporales)	Wood	1
Antrodiella onychoides (Egeland) Niemelä (Polyporales)	Dead wood	1
Armillaria (Fr.) Staude (Agaricales)	Wood/roots	1
Bjerkandera adusta (Willd.) P. Karst. (Polyporales)	Wood	1
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk (Stereales)	Wood	2
Botryobasidium vagum (Berk. & M.A. Curtis) D.P. Rogers [= *B. botryosum* (Bres.) J. Erikss.] (Stereales)	Wood	2
Brevicellicium olivascens (Bres.) K.H. Larss. & Hjortstam (Stereales)	Dead wood	1
Calocera pallidospathulata D.A. Reid (Dacrymycetales)	Dead wood	1
Calocera viscosa (Pers.) Fr. (Dacrymycetales)	Dead wood	1
Ceratobasidium cornigerum (Bourdot) D.P. Rogers (Ceratobasidiales)	Wood	2
Coniophora arida (Fr.) P.Karst (Boletales)	Wood	2
Coniophora olivacea (Pers.) P. Karst. (Boletales)	Dead wood	1
Coniophora puteana (Schumach.) P. Karst. (Boletales)	Wood	10
Coprinus micaceus (Bull.) Fr. (Agaricales)	Dead wood	1
Dacrymyces stillatus Nees (Dacrymycetales)	Dead wood	1, 2
Daedaleopsis confragosa (Bolton) J. Schröt. (Polyporales)	Wood	1
Ganoderma carnosum Pat. (Polyporales)	Wood/roots	1
Ganoderma lucidum (Curtis) P. Karst. (Polyporales)	Wood	1
Ganoderma resinaceum Boud. (Polyporales)	Wood	1
Globulicium hiemale (Laurila) Hjortstam [= *Cerocorticium hiemale* (Laurila) Jülich & Stalpers] (Stereales)	Wood	2
Gymnopilus penetrans (Fr.) Murrill (Cortinariales)	Dead wood	1
Gymnopus fusipes (Bull.) Gray (Agaricales)	Root	1
Hyphoderma argillaceum (Bres.) Donk (Stereales)	Wood	2
Hyphoderma praetermissum (P. Karst.) J. Erikss. & Å. Strid (Stereales)	Wood	2
Hyphoderma puberum (Fr.) Wallr. (Stereales)	Wood	1, 2
Hyphodontia alutaria (Burt) J. Erikss. [= *Kneiffiella alutaria* (Burt) Jülich & Stalpers] (Polyporales)	Wood	2
Hyphodontia arguta (Fr.) J. Erikss. (Polyporales)	Dead wood	1
Hyphodontia breviseta (P. Karst.) J. Erikss. (Polyporales)	Dead wood	1
Hyphodontia crustosa (Pers.) J. Erikss. (Polyporales)	Wood	1
Hyphodontia nespori (Bres.) J. Erikss. & Hjortstam [= *Kneiffiella nespori* (Bres.) Jülich & Stalpers] (Polyporales)	Wood	1,2
Hyphodontia pallidula (Bres.) J. Erikss. (Polyporales)	Dead wood	1
Hypholoma fasciculare (Huds.) P. Kumm. (Agaricales)	Dead wood	1

Table 3 *Continued*

Lacrymaria velutina (Pers.) Konrad & Maubl. (Agaricales)	Dead wood	1
Laetiporus sulphureus (Bull.) Bondartsev & Singer (Polyporales)	Wood	1
Leucogyrophana mollusca (Fr.) Pouzar (Boletales)	Dead wood	1
Lycoperdon pyriforme (Schaeff.) Pers. (Lycoperdales)	Dead roots	1
Marasmiellus candidus (Bolton) Singer (Agaricales)	Bark	1
Marasmius rotula (Scop.) Fr. (Agaricales)	Dead twigs	1
Mycena cinerella P. Karst. (Agaricales)	Leaves	1
Phellinus ferreus (Pers.) Bourdot & Galzin (Hymenochaetales)	Wood	1
Phellinus pini (Fr.) A. Ames (Hymenochaetales)	Wood	8
Phlebiella allantospora (Oberw.) Larss. & Hjortstam [= *Xenasmatella allantospora* Oberw.] (Stereales)	Wood	2
Phlebiella pseudotsugae (Burt) K.H. Larss. & Hjortstam [= *Xenasma pseudotsugae* (Burt)] (Stereales)	Wood	2
Phlebiella sulphurea (Pers.) Ginns & M.N.L. Lefebvre (Stereales)	Dead wood	1
Polyporus varius (Pers.) Fr. (Polyporales)	Dead wood	1
Postia balsamea (Peck) Jülich (Polyporales)	Wood	1
Postia sericeomollis (Romell) Jülich (Polyporales)	Wood	1
Postia stiptica (Pers.) Jülich (Polyporales)	Wood	1
Postia tephroleuca (Fr.) Jülich (Polyporales)	Wood	1
Postia wakefieldiae (Kotl. & Pouzar) Pegler & E.M. Saunders (Polyporales)	Wood	1
Psilocybe phyllogena (Peck) Peck (Agaricales)	Sawdust	1
Radulomyces confluens (Fr.) M.P. Christ. (Stereales)	Dead wood	1, 2
Radulomyces rickii (Bres.) M.P. Christ. (Stereales)	Dead wood	1
Ramaria stricta (Pers.) Quél. (Gomphales)	Wood	2
Resinicium bicolor (Alb. & Schwein.) Parmasto (Stereales)	Wood	2
Schizopora paradoxa (Schrad.) Donk (Stereales)	Wood	1, 2
Scytinostroma ochroleucum (Bres. & Torrend) Donk (Lachnocladiales)	Dead wood	1
Setulipes androsaceus (L.) Fr. (Agaricales)	Dead leaves	1
Sparassis crispa (Wulfen) Fr. (Cantharellales)	Dead wood	1
Steccherinum fimbriatum (Pers.) J. Erikss. (Stereales)	Dead wood	1
Stereum hirsutum (Willd.) Gray (Stereales)	Wood	1
Suillus tridentinus (Bres.) Singer (Boletales)	Wood	1
Thanatephorus cucumeris (A.B. Frank) Donk [= *Rhizoctonia solani* Kühn.] (Ceratobasidiales)	Damping-off	7
Tomentella Pat. sp. (Thelephorales)	Wood	2
Trametes versicolor (L.) Pilát (Polyporales)	Dead wood	1
Trechispora cohaerens (Schwein.) Jülich & Stalpers (Stereales)	Dead wood	1, 2
Trechispora farinacea (Pers.) Liberta (Stereales)	Wood	2
Trechispora microspora (P. Karst.) Liberta (Stereales)	Wood	2
Tubulicrinis sororius (Bourdot & Galzin) Oberw. [= *T. juniperina* (Bourdot & Galzin) Donk] (Stereales)	Wood	2
Tubulicrinis subulatus (Bourdot & Galzin) Donk (Stereales)	Wood	2
Vesiculomyces citrinus (Pers.) E. Hagstr. (Hericiales)	Dead wood	1
Vesiculomyces sp. (Pers.) E. Hagstr. (Hericiales)	Dead wood	1
Deuteromycotina		
Hyphomycetes		
Acremonium Link sp.	Leaves	4
Alternaria Nees sp.	Wood/twigs/leaves	3
Aspergillus ustus (Bainier) Thom & Church	Roots	1
Capnobotrys dingleyae S. Hughes	Wood/leaves	1
Cylindrocarpon destructans (Zinssm.) Scholten	Roots	1
Digitodesmium elegans P.M. Kirk	Wood	1
Endophragmiella eboracensis B. Sutton	Dead wood	1
Endophragmiella taxi (M.B. Ellis) S. Hughes	Dead twigs	1
Fusarium Link sp.	Wood/twigs/leaves	3, 11
Phomopsis (Sacc.) Bubák sp.	Wood	1
Phragmocephala stemphylioides (Corda) S. Hughes	Leaves/shoots	7, 8, 9
Sclerotium glaucoalbidum Desm.	Leaves	1
Sporidesmiella claviformis P.M. Kirk	Dead leaves	1
Sporidesmiella coronata (B. Sutton) P.M. Kirk	Dead leaves	1
Sporidesmiella longissima P.M. Kirk	Dead leaves	1
Sporidesmium goidanichii (Rambelli) S. Hughes	Dead leaves	1
Sterigmatobotrys macrocarpa (Corda) S. Hughes	Dead wood	1
Thysanophora penicillioides (Roum.) W.B. Kendr.	Dead leaves	1
Thysanophora taxi (Schneider) Stolk & Hennebert	Leaves	1
Torula Pers.	Roots	1
Tubercularia vulgaris Tode	Dying bark	1

Table 3 *Continued*

Coelomycetes		
Coleophoma empetri (Rostr.) Petr.	Leaves	1
Cryptocline taxicola (Allesch.) Petr.	Dying leaves	1
Diplodia taxi (Sowerby) De Not.	Dead leaves	1, 5
Fusicoccum taxi Died.	Leaves	1
Macrophoma taxi (Berk.) Berl. & Voglino	Leaves/shoots	7, 8, 9
Monochaetia cryptomeriae M. Wilson	Dead leaves	1
Pestalotia De Not. sp.	Saprophyte	5, 11
Pestalotiopsis funerea (Desm.) Steyaert	Leaves/shoots	7, 8, 9
Phoma allostoma (Lév.) Sacc.	Dead leaves	1
MYXOMYCOTA		
Arcyria cinerea (Bull.) Pers. (Trichiales)		1
Arcyria pomiformis (Leers) Rostaf. (Trichiales)		1
Calomyxa metallica (Berk.) Nieuwl. (Trichiales)		1
Ceratiomyxa fruticulosa (O.F. Müll.) T. Macbr. (Ceratiomyxales)		1
Colloderma oculatum (C. Lippert) G. Lister (Stemonitales)		1
Licea chelonoides Nann.-Bremek. (Liceales)		1
Licea marginata Nann.-Bremek. (Liceales)		1
Licea parasitica (Zukal) G.W. Martin (Liceales)		1
Licea perexigua T.E. Brooks & H.W. Keller (Liceales)		1
Licea scyphoides T.E. Brooks & H.W. Keller (Liceales)		1
Lycogala terrestre Fr. (Liceales)		1
Stemonitis nigrescens Rex (Stemonitales)		1

(v) Deuteromycotina

Caruso *et al*. (2000a) isolated 105 strains of endophytic fungi belonging to 25 different genera from inside wood, twigs and leaves samples of *T. baccata* growing in central-northern Italy. Of these *Alternaria* (Hyphomycete), *Fusarium* (Hyphomycete) and *Mucor* (Zygomycete) were the commonest. *Alternaria* was isolated from all materials analysed and is considered a 'resident genus of *Taxus* tissues' by the authors.

An *Acremonium* sp. has been isolated as an endophytic fungus of *T. baccata*. Leucinostatin A is one of several potentially toxic peptides produced by *Acremonium* sp. that have phytotoxic and antifungal properties. This peptide causes no visible symptoms in *T. baccata*, however, because it has an enzyme which transfers two glucosyl residues to leucinostatin A, markedly reducing the peptide's bioactivity. Moreover, the antifungal properties of this endophyte may contribute to the defence of its host (Strobel & Hess 1997). Leucinostatin A is especially active against the pathogenic fungus, *Pythium ultimum* Trow. (Mastigomycotina, Oomycota, Pythiales) (Strobel *et al*. 1997).

Diplodia taxi (Sow.) De Not. (Coelomycete) is associated with yellowing leaves of *T. baccata* (Siwecki 1978; Ridley 1994).

(vi) Epiphytes

The more frequent epiphytes recorded as growing on yew in south-west Ireland are given in Table 4. The smooth and flaking bark make it generally inhospitable for epiphytes (Kelly 1981) except in high humidity areas. Pilkington *et al*. (1994) recorded that the yews of a moist island in Loch Lomond, Scotland, have a number of epiphytes including *Vaccinium myrtillus*, *Dryopteris dilatata* and *Oxalis acetosella*, but also birch (*Betula pubescens* ssp. *carpatica*), holly (*Ilex aquifolium*) and rowan (*Sorbus aucuparia*). These trees were found

Table 4 Frequent epiphytes on yew trees in Reenadinna Wood, south-west Ireland (from Kelly 1981)

On tree bases and lower parts of trunk
Bryophytes
Isothecium myosuroides Brid.
I. myurum (Brid.) Brid.
Lejeunea cavifolia (Ehrh.) Lindb.
Marchesinia mackaii (Hook.) Gray
Metzgeria furcata (L.) Dum.
Neckera complanata (Hedw.) Hüben.

Lichen
Lobaria laetevirens (Lightf.) Zahlbr.

On branches and upper parts of trunk
Bryophytes
Drepanolejeunea hamatifolia (Hook.) Schiffn.
Frullania dilatata (L.) Dum.
F. fragilifolia (Tayl.) Gott., Lindenb. & Nees
F. germana (Tayl.) Gott., Lindenb. & Nees
  [= *F. teneriffae* (F. Weber) Nees]
F. microphylla (Gott.) Pearson
F. tamarisci (L.) Dum.
Harpalejeunea ovata auct. non-(Hook.) Schiffn.
  [= *H. molleri* (Steph.) Grolle]
Lejeunea ulicina (Tayl.) Gott. Lindenb. & Ness
  [= *Microlejeunea ulicina* (Tayl.) Evans]
Metzgeria furcata (L.) Dum.
Ulota bruchii Hornsch. ex Brid.
U. crispa (Hedw.) Brid.

Lichens
Normandina pulchella (Borrer) Nyl.
Pannaria cf. *pityrea* (DC.) Degel.
Sticta limbata (Sm.) Ach.

to grow as epiphytes in humus pockets but could also grow roots down through the hollow yew into the soil (chemical analyses of leaves added evidence that some of the 'epiphyte' trees were in fact rooted into the soil). Those trees rooted in the ground were being enveloped by the growing yew trunk, to become 'partner trees'. Of 791 yews looked at, 28 had partners and 60 had epiphytic trees. There were no differences seen between male and female yew trees. Wilks (1972) also mentions an oak (*Quercus*) growing epiphytically on a yew. Pilkington *et al*. (1994) quote a personal communication from A. Agnew in 1991 of a *Rhododendron ponticum* and a *Fraxinus excelsior* growing as partner trees on yew in south-west Wales.

(C) PLANT DISEASES

Taxus baccata is notably susceptible to *Phytophthora* sp. root disease, which is recorded by Strouts (1993) and Strouts & Winter (1994) as the only known fatal disease of yew in Britain. By contrast, yew is very resistant to honey fungus (*Armillaria* sp.) and there appears to be no authenticated cases of death due to honey fungus (Strouts & Winter 1994). Branch cankers are not uncommon. A branch dieback disease is common in *T. baccata* northwards to Derbyshire and Sheffield (first noted in the 1960s), associated with a girdling patch of dead bark or canker at the branch base, probably caused by a fungus (Strouts & Winter 1994).

Taxus baccata Aurea has golden yellow leaves when young. Blattny (1960) reports that the yellow leaf variegation agent is transmitted by grafting and Cooper (1979) uses this as evidence that the agent is viral.

Pratylenchus penetrans (a major root lesion nematode pest in woody plant nursery stock grown on light sandy soils) will lightly infest the roots of planted *T. baccata*, but is generally so little that in the Netherlands *T. baccata* can be used in a crop rotation strategy to control the pest (Bertrums 1998).

X. History

Using morphological characteristics of extant Taxaceae, Spjut (2000) concluded that, after radiation from south-west China, several species had evolved into Europe by the Tertiary period. He suggests that *Taxus baccata* arose from hybridization between an extinct Russian species (*T. contorta*) and Tertiary relics spreading north from North Africa.

It is likely that *Taxus* pollen was overlooked in the earliest palynological studies because it is susceptible to corrosion causing pollen grains to split open (Havinga 1967; Godw. Hist.; Środoń 1978). Pollen records do show, however, that *Taxus* was present in Europe during previous interglacial periods, starting with the Cromerian (450 000–700 000 yr BP) (Godw. Hist.; Środoń 1978) but was in greatest abundance in the warm, oceanic climate of the Hoxnian, 367 000–400 000 yr BP (West 1962; Godw. Hist.). Evidence includes the 'oldest known wooden artifact in the world', a spear of *T. baccata* found at Clacton, Essex (Godw. Hist.). *Taxus* pollen and macrofossils from the Hoxnian are common in Co. Galway, associated primarily with *Fraxinus* and *Alnus*, attributed to the abundance of fen woodland on limestone. Several periods of decline in *Taxus* are associated with the extension of acidic terrestrial peat which favoured such plants as *Picea*, *Abies* and *Rhododendron ponticum* (Godw. Hist.). At this time, yew spread further east than it currently does, reaching as far as Likhvin, south-west of Moscow (Sukatschev 1908).

There are isolated records of *Taxus* pollen from the late Anglian interglacial (< 400 000 yr BP) and early Wolstonian (*c*. 365 000 yr BP) but, according to Godwin (Godw. Hist.), these are likely due to secondary incorporation. However, *Taxus* appears to have been present in southern Europe, associated with *Abies*, during the Praclaux (*c*. 372 000 yr BP) and Landos (*c*. 339 000 yr BP) interglacials, which correspond most likely to Marine Oxygen Isotope Stages 9 and 11 (de Beaulieu *et al*. 2001; Tzedakis *et al*. 2001). *Taxus* pollen was also sparse through western Europe in the Ipswichian interglacial (75 000–128 000 yr BP) although *Taxus* was present. In Denmark, *Taxus* was again associated with wet soil conditions (with *Alnus* and *Fraxinus*) and was replaced by *Pinus* and *Picea* with progressive mor development (Andersen 1975; Wheeler 1992). In north-west Germany (Lower Saxony) a yew spear was found between the ribs of a straight-tusked elephant (*Hesperoloxodon antiquus* Falc.) in the equivalent of Ipswichian deposits (Movius 1950), in a woodland dominated by *Quercus* and *Betula*.

The spread of yew back into Britain and mainland Europe after the last ice age was comparatively later than in the last two interglacials and its proportion was considerably smaller. The earliest evidence for yew in Britain is in the late Boreal at the time of transition from pine to mixed deciduous forests (Godw. Hist.), reaching the limestone of north-west England nearly 7000 years ago (Birks 1982) and moving into Ireland in the Atlantic and Sub-Boreal, before 6000 yr BP (O'Connell *et al*. 1987, 1988; Mitchell 1988, 1990b).

It seems likely that yew reached its greatest European extent in the late Atlantic and Sub-Boreal (Averdieck 1971; Środoń 1978; Sarmaja-Korjonen *et al*. 1991; Peñalba 1994) and includes the yew and oak trunks formerly growing in the Thames basin and found buried in acidic peat under east London in 1995 (dated at more than 6000 yr BP). Indeed, yew was widespread in the Atlantic on calcareous peat, as in the Somerset Levels where yew grew in fen-carr dominated by *Alnus glutinosa*, *Betula* and *Quercus*, and in East Anglia in fen woods growing with *Quercus*, *Alnus*, *Fraxinus*, *Betula pubescens*, *Frangula alnus* and *Rhamnus catharticus* (Godwin & Clifford 1938; Godw. Hist.). Wheeler (1992) found yew at the base of fen peat, associated with a pre-fen woodland of *Quercus*, *Tilia*, *Corylus/Myrica* and *Ulmus* growing on clay. Some specimens near Ely, however, are recorded as being rooted in sandy gravel below the peat (Elwes & Henry 1906). Because *T. baccata* is not favoured by wet soils, and indeed is susceptible to poor drainage, it is speculated that the abundance of yew on wet soils in England and western Europe was due to the humid climate and poor calcareous soils reducing competition from other large trees, allowing more light into the understorey (Watts 1967; Svenning & Magård 1999). Nevertheless, yew grew well: a number of records in Britain and Ireland include yew stools of up to 2 m in diameter growing on peat (Adams 1905; Elwes & Henry 1906; Godw. Hist.). Yew twigs were used in the construction of the youngest of the Neolithic trackways in the Somerset Levels dated at 2115 ± 120 yr BP to 2890 ± 100 yr BP (Coles & Hibbert 1968; Coles *et al.* 1970). Thus, yew seems to have shown a late post-glacial spread in Britain much like *Fagus sylvatica*, but unlike the beech, it has been not nearly as successful in establishing itself as a widespread canopy component (Rodwell 1991; O'Connell & Molloy 2001).

The decline of yew at Wood Fen, north of Ely, at roughly the Sub-Boreal, was attributed to climatic dryness reducing the flooding of calcareous water into fenlands, allowing raised bogs to start growing, with the invasion of *Sphagnum* spp. and *Pinus sylvestris* (Godwin *et al.* 1935). The decline of yew on peatlands in Great Britain at the beginning of the Sub-Boreal was compensated for, to an extent, by its spreading into drier woodlands with the elm decline and with phases of limited clearance (coppicing) accompanied by cereal cultivation increasing (Waller & Hamilton 2000; O'Connell *et al.* 2001). *Taxus baccata* was an important component of the woodlands which regenerated between these phases of clearance. Macrofossil and pollen records reached a maximum in zone VIIb (*c.* 4000 years ago in the Sub-Boreal), including a number of archaeological remains (Godw. Hist.)

Despite these incursions into regenerating woodland, *T. baccata* started to decline, first in continental Europe and then in the British Isles, in the Sub-Boreal and into the Sub-Atlantic (e.g. Środoń 1978; O'Connell *et al.* 1988), partly attributable to the start of peat accumulation with wetter conditions. Yew was gone from the eastern Swiss Plateau by 6600 yr BP and was rare on the western plateau by 5000 yr BP (Haas & Richoz 1995). Favre & Jacomet (1998) collected 596 waterlogged branch wood specimens from four cultural layers of a late Neolithic site (dated around 5000 yr BP) in the north-eastern Swiss Plateau, on Lake Zurich, Switzerland. Seventy percent of the specimens consisted of twigs of *Corylus avellana*, *Abies alba* or *T. baccata*. Of these, yew twigs formed a remarkably high proportion (26.8% of all twigs), between 5 and 12.5 mm diameter. Favre & Jacomet speculated that the inhabitants had specific purposes for the yew and felled and traded yew timbers. *Taxus baccata* was first recorded in 5900 yr BP in the northern Iberian peninsula (Peñalba 1994), growing along with *Quercus*, *Corylus*, *Alnus* and *Pinus*, in patchy refugia situated at medium elevations. Peñalba observed that yew started declining at lower altitudes before 3000 yr BP, probably owing to human influence, relegating yew to higher altitudes: in northern Spain it now grows only as isolated individuals within beech forest. In the Mediterranean basin, García *et al.* (2000) note that *T. baccata* has become restricted to mountainous areas which they attribute to climatic regression and human activities. In southern Italy, *T. baccata*, along with *Carpinus betulus* and *Abies alba*, appeared *c.* 4000 years ago, and *T. baccata* and *Abies* became locally extinct about 2500 years ago presumably due to climatic change – and most likely increasing summer dryness (Watts *et al.* 1996).

Salisbury & Jane (1940) provide evidence of a later decline in Britain. At Maiden Castle in Dorset, they found yew to be common amongst charcoals of the Neolithic (*c.* 2500–2000 BC) and Early Iron Age (*c.* 400–200 BC) but absent from the Late Iron Age (50 BC–AD 50). They concluded that *T. baccata* was thus a local native, but declining, constituent of the vegetation. They also contended that yew had diminished in the south of England since Neolithic times owing to 'a steady augmentation of leached soil', but this is disputed by Godwin & Tansley (1941). O'Connell & Molloy (2001) suggest the decline was partly due to exploitation of the timber (the Tyrolean Iceman from this period had a bow stave and axe handle of yew wood – Spindler 1994) but more importantly due to increased grazing pressure. Yew recovery during periods of low human activity (such as in the Late Iron Age Lull, *c.* AD 100–300) is interpreted as further evidence of human impact (O'Connell & Molloy 2001; O'Connell *et al.* 2001).

Periods of expansion of yew in Ireland around 1880 yr BP (following an elm decline period) and a sharp decline around 1500 yr BP have been found in a number of studies (Watts 1984; O'Connell *et al.* 1987; Mitchell 1988, 1990a,b), the decline corresponding to a rise in anthropogenic indicators (see also Willerding 1968). Its current restricted distribution in western Ireland represents the vestiges of a previously more widespread tree; indeed County Mayo (Maigh Eo) translates as 'the plain of the yew' (Symes 1879).

The post-glacial distribution of *T. baccata* in the British Isles has been extensively modified by planting, from as early as the 9th century (Lyubenova & Nedelchev 2001). Many superstitions and myths have built up about the tree in relation to spirituality and connections with death and it seems likely that the Celts extensively planted yews (Lyubenova & Nedelchev 2001). Indeed, there are many theories as to why yews are so closely associated with churchyards in England and Scotland (Bowman 1837; Cornish 1946). On balance, it seems that early Christian missionaries took over pagan yew tree sites, under instruction from the Pope, to force conversion of the heathens. Given their long life, yews remained numerous in churchyards and indeed continue to be planted as symbols of Christianity due to the 'eternal life' of evergreen foliage and the symbolism of red berries and blood. Yew has also been used as a boundary marker and as a tombstone in unconsecrated ground (Williamson 1978).

The natural distribution of yew has been further blurred by extensive planting for its ornamental value (e.g. Voliotis 1986). Yew has been recorded historically in hedges in Anglo-Saxon charters and Domesday Book (Rackham 1990) and there has been extensive planting from the late sixteenth century as hedging, specimen trees and for topiary.

There are many archaeological records of the use of yew from Neolithic to Roman as, for example, spears, axe shafts and bows (Godw. Hist.). Yew pegs were also used as fastenings for the Neolithic trackways in the Somerset levels, and more esoterically, yew wood was used to sew together the timbers in the 'sewn boats' found at North Ferriby, Yorkshire, dating from 1600 and 750 BC (Wright & Churchill 1965). Coles *et al.* (1978) listed 18 artefacts made of yew from prehistoric Britain and Ireland including handles (for a dagger, knife and an axe), a spear shaft and bows. Mitchell (1990b) describes yew stakes beneath peat in County Mayo, Ireland, which are conjectured to have been part of a Bronze-age deer trap.

Archery with yew long bows is perhaps the most famous use of yew. Clark (1963) has discussed the prehistory of archery in north-western Europe. He concludes that the bow may have appeared in southern Europe and northern Africa around 15 000 BC and that it came into use in northern Europe during the 9th millennium BC. Its use declined after the 2nd millennium BC and it is likely that the Saxons reintroduced the weapon to England. While bows have been made of many woods, in particular ash and laburnum, the finest bows have traditionally been made of yew. Various British monarchs (Edward IV, Richard III and Elizabeth I) decreed that yews should be preserved and/or planted to maintain a supply of suitable bow wood, although the best wood undoubtedly came from continental Europe. Roger Ascham (1545; reprinted in English 1868) wrote a treatise on the art of long-bow shooting and the need for practice.

Despite the many uses of yew, from long bows to fine furniture (see Dallimore (1908) and Hartzell (1995) for summaries of the cultural history of yew), it is unlikely that yew woodlands have been actively planted and used for timber production.

Stands in south-east England (Rodwell 1991) and in Killarney Woods, Ireland (Turner & Watt 1939), may have been extensively felled to fuel the iron-smelting industry. More recently Kingley Vale in Sussex was used for wartime target practice (Williamson 1978).

XI. Conservation

Taxus baccata has become locally extinct or reduced to small isolated populations during the last 4000 years in many parts of Europe (Pax 1908; Tutin 1953; Czartoryski 1978; Tittensor 1980; Sarmaja-Korjonen *et al.* 1991; Peñalba 1994; Lewandowski *et al.* 1995; Watts *et al.* 1996; Svenning & Magård 1999) and the former Soviet Union (Pridnya 1984). It is now catalogued as a rare and endangered species prone to extinction in the Mediterranean mountains of southern Spain (García *et al.* 2000), Poland (Kepczynski & Peplinska 1995), Bulgaria (Lyubenova & Nedelchev 2001), in the eastern Transcaucasus (Safarov 1986) and Norway (Myking 2002). Pridnya (1984) reported the death of 3% of yews per year in the Caucasus mountains. García *et al.* (2000) note that in southern Spain, *T. baccata* is now restricted to a small number of isolated patches, most with fewer than 10–20 individuals dominated by senescent individuals with a low proportion of saplings and seedlings.

A number of causes have been put forward for the decline of yew. In the Mediterranean flora of southern Europe, at least, this may be due to the yew being left as a declining relict as the climate has become less oceanic (Anzalone *et al.* 1997). Elsewhere (and undoubtedly related to sub-optimum climate), decline has been variably attributed to herbivory of seeds or seedlings, heavy grazing by deer, competition for light against such trees as beech, adverse soil conditions (such as build-up of pathogens, autotoxicity or changed abiotic conditions), poor soil water relations and changes in microclimate, and fungal diseases (Czartoryski 1978; Król 1978; Pridnya 1984; Lewandowski *et al.* 1995; Holtan 2001).

Overall, however, a second major contributor to decline has undoubtedly been excessive felling (or at least felling at a faster rate than recruitment), noted in Ireland (Boate 1758 quoted in Lowe 1897), England (Tittensor 1980) and in mainland Europe (Svenning & Magård 1999; García *et al.* 2000; Vacik *et al.* 2001). Indeed, Svenning & Magård (1999) maintain that yew is one of the most negatively affected European trees by human intervention. This is no recent feature: the extreme rarity of yew in the Tyrol has been blamed on felling up till the 16th and 17th century to make yew bows for English armies (Spindler 1994); and in the east Carpathians in the 17th and 18th century the local Hucul population paid taxes in yew trees and Kontny (1937) calculated that over the two centuries 37 800 trunks were felled for taxes. More recently, there have been examples of yew being felled by landowners to prevent protected area status (e.g. Holtan 2001).

Ellenberg (1988) claims that *T. baccata* (and other trees) occur in central Europe on steep rocky slopes that have escaped disturbance, fire and logging. Vogler (1904) supported this idea as he found *T. baccata* was comparatively common on steep calcareous slopes and cliffs throughout Switzerland despite the prevailing impression that it was threatened by local extinction. The reasons given were lack of harvesting and grazing matched with the ability to grow there.

Taxus baccata populations have, however, been seen to expand where conditions are suitable (Carvalho *et al.* 1999; Seidling 1999). Active management can also help. In Denmark, only one yew population has survived (Worsøe 1985; Svenning & Magård 1999) whereas it was widespread 1000–2000 years ago (Nørrevang & Lundø 1981). But this population has expanded in tree number as a result of management by thinning and so letting in more light (Svenning & Magård 1999). Vacik *et al*. (2001) report that 'population viability management' methods show that a combination of silvicultural manipulation of stands to encourage crown growth and increasing public awareness of their vulnerability would increase the probability of survival of the endangered yew population of Bad Bleiberg by 75–95% compared to merely enclosing the trees in a reserve.

In Britain, the Forestry Commission (1994) recommended that rapid growth of yew can be promoted by felling the overstorey in yew-rich beech-ash woods. The yew will outcompete hardwood regeneration and dominate. However, once yew woodland is cut, it is more likely to regenerate to ash or birch in the first instance, with yew as a scattered understorey. Thus management should be restricted to only very occasional harvesting of yews. Around 50% of lowland yew woodlands in England are at present designated as Sites of Special Scientific Interest.

There is at present increasing research on the genetic make-up of yew populations and how this relates to conservation attempts (e.g. Hertel & Kohlstock 1996; Rajewski *et al*. 2000). Myking (2002) considers the life-history traits that influence the genetic variability of a number of species and concludes that *T. baccata* is potentially vulnerable to loss of genetic diversity. Lewandowski *et al*. (1995), however, show that loss of genetic variation in depleted populations is not necessarily a problem beause a strongly declining population in Poland showed high levels of genetic diversity. This is probably because *T. baccata* is an inherently genetically variable species compared with other conifers (Ledig 1986) and high genetic variation is encouraged by dioecy and wind pollination. However, Lewandowski *et al*. (1995) also note that new progeny show much higher levels of inbreeding, probably because of limited seed-dispersal and mating between close neighbours. Conversely, ideas of the conservation of local genetic resources of *T. baccata* have led to investigations on vegetative propagation by cuttings.

In the face of predicted climate change, Hulme & Jenkins (1998) conclude that 'it seems unlikely that climate change in the south-east of England could induce the population of *T. baccata* to move considering that the species is present in southern Italy, Greece and Spain'. And, indeed, modelling by Harrison *et al*. (2001) shows little change in *T. baccata* distribution under climate change scenarios.

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References

Adams, J. (1905) The occurrence of yew in a peat bog in Queen's County. *Irish Naturalist*, **XIV**, 34 (plus facing plate).

Allen, S.E. (1989) *Chemical Analysis of Ecological Materials*, 2nd edn. Blackwell Scientific Publications, Oxford, UK.

Allona, I., Collada, C., Casado, R. & Aragoncillo, C. (1994) Electrophoretic analysis of seed storage proteins from gymnosperms. *Electrophoresis*, **15**, 1062–1067.

Altmann, K.-H. (2001) Microtubule-stabilizing agents: a growing class of important anticancer drugs. *Current Opinion in Chemical Biology*, **5**, 424–431.

Andersen, S.T. (1975) The Eemian freshwater deposit at Egernsund, South Jylland, and the Eemian landscape development in Denmark. *Danmarks Geologiske Undersøgelser, Årborg*, **1974**, 49–70, plates 11–15.

Anzalone, B., Lattanzi, E., Lucchese, F. & Padula, M. (1997) The vascular flora of the Circeo National Park (Parco Nazionale del Circeo-Lazio). *Webbia*, **51**, 251–341.

Ascham, R. (1545) *Toxophilus: The Schole of Shootinge*. London, UK.

Aventis Pharma Ltd. (2002) *TAXOTERE® (docetaxel) for Injection Concentrate*. Aventis Pharma Ltd. http://www.taxotere.com/resources/piframes.html

Averdieck, F.-R. (1971) Zur postglazialen Geschichte der Eibe (*Taxus baccata*) in Nordwestdeutschland. *Flora*, **160**, 28–42.

Barker, M.G. & Ashenden, T.W. (1993) Foliar injury in young *Betula pendula* Roth, *Salix purpurea* L. & *Ilex aquifolium* L. trees and in propagated *Taxus baccata* L. shoots exposed to intermittent fog at a range of acidities. *Environmental Pollution*, **80**, 123–127.

Barnea, A., Harborne, J.B. & Pannell, C. (1993) What parts of fleshy fruits contain secondary compounds toxic to birds and why? *Biochemical Systematics and Ecology*, **21**, 421–429.

Bartkowiak, S. (1970) Ornitochoria rodzimych i obcych gatunków drzew i krzewów. [Ornithochory of indigenous and foreign species of trees and shrubs.]. *Arboretum Kórnickie*, **15**, 237–261.

Bartkowiak, S. (1978) Seed dispersal by birds. *The Yew – Taxus baccata L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 139–146. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Batten, L.A. (1976) Bird communities of some Killarney woodlands. *Proceedings of the Royal Irish Academy*, **76**, 285–313.

de Beaulieu, J.-L., Andrieu-Ponel, V., Reille, M., Grüger, E., Tzedakis, C. & Svobodova, H. (2001) An attempt at correlation between the Velay pollen sequence and the Middle Pleistocene stratigraphy from central Europe. *Quaternary Science Reviews*, **20**, 1593–1602.

Bebber, A. & Corona, E. (1986) Nota dendrocronologica su una trave di tasso (*Taxus baccata* L.). *Dendrochronologica*, **4**, 124.

Bell, P.R. & Hemsley, A.R. (2000) *Green Plants: Their Origin and Diversity*, 2nd edn. Cambridge University Press, Cambridge, UK.

Bertrums, E.J. (1998) Population decline of root lesion nematode (*Pratylenchus penetrans* Cobb) after a *Taxus baccata* crop. *Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen Universiteit Gent*, **63** (2B), 649–653.

Białobok, S. (1978) Possibilities of yew cultivation in an environment modified by man. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 147–149. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Birks, H.J.B. (1982) Mid-Flandrian forest history of Roundsea Wood National Nature Reserve, Cumbria. *New Phytologist*, **90**, 339–354.

Björkman, L. (1958) Idegranen (*Taxus baccata* L.) på Åland. *Acta Societatia Pro Fauna et Flora Fennica*, **74**, 1–18.

Blattny, C. (1960) Weiterer Beitrag zur Kenntnis der Nadelbaum virosen. *Preslia*, **32**, 414.

Bowman, J.E. (1837) On the longevity of the yew, as ascertained from actual sections of its trunk; and on the origins of its frequent occurrence in churchyards. *Magazine of Natural History*, **1**, 28–35, 85–90.

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.

Bugala, W. (1978) Systematics and variability. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 15–32. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Buhl, O., Falck, P., Jørgensen, B., Karsholt, O., Larsen, K. & Vilhelmsen, F. (2000) Fund af småsommerfugle fra Danmark i, 1999 (Lepidoptera). [Records of Microlepidoptera from Denmark in 1999 (Lepidoptera)]. *Entomologiske Meddelelser*, **68**, 121–131.

Burla, H. & Bachli, G. (1991) Notes on rearing drosophilid species from both cultivated and natural fruits. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **64**, 45–53.

Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America, 1, Conifers*. United States Department of Agriculture Forest Service, Agricultural Handbook 654. Washington, DC, USA.

Buschbom, U. (1968) Salzresistenz oberirdischer Sproßteile von Holzgewächsen I. Chlorideinwirkungen auf Sproßoberflächen. *Flora*, **157**, 527–561.

Caruso, M., Colombo, A.L., Crespi-Perellino, N., Fedeli, L., Malyszko, J., Pavesi, A., Quaroni, S., Saracchi, M. & Ventrella, G. (2000b) Studies on a strain of *Kitasatospora* sp. paclitaxel producer. *Annals of Microbiology*, **50**, 89–102.

Caruso, M., Colombo, A.L., Fedeli, L., Pavesi, A., Quaroni, S., Saracchi, M. & Ventrella, G. (2000a) Isolation of endophytic fungi and actinomycetes taxane producers. *Annals of Microbiology*, **50**, 3–13.

Carvalho, A., Rebelo, A. & Dias, J. (1999) Distribution and natural regeneration of yew trees in the National Parks of Peneda-Geres (Portugal) and Baixa Limia Serra-Xures (Spain). *Revista de Biologia*, **17**, 43–49.

Cecchi, F.A., Mariotti, L.M. & Tani, G. (1991) Ultrastructural observations on the megasporocyte of *Taxus baccata* L. Taxaceae in relation to megaspore behaviour. *Caryologia*, **44**, 45–54.

Chetan, A. & Brueton, D. (1994) *The Sacred Yew*. Penguin, London, UK.

Chira, E. (1964) Vplyv teploty na priebeh meiozy pelovych materskych buniek *Taxus baccata* L. *Biologia*, *XIX*, **4**, 235–244.

Christison, R. (1897) The exact measurement of trees. (Part 3). The Fortingall Yew. *Transactions of the Botanical Society of Edinburgh*, **13**, 410–435.

Clark, J.G.D. (1963) Neolithic bows from Somerset, England, and the prehistory of archery in north-western Europe. *Proceedings of the Prehistoric Society*, **29**, 50–98.

Clarke, M.L., Harvey, D.G. & Humphreys, D.J. (1981) *Veterinary Toxicology*, 2nd edn. Tindall, London, UK.

Coles, J.M., Heal, S.V.E. & Orme, B.J. (1978) The use and character of wood in prehistoric Britain and Ireland. *Proceedings of the Prehistoric Society*, **44**, 1–45.

Coles, J.M. & Hibbert, F.A. (1968) Prehistoric roads and tracks in Somerset, England. 1. Neolithic. *Proceedings of the Prehistoric Society*, **34**, 238–258.

Coles, J.M., Hibbert, F.A. & Clements, C.F. (1970) Prehistoric roads and tracks in Somerset, England. 2. Neolithic. *Proceedings of the Prehistoric Society*, **36**, 125–151.

Cooper, J.I. (1979) *Virus Diseases of Trees and Shrubs*. Institute of Terrestrial Ecology, Cambridge, UK.

Cooper, M.R. & Johnson, A.W. (1984) *Poisonous Plants in Britain and their Effects on Animals and Man*. Ministry of Agriculture, Fisheries and Food, Reference Book 161. HMSO, London, UK.

Cope, E.A. (1998) Taxaceae: the genera and cultivated species. *Botanical Review*, **64**, 291–323.

Cornish, V. (1946) *The Churchyard Yew and Immortality*. Frederick Muller, London, UK.

Creutz, G. (1952) Misteldrossel und Seidenschwanz. *Ornithologische Mitteilungen*, **4**, 67.

Czartoryski, A. (1978) Protection and conservation of yew. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 116–138. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Dallimore, W. (1908). *Holly, Yew and Box*. John Lane, London, UK.

Dallimore, W. (1964) A serious scale insect on yew. *Quarterly Journal of Forestry*, **43**, 65–67.

Daniewski, W.M., Gumulka, M., Anczewski, W., Masnyk, M., Bloszyk, E. & Gupta, K.K. (1998) Why the yew tree (*Taxus baccata*) is not attacked by insects. *Phytochemistry*, **49**, 1279–1282.

Dark, S.O.S. (1932) Chromosomes of *Taxus, Sequoia, Cryptomeria* and *Thuya*. *Annals of Botany*, **XLVI**, 965–977.

Davis, P.H. (1965) *Flora of Turkey*. Cambridge University Press, Cambridge, UK.

Delelis-Dusollier, A. & Géhu, J.-M. (1972) Aperçu phytosociologique sur les Fourres à *Taxus* de la basse Vallée de la Seine et comparaison avec ceux de l'Angleterre. *Documents Phytosociologiques*, **I**, 39–46.

Dempsey, D. & Hook, I. (2000) Yew (*Taxus*) species – chemical and morphological variations. *Pharmaceutical Biology*, **38**, 274–280.

Denis, J.N. (1988) A highly efficient, practical approach to natural taxol. *Journal of the American Chemical Society*, August 1988, 5917.

Denne, M.P. (1987) The tree resource of churchyards of Gwynedd, Wales. *Arboricultural Journal*, **11**, 33–52.

Dennis, E.B. (1964) Control of yew scale. *Plant Pathology*, **13**, 85–86.

Detz, H. & Kemperman, J. (1968) Zaaikalender van coniferen en loufhoutgewassen. *Proefstation Boksoop Jaarboek*, 163–174.

Devillez, F. (1978) Influence de la température sur la post-maturation et la germination des graines de l'if (*Taxus baccata* L.). *Bulletin de la Classe des Sciences de l'Academie Royale de Belgique*, 5^{e} série, **LXIV**, 203–218.

Di Sapio, O.A., Gattuso, S.J. & Gattuso, M.A. (1997) Morphoanatomical characters of *Taxus baccata* bark and leaves. *Fitoterapia*, **68**, 252–260.

Dickson, J.H. (1994) The yew tree (*Taxus baccata* L.) in Scotland – native or early introduction or both? *Scottish Forestry*, **48**, 253–261.

Dietz, H.H., Host, O. & Wiese, C. (1994) Yew poisoning in fallow deer in Denmark. *Dansk Veterinaertidsskrift*, **77**, 404–405.

Doss, R.P., Carney, J.R., Shanks, C.H., Williamson, R.T. & Chamberlain, J.D. (1997) Two new taxoids from European yew (*Taxus baccata*) that act as pyrethroid insecticide synergists with the black vine weevil (*Otiorhynchus sulcatus*). *Journal of Natural Products*, **60**, 1130–1133.

Duncan, R.W., Bown, T.A., Marshall, V.G. & Mitchell, A.K. (1997) *Yew Big Bud Mite*. Canadian Forest Service, Pacific Forestry Centre, Forest Pest Leaflet 79, Canada.

Eaton, R.A. & Hale, M.D.C. (1993) *Wood: Decay, Pests and Protection*. Chapman & Hall, London, UK.

Edlin, H.L. (1958) *The Living Forest*. Thames and Hudson, London, UK.

Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge, UK.

Elsohly, H.N., Croom, E.M. Jr, Kopycki, W.J., Joshi, A.S., Elsohly, M.A. & McChesney, J.D. (1997) Taxane contents of *Taxus* cultivars grown in American nurseries. *Journal of Environmental Horticulture*, **15**, 200–205.

Elwes, H.J. & Henry, A. (1906) *The Trees of Great Britain and Ireland*. Privately printed, Edinburgh, UK.

Erdemoglu, N. & Sener, B. (2001) Antimicrobial activity of the heartwood of *Taxus baccata*. *Fitoterapia*, **72**, 59–61.

Erdtman, E. & Tsuno, K. (1969) *Taxus* heartwood constituents. *Phytochemistry*, **8**, 931–932.

Faegri, K. (1960) *Maps of the Distribution of Norwegian Plants. 1. The Coast Plants*. Oslo University Press, Oslo, Norway.

Favre, P. & Jacomet, S. (1998) Branch wood from the lake shore settlements of Horgen Scheller, Switzerland: evidence for economic specialization in the late Neolithic period. *Vegetation History and Archaeobotany*, **7**, 167–178.

Ferguson, D.K. & Westhoff, V. (1987) An account of the flora and vegetation of Derryclare Wood, Connemara (Co. Galway), Western Ireland. *Proceedings of the Royal Irish Academy*, **C90**, 139–172.

Ferguson, I. (1995) An unusual foodplant for *Hedya pruniana* Hb. (Lep. Tortricidae). *Entomologist's Record and Journal of Variation*, **107**, 131–132.

Fiedler, H.J., Höhne, H. & Haupt, R. (1986) The influence of biological and ecological factors on the nutrient status of yew *Taxus baccata*. *Flora*, **178**, 141–155.

Forestry Commission (1994) *The Management of Semi-Natural Woodlands: Lowland Beech-Ash Woods*. Forestry Practice Guide 2. Forestry Commission, Edinburgh, UK.

Forster, W. & Wohlfahrt, T.A. (1981) *Die Schmetterlinge Mitteleuropas. Spanner (Geometridae)*. Frankische Verlagshandlung, Stuttgart, Germany.

Fuller, R.J. (1982) *Bird Habitats in Britain*. T. & A.D. Poyser Ltd, Calton, Staffordshire, UK.

Futak, J., Jasicova, M. & Schinday, E. (1966) *Flora Slovenska*, Vol. 2. Bratislava, Czechoslovakia.

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.

Gianinazzi, S., Schuepp, H. & Masson, J.P. (1995) *Arbuscular Mycorrhizas in Sustainable Soil-Plant Systems*. EC, Brussels, The Netherlands.

Godwin, H. & Clifford, M.H. (1938) Studies in the post-glacial history of British vegetation. I. Origin and stratigraphy of fenland deposits near Woodwalton, Hunts. II. Origin and stratigraphy of deposits in southern fenland. *Philosophical Transactions of the Royal Society of London, Series B, Biology Sciences*, **229**, 323–406.

Godwin, H., Godwin, M.E. & Clifford, M.H. (1935) Controlling factors in the formation of Fen deposits, as shown by peat investigations at Wood Fen, near Ely. *Journal of Ecology*, **23**, 509–535.

Godwin, H. & Tansley, A.G. (1941) Prehistoric charcoals as evidence of former vegetation, soil and climate. *Journal of Ecology*, **29**, 117–126.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley, Chichester, UK.

Guéritte, F. (2001) General and recent aspects of the chemistry and structure-activity relationships of taxoids. *Current Pharmaceutical Design*, **7**, 1229–1249.

Haas, J.N. & Richoz, I. (1995) Flora und vegetation im Schweizer Mittelland und im Jura. *Die Schweiz vom Paläolithikum bis zum Frühen Mittelalter, SPM II* (eds W.E. Stöckli, U. Niffeler & E. Gross-Klee), pp. 58–72. Schweizerische Gesellschaft für Ur- und Frühgeschichte, Basel, Switzerland.

Haeggström, C.-A. (1990) The influence of sheep and cattle grazing on wooded meadows in Åland, SW Finland. *Acta Botanica Fennica*, **141**, 1–28.

Hall, J.E., Kirby, K.J. & Whitbread, A.M. (2001) *National Vegetation Classification: Field Guide to Woodland*. Joint Nature Conservation Committee, Peterborough, UK.

Harley, J.L. (1959) *The Biology of Mycorrhiza*. Leonard Hill, London, UK.

Harley, J.L. & Harley, E.L. (1987) A checklist of mycorrhiza in the British flora. *New Phytologist Suppl*, **105**, 1–102.

Harrison, P.A., Berry, P.M. & Dawson, T.E. (2001) *Climate Change and Nature Conservation in Britain and Ireland: Modelling Natural Resource Responses to Climate Change (the MONARCH Project)*. Technical Report. UK Climate Impacts Programme, Oxford, UK.

Hartley, P.H.T. (1954) Wild fruits in the diet of British thrushes. A study in the ecology of closely allied species. *British Birds*, **47**, 98–107.

Hartzell, H.R. Jr (1991) *The Yew Tree: A Thousand Whispers*. Hulogosi, Eugene, Oregon, USA.

Hartzell, H.R. Jr (1995) Yew and us: a brief history of the yew tree. *Taxol: Science and Applications* (ed. M. Suffness), pp. 27–34. CRC Press, New York, USA.

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* CO$_2$-enrichment differ among species and depend on understorey light availability. *Global Change Biology*, **6**, 213–226.

Havinga, A.J. (1967) Palynology and pollen preservation. *Review of Palaeobotany and Palynology*, **2**, 81–98.

Havlin, J. & Folk, C. (1965) [Food and economic importance of the Starling.]. *Zoologické Listy*, **14**, 193–203.

He, L., Orr, G.A. & Horwitz, S.B. (2001) Novel molecules that interact with microtubules and have functional activity similar to Taxol. *Drug Discovery Today*, **6**, 1153–1164.

Heit, C.E. (1968) Thirty-five years' testing of tree and shrub seed. *Journal of Forestry*, **66**, 632–633.

Heit, C.E. (1969) Propagation from seed. Part 18: testing and growing seeds of popular *Taxus* forms. *American Nurseryman*, 15 January, 10–11, 118–128.

Hejnowicz, A. (1978) Anatomy, embryology and karyology. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 33–54. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Henslow, G. (1889) Yew trees in Berks. *Nature*, **XL**, 621.

Hepting, G. (1971) *Diseases of Forest and Shade Trees of the United States*. Agriculture Handbook no. 386. USDA Forest Service, USA.

Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecological Monographs*, **57**, 305–331.

Hertel, H. & Kohlstock, N. (1996) Genetische Variation und geographische Struktur von Eibenvorkommen (*Taxus baccata* L.) in Mecklenburg-Vorpommern. [Genetic variation and geographic structure of English yew (*Taxus baccata* L.) in Mecklenburg-Vorpommern (Germany)]. *Silvae Genetica*, **45**, 290–294.

Heymer, A. (1966) Beeren und Früchte als Vogelnahrung. *Beiträge zur Vogelkunde*, **12**, 95–102.

Hoffmann, G. (1958) Die eibereichen waldgesellschaften Mitteldeutschlands. *Archiv für Forstwesen*, **7**, no. 6/7.

Höllwarth, M. (1984) Entwicklung der Schwermetallgehalte von Eibennadeln an städtischen Standorten von 1975 bis 1982. [The development of heavy metal contents in needles of *Taxus baccata* at urban habitats 1975–82.]. *Angewandte Botanik*, **58**, 21–30.

Holtan, D. (2001) Barlinda *Taxus baccata* L. i Møre og Romsdal – på veg ut? [*Taxus baccata*. Møre og Romsdal county – a declining species?]. *Blyttia*, **59**, 197–205.

Hook, I., Poupat, C., Ahond, A., Guénard, D., Guéritte, F., Adeline, M.T., Wang, X.P., Dempsey, D., Breuillet, S. & Potier, P. (1999) Seasonal variation of neutral and basic taxoid contents in shoots of European Yew (*Taxus baccata*). *Phytochemistry*, **52**, 1041–1045.

Howard, A.L. (1944) The yew tree (*Taxus baccata*). *Nature*, **154**, 215–216.

Howard, P.J.A., Howard, D.M. & Lowe, L.E. (1998) Effects of tree species and soil physico-chemical conditions on the nature of soil organic matter. *Soil Biology and Biochemistry*, **30**, 285–297.

Hulme, M. & Jenkins, G.J. (1998) *Climate Change Scenarios for the United Kingdom: Scientific Report*. UK Climate Impacts Programme Technical Report no. 1. Climate Research Unit, Norwich, UK.

Hulme, P.E. (1996) Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation. *Journal of Ecology*, **84**, 853–861.

Hulme, P.E. (1997) Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia*, **111**, 91–98.

Hulme, P.E. & Borelli, T. (1999) Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology*, **145**, 149–156.

Hultén, E. & Fries, M. (1986) *Atlas of North European Vascular Plants: North of the Tropic of Cancer I-III*. Koeltz Scientific Books, Königstein, Germany.

International Seed Testing Association (ISTA) (1966) International rules for seed testing. *Proceedings of the International Seed Testing Association*, **31**, 1–152.

Interpretation Manual of European Union Habitats (1999) EUR 15/2. European Commission, Brussels, The Netherlands.

Jaziri, M., Zhiri, A., Guo, Y.-W., Dupont, J.-P., Shimomura, K., Hamada, H., Vanhaelen, M. & Homès, J. (1996) *Taxus* sp. cell, tissue and organ cultures as alternative sources for taxoids production: a literature survey. *Plant Cell Tissue and Organ Culture*, **46**, 59–75.

Jennewein, S. & Croteau, R. (2001) Taxol: biosynthesis, molecular genetics, and biotechnological applications. *Applied Microbiological Biotechnology*, **57**, 13–19.

Jetter, R., Klinger, A. & Schäffer, S. (2002) Very long-chain phenylpropyl and phenylbutyl esters from *Taxus baccata* needle cuticular waxes. *Phytochemistry*, **61**, 579–587.

Johnson, W.T. & Lyon, H.H. (1991) *Insects That Feed on Trees and Shrubs*, 2nd edn. Comstock Publishing Associates Cornell University Press, Ithaca, USA.

Jordan, W.J. (1964) Yew (*Taxus baccata*) poisoning in pheasants (*Phasianus colchicus*). *Tijdschrift voor Diergeneeskunde*, **89**, Suppl. 1, 187–188.

Kamppa, G. (1926) Dendrologinche Erfahrungen in Finnland. *Mitteilungen der Deutsche Dendrologischen Gesellschaft*, **26**, 192–194.

Kapuściński, S. (1947) Cis jako roślina żywicielska. [Yew as a host plant.]. *Wszechświat*, **9**, 267–272.

Kartusch, B. & Richter, H. (1984) Anatomische Reaktionen von Eibennadeln auf eine Erschwerung des Wassertransports in Pflanzenkörper. [Anatomical reactions of yew needles to an impairment of water transport in the plant body]. *Phyton*, **24**, 295–303.

Kelly, D.L. (1975) *Native woodland in western Ireland with especial reference to the region of Killarney*. PhD Thesis, University of Dublin, Ireland.

Kelly, D.L. (1981) The native forest vegetation of Killarney, south-west Ireland – an ecological account. *Journal of Ecology*, **69**, 437–472.

Kepczynski, K. & Peplinska, B. (1995) New localities of protected and rare plant species of the surrounding area of Rogozno Wielkopolskie (Part 1). *Acta Universitatia Nicolai Copernici Biologia*, **48**, 177–183.

Kite, G.C., Lawrence, T.J. & Dauncey, E.A. (2000) Detecting *Taxus* poisoning in horses using liquid chromatography/mass spectrometry. *Veterinary and Human Toxicology*, **42**, 151–154.

Klötzli, F. (1965) *Qualität und Quantität der Rehäsung in Wald- und Grünland-Gesellschaften des nördlichen Schweizer Mittellandes. [Quality and quality of Roe Deer Forage in the Northern Swiss Midlands]*. Veröffentlichungen des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel, in Zürich, 38 Heft. Hans Huber, Bern, Switzerland.

Knowles, J.W. (1949) Yew poisoning in cattle. *Veterinary Record*, **61**, 421–422.

Kontny, P. (1937) Aus des Vergangenheit der Eibe (*Taxus baccata* L.) in Polen. *Acta Societatia Botanicorum Poloniae*, **14**, 57–68.

Krenzelok, E.P., Jacobsen, T.D. & Aronis, J. (1998) Is the yew really poisonous to you? *Journal of Toxicology Clinical Toxicology*, **36**, 219–223.

Król, S. (1978) An outline of ecology. *The Yew – Taxus baccata L.* (eds S. Bartkowiak, S. Białobok, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 65–86. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Kučera, L. (1972) *Wundgewebe in der Eibe* (Taxus baccata *L.*). Eidgenössischen Technischen Hochschule Zürich, Switzerland, Dissertationdruckerel Leemann AG. Dissertation no. 4804.

Lange, O.L. (1961) Die Hitzeresistenz einheimischer immer- und wintergrüner Pflanzen im Jahreslauf. *Planta*, **56**, 666–683.

Larner, J.B. (1977) Sika deer damage to mature woodlands of south-western Ireland. *XIII Congress of Game Biologists* (ed. T.J. Peterle), pp. 192–202. Wildlife Management Institute and the Wildlife Society, Washington, DC, USA.

Larson, D.W., Matthes, U. & Kelly, P.E. (2000) *Cliff Ecology: Pattern and Process in Cliff Ecosystems*. Cambridge University Press, Cambridge, UK.

Laskaris, G., van der Heijden, R. & Verpoorte, R. (2000) Purification and partial characterisation of geranylgeranyl diphosphate synthase, from *Taxus baccata* cell cultures. An enzyme that regulates taxane biosynthesis. *Plant Science*, **51**, 97–105.

Lattin, J.D. (1998) *A Review of the Insects and Mites Found on* Taxus *spp. With Emphasis on Western North America*. General Technical Report, PNW-GTR-433. USDA Forest Service, Pacific Northwest Research Station, USA.

Ledig, F.T. (1986) Heterozygosity, heterosis, and fitness in outbreeding plants. *Conservation Biology: The Science of Scarcity and Diversity* (ed. M. E. Soule), pp. 77–104. Sinauer, Sunderland, Massachusetts, USA.

Lemer, B.R. (2001) *Roadside de-Icing Salts and Ornamental Plants*. Department of Horticulture. Purdue University Cooperative Extension Service, Landscape Horticulture, HO-142-W.

Lemieux, N., Maynard, B.K. & Johnson, W.A. (2000) A regional survey of deer damage throughout northeast nurs- [illegible] **18**, 1–4.

Levisohn, I. (1954) Occurrence of ectotrophic and endotrophic mycorrhizas in forest trees. *Forestry*, **27**, 145–146.

Lewandowski, A., Burczyk, J. & Mejnartowicz, L. (1995) Genetic structure of English yew (*Taxus baccata* L.) in the Wierzchlas Reserve: implications for genetic conservation. *Forest Ecology and Management*, **73**, 221–227.

Lilpop, J. (1931) Stanowisko cisow na Hysej Gorze pod Starym Zmigrodem. [The yew stand on Hysa Gora near Stary Zmigrod]. *Ochrona Przyrody*, **9**, 209.

Long, H.C. (1938) Poisonous Plants on the Farm. *Bulletin of the Ministry of Agriculture*, *London*, 75.

Lowe, J. (1897) *The Yew Trees of Great Britain and Ireland*. Macmillan, London, UK.

Lyubenova, M., Mirchev, S. & Nedelchev, R. (2001) Dendrochronological investigation of *Taxus baccata* L. from the common yew-beech forests in 'Central Balkan' National Park. *Third Balkan Scientific Conference,* **Part 1**, 108–115.

Lyubenova, M. & Nedelchev, R. (2001) Influence of human factors on population of *Taxus baccata* L. *Journal of Balkan Ecology*, **4**, 382–388.

Maly, K. (1930) Dendrologisches aus Illyrien. *Mitteilungen der Deutschen Dendrologischen Gesellschaft*, **42**, 127–136.

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and humid Atlantic zones. *Bioresource Technology*, **61**, 111–119.

O'Connell, M., Mitchell, F.J.G., Readman, P.W., Doherty, T.J. & Murray, D.A. (1987) Palaeoecological investigations towards the reconstruction of the post-glacial environment at Lough Doo, County Mayo, Ireland. *Journal of Quaternary Science*, **2**, 149–164.

O'Connell, M. & Molloy, K. (2001) Farming and woodland dynamics in Ireland during the Neolithic. *Biology and Environment: Proceedings of the Royal Irish Academy*, **101B**, 99–128.

O'Connell, M., Molloy, K. & Bowler, M. (1988) Post-glacial landscape evolution in Connemara, western Ireland with particular reference to woodland history. *The Cultural Landscape – Past, Present and Future* (eds H.H. Birks, H.J.B. Birks, P.E. Kaland & D. Moe), pp. 487–514. Cambridge University Press, Cambridge, UK.

O'Connell, M., Molloy, K. & McMahon, H. (2001) Reconstructing prehistoric farming activity and human impact at a fine spatial resolution: palaeoecological investigations at Mooghaun, Co. Clare, western Ireland. *Beiträge zur Siedlungsarchäologie und zum Landschaftswandel. Regensburger Beiträge zur Prähistorischen Archäologie*, **7**, 161–186.

Oliver, J. (1998) Plant defences versus mammals. *Botanical Society of the British Isles News*, **79**, 24–27.

Orr, A.B. (1952) Poisoning in domestic animals and birds. *Veterinary Record*, **64**, 339–343.

Page-Degivry, M.T. Le & Garello, G. (1973) La dormance embryonnaire chez *Taxus baccata*: influence de la composition du milieu liquide sur l'induction de la germination. *Physiologia Plantarum*, **29**, 204–207.

Panter, K.E., Molyneux, R.J., Smart, R.A., Mitchell, L. & Hansen, S. (1993) English yew poisoning in 43 cattle. *Journal of the American Veterinary Medical Association*, **202**, 1476–1477.

Parc, G., Canaguier, A., Landré, P., Hocquemiller, R., Chriqui, D. & Meyer, M. (2002) Production of taxoids with biological activity by plants and callus culture from selected *Taxus* genotypes. *Phytochemistry*, **59**, 725–730.

Parker, J. (1971) Unusual tonoplast in conifer leaves. *Nature*, **234**, 231.

Parmar, V.S., Jha, A., Bisht, K.S., Taneja, P., Singh, S.K., Kumar, A., Poonam, Jain, R. & Olsen, C.E. (1999) Constituents of the yew trees. *Phytochemistry*, **50**, 1267–1304.

Parsapajouh, D., Bräker, O.U., Habibi, H. & Schär, E. (1986) Etude dendroclimatologique du bois de *Taxus baccata* du nord de l'Iran. *Schweizerische Zeitschrift für Forstwesen*, **137**, 853–868.

Pavletic, Z. & Lieth, H. (1958) Der Lichtkompensationspunkt einiger immergrüner Pflanzen im Winter und im Frühjahr. *Bericht der Deutschen Botanischen Gesellschaft*, **71**, 309–314.

Pax, F. (1908) *Grundzüge der Pflanzenverbreitung in den Karpathen*. Verlag Wilhelm Engelmann, Leipzig, Germany.

Peace, T.R. (1962) *Pathology of Trees and Shrubs*. Clarendon Press, Oxford, UK.

Pehl, L. & Wulf, A. (2002) Nadelschäden an *Taxus baccata* L. durch *Cryptocline taxicola* (All.) Petr. [Needle disease on *Taxus baccata* L. caused by *Cryptocline taxicola* (All.) Petr.]. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, **54**, 266–268.

Peñalba, M.C. (1994) The history of the Holocene vegetation in northern Spain from pollen analysis. *Journal of Ecology*, **82**, 815–832.

Pennell, R.I. & Bell, P.R. (1986) The development of the male gametophyte and spermatogenesis in *Taxus baccata* L. *Proceedings of the Royal Society of London B*, **228** (1250), 85–96.

Pieroni, A. (1999) Gathered wild food plants in the upper valley of the Serchio River (Garfagnana), Central Italy. *Economic Botany*, **53**, 327–341.

Piffard, H.G. (1881) *A Treatise on the Materia Medica and Therapeutics of the Skin*. William Wood, New York, USA.

Pigott, C.D. (1969) The status of *Tilia cordata* and *T. platyphyllos* on the Derbyshire limestone. *Journal of Ecology*, **57**, 491–504.

Pilkington, N., Proctor, J. & Reid, K.I. (1994) The Inchlonaig yews, their tree epiphytes, and their tree partners. *Glasgow Naturalist*, **22**, 365–373.

Pisek, A. & Larcher, W. (1973) The normal temperature range. *Temperature and Life* (eds H. Precht, J. Christophersen, H. Hensel & W. Larcher), pp. 102–144. Springer-Verlag Berlin, Germany.

Pisek, A., Larcher, W., Moser, W. & Pack, I. (1969) Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. III. Temperaturabhangigkeit und optimaler Temperaturbereich der Netto-Photosynthese. *Flora*, **158**, 608–630.

Pisek, A., Larcher, W., Pack, I. & Unterholzner, R. (1968) Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. II. Temperaturmaximum der Netto-Photosynthese und Hitzeresistenz der Blätter. *Flora*, **158**, 110–128.

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.

Pisek, A. & Rehner, G. (1958) Temperaturminima der Netto – assimilation von Mediterranean und nordisch-alpinen Immergrünen. *Bericht der Deutschen Botanischen Gesellschaft*, **71**, 188–193.

Prat, H. (1926) Étude des mycorrhizes du *Taxus baccata*. *Annales des Sciences Naturelles (Botanique)*, **8**, 141–162.

Preston, C.D. & Hill, M.O. (1997) The geographical relationships of British and Irish vascular plants. *Botanical Journal of the Linnean Society*, **124**, 1–120.

Pridnya, M.V. (1984) Phytocoenotic status and structure of the Khosta common-yew population in the Caucasus Biosphere Reserve. *Soviet Journal of Ecology*, **15**, 1–6.

Pritchard, A.E. & Baker, E.W. (1951) The false spider mites of California (Acarina: Phytoptipalpidae). *Publications in Entomology, University of California, Berkeley*, **9**, 1–93.

Rackham, O. (1990) *Trees and Woodland in the British Landscape*. Dent, London, UK.

Rajewski, M., Lange, S. & Hattemer, H.H. (2000) Reproduktion bei der Generhaltung seltener Baumarten: das Beispiel der Eibe (*Taxus baccata* L.). [Problems of reproduction in the genetic conservation of rare tree species: the example of common yew (*Taxus baccata* L.)]. *Forest Snow and Landscape Research*, **75**, 251–266.

Ratcliffe, D.A., ed. (1977) *A Nature Conservation Review*. Cambridge University Press, Cambridge, UK.

Redding, L.W. (1971) *Resistance of Timbers to Impregnation with Creosote*. Forest Products Research Bulletin no. 54. HMSO, London, UK.

Redfern, M. (1975) The life history and morphology of the early stages of the yew gall midge, *Taxomyia taxi* (Inchbald) (Diptera: Cecidomyiidae). *Journal of Natural History*, **9**, 513–533.

Renwick, J. (1913) Notes on yew trees (*Taxus baccata* L.) in the Clyde area. *Glasgow Naturalist*, **5**, 19–33.

Richard, P. (1985) Contribution aéropalynologique a l'étude de l'action des facteurs climatiques sur la floraison de l'orme (*Ulmus campestris*) et de l'if (*Taxus baccata*). *Pollen Spores*, **27**, 53–94.

Richter, H. (1974) Erhöhte Saugspannungswerte und morphologische Veränderungen durch transversale Einschnitte in einem *Taxus*-Stamm. [Elevated suction tensions and morphological alterations caused by transverse cuts in a *Taxus* stem]. *Flora*, **163**, 291–309.

Ridley, G.S. (1994) Mycological records. 1: *Diplodia taxi* (Sowerby) de Notaris. *New Zealand Journal of Forestry Science*, **24**, 69–70.

Rodwell, J.S. (1991) *British Plant Communities*, Vol. 1 *Woodlands and Scrub*. Cambridge University Press, Cambridge, UK.

van Rozendaal, E.L.M., Kurstjens, S.J.L., van Beek, T.A. & van den Berg, R.G. (1999) Chemotaxonomy of *Taxus*. *Phytochemistry*, **52**, 427–433.

Ruguzov, I.A., Sklonnaya, L.U. & Chobotar, A.A. (1992) Pollination drop in conifers. *Botanicheskiĩ Zhurnal*, **77**, 40–52.

Safarov, I.S. (1986) Rare and disappearing species of eastern Transcaucasian USSR dendroflora and their preservation. *Botanicheskiĩ Zhurnal*, **71**, 102–108.

Sainz, M.J., Iglesias, I., Vilariño, A., Pintos, C. & Mansilla, J.P. (2000) Improved production of nursery stock of *Taxus baccata* L. through management of the arbuscular mycorrhizal symbiosis. *Acta Horticulturae*, **536**, 379–384.

Salisbury, E.J. (1927) On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London, B*, **216**, 1–65.

Salisbury, E.J. & Jane, F.W. (1940) Charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times. *Journal of Ecology*, **28**, 310–325.

Saniga, M. (2000) Štruktúra, produkčné a regeneračné pocesy tisa občajného v Štátnej Prírodnej Rezervácii Plavno [Structure, production and regeneration processes of English yew in the State Nature Reserve Plavno]. *Journal of Forest Science (Prague)*, **46**, 76–90.

Sarmaja-Korjonen, K., Vasari, Y. & Haeggström, C.-A. (1991) *Taxus baccata* and influence of Iron Age man on the vegetation in Åland S.W. Finland. *Annales Botanica Fennici*, **28**, 143–159.

Sax, K. & Sax, H.J. (1933) Chromosome number and morphology in the conifers. *Journal of the Arnold Arboretum*, **XIV**, 356–374 (plus two end plates).

Schneck, V. (1996) Studies on the influence of clone on rooting ability and quality in the propagation of cuttings from 40 to 350-year old yews (*Taxus baccata* L.). *Silvae Genetica*, **45**, 246–249.

Schweingruber, F.H. (1993) *Trees and Wood in Dendrochronology*. Springer, Berlin, Germany.

Seidling, W. (1999) Spatial structures of a subspontaneous population of *Taxus baccata* saplings. *Flora*, **194**, 439–451.

Senear, F.E. (1933) Dermatitis due to woods. *Journal of the American Medical Association*, **101**, 1527.

Shanker, K., Pathak, N.K.R., Trivedi, V.P., Chansuria, J.P.N. & Pandey, V.B. (2002) An evaluation of toxicity of *Taxus baccata* Linn. (Talispatra) in experimental animals. *Journal of Ethnopharmacology*, **79**, 69–73.

Siwecki, R. (1978) Diseases and parasitic insects of the yew. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 103–109. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Skorupski, M. & Luxton, M. (1998) Mesostigmatid mites (Acari: Parasitiformes) associated with yew (*Taxus baccata*) in England and Wales. *Journal of Natural History*, **32**, 419–439.

Smal, C.M. & Fairley, J.S. (1980a) Food of wood mice and bank voles in oak and yew woods in Killarney, Ireland. *Journal of Zoology*, **191**, 413–418.

Smal, C.M. & Fairley, J.S. (1980b) The fruits available as food to small rodents in two woodland ecosystems. *Holarctic Ecology*, **3**, 10–18.

Smit, M.P. (1992) Intoxicatie van lammeren door *Taxus baccata* en vleeskeuring. [*Taxus baccata* in lambs and meat inspection]. *Tijdschrift voor Diergeneeskunde*, **117**, 697–699.

Smith, C.O. (1942) Crown galls on species of Taxaceae, Taxodiaceae and Pinaceae as determined by artificial inoculations. *Phytopathology*, **32**, 1005–1009.

Snow, B. & Snow, D. (1988) *Birds and Berries*. T. & A.D. Poyser Ltd, Calton, Staffordshire, UK.

Sokolowski, S. (1921) Cisy na ziemiach Polskich i w krazach przyleglych. [Yew in Poland and neighbouring countries]. *Ochrona Przyrody*, **2**, 4–22.

Sorensen, A.E. (1984) Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology*, **53**, 545–557.

Spindler, K. (1994) *The Man in the Ice*. Weidenfeld & Nicolson, London, UK.

Spjut, R.W. (2000) *Introduction to Taxus*. http://www.worldbotanical.com/Introduction.htm

Sporne, K.R. (1974) *The Morphology of Gymnosperms*, 2nd edn. Hutchinson, London, UK.

Środoń, A. (1978) History of the yew in Poland. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 5–14. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Stace, C. (1997) *New Flora of the British Isles*, 2nd edn. Cambridge University Press, Cambridge, UK.

Strobel, G.A. & Hess, W.M. (1997) Glucosylation of the peptide leucinostatin A, produced by an endophytic fungus of European yew, may protect the host from leucinostatin toxicity. *Chemistry and Biology*, **4**, 529–536.

Strobel, G.A., Hess, W.M., Ford, E., Sidhu, R.S. & Yang, X. (1996) Taxol from fungal endophytes and the issue of biodiversity. *Journal of Industrial Microbiology*, **17**, 417–423.

Strobel, G.A., Torczynski, R. & Bollon, A. (1997) *Acremonium* sp.: a leucinostatin A producing endophyte of European yew (*Taxus baccata*). *Plant Science (Shannon)*, **128**, 97–108.

Strouts, R.G. (1993) *Phytophthora* root disease. *Arboriculture Research Note*, 58/93/PATH.

Strouts, R.G. & Winter, T.G. (1994) *Diagnosis of Ill-Health in Trees*. Research for Amenity Trees no. 2. HMSO/Forestry Commission, London, UK.

Strullu, D.G. (1978) Histologie et cytologie des endomycorhizes. *Physiologie Végétale*, **16**, 657–669.

Strullu, D.G. (1991) *Les Mycorrhizes des Arbres et Plantes Cultivées. Technique et Documentation*. Lavoisier, Paris, France.

Stützel, T. & Röwekamp, I. (1999) Female reproductive structures in Taxales. *Flora*, **194**, 145–157.

Suffness, M. (1995) *Taxol: Science and Applications*. CRC Press, New York, USA.

Sukachev, V.N. (1928) *Lesnye Porody. Sistematika Geografiya i Fitosociologiya ikh. Kvoinye Vip. I [Forest Trees Taxonomy, Range and Ecology Part I Coniferae]*. Moscow, Russia.

Sukatschev, W. (1908) Über des vorkommen der Samen von *Euryale ferox* Salisb. in einer interglazialen Ablagerungen in Russland. *Bericht der Deutschen Botanischen Gesellschaft*, **26**, 132–137.

Suszka, B. (1978) Generative and vegetative reproduction. *The Yew –* Taxus baccata *L.* (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 87–102. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Suszka, B. (1985) Conditions for after-ripening and germination of seeds and for seedling emergence of the English yew (*Taxus baccata* L.). *Arboretum Kórnickie*, **30**, 285–338.

Svenning, J.-C. & Magård, E. (1999) Population ecology and conservation status of the last natural population of English yew *Taxus baccata*. Denmark. *Biological Conservation*, **88**, 173–182.

Symes, R.G. (1879) *Memoirs of the Geological Survey*. HMSO, Dublin, Ireland.

Szaniawski, R.K. (1978) An outline of yew physiology. *The Yew – Taxus baccata L*. (eds S. Bartkowiak, W. Bugala, A. Czartoryski, A. Hejnowicz, S. Król, A. Środoń & R.K. Szaniawski), pp. 55–64. Foreign Scientific Publications, Department of the National Center for Scientific and Technical, and Economic Information (for the Department of Agriculture and the National Science Foundation, Washington, DC), Warsaw, Poland.

Szijj, J. (1957) The food biology of the Starling and its agricultural importance. *Aquila*, **63**–**64**, 71–101.

Tabbush, P. (1997) Estimating the age of churchyard yews. *Proceedings from Veteran Trees: Habitat, Hazard or Heritage?* Royal Agricultural Society of England and the Royal Forestry Society, March 1997.

Tabbush, P. & White, J. (1996) Estimation of tree age in ancient yew woodland at Kingley Vale. *Quarterly Journal of Forestry*, **90**, 197–206.

Tansley, A.G. & Rankin, W.M. (1911) The plant formation of calcareous soils. B. The sub-formation of the Chalk. *Types of British Vegetation* (ed. A.G. Tansley), pp. 161–186. Cambridge University Press, Cambridge, UK.

Tegetmeier, W.B. (1896) Pheasants poisoned by yew leaves. *Field, 28 November*, **2292**, 879.

Till, O. (1956) Über die Frosthärte von Pflanzen sommergrüner Laubwälder. *Flora*, **143**, 499–542.

Tittensor, R.M. (1980) Ecological history of yew *Taxus baccata* L. in southern England. *Biological Conservation*, **17**, 243–265.

van Tol, R.W.H.M., Visser, J.H. & Sabelis, M.W. (2000) Responses of the black vine weevil (*Otiorhynchus sulcatus*) to weevil and host-plant odours. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (NEV)*, **11**, 109–114.

Traczyk, T. (1953) Obserwacje nad rozmieszeniem cisa (*Taxus baccata* L.) w Sudetach. [Observations on the distribution of yew (*Taxus baccata* L.) in the Sudeten]. *Annales Universitatis Mariae Curie – Sklodowska Sectio C Biologia*, **8**, 103–119.

Turner, J.S. & Watt, A.S. (1939) The oakwoods (*Quercetum sessiliflorae*) of Killarney, Ireland. *Journal of Ecology*, **27**, 202–233.

Tutin, T.G. (1953) The vegetation of the Azores. *Journal of Ecology*, **41**, 53–61.

Tzedakis, P.C., Andrieu, V., de Beaulieu, J.-L., Birks, H.J.B., Crowhurst, S., Follieri, M., Hooghiemstra, H., Magri, D., Reille, M., Sadori, L., Shackletone, N.J. & Wijmstra, T.A. (2001) Establishing a terrestrial chronological framework as a basis for biostratigraphical comparisons. *Quaternary Science Reviews*, **20**, 1583–1592.

USDA (1948) *Woody-Plant Seed Manual*. Miscellaneous Publication no. 654. United States Department of Agriculture, Forest service, Washington, DC, USA.

USDA (1974) *Seeds of Woody Plants in the United States*. Agricultural Handbook 450. United States Department of Agriculture, Forest Service, Washington, DC, USA.

Vacik, H., Oitzinger, G. & Georg, F. (2001) Population viability risk management (PVRM) zur Evaluierung von *in situ* Erhaltungsstrategien der Eibe (*Taxus baccata* L.) in Bad Bleiberg. [Evaluation of *situ* conservation strategies for English yew (*Taxus baccata* L.) in Bad Bleiberg by the use of population viability risk management (PVRM)]. *Forstwissenschaftliches Centralblatt*, **120**, 390–405.

Vaishampayan, U., Parchment, R.E., Jasti, B.R. & Hussain, M. (1999) Taxanes: an overview of the pharmacokinetics and pharmacodynamics. *Urology*, **54** (6A Suppl.), 22–29.

Van Ingen, G., Visser, R., Peltenburg, H., Van Der Ark, A.M. & Voortman, M. (1992) Sudden unexpected death due to *Taxus* poisoning. A report of five cases, with review of the literature. *Forensic Science International*, **56**, 81–87.

Vesela, D., Saman, D., Valterova, I. & Vanek, T. (1999) Seasonal variations in the content of taxanes in the bark of *Taxus baccata* L. *Phytochemical Analysis*, **10**, 319–321.

Vidaković, M. (1991) *Conifers: Morphology and Variation*. (Translated by M. Šoljan). Grafički Zavod Hrvatske, Zagreb, Croatia.

Vogler, P. (1904) Die Eibe (*Taxus baccata* L.) in der Schweiz. *Jahrbuch der St. Gallischen Naturwissenschaftlichen Gesellschaft für das Vereinsjahr*, **1903**, 436–491.

Voliotis, D. (1986) Historical and environmental significance of the yew (*Taxus baccata* L.). *Israel Journal of Botany*, **35**, 47–52.

Von der Werth, J. & Murphy, J.J. (1994) Cardiovascular toxicity associated with yew leaf ingestion. *British Heart Journal*, **72**, 92–93.

de Vries, B.W.L. & Kuyper, Th.W. (1990) Holzbewohnende Pilze auf Eibe (T*axus baccata*). [Lignicolous fungi on yew (*Taxus baccata*).]. *Zeitschrift für Mykologie*, **56**, 87–94.

Wahl, P.-G., Kersten, W., Mehlan, W. & Stollewerk, D. (1992) Eine seltene Sensibisierung gegenüber Nadelbäumen. [A rare sensitization against coniferous trees]. *Allergologie*, **15**, 43–45.

Walker, K. & Croteau, R. (2001) Taxol biosynthetic genes. *Phytochemistry*, **58**, 1–7.

Waller, M.P. & Hamilton, S. (2000) Vegetation history of the English chalklands: a mid-Holocene pollen sequence from the Caburn, East Sussex. *Journal of Quaternary Science*, **15**, 253–272.

Watt, A.S. (1924) On the ecology of British beechwoods with special reference to their regeneration. II. The development and structure of the beech communities on the Sussex Downs. *Journal of Ecology*, **12**, 145–204.

Watt, A.S. (1926) Yew communities of the South Downs. *Journal of Ecology*, **14**, 282–316.

Watt, A.S. (1934a) The vegetation of the Chiltern Hills, with special reference to the beechwoods and their seral relationships. *Journal of Ecology*, **22**, 230–270.

Watt, A.S. (1934b) The vegetation of the Chiltern Hills, with special reference to the beechwoods and their seral relationships. II. The vegetation of the plateaus. *Journal of Ecology*, **22**, 445–507.

Watts, W.A. (1967) Interglacial deposits in Kildromin Townland, near Herbertstown, Co. Limerick. *Proceedings of the Royal Irish Academy, Section B*, **65**, 339–348.

Watts, W.A. (1984) The Holocene vegetation of the Burren, western Ireland. *Lake Sediments and Environmental History* (eds E.Y. Haworth & J.W.G. Lund), pp. 359–376. Leicester University Press, Leicester, UK.

Watts, W.A., Allen, J.R.M., Huntley, B. & Fritz, S.C. (1996) Vegetation history and climate of the last 15,000 years at Laghi di Monticchio, southern Italy. *Quaternary Science Reviews*, **15**, 113–132.

Webb, D. (1977) *An Irish Flora*, 6th edn. Dungalgan Press, Dundalk, Ireland.

Welch, H. & Haddow, G. (1993) *The World Checklist of Conifers*. The World Conifer Data Pool/Landsman's, Herefordshire, UK.

West, R.G. (1962) A note on *Taxus* pollen in the Hoxnian Interglacial. *New Phytologist*, **61**, 189–190.

Wheeler, A.J. (1992) Vegetational succession, acidification and allogenic events as recorded in Flandrian peat deposits from an isolated Fenland embayment. *New Phytologist*, **122**, 745–756.

White, J.E.J. (1998) *Estimating the Age of Large and Veteran Trees in Britain*. Forestry Commission Information Note 012. HMSO/Forestry Commission, London, UK.

Wiechert, J.M., Zwart, P. & Mathes, K. (2000) Eibenvergiftung in einem Schildkrötenbestand. [Yew-intoxication in tortoises]. *Der Praktische Tierarzt*, **81**, 167–171.

Wilks, J.H. (1972) *Trees of the British Isles in History and Legend*. Muller, London, UK.

Willaert, W., Claessens, P., Vankelecom, B. & Vanderhyden, M. (2002) Intoxication with *Taxus baccata*: cardiac arrhythmias following yew leaves ingestion. *PACE*, **25**, 511–512.

Willerding, U. (1968) Beiträge zur Geschichte der Eibe (*Taxus baccata* L.). Untersuchungen über das Eibenvorkommen in Plesswald bei Göttingen *Plesse-Archiv, Göttingen*, **3**, 1–155.

Williamson, R. (1978) *The Great Yew Forest – The Natural History of Kingley Vale*. Macmillan, London, UK.

Williamson, R. & Williamson, K. (1973) The bird community of yew woodland at Kingley Vale, Sussex. *British Birds*, **66**, 12–23.

Wilson, C.R., Sauer, J.M. & Hooser, S.B. (2001) Taxines: a review of the mechanism and toxicity of yew (*Taxus* spp.) alkaloids. *Toxicon*, **39**, 175–185.

Winter, T.G. (1983) *A Catalogue of Phytophagous Insects and Mites on Trees in Great Britain*. Booklet 53. HMSO/Forestry Commission, London, UK.

Wolff, R.L., Deluc, L.G. & Marpeau, A.M. (1996) Conifer seeds: oil content and fatty acid composition. *Journal of the American Oil Chemists Society*, **73**, 765–771.

Woods, B. & Calnan, C.D. (1976) Toxic woods. *British Journal of Dermatology*, **95** (Suppl. 13), 1–97.

Worsøe, E. (1985) Er taks (*Taxus baccata* L.) vildtvoksende i Danmark? [Does yew (*Taxus baccata* L.) grow wild in Denmark?]. *Flora og Fauna*, **91**, 22–26.

Wright, E.V. & Churchill, D.M. (1965) The boats from north Ferriby, Yorkshire, England, with a review of the origins of the sewn boats of the Bronze Age. *Proceedings of the Prehistoric Society*, **31**, 1–24.

Wyman, D. (1947) Seed collecting dates of woody plants. *Arnoldia*, **7**, 53–56.