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THE HOLOCENE HISTORY OF *TAXUS BACCATA* (YEW) IN BELGIUM AND NEIGHBOURING REGIONS

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ABSTRACT. — The current natural distribution of *Taxus baccata* L. in Belgium is limited to a few localities in the southern part of the country. In these localities, *Taxus* is predominantly growing on steep, calcareous slopes, which is believed to be its natural habitat in this part of the world. In Flanders, the northern part of Belgium, *Taxus* is considered not to be native and *Taxus* stands are interpreted there as being planted by humans or as garden escapes. The Holocene pollen and macrofossil data for *Taxus*, however, show a very different picture regarding abundance and geographical distribution, as well as habitat. It appears that during the Sub-boreal, *Taxus* grew in the coastal plain and the lower Scheldt valley, where it was part of the carr vegetation on peat. Before the end of the Sub-boreal, *Taxus* seems to have disappeared from this region, most probably because of the transition from the carr vegetation to (raised) bogs. Belgium is not the only case where such observations have been made. In other areas of northwestern Europe, *Taxus* also seems to have had a completely different distribution and ecology in the past, especially during the Sub-boreal.

An overview of the palaeobotanical finds of *Taxus baccata* from Belgium is here given, supplemented with finds from neighbouring regions. The Holocene distribution and palaeoecology of *Taxus baccata* are discussed in a broader northwest European context.

KEY WORDS. — *Taxus baccata* L., Belgium, Holocene, vegetation history, yew.

INTRODUCTION

During most of the Pleistocene interglacial periods, *Taxus* formed a much more important element of the vegetation of northwestern Europe than during the Holocene (AVERDIECK 1971, GODWIN 1975, ZAGWIJN 1992, LANG 1994). *Taxus* has been found in Belgium as early as the Tiglian-C5 interglacial period (ca. 2-1.8 million yrs BP; Pleistocene chronozones according to LANG 1994) (KASSE 1988) and seems to have had its greatest expansion in northwestern Europe during the Holstein interglacial (400 – 367 ka BP), a period characterised by a warm oceanic climate (JESSEN *et al.* 1959, WEST 1962, KELLY 1964, GODWIN 1975, WATTS 1985). High percentages of both *Taxus* pollen and macroremains have been found at several northwest European sites where Holsteinian sediments are preserved. High percentages of *Taxus* pollen have also been found at several sites in Belgium, in sediments dating from this period (DE GROOTE 1977, PONNIAH 1977, SOMMÉ *et al.* 1978). The most famous palaeobotanical record of *Taxus* dating from the Holstein interglacial, however, is a spear made of *Taxus* wood found at Clacton (Essex, UK; GODWIN

1975), which is also one of the oldest known artefacts made of wood.

During the last interglacial period before the Holocene, the Eemian (130 – 115 ka BP), *Taxus* also played a more important role in the vegetation in northwestern Europe than during the Holocene, although the pollen percentages are much lower than during the Holstein interglacial (BEHRE 1962, ANDERSEN 1975, WOILLARD 1979, LANG 1994). ZAGWIJN (1983, 1992) even distinguished a *Taxus* subzone in his zonation of the Eemian period in the Netherlands. In Belgium, both pollen and wood of *Taxus* have been found in Eemian peat deposits at Beernem (DE GROOTE 1977, DEFORCE 1997, KLINCK 1999).

During the present interglacial period, the Holocene, *Taxus* seems to have played a less important role in the vegetation. However, during the Sub-boreal (5 000 – 2 500 uncal. BP; Holocene chronozones according to MANGERUD *et al.* 1974), *Taxus* was more abundant and showed a completely different distribution and ecology than nowadays. The aim of this paper is to review the available data on the Holocene history of *Taxus* and to discuss its past distribution and ecology. Furthermore, the existing hypotheses for the Holocene *Taxus* decline will be evaluated in the light of the available palaeobotanical data.

PRESENT-DAY ECOLOGY AND DISTRIBUTION

There is no scientific agreement on the exact taxonomic position of the genus *Taxus*, which encompasses about seven closely related species scattered throughout the northern temperate region (VOLIOTIS 1986, DEMPSEY & HOOK 2000, THOMAS & POLWARD 2003). The species separation within the genus is equally disputed (VAN VUURE 1990, DELAHUNTY 2002, THOMAS & POLWART 2003), although recent genetic research (COLLINS *et al.* 2003) shows that the current species delimitations are well founded.

Taxus baccata L. (subsequently referred to as *Taxus*), the species native to Europe, is an evergreen needle-leaved gymnosperm shrub or tree, growing up to 28 m high. The species is slow-growing and long-living, reaching maturity only at ca. 70 years. It is extremely shade tolerant but can withstand full exposure to the sun (TUTIN *et al.* 1964, THOMAS & POLWART 2003). *Taxus* is normally dioecious, rarely monoecious and is wind-pollinated (TUTIN *et al.* 1964, THOMAS & POLWARD 2003). It flowers from February to April (RICHARD 1985).

Taxus occurs throughout most of Europe and some parts of northern Africa, although its distribution is very scattered. *Taxus* thrives best in regions with a mild, oceanic climate. Its distribution is limited by low temperatures in Scandinavia, a severe continental climate in eastern Europe and aridity and high temperatures in Turkey and north Africa (THOMAS & POLWART 2003). In the Mediterranean region, *Taxus* is confined to the higher mountains (TUTIN *et al.* 1964).

Taxus does not form pure monospecies stands (except in the Caucasus Mountains and on chalk and limestone in England) but belongs to diverse forest communities mainly composed of *Abies*, *Fagus*, *Carpinus*, *Alnus* and *Picea* (ELLENBERG *et al.* 1991, JAHN 1991, ISZULO & BORATYNSKI 2004).

In Europe, most of the natural stands of *Taxus* grow on well-drained calcareous soils, although the tree can grow on almost any soil, including silicious soils derived from igneous and sedimentary rocks (THOMAS & POLWART 2003). In most countries, *Taxus* is a declining or even threatened species. The reasons are thought to be deforestation, selective felling and grazing (MUHLE 1979, SVENNING & MAGÅRD 1999, NAVYS 2000, HOLTAN 2001, THOMAS & POLWART 2003, MYSTERUD & ØSTBYE 2004). Several protected areas have been established to conserve the species (SVALASTOG & HØLAND 1991, HARTZELL 1991, KRÓL 1993, BRANDE 2002), which also survives in a cultivated form as an ornamental tree in parks, gardens, and cemeteries (KRÜSSMANN 1972, SAINTENOY-SIMON 2006).

In Belgium, the current natural distribution of *Taxus* is limited to a few localities in the southern part of the country, namely the southern and western part of the Meuse district (Fig. 1; LAWALRÉE 1952, DUVIGNEAUD 1965, GALOUX 1979, VAN ROMPAEY & DEVOSALLE 1979, SAINTENOY-SIMON

1983, 2006, LAMBINON *et al.* 1998). At these localities, *Taxus* predominantly grows on steep, calcareous slopes, which are believed to be its natural habitat in the region (LAMBINON *et al.* 1998). *Taxus* grows there together with *Fagus sylvatica*, *Carpinus betulus*, *Quercus robur*, *Q. petraea*, *Tilia platyphyllos* and, sometimes, *Ulmus* spp. and *Corylus avellana* (DUVIGNEAUD 1965, GALOUX 1979). In Flanders, the northern part of Belgium, *Taxus* is considered not to be native and *Taxus* stands are interpreted there as having been planted by humans or as escapes

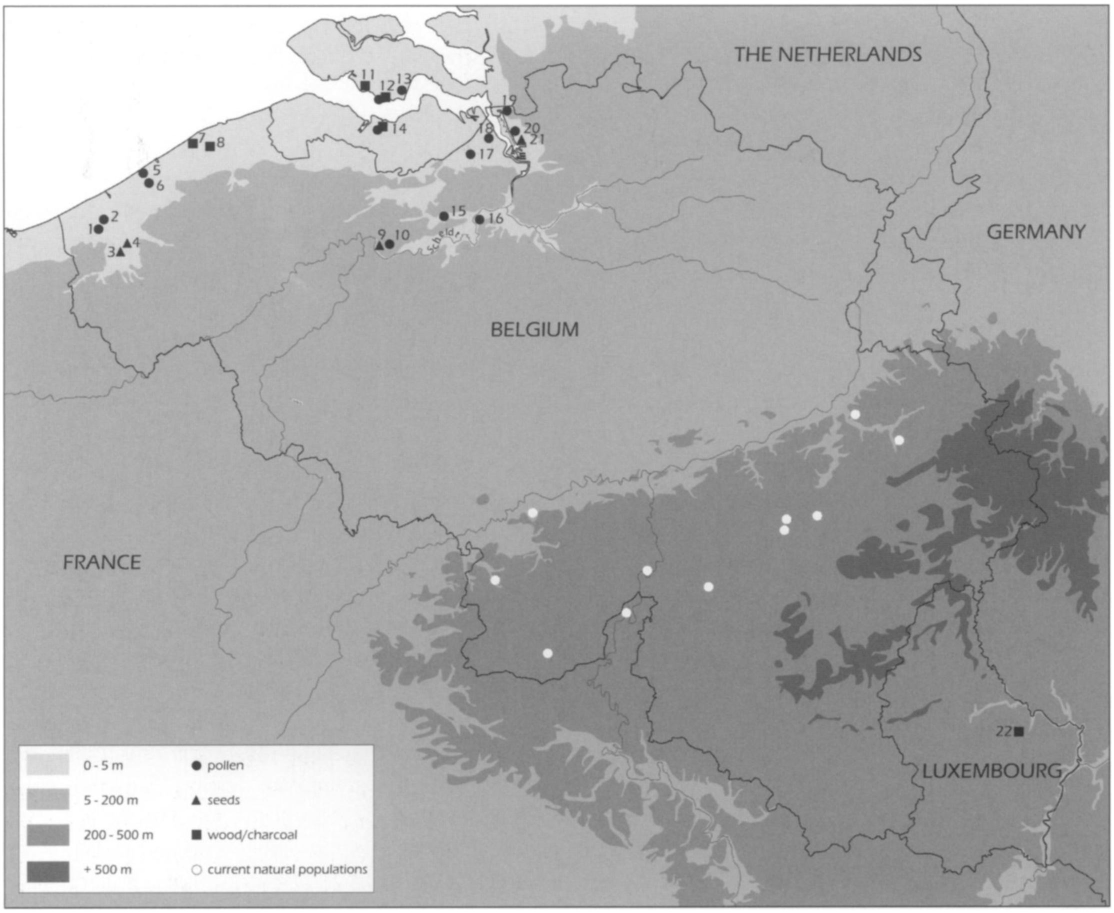

Fig. 1. Map showing both the current natural distribution and subfossil finds of *Taxus baccata* in Belgium: white dots denote natural *T. baccata* populations (data from LAWALRÉE 1952, VAN ROMPAEY & DEVOSALLE 1979, SAINTENOY-SIMON 2006, VAN LANDUYT *et al.* 2006, and MAES *et al.* 2006); black symbols denote Holocene palaeobotanical records of pollen, seeds and wood/charcoal of *Taxus*. (1) Avekapelle 363 (BAETEMAN & VERBRUGGEN 1979); (2) Booitshoeke (BAETEMAN & VERBRUGGEN 1979); (3) Oudekapelle (STOCKMANS & VANHOORNE 1954); (4) Sint-Jacobs-Kapelle (STOCKMANS & VANHOORNE 1954); (5) Raversijde (DEFORCE & BASTIAENS, in press); (6) Leffinge (BAETEMAN *et al.* 1981); (7) Wenduine (MERTENS 1958); (8) Blankenbergse vaart - Zuid (ALLEMEERSCH 1991); (9) Heusden (STOCKMANS 1945); (10) Laarne – Damvallei (VERBRUGGEN 1971); (11) Borsele (NL)(VAN RIJN 2001); (12) Ellewoutsdijk (NL)(VAN RIJN 2003, VAN SMEERDIJK 2003); (13) Baarland (NL)(DE JONG 1986); (14) Terneuzen (MUNAUT 1967a,b); (15) Waasmunster – Pontrave (MERCKX 1996); (16) Weert (MINNAERT 1982); (17) Verrebroek (DEFORCE *et al.* 2005); (18) Doel (MINNAERT & VERBRUGGEN 1986); (DEFORCE *et al.* 2005); (19) Zandvliet (MUNAUT 1967a); (20) Oorderen (MUNAUT 1967a); (21) Kruisschans (VANHOORNE 1951); (22) La Karelslé (Waldbillig, eastern Gutland, Luxembourg) (PERNAUD 2001).

from gardens and parks (LAMBINON *et al.* 1998, MAES *et al.* 2006).

In other parts of northwestern Europe, the natural distribution of *Taxus* is also mainly confined to soils on limestone and other types of well-drained, base-rich soils (UK and Ireland: TITTENSOR 1980, KELLY & KIRBY 1982, STACE 1997, PRESTON *et al.* 2002; The Netherlands: WEEDA *et al.* 1985; Germany: JÄGER & WERNER 2002; France and Switzerland: PALESE & AESCHIMANN 1990; Scandinavia: JONSELL 2000, MOSSBERG & STENBERG 2003).

PALAEOBOTANICAL RECORDS OF *TAXUS*

THE POLLEN DATA

Characteristics of Taxus *pollen*

Taxus pollen is spherical to obtusely angular, its size ranging between 19.3 and 29.8 µm after acetolysis (AVERDIECK 1971, BEUG 2004). *Taxus* pollen does not have sacci and is inaperturate. The exine is intectate and has a scabrate or microgemmate sculpturing (MOORE *et al.* 1991, BEUG 2004). Regarding identification, confusion might be possible with pollen of *Juniperus*, *Populus*, *Rhynchospora* and *Quercus* (AVERDIECK 1971, ZOLLER 1981, MOORE *et al.* 1991, BEUG 2004). The pollen grains frequently split and are sensitive to corrosion (HAVINGA 1967, AVERDIECK 1971, ROHR & KILBERTUS 1977, BRADSHAW 1978). Although *Taxus* is an anemophilous tree, the pollen representation in surface samples near *Taxus* stands seems to be rather low and decreases sharply with increasing distance from the *Taxus* stand (HEIM 1970, NORYSKIEWICZ 2003). These factors, in combination with the lack of distinctive features such as sacci, apertures or a distinctive exine sculpturing, make it likely that *Taxus* pollen was not recognised in some of the earlier palynological studies (KÜSTER 1994), or at sites where conditions for pollen preservation were poor. During the palynological investigation of Wood Fen (Ely, UK; GODWIN *et al.* 1935), for example, no *Taxus* pollen was found while several trunks and even the pollen-bearing cone scales of *Taxus* were present in the investigated peat sequence. Similarly, pollen analysis of peat sequences from Kruisschans (Antwerp, Belgium; VANHOORNE 1951), Oudekapelle (Diksmuide, Belgium; STOCKMANS & VANHOORNE 1954) and Sint-Jacobs-Kapelle (Diksmuide, Belgium; STOCKMANS & VANHOORNE 1954) did not reveal *Taxus* pollen during the palynological research, while several *Taxus* seeds were recovered from the same peat sequences investigated.

Holocene Taxus *pollen records from Belgium and immediate surroundings*

Holocene records of *Taxus* pollen from Belgium are not very abundant. Out of a total of 370 palynological studies from all over Belgium that were reviewed (DEFORCE & BASTIAENS 2006), only 12 contained substantial records of *Taxus*. Sites where *Taxus* occurred in only one or a few samples, and with a frequency of less than 1%, are not included in the overview presented here, as this might represent long-distance transport. On the other hand, it must be remembered that in some of the older analyses, *Taxus* pollen was very probably overlooked, as already discussed above. Three additional records derived from the southwestern Netherlands, close to the Belgian border, are included in the discussion.

Together, the records show two remarkable characteristics: (1) they are all situated in the coastal plain and the lower Scheldt valley (Fig. 1), and (2) they can all be dated from the Subboreal. Some of these dates only rely upon biozonation as the interpretation of the older diagrams is not supported by radiocarbon dating. But still, the available ^{14}C dates (Table 1) allow the conclusion that *Taxus* appears in pollen diagrams in Belgium and the southern Netherlands between 4750 ± 140 uncal. BP (Oorderen) and 4280 ± 130 uncal. BP (Terneuzen). At all sites *Taxus* percentages remain rather low, varying between 2 and 6%. The percentages are higher only at Zandvliet (10.1%) and Ellewoutsdijk (16%). *Taxus* disappears from the pollen diagrams between 4035 ± 30 uncal. BP (Raversijde) and 3510 ± 45 uncal. BP (Baarland) (Table 1).

Table 1. Radiocarbon dates of the start and end of the *Taxus* curve in Holocene pollen diagrams from Belgium and the southern Netherlands. Radiocarbon dates are calibrated using CALIB 5.0.2 (STUIVER & REIMER 1993) and the INTCAL04 calibration data set (REIMER *et al.* 2004).

Nr (cf. Fig. 1)	Site	Start *Taxus*-curve ^{14}C yr BP	cal. BP (2 σ)	Lab. code	End *Taxus*-curve ^{14}C yr BP	cal. BP (2 σ)	Lab. code	Reference
5	Raversijde	Before 4395 ± 30	4866 - 5045	KIA-20051	4035 ± 30	4422 - 4778	KIA-24488	DEFORCE & BASTIAENS, in press
12	Ellewoutsdijk	Before 4460 ± 50	4885 - 5296	UtC-12055	-	-	-	VAN SMEERDIJK 2003
14	Terneuzen I	4280 ± 130	4451 - 5287	Lv-116	Before 3500 ± 110	Before 3481 - 4083	Lv-118	MUNAUT 1967a, GILOT 1997
14	Terneuzen III	4590 ± 110	4962 - 5584	Lv-123	3750 ± 100	3868 - 4415	Lv-122	MUNAUT 1967a, GILOT 1997
13	Baarland	Before 4440 ± 40	Before 4876 - 5282	GrN-14268	3510 ± 45	3644 - 3899	GrN-10252	DE JONG 1986, 1987
19	Zandvliet VIII	4480 ± 110	4845 - 5449	Lv-256	Before 3780 ± 160	Before 3697 - 4781	Lv-255	MUNAUT 1967a, GILOT 1997
20	Oorderen II	4750 ± 140	5044 - 5751	Lv-251	3800 ± 70	3986 - 4413	Lv-250	MUNAUT 1967a, GILOT 1997

THE SEED DATA

Characteristics of Taxus seeds

The seeds of *Taxus* are highly characteristic: they are large (6-8 mm) and ellipsoid-ovoid with a tapering upper end, and rounded to slightly triangular or biconvex in section; their surface is smooth. Seeds cannot be mistaken for any other species. When fresh, seeds are surrounded by a conspicuous reddish aril. This aril is the only non-toxic part of *Taxus*, and it is eaten and digested by birds and small mammals, while the seed itself passes the intestinal canal undamaged (WEEDA *et al.* 1985). Birds are the main agent of seed dispersal (ZOLLER 1981, THOMAS & POLWART 2003), which occurs from September into the winter (ZOLLER 1981, BOUMAN *et al.* 2000). As the fleshy aril does not preserve, palaeobotanical finds of *Taxus* seeds always lack that part.

Holocene Taxus *seed records from Belgium and immediate surroundings*

A small number of Holocene records of seeds of *Taxus* are known from Belgium: subfossil seeds have been found at Oudekapelle (STOCKMANS & VANHOORNE 1954) and Sint-Jacobs-Kapelle (STOCKMANS & VANHOORNE 1954), in the western coastal area, and at Kruisschans (VANHOORNE 1951) and Heusden (STOCKMANS 1945), both along the river Scheldt (Fig. 1).

These finds originate from the same restricted region that yielded subfossil pollen, i.e. the coastal area and the lower Scheldt valley. The *Taxus* seeds have all been recovered from peat deposits, none of which have been dated by radiocarbon analysis. Nevertheless, all finds can be attributed to the Late Atlantic or Sub-boreal on the basis of their position in the lower part of the so-called surface peat (see further), or of pollen analysis carried out on the same peat sequences (VANHOORNE 1945, VANHOORNE 1951, STOCKMANS & VANHOORNE 1954).

WOOD AND CHARCOAL DATA

Characteristics of Taxus *wood and charcoal*

The wood of *Taxus* is very dense, hard, elastic and resistant to decay (ZOLLER 1981). The sapwood is white to yellowish; the heartwood is red and colours orange-brown after contact with the air. Owing to its good elasticity, it has been a very popular timber for the production of tools and weapons, in particular bows (ZOLLER 1981, LANTING *et al.* 1999, GALE & CUTLER 2000). *Taxus* wood and charcoal are easy to differentiate from that of other European gymnosperms, on account of the distinct spiral thickenings in the tracheid walls and the absence of resin canals in the former (GROSSER 1977, SCHWEINGRÜBER 1990, GALE & CUTLER 2000).

Holocene Taxus *wood and charcoal records from Belgium and immediate surroundings*

Subfossil Holocene wood remains of *Taxus* from Belgium are only known from Blankenberge (ALLEMEERSCH 1991) and Wenduine (MERTENS 1958). At Blankenberge, *Taxus* wood was found embedded in a peat deposit dating from the late Atlantic or the Sub-boreal. At Wenduine, a fragment of *Taxus* wood was found in an archaeological site dating from the Roman period (57 BC – 402 AD; archaeological periods according to SLECHTEN 2004).

In the southern part of the Netherlands, subfossil wood of *Taxus* has been found at Terneuzen (MUNAUT 1967a,b), Borsele (VAN RIJN 2001) and Ellewoutsdijk (VAN RIJN 2003). At Terneuzen, several *Taxus* stems have been recovered from peat deposits but they have not been dated and their stratigraphic position has not been recorded. However, it is very likely that the stems derive from the same levels from which *Taxus* pollen was recovered, which would place the wood fragments in the Sub-boreal (MUNAUT 1967a, GODWIN 1968). At Borsele and Ellewoutsdijk, the *Taxus* finds were partly preserved in the peaty soil and consisted of wooden poles that were used as parts of Roman Age buildings. One *Taxus* pole from Borsele was radiocarbon-dated at 4690 ± 60 uncal. BP (several poles made from *Pinus sylvestris* gave similar dates) (SIER 2001). The *Taxus* poles from Ellewoutsdijk were not dated by radiocarbon analysis but a pole from *P. sylvestris* from the same buildings was dated at 4480 ± 25 uncal. BP. The only possible explanation for the time gap between the time of the construction and the much older age of part of the construction wood is that at these sites during Roman times, subfossil wood was used for the construction of buildings (VAN RIJN 2003). As inferred from the pollen analysis of Ellewoutsdijk (VAN SMEERDIJK 2003) and the palaeogeographical map of the region (VOS & VAN HEERINGEN 1997), these sites were situated in an almost treeless peat-bog environment during the Roman Age, which might explain the use of subfossil material.

The *Taxus* wood found at the Roman site of Wenduine (MERTENS 1958) has not been dated but it might represent subfossil wood too, given that Wenduine was also situated in a peat bog or a peri-marine environment during Roman Age (ALLEMEERSCH 1991, ERVYNCK *et al.* 1999).

Charcoal from *Taxus* has been found in La Karelslé, eastern Gutland (Luxemburg) (Fig. 1), in archaeological cave deposits. A few fragments derive from deposits dating from the Middle Neolithic (4 500 – 3 500 BC; which corresponds to the Late Atlantic) while rather large amounts have been recovered from Late Bronze Age deposits (1 100 – 800 BC, corresponding to the Late Sub-boreal) (PERNAUD 2001). This is rather surprising as there is no evidence for the extension or even presence of *Taxus* in any of the Holocene palynological records from Luxemburg (PERNAUD 2001), eastern Belgium and the Gaume district (COUTEAUX 1969a,b), the Plateau des Tailles area (MULLENDERS & KNOP 1962) or the French Ardennes (MULLENDERS 1960, LEFEVRE *et al.* 1993).

All dated finds of Holocene *Taxus* wood and charcoal are of Late Atlantic or Sub-boreal age and, except for the charcoal from Gutland, all finds were excavated in the Belgian coastal plain or the Scheldt estuary.

HOLOCENE PALAEOBOTANICAL RECORDS OF *TAXUS* FROM OTHER PARTS OF NORTHWESTERN EUROPE

Probably one of the earliest mentions of *Taxus* occurring in peat deposits was made by STARING (1983, re-edition from 1856). The author expressed his surprise about the presence of subfossil *Taxus* wood in Dutch peat deposits, in contrast with the 19th century distribution of *Taxus* in The Netherlands and elsewhere in Europe. That *Taxus* grew on peat has been further demonstrated by the finds of subfossil wood at Ely (UK), described by Miller and SKERTCHLEY (1878) and discussed by GODWIN *et al.* (1935). Another early observation of *Taxus* trunks recovered from peat deposits was made at Ballyfin Bog (Ireland) by ADAMS (1905), who stated that similar finds were so plentiful in former times that farmers in the neighbourhood used the wood for gate posts, house roofs, etc.

FIRBAS (1949) reviewed Holocene records of *Taxus* wood from Germany, both from natural peat deposits and from archaeological contexts including several trunks from peat deposits from the coastal lowlands of Ostfriesland. Other finds of *Taxus* wood recovered from peat deposits in Germany are listed by HAYEN (1960, 1966) and AVERDIECK (1971).

Next to these finds of subfossil wood, there are also numerous pollen diagrams from northwestern Europe, showing a distinct *Taxus* curve, mostly during the Sub-boreal (for northwestern Germany, see AVERDIECK 1971, 1983, HAYEN 1960; for Ireland: O'CONNELL *et al.* 1988, MITCHELL *et al.* 1996, MOLLOY & O'CONNELL 2004; for England: GODWIN 1975, PEGLAR 1993a,b, GREIG 1996, BATCHELOR *et al.* 2004; for northwestern France: VAN ZEIST 1964; for Sweden: BERGLUND 1966, for Finland: SARMAJA-KORJONEN *et al.* 1991).

DISCUSSION

From the Holocene palaeobotanical records of *Taxus* presented, it is clear that this tree was more abundant and had a different distribution during the Sub-boreal in northwestern Europe compared to nowadays.

Taxus occurs sporadically in pollen diagrams from England (BIRKS 1982, GODWIN 1975), Ireland (HUANG 2002) and Sweden (BERGLUND 1966) from the Late Boreal or early Atlantic onwards. For Belgium, the earliest post-glacial palaeobotanical records of *Taxus* date from the late Atlantic or early Sub-boreal. All the other palaeobotanical records from Belgium and the southern Netherlands can be dated from the Sub-boreal as well. Not only in Belgium, but also in other parts of northwestern Europe (see 3.4), *Taxus* shows a maximum in pollen diagrams during the Sub-boreal.

DISTRIBUTION AND HABITAT OF *TAXUS* DURING THE SUB-BOREAL

Most of the finds of subfossil pollen, seeds and wood of *Taxus* in Belgium and the southern part of the Netherlands are situated in the coastal lowlands and more precisely in the area where the so-called 'surface peat' or 'Holland peat' occurs in the subsoil. This surface peat was formed during the mid Holocene when the postglacial sea-level rise began to slow down and coastal barriers could develop (BAETEMAN 1981, 1999, VOS & VAN HEERINGEN 1997). These coastal barriers closed the coast almost completely and initiated mire development. At the time of the maximal expansion of the peat, in the Sub-boreal, the mires stretched nearly continuously from Calais in northwestern France to southwestern Denmark, including the coastal plain of Belgium, the western part of the Netherlands and the lower Scheldt valley (PONS 1992).

According to PONS (1992), this surface peat shows more or less the same general development in the coastal plain in Flanders and the southwestern part of the Netherlands. On the salt marshes of the regression surface brackish fens developed, forming *Phragmites* (*-Scirpus*) peat. Gradually, desalinisation and decreasing amounts of available nutrients resulted in *Carex-Phragmites* fens, which changed into mesotrophic *Betula-Alnus* carr, sometimes with some *Pinus*. This phase of carr peat is followed by a transition to *Sphagnum* peat and, in most places, the development of raised bogs resulting in the formation of *Sphagnum*-Ericaceae peat. Peat growth ended because of marine transgressions and fluvial sedimentation between the Late Sub-boreal and the Late Middle Ages, depending on the location, which resulted in the covering of the peat with marine and alluvial clay deposits (JANSSENS & FERGUSON 1985, DENYS & VERBRUGGEN 1989, ALLEMEERSCH 1991, PONS 1992). The upper part of the surface peat is often lacking as a consequence of marine erosion or medieval and post-medieval peat extraction (BAETEMAN *et al.* 2002, BAETEMAN 2005). Macroremains of *Taxus* from the coastal plain of Belgium and the southern Netherlands (Fig. 1), except those associated with archaeological sites, have all been recovered from the part corresponding to the carr-phase of the peat profiles. They were associated with seeds and other macroscopic remains of plants typical of an alder/birch carr or fen vegetation composed of, e.g., *Alnus glutinosa*, *Betula* sp., *Comarum palustre*, *Carex paniculata*, *Carex pseudocyperus*, *Lysimachia vulgaris*, *Lycopus europaeus* and *Thelypteris palustris* (VAN HOORNE 1951, STOCKMANS & VANHOORNE 1954, ALLEMEERSCH 1991). The occurrence of *Taxus* in pollen diagrams from these areas also corresponds with the carr-phase of the analysed peat profiles (e.g., MUNAUT 1967, DEFORCE & BASTIAENS in press).

The fact that, at sites mentioned above, *Taxus* was actually part of the local vegetation community has been ignored or even denied by several authors as it does not seem to correspond with the present day ecology and distribution of this tree. VAN SMEERDIJK (2003: 161-162), for example, argued that the high percentages of *Taxus* pollen at Ellewoutsdijk and Baarland must be explained by transport by the river Scheldt and thus must originate from a more inland area. However, the fact that *Taxus* wood has been discovered at Ellewoutsdijk and at the nearby Terneuzen, does not support this hypothesis. Besides, the river Scheldt followed a more northern route at that time and did not flow near Ellewoutsdijk or Baarland (VOS & VAN HEERINGEN 1997, DENYS & VERBRUGGEN 1989). Many other records of pollen and macroremains of *Taxus* from peat deposits, often in areas without any fluvial activity, indicate that *Taxus* actually did grow on peat. In fact, this is not an entirely new observation as Godwin already remarked, based on his research at Wood Fen (Ely, UK; GODWIN *et al.* 1935), at Woodwalton Fen (Hunts, UK; GODWIN & CLIFFORD 1938) and on the *Taxus* finds at Terneuzen (The Netherlands; GODWIN 1968), that "*Taxus* almost certainly had an extensive natural occurrence upon peat land, although natural communities of this kind can no longer be pointed out" (GODWIN 1968: 737).

It has to be stressed here that palaeobotanical data are generally sparse for chalk regions, since the geological and topographical conditions in these regions are unsuitable for the formation and preservation of stratified peat (TITTENSOR 1980). This could, of course, bias the reconstruction of the Holocene distribution of *Taxus* presented. However, this objection may be valid for the areas with actual natural *Taxus* populations in Belgium (Fig. 1) but this is not true for the areas both to the northwest and to the southeast of this region. For those areas, Holocene pollen diagrams and other palaeobotanical data are available, but no *Taxus* pollen were recorded outside the coastal area and the lower Scheldt valley, one exception being the records of *Taxus* charcoal from Gutland (Luxembourg).

THE *TAXUS* DECLINE

At the above-mentioned sites from Belgium and surrounding regions, *Taxus* disappears in the pollen diagrams during the second half of the Sub-boreal, around 3 500 uncal. BP (see Table 1). Similarly, no botanical macroremains of *Taxus* have been found that are younger than the end of the Sub-boreal. In pollen diagrams from other sites situated in the lowlands of northwestern Europe, *Taxus* disappears as well, or shows a strong decline, before the end of the Sub-boreal.

The Holocene decline of *Taxus* in northwestern Europe is generally attributed to competition with *Fagus* and *Carpinus*, deforestation, selective felling and grazing (FIRBAS 1949, AVERDIECK 1971, ZOLLER 1981, SVENNING & MAGÅRD 1999, NAVYS 2000, HOLTAN 2001, THOMAS & POLWART 2003). However, these explanations are all based on the actual ecology and distribution of *Taxus*, i.e., *Taxus* growing on well-drained calcareous soils. For the decline of *Taxus* growing in a fen carr environment, other explanations must be sought.

The most common explanation for the Sub-boreal *Taxus* decline is competition with *Fagus* and *Carpinus* (FIRBAS 1949, AVERDIECK 1971, MUHLE 1979). Recent research showed that a

Taxus population in Denmark increased after thinning the tree canopy, especially by felling beech (SVENNING & MAGÅRD 1999). Other research demonstrated, however, that regeneration of *Taxus* could be rather successful under the canopies of several broadleaved trees, including *Carpinus betulus* (ISZKULO & BORATYNSKI 2004). Moreover, as *Fagus* and *Carpinus* only grow on well-drained soils (ELLENBERG *et al.* 1991), light competition with these two taxa cannot have played a role in the decline of *Taxus* growing in wet conditions.

Another explanation for the *Taxus* decline could be deforestation, but the pollen diagrams from Belgium and the southern Netherlands do not indicate deforestation during the period of the *Taxus* decline. There are also no indications for agriculture or other forms of intensive human impact on the vegetation in the coastal lowlands during the Sub-boreal (VOS & VAN HEERINGEN 1997, ERVYNCK *et al.* 1999).

Selective felling of *Taxus*, for its valuable wood or to avoid cattle poisoning, has been proposed as another explanation for the *Taxus* decline at several sites in northwestern Europe (SARMAJA-KORJONEN *et al.* 1991, SVENNING & MAGÅRD 1999, O'CONNELL & MOLLOY 2001). From the Neolithic onwards, *Taxus* was probably the most used wood for the manufacture of bows (CLARK 1963, LANTING *et al.* 1999, BEUKER 2002). Many other wooden implements were made from *Taxus* as well (GODWIN 1975, COLES *et al* 1978, GALE & CUTLER 2000). However, since human populations and activities were almost absent during the Sub-boreal, in the region under consideration here, these explanations can also be rejected (VOS & VAN HEERINGEN 1997, ERVYNCK *et al.* 1999, LOUWE KOOIJMANS *et al.* 2005).

In several forests of northwestern Europe, it has been observed that *Taxus* recruitment suffers from browsing by roe deer, *Capreolus capreolus* (GARCIA & OBESO 2003, MYSTERUD & ØSTBYE 2004). The branchlets, needles and seeds of *Taxus* contain a poisonous alkaloid, a lethal toxin for many species including horses, cows, goats and humans (JORDAN 1964, SCHULTE 1975). Only a few animals including roe deer are not sensitive to it; they like to nibble the yew branchlets and cause tangible damage to the trees (MYSTERUD & ØSTBYE 1995, 2004 NAVYS 2000). Fully-grown *Taxus* trees are largely resistant to the nibbling; even after a tree is cut down, green shoots appear from the stump. On the other hand, recent research has demonstrated that roe deer browsing reduces *Taxus* recruitment (HULME 1996, GARCIA & OBESO 2003, MYSTERUD & ØSTBYE 2004). In general, although roe deer occur in wetland habitats (DANILKIN 1996, BARANCEKOVA 2004), it is very unlikely that the Sub-boreal *Taxus* decline can be explained by roe deer –browsing, as there are no indications for an increase in their population at that time.

One more possible explanation for the *Taxus* decline would be a climate change. There is no evidence, however, for a major change of the climatic conditions in northwestern Europe around 3 500 uncal. BP (DAVIS *et al.* 2003). As Belgium and the southern Netherlands are not situated near the limits of the natural distribution of *Taxus*, it is unlikely that a minor change in climatic conditions would have caused the *Taxus* decline.

In conclusion, although some of the above-mentioned explanations for the *Taxus* decline might hold true for *Taxus* stands growing on well-drained, mineral soils or in regions where human impact was more intense (TITTENSOR 1980, O'CONNELL & MOLLOY 2001), they are not suitable to explain the Sub-boreal decline of *Taxus* in the coastal area of Belgium and the southern Netherlands. As a more likely explanation for the decline of *Taxus* in Belgium and the southern Netherlands, a change of the environment in which *Taxus* grew can be proposed. In most places in the coastal area and the Scheldt estuary, this environmental change could consist of the already mentioned transition from the carr peat phase, in which most of the palaeobotanical records of *Taxus* can be situated, to ombrotrophic moss peat and, in most places, the development of raised bogs resulting in the formation of *Sphagnum*-Ericaceae peat (ALLEMEERSCH 1986, 1991, PONS 1992, VERBRUGGEN *et al.* 1996, DEFORCE & BASTIAENS in press.). Especially the pollen diagrams from Oorderen (MUNAUT 1967) and Raversijde (DEFORCE & BASTIAENS in press) show very clearly that *Taxus* indeed disappears with the transition to ombrotrophic conditions, illustrated by the increase of *Sphagnum* and *Calluna*/Ericaceae.

In the inland part of the lower Scheldt valley, where no ombrotrophic peat occurs on top of the fen-carr peat deposits, the end of the peat growth was caused by the deposition of alluvial loam and clay, as a consequence of agricultural practices (VERBRUGGEN *et al.* 1996, HUYBRECHTS 1999).

CONCLUSIONS

All Holocene palaeobotanical records of *Taxus* from Belgium and the southern Netherlands show three remarkable characteristics: (1) they all are situated in the coastal plain and the lower Scheldt valley, (2) they all date from the Sub-boreal and (3) they all indicate that *Taxus* grew on peat. This strongly contrasts with the recent distribution and ecology of *Taxus*, the current natural distribution of *Taxus baccata* L. in Belgium being limited to a few localities in the southern part of the country, all situated on steep, calcareous slopes.

The Holocene occurrence of *Taxus* in the coastal plain in Belgium, and probably in several other lowland areas in northwestern Europe, correlates with the carr peat phase of the surface or Holland peat, which was mainly formed during the Sub-boreal. The decline and disappearance of *Taxus* in northern Belgium and the southern Netherlands during the second half of the Sub-boreal are most likely the result of the transition of these coastal marshes from a fen-carr environment to ombrotrophic bogs.

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