W13

Taxus baccata woodland

Synonymy

Yew-woods Tansley & Rankin 1911, Watt 1926, Tansley 1939, Ratcliffe 1977.

Constant species

Taxus baccata.

Rare species

Buxus sempervirens.

Physiognomy

Only rarely can such species-poor vegetation as mature Taxus baccata woodland present such a memorable spectacle. Taxus is the only constant woody species here, indeed the only constant, being an uncompromising dominant in a canopy that is rarely higher than 10 m but typically closed and very dense. Beyond the outer margins of stands, which can be wind-pruned and surrounded by a fringe of shrubs and climbers of the neighbouring scrub, Taxus reigns supreme in sometimes quite extensive stretches of striking floristic poverty and uniformity. In such a scene, the different character of the individual trees is very impressive, with pioneers of venerable appearance, richly branched from the ground and often with their trunks fused into weird shapes, and, between them, younger trees, less branched but frequently grown up lop-sided in the shade of the earlier invaders (Watt 1926, Williamson 1978).

No other tree is more than occasional throughout the community, though *Sorbus aria* is a very characteristic associate and, in one sub-community, it becomes a little more frequent, its crowns characteristically taller than the *Taxus* canopy and, with their dusty white foliage, forming a sharp contrast to the sea of dark green around. Quite commonly, it carries *Viscum album*. Emergent *Fraxinus excelsior* can also sometimes be seen and, rarely, there can be widely-scattered *Fagus sylvatica*, *Acer pseudoplatanus* or *Quercus robur*.

The picture beneath the Taxus is characteristically

gloomy and bare. In the first place, there is no true understorey here. Associated shrubs are rare, except around the margins of stands and in gaps, and usually there is nothing more than a few sparse and spindly specimens of Sambucus nigra and a very occasional drawn-up Ilex aquifolium or Crataegus monogyna. Although seedlings of Taxus appear in large numbers in most years, they disappear by autumn and saplings occur only rarely. Where the canopy is a little thinner there may be some young Fraxinus or A. pseudoplatanus. In a few stands, Buxus sempervirens is a distinctive associate, and it can grow up as a very local canopy dominant.

One other frequently noticeable feature beneath the trees is the amount of dead woody remains of plants from the preceding scrub. *Juniperus communis*, a locally important precursor to *Taxus*, can be especially distinctive with its very persistent contorted skeletons, the wood smelling strongly of cigar-boxes, marking the base of each yew as a long-redundant nurse (Figure 23).

The field layer is typically very sparse indeed: at most there is but a thin and patchy cover of herbs and quite often just a bare expanse of soil and rock with brown carpets of slowly-rotting yew needles. The most frequently encountered species is Mercurialis perennis with very occasional Urtica dioica, Hedera helix, Brachypodium sylvaticum, Arum maculatum, Rubus fruticosus agg., Viola spp., Glechoma hederacea and Fragaria vesca, all of them plants found in other of our more calcicolous woodlands, though often with an abundance and luxuriance that is quite unknown here.

Bryophytes, too, are generally extremely poorly developed. Eurhynchium praelongum is, at most, occasional and, even then, its cover is low and other species occur only as infrequent small patches: Fissidens viridulus, Ctenidium molluscum, Eurhynchium murale, Thuidium tamariscinum and Brachythecium velutinum on soil and stones, Mnium hornum on twiggy litter and Isopterygium elegans on humus.

Sub-communities

Sorbus aria sub-community. S. aria is a fairly frequent woody associate of Taxus here, its scattered crowns breaking the yew canopy at about 2 or 3 trees ha⁻¹, and, more rarely, there can be some Fraxinus, Fagus, Q. robur or A. pseudoplatanus. In most stands, Sambucus is the only shrub, but it is in this kind of Taxus woodland that Buxus can become locally important, forming a patchy slightly lower tier beneath the yew or growing up amongst it, its sinuous trunks and dense terminal branching producing a very distinctive effect.

Only exceptionally is there anything that could remotely be termed a field layer here. Mercurialis is totally absent and quite often there are no herbs at all: sometimes a diligent search may reveal a single individual of plants like Arum maculatum, Viola spp. or Fragaria vesca and very rarely there can be some frail-looking Hedera. More often, the ground is completely bare apart from carpets of litter over exposed flinty soil and tumbles of talus. On more stable patches of soil or on rock fragments, some bryophytes can be present.

Mercurialis perennis sub-community. In this sub-community, Taxus is almost always the sole canopy tree with only very infrequent S. aria or Fraxinus. But the cover can be a little (only a little) more open and this can permit a more frequent and somewhat denser growth of Sambucus beneath, sometimes with sparse Ligustrum

Figure 23. Canopy physiognomy in *Taxus* woodland at Juniper Bottom, Surrey.

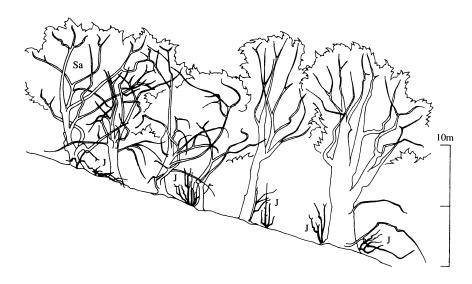
The section shows first- and second-generation yews with occasional whitebeam (Sa) and a cemetery of junipers (J).

vulgare, Euonymus europaeus and Cornus sanguinea and scrambling Clematis vitalba or Tamus communis.

Herbs, too, are a little more numerous and of somewhat greater cover here. *Mercurialis* is constant, though it is rarely more than patchily abundant and sometimes wilted by August, and there can be some *Urtica dioica* and scattered *Brachypodium sylvaticum*, *Rubus*, *Viola* spp. and *Fragaria*. *Iris foetidissima* is a striking associate at some localities and the characteristic Fagion gap species, *Atropa belladonna* and *Inula conyza*, can occur. Sparse seedlings of *Taxus* and *Fraxinus* may also be found. But such abundance is very much a comparative thing and, again, the bulk of the ground is often quite bare apart from occasional bryophytes.

Habitat

Taxus is an occasional and sometimes prominent associate in various kinds of British woodlands, most notably the Fraxinus-Acer-Mercurialis and Fagus-Mercurialis woodlands, but only very locally does it attain dominance in the type of extensive and uniform canopy characteristic of this community. Existing stands of the Taxus woodland are typically associated with moderate to very steep limestone slopes carrying shallow, dry rendzinas. With a single striking exception on the Durham Magnesian Limestone, the community is confined to the Chalk of south-east England where it characteristically occurs along the sides and bottom of dry valleys and on scarps. Here, the soils are generally grey rendzinas of the Upton series (Soil Survey 1983), thin, often rich in downwashed flints and poor in earthworms. Along valley bottoms, the *Taxus* woodland may extend on to somewhat deeper and moister soils derived from head. Many sites face south with slopes experiencing increased insolation and wind-exposure.



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In such situations, the ultimate success of *Taxus* seems to depend on its ability to capitalise, slowly but inexorably, on a more prolific colonisation than other potential invaders, such as *Fagus* and *Fraxinus*, are able to achieve. Both these species probably have difficulty in sustaining growth on the drier and more exposed sites here. In addition, *Taxus* may gain some initial advantage, at least against *Fagus*, by its prolific and regular fruiting and by having seeds that are bird-distributed: yew fruits are eaten in formidable quantities by certain birds, notably by winter-flocking members of the thrush family which disgorge or excrete the seeds (Williamson 1978, Fuller 1982). The seeds are also hoarded and eaten by rodents.

Taxus can invade ungrazed grasslands directly (Williamson 1978), but its progress is very much assisted by the presence of scrub and the existence of some younger stands of the community can be traced to particular episodes of grazing relaxation on the south-eastern Chalk, as in the period of agricultural neglect in the 1920s (Watt 1926) or after myxomatosis (Williamson 1978). Scattered bushes may be important in providing breaks in the intact sward with patches of shaded and sheltered bare soil beneath them but, more importantly, they offer protection from remaining browsers. For, contrary to some early views (e.g. Tansley & Rankin 1911) and to popular opinion, Taxus foliage is not deadly to all larger herbivores, at least not invariably (see Lowe 1897), and is quite regularly browsed by rabbits, hares, deer and sheep, though not usually by cattle and horses which can suffer quick and fatal effects (Watt 1926, Williamson 1978); rabbits also bark stems and branches (Elwes & Henry 1906). Initial invasion is thus very much controlled by the distribution of resistant shrubs, most notably by the unpalatable Juniperus, itself a plant of local distribution and one tolerant of exposed sites with dry soils where Taxus can do well. In many of the areas examined by Watt (1926), every young juniper had its protected cluster of yew seedlings and every maturing yew its dying or dead juniper. Other shrubs too, he found, such as Crataegus and Prunus spinosa, offered some defence against browsers, though they did not provide such complete or consistent protection to the young Taxus. Moreover, on the deeper, moister soils where these shrubs tended to replace Juniperus as the scrub dominant, other trees, notably Fraxinus, increased in importance as invaders.

Once established within scrub, a further feature aids the survival of *Taxus* against other tree species, probably even against *Fagus*, and that is its extreme tolerance of shade. Saplings can persist, growing very slowly, for very many years before breaking through and, though estimates and borings usually give *Taxus* 4–12 annual rings cm⁻¹, shaded trees can show as many as 20 (Edlin 1958, Newbould 1960, Williamson 1978). Moreover,

Taxus can survive its own formidable shade and family groups of trees are a very characteristic feature of young yew woods, especially where invasion has occurred within more open scrub, and they can sometimes still be discerned within mature stands (Watt 1926).

Without exception, all other woody and herbaceous associates of the scrub suffer from the severely-reduced light as the *Taxus* canopy closes. Well-grown *Fraxinus* or *Sorbus aria*, which have outstripped *Taxus* in the early years, may persist as emergents in mature stands or reappear in gaps, but the bulk of these are not replaced as they die and the groups of the longer-lived *Taxus* fuse into a virtually continuous cover. Likewise, it is only in gaps that there is any substantial development of shrubs, herbs or bryophytes characteristic of the base-rich soils here and, even then, plants such as *Sambucus* and *Urtica*, reflecting the enrichment provided by past rabbit-infestation, may be more prominent.

The striking impoverishment of the flora under Taxus is probably also a reflection of intense root competition in soils which are often already dry. Like Fagus, Taxus has a very extensive horizontal root system with a thick felted mat ramifying the soil near the surface. And, in extreme situations, it can survive rooted into virtually bare rock from the surface of which almost all else has disappeared. This is well seen on the slopes above the river Mole at Box Hill in Surrey where Taxus and Buxus persist on very steep ground which is being actively undercut, their roots exposed on the down-slope side, their trunks piled with tumbled rubble above, and the surface of the bedrock washed clean by sheet-rain erosion.

Apart from a romanticised, though real, function as a source of wood for longbows and as a provider of material much prized for turnery, carving and veneering, it seems doubtful whether our *Taxus* woodlands have ever been actively treated for timber production. Stands may have been extensively felled to fuel the ironsmelting industry of the south-east and, more recently, in the renowned woods of Kingley Vale in Sussex, yews were used for wartime target practice (Williamson 1978). *Taxus* has been very widely planted throughout the country, though usually as hedging or for solitary ornament and groups seldom comprise more than a few trees. These eventually develop the characteristically bare floor but are scarcely a substitute for natural stands with their long and complex topographic associations.

It is possible that some occurrences of *Buxus* in British woodlands originate from planting but, as Pigott & Walters (1953) demonstrated, there is no convincing evidence that this species is not a native in this country (see also Godwin 1975). Its consistent association with *Taxus*, both in this community and in related kinds of *Fagus-Mercurialis* woodland, in sites which are characterised by steep, unstable slopes and shallow soils

(matched in many of its French localities), argue strongly for a natural origin and its patchy occurrence may relate to sporadic survival right through the Forest Maximum (Pigott & Walters 1953). Stands of pure *Buxus* scrub can also be found very locally in Britain, notably at Ellesborough Warren in Buckinghamshire and at Boxwell in Gloucestershire (Ratcliffe 1977). At the latter site, which has been known since the time of Domesday, the trees have been coppiced: box-wood is prized for turnery and carving and for providing endgrain blocks for engraving (Clapham & Nicholson 1975). These stands have not been sampled but their typically sparse associated flora includes *Sambucus* and the herbs typical of the *Taxus* woodland.

Zonation and succession

Typically, the Taxus woodland is found in close association with grasslands and scrub which reflect grazingrelaxation over the south-eastern Chalk. Thus, stands can be found in mosaics and zonations with a complete sequence of vegetation types from close-cropped turf of the Festuca-Avenula grassland, rank swards dominated to varying degrees by coarse grasses such as Bromus erectus, Brachypodium pinnatum, Avenula pubescens, Festuca rubra and Arrhenatherum elatius, and various kinds of Crataegus-Hedera scrub. Where rabbit-infestation has become important again, patches of Festuca-Hieracium-Thymus grassland or stands of Urtica dioica may also occur. The exact disposition of these communities, their proportions and the age structure of the Taxus woodland can reflect long and complex histories of grazing by stock and wild herbivores. Much of this information is now irrecoverable though, as Williamson (1978) has shown at Kingley Vale, the effects of recent particular events can often be revealed by careful observation.

It was from a consideration of spatial patterns in a number of sites in the South Downs that Watt (1926) proposed his scheme for the general seral development of the Taxus woodland. From the varied examples of Taxus invasion, Watt characterised two main trends in succession associated with the proportional importance in the protective scrub of Juniperus and Crataegus. Where the former predominated, as on shallower soils in more exposed sites, its greater resistance to browsing allowed *Taxus* to gain a more extensive and rapid hold; among Crataegus, invasion was slower and more diffuse. On the deeper and somewhat moister soils typical of Crataegus scrub, Fraxinus also became increasingly important so that, in the more gradual progress to a closed Taxus cover, an intermediate stage of 'yew-ash wood' supervened. Eventually, however, Taxus exerted its overwhelming dominance throughout, often leaving just either dead juniper nurses beneath or occasional emergent ash to give any clue as to the particular origin of a stand.

As Watt went on to demonstrate (Watt 1934a, b), exactly the same kinds of seral development are characteristic of succession to the Fagus-Mercurialis woodland, though in that community the generally richer survival of different field layers in mature stands provides a lasting indication of the scrubby precursors and the edaphic conditions which they favour. But the great similarity of the successions does raise the question of why Fagus should invade and triumph in some situations and Taxus in others. The answer probably lies in the greater tolerance of Taxus of drier, more exposed conditions but, in many marginal cases, the success of the latter may be due to its more reliable fruiting and better seed-dispersal. Even so, Taxus-dominance of the kind seen here is a very local phenomenon. Like Fagus, it seems to have shown a late post-Glacial spread in Britain (Firbas 1949, Godwin 1975) but it has been nowhere near as successful in establishing itself as a widespread canopy component.

Once developed, however, the *Taxus* woodland is a climax community which cannot naturally be replaced by Fagus, or any other canopy dominant tolerant of base-rich soils, without death of the yews or felling. Some existing stands contain very old trees, though probably not as old as Watt (1962) thought: 500 years, rather than 1000, seems to be a more accurate estimate for the most ancient individuals at Kingley Vale (Newbould 1960, Williamson 1978). Stands of the community may, of course, have been in occupation in such sites for much longer, though, as Watt (1926) showed, the Taxus woodland tends to show small-scale migrations around Chalk coombes, colonising first in the head, then along the flanks and eventually, after many generations, dying from behind and invading again. In many sites, afforestation of surrounding plateau and slopes with mixtures of Fagus and conifers has isolated stands of the community, reduced their room for manoeuvre and destroyed their grand landscape context.

Distribution

The Taxus woodland is almost wholly confined to the Chalk of the North and especially the South Downs with some stands in gaps on the Chilterns. A stand of Taxus-dominated woodland on the Magnesian Limestone at Castle Eden Dene in Durham is included here but local prominence of Taxus on the Carboniferous Limestone around Morecambe Bay is best considered as variation within the north-western Fraxinus-Acer-Mercurialis woodland.

Affinities

British stands of *Taxus* woodland have long attracted the admiration of Continental ecologists but it is not easy to accommodate them in phytosociological 238 Woodlands and scrub

schemes. Tüxen (1952) and Delelis-Dusollier & Géhu (1972) allocated samples of fairly species-rich yew scrub from south-east England to a *Roso-Sorbetum ariae* which they saw as the British equivalent to the *Taxo-Prunetum mahalebis*, a community of Chalk cliffs along the Seine (Delelis-Dusollier & Géhu 1972). These woodlands did not accommodate species-poor mature stands

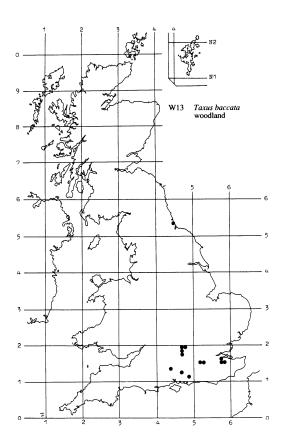
and their equivalent in this scheme is part of the Crataegus-Prunus scrub. The Taxus woodland as understood here is probably best seen as part of the Fagion alliance in the Querco-Fagetea, alongside the Fagus-Mercurialis woodland and European communities like the Taxo-Fagetum Elter 1947.

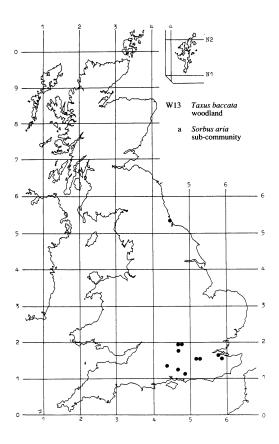
Floristic table W13

	a	ь	13
Taxus baccata	V (9–10)	V (6-10)	V (6-10)
Fraxinus excelsior	I (3)	I (4)	I (3-4)
Sorbus aria	III (3-5)	I (4-6)	II (3–6)
Fagus sylvatica	I (3)		I (3)
Acer pseudoplatanus	I (4)		I (4)
Quercus robur	I (3)		I (3)
Sambucus nigra	II (3–4)	III (2–5)	III (2-5)
Crataegus monogyna	I (1-2)	I (1–2)	I (1–2)
Ilex aquifolium	I (1-2)	I (1–2)	I (1–2)
Buxus sempervirens	II (4–8)		I (4-8)
Fraxinus excelsior sapling	I (2)		I (2)
Acer pseudoplatanus sapling	I (3)		I (3)
Taxus baccata sapling		I (4)	I (4)
Euonymus europaeus		I (3)	I (3)
Ligustrum vulgare		I (3)	I (3)
Arum maculatum	I (2)		I (2)
Ctenidium molluscum	I (6)		I (6)
Rhynchostegium murale	I (2)		I (2)
Brachythecium velutinum	I (3)		I (3)
Mercurialis perennis		V (1-9)	III (1–9)
Eurhynchium praelongum	I (2)	II (1-3)	I (1-3)
Clematis vitalba	I (3)	II (1–4)	I (1-4)
Fissidens viridulus	I (3)	II (1-4)	I (1-4)
Urtica dioica		II (1-2)	I (1-2)
Taxus baccata seedling		II (1-2)	I (1-2)
Atropa belladonna		I (2-3)	I (2-3)
Inula conyza		I (1-2)	I (1–2)
Glechoma hederacea		I (3)	I (3)
Fraxinus excelsior seedling		I (2)	I (2)
Iris foetidissima		I (7)	I (7)
Thuidium tamariscinum		I (4)	I (4)
Isopterygium elegans		I (3)	I (3)
Brachypodium sylvaticum		I (2)	I (2)
Tamus communis		I (3)	I (3)
Eupatorium cannabinum		I (3)	I (3)

Viola reichenbachiana/riviniana	I (2-3)	I (1-2)	I (1-3)
Rubus fruticosus agg.	I (1)	I (1-3)	I (1-3)
Mnium hornum	I (1)	I (2-3)	I (1-3)
Hedera helix	I (8)	I (2)	I (2–8)
Fragaria vesca	I (2-3)	I (3)	I (2-3)
Rhytidiadelphus loreus	I (2)	I (1)	I (1–2)
Number of samples	11	11	22
Number of species/sample	4 (1–8)	7 (4–10)	6 (1–10)
Tree height (m)	9 (6–10)	10 (8–20)	10 (6–20)
Tree cover (%)	100	97 (90–100)	98 (90-100)
Shrub height (m)	1 (1–2)	3 (1–4)	2 (1-4)
Shrub cover (%)	1 (0-5)	6 (0–15)	4 (0–15)
Herb height (cm)	8 (5–10)	40 (2060)	24 (5-60)
Herb cover (%)	6 (0–60)	27 (1–90)	15 (0-90)
Ground height (mm)	20 (10–30)	10	15 (10-30)
Ground cover (%)	5 (0–30)	1 (0-3)	3 (0–30)
Altitude (m)	174 (76–205)	161 (76–205)	167 (76–205)
Slope (°)	15 (5–30)	15 (0–30)	15 (0–30)

- a Sorbus aria sub-community
- b Mercurialis perennis sub-community
- 13 Taxus baccata woodland (total)





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