W21
Crataegus monogyna-Hedera helix scrub

Synonymy
Scrub and Chalk scrub *auct. angl.*; Scrub associations Tansley 1911; Progressive scrub Moss 1913; Retrogressive scrub Moss 1913; Thicket scrub Salisbury 1918*b*; Woodland scrub Salisbury 1918*b*; *Fruticetum* Tansley 1939 *p.p.*

Constant species
Crataegus monogyna, *Rubus fruticosus* agg., *Hedera helix*.

Rare species
Himantoglossum hircinum, *Orchis militaris*, *O. purpurea*, *O. simia*, *Silene nutans*, *Seseli libanotis*.

Physiognomy
The *Crataegus monogyna-Hedera helix* scrub is a compendious community which includes most of the seral thorn scrub and many hedges in the British Isles. The vegetation is always dominated by various mixtures of smaller trees and shrubs, undershrubs and woody climbers and sprawlers but physiognomically it is quite diverse and sometimes difficult to separate from more open herbaceous vegetation with scattered woody plants on the one hand and woodland on the other. Typically, however, the woody cover of the community as defined here is dense, often closed or almost so, such that half-and-half mixtures of grassland and scrub would be considered as mosaics of this kind of vegetation and others. The canopy can, however, be quite low, sometimes little more than a metre high and only rarely more than 5 m. But, although stands can be very uneven-topped, where once discrete groups of shrubs, trees and undershrubs are coalescing, the woody cover is characteristically unstratified. Saplings of some species of taller trees are common in the community and occasional specimens may protrude a little but they never form an overtopping canopy.

In floristic terms, the woody component of this vegetation is quite varied, being influenced not only by edaphic differences but also by the availability of seed-parents and the vagaries of dispersal and establishment; and, once the canopy has begun to close, there is some competitive interplay between certain of the species. However, a strong common element is provided by various spinose plants. *Crataegus monogyna* is the most frequent of these overall and it is often the most abundant tree: it is usually among the first invaders of the various kinds of neglected herbaceous vegetation from which the community often develops and, except on shallower soils (usually rendzinas here), it can be very abundant from the start. It is also the most widely planted species of hedges, and in younger stretches, it may be the sole dominant. *C. laevigata*, by contrast, is very rare, though it may appear in stands developing within or close to long-established woodlands in southern Britain (Ross in Tansley 1939, Bradshaw 1953). The other common thorny tree here is *Prunus spinosa*: it is somewhat less frequent overall than *C. monogyna* but it is often prominent in situations where established bushes can sucker in to developing scrub and it probably has an edge over hawthorn on heavier, moister soils. It is also more resistant to salt-spray than *C. monogyna* and tends to replace it as the common dominant on exposed sea-cliffs, although much coastal blackthorn scrub is better placed in the *Prunus-Rubus* community. Feral *Prunus domestica* (often recognisably ssp. *insititia*) is sometimes found in hedges or other stands of the *Crataegus-Hedera* scrub, not always close to settlements.

After *C. monogyna*, the commonest member of the community is *Rubus fruticosus* agg. which is often very abundant here on all but the driest soils, forming clumps of decumbent, arching or erect shoots which can fuse into an impenetrable tangle among the taller trees and sprawl over their lower branches. Where scrub is developing from established woodland or actively spreading, the Rubi often occur as an advancing front over which other trees can leapfrog to colonise the open ground beyond, so that a complex patchwork of young trees and bramble patches develops (e.g. Tansley 1922). Thick

Rubus is densely shading (many taxa are also partly evergreen) and may hinder the establishment of tree seedlings, dense clumps persisting as enclaves among the taller areas of scrub; though, where the canopy of existing trees closes over, the brambles are themselves shaded out to a sparse cover or totally eliminated. Where the scrub has stabilised, *Rubus* may remain dominant in what is essentially a distinct marginal band of the *Rubus-Holcus* underscrub, as along uncut hedgebanks. On drier soils where the community develops, especially more calcareous ones, the procumbent *Rubus caesius* can be found but *R. idaeus* is rather rare here.

Roses, too, can be a prominent feature of the *Crataegus-Hedera* scrub, readily colonising even quite rank herbaceous vegetation. *Rosa canina* agg. is the commonest taxon (*R. dumalis* has been distinguished in some more northerly stands) and it can form large irregular bushes with arching stems up to 3 m tall. Less frequent among the shrubby roses, but rather characteristic of early stages in the invasion of chalky soils, are *R. rubiginosa* and, much more local, *R. agrestis*. Another Rubiginosae rose, *R. micrantha*, has a less marked preference for calcareous soils. Of different habit is *R. arvensis*, which occurs occasionally throughout, as a decumbent bush or, much more conspicuously, as a sprawler, its long shoots reaching several metres in height in the crowns of shrubs and trees. *R. pimpinellifolia* occurs locally, though sometimes in considerable abundance, over sandy soils and limestones.

Few other small trees or shrubs are found with any frequency throughout the *Crataegus-Hedera* scrub. *Corylus avellana*, for example, is rather uncommon. It prefers deeper and moister profiles, so does best in situations where there are pockets of soil among barer rocky ground, where it can be locally abundant, as over limestone talus admixed with soil (e.g. Merton 1970), on pavements with downwash into grikes, or over spoil and made slopes, as on railway embankments (e.g. Sargent 1984). It can also figure prominently in stands developed from degenerating woodland (as in Moss's (1913) 'retrogressive scrub'), clear-felled and abandoned woodland or mis-managed coppice. *Ilex aquifolium* is even scarcer: it can invade closed ungrazed swards, but is commoner on more base-poor soils than are usual here and most of the scrubby vegetation in which it is prominent (like the New Forest holms: Peterken & Tubbs 1965) is best considered as immature stands of less calcicolous oak-birch or beech woodland. The peculiar holly scrub of Dungeness is again developed in association with heath (Scott 1965, Peterken & Lloyd 1967). However, *Ilex* can be locally prominent here and is especially abundant in some areas in hedgerow stands, where there are sometimes suspicions that it has been planted (Peterken & Lloyd 1967). One further infrequent associate is *Salix cinerea* which is occasionally encountered on heavier, moister soils.

Some other species are common but very much confined to particular kinds of *Crataegus-Hedera* scrub. On more naturally eutrophic or disturbed and enriched soils, *Sambucus nigra* is very frequent and locally abundant. It is characteristic here of two sub-communities on mesotrophic mull profiles and on made or fragmentary soils in industrial landscapes and derelict land (in the latter situations sometimes being accompanied by prominent bushes of the garden-escape *Buddleja davidii*); but it also marks out sites of local enrichment on more impoverished calcareous soils, being especially associated with rabbit warrens on the Chalk. Much more distinctive of the more calcicolous kinds of scrub included here is a group of species of which *Viburnum lantana*, *Cornus sanguinea* and *Ligustrum vulgare* are the strongest preferentials with *Rhamnus catharticus* and *Euonymus europaeus* less markedly confined and *Juniperus communis* ssp. *communis* as a locally abundant member.

This type of vegetation is also richer in climbers than are other kinds of *Crataegus-Hedera* scrub with *Tamus communis* and *Clematis vitalba* preferentially frequent. *Lonicera periclymenum* occurs more evenly throughout the community and *Hedera helix* is sometimes seen among the crowns of the trees, though it is more characteristic as a ground-growing plant here. Towards the south-west, *Rubia peregrina* can be found.

The other common group of woody plants in the *Crataegus-Hedera* scrub comprises saplings of certain woodland canopy trees. Frequently, such species invade together with or even in advance of the smaller trees and shrubs, coexisting for some time in a single irregular stratum before they overtop them. The commonest overall is *Fraxinus excelsior* with *Acer pseudoplatanus* more occasional and more obviously confined to moister profiles. Also preferential to heavier soils is *Quercus robur*, much better able to colonise unwooded ground than it is to regenerate under more closed canopies and, with its large food supply in the seed, able to grow up through quite rank swards (Jones 1959). *Acer campestre* is also a little more common on moister soils and to the west and north *Ulmus glabra*. On more eutrophic moist soils, suckering elms of the *procera* and *carpinifolia* sections can also be very prominent here, often spreading from planted trees around settlements and in hedgerows over neglected farmland and abandoned gardens, their dense clones showing the characteristic rounded or semi-circular plan (e.g. Rackham 1975, 1980, Peterken 1981). Saplings of *Fagus sylvatica* can also be found, but they tend to occur only in fairly close proximity to seed-parents and their abundance is very much controlled by the sporadic pattern of masting. Where good mast years have coincided with agricultural neglect near to beech woodland (as in the situations recorded by Watt 1924,

1934*a*, *b*), *Fagus* can figure prominently in this community on both deeper and moister (though not strongly-gleyed) profiles and dry soils. Other trees occasionally found on free-draining, more calcareous soils are young *Taxus baccata* and *Sorbus aria*.

The field layer beneath the more or less continuous woody covers included in the *Crataegus-Hedera* scrub is typically species-poor. The most characteristic feature throughout is a ground carpet of *Hedera helix* which is often very abundant here, frequently accounting for the bulk of the cover and a good indicator of the uninterrupted canopy expansion and slowly-deepening shade that distinguishes many stands. Also typical, though clearly preferential to more eutrophic and disturbed soils (that is, those situations where *Sambucus* tends to occur) are *Urtica dioica* and *Galium aparine* though, throughout, these species are only abundant where the canopy is thinner, becoming more confined to enclaves and margins as the shrub and tree cover closes. On lighter, more calcareous and impoverished soils, *Urtica* and *Galium* continue to be represented sporadically (often around areas of local enrichment like rabbit burrows) but a more frequent indicator of disturbance is *Brachypodium sylvaticum*. This grass is a characteristic plant of scrub that has developed over ploughed and abandoned sites over limestones (commonplace, for example, after wartime ploughing campaigns on marginal land) but is also widely found where the community has sprung up on disturbed, base-rich soils over limestone screes and spoil. It can also mark out areas of scrub which have developed by run-down of a pre-existing woodland cover, though it is by no means an infallible indicator of this kind of origin.

Two other groups of herbs characterise the community. The first comprises species typical of more calcicolous Carpinion and Fagion woodlands and these are best represented in more long-established stands well on their way to maturity and in scrub that has developed adjacent to existing woodland of this kind or by its degeneration. *Mercurialis perennis* is the commonest and most distinctive of this suite and, like *Hyacinthoides non-scripta* and *Anemone nemorosa*, which are much less frequent and more obviously preferential to moister soils over which the community occurs, it is slow to appear in or spread into newly-developing stands. Other members of this group include *Arum maculatum*, *Geranium robertianum*, *Phyllitis scolopendrium*, *Stachys sylvatica* and *Circaea lutetiana* with, on moister soils, *Poa trivialis* and *Glechoma hederacea* and, towards the south, *Iris foetidissima*, all of which are encountered occasionally. Plants of less base-rich woodlands are generally more scarce here, though *Silene dioica* and *Stellaria holostea* occur in some stands. *Holcus mollis* is very patchy and *Pteridium aquilinum* infrequent and usually sparse, though it can show local abundance among more open patches with brambles. On strongly-gleyed soils, *Juncus effusus* and *Deschampsia cespitosa* can be found.

The other group of species occurring here consists of plants which have either survived from the preceding herbaceous vegetation or which have appeared among degenerating scrub, usually the former. By and large, they are shade-intolerant and thus very much confined to more open enclaves and margins, so their frequency among these generally closed canopies is low. Nonetheless, such species can give this kind of scrub considerable floristic diversity and where some grazing or mowing has stabilised the vegetation, they may become a more or less permanent feature among or fronting the trees and shrubs. Grassland assemblages are most frequently encountered with, on less calcareous soils, Arrhenatherion plants such as *Arrhenatherum elatius*, *Holcus lanatus* and *Heracleum sphondylium* and, on more calcareous ones, Mesobromion species like *Bromus erectus*, *Brachypodium pinnatum* and *Sanguisorba minor*. Where the community occurs on more disturbed ground, weedy plants such as *Lamium purpureum*, *Stellaria media*, *Cirsium arvense*, *Arctium minus* agg. and *Bromus sterilis* can occur or, on more calcareous soils, *Erigeron acer*, *Inula conyza*, *Hypericum perforatum* and *H. montanum*. Some of the orchids which can be found in rather more open stands of the community, sometimes in local abundance, may also benefit from the ground disturbance with which the development of this scrub is often associated or from the structural changes that invasion of trees and shrubs involves. Among the species encountered here are *Ophrys insectifera*, *Plantanthera bifolia*, *P. chlorantha* and the rarer *Himantoglossum hircinum* (Good 1936), *Orchis simia*, *O. purpurea* and *O. militaris* (Farrell 1985).

Bryophytes are generally sparse in this vegetation and few species occur more than occasionally. *Eurhynchium praelongum* is the commonest with *Brachythecium rutabulum*, *Plagiomnium undulatum* and *Eurhynchium confertum*.

Sub-communities

***Hedera helix-Urtica dioica* sub-community.** These are species-poor scrubs with a dense canopy that is most often dominated by *Crataegus* or various mixtures of hawthorn, *Prunus* and *Sambucus* with patches and/or a marginal fringe of *Rubus* and *Rosa canina* agg. *Corylus* and saplings of *Fraxinus* occur occasionally but other shrubs and trees are generally scarce, though to the west and north, young *Acer pseudoplatanus* can be locally prominent. Other stands, especially on the heavy clays of the Midlands and East Anglia, are dominated by young suckers of *procera* or *carpinifolia* elms, both in hedges, which are common in this sub-community, and

in field scrubs produced by spread from existing trees. On wastelands, *Buddleja* sometimes figures prominently and other garden-escapes like *Lupinus arboreus* and *Laburnum anagyroides* can be locally abundant.

Under the typically densely-shading canopy, the field layer is usually impoverished and sometimes very sparse, though *Hedera* can be extensive as a ground carpet. The only other common plants are *Urtica* and *Galium aparine* and even these may be reduced to sparse and puny individuals beneath thicker covers. *Poa trivialis* and *Glechoma hederacea* sometimes occur on moister soils or, in drier situations, *Brachypodium sylvaticum* but these are generally very infrequent. Somewhat more common and slightly preferential to this sub-community are *Silene dioica* and species of rank and more weedy Arrhenatherion swards, especially *Arrhenatherum* itself, *Heracleum sphondylium*, *Holcus lanatus* and also *Elymus repens*, *Calystegia sepium*, *Bromus sterilis*, *Cirsium arvense* and *Arctium minus* agg. *Pteridium* also occurs very occasionally, sometimes in abundance. Often, mixtures of these species occur patchily throughout the scrub and may represent survivors of herbaceous vegetation that is being gradually eclipsed but, along narrow verges, they often form a permanent fronting fringe to hedgerow scrub, being stabilised by mowing.

***Mercurialis perennis* sub-community.** In both canopy and field layer, this sub-community is a little richer than the last, having a composition that approximates to that of young calcicolous Carpinion woodland, particularly that of moister, eutrophic soils. *Crataegus*, *Prunus* and *Sambucus* are still very common here and mixtures of these species often dominate; *Rubus* and *Rosa* spp. (including rather more *R. arvensis* here) are also usually prominent within and around stands. But with some *Corylus*, frequent saplings of *Fraxinus* and *Acer pseudoplatanus*, occasional preferential occurrences of young *Quercus robur* and *Acer campestre* and sparse records for *Euonymus* and *Cornus*, the floristics of the woody cover are often qualitatively indistinguishable from the *Fraxinus-Acer-Mercurialis* woodland. Quantitatively, however, the balance of the various components is different and structurally the vegetation is dominated by smaller woody plants, having a canopy usually around 5 m high with occasional taller emergent trees. In some stands fairly close to mature *Fagus*, beech saplings may be locally abundant and other tracts are dominated by young elm suckers.

Such stands may be very dense but usually here the canopy is a little more open and the presence of some less heavily shading trees makes for greater lighter penetration. This, together with the probably greater age of these scrubs, means that a richer and more extensive field layer can develop. *Hedera* is still often extensive as a ground carpet and patches of *Urtica* and *Galium aparine* are very common but *Mercurialis* is now much increased in frequency, though it usually occurs as discrete clonal patches rather than as a continuous sheet. Also preferential here are *Arum maculatum*, *Poa trivialis*, *Glechoma hederacea*, *Hyacinthoides non-scripta*, *Allium ursinum* and, on spring-waterlogged soils, *Anemone nemorosa*.

Bryophytes are more frequent here than in the last sub-community, though their cover is typically low with *Eurhynchium praelongum* and *Brachythecium rutabulum* forming sparse wefts.

***Brachypodium sylvaticum* sub-community.** The composition of the woody cover here is very much as in the *Hedera-Urtica* sub-community except that *Sambucus* is much reduced in frequency and there are occasional records for more calcicolous species like *Ligustrum*, *Cornus*, *Rhamnus* and *Viburnum lantana*. *Juniperus* and young *Taxus* can also be found in some stands but none of these species is as common as in the *Viburnum* sub-community. *Fagus* saplings can be locally prominent and some stands are dominated by elm suckers.

In the field layer, *Hedera* remains frequent and often abundant but *Urtica* and *Galium aparine* are rather uncommon and usually of low cover. Much more obvious here is *Brachypodium sylvaticum* with occasional *Fragaria vesca* and *Viola riviniana*. Other species can be quite numerous, though no other plants are preferential: rather, there are scattered individuals of a wide variety of species occurring throughout the community or more frequently in other sub-communities, including *Silene dioica*, *Holcus mollis*, *H. lanatus*, *Cirsium arvense*, *Pteridium aquilinum* (on somewhat less base-rich soils), *Mercurialis perennis*, *Arum maculatum*, *Geranium robertianum* and *Phyllitis scolopendrium* (on rather more base-rich soils). Bryophytes are poorly represented with only very occasional *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Plagiomnium undulatum*.

***Viburnum lantana* sub-community:** Chalk scrub association Tansley & Rankin 1911: Limestone scrub Moss 1911; Progressive scrub Moss 1913 *p.p.*; Retrogressive scrub Moss 1913; Chalk scrub Tansley 1925, Smith 1980; Juniper scrub Watt 1934*a*; Hawthorn scrub Watt 1934*a* *p.p.*; *Clematito-Prunetum* Shimwell 1968*a*; *Crataegus-Rosa pimpinellifolia* community Shimwell 1968*a*; *Geranio-Coryletum* Shimwell 1968*a*; Southern mixed shrub communities Duffey *et al.* 1974. In terms of its woody component, this is by far the most distinctive kind of *Crataegus-Hedera* scrub. In the first place, various of the general community species show a reduction in frequency or abundance here, tending to be better represented on deeper soils which are in the minority. *Prunus spinosa*, for example, is less common than usual and *Crataegus* and *Rubus fruticosus* agg., though still frequent, often have lower cover than else-

where. *Corylus*, too, favours deeper soils though it performs well on rubbly slopes with admixed talus and soil. *Sambucus* is local and distinctly associated with disturbed and enriched sites but, since these can be widespread, it figures fairly frequently. But, more obviously, various other species are strongly preferential to this sub-community, *Viburnum lantana*, *Cornus* and *Ligustrum* becoming constant and *Juniperus* occurring more frequently than elsewhere. Roses are also often conspicuous with *R. rubiginosa*, *R. micrantha* and, more locally, *R. agrestis* and *R. pimpinellifolia* being recorded along with *R. canina* agg. and *R. arvensis*. *Rubus caesius* can occur in the early stages of colonisation. Among the woodland canopy trees represented by saplings, there are also some distinctive features. Young *Fraxinus* and, on deeper soils to the west and north, *Acer pseudoplatanus* are common and there can be some *Fagus sylvatica* near to established seed-parents, but more frequent than usual are *Taxus* and *Sorbus aria*. *Quercus robur* saplings, on the other hand, are very scarce. The other prominent component comprises climbers. *Hedera* and *Lonicera* are occasionally seen among the tree and shrub canopies but much more characteristic here are *Tamus* and *Clematis*.

When rich mixtures of these species are present, this kind of scrub can present a splendid sight, especially when the deciduous species get their autumn colours and the plants are in full fruit. As always, there is considerable physiognomic variation between stands, with some more open and others almost closed, though, in line with the general definition of the community, less dense woody covers should be considered as scrub/grassland mosaics. There are also differences in the canopy composition in relation to regional and local climate and soils. Many of the preferentials, for example, have a distinctly Continental distribution in Britain, being best represented on the Chalk of the south and east and becoming increasingly scarce in moving to the north-western limit of the *Crataegus-Hedera* scrub (e.g. Pigott & Huntley 1978). And, among these, *Cornus* seems especially well adapted to the colonisation of more impoverished soils by rapid and prolific seed germination (Lloyd & Pigott 1967), after which it can sucker profusely and become locally dominant. Then, there is the tendency for *Juniperus* (and sapling *Taxus*) to be associated with shallower, drier soils on steeper, more exposed slopes, a preference which, in contrast to the quantitative prominence of *Crataegus* on deeper, moister soils on gentler, sheltered slopes here, led Watt (1934*a*) to propose his classic two-sere view of scrub and beechwood development on the Chilterns. *Crataegus-Hedera* scrubs with *Juniperus* have not been widely sampled but available data suggest that both types of Watt's scrubs can be accommodated in this single sub-community.

The field layer beneath denser woody covers here is not especially distinctive. *Hedera* and *Brachypodium sylvaticum* are the commonest species and the occasional presence of plants such as *Mercurialis perennis*, *Arum maculatum* and *Geranium robertianum* gives the vegetation something of the appearance of the *Mercurialis* sub-community, though associates of moister soils like *Poa trivialis* and *Glechoma hederacea* are very scarce. In more open places, there can be greater enrichment. On shallower, rocky soils, *Teucrium scorodonia* and *Origanum vulgare* are very characteristic of this kind of scrub and there can be some *Hypericum perforatum*, *H. montanum* and more ephemeral species such as *Erigeron acer* and *Inula conyza*. In places with local soil enrichment, as where this scrub is colonising around rabbit burrows, *Urtica* and *Galium aparine* can be prominent together with plants like *Verbascum thapsus*, *Atropa belladonna* and *Solanum dulcamara* among an abundance of *Sambucus*. Then, where invasion is occurring over more intact soil covers, there may be survivors of the preceding herbaceous vegetation, an often extremely rich calcicolous grassland element in the more open mosaics characteristic of the early stages of scrub development but, with increasing canopy closure, generally limited to ranker grasses like *Bromus erectus* or *Brachypodium pinnatum* with dicotyledons such as *Sanguisorba minor* and *Helianthemum nummularium* which are able to grow up through the tall sward. Some of the rarer orchids noted above are particularly associated with these kinds of transition: some of the stations of *Orchis simia*, *O. purpurea* and *O. militaris* (Farrell 1985) occur in more open stands of this sub-community and much of the spread of *Himantoglossum hircinum* early in this century has been around this scrub (Good 1936). Another rarity which seems to be closely related to rank grassy scrubs of this type is *Seseli libanotis* (Dony 1953).

Also best considered here is the distinctive kind of vegetation described from Derbyshire by Moss (1913) as 'retrogressive *Corylus* scrub' and defined by Shimwell (1968*a*) as the *Geranio-Coryletum*. This open scrub would, strictly speaking, be considered in this scheme as a complex mosaic of the *Viburnum* sub-community with the local calcicolous grassland, but it has some other peculiar floristic features. Although the woody cover is generally orthodox, *V. lantana* is already scarce this far north and *Corylus* is unusually abundant. Furthermore, although *Brachypodium sylvaticum*, *Teucrium* and *Origanum* are frequent, together with some common woodland herbs like *Mercurialis perennis*, *Viola riviniana* and *Melica uniflora*, there is a very striking mixture of species with strong northern affinities, such as *M. nutans*, *Trollius europaeus* and *Rubus saxatilis* with others like *Geranium sanguineum*, *Convallaria majalis*, *Silene nutans* and *Aquilegia vulgaris* that seems to indicate rather specialised environmental and historical relationships.

Bryophytes are usually not numerous or abundant in more closed stands of the *Viburnum* sub-community but the usual *Eurhynchium praelongum* and *Brachythecium rutabulum* are sometimes accompanied by *Ctenidium molluscum*, *Thuidium tamariscinum* or *Fissidens cristatus*.

Habitat

The *Crataegus-Hedera* scrub is the typical sub-climax woody community of circumneutral to base-rich soils throughout the British lowlands. It usually develops by the invasion of neglected bare ground or untreated herbaceous vegetation or where woodland has been degraded and its floristics and physiognomy reflect its transitional and unstable character as well as being related to edaphic and climatic variation. Hedgerow stands are often of planted origin but, even where the establishment of a woody cover is more natural, human influence affects colonisation through the previous treatment of the ground and the availability of seed-parents; and re-imposition of grazing, mowing or burning can halt or reverse the successional process at any stage.

The most important factor governing the development of the community in the intensively-used British landscape is the disruption of the stability of the existing ground cover. Sometimes, this happens naturally and exposes fresh bare surfaces, as where the woody species of this scrub have invaded directly or early in the colonisation of landslips in softer deposits (splendidly seen on the Axmouth–Lyme Regis Undercliffs: Ratcliffe 1977) or of fresh talus and rock falls beneath harder cliffs. But, very often here, such disruption is to some extent artificial. The *Crataegus-Hedera* scrub has developed widely, for example, on many kinds of neglected made ground (on derelict land, over spoilheaps and on verges and embankments: e.g. Sargent 1984) and on cultivated land that has been abandoned (in gardens, allotments and arable fields: e.g. Brenchley & Adam 1915, Salisbury 1918*b*, Tansley 1939, Lloyd & Pigott 1967). It is also extremely common where grasslands, previously maintained as plagioclimax vegetation, have been subject to a relaxation of grazing and/or mowing, with stands widely distributed over neglected pastures, meadows, verges, commons and graveyards (e.g. Watt 1924, 1934*a*, Tansley 1939) and on land that has experienced some decline in natural herbivore populations, notably rabbits following myxomatosis (e.g. Thomas 1960, 1963, Wells 1969).

The *Crataegus-Hedera* scrub includes most of the more well-established woody vegetation that develops in such varied situations as these except where the soils are either markedly acid or strongly waterlogged. In the former case, it is generally replaced by the *Ulex-Rubus* scrub or various kinds of ericoid heath which are often colonised by birch (and, seeding in from plantations, pine); on wetter ground, by young woodlands with *Salix cinerea*, *Betula pubescens* and *Alnus*. Apart from brambles, none of these species is common here, though pine can figure locally, even among *Juniperus* (Ward 1973) if there is an abundant seed source nearby. But, within these very broad limits, the soils here are very variable, ranging from man-made raw soils on rock waste and demolished buildings, through man-made soils on restored ground, new verges and hedgebanks, to more natural profiles of different degrees of maturity. In terms of base-status, the soils run from quite base-poor brown earths to very base-rich and calcareous rendzinas; and the drainage of the profiles varies from impeded (surface-water gleys being especially important) to excessive; some soils are highly eutrophic, others are very poor in nutrients.

Some of the woody colonisers characteristic of the *Crataegus-Hedera* scrub are able to invade and establish over virtually the whole spectrum of these soils and it is these more catholic species that provide the core of the floristic definition of the community. *Crataegus*, *Prunus*, *Rubus fruticosus* agg. and *Rosa canina* agg. are well represented throughout and are often among the first colonisers, fading in quantitative importance only on the most shallow and dry profiles. Among the woodland trees that invade early, both *Fraxinus* and *Acer pseudoplatanus* are also relatively undemanding as far as soil conditions are concerned.

Below this general level, there are some clear edaphic preferences among other woody species which help to define the different kinds of *Crataegus-Hedera* scrub. *Sambucus*, for example, is distinctly associated with more eutrophic soils, though the source of the enrichment is very varied. Some of the profiles here are naturally richer than others and the preferential frequency of *Sambucus* in the *Hedera-Urtica* and *Mercurialis* sub-communities is partly a reflection of the fact that many soils under these kinds of scrub are mulls, rather than more oligotrophic rendzinas which predominate in the *Brachypodium* and *Viburnum* sub-communities. The former sub-communities are also common on abandoned arable land which has received some additions of fertiliser in the past and in a wide variety of situations where there has been or continues to be some kind of ground disturbance. In the *Brachypodium* and particularly the *Viburnum* sub-community, *Sambucus* often marks areas of more local enrichment, as around rabbit burrows, where its success is enhanced because of the unpalatable nature of its bark. Suckering elms of the *procera* and *carpinifolia* groups also tend to be commoner on the more eutrophic soils of the *Hedera-Urtica* and *Mercurialis* sub-communities, though it is not clear whether they are responding to or helping produce enrichment (Martin & Pigott 1975, Rackham 1975, 1980).

Among the more eutrophic kinds of *Crataegus-*

Hedera scrub, there are further differences among the woody species related to soil moisture. *Quercus robur* and, especially in more southerly stands, *Acer campestre* and suckering elms are all preferentially frequent invaders in the scrub of the *Mercurialis* sub-community which is particularly characteristic of ill-draining clays and shales with stagnogleys and pelosols in abandoned arable land and neglected pastures in the Midlands and East Anglia (e.g. Brenchley & Adam 1915, Ross in Tansley 1939).

Generally, the soils of the other types of *Crataegus-Hedera* scrub are more free-draining and, among these, the major edaphic influence is related to base-status. The *Hedera-Urtica* sub-community is typical of less base-rich profiles, many of them fragmentary soils over non-calcareous waste or made soils on verges and hedge-banks, others more natural brown earths on neglected agricultural land. By contrast, the soils of the *Brachypodium* and particularly the *Viburnum* sub-community are characteristically base-rich and calcareous, in the latter type of *Crataegus-Hedera* scrub often classic rendzinas where extreme base-richness is combined with excessive drainage and impoverishment. Much of the very distinctive richness of the canopy of the *Viburnum* sub-community comes from the preferential frequency of more calcicolous species: *Viburnum lantana*, *Cornus*, *Ligustrum* and, to a lesser extent, *Rhamnus* and *Euonymus* are all best represented here, together with a number of less common roses, like *R. rubiginosa*, *R. agrestis* and *R. pimpinellifolia*, and *Clematis*. Most of the southern British localities of *Juniperus* are also on the more shallow and calcareous of these rendzinas (Watt 1934*a*), though the differential survival of this shrub on more marginal land may give us only a partial view of its edaphic preferences in this part of the country (Ward 1973). Among invading woodland trees, the more calcicolous *Taxus* and *Sorbus aria* are preferential here and, where seed-parents are near, *Fagus* can figure prominently, out-performing *Q. robur* on these shallower soils and only giving way to *Taxus* in more extreme conditions (Watt 1926, 1934*a*).

The *Viburnum* sub-community is by no means confined to rendzinas over Chalk: it occurs on calcareous, lithomorphic soils over other limestone bedrocks and waste as far north as the southern Lake District. But it is best represented to the south and east, where Chalk is the predominant limestone, because many of its distinctive calcicolous woody species happen to have strongly Continental affinities, becoming increasingly scarce towards the north and west where summers are cooler and shorter. No single isotherm provides a precise limit for this kind of *Crataegus-Hedera* scrub and, though a mean annual maximum temperature of 26 °C (Conolly & Dahl 1970) marks a crude final boundary for the sub-community as a whole, some species (*V. lantana* itself, for example) have a distribution more strictly confined to the warmest parts of the country. Others, like *Juniperus*, occur widely further north (though on different kinds of soils) and yet are rather local in their distribution to the south. Among the colonising woodland trees, *Taxus* is likewise local and *Fagus*, though of Continental range through Europe, is of restricted natural occurrence in Britain, though it often colonises in this scrub from planted stock far to the north of its limit.

A number of factors are of very considerable importance in limiting the ability of the woody species of the community to colonise the various climatic and edaphic situations they prefer, and this means that stands, especially younger ones, can show great diversity, even within individual sub-communities. The physical character of the existing ground cover is one: whether it is bare (and then, whether it is stable or not) or already occupied by herbaceous vegetation (and then, how rank this is). *Fraxinus*, for example, is able to get a hold on quite mobile talus, *Corylus* favouring more stable and finer material admixed with soil, *Acer pseudoplatanus* faring especially well on grossly-disturbed and abandoned sites like old spoil heaps. In Cressbrook Dale in Derbyshire, Scurfield (1959) and Merton (1970) demonstrated how much of the scrub and young woodland springing up on barer ground (and belonging mostly to the *Brachypodium* and *Viburnum* sub-communities) was dominated by variation in the proportions of these species according to their substrate preferences. One other species which can rapidly colonise open, shallow and very impoverished limestone soils here is *Cornus*: it has the advantage of a berry containing two seeds which germinate very quickly provided there has been a cold pre-treatment and it can become very prominent in stands of the *Brachypodium* and especially the *Viburnum* sub-community which have grown up on marginal Chalkland, ploughed once and then abandoned (Lloyd & Pigott 1967: see also Tansley 1922). On enriched bare soils, where the *Hedera-Urtica* sub-community often develops, *Sambucus* (and the garden-escape *Buddleja*) often get an early hold, sometimes in more unorthodox situations, as where such scrub develops up the walls of half-demolished buildings.

Other species are able to colonise closed swards, even quite rank ones. *Crataegus*, *Prunus*, *Rubus fruticosus* agg. and *Rosa canina* agg. are all plants which favour somewhat deeper and moister soils than are characteristic of the above situations, but they can also grow through a herbaceous cover and commonly come to dominate in all kinds of *Crataegus-Hedera* scrub derived from grasslands where grazing or mowing have been relaxed. On heavier, moister soils, *Q. robur* is also a characteristically early invader, well adapted, with its big seeds that benefit from a cover of litter, to growing through ranker herbage (Jones 1959). *Procera* and *carpinifolia* elms, as well as *Prunus* and in some areas *Populus tremula*, can circumvent competition from

taller plants by suckering under the vegetation, and these species may dominate locally where established trees have spread into overgrown woodland rides or fields adjacent to hedges.

A second factor influencing colonisation is the supply of seed of the woody species, more particularly the location of seed-parents and dispersal from them. Some plants here are extremely widely distributed, notably *Crataegus* which has been universally planted in lowland hedges, and *Rubus fruticosus* agg. which is so catholic as to figure, as one taxon or another, in a very wide variety of vegetation types; this undoubtedly gives these species some advantage in the invasion of newly-available ground. Others benefit from having been planted nearby too, like *Fagus*, which can seed into this kind of scrub well beyond the area where it is a natural forest dominant. On the other hand, there are species like *Juniperus* which are rather localised and which may have declined to such critically low levels in some areas as to be able to re-expand only with difficulty, even were conditions for establishment to become suitable (Ward 1973).

As far as dispersal is concerned, it is noteworthy that many of the most successful species of the *Crataegus-Hedera* scrub, both generally and among the preferentials of more calcareous soils, have brightly-coloured and fleshy fruits attractive to birds, among which larger members of the thrush family seem to be particularly important as dispersal agents, flocking in large numbers in winter and often totally depleting the crop (Fuller 1982). These species show diet preferences, though this varies with availability (Hartley 1954) and no systematic work seems to have been done on the effectiveness of these birds in dispersing particular trees or shrubs. Heavier fruits like acorns and hazel nuts are often dispersed by small mammals, and the former by larger birds, especially jays, sometimes over considerable distances: acorns, for example, can be carried up to 200 m from the parent tree (Mellanby 1968) and this can give *Q. robur* some advantage in this community over *Fagus*, whose fruits often just drop from the tree (Watt 1923, 1925). Other important invaders such as *Fraxinus* and *Acer pseudoplatanus* have fruits which can be wind-dispersed and prevailing wind direction may be a controlling factor in their prominence. In considering the invasion of pastures where grazing has been relaxed, it should also be remembered that many of the commonest woody species of this scrub are already present in many swards as very small individuals, a few centimetres high and growing very slowly, but able to get away quickly if unchecked.

Once established in such situations, those species which are well armed with thorns or prickles are protected to some extent against renewed herbivore predation and can offer some shelter to new woody invaders that may not be so resistant. Other species benefit by being unpalatable: *Sambucus*, for example, once established around rabbit burrows, is largely immune from barking by these animals and *Juniperus* can play a crucial role in protecting young *Fagus* and *Taxus* which grow up in the *Viburnum* sub-community (Watt 1926, 1934*a*). Tighter canopies of early invaders can also offer shelter from wind in exposed situations. However, as soon as the cover of trees and shrubs begins to close, the influence of shade begins to outweigh any protective effect for those species more sensitive to reduced light penetration. Rubi and roses in particular tend to become more confined to the margins of all the different kinds of *Crataegus-Hedera* scrub or to enclaves where they established themselves early as a thick, smothering cover that precludes invasion of taller species; and young saplings of many of the trees, notably *Fraxinus* and *Acer pseudoplatanus*, can be overtaken and shaded out. Where *Juniperus* figures in the *Viburnum* sub-community, it too is eventually killed by its crowding neighbours, often by the shade-tolerant *Taxus* which it nurses but which eventually overtops it (Watt 1926).

The increasing canopy shade, and probably also intense root-competition, are the major factors responsible for the characteristically impoverished field layer of the *Crataegus-Hedera* scrub. As defined here, the community includes only denser stands of scrub within which there is usually but scanty survival of any pre-existing herbaceous vegetation: such elements can be a continuing source of enrichment in younger, more open mosaics or stabilised zonations (see below) but, with the advance of scrub development, they become progressively confined to margins and any remaining uncolonised areas. Those plants which do persist vary considerably, particularly in more disturbed situations where there can be many low-frequency adventives, but the recognisable assemblages described above usually differ according to soil conditions and the particular pattern of treatment and neglect of the vegetation in the period before the scrub developed. Where grasslands have been colonised, the survivors are typically important species of ranker swards (unless grazing or mowing have been re-imposed around the scrub) with Arrhenatherion assemblages on the less base-rich soils, represented here in the *Hedera-Urtica* sub-community, Mesobromion species on the more base-rich, as in the *Viburnum* sub-community. Where waste ground or abandoned arable land has been invaded, Arrhenatherion plants may figure again where there has been time for the establishment of an intervening grassy phase before the woody species have colonised. On more calcareous soils, *Brachypodium sylvaticum* is a more persistent survivor from abandoned ploughland, being more shade-tolerant than most of the other grassland herbs: both the *Brachypodium* and *Viburnum* sub-communities probably include

stands which have developed in this kind of situation. Where trees and shrubs colonise more open ground directly, weeds often remain prominent for some time with coarser, eutrophic species on richer soils; on shallow rendzinas that have been ploughed and abandoned, there may be remnants of the distinctive dicotyledon-dominated calcicolous floras characteristic of impoverished, base-rich soils, often preferentially invaded by *Cornus* to produce scrub of the *Viburnum* sub-community (e.g. Lloyd & Pigott 1967).

On the positive side, the single most obvious response to the deepening shade, the great spread in all kinds of *Crataegus-Hedera* scrub of the ground carpet of ivy, marks a floristic convergence in the middle years of the community, as the variety of the preceding herbaceous floras is finally extinguished and before there is any obvious development of a rich woodland element. The prominence of the other more or less common component of the community, *Urtica* and *Galium aparine* may also be partly an indirect response to shade. On more disturbed, enriched soils, these species are often present before the scrub develops but, where closed swards are being invaded, they typically appear with the trees and shrubs, perhaps responding to the appearance of patches of enriched bare ground where other herbs have succumbed to the shade and decayed, releasing a flush of nutrients. In some cases, the use of scrub as bird-roosts may play a part in soil eutrophication.

The *Crataegus-Hedera* scrub can remain in this very dense and dark phase for considerable periods of time with often little more than a sparse carpet of ivy beneath or sometimes total extinction of the field layer. But, where succession progresses, a new phase of enrichment with the appearance of woodland herbs ensues and this community includes such transitional vegetation prior to the development of the distinctive woodland canopy. The initiation of this stage is partly a function of the opening up of the woody cover, as overtopped small trees and shrubs thin out to leave some gaps. Some existing species, like *Hedera*, *Urtica*, *Galium aparine* and *Brachypodium sylvaticum*, can show a renewed expansion, providing some floristic continuity and *Rubus* may spread again as an underscrub, but distinctive woodland species now begin to appear too. However, since some of the most important of these, notably *Mercurialis*, *Hyacinthoides* and, on moister soils, *Anemone*, are very slow to spread, there may be a very considerable time-lag before anything like a full complement of herbs develops, a feature very well seen in the colonisation of Geescroft Wilderness at Rothamsted (Brenchley & Adam 1915, Tansley 1939, Pigott 1977). Although no data on the age of the stands included here were available, it seems likely that the most long-established scrubs are those of the *Mercurialis* sub-community where the elements of a richer kind of Carpinion or Fagion woodland are well represented. Some stands in the *Hedera-Urtica* sub-community have a field layer similar to that of less calcicolous Carpinion woodland.

Zonation and succession

Zonations between the *Crataegus-Hedera* scrub and other vegetation types are very varied but they usually represent stages in diverse successions between open ground or herbaceous vegetation on the one hand and woodland on the other, sometimes progressive, sometimes stabilised, sometimes moving in reverse and often represented by only part of the full sequence of communities. Surprisingly, in view of the very widespread occurrence of these successions, very few systematic studies of their operation have been undertaken. Potentially valuable early studies (e.g. Salisbury 1918*b*, Tansley 1922, Tansley & Adamson 1915, Brenchley & Adam 1915, Ross in Tansley 1939, Hope-Simpson 1940*b*, 1941*b*) were, for one reason or another, not followed through in detail and what other knowledge we have usually comes from comparison of different stands at different stages of development (e.g. Watt 1926, 1934*a*, Scurfield 1959, Merton 1970, Duffey *et al.* 1974) or more generalised observations (e.g. Thomas 1960, 1963). We are therefore much in need of long-term investigations of the progression of even the most ordinary processes here.

Active and direct scrub colonisation of recently- or grossly-disturbed substrates is more common in artificial habitats like urban and industrial wasteland than in naturally unstable situations which are quite rare in the subdued landscape of lowland Britain. On neglected derelict land, the *Crataegus-Hedera* scrub is usually represented by the *Hedera-Urtica* sub-community springing up among mosaics of weed communities or weedy Arrhenatherion swards, together with *Rubus-Holcus* underscrub. Patterning is often rather chaotic and progression to woodland uncommon, partly because of the frequently recent and continuing disturbance and partly because, in more extensive sites, seed-parents of canopy trees can be quite rare. But *Acer pseudoplatanus* sometimes becomes very prominent and less isolated sites may have patchy stands of the *Holcus lanatus* sub-community of the *Quercus-Pteridium-Rubus* woodland, dominated by sycamore with a little ash and *Q. robur*, which have perhaps developed from the scrub.

Similar mixtures of weedy vegetation with scrub of the *Hedera-Urtica* sub-community can characterise abandoned ploughland on less base-rich brown earths. The frequency of this kind of site has varied according to the vagaries of the agricultural economy, fields sometimes falling into neglect when arable cultivation became unprofitable or in periods when incentives for ploughing pushed such cultivation on to marginal land that proved too intractable. Colonisation of such aban-

doned ground by woody species can follow diverse courses but with generally abundant supplies of seed in hedges and woodlands nearby, it is often more rapid and orthodox than on derelect land and some of the classic descriptions of the development of the *Crataegus-Hedera* scrub relate to such situations (Salisbury 1918*b* Brenchley & Adam 1915, Ross in Tansley 1939). As before, it seems likely that the *Hedera-Urtica* sub-community develops into some kind of *Quercus-Pteridium-Rubus* woodland on more base-poor soils or, where *Fagus* figures prominently among the invading trees, into the *Fagus-Rubus* woodland (e.g. Watt 1924, 1934*b*). On more base-rich but heavy soils, very common over the claylands of the Midlands and East Anglia, succession is more likely to lead to the *Fraxinus-Acer-Mercurialis* woodland with the *Mercurialis* sub-community perhaps supervening between the *Hedera-Urtica* sub-community and richer forms of this forest; or the latter kind of *Crataegus-Hedera* scrub may develop directly to the *Hedera* sub-community of the *Fraxinus-Acer-Mercurialis* woodland, as seems to have happened on Broadbalk Wilderness at Rothamsted (Brenchley & Adam 1915, Tansley 1939) and in the Hayley Triangle (Rackham 1975).

Zonations involving the *Hedera-Urtica* and *Mercurialis* sub-communities are also common on less and more base-rich brown earths in lowland agricultural landscapes where scrub development has been precipitated by a decline in grazing by stock or wild herbivores, notably rabbits, or by neglect of mowing in field corners or more inaccessible parts of meadows. Usually, in such cases, weedy elements figure little among the associated herbaceous vegetation, grasslands being more prominent. Typically, on these often quite enriched soils, these are mesotrophic swards like the *Lolio-Cynosuretum* or the *Centaureo-Cynosuretum* or, more often in direct contact with the scrub, rank *Arrhenatheretum* or, on moister soils, the *Deschampsia-Holcus* grassland. *Rubus-Holcus* underscrub again frequently forms a fringe between the grassland and the scrub. On sea-cliffs, where the *Crataegus-Hedera* scrub can develop in more sheltered situations, these grasslands are replaced by sequences of more maritime swards like the *Festuca-Holcus* or *Festuca-Daucus* grasslands or, where there is some grazing, the *Festuca-Plantago* grassland. In such situations, progressions to woodland are rare, but on neglected inland pastures and meadows the *Crataegus-Hedera* scrub seems to follow the same sequence as in successions on open ground, to *Quercus-Pteridium-Rubus* or *Fagus-Rubus* woodland on less base-rich soils or to *Fraxinus-Acer-Mercurialis* woodland on the more base-rich but moist soils.

On base-rich but more free-draining rendzinas, zonations typically involve the *Brachypodium* or *Viburnum* sub-communities and on freely-weathering limestone slopes free of heavy grazing, a situation seen especially well on Carboniferous Limestone exposures following myxomatosis, complete sequences from open fern-dominated vegetation, through tussocky *Arrhenatherum* to these kinds of *Crataegus-Hedera* scrub and woodland, can be found (e.g. Merton 1970). Usually, on Carboniferous Limestone, most of which lies beyond the natural limit of *Fagus*, different kinds of *Fraxinus-Acer-Mercurialis* woodland represent the climax forest, with the *Geranium* sub-community predominating on steeper screes that have acquired a woodland cover fairly recently (Pigott 1960, 1969, Merton 1970). Longer-established *Fraxinus-Acer-Mercurialis* woodland, among which open areas of *Viburnum* sub-community scrub can be found on rocky knolls, is very locally of the *Teucrium* sub-community (Moss 1913, Pigott 1960, 1969, Shimwell 1968*a, b*).

On the gentler landscapes of the more southerly limestones like the Chalk and Oolite, zonations between the *Brachypodium* and *Viburnum* sub-communities and more open vegetation are often associated with artificially-disturbed sites like spoil heaps and quarry floors (e.g. Tansley 1922, Tansley & Adamson 1925, Hope-Simpson 1940*a*, 1941*a*) and rabbit warrens (Tansley 1939). In such places, these kinds of *Crataegus-Hedera* scrub can be found in mosaics with the calcicolous weedy vegetation of the Atropion alliance of the Epilobietea. On more impoverished and disturbed limestone soils, such as are exposed by ploughing and abandonment of very shallow rendzinas, the *Viburnum* sub-community can be seen developing among open swards of the *Festuca-Thymus-Hieracium* grassland (Lloyd & Pigott 1967).

Where scrub develops at a later stage in successions from open ground over limestones or invades long-established grasslands where grazing has been relaxed, the *Brachypodium* and *Viburnum* sub-communities are typically found in mosaics with closed Mesobromion swards. What these are depends partly on the regional and local climate, partly on the soil conditions and partly on the grazing regime before scrub invasion. By and large, the distribution of these two kinds of *Crataegus-Hedera* scrub coincides with the range of the major lowland plagioclimax calcicolous grassland, the *Festuca-Avenula* sward, and different types of this community usually constitute the starting point for successions; towards the north-west, there is a small overlap with *Sesleria albicans* swards, the *Sesleria-Scabiosa* and *Sesleria-Galium* grasslands; along the oceanic seaboard of the west and south, the *Festuca-Carlina* grassland can show sporadic progression to scrub, though the edaphic and climatic conditions characteristic of this sward are usually too extreme to support any growth of woody species.

Most of the trees and shrubs of the *Brachypodium* and

Viburnum sub-communities can invade (or, if suppressed saplings are already present, get away in) these grasslands once grazing is relaxed but, quite often, a coincidental spread of ranker grasses means that scrub development is occurring among mosaics of these swards and grasslands dominated by *Bromus erectus* and/or *Brachypodium pinnatum* (especially to the south) or *B. sylvaticum* or, on somewhat deeper soils, *Festuca rubra, Avenula pubescens* or *Arrhenatherum elatius*. And, among these latter communities, the advance of scrub may be accompanied by a fringe of *Rubus-Holcus* underscrub, a feature well seen in Tansley's (1922) account of invasion at Downley Bottom on the South Downs. After the demise of rabbits with myxomatosis in the mid-1950s, mixtures of all these vegetation types have become extremely common, particularly on the southern Chalklands (e.g. Thomas 1960, 1963, Wells 1969, Ratcliffe 1977). Although advanced scrub development in this kind of landscape usually results in a great floristic impoverishment, more open mosaics of short swards, rank grasslands and scrub on limestones represent one of the richest complexes of vegetation types that are found in lowland Britain, with a structural variety that can be of importance to the diversity of invertebrate and bird populations (e.g. Duffey *et al.* 1974, Smith 1980, Fuller 1982).

Post-myxomatosis successions are too young for any extensive progression to mature forest yet to have occurred but, over much of the southern Chalk, the *Fagus-Mercurialis* woodland is probably the natural climax community on moderately free-draining rendzinas, with the *Taxus* woodland replacing it locally on slopes with a warmer topoclimate (Watt 1926, 1934*a*). Beyond the natural limit of beech, such successions probably terminate in the *Fraxinus-Acer-Mercurialis* woodland with *Fraxinus* and *Acer pseudoplatanus* very well represented in younger, secondary canopies.

In all these different kinds of succession, scrub advance can be halted by a re-imposition of grazing or mowing which typically results in sharp boundaries between the grassland and scrub quite unlike the gradual and uneven transitions of active colonisation. Such abrupt zonations are the norm on hedgebanks where linear stands of *Crataegus-Hedera* scrub, often of planted origin though sometimes the remnants of woodlands adjacent to the path or road, are fronted by mesotrophic or calcicolous grasslands artificially maintained, usually by mowing, with perhaps a very condensed zone of *Rubus-Holcus* underscrub between. All the sub-communities can be found in such zonations, the particular arrangement of the scrub, underscrub and grassland components varying according to the verge and hedgebank structure, something which often shows marked regional differences along older routes. Similar condensed transitions can be seen where the *Crataegus-Hedera* scrub occurs as a marginal fringe to mature woodland.

Very heavy grazing or cutting or burning of scrub followed by grazing and mowing can reverse successions to the *Crataegus-Hedera* scrub though it is probably very difficult to restore the richer, more long-established swards from which the seral progressions often start, especially where scrub invasion is well advanced and destruction of the trees and shrubs involves great disturbance. Then, the scrub is likely to be replaced by weedy vegetation or rank Arrhenatherion grasslands. Gradual scrub destruction by long-continued grazing is probably more successful in restoring richer herbaceous communities and some stands of the community may represent an intermediate stage on a retrogressive sere from woodland back to grassland, initiated and maintained by grazing (Moss 1913).

Distribution

The *Crataegus-Hedera* scrub is widely distributed through the British lowlands. The *Brachypodium* and *Viburnum* sub-communities are generally confined to areas with more free-draining calcareous soils so their ranges reflect the occurrence of drift-free limestones; and the latter type is much better represented in the warmer south and east, having its centre of distribution on the Chalk. The *Mercurialis* sub-community is concentrated on more heavy-textured base-rich soils, being especially common in areas with clays and shales or ill-draining superficials.

Affinities

The community brings together a wide variety of previously described vegetation types often simply termed 'scrub', or 'Chalk scrub' in the case of the *Viburnum* sub-community, and only rarely (e.g. Shimwell 1968 *a, b*) subjected to more detailed phytosociological analysis. Available data are relatively few and, pending further investigation, it seems best to retain the types distinguished here within the same community. The *Crataegus-Hedera* scrub thus contains most of the more well-established British woody vegetation of the order Prunetalia, often placed in a distinct class of scrubs and underscrubs, the Rhamno-Prunetea, though incorporated by Ellenberg (1978) into the Querco-Fagetea. The community is best accommodated among the more calcicolous scrubs of the Berberidion alliance, though the *Hedera-Urtica* sub-community has affinities with the Rubion subatlanticum. Similar vegetation types have been described from Germany (Tüxen 1952, Ellenberg 1978) and The Netherlands (Westhoff & den Held 1969).

Floristic table W21

	a	b	c	d	21
Crataegus monogyna	V (1–10)	IV (2–8)	IV (1–8)	V (2–8)	V (1–10)
Rubus fruticosus agg.	V (1–10)	III (2–7)	IV (2–6)	V (2–8)	IV (1–10)
Prunus spinosa	III (1–9)	II (2–9)	III (1–10)	II (3–6)	III (1–10)
Fraxinus excelsior sapling	II (1–4)	III (3–7)	II (1–10)	III (3–4)	III (1–10)
Rosa canina agg.	III (1–7)	II (1–5)	II (4–6)	III (3–7)	III (1–7)
Corylus avellana	II (1–7)	II (4–8)	II (3–5)	II (4–6)	II (1–8)
Rosa arvensis	I (2)	II (2–5)	I (1)	I (1–4)	I (1–5)
Acer pseudoplatanus sapling	I (2–6)	II (3–7)	I (3)	II (3–5)	I (2–7)
Lonicera periclymenum	I (2–5)	I (3–4)	I (1–4)	I (3–5)	I (1–5)
Euonymus europaeus	I (1–3)	I (3–4)	I (4)	I (3)	I (1–4)
Ilex aquifolium	I (1–2)	I (1–9)	I (1–2)	I (4)	I (1–9)
Salix cinerea	I (7)		I (1–8)	I (5)	I (1–8)
Rhamnus catharticus	I (4)		I (4–5)	I (4–5)	I (4–5)
Betula pendula sapling	I (3)	I (3)	I (7)		I (3–7)
Fagus sylvatica sapling		I (4–7)	I (1–4)	I (1–4)	I (1–7)
Sambuca nigra	III (1–6)	III (1–6)	I (4)	II (1–4)	II (1–6)
Quercus robur sapling	I (1)	II (3–9)	I (5)	I (3)	I (1–9)
Acer campestre	I (1–4)	II (3–5)	I (3)	I (1–4)	I (1–5)
Ulmus procera/carpinifolia suckers	I (1–8)	II (4–10)	I (9–10)		I (1–10)
Malus sylvestris	I (1–2)	I (1–4)			I (1–4)
Ulmus glabra sapling	I (1)	I (1–6)			I (1–6)
Crataegus laevigata		I (3)			I (3)
Ligustrum vulgare	I (1–5)	I (1–6)	II (2–5)	V (1–5)	II (1–6)
Viburnum lantana	I (4)	I (4)	I (4–8)	V (4–8)	II (4–8)
Cornus sanguinea	I (5)	I (3–6)	I (3–6)	IV (3–6)	I (3–6)
Tamus communis	I (3)	I (1–4)	I (1–4)	III (1–4)	I (1–4)
Clematis vitalba		I (3)	I (1–6)	III (1–4)	I (1–6)
Taxus baccata sapling	I (8)	I (7)	I (3–8)	II (3)	I (3–8)
Juniperus communis communis			I (4–8)	II (4–7)	I (4–8)
Sorbus aria sapling				I (4–5)	I (4–5)
Hedera helix	IV (2–10)	IV (3–10)	IV (1–10)	IV (6–10)	IV (1–10)

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Urtica dioica	IV (1–8)	IV (1–10)
Galium aparine	IV (1–7)	IV (2–8)
Silene dioica	II (2–5)	I (4)
Heracleum sphondylium	II (1–4)	I (1–3)
Holcus lanatus	II (3–5)	I (2)
Arrhenatherum elatius	II (1–6)	
Elymus repens	I (3–6)	
Calystegia sepium	I (1–5)	
Mercurialis perennis	I (1–6)	IV (2–7)
Eurhynchium praelongum	I (1)	III (1–8)
Arum maculatum	I (1–5)	III (2–5)
Poa trivialis	I (3–7)	II (2–7)
Glechoma hederacea	I (1–5)	II (2–6)
Brachythecium rutabulum	I (1)	II (1–6)
Hyacinthoides non-scripta		II (2–6)
Allium ursinum	I (5)	I (3–8)
Anemone nemorosa		I (2–7)
Brachypodium sylvaticum	I (1–6)	I (1–4)
Fragaria vesca		
Viola riviniana		
Teucrium scorodonia		
Origanum vulgare		
Bromus erectus		
Brachypodium pinnatum		
Sanguisorba minor		
Stachys sylvatica	I (1–3)	I (2–5)
Geranium robertianum	I (1–2)	I (3–5)
Phyllitis scolopendrium	I (1–5)	I (4–6)
Iris foetidissima	I (3)	I (3–4)
Pteridium aquilinum	I (2–8)	I (1–2)
Circaea lutetiana	I (4)	I (2–3)
Stellaria holostea	I (1–3)	I (2)
Dryopteris filix-mas	I (1)	I (1–3)
Dactylis glomerata	I (1–3)	I (1–2)

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II (3–4)	II (3–4)	III (1–10)
II (3–5)	III (1–4)	III (1–8)
I (1–5)	I (5)	I (1–5)
I (1–4)	I (4)	I (1–4)
I (4–6)		I (2–6)
I (4)		I (1–6)
		I (3–6)
		I (1–5)
I (2–3)	II (2–7)	II (1–7)
II (1–6)	II (2–6)	II (1–8)
I (1–4)	II (2–4)	II (1–5)
I (1–2)	I (1)	I (1–7)
I (3)	I (2)	I (1–6)
I (4–5)	I (5)	I (1–6)
		I (2–6)
		I (3–8)
		I (2–7)
IV (1–9)	IV (3–6)	III (1–9)
II (2–4)	II (2–3)	I (2–4)
II (1–7)		I (1–7)
I (3–6)	II (1–4)	I (1–6)
	II (1–3)	I (1–3)
	II (2–5)	I (2–5)
	II (1–5)	I (1–5)
	II (1–3)	I (1–3)
I (4)	I (2)	I (1–5)
I (1–6)	I (1–6)	I (1–6)
I (2–7)	I (1–6)	I (1–7)
I (4)	I (3–4)	I (3–4)
I (1–3)		I (1–8)
I (2)		I (2–4)
I (4)		I (1–4)
I (1)		I (1–3)
		I (1–3)

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Floristic table W21 *(cont.)*

	a	b	c	d	21
Rumex sanguineus	I (1–4)	I (3)			I (1–4)
Moehringia trinervia	I (1–2)	I (3)			I (1–3)
Torilis japonica	I (1–2)	I (3)			I (1–3)
Lamium purpureum	I (3)	I (3)			I (3)
Stellaria graminea	I (4)	I (2)			I (2–4)
Stellaria media	I (1)	I (3)			I (1–3)
Arctium minus agg.	I (5)	I (3)			I (3–5)
Holcus mollis	I (2)		I (3–6)		I (2–6)
Cirsium arvense	I (4)		I (1–3)		I (1–4)
Ranunculus repens	I (1–2)		I (2)		I (1–2)
Bromus sterilis	I (3–4)		I (1)		I (1–4)
Potentilla sterilis	I (1)		I (2–3)		I (1–3)
Plagiomnium undulatum		I (3–4)	I (4–7)		I (3–7)
Juncus effusus		I (3)	I (4)		I (3–4)
Geum urbanum		I (2)	I (1)		I (1–2)
Eurhynchium confertum		I (3)	I (3)		I (3)
Rubia peregrina			I (3–5)	I (5)	I (3–5)
Number of samples	30	34	20	31	115
Number of species/sample	11 (4–24)	15 (6–27)	16 (7–29)	14 (8–18)	14 (4–29)
Shrub height (m)	3 (1–8)	5 (1–15)	2 (1–5)	3 (2–3)	3 (1–15)
Shrub cover (%)	97 (80–100)	87 (60–100)	91 (25–100)	98 (90–100)	92 (25–100)
Herb height (cm)	78 (10–150)	46 (15–150)	35 (10–150)	42 (20–150)	46 (10–150)
Herb cover (%)	73 (5–100)	91 (50–100)	79 (5–100)	77 (10–100)	81 (5–100)
Ground height (mm)	10	18 (10–40)	20 (10–40)	10	15 (10–40)
Ground cover (%)	1 (0–50)	11 (0–85)	16 (0–100)	17 (0–85)	9 (0–100)
Altitude (m)	87 (4–270)	73 (2–150)	82 (5–130)	60 (10–130)	66 (2–270)
Slope (°)	2 (0–40)	4 (0–50)	7 (0–40)	7 (0–30)	4 (0–50)

a *Hedera helix-Urtica dioica* sub-community
b *Mercurialis perennis* sub-community
c *Brachypodium sylvaticum* sub-community
d *Viburnum lantana* sub-community
21 *Crataegus monogyna-Hedera helix* shrub (total)

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