

Biological Flora of the British Isles: *Juniperus communis* L.

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Summary

1. This account reviews information on all aspects of the biology of *Juniperus communis* that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history and conservation.

2. *Juniperus communis* (juniper) is an evergreen dioecious gymnosperm shrub with two main population centres in Britain, one on chalk downlands of southern England and the other in northern England and Scotland. British populations are divided into two main subspecies although there is overlap in genetic and morphological features. Subspecies *communis* varies from a spreading shrub to an erect tree characteristic of calcareous soils in southern England, various soils in the Scottish highlands, while ssp. *nana* is a small procumbent shrub, restricted to well-drained bogs and, more usually, rocky outcrops, generally as a minor component of upland heaths and montane scrub. Both subspecies are drought and frost tolerant, although sensitive to fire. A third subspecies, *hemisphaerica*, primarily found in mountains of southern Europe has two small populations on maritime cliffs in the UK.

3. Although not very palatable, *J. communis* is grazed by small and large mammals when food is short, particularly in winter. Its low palatability is derived from oils found in the needles, cones and wood, dominated by monoterpenes. These have been extensively used in folklore medicine and to flavour alcoholic drinks, and are being investigated for new medicinal uses.

4. *Juniperus communis* ssp. *communis* is a characteristic light-demanding invader of pasture but has declined due to agricultural expansion, erosion, overgrazing, fire and poor regeneration, such that it is now rare and threatened across lowland/southern Europe. Although susceptible to overgrazing, some grazing can be beneficial to create the open sward necessary for seedling establishment. Other limits to regeneration are: progressively ageing stands in which male plants predominate; increasing fragmentation of stands that reduces pollination efficacy; and high seed dormancy with consequent variable germinability.

Key-words: climatic limitation, communities, conservation, ecophysiology, geographical and altitudinal distribution, germination, herbivory, mycorrhiza, parasites and diseases, reproductive biology, soils

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Pinopsida (Coniferae), Cupressaceae. The junipers are a taxonomically difficult group, composed of about 68–80 species, mainly shrubs and small trees, distributed over temperate and subtropical regions of the northern hemisphere, although *Juniperus procera* also grows along the rift mountains of East Africa into the southern hemisphere (Adams & Demeke 1993; Adams 2004).

Juniperus communis is a native evergreen gymnosperm shrub or small tree to 11(17) m. Bark reddish-brown, usually thin, often peeling in long strips. Young shoots triangular with projecting ridges. Twigs terete, slender, smooth and often shiny, triangular between the nodes, spreading in three dimensions, not flattened into one plane as in other genera of the Cupressaceae. Buds c. 3 mm long with acuminate scales. Adult foliage is not found in this species of juniper. Juvenile foliage needle-like to narrowly oblong, 5–12(15) mm long, acute apex, jointed at base, very prickly, erect to patent; leaves borne in whorls of three, persisting for three years, sessile, keeled and with a single broad white stomatal band on the upperside, sometime divided by a green line towards the base, often with an abaxial resin gland. Usually dioecious. Male cones (strobili) c. 8 mm, solitary, maturing and shed annually, cylindrical, with (2)3–6(9) whorls of stamens; pollen wingless. Female strobilus axillary, c. 2 mm and green when young, 5–10 mm and globose or rather longer than broad, surrounded at base by minute scale-like bracts, persisting when mature; a true cone although the 3–16 scales do not become hard and woody but remain fleshy, \pm fused together and berry-like, black with a blue bloom when ripe. Seeds not winged, elongated, ovoid, three-cornered, with grooves and resin pockets over the whole seed, one seed per cone-scale, 1–3(6) seeds per cone, each 4–5 mm long, embedded in the resinous, mealy pulp and retained within the cone at dispersal. Female cones ripen the second or third year.

Juniperus communis is a variable species, with the two extremes of variation usually regarded as separate subspecies in the British Isles – *ssp. communis* and *ssp. nana*. There are also frequent intermediates between these and two further subspecies are normally recognized – *ssp. hemisphaerica* and *ssp. depressa* – although at least 30 varieties have been recognized (Adams 2004). Poveda *et al.* (2002) demonstrated clear differences between *ssp. nana* and *ssp. depressa* based on the alkane composition of cuticular waxes. There appears, however, to be no clear genetic distinction between all populations of *ssp. communis* and *ssp. nana* and so differentiation between subspecies may not be reliable (Vines 1998, cited in Adams *et al.* 2002; Adams & Pandey 2003; Plantlife 2004). Sullivan (2001) concluded that in north-west Scotland if > 40% of leaves on a bush are abruptly pointed it was *ssp. nana*, while < 40% indicated *ssp. communis*. Filipowicz *et al.* (2006) found no difference between the two subspecies on the basis of chloroplast DNA or monoterpene content. Similarly, Guerra Hernández *et al.* (1987) found little difference in

volatile distillates. Miller (1974) suggested that the two subspecies can be differentiated by wood anatomy, specifically average and maximum tracheid lengths and distribution of ray height frequencies, but again there is some overlap. In the light of these uncertainties, Adams (2004) relegated all these subspecies to varieties; in this account, however, we follow *Flora Europaea* in referring them to subspecies.

Juniperus communis ssp. *communis* (ssp. *eu-communis* Syme; var. *arborescens* Gaud.; var. *montana* Niell.-non-Ait.; var. *vulgaris* Ait.) is the more frequent and forms a spreading shrub to an erect tree, but is very variable and can sometimes be prostrate, undoubtedly in response to environmental conditions (Lebreton & Bayet 1994). Sullivan (2001) considered plants apparently intermediate to *ssp. nana* to be *ssp. communis*. Leaves are mostly 8–20 \times 1–1.5 mm, loosely set, patent, spreading at almost right angles to the stem, gradually tapering to a sharp point so that branchlets are prickly to the touch. Mature female cone globose usually with one seed. Very local but often common throughout lowland Britain and Ireland on both limestone and acid soils, especially on the chalk downs of southern England and the Scottish Highlands.

Juniperus communis ssp. *nana* (Hook.) Syme (ssp. *nana* (Willd.) Syme; ssp. *alpina* Celak.; ssp. *alpina* (Sm.) Celak.; ssp. *alpina* (S.F. Gray) Celak.; ssp. *alpina* (Neilr.) Celak.; var. *montana* Ait.; var. *saxatilis* Pall.; *J. alpina* (Sm.) S.F. Gray; *J. densa* Gord.; *J. pygmaea* K. Koch; *J. sibirica* Burgsd.; *J. nana* Willd.; *J. vulgaris* Kohler nom. nud.; see Christensen (1985)) is a procumbent shrub often < 10 cm high. Leaves mostly 4–12 \times c. 1.5 mm, closely set, ascending or loosely appressed, abruptly tapered to a short but sometimes blunt point such that the branchlets are scarcely sharp to the touch. Female cone longer than broad, normally with up to three seeds. Rocks and moors mostly in the uplands, exposed coastal areas and lowland bogs of north Wales, north-west England, western Ireland and central and north-west Scotland; absent from southern England.

Juniperus communis ssp. *hemisphaerica* (J. & C. Presl) Nyman (ssp. *depressa* Steven) is intermediate between the last two subspecies, forming a low compact shrub, leaves mostly 8–20 \times 1.3–2 mm, closely set, patent, gradually tapering to a sharp point so that branchlets are prickly to the touch. It is found mainly in mountainous areas of southern Europe and north-west Africa (Quèzel & Barbero 1989) and in the UK is, according to Preston *et al.* (2002), confined to two tiny populations on low maritime cliffs on the Lizard Peninsula, Cornwall, and in Pembrokeshire. Stace (1997) commented that the identity of these plants needs confirmation.

Juniperus communis ssp. *depressa* (Pursh) Franco is restricted to North America and is not considered further here. The many other possible varieties, including var. *hondoensis* and var. *nipponica* from Japan and Taiwan and var. *megistocarpa* from eastern Canada (Adams *et al.* 2002, 2003) are also omitted from this account since they do not occur in the British Isles.

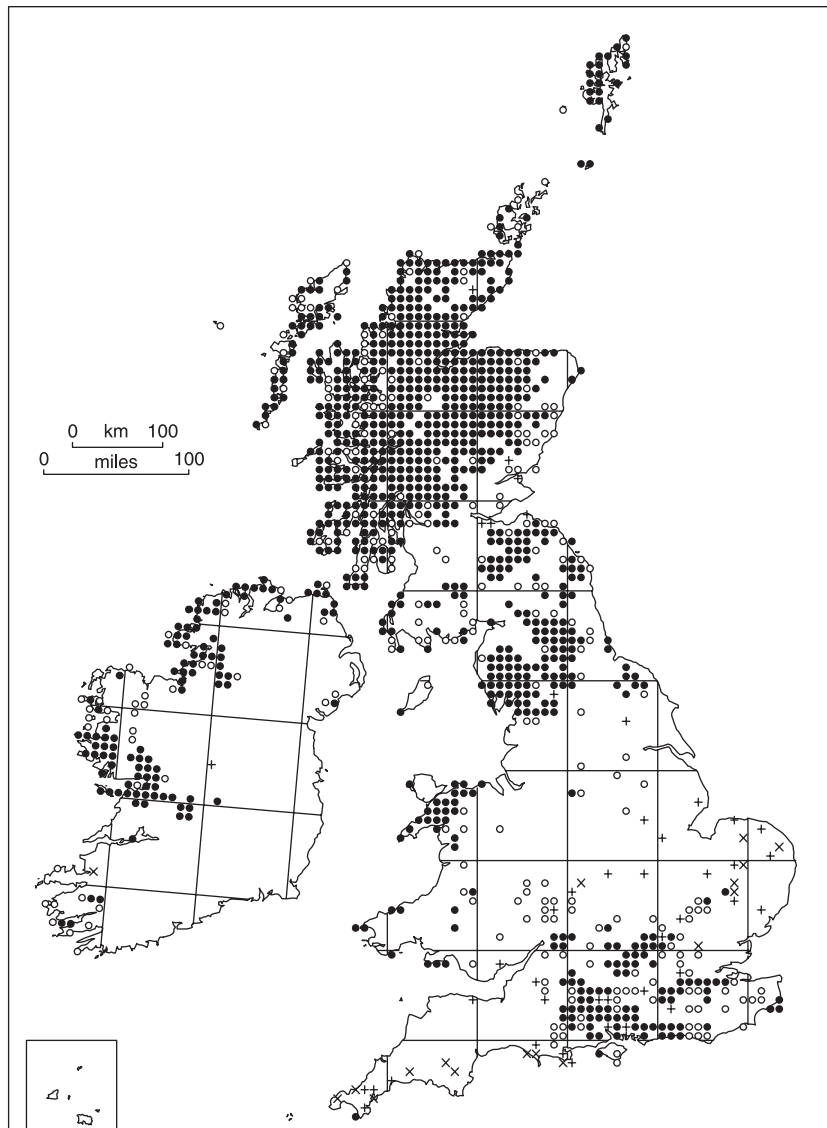


Fig. 1. The distribution of *Juniperus communis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards, (○) pre 1950; introduced: (+) 1950 onwards, (x) pre 1950. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society of the British Isles.

I. Geographical and altitudinal distribution

Juniperus communis has a wide distribution in Britain (Fig. 1) from west Cornwall and Kent and Dorset northwards to Hertford and Carmarthen, North Wales, Lancashire and Yorkshire northwards to Orkney. In Ireland it occurs mainly in the west: Kerry, Cork, from Clare and Tipperary northwards to Derry, Down and Antrim. The distribution is discontinuous with main population centres in the north (mostly in Scotland and more rarely in northern England) and the chalk downlands of southern England with scattered populations elsewhere. It is locally abundant in Cumbria, County Durham and Northumberland. The natural distribution of juniper in Britain has undoubtedly been reduced by burning and excessive grazing.

Juniperus communis ssp. *communis* (Fig. 2) is characteristic of the lowlands, including the distinctive

communities on chalk in southern England, but extends onto suitable sites in northern England and Scotland. In northern England, most juniper colonies lie between 180 m and 420 m (Clifton *et al.* 1997) but the high altitude *Juniperus–Oxalis* woodland (W19) in north-east Britain lies between 300 m and 650 m (Rodwell 1991), with an altitudinal limit of individuals ascending to 975 m at Braeriach, Aberdeenshire (Preston *et al.* 2002). Juniper here and other places in the Cairngorms, such as Creag Fhiachach, is probably the closest approach to a natural treeline in Britain. *Juniperus communis* ssp. *nana* has a smaller range, restricted to the uplands of North Wales, Cumbria and Scotland plus a number of populations scattered around Northern and Southern Ireland (Fig. 3). As an occasional component of montane (subalpine) scrub in the northern corries of Cairn Gorm, it occurs between 450 and 850 m (Scott 2000) and in Wales up to 800 m (Y

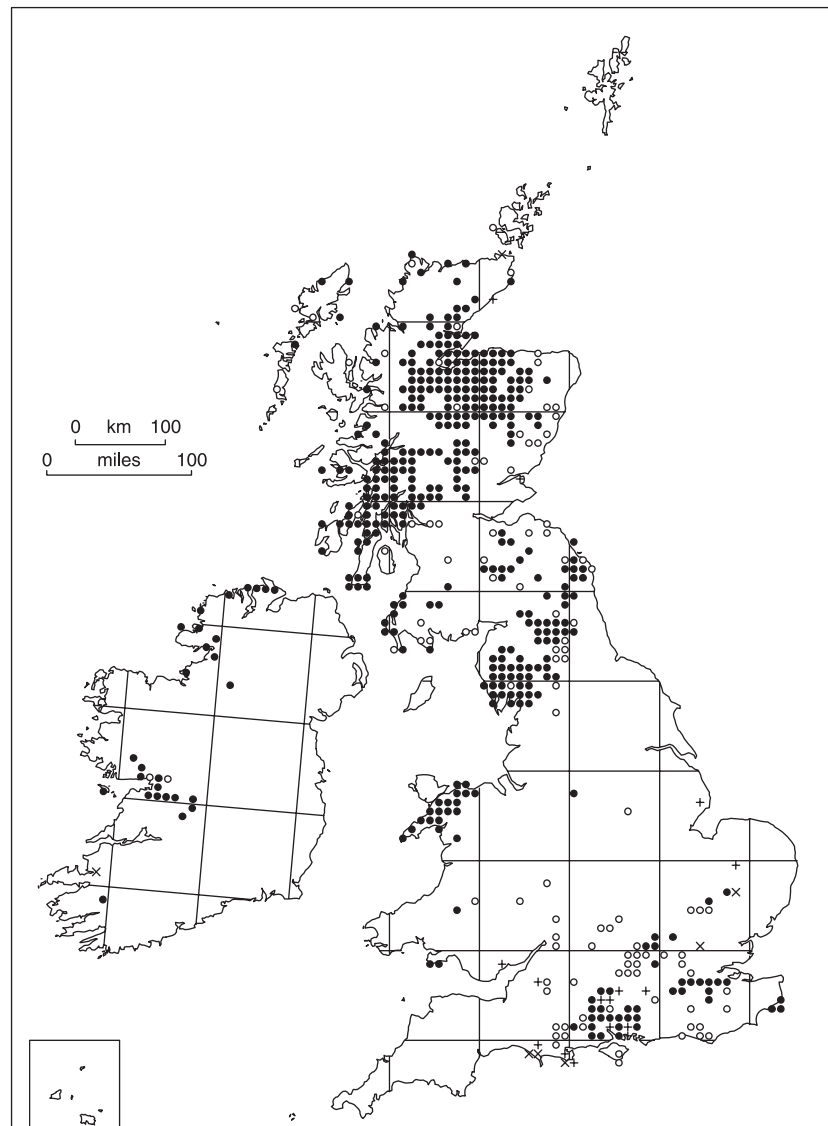


Fig. 2. The distribution of *Juniperus communis* ssp. *communis* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards, (○) pre 1950; introduced: (+) 1950 onwards, (×) pre 1950. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society of the British Isles.

Lliwedd, Caernarvonshire; Preston *et al.* 2002) and down to sea level in the north and west of Scotland. *Juniperus communis* ssp. *hemisphaerica* is found mainly in mountainous areas of south Europe and north-west Africa and in the UK is, according to Preston *et al.* (2002), confined to two tiny populations on low maritime cliffs on the Lizard Peninsula, Cornwall, and in Pembrokeshire.

Juniperus communis has one of the widest global distributions of any gymnosperm, occurring throughout most of Europe (except the Azores, Balearic Islands and Crete; Fig. 4), north Africa, north Asia southwards to the Himalaya, and North America from the mountains of north California to Pennsylvania. In the north of its range, *J. communis* has a wide, continuous distribution, being increasingly confined to scattered and isolated mountain areas in the south.

In Spain, *J. communis* ascends to 1600–2500 m (García *et al.* 1999a). *Juniperus communis* ssp. *communis* is globally the most widespread subspecies with ssp. *hemisphaerica* occurring in the mountains of southern Europe (including Sicily) while ssp. *nana* is found in the higher mountains of Europe, including those of the Mediterranean and the islands of Corsica and Sardinia (Lebreton *et al.* 2000; Gerasimidis *et al.* 2006) descending to coastal rocks and cliffs along north Atlantic coasts.

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

In southern England *Juniperus communis* ssp. *communis* is associated with steep, exposed slopes with shallow

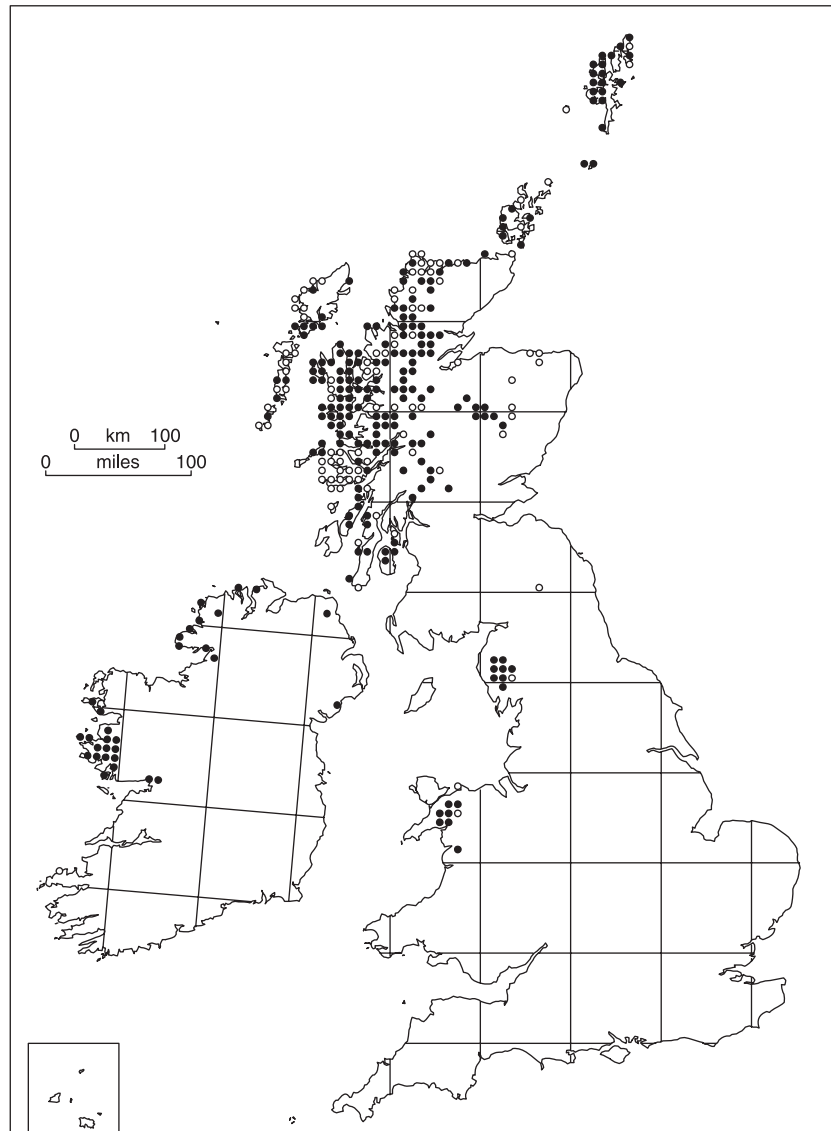


Fig. 3. The distribution of *Juniperus communis* ssp. *nana* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards, (○) pre 1950. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society of the British Isles.

drought-prone soils, whereas in northern England and Scotland it occurs in more mesic conditions attributable to higher rainfall, soil flushing or north-facing slopes. *Juniperus-Oxalis* woodland in the east-central Highlands of Scotland is found where the climate has a distinct continental nature with comparatively low rainfall (800–1200 mm year⁻¹ or about 160 wet days year⁻¹). In the Scottish Borders, juniper grows on slopes from zero to 95% (McBride & Borders Forest Trust 1998). By contrast, *J. communis* ssp. *nana* is found in moister areas of > 1600 mm year⁻¹ of precipitation and with more than 220 wet days annually (McGowan *et al.* 1998), where snow tends to be blown clear of the vegetation and there is severe wind pruning. Snow may be detrimental to spp. *nana*: Sullivan (2001) mentioned a stand in Strathdearn that suffered almost 100% mortality after being snow-covered for around six weeks in the severe winter of 1983–4. It occupies flat

to gently sloping land with a moderately sheltered, predominantly southerly aspect. Large areas of north-west Scotland that appear to offer suitable habitat are nevertheless devoid of ssp. *nana* (Poore & McVean 1957; Thompson & Brown 1992). *Juniperus communis* ssp. *hemisphaerica* is restricted to exposed lowlands near sea-level (Preston *et al.* 2002). In continental Europe, *J. communis* is typical of harsh environmental conditions and nutrient-deficient soils (García *et al.* 2000b). Rodwell (1991) commented that *Juniperus-Oxalis* woodland in the east-central Highlands of Scotland was found in areas with annual accumulated temperatures of 280–550 °C, a mean annual maximum temperature below 23 °C, and the lowest February minima of any part of the country; snow-fall was moderate but morning snow-lie occurred on more than 60 days year⁻¹ and late frosts were very frequent.

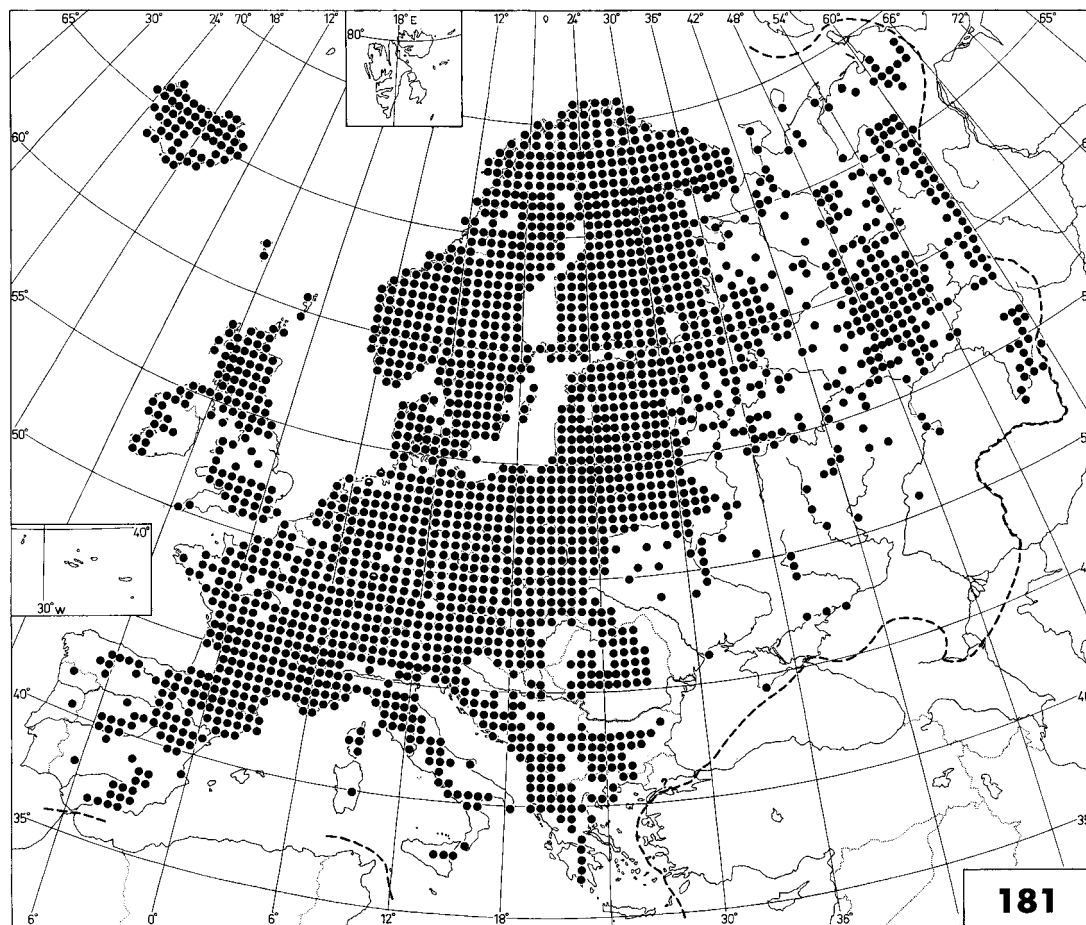


Fig. 4. European distribution of *Juniperus communis* (reproduced from *Atlas Florae Europaeae*, vol. 2, 1973, by permission of the Committee for the Mapping of the Flora of Europe and Societas Biologica Fennica Vanamo).

(B) SUBSTRATUM

In the south, *J. communis* ssp. *communis* occurs predominantly on calcareous soils (with some on acidic heath; Ward 1973) but is largely indifferent to soil in the north, growing on all free-draining soils, particularly limestone, slate and quartzite, but avoiding waterlogged and the most excessively drained soils. In between these geographical extremes, juniper is mostly found on Carboniferous Limestone in the northern Pennines, although a few populations are found on acidic soils of the andesitic lavas of the Cheviots and the crags of Whin Sill (Clifton *et al.* 1997).

Juniperus communis ssp. *nana* is restricted to rock outcrops and the better drained parts of blanket bog. In north-west Scotland, it is generally found on weathered acidic scree or debris with a surface mosaic of rock, bare soil and vegetation (McGowan *et al.* 1998). On deeper soils it occurs mainly on free draining peat < 30 cm deep, often with a mineral content. In Scotland, ssp. *communis* has been recorded as growing on soils between pH 4.1–5.7 (Forbes & Proctor 1986) and ssp. *nana* pH 3.7–4.9 (Sullivan 2001). *Juniperus communis* ssp. *hemisphaerica* at the Lizard grows on broken, rocky slopes over serpentine rocks where cattle tracks act as fire-breaks; in Pembrokeshire it occurs in

wind-pruned coastal scrub and dwarf heathland near sea-level (Preston *et al.* 2002). Both subspecies *nana* and *communis* are tolerant of poor soils and, like birch, have the reputation of being soil improvers (Phillips 1910; Miles & Kinnaird 1979a).

III. Communities

In calcareous habitats, *Juniperus communis* is found in two grasslands (Rodwell 1992). *Juniperus communis* (approaching ssp. *nana* in its procumbent habit) is a fairly abundant and frequent member of the *Salix repens*–*Empetrum nigrum* ssp. *nigrum* subcommunity of the *Dryas octopetala*–*Carex flacca* heath (CG13) in the lowlands of north-west Scotland. In southern England *Juniperus communis* ssp. *communis* is an infrequent and scarce member of the *Fragaria vesca*–*Erigeron acer* and the *Medicago lupulina*–*Rumex acetosa* subcommunities of the *Festuca ovina*–*Hieracium pilosella*–*Thymus praecox*/pulegioides grassland (CG7). Ssp. *communis* has also been seen as an important colonizer of swards of the *Cladonia* subcommunity after myxomatosis, forming open scrub at Porton Down, Wiltshire, in a nutrient-poor grassland type most similar to the Brecklands of East Anglia. Indeed, in the early 1970s, Porton Down contained around

a quarter of the juniper bushes of southern England according to Wells *et al.* (1976) although they have subsequently declined in number (Ward & King 2006), partly due to increased rabbit numbers.

Juniperus communis ssp. *communis* is also locally abundant in the *Crataegus monogyna*–*Hedera helix* scrub (W21), especially within the *Viburnum lantana* subcommunity confined to free-draining calcareous soils, and best represented on the Chalk of the south-east. *Taxus baccata* and *Sorbus aria* are the most frequent trees. *Juniperus communis* is associated with shallower, drier soils on steeper and more exposed sites and is the main nurse plant necessary for the establishment of yew seedlings (Watt 1934), leading to *Taxus baccata* woodland (W13) in the south-east and elsewhere, such as the sea cliffs of the Great Orme and the Little Orme of northern Wales (Larson *et al.* 2000). Juniper establishes on more exposed, steeper slopes and drier, shallower soils than *Crataegus monogyna*, conditions more suitable for the establishment of yew. Moreover, juniper provides a better defence against herbivores.

The wind-swept short carpets of shrubs typical of the *Armeria maritima* subcommunity of the *Calluna vulgaris*–*Scilla verna* heath (H7) on cliffs of the west coast of Britain contain scattered bushes of *Juniperus*. *Juniperus communis* is also a minor component of a number of upland and northern heaths. Birks (1977) suggested that, based on modern treelines in Scandinavia, juniper once formed a belt of scrub between the tree-line of pine and birch in the Cairngorms and the dwarf-shrub heath above. Moorland areas in the eastern Highlands of Scotland can contain small scattered bushes of *J. communis* ssp. *communis*. These correspond to the *Calluna vulgaris*–*Vaccinium myrtillus* heath (H12), especially in the more species rich *Vaccinium vitis-idaea*–*Cladonia impexa* subcommunity and to a lesser extent the more open *Galium saxatile*–*Festuca ovina* subcommunity. In the north-west Highlands, where the heather is severely wind-trimmed (*Calluna vulgaris*–*Racomitrium lanuginosum* heath, H14) there are scattered records of *J. communis*, generally ssp. *nana*, usually in low abundance although it can be locally abundant and reach up to 50% cover in the diverse shrub-mat of the *Arctostaphylos uva-ursi* subcommunity. *Juniperus communis* ssp. *nana* is also found in some stands of the *Loiseleuria procumbens*–*Cetraria glauca* subcommunity of the *Calluna vulgaris*–*Arctostaphylos alpinus* heath (H17) on very exposed ridges of higher altitudes in north-west Scotland, and to a lesser extent at lower altitudes in the *Viola riviniana*–*Thymus praecox* subcommunity of the *Vaccinium myrtillus*–*Racomitrium lanuginosum* heath (H20). At the lowest altitudes in shaded, moist habitats, ssp. *nana* is a very occasional addition in the *Calluna vulgaris*–*Vaccinium myrtillus*–*Sphagnum capillifolium* heath (H21).

In these heaths, however, *Juniperus* is most common, by definition, in the *Calluna vulgaris*–*Juniperus communis* ssp. *nana* heath (H15) where it is a more or less constant dominant in the shrub-mat. Here, the shrub-mat is

often severely wind-pruned to less than 10 cm thick. *Calluna vulgaris* and *Erica cinerea* together with a number of other ericaceous species are frequent, although not dominant, and the sheltered, oceanic conditions encourage high bryophyte diversity. This heath is restricted to the western seaboard of north-west Scotland and some of the western islands, especially Skye. Over the typical quartzite substrate it forms a characteristically discontinuous mosaic of islands with very sparse cover on the intervening bare rock. It typically occurs at the junction of the sub- and low-alpine zones situated between mires below and fell-field above. Although it is best developed on cool shady slopes which are blown clear of snow, it is comparatively more sheltered compared to other heath types in the area (such as the *Calluna*–*Racomitrium* and *Calluna*–*Arctostaphylos alpinus* heath). The best examples on Beinn Eighe and Foinaven cover a number of hectares (Poore & McVean 1957; Pl. Comm. Scot.) but the extent of this community may have been greatly reduced by burning, to which the juniper is very sensitive, and it now covers < 800 ha (Sullivan 2001). Sullivan found that junipers in H15 stands were twice as old as in other communities emphasizing the lack of recent disturbance. Fire may explain the many scattered plants of *J. communis* ssp. *nana* throughout the many different heath types, which are partly differentiated from *Calluna*–*Juniperus* heath by the absence of juniper. Durno & McVean (1959) traced this heath on Beinn Eighe back to Sub-Atlantic times and concluded that the current stands are a relic of a previously much more widespread community type. On the east-central Highlands where the climate is more continental, the *Calluna*–*Juniperus* heath is replaced by the more calcifugous *Juniperus*–*Oxalis* scrub.

Juniperus communis ssp. *communis*–*Oxalis acetosella* scrub (W19) is a community of high altitudes, mostly within the colder and relatively dry parts of north-west Britain, and is the characteristic montane scrub vegetation in the east-central Highlands of Scotland, especially in damp hollows and on north-facing slopes in heather moorland. Isolated stands are found in southern Scotland, Northumberland, the Pennines and the Lake District. Ideally, the *Juniperus*–*Oxalis* woodland forms a fringe between submontane woodland (such as *Pinus*–*Hylocomium*, see below) and montane heath. In many areas, however, the *Juniperus*–*Oxalis* woodland persists as a fragmentary belt above a wide zone that is now largely converted to heath and grassland (Pl. Comm. Scot.). Juniper is the most abundant woody species, though some stands support an over-canopy of birch (almost always *Betula pubescens* ssp. *carpatica*) made up of multi-stemmed, bushy growth < 10 m high. The juniper may form a closed canopy but this is unusual and most stands are variably patchy with an overall cover of less than 60%. Ericaceous plants, particularly *Vaccinium myrtillus* and to a lesser extent *V. vitis-idaea* and *Calluna vulgaris*, are major elements of this woodland where the shade and

grazing are not too high. Ferns are also a prominent component and although no one species is constant, *Gymnocarpium dryopteris*, *Thelypteris phegopteris* and *Blechnum spicant* are common. They undoubtedly benefit from the shelter, shade and protection from grazing afforded by fairly close-set but not too densely crowded juniper. These woodlands are also comparatively herb-rich (with a number of species at the edges of their ranges) and bryophyte-rich.

Juniperus–Oxalis woodland can be divided into two subcommunities. On more acidic soils, the *Vaccinium vitis-idaea–Deschampsia flexuosa* subcommunity includes the more heathy and calcifugous stands in which there is often a rather open cover of juniper bushes and an abundance of ericaceous subshrubs and bryophytes. The herb flora is fairly typical of the whole community (the only vascular plant particular to this subcommunity is *Deschampsia flexuosa*) but it is the bryophytes that give this community its distinctive character, particularly *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, *Pleurozium schreberi*, *Hypnum cupressiforme* and *Dicranum majus*. The subcommunity takes on an interesting form in the Morrone Birkwoods in north-east Scotland where spatial patterning is built around a hummock-hollow topography, with the ericoids mostly at the tops of the hummocks on highly organic soil and the herbs in the less humic hollows (Huntley & Birks 1979a). This subcommunity is probably the nearest UK equivalent to the extensive subalpine birch–juniper scrub of Scandinavia (Huntley & Birks 1979a,b). The *Viola riviniana–Anemone nemorosa* subcommunity is restricted to more fertile areas. Here, the juniper canopy tends to be denser than in the *Vaccinium–Deschampsia* subcommunity and, although *Vaccinium myrtillus* remains very frequent, the ericoid sub-shrubs are overall sparser often leading to more open looking vegetation. A dense grass cover between the juniper bushes is characteristic of this subcommunity, particularly *Agrostis capillaris*, *A. canina* ssp. *montana* and *Anthoxanthum odoratum*, and, distinctive to this subcommunity, *Festuca ovina*, *F. rubra* and *Holcus mollis*. *Deschampsia flexuosa*, by contrast, is scarce and only rarely abundant. The herb flora is more typical of less acidic, dry, impoverished soils, particularly *Viola riviniana* and *Anemone nemorosa*. The bryophyte layer tends to be characterized by *Rhytidiadelphus triquetrus* and *Plagiomnium undulatum*.

The *Juniperus–Oxalis* woodland merges into three other woodland types, where, in each, *Juniperus communis* (presumably all ssp. *communis*) is found in decreasing amounts, restricted to more open areas. On acidic, impoverished soils *Juniperus–Oxalis* woodland creates a transition mosaic with the *Rhytidiadelphus triquetrus* subcommunity of the *Quercus petraea–Betula pubescens–Dicranum majus* (W17) woodland. On strongly leached soils, it merges into *Pinus sylvestris–Hylocomium splendens* woodland (W18). Similarly, on less acidic and more fertile soils, particularly in eastern Scotland, a reducing amount of juniper and an increase

in birch marks the gradual transition to *Quercus petraea–Betula pubescens–Oxalis acetosella* (W11) woodland. Quite where the line is drawn between these woodland types is primarily dependent upon the relative abundance of the key species; decreasing juniper and increasing birch (W11 and W17) or pine (W18) marking the transition away from *Juniperus–Oxalis* woodland. Although *Juniperus–Oxalis* woodland may be a climax community under extreme conditions, it may also be that some of the lower altitude stands represent degraded versions of these woodlands where the pine and birch have been destroyed leaving a relict understorey stabilized by grazing (preventing tree re-invasion). Others might be seral shrub communities. As montane scrub, *Juniperus–Oxalis* woodland occupies the same position as the juniper scrub of the ‘lower alpine’ zone in Scandinavia in such communities as the *Junipereto–Betuletum nanae myrtilletosum* although the juniper there is ssp. *nana* and there is no evidence of a similar association between juniper and *Betula nana* in Scotland (Rodwell 1991). Juniper scrub has been recorded as a seral stage in primary succession on moraine in northern Sweden: *Alnus incana–Sorbus aucuparia–Juniperus communis–Picea abies*, with juniper appearing after 50–60 years and persisting until Norway spruce dominates at around 200 years (Svensson & Jeglum 2003).

In mainland Europe, *Juniperus communis* is the dominant woody component of high-mountain shrublands of the Sierra Nevada, Spain, above the treeline, between 1600 m and 2500 m and apart from occasional *Berberis vulgaris*, is the only fleshy-‘fruited’ species in the shrubland. Poldini *et al.* (2004) presented a syntaxonomic scheme for the subalpine vegetation of the south-eastern Alps. Within the basic *Erico–Pinetea*, *Juniperus communis* ssp. *nana* is a minor component of the coenoses *Rhododendro hirsuti–Pinetum prostratae*, *Erico carnae–Pinetum prostratae* and *Sorbo chamaemespili–Pinetum mugo*, and is a diagnostic species of the *Rhodothamno chamaecisti–Juniperetum alpini* (equivalent to the *Rhododendro hirsuti–Juniperetum* of the Balkan Alps, the more acidic *Junipero–Arctostaphyletum* of the Central Alps and several coenoses of the alliance *Daphno oleoidis–Juniperion alpinaea* of the Apennines, and corresponding to Habitat Classification 4060 and Corine biotope 31.431). In the *Vaccinio–Picetea*, subspecies *nana* is diagnostic of the coenoses *Rhododendretum ferruginei* and *Rhododendro ferruginei–Pinetum prostratae* on more southern and steeper slopes, and a minor component of *Vaccinium vitis-idaea–Callunetum vulgaris* on shallower acid soils and dry bogs. All three correspond to Habitat Classification 4060 and Corine biotope 31.42 A. In north-west Africa, Quèzel & Barbero (1989) proposed a new association of *Cynosuro balansae–Juniperetum hemisphaericae* within the new alliance *Lonicero kabylicae–Juniperion hemisphaericae* from the Djurdjura Mountains in Algeria between 1700 m and 2300 m, where there is protection from grazing by sheep and goats. They have described it as a unique community as it is dominated by

Juniperus communis ssp. *hemisphaerica*, unlike in the rest of the high Atlas Mountains where ssp. *hemisphaerica* is a very minor component. They have suggested that this community is similar to the communities of some of the high mountain ranges of southern Europe.

In the lowlands, Barkman (1985) assigned the dense, ungrazed *Juniperus communis* shrub on the poor, dry, acidic soils of north-central Europe to two associations: the eastern *Helichryso–Juniperetum* in Poland and the western *Dicrano–Juniperetum* in the area between east Germany, southern Sweden and central Netherlands. The latter can be subdivided into a north-east group of two subassociations and a south-west group of six subassociations.

In Eastern Europe, *J. communis* is a prominent component in the succession on abandoned agricultural land, being one of the first shrubs to invade the herb-rich seres (Faliński 1980a, 1998). Juniper remains a common component of the developing *Populus tremula–Pinus sylvestris* woodland and an occasional element in the climax pine forest.

IV. Response to biotic factors

Juniper is not very palatable but browsing by deer, cattle or sheep can significantly affect the shape of bushes and reduce their height. In Teesdale, Gilbert (1980) recorded that horses can kill juniper by gnawing the bark. In extreme cases, large animals such as deer, cattle and horses can open up and fragment dense stands and possibly even eliminate juniper (Huntley & Birks 1979a; Gilbert 1980; Borders Forest Trust 1997). Death by debarking can also result from red deer rubbing the velvet from antlers, and fraying by roe deer (Miles & Kinnaird 1979b). In a garden experiment, Grubb *et al.* (1999) found that out of 11 common British shrubs, juniper was the least damaged by rabbits, after *Sorbus aria*. However, rabbits can be very damaging to juniper, particularly in southern England, as a result of browsing and bark stripping when rabbit numbers are high (Ward & King 2006). In Glen Feshie, Miller *et al.* (1982) found juniper and birch were less severely browsed by deer than pine or rowan saplings but gorse and juniper were more heavily browsed by mountain hares (*Lepus timidus* L.) than rowan, willow or birch in winter when snow covered other moorland vegetation (Hewson 1977). The leaves, bark and twigs of juniper were eaten by hares. Subspecies *nana* appears to respond least favourably to grazing, since a survey by McGowan *et al.* (1998) found most plants in areas with little grazing. Also, the biggest plants (where 40% were over 1 m² canopy area) were found at Invernaver, where grazing pressure was light, compared to a site on Skye that was heavily grazed by sheep and deer, where all plants were < 100 cm² and in poor condition. A later study by McGowan *et al.* (2004) in northern Scotland found that female plants of ssp. *nana* suffered more winter grazing than male plants: over the five sites investigated, 30.2% of old shoots were grazed from

female plants compared to 33.0% on unsexed plants (probably female) and 17.5% on male plants. The proportion of old shoots grazed was similar across the size range of female plants, but declined with size on male plants from 20% to 25% on small plants (< 500 cm²) to nearly zero on large plants (> 1 m²).

Grazing of seedlings and young plants can play an important role in limiting regeneration. Juniper seedlings are more vulnerable to herbivory than mature plants and are attacked by slugs, mice and other small rodents, rabbits, sheep and deer (Miles & Kinnaird 1979a; Gilbert 1980; Banks 2001). Miller & Cummins (1982) found less seedling grazing with altitude in Scotland since red deer (*Cervus elaphus* L.) spend more time at lower altitudes, especially in winter. Miles & Kinnaird (1979b) noted that saplings were most susceptible to browsing when they emerged from the field layer. Over a 4-year period in Glen Feshie, they found an average of 31% mortality of unprotected seedlings of juniper, birch, Scots pine and rowan compared to 4% in plots from which red deer were excluded.

Seeds are also at risk: McVean (1966) observed that direct sowing of juniper seed in Scotland was unlikely to succeed where mice were abundant. Pigott (1956) and Gilbert (1980) commented on the scarcity of young junipers in *Juniperus–Oxalis* woodlands.

Some grazing may be essential to juniper regeneration by opening up dense vegetation (Vedel 1961; Ward 1973; Fitter & Jennings 1975; Gilbert 1980; also see XI). Svensson & Jeglum (2000) observed that in northern Sweden, where domestic grazing or mowing has been common, large thickets of juniper have developed and persisted. Rosén (1988) found that juniper establishment in southern Sweden reached 814 seedlings a year in a cattle-grazed 50 × 50 m plot of limestone heath, compared to a maximum of 349 in a similar ungrazed plot. However there was evidence that grazing interacted with weather in a severe drought of 1983; a much higher number of seedlings was killed in the grazed plot than in ungrazed plots, presumably due to the dense sward protecting the seedlings from drought.

In the Mediterranean high mountains of eastern Spain, *J. communis* ssp. *hemisphaerica* is strongly associated with prostrate shrubs of *J. sabina*. Verdú & García-Fayos (2003) noted that all seeds of *J. communis* were found beneath *J. sabina* shrubs. Seventy-five percent of the female *J. sabina* shrubs sampled (15 of 20) had *J. communis* seeds on the ground beneath while only 25% of males had seeds beneath. Moreover, 42% of the female plants of *J. sabina* sampled had *J. communis* adult plants rooted beneath them, compared to 25% of males. Although the percentage of *J. sabina* canopy cover in the study area was only 25%, 86.4% (of 81) of *J. communis* individuals were associated with *J. sabina* shrubs. This was attributed to the seeds of both junipers being dispersed by birds that are attracted primarily to female bushes. The presence of *J. communis* did not affect subsequent performance of the nurse plants

but growth and reproductive capacity were reduced in *J. communis* plants under *J. sabina* (Verdú & García-Fayos 2004).

Juniperus communis also has significant effects on other plant species. Plants growing in the open centre of older juniper shrubs or rings of its bushes, including seedlings of rowan and yew, may have some degree of protection from large herbivores (Watt 1934; Tansley, Br. Isl.; Miles & Kinnaird 1979b). Juniper also acts as a nurse plant for other organisms by ameliorating or changing environmental conditions. For example, in the dry grasslands of central Hungary, terricolous lichens such as *Cladonia rangiformis* and mosses such as *Hypnum cupressiforme* and *Polytrichum juniperinum* are found only under the shade of juniper where they benefit from a reduction in high light fluxes in summer (Kalapos & Mázsza 2001). In eastern Poland, Faliński (1998) observed that the invasion of juniper into abandoned agricultural land caused the developing moss-lichen sward to break up, creating dry bare ground around the base of the shrubs; the bare ground was then invaded by sand therophytes such as *Teesdalia nudicaulis*, *Cerastium semidecandrum*, *Myosotis stricta* and, particularly, *Spergula morisonii* and the grass *Corynephorus canescens*. As the juniper bushes became wider, the therophytes grew increasingly further away from the shrub base which in turn was invaded by liverworts and several *Cladonia* species. Herbaceous and woody plants progressively invaded but the lichen-moss layer continued to develop under the bushes, dominated by forest species such as *Pleurozium schreberi*, *Dicranum polysetum* and *Cladonia* species. In central France, *J. communis* along with *Buxus sempervirens* is a nurse plant for the establishment of *Quercus humilis*, improving germination conditions and protecting seedlings from grazing (Rousset & Lepart 1999).

V. Response to environment

(A) GREGARIOUSNESS

Northern British juniper stands are characteristically patchy with a cover normally of less than 60% (Rodwell 1991; McBride & Borders Forest Trust 1998). The patchiness is exacerbated by overgrazing, which dissects large stands into fragments. Clifton *et al.* (1997) found that of 83 sites examined in northern England only 5 (6%) included areas of juniper classified as dense. Most colonies consisted of relict scattered bushes. McBride & Borders Forest Trust (1998) observed that in the Scottish Borders 45% of juniper colonies surveyed consisted of < 50 scattered isolated bushes, and one large colony contained 31% of the Borders' junipers.

Faliński (1980a) recorded that junipers seeding into old fields in Poland were randomly distributed although local aggregation could occur along ruts and furrows, with up to 30 000 individuals ha⁻¹ (Faliński 1980b). In older populations, Faliński (1980a) and Rosén (1988) in Sweden found that junipers between 15 and 49 years

old showed clear aggregation. This was less pronounced for older plants (50–79) and the oldest junipers (80–116 years) were scattered. Faliński (1980a,b) attributed clumping of young plants to seedling establishment in the immediate vicinity of parent plants. Rosén (1988), working in denser stands, found that seedling establishment was aggregated within the openings between shrubs and, within these openings, seedlings were clumped in the most open areas with fewest near the older shrubs, despite open areas being the sites of lowest seed deposition by birds. This may be a response to shade or water competition with established shrubs. Rosén suggested that the former is more likely since, in the very shallow soil, juniper roots were close to the surface, spreading at least 4–5 m from the parents and so most new seedlings were within the root-spread of established individuals. Nevertheless, Gilbert (1980) stated that in 15 years he had never seen a young juniper grow within the root-spread of a parent bush in Britain.

The degree of past gregariousness is indicated by genetic variation. Van der Merwe *et al.* (2000) found a high level of genetic variation between populations of juniper in Britain. English, Welsh and northern Scottish populations appeared genetically discrete (even when separated by only 1 km) but those in the Scottish Borders showed little between-population diversity, suggesting more recent fragmentation of the metapopulation (Borders Forest Trust 1997). Genetic diversity within populations is large, even if the population size is small; in a DNA analysis in the Borders it was found that 93% of RAPD variation was within populations and only 7% between populations (Borders Forest Trust 1997), suggesting a large gene pool with substantial gene flow between populations and therefore low genetic isolation. Oostermeijer & de Knegt (2004) suggested that in eastern Dutch heathlands, gene flow was probably now reduced because of population fragmentation but genetic inbreeding was unlikely to explain current decline. At a coarser scale, Vargas (2003) noted a lack of variation in nuclear DNA from Iceland to the Caucasus in both subspecies *nana* and *communis*, suggesting a recent colonization across Europe with multiple colonization patterns at a local scale. More recent studies on genetic diversity in *J. communis* have begun using nuclear microsatellites (e.g. Michalczyk *et al.* 2006).

(B) PERFORMANCE IN VARIOUS HABITATS

Juniper is a characteristic invader of pasture and, as such, can survive in open woodland but it is intolerant of heavy shade. Thus in abandoned fields in Poland, pioneer herbaceous swards are invaded after 5–12 years by juniper, which then progressively dominates until the developing canopy of *Populus tremula* and open *Pinus sylvestris* leads to its decline – but not eradication (Faliński 1980a). Clifton *et al.* (1997) noted that junipers under dense woodland shade in Northumberland were

tall and moribund, with discoloured foliage, and were liable to be killed off by developing birch and oak woodland. However, Miles & Kinnaird (1979a) stated that maximum height growth of seedlings in dense shade was around 2 cm for *Betula pubescens* and *B. pendula*, 5 cm for juniper and 8 cm for *Pinus sylvestris*, suggesting that juniper (presumably *ssp. communis*) could establish in taller vegetation than the native birches. Certainly, Miles & Kinnaird (1979a) recorded that juniper seedlings could survive overtopping by grass dense enough to kill birch, and have been seen to survive being covered by grass for 3–4 years and still been slowly growing upwards. Subspecies *nana* tends to grow against or over rocks which McGowan *et al.* (1998) interpreted as a need for microsites of reduced competition from *Calluna vulgaris* or a favourable microsite for establishment.

Trials in Scotland by the Forestry Commission (Broome 2003) on fairly fertile grasslands in Moray showed that the survival and growth of 25-cm tall junipers were significantly higher over the 5 years from planting when surrounding vegetation was treated with herbicide one or more times each year. Survival was similar on the herbicide plots (98% under multi-herbicide treatments; 84% when treated with herbicide once per year) but this was significantly greater than the 46% survival on control plots. Differences in growth were not significant between the multi- and annual-herbicide treatments but were significantly greater than in the control after 5 years in terms of height increment (43.2 cm and 39.1 cm compared to 30.0 cm, respectively), root collar diameter (20.1 cm, 20.7 cm and 10.9 cm, respectively) and shoot length increment (58.3 cm, 54.0 cm and 39.9 cm, respectively). The positive effect of the herbicide treatments was still evident in shoot growth 10 years after planting even though there had been no herbicide applied for 5 years.

In extreme climatic environments, such as the short growing season and low winter temperatures of higher altitudes, or severe summer drought in Mediterranean mountains (García & Zamora 2003), the reproduction of juniper declines, and it persists by longevity, reproducing during favourable periods. In the mountains of east Spain, *Juniperus communis* usually establishes under the protection of *J. sabina*, but under the more favourable growing conditions on flatter, deeper and wetter soils of formerly cultivated valley bottoms *J. communis* establishes in the open and forms stands up to 3.5 times denser than those on the slopes (Verdú & García-Fayos 2003). Climate and competition inevitably interact to alter the performance of juniper. Miller & Cummins (1982) in the Cairngorm Mountains of Scotland similarly found variation in juniper densities with altitudinal zone: pine forest (411–530 m), 57 ha⁻¹ (of which 50 ha⁻¹ (88%) were over 10 mm basal stem diameter); pine-juniper scrub (531–590 m), 745 ha⁻¹ (633 ha⁻¹ (85%) > 10 mm diameter); juniper scrub (591–670 m) 287 ha⁻¹ (137 ha⁻¹ (48%) > 10 mm diameter); montane heath (671–750 m) 3 ha⁻¹ (0% > 10 mm).

Juniperus communis ssp. communis naturally shows a great range of canopy shapes and sizes through its range, varying from decumbent shrubs < 1 m high to pyramidal, conical or narrow cylindrical forms normally up to 5 m high but exceptionally up to 17 m. This can be partially attributed to shade, grazing and, in upland areas, to exposure since bushes become shorter and squatter with increasing altitude (Ratcliffe 1977; Gilbert 1980). However, some of this variation in shape is undoubtedly genetic since the forms persist in cultivation, offspring resemble the parent bush in shape, and mature males tend to be taller than females (Ward 2007). Given the great variation in shape within a population, the genetic control is probably governed by relatively few genes (McVean 1992). Bush shape also changes with age as inner branches die from self-shading and older bushes tend to fall open (Rodwell 1991).

Estimating the age of juniper bushes can be difficult because of the numerous and often eccentric stems containing rot, but the evidence suggests that bush longevity increases with latitude, probably due to more extreme climatic conditions leading to slower growth (Ward 1982; Clifton *et al.* 1997). Individuals exceeding 100 years have been found on the chalk downs in southern England (Ward 2007) and over 200 years old in northern England (Malins-Smith 1935; Kerr 1968; Gilbert 1980; Clifton *et al.* 1997) with one individual of 255 years old recorded from the stand at Upper Teesdale in 1987 (Ward 2004a). Rosén (1988) found juniper bushes up to 116 years old in southern Sweden, and Kallio *et al.* (1971) suggested that juniper may survive for 1000 years in Lapland. Faliński (1980a,b) found a positive relationship between age and height of juniper in Poland up to 20 years old, which could be used for dating individuals. Elwes & Henry (1906) recorded junipers with trunks up to 2 m in girth (64 cm diameter) in Britain.

The age of many stands, particularly even-aged ones, may reflect invasion following disturbance. Wells *et al.* (1976) found two stands at Porton Down, Wiltshire, with mean ages of 75.2 ± 11.4 and 71.1 ± 14.5 (SD) years and with the oldest bush being 98 years old in 1976, growing on land that was described as pasture in tithe surveys of the 1830s. The invasion of juniper probably reflects declining grazing pressure from cattle and sheep at the end of the 19th century. Similar invasions occurred following the outbreak of myxomatosis in 1954.

Juniper is slow-growing and in a garden experiment at Cambridge Grubb *et al.* (1999) found that of 11 angiosperm native shrubs and trees, juniper was the slowest growing, reaching a mean of 273 ± 26 (SE) cm after 12 years (having been planted as 2-year-old seedlings), almost half that of the most vigorous trees such as hawthorn (*Crataegus monogyna*). Average basal area of these shrubs aged 14 years old was 47.5 cm² divided between 1 and 4 stems. In northern England and Scotland, growth rates are typically 3–5 cm in

height per year (Gilbert 1980; Broome 2003). But age is obviously an important compounding factor and in Britain juniper grows most rapidly when between 5 and 20 years of age. Ward (1973) measured heights of 15 cm at 5 years of age (an average of 3 cm year⁻¹) and 150 cm at 20 years (7.5 cm year⁻¹). Ward (2007) found, in a young population, that mean growth rate of male trees was 8.07 ± 3.32 (SD) cm year⁻¹ whereas female trees showed a mean growth rate of 6.66 ± 3.20 cm year⁻¹. In an old population, she found a lower growth rate of 4.34 ± 2.59 cm year⁻¹ (males) and 4.81 ± 2.58 cm year⁻¹ (females). In the colder climate of Russia, Vorob'eva (1975) measured slower growth rates: 0.8–1.5 cm year⁻¹ between 1 and 6 years old, 3–5 cm year⁻¹ between 14 and 17 years and 5–6 cm year⁻¹ for mature individuals. Raatikainen & Tanska (1993) found an average growth rate of 4.4 cm year⁻¹ for bushes 8–52 years old in southern Finland. Ward (1982) measured growth in stem radius (i.e. ring widths) of 0.03–1.97 mm year⁻¹ in southern England, similar to that found in Belgian heathland of 1.1 mm year⁻¹ (range of 0.6–1.78 mm year⁻¹; $n = 9$; Verheyen *et al.* 2005), and also at Moughton Fell, Yorkshire, with an average of 0.04 mm year⁻¹ in a 12 years old juniper and a maximum of 0.64 mm year⁻¹ in a 70-year-old individual (Malins-Smith 1935). McBride & Borders Forest Trust (1998) estimated growth in stem radius in the Scottish Borders to be 0.5–1 mm year⁻¹ for the first 40 years after which it slowed considerably. Malins-Smith (1935), however, found that most individuals at Moughton Fell had shown a sudden increase in growth after 15–25 years of 1.3–3.4 times the previous circumference growth per year, attributed to gaining sufficient height to break-free of rabbit attack. He also observed that growth was slower on limestone than on more acidic, deeper soils, quoting the example of a 70-year-old juniper having a circumference of less than 9 cm on limestone compared to 28 cm on 'more favourable soil' (podzol c. 30–40 cm deep above bedrock). However, in the same study, the majority of recent regeneration (plants < 25 years old) was found on the limestone.

(C) EFFECT OF FROST, DROUGHT, ETC.

Juniper is frost tolerant and in Scandinavia only during the coldest winters is there damage to needles, strobili and immature cones; then needle death can reach up to 40%, coupled with 50% loss of first-year cones (Raatikainen & Tanska 1993). Juniper woodland in the east-central highlands occurs where late frosts are frequent (Rodwell 1991). In the Austrian Alps, *J. communis* ssp. *nana* showed a frost resistance (LT₅₀) during the growing season of -9.9 °C (Taschler & Neuner 2004), the highest resistance of the woody plants tested. Heavy wet snow can cause breakage of branches and may relate to the lack of taller junipers at higher altitudes; snow damage is also found at lower altitude where supporting scrub has been cleared leaving weak junipers (L.K. Ward, personal communication).

Juniper appears to be tolerant of all but the severest drought. Gilbert (1980) noted a number of possible reasons for poor juniper regeneration in Teesdale but included the exceptional drought of 1976. On the thin limestone soils of the Alvar grasslands of Sweden, Rosén (1995) found that mortality was highly synchronized with severe drought and García *et al.* (1999b) suggested that drought was the most probable cause of ageing populations found in Mediterranean mountain juniper populations. By contrast, juniper is intolerant of flooding (Glenz *et al.* 2006). On three sites of contrasting soil water content (Hill *et al.* 1996), it was found that the sex ratio of female to male trees was around 1 : 1 on the drier sites but 11 : 1 on the waterlogged site, suggesting that male trees are less tolerant of waterlogging. Foliar carbon discrimination ($\delta^{13}\text{C}$) was more negative for both sexes on the waterlogged site.

Juniperus communis ssp. *communis* is tolerant of low severity fires but high severity fires (i.e. in high fuel loads) can be fatal. Faliński (1998) found that fire in open, young *Pinus sylvestris* woodland with an understorey of juniper and *Populus tremula* in Poland killed 70% of junipers within the scrub and 100% of those in dense grasses, with no signs of re-sprouting. Similarly, intense moorland fires in the UK kill or seriously damage juniper. Mallik & Gimingham (1985) found that *J. communis* did not survive a temperature of 800 °C and although surviving 400 °C and 600 °C showed poor vegetative regeneration at the latter temperature. Of the heathland plants tested in this study, *J. communis* was the most susceptible to fire. In north-east England, where recorded fires were probably of lower intensity, only isolated individuals were killed (Clifton *et al.* 1997). Indeed, fire may be a useful tool in rejuvenating declining stands by encouraging natural regeneration (Kerr 1968; Miles & Kinnaird 1979a). Juniper does not often sprout, nor does it have an effective soil seed bank, so regeneration after fire is from seeds from surviving individuals (García *et al.* 1999b). *Juniperus communis* ssp. *nana* is very sensitive to burning (Poore & McVean 1957; McVean 1961) and the disappearance of *Calluna*-*Juniperus* heath has been ascribed in some instances to a single fire (Pl. Comm. Scot.).

VI. Structure and physiology

(A) MORPHOLOGY

Juniper is usually a multi-stemmed shrub, or sometimes a small tree. The canopy form varies from a prostrate, mat-forming shrub to upright. In Perthshire, Forbes & Proctor (1986) found 65% of mature junipers were bushy, 8% columnar and 27% spreading. Female bushes tend to be smaller and more multi-stemmed (Ward 1973; Verheyen *et al.* 2005) although in young stands at Porton Down females have been seen to be taller than the males (Ward 2007). In older stands, males were significantly taller (Ward 2007). The differences in form are known to be due to genotypic and

phenotypic variation (Turesson 1961). Mature bark is thin (< 6 mm), resinous, reddish-brown, shredding and scaly.

Shoots are either erect or spreading and very shiny; initially they are greenish-yellow, turning reddish-brown with age (Vedel & Lange 1978). Growth of the trunk is frequently one-sided with many incomplete rings, commonly due to browsing damage. Stoma width was measured as $14.55 \pm 1.55 \mu\text{m}$ wide (mean \pm SD, $n = 20$) in Scandinavia by Sweeney (2004). Stomatal density of juniper was measured as 89.85 ± 3.06 (SD) mm^{-2} from Pisa, Italy (Tognetti et al. 2000b), 229 mm^{-2} in the UK (Woodward & Kelly 1995) and $262 \pm 12.3 \text{ mm}^{-2}$ (SE, $n = 10$) on material from the French Alps.

Using herbarium specimens, Peñuelas & Matamala (1990) and Woodward & Kelly (1995) determined that historic increases in carbon dioxide concentration have led to a decrease in stomatal density of *J. communis*. Woodward & Kelly (1995) demonstrated a change from 329 mm^{-2} to the current 229 mm^{-2} , a decrease of 30.4%.

Like *Taxus baccata*, the wood of *Juniperus communis* shows a gradual transition from early to late wood within each annual ring, a distinct annual ring boundary and no resin canals (although resin canals are found in the cones; Klimko & Jankowska 1998). Wood density is $0.53 \pm 0.02 \text{ g cm}^{-3}$ (mean \pm SE) (Grubb et al. 1999). A description of wood anatomy in *J. communis* can be found in Gross & Ezerietis (2003).

Juniperus communis has spherical pollen grains which on preservation usually split into two hemispherical parts (due to swelling of the middle exine layer), each of which normally rolls into a spindle shape. Each grain has a small circular pore which is readily recognizable in intact grains. The surface is covered in stalked, spherical gemmae or granules (Southworth 1986) which often become detached during fossilization or preparation, and are generally sparser than those found on *Taxus baccata* pollen grains, which they resemble (Godw. Hist.; Andrew 1984).

(B) MYCORRHIZA

Ectomycorrhizas have occasionally been reported for *J. communis*, including ssp. *nana* (Dominik 1951; Dallimore & Jackson 1966; Reinsvold & Reeves 1986). There are records of species of *Juniperus* in Europe forming ectomycorrhiza with *Cenococcum geophilum* Fr. (Ascomycota: Incertae sedis) (Harley & Harley 1987). Belomesyatseva (2002, 2004) listed the following mycorrhizal fungi on *J. communis* in mainland Europe, mostly probably forming ectomycorrhizas: *Suillus luteus* (Fr.) Gray, *Xerocomus badius* (Fr.) Gilb. (both Basidiomycota: Boletales), *Amanita gemmata* (Fr.) Bertillon, *A. muscaria* (L.) Pers. (both Basidiomycota: Agaricales) and *Elaphomyces muricatus* Fr. (Ascomycota: Eurotiales). Belomesyatseva also assumed there to be an association between *J. communis* and *Paxillus involutus* (Fr.) Fr. (Basidiomycota: Boletales). However, the formation of ectomycorrhiza appears to be a facultative relationship.

Endomycorrhizas are more common (Lihnell 1939; Dominik 1951; Reinsvold & Reeves 1986). Błazkowski et al. (1998) found the following arbuscular fungi (Glomeromycota) associated with *J. communis* in Poland: *Acaulospora lacunosa* Morton, *A. paulinae* Błazk., *Glomus deserticola* Trappe, Bloss & Menge, *G. constrictum* Trappe, *G. dominikii* Błazk., *G. fasciculatum* (Thaxt.) Gerd. & Trappe, *G. ?geosporum* (Nichol. & Gerd.) Walker, *G. ?heterosporum* Smith & Schenck, *Scutellospora dipurpureascens* Morton & Koske and *S. pellucida* (Nicol. & Schenck) Walker & Sanders. They also found *Glomus fuegianum* (Speg.) Trappe & Gerd. associated with arbuscular mycorrhizas.

(C) PERENNATION: REPRODUCTION

Juniperus communis is a chamaephyte or phanerophyte depending upon growth form. Under continental climates reproduction appears to be entirely by seed but, in the more oceanic climate of England, rooting of decumbent branches by layering is fairly common in the north although rare in southern England (Ward 1973; Clifton et al. 1997). It is unclear whether these branches survive when the original shrub dies. Sullivan (2001) suggested that layering is uncommon in spp. *nana* but when it does occur it is typically away from the prevailing winds and rooting can occur > 1 m from the origin, the stem in between sometimes being bare of leaves. Faliński (1980a) noted that vegetative perennation is exceptionally rare in Poland. *Juniperus communis* can be propagated artificially through cuttings, seed or grafting. Pragmatically, it is easier to establish juniper from cuttings (Dearnley & Duckett 1999; see Broome 2003 for recommended methods).

(D) CHROMOSOMES

$2n = 22$ (Lökvist 1963, cited in Moore 1982). Hall et al. (1973) surveyed the 20 cultivated junipers of the Morton Arboretum near Chicago and found that most had 22 pairs of chromosomes but three species in section *Sabina* were tetraploid ($2n = 44$).

(E) PHYSIOLOGICAL DATA

(i) Light

Juniperus communis is light-demanding; it is intolerant of deep shade (< 1.6% daylight) (Grubb et al. 1996) but will survive and grow in as little as 20.5% daylight (Humphrey 1996). Humphrey found that thinning a 40-year-old Scots pine forest near Inverness, Scotland, to increase light flux to 25.3% made no significant difference to juniper survival or height growth. In Sweden, the minimum light in the autumn for gross CO_2 uptake was 300–400 lux (c. $0.4\text{--}0.6 \text{ W m}^{-2}$) (Ungerson & Scherdin 1965), whereas the compensation point was 3000 lux (c. 4.4 W m^{-2}). The latter rose to 7500 lux (c. 11 W m^{-2}) in the spring. Juniper also seems

resistant to high UV levels. Brzezinska *et al.* (2005) reported that juniper exposed to elevated levels of UV-B radiation (at $16 \text{ kJ m}^{-2} \text{ day}^{-1}$) for several weeks did not show the normally expected decrease in carbohydrate accumulation (due to disruption of photosynthetic enzymes) but did show an unexpected increase in chlorophyll a and b levels.

(ii) Water relations

Juniper is generally drought tolerant (e.g. Lysova 1980). Dodd & Poveda (2003) found that the alkane chains in cuticular waxes of *Juniperus communis* var. *saxatilis* [= *nana*] were longest at low and high elevations in the Pyrenees. This correlated with temperature and an aridity index, and is possibly a result of adaptation to minimize cuticular transpiration during hot summer temperature at low elevation and physiological drought caused by freezing temperatures at high elevation.

The relatively low stomatal resistance of *J. communis*, measured by Smith (1980) as 260 s m^{-1} , when combined with low wind speed ($< 30 \text{ cm s}^{-1}$) produces a thick aerodynamic (or boundary layer) resistance about the leaves. This was sufficient to improve water use efficiency by 34%, compared to 48% in *Pinus contorta* and 57% in *Abies lasiocarpa* (Smith 1980). The juniper used in this study is presumed to be ssp. *depressa* but the conclusion that this boundary layer would significantly aid the water regulation of low-growing junipers (which are usually in areas of low windspeed) would seem applicable to British subspecies.

Tognetti *et al.* (2000b, 2002) studied the long-term effects of atmospheric CO_2 enrichment on water relations in *Juniperus communis* and two other woody shrubs (*Erica arborea* and *Myrtus communis*) growing near CO_2 -emitting springs in Pisa, Italy. Based on distances from the CO_2 springs, physiological measurements were made on shrubs that had experienced atmospheric CO_2 concentrations of about 360 and 700 p.p.m. for their entire lifetimes. Common responses to elevated CO_2 were evident in all three species: reduced leaf stomatal conductances; increased leaf water potentials; greater relative water contents as leaf water potentials declined with drought; altered elastic cell-wall properties giving greater capacity for water uptake from the soil; higher turgor potentials during a mid-season drought (soil water content approaching 12%); and higher (less negative) pre-dawn and midday water potentials especially between July and September when drought was severe. Tognetti *et al.* (2001) additionally found that juniper had a lower percentage of xylem embolism in drought conditions compared to the other two species, suggesting it is the most drought-tolerant of the three species. Tognetti *et al.* (2000b) interpreted these data to indicate that plants growing near the CO_2 vent were either conserving soil water due to direct effects of elevated CO_2 concentrations on leaf conductance or that they had improved access to soil water due to a deeper root system. As atmospheric CO_2

content rises, it is likely that enhanced rates of photosynthesis will lead to greater carbohydrate synthesis and the accumulation of osmotically active solutes in leaves, which would decrease leaf water potentials (Tognetti *et al.* 2000a, 2002). These responses suggest that juniper will develop increasingly greater tolerances of drought as CO_2 levels continue to rise, and that it may be able to expand its range into areas that have historically been too dry to support its growth and successful reproduction. This fits with the assertion by García (1998b) and García *et al.* (1999b) that the establishment of juniper under Mediterranean conditions is currently limited by summer water stress.

(iii) Temperature

Juniperus communis is cold-tolerant and will survive to a minimum of 150 growing degree days (calculated after budburst and using a 5°C threshold); this is comparable to *Betula pubescens*, and compares with 500 growing degree days for *Pinus sylvestris* and 1000 for *Taxus baccata* (Sykes *et al.* 1996). Ungerson & Scherdin (1965) have shown that the minimum temperature in midwinter for net CO_2 assimilation in *J. communis* is -4.9°C . The respiration limit in midwinter is -9.0°C .

Comparing pollen production with mean annual temperatures along a transect from Estonia to northern Finland, Seppä *et al.* (2004) concluded that the optimum temperature for *J. communis* pollen production was 1.5°C . This is very similar to *Pinus sylvestris* (1.7°C); only 25 taxa of the 102 investigated had a lower temperature threshold than juniper.

(iv) Nutrition

Juniper is typically found on low nitrogen soils and has been classified in Hill *et al.* (1999) as having a low nitrogen requirement (an indicator value of 3 on a scale of 1 to 9). Fertilizer trials in Scotland by the Forestry Commission (Broome 2003) found that on poor to medium upland brown earths at Moray, applications of phosphorus at 60 kg ha^{-1} had no significant effect on survival or growth of planted junipers. On nutrient deficient peaty podzols at Lochaber, various low applications of N, P and K had no effect on survival of planted junipers but application of N at 150 kg ha^{-1} significantly improved height growth over 2 years (11.1 cm without N, 14.0 cm with N) and root collar diameter growth (3.21 mm without N, 5.94 mm with N). The other nutrients by themselves had no effect but K (100 kg ha^{-1}) with N increased height growth, and P (90 kg ha^{-1}) with N increased root collar diameter growth. The comparatively small effect of fertilizers points to juniper being well-adapted to nutrient-poor conditions. This is supported by the findings of Grubb *et al.* (1996) that growth on calcareous soils is limited by available light rather than P and N. Subspecies *nana* appears to be less tolerant of high N levels and after 4 years of applying NPK to an ultrabasic ranker

on an exposed ridge of the Isle of Rum (Ferreira & Wormell 1971), juniper (presumed to be spp. *nana*) disappeared.

Peñuelas *et al.* (2001) measured annual averages of leaf mineral concentrations of *J. communis* growing by a natural CO₂ spring (700 p.p.m.) and from a nearby control site (360 p.p.m.) in Mediterranean Italy. Juniper growing by the spring had higher levels of the following (control content in mg g⁻¹, percentage increase by the spring; data interpolated from figures): Fe 0.055, 18%; Mg 1.8, 22%; Ca 12, 25%; Mn 0.8, 38%; K 3.5, 40%; Ti 0.00015, 130%; S 0.7, 700%; Al 0.036, 1340%. By comparison, those by the spring had lower levels of the following (control content in mg g⁻¹, percent decrease by the spring; data interpolated from figures): C 480, 2%; Co 0.121, 21%; Ba 0.017, 53%. The following were not significantly different (data for control plants in µg g⁻¹ ± SE): P 672 ± 35; Na 72 ± 22; Zn 23 ± 2; Si 19 ± 6; Cu 4 ± 2; Ni 1 ± 0.3; Cr 2 ± 0.48; Pb 2 ± 1; Mo 0.87 ± 0.17; V 0.19 ± 0.08; Cd 0.011 ± 0.006; N 8400; Sr 24, B < 5 (the last three interpolated from a figure). Čeburnis & Steinnes (2000) found similar levels of Pb, Cd, V, Cr, Zn and Mn in leaves in Lithuania as in the above controls, with the addition of 0.14 µg g⁻¹ of As. On a British serpentine soil, *J. communis* was found to have leaf concentrations (µg g⁻¹) of Ni 32.0, Cr 15.0, Co 7.6 and Fe 310 (Johnston & Proctor 1977). While these are much higher than the concentrations given above, they were the lowest of the serpentine species analysed. Tognetti & Peñuelas (2003) looked more closely at seasonal changes in N and C at the same springs as Peñuelas *et al.* (2001) and reported that total leaf nitrogen content was significantly higher in early spring in plants near the CO₂ spring (control: c. 0.68%; CO₂ spring: c. 0.96% dry mass; data interpolated from figure), after which it increased in the control leaves over the summer to equal that at the CO₂ spring. Conversely, the δ¹³C content of leaves was negatively affected by atmospheric enrichment through the year (in early spring, control: -33; CO₂ spring; -27 δ¹³C [‰]). As a consequence, the total C : N ratio in control junipers in early spring was significantly higher (control: c. 50; CO₂ spring: c. 75), declining to match that of the CO₂ spring plants.

Although annual leaf N was not altered by the elevated level of CO₂, Peñuelas & Matamala (1990) using herbarium specimens of trees, shrubs and herbs, including juniper, found that changes in CO₂ over the industrial period (from 278 to 348 p.p.m.) had led to a decrease in leaf N content and stomatal density, and no significant change in leaf C and S content (individual data for juniper not given). In *J. communis* from northern Scandinavia, Rundgren *et al.* (2003) measured N content of fresh leaves at 1.30% with a C : N ratio of 40.3.

(v) Other aspects

Čeburnis & Steinnes (2000) looked into using juniper and *Picea abies* as biomonitors of atmospheric

deposition of heavy metals in Lithuania. Juniper and spruce needles consistently showed significantly lower concentrations of these heavy metals (except Mn and Zn) than mosses collected at the same site, typically < 10%. Although the needles could accumulate metals from the atmosphere, the low retention and the uncertainty of how much this was supplemented by uptake through the roots, showed juniper to be a poor biomonitor of atmospheric deposition.

On heavy metal rich soils in Bulgaria, Atanasova *et al.* (2004) found that junipers had shorter current-year shoots and lower fresh and dry mass compared to control plants. This may have been partly due a reduced water supply (indicated by lower water content compared to control plants) but analyses suggested lower cytokinin export from the roots or altered cytokinin metabolism producing less biologically active cytokinins. The effect of gibberellic acid sprayed onto *Juniperus communis* 'Suecia' in containers depended upon timing (Grzesik & Joustra 1990). When added before growth started, 800 mg L⁻¹ resulted in taller plants than 400 mg L⁻¹; when applied at later stages of growth, concentration had no effect. Gibberellic acid was also seen to reduce branching.

(F) BIOCHEMICAL DATA

Wolff *et al.* (1996) examined fatty acid composition in 25 conifer species, and found that *J. communis* had the highest concentrations of Δ5-unsaturated polymethylene-interrupted fatty acid (Δ5-olefinic acids). Mastelić *et al.* (2000) isolated 22 glycosidically bound volatile compounds (aglycones) from the needles of female junipers in Croatia. Long chain alcohols (polyprenols) have also been isolated from juniper needles (Sasak *et al.* 1976; Øezanka & Votruba 2001). Juniper also has a high content of condensed tannins (Frutos *et al.* 2002; Kamalak *et al.* 2004; see IX(A)(i)). The total carotenoid content of *J. communis* was measured at 197.1 µg g⁻¹ dry mass, the highest of 15 species of gymnosperms measured (range 57.4–197.1 µg g⁻¹ dry mass) (Czeczuga 1987). The dominant carotenoid, rhodoxanthin, was found not to vary in concentration significantly between sun and shade leaves and amounted to 14% of total carotenoids (Czeczuga 1986, 1987). Juniper cones generally contain 0.5–2% of essential oil together with flavonoids (Kowalska 1980; Lamer-Zarawska 1980; Hiermann *et al.* 1996), condensed tannins (Friedrich & Engelshowe 1978), fatty acids and sterols (Guerra Hernández *et al.* 1988). In a seasonal study of energy contents of storage materials in five gymnosperms (Distelbarth *et al.* 1984), *J. communis* showed the highest lipid contents in leaves in late summer (3–5 kJ g⁻¹ dry mass), highest starch in bark in early spring (1–1.5 kJ g⁻¹ dry mass) and a high overall total energy content of storage substances in leaves in late winter and early spring (7–8 kJ g⁻¹ dry mass). The latter was the highest of the 5 species. In the same study, the nitrogen content of the leaves of *J. communis* was

found to be highest in late summer and autumn at around 2% dry mass.

Terpenes have been particularly well studied. Oil extracted from juniper is known to be diverse: Butkiene *et al.* (2006) identified 149 different constituents making up 94.9–99.2% of the oils from Lithuanian material. Monoterpenes and sesquiterpenes make up the bulk of this (92–99%) although the balance between these two groups is very variable (monoterpenes: 55–90%; sesquiterpenes: 13–42%) (Butkiene *et al.* 2006; Cavaleiro *et al.* 2006; Damjanovic *et al.* 2006). Sixteen different diterpenes have also been isolated from juniper leaves, including ssp. *hemisphaerica* (Pascual Teresa *et al.* 1980; San Feliciano *et al.* 1991). Vernin *et al.* (1988) identified 64 sesquiterpenes from French juniper leaves. The largest components of the monoterpenes are usually α -pinene (17–77%) and sabinene (0.2–41%) (Sybilska *et al.* 1994; Valterová *et al.* 1997; Mastelić *et al.* 2000; Butkiene *et al.* 2006). As can be seen, sabinene is particularly variable and may be more abundant than α -pinene: Looman & Svendsen (1992) found the main oil components of *Juniperus communis* var. *saxatilis* [= *nana*] in the mountains of central Norway to have an average ratio of α -pinene : sabinene : limonene of 21 : 45 : 5. Adams (1998) found juniper oil from Sweden to be low in sabinene (0.7%) compared to 14.7% in Greece and 41.4% in Italy. Other constituents of juniper oil (with typical values listed by Stanić (1998) from Croatian material) include: β -pinene (12.9%), champhene (10.4%), terpinen-4-ol (8.5%), borneol (4.3%), limonene (3.9%), caryophyllene (2.6%), α -terpineol (1.4%), cineole (1.1%), myrcene, *g*-terpinene, terpinolene, β -phellandrene and germacrene-D (Vernin *et al.* 1988; Chatzopoulou & Katsiotis 1993; Hiltunen & Laakso 1995; Wolff *et al.* 1996; Stanić *et al.* 1998; Øezanka & Votruba 2001; Frutos *et al.* 2002; Kamalak *et al.* 2004; Cavaleiro *et al.* 2006).

The qualitative and quantitative composition of the essential oil varies depending on method of extraction (Chatzopoulou *et al.* 2002), geographical origin (Hörster 1974a,b; Schilcher & Heil 1994; Koukos & Papadopoulou 1997; Ochocka *et al.* 1997), season (Ochocka *et al.* 1997) and climate. The proportion of pinenes is greatest in trees grown at low altitudes (Stoyanova 1993) and under cold conditions (Looman & Svendsen 1992). Kallio & Jünger-Mannermaa (1989) compared the volatile terpenes of samples collected at different distance from the coast in Finland and found changes in the relative content of humulene (2.4% inland compared to 1.1% at the coast), α -terpinolene (from 0.84% to 0.53%) and the total amount of β -elemene, caryophyllene & terpinen-4-ol (from 4.7% to 1.9%).

Oil can be extracted from needles, cones and wood (Berta 1993; Stanić *et al.* 1998); relative yields (w/w) were reported in *J. communis* ssp. *nana* as 0.78%, 0.70% and 0.12% (Marongiu *et al.* 2006). Qualitative differences have been found between oils from different plant parts. Gonny *et al.* (2006) working with ssp. *nana* found

the oils of leaves, cones and wood to be rich in monoterpenes but root oil was dominated by sesquiterpenes with low amounts of monoterpenes. Shahmir *et al.* (2003) reported that leaves from north Iran contained sabinene (40.7%), α -pinene (12.5%), terpinen-4-ol (12.3%) while cones contained sabinene (36.8%), α -pinene (20%), limonene (10.6), germacrene-D (8.2%) and myrcene (4.8%). Marongiu *et al.* (2006) examining ssp. *nana* from Italy noted that leaf oils were made up of limonene (36.2%), β -selinene (15.2%) and α -terpinyl acetate (5.3%) whereas oil from cones was composed chiefly of limonene (40.1%), germacrene D (17.2%) and α -pinene (4.7%), and the small amount of oil derived from wood consisted of limonene (8.9%), α -terpinyl acetate (9.7%) and germacrene D (8.6%). Butkiene *et al.* (2006) working in Lithuania found that oil from unripe cones contained a larger amount of α -pinene than oil from leaves or ripe cones from the same plant. The amount of myrcene was larger in cone than leaf oil and increased during ripening; the opposite trend was found for beta-phellandrene.

Oils from juniper have proved useful for controlling pig sarcoptic mange mites *Sarcoptes scabiei* var. *suis* (Mägi *et al.* 2006), interfering with the development of the tobacco caterpillar *Spodoptera litura* (Vardhini *et al.* 2001) and as antifungal and antibacterial agents (Filipowicz *et al.* 2003; Jimenez-Arellanes *et al.* 2003) although not reliably against bacteria such as *Staphylococcus aureus*, *Escherichia coli* or *Pseudomonas aeruginosa* nor the yeast *Candida albicans* (Angioni *et al.* 2003).

VII. Phenology

Juniperus communis ssp. *nana* in Scotland produces strobili between March and June; ssp. *communis* between May and June, exceptionally to the beginning of July (Faliński 1998; McGowan *et al.* 1998). In southern Finland, Raatikainen & Tanska (1993) found that male strobili opened when the effective temperature sum reached approximately 183 °C (178–190 °C; time unit and temperature threshold not stated) starting between 23 May and 7 June in open areas and some 3–6 days later in the forest. Strobili lasted for 7–12 days. Female strobili open later than males (Ward 1973), variably recorded as a few days in Finland (Raatikainen & Tanska 1993) and by 3–4 weeks in Poland (Faliński 1998).

Green cones start forming in June and in the second half of July become dark green, attaining a diameter of c. 5 mm and a mass of 70–80 mg. Following fertilization 12–13 months after pollination, the mass doubles by July in the second year when the cones turn matt blue-black and the mass then declines due to water loss. In the third year (i.e. after 2 years) the cones ripen in September to October and are taken by birds. Ottley (1909) gave detailed timing of gametophyte development and fertilization in *J. communis* in Massachusetts which he regarded as 4 weeks ahead of Sweden as

reported by Norén (1904): strobili appeared on 28 March with ovules developing by 1 May; pollination took place between 22 April and 9 May with the aid of a pollination drop; fertilization occurred the following year between 17 and 21 June. Seeds normally germinate March–April although sporadic germination can occur through to September (Sullivan 2001).

VIII. Strobilus (cone) and seed characters

(A) STROBILUS BIOLOGY

Juniperus communis is usually dioecious, occasionally monoecious (Ottley 1909); Renner (1905) noted hermaphrodite strobili but these have not been reported elsewhere. Raatikainen & Tanska (1993) found that the density of male strobili in southern Finland was approximately 1.5 times that of female strobili. Pollination is anemophilous with pollen being caught in a pollination drop of *c.* 0.3 mm diameter of sugary fluid secreted by the nucellus. The pollination drop appears in the morning and remains in place for up to 7–10 days but is reabsorbed in as little as 10–15 min following the arrival of pollen (or substitute such as talc or coal dust) (Mugnaini *et al.* 2002). Successful pollination obviously depends upon many factors but forest cover and late frosts appear particularly important. In southern Finland, Raatikainen & Tanska (1993) estimated that each male strobilus of juniper produced $206\text{--}280 \times 10^3$ pollen grains, with suboptimal plants (such as those growing under forest shade) producing the lowest number, reducing likely pollination success. These authors also found that the number of strobili was very low after a very cold winter in 1984–85, particularly in males which opened earlier than the females. As a consequence, in 1985 only 38% of female strobili in open-area junipers developed a cone and only 11% of the junipers under a spruce canopy, resulting in 36.9 ± 25.6 (SD) g of cones per juniper bush in the open and 4.3 ± 7.2 g per juniper in the forest. This compares to mean and maximum cone production per bush under more optimal conditions in Poland of 66.5 g and 997 g, respectively, in 20 years old stands (Faliński 1980a). Faliński (1998) recorded a record-breaking bush in south-east Poland bearing 59 267 cones with a mass of 1594 g.

Cones are produced annually and take 3 years to mature. Pollination occurs in spring but fertilization is delayed by 12–13 months; the pollen during this time is stored on the megasporangial scales. The female cone begins significant development as the pollen tube elongates. Female strobili normally contain three ovules and thus produce 1–3 seeds (although up to 6 is possible). Raatikainen & Tanska (1993) observed that the proportion of three-seeded cones was greater in the open than under forest shade (43.8% and 2.6%, respectively: 1985 data) but the proportion of one-seeded cones was the reverse (23.0% in the open and 78.1% in the forest). If none of the ovules is pollinated,

the cone is usually aborted in the second year (coinciding with the normal fertilization time) (Rouault *et al.* 2004). This was demonstrated in the Sierra Nevada of Spain by García (1997) who found an average of $56 \pm 2.6\%$ (SE, $n = 75$, range 5–91%) of cones aborted. Seedless cones may, however, hang on the plant for a long time; García (1997) observed that these were smaller and drier than healthy cones, and became shrivelled and grey, but further north only a small proportion shrivel in this way and most are indistinguishable from cones with viable seeds (L.K. Ward, personal communication).

The fresh mass of cones in mainland Europe varies between 80 mg and 110 mg, with a dry mass of 22–72 mg, of which 59–82% is cone material and the rest seeds (Jordano 1993; Raatikainen & Tanska 1993; Obeso & Herrera 1994). The large range of mass is largely attributable to the variable number of seeds. Jordano (1993) reported an average content of the pulp (dry mass) of 11.5% lipid, 4.4% protein and 44.1% fibre content.

Juniper begins reproducing at the comparatively young age of 6–8 years old (Raatikainen & Tanska 1993) although Faliński (1980a, 1998) reported male strobili appearing on bushes as young as 5 years old in Poland. In garden experiments in Cambridge comparing 11 angiosperm shrubs and trees, Grubb *et al.* (1999) found that juniper began producing strobili in its fifth year after planting out as 2-year-old seedlings, younger than any other shrub. Bushes are typically 20–50 cm high at first strobilus production (e.g. Faliński 1980a, 1998). In the experiments of Grubb *et al.* (1999), juniper was the shortest of all shrubs at first reproduction at 30–40 cm. In dense stands, reproduction is delayed in both sexes until 10–25 years old (Ward 1973; Vorob'eva 1975; Faliński 1980b). The proportion of individuals producing strobili (and by implication cone yield) increases with age up to 20–30 years after which it declines (Faliński 1980a, 1998; Raatikainen & Tanska 1993). In young plants (< 21 years old), Faliński (1980b) found > 70% of individuals were reproductive but in the oldest stands < 10% of individuals produced seed. At Porton Down, southern England, very old junipers have been seen to produce fewer seed per bush than younger, healthier individuals but the number of viable seeds per cone may be higher in the old plants (L.K. Ward, personal communication). In older individuals, strobili are increasingly restricted to the top of the canopy (Faliński 1998).

In Poland, juniper bushes 12–14 years old (hence 6–8 years after commencing reproduction) began to show clear year-to-year differences in intensity of strobilus production (Faliński 1998). Thereafter, enhanced strobilus production occurred every other year, or every third year in older populations, with perhaps a longer cycle of 4 years in southern Spain (García *et al.* 2002). This 'masting' may or may not be synchronous between regions; García *et al.* (2001) showed that annual variation in cone production and cone size was not synchronous between regions in Spain. True masting is

unlikely in juniper given its dependence on birds for seed dispersal, and García *et al.* (2002) pointed out that transitions between large and small crops are gradual between years despite large interannual variation of 10^3 – 10^6 cones ha^{-1} , allowing predators to track annual changes.

Young juniper populations (8–15 years old) are usually dominated by male plants (female : male ratio of 1 : 2.5) while mature populations are more equally divided, sometimes with females outnumbering males (up to 1 : 0.4) (Faliński 1980a,b; Ward 1982; Forbes & Proctor 1986; Raatikainen & Tanska 1993; Clifton *et al.* 1997). However, in a long-term study, Ward (2007) reported that in a 23-year old population, the female : male ratio was 1 : 1.13 and this changed by the time the population was 46 years old to 1 : 1.32, showing a greater male bias with increasing age. A very old population (97 years old) changed from a female : male ratio of 1 : 1.51 to 1 : 2.10 by the time the population was 120 years old (Ward 2007). Ward suggested that this was due to a longer life span in males and males having a greater resistance to terminal disease. Variations are apparent: Forbes & Proctor (1986) found in Perthshire that while the overall sex ratio of female : male was 1 : 0.9 in a mature stand, plants < 20 cm girth had a predominance of females (female : male ratio of 1 : 0.65), with almost half of the plants of unknown sex. In *Juniperus communis* ssp. *alpina* [= *nana*] the sex ratio (female : male) has been seen to decrease significantly with elevation in the Spanish Sierra Nevada (Ortiz *et al.* 2002). The production of filled seeds was also greater above 2600 m due to better wind pollination.

(B) HYBRIDS

A hybrid between *Juniperus sabina* L. and *J. communis*, named *J. × kanitzii* Csató, was described in Hungary in 1886 (Dallimore & Jackson 1966). Hybrids between different species are probably not uncommon where distributions overlap. This is confounded, however, by a lack of understanding of the natural range of physiognomic variation in different species and those of their hybrids.

(C) SEED PRODUCTION AND DISPERSAL

Faliński (1980a) calculated a mean and maximum number of female cones ('berries') per individual plant of 1112 and 22 625, respectively, in eastern Poland, corresponding to a maximum cone production of 1.47 million ha^{-1} . This compares to 400 000 cones per ha in years of medium to high production in the Sierra Nevada of Spain (García *et al.* 1996 reported in García *et al.* 1999a).

Seed production of *Juniperus communis* has been reported as up to 700 000 seeds ha^{-1} in the Sierra Nevada of Spain (García *et al.* 1996 reported in García *et al.* 1999a) and 810 000–5425 000 ha^{-1} in southern Finland but reducing to 85 000 ha^{-1} under the shade of

spruce forest (Raatikainen & Tanska 1993). García (2001) estimated the number of seeds on the ground to be 142 and 219 seeds m^{-2} in the Sierra Nevada during 1994 and 1995, respectively. García *et al.* (2000b) reported that seed production of *J. communis* throughout its range in Europe varies in response to geographical variations and climatic gradients. It has been postulated by several workers, that production of seeds and seed fertility decrease dramatically in the populations of most tree species in the northern regions due to stressful climate (Pigott & Huntley 1981; Pigott 1989).

The average mass of fresh seed of *J. communis* ssp. *communis* has been reported as 12–27 mg ($n = 10$) (Obeso & Herrera 1994) and 12.47 ± 0.15 mg (SE, n unknown) (García *et al.* 2000a) in south-east Spain, 12.3 in the Swiss Alps (Pluess *et al.* 2005) and 12.91 ($n = 17$) in the French Alps. *Juniperus communis* ssp. *nana* fresh seed mass in the Swiss Alps was measured as 10.5 mg (14% less than the lowland ssp. *communis*) (Pluess *et al.* 2005).

Little is known of the dispersal agents of *Juniperus communis* ssp. *nana* seed. Seeds of ssp. *communis*, however, are known to be dispersed by wind, gravity, hares, sheep or birds (Vedel 1961; Piotta *et al.* 2003). Ward (1973) and Rosén (1988) both mentioned that junipers are often associated with sheep walks but the precise reasons are not known. Rosén (1988) also suggested that, in Sweden, strong winds may blow seeds long distance over frozen snow. Birds, however, are considered the most important seed dispersal agents. The main dispersers in Britain are the mistle thrush (*Turdus viscivorus* L.), blackbird (*T. merula* L.) and song thrush (*T. philomelos* C.L. Brehm) although the small cone size makes them available to even small birds such as the robin (*Erithacus rubecula* L.), cuckoo (*Cuculus canorus* L.) and in Scotland possibly grouse (species unstated) and crested tits (*Parus cristatus* L.) (Darling & Boyd 1969).

Elsewhere in Europe, the ring ouzel (*Turdus torquatus* L.), mistle thrush, fieldfare (*T. pilaris* L.) and waxwing (*Bombycilla garrulus* L.) make extensive use of juniper berries (García *et al.* 1999a). In the Spanish highlands, Jordano (1993) observed that 97.6% of feeding records were by *Turdus* species, and that the mistle thrush and ring ouzel showed the highest reliance on juniper berries which made up more than one third of their diet. Both birds feed almost exclusively on juniper berries in late summer/winter when juniper cone remains and seeds form > 90% of their droppings (Zamora 1990). The ring ouzel can disperse more than 65% of the juniper seed crop each year compared to a total removal by frugivorous birds of 53–89% (Zamora 1990; García 2001). García *et al.* (1999a) found that these two thrushes strongly selected against unripened aborted cones and also those heavily infected with a scale insect *Carulaspis juniperi* (Bouche) and a seed predator chalcid *Megastigmus bipunctatus* (Swed.). Cones infected with the scale insect were rejected visually (especially by the ring ouzel) and those with the chalcid following beak

manipulation. Since both insects reduce the number of viable seeds in a cone, and since unripe and aborted cones do not contain viable seeds, the birds' selective feeding behaviour results in a seed bank voided in their faeces composed almost entirely of viable seeds, and so with a higher percentage viability than in the pre-dispersal stock. Nevertheless, García (2001) noted that only 3.6–5.5% of dispersed seeds were viable.

García & Ortiz-Pulido (2004) found in Spain that the abundance of bird frugivores was seldom affected by juniper berry abundance at the local scale, but clearly responded to berry abundance at the landscape scale. Jordano (1993), however, found spatial coupling of local berry production of several species of juniper (including *Juniperus communis*) and the abundance of wintering *Turdus* species across southern Spain.

Many of the dispersed seeds end up beneath shrubs as the birds rest to defecate. In Spain, García *et al.* (1996 reported in García *et al.* 1999a) found that open patches of ground receive < 1% of the juniper seeds dispersed by birds. Juniper seeds may end up beneath other junipers since birds frequently use juniper as a perch. In a garden experiment, Kollmann & Grubb (1999) showed that of 10 European tall-shrub species, *Juniperus communis* was intermediate in terms of the number of seedlings of fleshy-'fruited' species found beneath the canopy although inferior to *Crataegus monogyna*.

(D) VIABILITY OF SEEDS: GERMINATION

Seed viability is variable, from nearly zero to 75–80% in spp. *communis* (Johnsen & Alexander 1974; Ward 1982; Forbes & Proctor 1986) and up to 60–75% in spp. *nana* (Sullivan 2001). It is higher in the more northern and mountainous parts of Europe (García *et al.* 2000a) but declines towards its northern European limit and especially towards its southern limits in the mountains of the Mediterranean region (García *et al.* 2000b).

Poor viability is usually primarily due to age of the juniper bush, insect predation and empty seeds (due to pollination failure or seed abortion during development leaving seeds with an undeveloped embryo which are indistinguishable from filled seeds since the thick seed coat makes up to 75% of the mass of the seed; Pack 1921). Up to 98% seed abortion has been recorded at Porton Down (L.K. Ward, personal communication). Apparently poor germination can also be due to dormancy (see below). Viability of seed from young junipers is usually high (80%; Ward 1982) decreasing to 3–5% or even lower in old individuals (Pack 1921; Ward 1982; Diotte & Bergeron 1989; Verheyen *et al.* 2005). Verheyen *et al.* (2005) also reported that seed from a moribund stand in Belgium with 3% viability resulted in a seedling emergence rate of 0.16% in a glasshouse trial. By contrast, Forbes & Proctor (1986) found no correlation between girth of individuals and seed viability.

In a European-wide survey, García *et al.* (2000b, 2002) found the highest number of seeds per cone

towards the southern end of juniper's range in the Iberian Peninsula; an average of around 2.3 seeds per cone compared to as low as around 1.4 in the Saian Mountains in Siberia within the central range of the species (figures estimated from diagrams). This was associated, however, with the lowest number of filled seeds per cone (estimated by cutting open the seeds as an average of 0.4 per cone in Spain compared to 1.2 in the Saian Mountains). This is attributable to high rates of seed predation in the Iberian Peninsula (up to c. 30%), and to higher rates of empty seeds (above 70% at most sites in the Iberian Peninsula, compared to 18% in the Saian Mountains). They found that seed predation was independent of latitude (being high in the Iberian Peninsula but higher in Sweden – c. 39%) but the proportion of unfilled seeds was highest towards the southern and northern limits ($r^2 = 0.77$, $P = 0.005$, polynomial regression analysis). As a result, the percentage of filled seeds (and therefore presumably viable) averaged less than 11% in Iberian regions, with a lowest value of 1.4%, compared to 80% in the Saian Mountains. The high proportion of empty seeds is undoubtedly due to sub-optimal climatic conditions affecting pollination and fertilization but García *et al.* (2000b) suggested that it could also be due to inbreeding depression amongst the naturally fragmented (and now increasingly so) populations. However, genetic testing (see XI) suggests that this is unlikely to be a major factor.

García (1998a) gave further information on the role of insect pests in viability. Monitoring six populations over 3 years they found that 70% of ripe cones contained no viable seeds. Fruits attacked by the seed-predating chalcid *Megastigmus bipunctatus* or the scale insect *Carulaspis juniperi* in the Sierra Nevada of Spain produce fewer seeds (especially when attacked by the former). Moreover, fewer of these seeds were viable in cones attacked by insects, especially in the presence of the scale insect, possibly due to fruit dehydration promoting seed abortion.

Juniperus communis does not have a long-term seed bank (e.g. Thompson *et al.* 1997), but germination is commonly delayed, sometimes by up to 3–5 years (McVean 1966; Broome 2003) and frequently requires two winter seasons for maximal germination. Establishment experiments by the Forestry Commission (Broome 2003) in the north-west Highlands of Scotland found that, following 15 months of artificial stratification, seedlings continued to emerge for 5 years with the peak in germination (representing c. 80% of total germination) occurring 2 years and 7 months after the start of the experiment (i.e. the spring of the third year after the start of stratification). Very similar results were found in trials using seed from the east and central Highlands by Miles & Kinnaird (1979a). Miles (unpublished, reported in Miles & Kinnaird 1979a) observed that seeds from the Highlands of Scotland began to germinate in the second spring after collection if sown or stratified out of doors immediately after collection

in autumn. Germination occurred sporadically between February and September and continued over 2–3 years. In the Sierra Nevada of Spain, cumulative germination reached 36% in the second and third springs after sowing (García 2001).

Dormancy in juniper seeds appears to be due to both a hard, thick semi-permeable seed coat, impregnated with lignin, and to immaturity of the embryo, which requires a time to develop (after-ripening) before germination (Pack 1921; Zheronkina 1974). Germination can be improved greatly by pre-sowing treatments (e.g. Johnsen & Alexander 1974) but their efficacy varies depending upon seed source and has led to uncertainty about the best treatment. Pack (1921) noted that the germination rate of seeds that were not placed in a dry storage for after-ripening was only around 1%. Cold-moist stratification for 12–60 weeks (Broome 2003) or two periods of cold stratification at 3.5 °C for 90 days separated by 60–90 days at 20 °C (Plantlife 2004) have been found to increase juniper germination. In the case of the latter, germination of 70–75% over 20–30 days has been found. A warm-moist stratification at 20 °C for 4–12 weeks prior to cold-moist stratification for 3–7 months has also proved effective (Lemoine-Sébastien 1958; Miles & Kinnaird 1979a; Diotte & Bergeron 1989; Piotto *et al.* 2003). The warm period is thought to enhance the elimination of germination inhibitors and promote the production of germination promoters. Trials by the Forestry Commission (Broome 2003) in Scotland found that a warm period did not consistently improve germination but the combination of warm-moist stratification and a long (38 week) cold-moist stratification produced germination of over 60%.

High temperatures, alternating temperatures, freezing and thawing, removal of the seedcoat, the application of hydrogen peroxide, 1% citric acid (followed by stratification), dilute acids, carbon dioxide, or light have also been advocated to stimulate germination with variable success. Indeed, Broome (2003) found that freezing to –13 °C for one week during the winter following sowing appeared to reduce germination from the expected 50–60% to less than 30%. Once dormancy has been broken, however, germination occurs even at 0 °C (Miles unpublished, reported in Miles & Kinnaird 1979a). McVean (1966) reported that adding ground rock sulphate adversely affected germination of juniper but not that of other woody species tried.

Forestry Commission trials in Scotland (Broome 2003) showed that germination more than doubled when clean seeds were sown rather than whole cones. This is supported by observations that more seedlings germinate beneath bird perches than where berries have fallen from the bush. McVean (1966) found the best germination was achieved from fragmented cones and he considered that good contact with the ground was more important than either stratification over winter or time of sowing (spring or autumn).

For the reasons outlined above, emergence of seedlings under field conditions is very unpredictable

(e.g. Gilbert 1980; Clifton *et al.* 1995). Early establishment of seedlings (< 20 cm tall) requires the unshaded conditions of bare ground or a short sward (Ward 1973; Miles & Kinnaird 1979a). Grubb *et al.* (1996) reported that seedlings suffered high mortality in 32–38% full sunlight, significantly higher than seedlings in less shaded conditions. However, the lack of cover for rodents may be as important as the lack of shade. Favourable germination conditions are moist, compact soil with sufficient oxygen diffusion (Diotte & Bergeron 1989). Subsequent survival of seedlings is very dependent upon favourable weather conditions (e.g. Ward 1981; Rosén 1988). For example, at the southern limit of juniper in the Iberian Peninsula García (2001) found that first-year mortality may be as high as 75–80% and he estimated that only 6 out of 10 000 seeds will produce a seedling surviving its first year.

(E) SEEDLING MORPHOLOGY

Germination is epigeal (Farjon 1998). First-year juniper seedlings have two elongated bluish cotyledons (1.5–2 times the length of normal leaves) and an apical cluster of needles (Gilbert 1980). Needles are initially in pairs or whorls of four and are produced in whorls of three only in the fourth or fifth year (Vorob'eva 1975; Sullivan 2001). Seedling development is shown in Fig. 5.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

(i) *Mammalia*

Juniper is not very palatable, which can be attributed to high levels of monoterpenoids that can cause digestive and kidney problems, abortion (attributed to isocupressic acid) and even death in goats and cattle (Gardner *et al.* 1998; Phillip 2003). Yet many large mammals have been recorded browsing and grazing, including deer, moose, cattle, horses and sheep, usually when other forage is scarce or of poorer quality, as has also been observed in yew (Thomas & Polwart 2003). Herbivory is thus particularly common in winter and early spring when other forage (especially on deciduous plants) is scarce (Fitter & Jennings 1975; Cummins & Miller 1982). For example, Miller (1971) noted that junipers in Glen Feshie were browsed by red deer primarily from December to March, particularly during snowy conditions, and avoided in summer. Similarly, Fitter & Jennings (1975) found grazing by sheep in the Chilterns was restricted primarily to winter when other forage was scarce. Buttershøn & Buttershøn (1985) similarly noted that the severity of sheep grazing of juniper in Denmark was highest when it was surrounded by nutrient-poor vegetation such as *Deschampsia flexuosa* and *Calluna vulgaris*. In Sweden, Shipley *et al.* (1998) found that moose (*Alces alces* L.) ate mostly *Pinus sylvestris* and *Salix* spp. while juniper

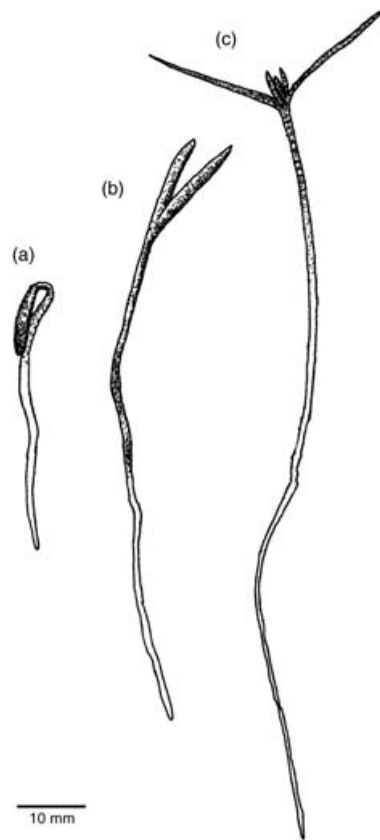


Fig. 5. Germination and seedling development of *Juniperus communis* at (a) 1, (b) 2 and (c) 12 days.

accounted for only 4–7% of the diet mass. However, this undoubtedly reflects the relative scarcity of juniper since juniper was the most actively sought conifer (compared to *Pinus sylvestris* and *Picea abies*) but some way behind the tree most sought, *Sorbus aucuparia*. The preference for juniper over other conifers may be linked to it having a low phenolic content (0.4% dry mass compared to 4.9% and 2.3% in *Pinus sylvestris* and *Picea abies*, respectively) and also to it having a low fibre content (46% dry mass as neutral detergent fibre, compared to 55% and 57% in the other two species, respectively). Analyses of *J. communis* in eastern N. America showed that the berries have a fairly low crude protein content (3.7% of dry mass) but a high crude fat content of 14.3% and a gross energy content of 4.96 kcal g⁻¹ (Decker *et al.* 1991). From the analysis of condensed tannins in the leaves of various shrub species in a grazed area in Spain (Frutos *et al.* 2002), *J. communis* showed total condensed tannins of 197 g kg⁻¹ dry mass in the winter and 230 g kg⁻¹ in the summer, higher than the level of 176 g kg⁻¹ considered to inhibit food absorption. In Turkey, Kamalak *et al.* (2004) reported a value of total condensed tannins for *Juniperus communis* of 213 g kg⁻¹.

Mountain hares (*Lepus timidus* L.) have been seen to largely avoid juniper in Sweden (Hjältén 1992) but to browse it in Finland (Raatikainen & Tanska 1993). Miles (unpublished, reported in Miles & Kinnaird

1979b) stated that brown hares (*L. capensis* L.) and rabbits (*Oryctolagus cuniculus* L.) cause basal stripping of juniper bark in the UK. Feeding by lagomorphs, as described above, is usually more common in winter. Mátrai *et al.* (1998) observed that rabbits in Hungary used juniper patches as preferred sites for burrowing and hiding, and juniper formed 19% of their winter diet. Faecal pellets from rabbits grazing juniper have a strong juniper smell and Bilkó *et al.* (1994) commented that the smell is critical in passing the juniper eating habit from does to their offspring; such offspring preferred juniper over other plant species. In the western Italian Alps, *J. communis* appeared in 3% of faecal pellets of small *Mustela* species, appearing at the seasons of greatest cone availability (summer and autumn) (Remonti *et al.* 2007).

Juniper cones and seeds are very palatable to small mammals, especially the woodmouse (*Apodemus sylvaticus* L.) (Gilbert 1980; Hester 1995; García *et al.* 2000a) and possibly bank voles (*Clethrionomys glareolus* Schreber) and field voles (*Microtus agrestis* (L.)). Raatikainen & Tanska (1993) found that 40% of unripe cones in southern Finland in 1985 were eaten by small mammals, possibly voles. In areas with scattered juniper bushes, woodmice appear to be attracted by high cone densities (García *et al.* 2001). This fondness for juniper undoubtedly explains why direct sowing of seeds in the field without protection is usually unsuccessful (Miles & Kinnaird 1979a). In Spain, García *et al.* (2000a) noted that woodmice consume seeds both from green and ripe cones whilst still on the plant and also from those fallen below. They will also eat seeds from bird faeces after dispersal. These authors also found that woodmice attack empty and full seeds but quickly discard empty seeds after an initial bite. Seed predation was independent of the number of full or empty seeds in experimentally presented clusters, and so it seems unlikely that the production of empty seeds is an adaptation to reducing predation (García *et al.* 2000b).

In Sweden, extract of *J. communis* cones have been shown to have moderate anti-inflammatory effects in the two assays tested (Tunón *et al.* 1995). Humans have used the cones and extracted oils of *Juniperus communis* (often for centuries) as a diuretic, an antiseptic (bacterial and fungal), an abortifacient, for diabetes treatment and for foot complaints (Sánchez de Medina *et al.* 1994; Stanić *et al.* 1998; Petlevski 2001; Barnes 2003; Viegi *et al.* 2003; Anderson 2004; Pepeljnjak *et al.* 2005) although other species may be more effective (e.g. Cavaleiro *et al.* 2006) and an overdose can prove fatal. The cones (berries) are still used to flavour gin (Vichi *et al.* 2005) and other regional European spirits and beers (McNeill 1910; Webster 1978). In Poland, juniper beer (*psiwo kozicowe*) is still brewed in the Kurpie region and the berries are widely used as a spice especially in *kielbasa jalowcowa* sausages (Łuczaj & Szymański 2007). A specialized literature exists on commercial oil extraction from juniper (e.g. Chatzopoulou *et al.* 2002); the active ingredients are primarily

monoterpene and sesquiterpene hydrocarbons (see section VI (F)). *Juniperus communis* wood has been shown to be useful for artificial bone implants; the essential oils released into the body would be tolerated at the likely concentrations (Gross & Ezerietis 2003). The Carrier people of British Columbia use and have traditionally used a decoction of *J. communis* branch and berries which is drunk for the treatment of kidney infections (Ritch-Krc *et al.* 1996). In British Columbia, branches of *J. communis* are fed to ruminants to prevent worms and berries are used against liver fluke (Lans *et al.* 2007). Juniper oil is also used by herdsmen in the Montseny region of Catalonia (eastern Pyrenees) to prevent or cure helminthiasis (Bonet & Vallès 2007).

In the mountains of the Mediterranean, *J. communis*, along with other junipers, has been extensively used for fuel, relegating their survival to marginal areas (Verdú & García-Fayos 2003). In Upper Teesdale, juniper wood was previously used as the base of haystacks and as firewood (Gilbert 1980), and as a smokeless fuel for illicit whisky stills in the Scottish highlands (Borders Forest Trust 1997). In Norway, juniper has had a wide variety of traditional uses including fencing (Høeg 1981; Austad & Hauge 1990).

(ii) Aves

The main dispersers in Britain are the mistle thrush (*Turdus viscivorus*), blackbird (*T. merula*) and song thrush (*T. philomelos*), as described in VIII (C), but few birds appear to consume the seed. Crested tits (*Parus cristatus* L.) are associated with junipers in Scottish pinewoods but it is not clear how much they feed on juniper cones or seeds (Borders Forest Trust 1997). In the Chilterns, Snow & Snow (1988) noted that juniper berries are of little interest to birds other than mistle thrushes which sometimes defend juniper bushes against other birds. In Finnish Lapland, the berries and needles of *J. communis* make a minor contribution to the autumn diet of hazel grouse (*Tetrastes bonasia* L.) (Salo 1971), while Pulliainen (1982) reported that *J. communis* berries are an important constituent of the autumn diet of black grouse (*Lyrurus tetrix* L.) in the Finnish taiga. Feeding experiments have shown that *J. communis* fruits should provide a nutritious food for wild turkeys (*Meleagris gallopavo* L.) in eastern North America, especially in winter when snow covered their preferred food of acorns (Decker *et al.* 1991).

(iii) Acarina

Three mites are specifically associated with *Juniperus communis* in the UK (Ward 1977): *Pentamerismus erythreus* (Ewing) (Acarina, Tenuipalpidae), *Oligonychus ununguis* (Jac.) (Acarina, Tetranychidae) and *Trisetacus quadrisetus* (Thom.) (Acarina, Eriophyiidae). All three feed on shoots and leaves and the last has also been found feeding on buds, stems and galls (Ward 1977) and is a severe pest in southern England; > 80% of

seeds have been seen affected on individual bushes at Bulford, Wiltshire (L.K. Ward, personal communication). *Trisetacus quadrisetus* appears absent from northern Britain and is only a scarce gall mite of juniper cones and needles in the eastern Sierra Nevada and southern Finland (Raatikainen & Tanska 1993; García 1998a). *Trisetacus juniperinus* (Nalepa) has been observed causing galls on *J. communis* in the UK. In a survey of juniper at Newtimber Hill, South Downs, between 1976 and 1981, Bristow (1981) found that an unidentified species of *Trisetacus* (not *T. quadrisetus*) was found in 72–97% of female cones ($n = 100$ each year), resulting in total destruction of the contained seeds. Up to 390 mites were found per cone. She suggested that ladybirds (Coleoptera: Coccinellidae) were the most likely dispersing agents of the mites. *Trisetacus quadrisetus* acts in a similar way, the mites entering the cones at pollination. Affected cones are slightly larger with the seeds protruding from the distorted tip; the seed wall of affected seeds is larger, fluted and thinner than unaffected seeds (L.K. Ward, personal communication).

In Norway, *J. communis* was the only plant taxa of 62 investigated to carry all eight identified species of *Typhlodromus* (Acarina, Phytoseiidae), with high numbers of *T. ernesti* Ragusa & Swirski and *T. laurae* Arutunjan, smaller numbers of *T. baccettii* Lomb., *T. bichaetae* Karg, *T. eucervix* Karg & Edland, *T. phialatus* Athias-Henriot and *T. pyri* Scheuten, and the only host to carry *T. norvegicus* Edland & Evans (Edland & Evans 1998). These are predatory mites.

(iv) Insecta

Kennedy & Southwood (1984) listed a total of 32 species of phytophagous insects associated with *Juniperus communis* in Britain, putting it midway up the league table of 28 UK tree groups used. Ward (1977) lists 35 species including eight introduced species and one hemipteran, *Pitedia juniperina*, formerly found in Surrey and Kent and presumed extinct. Table 1 gives the current expanded list. Coleopterans are sparse. Ward (1977) also included data of over one hundred common insects collected from juniper in southern England but which are not necessarily using the juniper as such. Some insects may use juniper as a surrogate food plant in lieu of their main host; for example, the psyllid *Trioza apicalis* (Hemiptera: Psylloidea) breeds on *Daucus carota* in Sweden but is also found to survive on *J. communis* (Kristoffersen & Anderbrant 2007) perhaps because both contain high levels of the monoterpene sabinene (Valterová *et al.* 1997). The assertion by Ward (1977) that *J. communis* and *Taxus baccata* support different insect faunas is largely true since comparison of Table 1 with data in Thomas & Polwart (2003) shows only three lepidopterans in common: *Blastobasis lignea*, *Deileptenia ribeata* and *Ditula angustiorana*. Insects and mites of the Cupressaceae have more in common with the Pinaceae

Table 1. Insects recorded from *Juniperus communis* in Britain. The Cecidomyiidae nomenclature follows the revision of Harris *et al.* (2006)

Species/classification	Source	Ecological notes
HEMIPTERA		
Acanthosomatidae		
<i>Elasmostethus tristriatus</i> (F)	1, 2, 3	Mostly southern; on branches; spread to many garden and ornamental junipers
[= <i>Cyphostethus tristriatus</i> (F)]		
Diaspididae		
<i>Carulaspis juniperi</i> (Bouche)	1	Introduced, on native juniper; shoots and leaves
<i>C. minima</i> (Tar.)	1	Introduced; shoots and twigs
Lachnidae		
<i>Cinaria cupressi</i> (Buckton)	1	Introduced; on shoots of spp. <i>communis</i> and ssp. <i>hemisphaerica</i>
<i>C. fresai</i> Blanch.	1	Introduced; on branches
<i>C. juniperi</i> (De Geer)	1, 2, 4, 5	Colonies amongst new needles; on spp. <i>nana</i>
<i>C. tujafilina</i> (Del Guercio)	1	On branches
Lygaeidae		
<i>Eremocoris abietis</i> (L.)	1, 2	Rare, in litter
<i>E. fenestratus</i> (Herr.-Sch.)	1, 2	Rare, in litter
<i>Orsillus depressus</i> Dall.	6	Introduced; on Cupressaceae in gardens in Surrey and recorded on juniper in Europe
Miridae		
<i>Dichrooscytus rufipennis</i> (Fall.)	2	
<i>D. valesianus</i> (Mey-Dur.)	1	Shoots and leaves
<i>Zyginus nigriceps</i> (Fall.)	1	Shoots and leaves; Cairngorms
<i>Lygocoris contaminatus</i> Fall.	1	Usual host <i>Betula</i> spp.
<i>Lygus punctatus</i> (Zett.)	7	Usual host <i>Teucrium scorodonia</i>
Pemphigidae		
<i>Gootiella tremulae</i> Tullgren	8	Very rare; on roots of old native stands
Pentatomidae		
<i>Aelia rostrata</i> Boheman	9	Cereal crop pest that hibernates on juniper in Spain
<i>Pitedia juniperina</i> (L.)	1, 2, 10	On fruits; rare or extinct; destroys seeds in southern Finland
Pseudococcidae		
<i>Planococcus vovae</i> (Nas.)	2, 11	Introduced; including ssp. <i>nana</i>
THYSANOPTERA		
Thripidae		
<i>Thrips juniperinus</i> L.	1, 2	Shoots and pollen; northern
[= <i>Thrips junipericola</i> Mor.]		
NEUROPTERA		
Coniopterygidae		
<i>Aleuropteryx juniperi</i> Ohm	12	A predator of scale insects on juniper; record from Box Hill in 1970
Raphidiidae		
<i>Raphidia maculicollis</i> (Stephens)	13	Snake fly; wood feeder; Porton (Blakes Firs) Wiltshire; Usually associated with <i>Pinus</i> in the south
LEPIDOPTERA		
Blastobasidae		
<i>Blastobasis lignea</i> Wals.	1	Introduced; reared from fruit and leaves
Cochylidae		
<i>Aethes rutilana</i> (Hüb.)	1, 14	Leaf webber in southern England; miner on ssp. <i>nana</i> ; Arbonne juniper forest, Seine-et-Marne, France
Gelechiidae		
<i>Dichomeris juniperella</i> (L.)	1	Leaf webber; recorded from Cairngorms only
<i>D. marginella</i> (F)	1, 14	Leaf webber and miner; southern British Isles; Arbonne juniper forest, Seine-et-Marne, France
<i>Gelechia sabinella</i> Zell.	14	Arbonne juniper forest, Seine-et-Marne, France
<i>Teleiodes vulgella</i> (Hüb.)	2	Leaf webber
Geometridae		
<i>Deileptenia ribeata</i> (Clerck)	1	Has been reared on <i>J. communis</i>
<i>Eupithecia indigata</i> (Hüb.)	15	
<i>E. intricata</i> (Zett.)	1	Shoots and leaves
<i>E. intricata arceuthata</i> (Frey.)	1, 15	Introduced 1942; southern; very rare but spreading; also
<i>E. intricata helveticaria</i> (Boisduval)	14	Arbonne juniper forest, Seine-et-Marne, France
<i>E. intricata hibernica</i> Mere.	1	Associated with ssp. <i>nana</i> in Ireland
<i>E. intricata milleraria</i> Wnuk.	1	In northern Britain
<i>E. phoeniceata</i> (Ramb.)	1	Introduced 1959; spreading; shoots and leaves
<i>E. pusillata</i> (Den. & Schiff.)	1, 14	Shoots and leaves; including ssp. <i>nana</i> ; Arbonne juniper forest, Seine-et-
<i>E. tantillaria</i> (Bois.)	15	Marne, France
<i>Gelechia sabinella</i> (Zell.)	16	Gardens in suburbs of North London

Table 1 Continued

Species/classification	Source	Ecological notes
<i>Gelechia senticetella</i> (Staud.)	17	Possibly established in the UK – ex garden centre?
<i>Odontoptera bidentata</i> (Clerck)	18	
<i>Thera cognata</i> (Thunb.)	1, 2	Shoots and leaves; not in south-east England; on ssp. <i>nana</i>
<i>T. cupressata</i> (Geyer)	15	First recorded in 1985; spreading
<i>T. juniperata</i> (L.)	1, 14	Shoots and leaves; Arbonne juniper forest, Seine-et-Marne, France
Noctuidae		
<i>Lithophane leautieri hesperica</i> Bours.	1, 19	Introduced 1951, recorded at Porton; spread north to Midlands; shoots and cones
Tortricidae		
<i>Archips oporana</i> (L.)	2	Webber and miner
<i>Cacoecimorpha pronubana</i> (Hüb.)	2	Webber
<i>Ditula angustiorana</i> (Haw.)	20	
<i>Pammene juniperana</i> Mill.	14	Arbonne juniper forest, Seine-et-Marne, France
Yponomeutidae		
<i>Argyresthia abdominalis</i> Zell.	1, 14	Leaf miner; southern England; Arbonne juniper forest, Seine-et-Marne, France
<i>A. arceuthina</i> Zell.	1, 14	Shoot miner; Arbonne juniper forest, Seine-et-Marne, France
<i>A. aurulentella</i> Staint.	1	Leaf miner
<i>A. dilectella</i> Zell.	1	Shoot miner
<i>A. praecocella</i> Zell.	1, 14	Fruit miner; Arbonne juniper forest, Seine-et-Marne, France
<i>A. trifasciata</i> Staud.	21	From Hampstead assumed ex garden
COLEOPTERA		
Buprestidae		
<i>Lampra festiva</i> L.	14	Arbonne juniper forest, Seine-et-Marne, France
<i>Melanophila acuminata</i> (De Geer)	2	Rare
Cerambycidae		
<i>Rhagium bifasciatum</i> F.	1	Rotting wood, Birk Fell, Westmorland
<i>Callidiellum rufipenne</i> (Motsch.)	22	Established on juniper in Italy; native to East Asia
<i>Chlorophorus pilosus glabromaculatus</i> (Goeze)	23	Larvae on juniper in Italy
<i>Semanotus ruscicus</i> (F)	2	South-east; central Europe
<i>Strangalia melanura</i> (L.)	13	Wood feeding; Yarnbury Castle, Wiltshire
Melandryidae		
<i>Melandrya barbata</i> (F)	2	
Melyridae		
<i>Dasytes niger</i> L.	13	Wood feeding; males and females; Porton (Blakes Firs), Wiltshire
Scolytidae		
<i>Phloeosinus thujae</i> (Perris)	1, 2	Wood under recently dead bark; southern England
Scraptidae		
<i>Anaspis maculata</i> Fourcroy	13	Wood feeding; Wiltshire and Surrey
HYMENOPTERA		
Diprionidae		
<i>Monoctenus juniperi</i> (L.)	1	Shoots and leaves; Cairngorms only?
Eulophidae		
<i>Dicladocerus euryalus</i> (Hal.)	24	Parasite reared from <i>Argyresthia</i> sp. on juniper
Torymidae		
<i>Megastigmus bipunctatus</i> (Swed.) [= <i>M. kuntzei</i> Kap.]	1, 2	Seeds; on ssp. <i>nana</i> ; England only?
<i>M. spermotrophus</i>	25	Seed chalcid native to North America
DIPTERA		
Cecidomyiidae		
<i>Arceuthomyia valerii</i> (Tav.)	1	Buds galled; wrongly identified in Britain?
<i>Oligotrophus juniperinus</i> (L.)	1, 2	Buds galled; northern including on ssp. <i>nana</i>
<i>O. panteli</i> Kief.	1	Buds galled; only on ssp. <i>nana</i>
<i>O. schmidti</i> Rüb.	1	Buds galled
<i>O. gemmarum</i> Rüb. (new combination (Harris <i>et al.</i> 2006))	1, 2	Buds galled; includes ssp. <i>nana</i>

Data taken from: (1) Ward (1977), (2) Phytophagous Insects Database, (3) Allen (1984), (4) Scheurer (1991), (5) Danielsson & Carter (1992), (6) Hawkins (1989), (7) Woodroffe (1971), (8) Carter & Danielsson (1993), (9) Sanchez-Boccherini & Gallego (1981), (10) Raatikainen & Tanska (1993), (11) Williams (1984), (12) Ward (1970), (13) L.K. Ward, pers. comm., (14) Leraut (1978), (15) Hatcher & Winter (1990), (16) Agassiz (1978), (17) Agassiz (1989), (18) Wakeley (1957), (19) Ward (1991b), (20) Bradley *et al.* (1973), (21) Emmet (1982), (22) USDA (1999), (23) Sama & Bassetti (1980), (24) Askew & Godfray (1987), and (25) Rouault *et al.* (2004).

than the Taxaceae (Ward *et al.* 2003). In southern England the number of species of phytophagous fauna has been seen to be highly positively related to the number of bushes in an area (Ward & Lakhani 1977).

Insects can have a significant impact on juniper. Miles & Kinnaird (1979a) reported that in their experience, 80% of juniper seeds in the central and east Highlands were parasitized by an unknown species of insect. Similarly, in the Sierra Nevada of Spain García (1997) found that the seed predator chalcid *Megastigmus bipunctatus* attacked $33.6 \pm 2.3\%$ (SE, $n = 75$, range = 1–83%) of cones per plant and that at least 20% of plants had more than 50% of cones damaged. He also reported that while the scale insect *Carulaspis juniperi* attacks more cones per plant ($54.2 \pm 3.7\%$; $n = 29$, range = 0–85.7), only 3.5% of plants showed more than 50% of their cones heavily attacked. In Britain, caterpillars of the small webber moth *Dichomeris marginella* causes sufficient damage to the needles and branches of juniper by mining that it is listed as a pest by the Forestry Commission (Borders Forest Trust 1997).

The aphid *Cinara juniperi* is common on 1-year old shoots (and less frequently on 2-year old shoots) in the Carpathian Mountains of Poland. Although these have been recorded at low densities (5–60 aphids per shrub), they are sufficient to inhibit shoot growth and can lead to browning of the needles, certainly reducing their ornamental value (Jaśkiewicz 2000, 2003). This aphid is, however, a food source for a range of insects and as such is of importance in maintaining the diversity of insects in this area although none is dependent solely on juniper. The aphid is predated by individuals of Araneida (Arachnida), unidentified earwigs (Dermaptera), hoverfly larvae (Diptera: Syrphidae) and especially larvae of lacewings (Neuroptera, Chrysopidae) and the ladybird *Chilocorus bipustulatus* L. (Coleoptera: Coccinellidae) (Jaśkiewicz 2003). Three to four percent of the aphids were parasitized by *Aphidus ervi* Haliday (Hymenoptera: Aphididae) which in turn were parasitized by several hymenopterans – *Charpis victix* Westw. (Cynipidae), *Coruna clavata* Walker (Pteromalidae), *Asaphes vulgaris* Walker (Pteromalidae), *Leptomastidea bifasciata* (Mayr) (Encyrtidae) and *Dendroceus carpentieri* Curtis (Megaspilidae) (Jaśkiewicz 2003).

Several insects introduced into Britain are spreading rapidly, for example: *Eupithecia phoeniceata* (Lepidoptera, Geometridae) first found in 1959; *E. intricata* ssp. *arceuthata* first recorded 1942 and subsequently spread along the southern coast; and *Lithophane leautieri* ssp. *hesperica* (Lepidoptera, Noctuidae) first recorded in 1951 (L.K. Ward, personal communication; see Table 1 for details of the insects). Other insects have become common by successfully spreading from native juniper to garden and other ornamental Cupressaceae. This includes species native to the UK such as the juniper shieldbug *Elasmostethus tristriatus* (Hemiptera, Acanthosomatidae), and non-native species such as *Carulaspis juniperi* (Hemiptera, Diaspididae) (Allen 1984; L.K. Ward, personal communication). Strong

(1979) pointed out that insect species with declining populations tend to be monophagous on *J. communis*, while those expanding their range are capable of living on several host species.

(B) PLANT PARASITES AND EPIPHYTES

Appendix S1 (see Supplementary material) lists the fungi and myxomycota directly associated with *J. communis*. Four hundred and ninety six species are listed. The Fungal Records Database of Britain and Ireland (see Appendix S1) includes 82 records of fungi and slime moulds recorded on *Juniperus communis* in Britain, compared to 551 for *Taxus baccata* and 1524 for *Pinus sylvestris*. Belomesyatseva (2002) reported 207 species of fungi on *J. communis* in Belarus (but lists just the 133 genera). Of the British species, 58.7% are anamorphic fungi, 23.8% ascomycota and 17.5% basidiomycota (Appendix S1). Over a third (36.7%) of the fungi species were of cosmopolitan distribution, 32.2% Holarctic, 13.6% Palaearctic, 11.5% European, 3.4% Mediterranean and 2.6% adventive. Saprobic fungi dominated (70.6%), split between those in the rhizosphere (31.1%) and on dead wood (30.5%); others were parasites (27.2%, including 10.7% obligate parasites of needles) and 2.1% 'mutualists'.

At Porton Down, Wiltshire, dead or dying branches of old juniper bushes were found covered by foliose lichens including *Hypogymnia (Parmelia) physodes* by Wells *et al.* (1976), and Gilbert (1980) reported the lichen *Cetraria pinastri* and the liverwort *Lophozia longidens*, both usually associated with the Scottish Highlands, on junipers at Upper Teasdale. Aragón & Martínez (1999) reported the following lichens on *Juniperus communis* ssp. *hemisphaerica* from the Sierra de Alcaraz in eastern Spain: *Lecanora chlarotera* Nyl., *Lecidella elaeochroma* (Ach.) Choisy, *Melaspilea proximella* Nyl. ex Norri., *Ochrolechia szatalaensis* Verseghy and *Pertusaria paramerae* Crespo & Vezda.

Belomesyatseva (2004) noted the following lichens on *J. communis* in Eastern Europe: *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng., *C. coniocraea* (Flörke) Spreng., *C. cornuta* (L.) Hoffm., *Lecanora symmicta* (Ach.) Ach., *Hypogymnia physodes* (L.) Nyl., *Parmeliopsis hyperopta* (Ach.) Arnold, *Vulpicida juniperinus* (L.) Mattsson & M.J. Lai and *V. pinastri* (Scop.) Mattsson & M.J. Lai.

Rios-Insua (1984) reported that the dwarf mistletoe *Arceuthobium oxycedri* (native to Cupressaceae in Spain, Morocco and east through the Mediterranean) was sufficiently dense on juniper near Madrid, central Spain, to cause damage and warrant chemical control. It has also been seen in France and Italy.

(C) PLANT DISEASES

Juniperus communis is the primary host of the rusts *Gymnosporangium clavariiforme* and, to a lesser extent and in the north, *G. cornutum* (Basidiomycota: Uredinales) throughout Europe. These rusts are

systemic, perennial, and produce teliospores and basidiospores in spring that are transported by wind to the alternative hosts, *Crataegus monogyna* and *Sorbus aucuparia*, respectively (Wennström & Eriksson 1997). Juniper can be seriously injured by *Gymnosporangium* which forms golden gelatinous patches surrounding the stems (Dallimore & Jackson 1966) and removal of hawthorn around juniper populations on chalk is a common management practice. Lygis *et al.* (2004) found in Scots pine stands in eastern Lithuania that while the fruiting bodies of the root rot *Heterobasidion annosum* (Basidiomycota: Russulales) were found on only 13.1% of all sampled juniper trees and stumps, it was found on 76.2% of all dead junipers sampled and juniper may thus be a significant source of infection for establishing pines.

A number of fungi have been noted as especially prevalent or virulent on junipers in Britain, including the needle cast fungus *Lophodermium juniperinum* (Ascomycota: Rhytismatales), the juniper twig blight *Phomopsis juniperivora* (Ascomycota: Diaporthales) (Gilbert 1980) and the root rot *Phytophthora cinnamomi* (Oomycota: Pythiales). Outside the UK, juniper tip blight, which causes a progressive dying back of twigs and branches on a number of *Juniperus* species, is caused by *Phomopsis juniperovora*, *Kabatina juniperi* (Ascomycota: Incertae sedis) or *Sclerophoma pythiophila* (Ascomycota: Dothideales).

X. History

Pollen of *Juniperus communis* ssp. *communis*, as discussed in VI (A), is fragile but readily identified in deposits by the fact that it splits open and each half curls into a cylinder (Godw. Hist.). Pollen is produced abundantly but only poorly dispersed so values greater than 5% are regarded as indicative of a strong local presence (Huntley & Birks 1983). Indeed, Schofield *et al.* (2007), in a modern study in Greenland, found that even when juniper was locally dominant (55–65% cover), juniper pollen was still < 2.4% of all pollen extracted from moss polsters. Pollen production of ssp. *nana* is low (Birks 1973) and is poorly represented in surface pollen samples. Pollen and peat stratigraphy analyses at Beinn Eighe led Durno & McVean (1959) to propose that the communities of ssp. *nana* are a vestige of a more continuous post-glacial cover.

Parts of *J. communis*, such as leaves and wood, are readily preserved as subfossils and more recent artefacts, especially if lying in water. Juniper wood implements dating back to AD 850 were documented by Larsen (1990). The essential oils and the dense wood structure of slow-growing bushes without large resin canals favour preservation (Gross & Ezerietis 2003). Willis & van Andel (2004) reviewed the evidence that *Juniperus communis*, and other trees, survived in central and eastern Europe at the height of the last glaciation, 30 000–33 000 BP. González-Sampérez & Utrilla (2003) analysing hyena coprolites for pollen found evidence of

juniper woodlands in northern Spain between 50 700 and 30 900 BP. *Juniperus communis* along with *Populus tremula*, *Salix caprea*, *Betula pubescens*, *Sorbus aucuparia* and *Prunus padus* closely followed the ice recession in the early Holocene and were established in Norway and Sweden by the Allerød (12 000–11 000 BP) (Kullman 1998; Myking 2002) at which point it was undoubtedly widespread through western Europe, especially in the Alps (Huntley & Birks 1983), and into eastern Europe (Rybnickova & Rybnicek 2006). *Juniperus communis* ssp. *communis* was present in Ireland by 12 500 BP (Molloy & O'Connell 2004) and, due to its rapid rate of colonization (Van der Merwe *et al.* 2000), was one of the first Holocene trees and spread over much of its present British range by 11 000–9500 BP (Godw. Hist.; Tipping 1987). Certainly in Shetland there was a peak in pollen levels at 9350 BP (Bennett *et al.* 1992) that occurred at the same time as that of *Corylus avellana*. In the Orkney Islands the juniper peak follows the *Corylus* peak (Moar 1969), whilst in the western Isles and mainland Scotland it precedes it (e.g. Birks & Williams 1983; Gear & Huntley 1991) suggesting successional differences. In western Norway, for example, *J. communis* colonization is increasingly delayed further north, probably attributable to slower rates of invasion further north (Kristiansen *et al.* 1988). Climate is also undoubtedly important: *J. communis* pollen in Icelandic lake deposits has been interpreted as a succession of herb-rich tundra to dwarf shrubs including juniper from 8800 to 7800 BP (Rundgren 1998). Juniper pollen increased from 10% to 15% frequency to 25–35% during this period, possibly reflecting wetter, warmer and more variable winters. Successional differences may also be due to other factors such as grazing. In Ireland, the replacement of *Salix* scrub by *Juniperus* around 12 500 BP has previously been interpreted as due to climatic deterioration. However, Bradshaw & Mitchell (1999) in reviewing the evidence suggested that the demise of willow was more likely to be due to preferential grazing by the giant Irish deer (*Megaloceros giganteus*) – perhaps due to the willow's higher phosphorus content – whose increasing numbers subsequently led to the domination of grasses around 12 000 BP.

Juniper has undoubtedly increased and declined many times in local areas due to changes in climate, competition and human activities, including the clearing and abandonment of land (e.g. Schwartz *et al.* 2005), and changes in grazing. For example, in the Aran Islands of Western Ireland, juniper was prominent in the early Holocene but declined thereafter, presumably due to increased competition (Molloy & O'Connell 2004). Juniper then increased during the period 400–100 BC and again during the Late Iron Age Lull from AD 100–500, due to reduced human pressure. It declined at the end of the lull, probably due to being shaded out by *Taxus baccata*, followed by a dramatic decline from AD 500–1230 due to renewed human impact, with extinction during the last century, possibly through its use in Palm Sunday ceremonies (Webb

1980). Human activity has not always been detrimental and under certain circumstances has favoured juniper. Huttunen (1980) reported that the spruce forest of southern Finland was progressively invaded by *J. communis* after slash and burn agriculture started in AD 200–300. By the early 14th Century, juniper was common as a result of increasing fire frequency and grazing pressure allied with soil impoverishment. Subsequent changes in populations appear to have been related primarily to changes in grazing pressure; higher grazing pressures resulting in more juniper.

Extensive felling of woodland where juniper occurred as an understorey would have allowed juniper to expand and survive through reduced competition. Certainly, pollen records from the alluvial fill of the Ouse valley, East Sussex, suggest that juniper expanded from patches of scrub following extensive woodland clearance after the Bronze Age (Waller & Hamilton 2000). Similarly, the cutting of birch, pine and other trees for timber over the past few centuries may explain why some *Juniperus-Oxalis* stands in Scotland are on such a range of soils: these represent degraded mixed pine–birch–juniper forest which developed in the Boreal period (McVean 1961; Birks 1977; O’Sullivan 1977). Many stands in Britain appear to be of comparatively recent origin and are just a few centuries old.

XI. Conservation

In Norway, Myking (2002) considered that the life-history traits of *J. communis* (a large geographical range, widely scattered within its range, good seed production and dispersal, and an early successional invader) should make it a viable species in the long term, and this is undoubtedly true in the UK. There is, however, widespread concern that the communities in which it forms a dominant component are becoming increasingly scarce (especially in England; Ward 1973, 1981; Wells *et al.* 1976; Ward & King 2006). In Sussex, southern England, Ward & King (2006) found that 56% of juniper populations became extinct between 1970 and 2003, and bush numbers fell from 4767 to 1465, a 69% loss. In Northern England (County Durham and Northumberland, excluding Upper Teesdale), Clifton *et al.* (1997) recorded a 30% decline in the number of juniper bushes over the 21 years up to 1994; a loss of 1.5% per year. Of the 130 colonies inspected, 16% had disappeared, 54% had declined in size, 19% were stable and 11% had increased in size. The colonies remaining in 1994 were mostly small (79% had < 50 bushes and 61% < 25 bushes) and only 16% of colonies had > 100 bushes and just 5% > 200 bushes. In comparison, Gilbert (1980) estimated that the largest collection of juniper stands in England at Upper Teesdale National Nature Reserve, County Durham (excluded from the study of Clifton *et al.* 1997) had an estimated 15 000–20 000 bushes. Many authors have also noted that young junipers are scarce in many British stands (e.g. Pigott 1956; Gilbert 1980).

Juniper is also rare and threatened in Belgium (Burny 1985; Frankard 2004; Verheyen *et al.* 2005), northern Germany (Pott & Hüppe 1991), the Netherlands (Oostermeijer & de Knecht 2004), Poland (Boratynski 1985) and within the city of Zurich, Switzerland (Landolt 1994). The last large Belgian population decreased by 36% between 1980 and 2003, changing from a relatively immature to a mature population with low vitality (64% of individuals exhibiting significant needle loss) and little regeneration (Verheyen *et al.* 2005). There has also been a marked decline in other parts of lowland western Europe (e.g. Lemoine-Sébastien 1966; Götz 1979) along with increased population fragmentation (e.g. Verdú & García-Fayos 2003). However, in cooler and moister areas, such as parts of Scandinavia, reduced grazing has led to a rapid expansion in juniper density and is causing a conservation problem in its own right (Rosén 1988).

The increasing rarity of juniper in Britain has led to the creation of a Biodiversity Species Action Plan to counter its decline (JNCC 2001). Juniper scrub has also been formally identified as a nationally scarce woodland type in Britain and, as of 1995, seven Sites of Special Scientific Interest have been notified wholly or partly for their *Juniperus-Oxalis* stands (Clifton *et al.* 1995). Stands have also been identified within the EU Habitats Directive due to their threatened European status (Department for Environment, Food and Rural Affairs, undated); Annex I habitats include *Juniperus communis* formations on heaths or calcareous grasslands (EU Code 5130; currently 33 special areas of conservation) and coastal dunes with *Juniperus* species (EU Code 2250; currently 2 SACs) (Joint Nature Conservation Committee; www.jncc.gov.uk).

Long-standing causes of decline such as agricultural expansion, overgrazing, shading by secondary woodland, large-scale erosion and fire that damage and destroy *mature* plants are still a major problem (e.g. Huntley & Birks 1979b; Gilbert 1980; Ward 1981; Clifton *et al.* 1997; Ward & King 2006) although the precise effects of each of these and their interactions are still largely unknown. Many authors, however, state that the main cause of the juniper decline is a lack of regeneration leading to increasingly even-aged, moribund old populations with senescent bushes increasingly susceptible to disease and windthrow (Clifton *et al.* 1997), and with no replacements (Ward 1973; Fitter & Jennings 1975; Gilbert 1980; Ward 1981; Hester 1995). At two study sites on the Porton Ranges, Hampshire, UK, no regeneration had been observed for 37 years (Ward 2007). In the Scottish Borders, McBride & Borders Forest Trust (1998) found regeneration in only 19 of the 80 colonies, and most of the individual bushes in these stands were over a century old. Similarly, Clifton *et al.* (1997) found young plants in only 12% of sites in County Durham in 1994, and no seedlings at all.

The decline in regeneration is partly attributable to a reduction in viable seed production. This is a facet of older stands having a reduced capacity to produce seed

with age (Ward 1982) but also habitat fragmentation reducing pollination efficacy and reducing the number of overwintering thrushes and hence seed dispersal (Livingston 1972; Snow & Snow 1988). Ward (1973) reported that, in southern England, smaller stands tend to be increasingly isolated as declining colonies increasingly retreat towards centres of aggregation, increasing the likelihood that these small stands will die out and not be replaced; she found that the mean distance between present-day sites was 1.91 km but the mean distance of extinct stands to the nearest living stand was 10.45 km. The major bottleneck in regeneration, however, is undoubtedly seed germination and early seedling survival. Gilbert (1980) calculated that the chance of a 2-year-old seedling surviving for 10 years was 1 in 50.

Competition with other plants can reduce establishment. Thus, poor seedling recruitment in Belgium is attributed, at least partly, to the expansion of *Molinia caerulea* due to atmospheric nitrogen pollution (Verheyen *et al.* 2005). Dense vegetation can also provide shelter for small mammals leading to increased seed predation (McVean 1966). Nevertheless, regeneration in Scotland has been noted in tall heather and bracken which acts to keep out large herbivores such as sheep (McBride & Borders Forest Trust 1998). In a similar way, Livingston (1972) found that rocks in pasture helped juniper seedling survival in New England.

In northern England, at least, it seems that regular ground disturbance by quarrying, mining (Gilbert 1980), erosion or unregulated grazing (Clifton *et al.* 1997), preventing scrub development (Dearnley & Duckett 1999), has helped provide the bare ground most suitable for juniper establishment. Indeed, Clifton *et al.* (1997) found that in northern England, 80% of colonies with young juniper were associated with eroding sites. Grazing, however, is a two-edged sword. Juniper seedlings do poorly in ungrazed conditions due to excessive shade and benefit from bare ground or a short sward with little shade, such as produced by moderate to heavy grazing (Ward 1973; Fitter & Jennings 1975; Miles & Kinnaird 1979a; Gilbert 1980; Ward 1973, 1982). However, subsequent grazing must be very light if the seedlings are to survive, which explains why seedling survival is better with summer rather than winter grazing (Fitter & Jennings 1975). Thus regeneration may depend more on a sudden relaxation of grazing than continuously low herbivore numbers (Ward 1973; Fitter & Jennings 1975). This may account for the expansion of many juniper populations in southern England with the outbreak of myxomatosis in the 1950s (Thomas 1960, 1963; Ward 1973) and the reduction in regeneration once rabbit numbers recovered (Ward & King 2006), although it is not clear whether these were from seed or growth of suppressed plants.

In the same way, although fire can devastate mature stands, burning may aid regeneration in some situations. Thus Miles & Kinnaird (1979a) recorded the first

regeneration seen in years after an accidental fire at Tynron in Dumfries, and Sykes (1976) noted the same in the Tynron Juniper Woodland National Nature Reserve, yet McBride & Borders Forest Trust (1998) found no regeneration following heather burning in two juniper colonies. The underlying reason was probably different post-fire grazing pressure.

Climate also has a large influence on establishment. Juniper populations in northern Europe and northern Spain have been noted as having a high proportion of young individuals compared to populations in Mediterranean mountains, suggesting a lack of recent regeneration in the latter (Austad & Hauge 1990; Rosén 1998; García *et al.* 1999b; García *et al.* 2000b), ascribed to drought-induced seedling mortality in the Mediterranean climate. Conversely, at the northern end of its range, the establishment of juniper (especially *ssp. communis* which favours well-drained soil; McVean 1966) is likely to be susceptible to increased rainfall. Climate change, allied with fire and grazing, may lead to a contraction of juniper's range (Hester 1995) although climate change by itself is unlikely to be seriously damaging to such a widespread species (Ohlemüller *et al.* 2006).

Active management has been used in a number of regions to encourage natural regeneration (Ward 1991a; Sutherland 1993). The Forestry Commission (Broome 2003) suggested that juniper is best established from seed, not mixing material from populations that are more than 1 km apart to maintain genetic integrity. Protection of seed from mice using 15-cm high mesh guards around each seed-plant has proved successful (McBride & Borders Forest Trust 1998). Pragmatically, however, it is easier to establish juniper from cuttings (Dearnley & Duckett 1999; Broome 2003) as has been attempted at Teesdale (L.K. Ward, personal communication). Fencing to control grazing generally allows the vegetation to become too rank for successful juniper establishment, and in Scotland encourages rabbits which strip the bark from juniper stems in winter (McBride & Borders Forest Trust 1998).

Less is known about *J. communis ssp. nana*. Although locally plentiful, many populations are small and isolated, probably representing remnants of a once more widespread distribution, contracted because of its sensitivity to burning and grazing (Pl. Comm. Scot.; Hester 1995; Preston *et al.* 2002). A scarcity of young plants has been noted (McGowan *et al.* 1998) which may be due to grazers removing cones before they ripen (especially as female plants are preferentially grazed; McGowan *et al.* 2004), or a shortage of female plants in the communities or a lack of suitable microsites for establishment. It may be possible that, like *ssp. communis*, localized disturbance, periodic heavy grazing or abandonment of cultivation would aid its establishment. Climate change may benefit *ssp. nana* by allowing its expansion into the alpine vegetation of Mediterranean summits (Sanz-Elorza *et al.* 2003).

The conservation of juniper has implications for its associated vegetation communities and fauna. For example, the gall fly *Schmidtiella gemmarum* Rubsaamen (Diptera: Cecidomyiidae) has become locally extinct in an area of juniper decline due to encroaching tree cover (Ward 2004b). In southern England the number of species of phytophagous fauna has been seen to be positively related to the number of bushes in an area (Ward & Lakhani 1977); regression analysis showed that the number of bushes explained 77% of the variation in numbers of arthropod species. Ward (1973) suggested that sites with continuous populations of > 100 bushes are of greatest conservation value while Ward & Lakhani (1977) showed that a site in southern England with 300 juniper bushes had a probability of 5% of containing all 15 of the commoner arthropod species expected and a site with around 3000 bushes had a probability of 50% of containing all 15. Insects feeding on berries are at greater risk of extinction than those that feed on foliage (Ward 1981). Gillings & Fuller (1998) recorded 18 species of birds breeding in juniper scrub in the east of Scotland. The other side of the coin is that juniper can be detrimental to biodiversity if it invades a rich habitat: Rejmánek & Rosén (1988) found a significant decrease in the biodiversity of limestone grasslands in Sweden when juniper exceeded 75% cover, and the field and ground layers of the vegetation took at least 3–4 years to recover when the juniper was cleared (Rosén & Bakker 2005). The re-establishment of the alvar vegetation in Oland by eliminating *J. communis* is summarized by Rosén (2006). Small patches of juniper were left to encourage biodiversity.

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Supplementary material

The following Supplementary material is available for this article:

Appendix S1. Fungi and slime moulds directly associated with *Juniperus communis*, with references to the sources of information.

This information is available as part of the online article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01308.x>

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