# *Hedera helix* L.

DANIEL J. METCALFE

*CSIRO Sustainable Ecosystems and Rainforest CRC, Tropical Forest Research Centre, PO Box 780, Atherton, QLD, 4883, Australia† and Biology Division, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton, UK*

Araliaceae, Schefflereae. Climbing, sometimes reaching 30 m, or prostrate and creeping, forming extensive carpets. Woody stems up to 25 cm diameter, young twigs pubescent with stellate to peltate hairs, and densely furnished with adventitious roots. Leaves petiolate, simple, alternate, exstipulate, coriaceous, glabrous, evergreen; those of climbing or creeping stems 4–10 (–25) cm, palmately lobed with 3–5 triangular, entire lobes; leaves of flowering stems 6–10 cm, entire, ovate or rhombic. Leaves shining, dark green above, often with pale veins, paler green below; may become pale green/yellow in late summer, and upper surface sometimes tinged with purple in winter. Flowers actinomorphic, *c.* 20 in terminal globose umbels, which may be arranged into panicles. Sepals 5, very small, deltate. Petals 5(–6), yellowish-green, 3–4 mm, triangular-ovate, somewhat hooded at apex; free. Flowers hermaphrodite, stamens 5; ovary inferior, 5-celled, styles joined into a column. Nectar secreted by a domed disk surrounding the styles. Peduncle, pedicels and receptacle stellate-tomentose; pedicels not jointed. Fruit a berry, bluish- or greenish-black (rarely yellow or white), globose, 6–8 mm. Pulp purple, seeds 1–5, *c.* 35 mg dry mass, rugose, whitish; embryo small, endosperm ruminate.

There is considerable disagreement over the taxonomy of the ivies (*Hedera* spp.), with the number of European species being cited as between one and six. Three subspecies of *Hedera helix* L. (hereafter 'ivy') are recognized in Fl. Eur.: ssp. *helix*, ssp. *poetarum* and ssp. *canariensis*. 'Hedera hibernica' ('Irish ivy') is recognized only as a horticultural form that is somewhat intermediate between *H. helix* ssp. *helix* and ssp. *canariensis*. Stace (1997) places ssp. *canariensis* with *H. algeriensis* Hibberd, and recognizes '*H. hibernica*' as a subspecies of *H. helix* – ssp. *hibernica* (G. Kirchn.) D.C. McClint, along with ssp. *helix* (the common British ivy) and the yellow-fruited garden-escape ssp. *poetarum* Nyman, from the Mediterranean. Recent molecular data suggest that ssp. *helix* and ssp. *hibernica* may represent distinct species, with ssp. *helix* being the (diploid) maternal parent of the tetraploid ssp. *hibernica* (Ackerfield & Wen 2003). They are distinguishable by their cpDNA phylogeny, by their trichome morphology and by aspects of their ecology (McAllister 1981; McAllister & Rutherford 1990; Ackerfield & Wen 2002, 2003; Grivet & Petit 2002). Throughout this account Irish ivy will be treated as ssp. *hibernica* of *H. helix*, as in much of the older literature the subspecies concerned have not been distinguished. Hundreds of cultivars of *H. helix* and its subspecies are recognized in the horticultural trade.

## I. Geographical and altitudinal distribution

Ivy is common throughout the British Isles, except for parts of northern Scotland (Bot. Irl.; Fl. Br. Isl.), with recorded introductions to northern and eastern Scotland, and to Shetland (Preston *et al.* 2002; Fig. 1). The subspecies are undoubtedly under-recorded but *H. helix* ssp. *helix* is widely distributed (Fig. 2) and *H. helix* ssp. *hibernica* has a predominantly western natural distribution, with extensive introductions elsewhere (Fig. 3). Ivies occur from sea level to 615 m in Ireland, to 550 m in Wales and Scotland and to 480 m in England (Atl. range Br. Pl.).

A central European species *sensu* Ellenberg (1988), ivy has a southerly and westerly distribution in Europe, extending from north Africa and the Mediterranean to Norway (60°32′ N) and eastwards to Latvia and Ukraine, Armenia, Georgia and Iran (Fig. 4). It occurs sparsely north of the Alps in central Europe, and is absent from northern and eastern Russia, eastern Poland, the Faroes, Finland, Iceland and Svalbard. The ssp. *hibernica* is most common along the Atlantic coast of Europe from Ireland to south-west Spain, while ssp. *helix* occupies central and eastern Europe as far as the Ukraine. Ivy has naturalized and become common in Australia, Brazil, Canada, Hawaii, New Zealand and the United States (Laroque 1998, cited in Grivet & Petit 2002), and has also been introduced to India and South Africa.

## II. Habitat

### (A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Ivy tends to be limited to sheltered sites, particularly on higher ground, where it becomes increasingly sparse
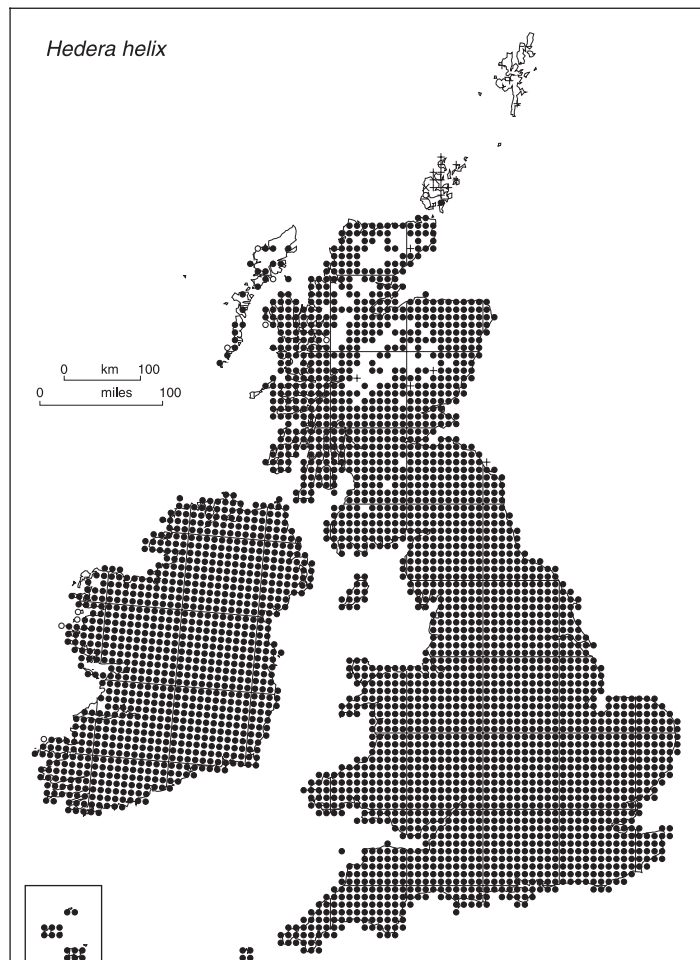
**Fig. 1** The distribution of *Hedera helix* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards; introduced (×) pre 1950, (+) 1950 onwards. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society if the British Isles.

even in southern England (Snow & Snow 1988). Macleod (1983, cited by Snow & Snow 1988) found in the Cotswolds that plants growing above 265 m a.s.l. had fewer, smaller and later ripening fruit than plants growing below 80 m a.s.l. At higher, cooler latitudes fruit production also becomes limited; indeed ivy rarely flowers and is apparently unable to reproduce sexually in its northernmost populations in Sweden and the northern regions of the former Soviet Union, where populations isolated by global cooling at the end of the Atlantic period, *c.* 5 thousand years before present (5 kyr BP), have maintained themselves by vegetative reproduction (Fröman 1944; Hafsten 1956; Poyarkova 1973, cited in Ackerfield & Wen 2003).

Ivy is an Atlantic element of the European flora *sensu* Dahl (1998), having an essentially southern and western distribution. Ivy is classified as European southern-temperate by Preston & Hill (1997); more strictly, ssp. *helix* is European southern-temperate and ssp. *hibernica* is Oceanic southern-temperate (Preston *et al*. 2002). Ellenberg (1988) noted that ivy is an indicator of fairly warm conditions from lowland to high

mountain sites but especially in submontane to temperate regions. Ivy develops and fruits normally in areas with cool to warm summers (mean temperature of warmest month > 13 °C) but not areas with cold winters (mean temperature of coldest month > −1.5 °C, Iversen 1944). Within the Scandinavian-Atlantic sub-element the occurrence of ivy is limited by an isotherm of ≥ −4 °C (Fröman 1944; Hafsten 1956).

### (B) SUBSTRATUM

Ivy is tolerant of all but the most acid (< pH 4), waterlogged or very dry soils. It is favoured by moist fertile or very fertile soils ranging from fairly dry to slightly damp; so it is common on heavier clay-rich soils and less abundant on poor and well-drained sandy soils (Tansley, Br. Isl.; Grime *et al.* 1988; Snow & Snow 1988). McAllister & Rutherford (1990) report that ssp. *hibernica* but not ssp. *helix* can be found just above the spring tide high water level on coastal shingle banks. In Europe ivy grows in beech woods on the slightly moist limestone soils of the Swiss Jura, on dry slopes and
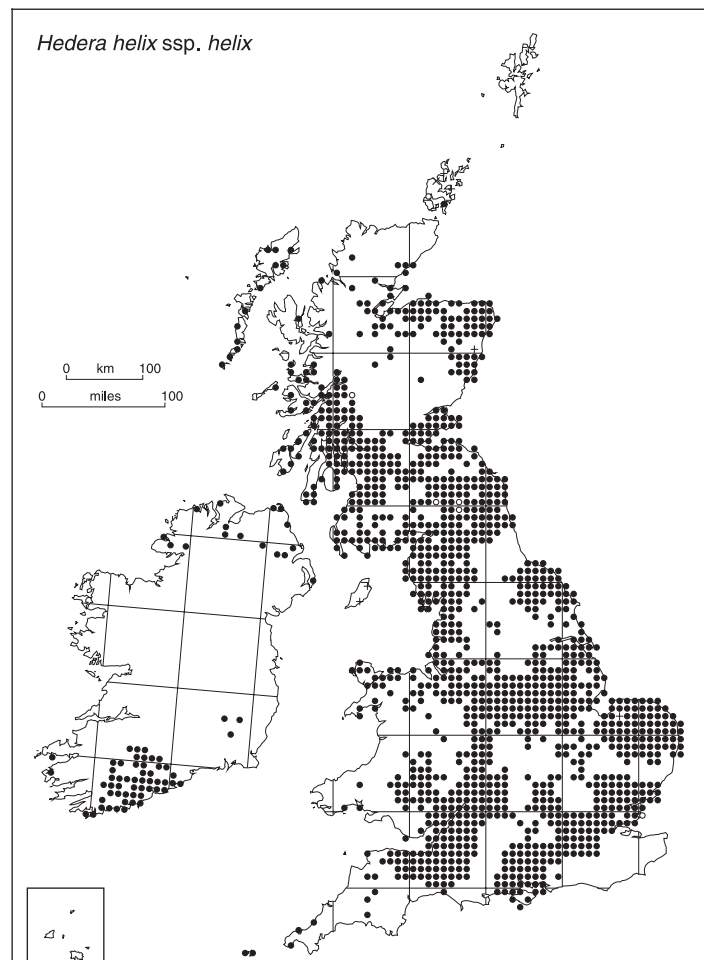
*Hedera helix* ssp. *helix*

**Fig. 2** The distribution of *Hedera helix* ssp. *helix* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards; introduced (×) pre 1950, (+) 1950 onwards. 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 if the British Isles.

brown mull soils, and on more fertile soils in the more oceanic, temperate oak woods (Ellenberg 1988).

### III. Communities

Ivy is found in most types of woodland (21/25 types of Rodwell, 1991; Tansley, Br. Isl.; Ir. Pfl.), although it is characteristic of secondary rather than ancient woodland (Rackham 1990) as it is a poor colonizer of existing woodland. It is a constant in some subcommunities of *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland (W8), *Quercus robur–Pteridium aquilinum–Rubus fruticosus* woodland (W10) and *Fagus sylvatica–Mercurialis perennis* woodland (W12). It is also a constant in *Crataegus monogyna–Hedera helix* scrub (W21 of Rodwell 1991) which includes most seral thorn scrub and many hedges, and its invasion of open ground is typically associated with hawthorn succession (Grime *et al*. 1988). Ivy is a relatively uncommon (< 20% of samples) constituent of *Arrhenatherum elatior* grassland (MG1 of Rodwell 1992), occurring in the *Filipendula ulmaria* and *Urtica dioica* subcommunities, and in the

*Bromus* (*Anisantha*) *sterilis* variant of the *Festuca rubra* subcommunity, where it may form a sparse ground cover with *Glechoma hederacea*. Near the coast, ivy is a preferential species in the *Ranunculus ficaria* subcommunity of the *Festuca rubra–Hyacinthoides non-scripta* maritime bluebell community (MC12). In open habitats ivy is a conspicuous member of the *Urtica dioica–Galium aparine* community (OV24), sometimes forming patchy ground cover in the *Arrhenatherum elatius–Rubus fruticosus* agg. subcommunity. Ivy is also present in two subcommunities of the *Epilobium* (*Chamerion*) *angustifolium* community (OV27), is an associate of the *Parietaria diffusa* community (OV41), and is occasionally favoured in the *Cymbalaria muralis* community (OV42; Rodwell 2000). The species most similar in habitat 'preference' include *Bromopsis ramosa*, *Elymus caninus*, *Geum urbanum*, *Melica uniflora* and *Mercurialis perennis* (Grime *et al*. 1988). In Europe ivy grows in continental beech woods and the more oceanic, temperate xerothermic mixed oak woods and oak–hornbeam woods; ivy is characteristic of *Querco–Fagetea* broadleaved woods and scrub on more fertile soils
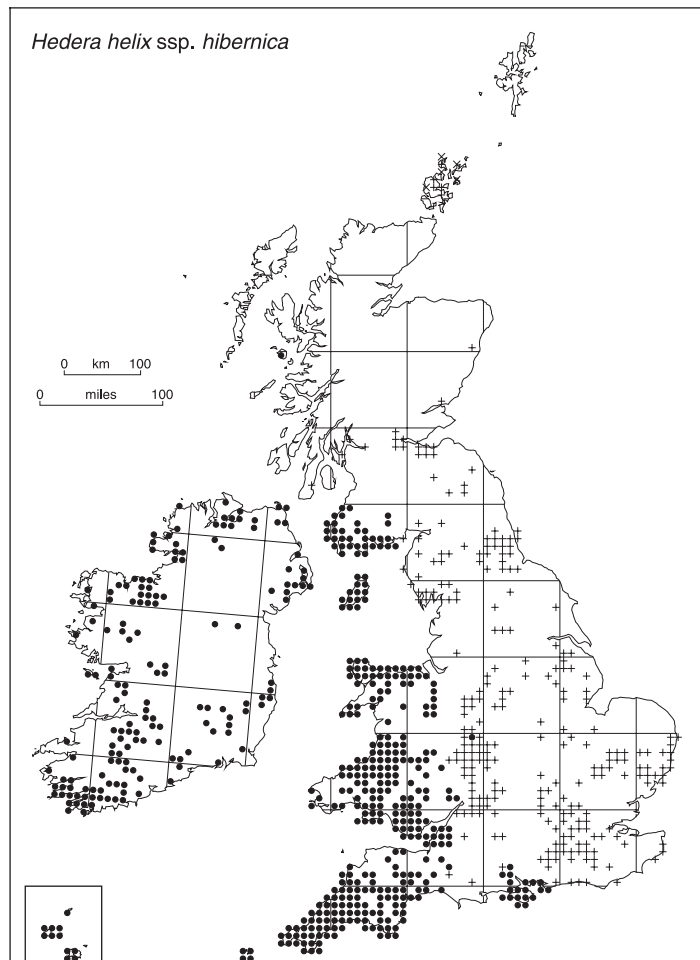
**Fig. 3** The distribution of *Hedera helix* ssp. *hibernica* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. Native: (●) 1950 onwards; introduced (×) pre 1950, (+) 1950 onwards. Mapped by H.R. Arnold, using Dr A. Morton's DMAP software, Biological Records Centre, Centre for Ecology & Hydrology, Monks Wood, mainly from data collected by members of the Botanical Society if the British Isles.

and the *Querco–Fagetea* hedge communities (Ellenberg 1988).

## IV. Response to biotic factors

Ivy tends to become established from seed in disturbed or more open habitat, and does not appear to compete strongly with established woodland ground flora species, though it can avoid shading effects by climbing (Rodney Helliwell, pers. comm.). However, McAllister & Rutherford (1990) report that ssp. *hibernica* can compete successfully with *Dryopteris filix-mas*, *Filipendula ulmaria*, *Mercurialis perennis*, *Poa pratensis*, *Pteridium aquilinum*, *Rubus latifolius* and *Rumex crispus*, whereas ssp. *helix* cannot. Cutting and grazing generally reduce the competitive abilities of ivy, and it shows low tolerance of fire when it does burn. However, being evergreen and with a relatively high water content, ivy is slow to burn and will not readily spread fire well. Consequently, ground planting with ivy has been proposed to reduce fire risk in seasonally dry areas (e.g. Utah Bureau of Land Management 2001).

## V. Response to environment

### (A) GREGARIOUSNESS

Largely dispersed by birds, several ivy seeds may be deposited in a single dropping; all of these may germinate, so clusters of seedlings are frequently found together, at densities of up to 50 m$^{-2}$ (Bottema 2001). As it grows, ivy often continues to maintain its own company, and many stems, often of different ages, may be seen climbing walls and trees. In woodland habitats, ivy frequently forms a dense ground cover occupying large areas and made up of many individuals. Plants are more solitary in less favourable habitats.

### (B) PERFORMANCE IN VARIOUS HABITATS

Ivy grows most vigorously in shaded, moist sites on heavy, fertile soils, and where it occurs in woodland it is frequently dominant in the field layer. This behaviour makes it very invasive as an exotic (e.g. Thomas 1998; California Exotic Plant Pest Council 1999). Ivy's aggressive

**Fig. 4** Approximate natural distribution of *Hedera helix* in Europe, North Africa and western Asia, where it occurs increasingly sparsely towards the eastern part of its range.

and communal growth on trees has led to it being generally considered a forest weed (e.g. Horne 1952); Rackham (1990) notes that Theophrastus (372–287 BC) thought that ivy kills the tree on which it grows though seemingly from little actual evidence. Vigorous foliar growth in the canopy of trees is usually restricted to moribund individuals, as healthy trees tend to have a sufficiently thick canopy to suppress growth of the fertile shoots of ivy, although ash (*Fraxinus excelsior*) may permit enough light to penetrate the canopy for even a healthy tree to be infested (Mitchell 1975). Weak trees may suffer from constriction by multiple ivy stems joining around the bole, and trees with luxuriant ivy growth in their canopies may be at an increased risk of wind throw. However, an unpublished experiment conducted by the late Mr Arthur Arnold near Wickham, Hampshire, between 1890 and 1942 suggested no effect of ivy on the height, average girth or cubic content of oak trees when half of the trees in a wood were kept clear of ivy, and the other half were permitted to support extensive ivy growths. Similarly, no significant differences were found between growth rings of host and non-host trees in a French study (Trémolières *et al.* 1988). Ellenberg (1988) reports that ivy is fairly tolerant of different soils in France and north-west Germany, but that it becomes confined to more fertile oak–hornbeam forests further to the east.

Ivy seedlings will establish in understorey conditions with evergreen shade (Sack 2004), although seedlings are more usually found in less shaded conditions; ivy invasion of woodlands and forests is associated with natural disturbance (Schnitzler 1995) or plantations (Rodney Helliwell, pers. comm.). Well-lit conditions are necessary for reproductive success, but in the allu-

vial forests of the Rhine, plants above 4 m in height may flower even under a closed canopy due to a preponderance of lightly shading canopy trees such as *Fraxinus excelsior*, *Populus* spp. and *Ulmus minor* (Schnitzler 1995).

### (C) EFFECT OF FROST, DROUGHT, ETC.

Ivy is intolerant of winter cold (mean temperature of coldest month ≤ −2 °C, Iversen 1944), this factor appearing to determine the limits to its northern and eastern distribution in Europe (see also Hafsten 1956). Ellenberg (1988) suggested that winter frosts may cause the trend for ivy to cease climbing trees and become more of a terrestrial creeper as it moves east in Europe. Flowers produced late in the autumn are susceptible to frost (Grime *et al.* 1988) and early ripening fruit may be caused to wither and abort by excessive cold (Snow & Snow 1988). However, induced tolerance may permit survival of temperatures down to −25 °C, as a result of increasing concentrations of water-soluble proteins and sugars in the leaves (Parker 1962; Street & Öpik 1984).

Drought is unlikely to be of major significance to UK populations, but it is suggested that critical levels of summer drought determine Mediterranean distributional limits (Huntley & Birks 1983). However, ivy is notably tolerant of seasonal drought, and so might be more advantaged relative to other woodland species in moister forests as climates become drier (Sack & Grubb 2002).

Ivy is relatively resistant to sulphur dioxide pollution (Bannister 1976) and resistant to the effects of limestone dust (Grime *et al.* 1988). Though frequently appearing chlorotic, ivy grows abundantly on chalk cliffs in southern England, but it is very sensitive to salt (Bannister 1976).

## VI. Structure and physiology

### (A) MORPHOLOGY

Ivy is very variable in life form: it may be a perennial herbaceous vine or climber, a herb, a woody subshrub, or rarely a tree. Woody stems may grow vertically up tree trunks, cliffs and walls, or grow horizontally on the woodland floor to form a continuous carpet – this capacity to extend over soil-less habitats from a base rooted in soil is unique in the British flora (Grime *et al.* 1988). Only the vertical stems bear reproductive shoots, which are physiologically adult and bear large, spirally arranged, radially symmetrical ovate leaves. Juvenile plants or parts of plants bear alternately arranged, palmately lobed shade-leaves, and it is typically this growth phase that produces adventitious roots. The natural switch in morphogenesis from juvenile to adult phase is a consequence of differential DNA replication, resulting in changes to both the quality (through heterochromatin under-replication) and quantity (through polyploidization) of DNA expressed in adult tissue

(Schäffner & Nagl 1979); artificial application of auxin may also promote flowering in juvenile forms (Zeeuw & Leopold 1956, cited in Sinott 1960). Mature-leaf forms may be forced to revert to juvenile forms with gibberellic acid (Robins 1957, cited in Sinott 1960; Rogler & Hackett 1975; Wareing & Frydman 1976; Zimmerman *et al*. 1985), or through cold shock or X-ray irradiation (Frank & Renner 1956, cited in Sinott 1960). Reversal may also occur naturally in low light and high temperatures, and cuttings from the adult phase may revert to juvenile phase (Davis *et al*. 1992).

Stellate trichomes on new shoot tips give a grey-white pubescent effect that diminishes as laminar growth separates them. A trichome consists of a central stalk from the apex of which radiate a variable number of unicellular rays. These rays may stand up giving the appearance of pubescence in ssp. *helix,* or lie flat along the laminar surface in ssp. *hibernica* (McAllister & Rutherford 1990). Leaf thickness ranges from 230 μm in juvenile leaves to 330 μm in adult ones (Poethig 1990). Stomata are present on the lower (abaxial) surfaces of leaves only, at a density of 125–240 mm$^{-2}$; guard cell length is 22–30 μm (Sack *et al*. 2003a; Sack *et al*. 2003b). Specific leaf area (SLA) is *c*. 200 cm$^2$ g$^{-1}$ in shade, but nearer to 100 cm$^2$ g$^{-1}$ in sun. Typical leaf characteristics are: lamina area *c*. 50 cm$^2$; lamina volume *c*. 1.4 cm$^3$; foliar water content is relatively high at *c*. 230 g H$_2$O 100 g$^{-1}$ leaf dry mass (65–70% wet mass), although declining from juvenile to mature plants (Baldini *et al*. 1997; Sack *et al*. 2003a; Sack *et al*. 2003b). The wood is typically light-coloured and soft (Metcalfe & Chalk 1957); wood density is *c*. 530 kg m$^{-3}$.

Seedlings grow a single slender primary root, which extends vertically to bear many short, fine branches, some of which develop into prominent horizontal secondaries with lateral branches. Larger juveniles root adventitiously from the nodes of the above-ground creeping stem. Still larger plants use adventitious roots for climbing. Fine root diameter is 300–500 μm. Root architecture is highly dissected. Root mass fraction (RMF) is moderately high at *c*. 0.28 (Sack *et al*. 2003b).

### (B) MYCORRHIZA

Ivy is typically mycorrhizal, but possibly not with a normal arbuscular type, as no arbuscules have been reported (Harley & Harley 1987; references therein). Mycorrhizas are also associated with the adventitious roots produced by juvenile shoots (Grime *et al*. 1988).

### (C) PERENNATION: REPRODUCTION

Flowers are produced on well-lit, aerial, adult shoots from about 10 years old (Clark 1983). Flowering begins in late August and may continue into November in the UK or as late as January in southern Europe. Flowers are produced in panicles of 1–6 umbels, the terminal umbel flowering first, followed by successive umbels back to the leafy growth. Anthesis begins 1–2 days before

production of nectar, the stamens falling from the plant about 7 days after anthesis. Bottema (2001) estimates daily pollen presentation on a 28-year-old plant to be 1.27–2.03 × 10$^9$ grains. Nectar is produced on the floral disc for 1–3 days; the flowering process is more drawn out at the beginning of the flowering period in late summer – by mid autumn the progression from bud through anthesis and nectar production to shedding of ephemeral components may take only 3 days. Typically only one umbel per panicle develops into fruit, normally the terminal one, but should that be removed later-flowering umbels may develop instead of being aborted. The fruit is a purple-black berry (occasionally yellow, Fl. Wilt., although this record may reflect a misidentification of ssp. *poetarum*), size 5.5–7.5 × 5.5–8.7 mm, and up to 0.33 g fresh weight; pulp dry mass 15–52 mg, pulp constituents up to 31.9% lipid, 5% protein, 16.1% fibre, 47.4% non-structural carbohydrate and 0.5% ash (Herrera 1987; Snow & Snow 1988; Obeso & Herrera 1994). The berries contain 1–5 seeds up to 6.8 × 4.8 mm, fresh weight 20–60 mg, dry weight 17–50 mg (Grime *et al*. 1988; Obeso & Herrera 1994; Laura Kennison, unpublished undergraduate dissertation). Seeds are mainly bird-dispersed and germinate after 7–10 days; light and the presence of the fruit pulp inhibit germination. There is no persistent seed bank. Vegetative propagation is probably more important than sexual reproduction in areas where ivy is already present, through rooting and patch-forming.

### (D) CHROMOSOMES

*Hedera helix* ssp. *helix* 2*n* = 48; ssp. *hibernica* 2*n* = 96 (Chr. Atl.; Fl. Eur.; Vargas *et al*. 1999). It has been suggested that the generic base number is possibly *x* = 12, making ssp. *helix* 2*x* and ssp. *hibernica* 4*x* (Mabberley 1997), although in a survey of all 13 *Hedera* spp. Vargas *et al*. (1999) suggested that the basic number is probably *x* = 24. Diploid cell DNA content of juvenile leaves 3.6 pg, of adult phase leaves 6.2 pg (Schäffner & Nagl 1979).

### (E) PHYSIOLOGICAL DATA

#### (i) Light

Phenotypically, juvenile leaves are shade leaves and adult leaves are sun leaves. Juvenile leaves have lower photosynthetic capacity and offer only limited acclimation to high light fluxes (Hoflacher & Bauer 1982; Bauer & Thöni 1988). Ivy performs relatively well as a seedling in the understorey, having a relatively low light compensation point (PAR 30 μmol m$^{-2}$ s$^{-1}$) and light requirement for 90% of maximum photosynthesis (360 μmol m$^{-2}$ s$^{-1}$) compared to other climbing plants (Carter & Teramura 1988). Ellenberg (1988) classified ivy as a semi-shade plant of 5–10% relative light flux, and Sack *et al*. (2003b) reported that ivy will persist, despite repeated drought, in irradiance *c*. 3% of full

sunlight or less. Adult leaves always have a greater photosynthetic capacity than juvenile leaves (*c.* 1.5 times higher, Bauer & Bauer 1980), even when comparing juvenile and adult leaves from the same plant. Juvenile leaves may show limited acclimation to moderately high light during leaf development, or even on exposure to higher light after full development, although it took about 6 weeks of exposure to result in an increase in net photosynthesis (Bauer & Thöni 1988). Such acclimation behaviour suggests an ability to modify leaf structure to maximize photosynthesis when deciduous species lose their leaves, although leaves which experience a rapid increase in incident light at leaf fall are photoinhibited, and may suffer reduced net photosynthetic rates all winter (Oberhuber & Bauer 1991). Damage in photoinhibited leaves may be repaired in spring, after which the leaves continue functioning as normal. Sun leaves and north-facing leaves which are not exposed to a significant increase in ambient light in autumn do not show reduced net photosynthesis until affected by low temperatures (Oberhuber & Bauer 1991).

Ivy shows moderate morphological plasticity in shade, as expected of a shade-tolerator, with higher SLAs and lower RMFs when grown in deeper shade (Sack & Grubb 2002), and moderately higher chlorophyll content per unit mass in shade (Sack *et al.* 2003b). Chlorophyll content chl *a* 0.56 mg g$^{-1}$ fresh weight, chl *b* 0.28 mg g$^{-1}$ FW (Baldini *et al.* 1997). Ivy leaves show maximum absorbance between 400 and 700 nm, with a slight reduction in absorbance at around 550 nm; absorbance is greater from the adaxial than the abaxial surface due to increased reflection but not transmittance (Baldini *et al.* 1997). Leaves continue to absorb some energy between *c.* 700–1350 nm, across which range there is also a sharp increase in both reflectance and transmittance (Eller 1979, cited in Holm 1989). Relative growth rates (RGR) are affected by light quality, with relative growth rate in low red : far-red light only 68% of that in neutral shade of the same magnitude (Sack & Grubb 2002).

### (ii) Water relations

Ivy is classified by Ellenberg (1988) as a moist-site indicator, being found mainly on soils of average dampness, and absent from both wet ground and places which may dry out. Ivy seedling density was strongly positively correlated with soil moisture under 10 shrub and one tree species, even though seedlings were still significantly present in the driest sites (Kollmann & Grubb 1999). Water use efficiency for juvenile plants growing in shaded conditions was one of the lower values determined for eight climbers, at 6.3 mmol $CO_2$ mol$^{-1}$ $H_2O$ (Carter & Teramura 1988), and ivy seedling survival was high relative to many other woody species growing in shade under a deciduous experimental scrub (Kollmann & Grubb 1999). Sack (2004) showed that ivy seedlings survived significantly longer under extreme drought in deeply shaded (3% ambient light) than in well lit (30% light) conditions, and suggests that shade plays a protective role for the essentially shallow-rooted seedlings, reducing evaporative demand and the impact of photoinhibitory irradiances. Ivy exhibits very low cuticular conductance (for juvenile-type leaves *c.* $1.9 \times 10^{-4}$ kg m$^{-2}$ s$^{-1}$ MPa$^{-1}$), with even adult leaves under high irradiance losing very little water (Ellenberg 1988; Sack *et al.* 2003a). Other leaf hydraulic characteristics are presented in Sack *et al.* (2003a).

### (iii) Temperature

As befits a member of a largely tropical family, ivy benefits from warm summers and is disadvantaged by frosty winters. Although weeks of mild frosts appear to limit the distribution of ivy, tolerance of much more severe frosts may be induced. Low but non-freezing temperatures can induce a frost tolerance to about −12 °C; mild frosts (0 °C to −5 °C) will induce frost hardiness to −16 °C; severe frosts of −10 °C are needed to induce resistance of −20 °C to −24 °C (Bauer & Kofler 1987). The mechanism of frost tolerance seems to include increased concentrations of water-soluble proteins and both concentrations and diversity of soluble sugars (Parker 1962; Fischer & Feller 1994), and the development of anthocyanin pigments (Parker 1962). Induced frost tolerance was accompanied by increases in the phospholipid but not galactolipid fractions of the membrane lipids, membrane augmentation accompanied by an increase in the length of the thylakoids but not chloroplast numbers. Membrane desaturation also took place, again within the phospholipid fraction, with a decline in the palmitic acid proportion in favour of linoleic, and to a lesser extent linolenic acids (Senser & Beck 1984). Net photosynthesis declines with increasing degree of frost, but rises again rapidly with increased warmth; leaf assimilatory enzyme proteins are conserved through the winter allowing ivy to make use of short periods of warmth, and to start assimilation as early as possible in the spring (Fischer & Feller 1994). Photosynthetic depression in frost-hardened leaves does not appear to be caused by feedback inhibition via assimilate accumulation (Bauer *et al.* 1996). The soluble sugar content of leaves peaked in January, total proteins and carbohydrates increased between February and May (by 50% and 200%, respectively), the latter due to starch accumulation (Fischer & Feller 1994). There was re-translocation of solutes to newly growing foliar material in May; total sugars declined in spring, increased in late summer and then declined again in late November (Parker 1962). In summer only three sugars were found in the leaves (sucrose, glucose and fructose) but in winter six or possibly seven sugars were present (the above three, plus stachyose, raffinose, xylose and possibly arabinose). Anthocyanins are undetectable in summer but develop in autumn, as leaves take on their red/purple tints, and decline in spring at the same time as sugars (Parker 1962).

### (iv) Nutrition

Ivy is a photosynthetic autotroph, utilizing the C3 photosynthetic pathway.

### (F) BIOCHEMICAL DATA

Ivy foliage is eaten by a range of mammals (see section IX(A)), the apical portions (leaves and shoots < 1 cm diameter) having an *in vitro* organic matter digestibility of *c*. 63%, and containing *c*. 44% fibre, 17% lignin, 1% silica and 9% crude protein. This composition meets the minimum requirements for deer forage and accounts for the utilization of ivy as a primary forage item in autumn/winter studies (González-Hernández & Silva-Pando 1999). However, leaf extracts containing α-hederin have been shown to have appetite-suppressing and insecticidal action on larvae of three noctuid moth species (Hubrecht 1988). The toxic α- and β-hederins are derived from the hydrolysis of hederasaponins A and B (Cooper & Johnson 1984). Frohne & Pfänder (1984) detected triterpenoid saponins in all parts, and at least four triterpenoid saponins have been extracted from the fruit of ivy; all of these showed molluscicidal activity at ≤ 15 p.p.m. (Hostettmann 1980). A list of additional chemicals isolated from various plant fractions is available from The Phytochemical Database (Beckstrom-Sternberg & Duke 1994). Cooper & Johnson (1984) report toxicity to cattle (leaves and berries), deer, sheep, dogs and chickens (latter by seeds), although see section IX. Mineral nutrient content of newly fallen leaf litter collected in a riparian Rhine forest, France, was: N = 0.80 g 100 g$^{-1}$ dry matter, P = 0.031 g 100 g$^{-1}$, K = 0.77 g 100 g$^{-1}$, Mg = 0.31 g 100 g$^{-1}$; the C : N ratio was 56.9 (Badre *et al*. 1998). The content of water-soluble compounds in fresh leaves was 18% of leaf dry matter, and the content of phenols was 1.03%; tannins were absent (Trémolières & Carbiener 1985, cited in Badre *et al*. 1998).

The fruit pulp has a high lipid content (32%), moderate protein content (5%) and low soluble carbohydrate content (47%) compared to other British bird-dispersed fruits (Krajewska 1981; Snow & Snow 1988). The fatty acid content of the seeds is as follows: 5% palmitic, 20% oleic, 13% linoleic and 62% petroselenic (Gibbs 1974). Krajewska (1981) isolated oleanolic acid from fruits, flowers and leaves. Mild toxicity of the fruit may prevent too many being eaten at a single time by a single disperser; cyanogenic glycosides are present in the pulp but not seeds of unripe ivy berries, and at lower levels in the pulp of ripe berries. The flavonoid rutin is present in the pulp but not seeds of both unripe and ripe berries. The saponin β-hederin is detectable in ripe but not unripe seeds and pulp, and the saponin hederagenin 3-O-β-L-arabinopyranoside is present in the pulp of both unripe and ripe berries, but only in the seeds from unripe fruit (Barnea *et al*. 1993).

The sap of ivy may cause dermatitis in man (Cooper & Johnson 1984), the allergens being the polyacetylenes falcarinol and didehydrofalcarinol (García *et al*. 1995);

skin reactions have also been attributed to the alkaloid emetine (Mahran *et al*. 1975). Turton (1925) reported the poisoning of a child by eating ivy leaves. Forsyth (1968) reports that an infusion of leaves may be used as a fomentation for bruises, and to remove shiny patches from clothes!

In terms of chemical control of ivy, the foliage is resistant to 2,4-D and mildly resistant to 2,4,5-T in water, although the dormant shoot is susceptible to 2,4,5-T diluted in oil; the stump or stem may also be controlled with ammonium sulphamate in water (Fryer & Makepeace 1978). The systemic herbicides triclopyr amine and triclopyr ester are also effective control agents (Swearingen & Diedrich 2000).

## VII. Phenology

The main period of leaf initiation is in April to May, although leaves are produced almost continuously from March to October (D.J. Metcalfe and L. Sack, unpublished data); the main litterfall period is also in late spring with litter biomass of *c*. 0.8 t ha$^{-1}$ recorded from arboreal ivy in the Rhine forests of Alsace, France (Badre *et al*. 1998). Leaves are long-lived (3–4 years), but show seasonal changes in chlorophyll content, with leaf chlorophyll concentration dipping in mature leaves in early April, synchronously with the onset of leaf flushing, and recovering back to 'normal' levels within 3–4 weeks. Juvenile leaves showed some tendency for leaf chlorophyll content to decline in mid-winter. All leaves show a huge increase in anthocyanin levels during the cold months (D.J. Metcalfe and L. Sack, unpublished data).

Floral initiation consists of a pre-floral stage, which does not require specific environmental conditions, followed by a stage of floral initiation that requires an inductive process in short days (12 h photoperiod) followed by expression under long days (16 h photoperiod) at a specific temperature: 16 °C near optimal, 21 °C near upper limit (Wallerstein & Hackett 1989). Consequently, ivy is one of the latest flowering of all woody species, typically flowering in September, although sometimes as early as August or as late as November. The season is later farther north in the country (UK Phenology Network 2001). This disharmony between flowering season and the weather may reflect the origins of ivy in warmer conditions during the Tertiary (Ackerfield & Wen 2003; see section X). There are about 20 flowers in each umbel, and 3–5 umbels in a panicle; flowers in an umbel open more or less synchronously, while umbels flower sequentially, with the terminal umbel flowering first. Early flowering plants may bear ripe fruit in November, late-flowering plants not until May or even June, but most ripen fruit in March or April (Snow & Snow 1988).

## VIII. Floral and seed characters

### (A) FLORAL BIOLOGY

Ivy flowers in brightly lit or lightly shaded sites from late August until late November, unless early frosts kill

remaining buds. Flowers are hermaphrodite, protandrous or homogamous, and are insect pollinated. The anthers are bright yellow, turning brownish-yellow and falling off quickly (1–3 days) after anthesis, after which the stigma is mature and the disk secretes nectar more actively. Nectar-producing flowers glisten, compensating for the diminution in conspicuousness resulting from the loss of anthers. Insects visiting the first stage (effectively male) flowers have the undersides of their abdomens dusted with pollen, which they deposit on the stigmas of second stage (female) flowers (Knuth, Poll. II). These insect visitors effect cross-pollination, as self-pollination would seem to be ineffective (Wittrock 1886, in Knuth, Poll. II). A wide range of insects may be seen to visit ivy flowers; often swarms of flies and Hymenoptera are in attendance at sunlit inflorescences (Table 1). Ivy may be completely dependent on flies for pollination in northern countries, or rely exclusively on vegetative reproduction at the extreme northern limit of its range. (Fröman 1944; Fægri & van der Pijl 1979).

### (B) HYBRIDS

Wild populations show considerable variation, which may in part be due to hybridization, but also to the tendency of juvenile shoots to mutate freely, giving rise to various foliage and growth habits. These may by propagated by cuttings or layers by horticulturists to provide the many commercially available cultivars, of which at least 89 are commonly available (Bailey & Bailey 1976). *Hedera helix* ssp. *helix* is a diploid, and although it frequently grows in close proximity to the tetraploid (ssp. *hibernica*), no triploids have yet been identified (McAllister & Rutherford 1990). However, chloroplast microsatellite markers show some genetic mixing, and shifts in ploidy or hybridization and introgression are possible (Grivet & Petit 2002; references therein). The intergeneric hybrid × *Fatshedera lizei*, which arose in Lizé Frères nursery, Nantes, in 1910, occurred between *Fatsia japonica* 'Moseri' × *Hedera helix* cv, but has not been repeated (Mabberley 1997).

### (C) SEED PRODUCTION AND DISPERSAL

Seeds are dispersed from November/December until as late as June, although Snow & Snow (1988) recorded a feeding peak in April and most European records are of berry consumption in April and May. In a hard winter the majority of fruit are taken in January and February. The prime dispersers are the thrushes (Table 2), though other birds including woodpigeons will take fruit and may disperse seed; woodpigeons also take large numbers of unripe berries and may destroy 78% of the seed crop (Snow & Snow 1988). Roe deer will take some ripe fruit, so may act as dispersers also (Hélène Verheyden-Tixier, pers. comm.), as do martens (Trémolières *et al*. 1988).
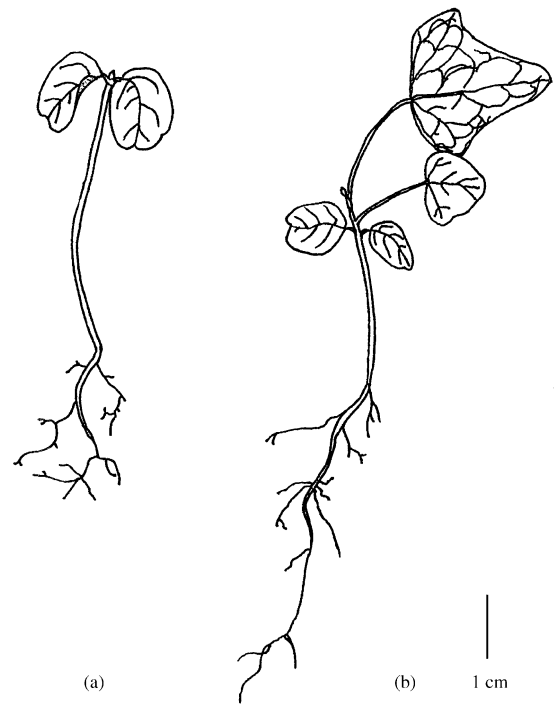
**Fig. 5** Development of *Hedera helix* seedlings, (a) 2 weeks and (b) 1 month after germination. See also Muller (1978).

### (D) VIABILITY OF SEEDS: GERMINATION

Seeds normally start to germinate within 6–14 days of planting, although dormancy of cleaned seeds (manually cleaned or seeds regurgitated by blackbirds or starlings) may last for up to 30 days; cleaning results in nearly 100% germination (Clergeau 1992; D.J. Metcalfe, unpublished data). Seeds planted within the fruits may remain dormant for up to 57 days, associated with *c*. 40% seed mortality. Drying of fruits kills all seeds (Clergeau 1992). Germination is epigeal, and may to some extent be inhibited by light. There does not appear to be any extended period of seed dormancy or the formation of a soil seed bank (Warr 1991; Kjellson 1992).

### (E) SEEDLING MORPHOLOGY

After germination the elongating hypocotyl carries the seed coat upwards on the cotyledons, which shed it as they expand (Fig. 5). Seedlings rapidly develop skototropic (shade-seeking) shoots which increases their chances of encountering a vertical structure up which to climb; leaves remain positively phototropic.

## IX. Herbivory and disease

### (A) ANIMAL FEEDERS OR PARASITES

Despite the presence of a range of secondary metabolites in the foliage, a number of vertebrate species will browse ivy, including red, roe and fallow deer. Roe deer (*Capreolus capreolus* L.) show a distinct preference for ivy during the autumn and winter, when it may form

**Table 1** Insect flower visitors recorded for ivy. Based on British data unless indicated (*) as being a European observation. Arrangement of taxa into families of Diptera after Chandler (1998) and Hymenoptera after Fitton *et al.* (1978)

| Species | Family | Reference |
| --- | --- | --- |
| Dermaptera | | |
| *Forficula auricularia* L. | Forficulidae | 2* |
| Diptera | | |
| *Phytomyza* sp. | Agromyzidae | 1 |
| *Anthomyia* sp. A | Anthomyiidae | 1 |
| *Anthomyia* sp. B | Anthomyiidae | 1 |
| *Bolitophila fusca* Mg. | Bolitophilidae | 1 |
| *Calliphora vicina* Robineau-Desvoidy | Calliphoridae | 1, 3 |
| *Calliphora vomitoria* L. | Calliphoridae | 2*, 3 |
| *Lucilia caesar* L. | Calliphoridae | 3 |
| *Lucilia cornicina* Fallén | Calliphoridae | 2* |
| *Lucilia* sp. | Calliphoridae | 1 |
| *Melinda gentilis* Robineau-Desvoidy | Calliphoridae | 3 |
| *Onesia sepulcralis* Mg. | Calliphoridae | 1 |
| *Pollenia amentaria* Scopoli | Calliphoridae | 3 |
| *Pollenia rudis* Fabricius | Calliphoridae | 1, 3 |
| *Metriocnemus* sp. | Chironomidae | 1 |
| *Orthocladius* sp. | Chironomidae | 1 |
| *Chloropsica ornata* Mg. | Chloropidae | 1 |
| *Drosophila graminum* Fallén | Drosophilidae | 1 |
| *Hydrellia griseola* Fallén | Ephydridae | 1 |
| *Aricia lardaria* Fallén | Muscidae | 1 |
| *A. lucorum* Fallén | Muscidae | 1 |
| *Graphomya maculata* Scopoli | Muscidae | 3 |
| *Limnophora* sp. | Muscidae | 1 |
| *Mesembrina meridiana* L. | Muscidae | 3 |
| *Neomyia cornicina* Fabricius | Muscidae | 3 |
| *Phaonia rufiventris* Scopoli | Muscidae | 3 |
| *Trichophthicus cunctans* Mg. | Muscidae | 1 |
| *Sciara* sp. | Mycetophilidae | 1 |
| *Sarcophaga carnaria* L. | Sarcophagidae | 3 |
| *Scathophaga stercoraria* L. | Scathophagidae | 1, 3 |
| *Dasysyrphus albostriatus* Fallén | Syrphidae | 3 |
| *Epistrophe* sp. | Syrphidae | 3 |
| *Episyrphus balteatus* De Greer | Syrphidae | 3 |
| *Eristalis tenax* L. | Syrphidae | 1, 3 |
| *Eupeodes corollae* Fabricius | Syrphidae | 3 |
| *Eupeodes luniger* Meigen | Syrphidae | 3 |
| *Helophilus pendulus* L. | Syrphidae | 3 |
| *Helophilus* sp. | Syrphidae | 2* |
| *Melanostoma mellinum* L. | Syrphidae | 3 |
| *Melanostoma scalare* Fabricius | Syrphidae | 3 |
| *Melangyna* sp. | Syrphidae | 3 |
| *Meliscaeva auricollis* Meigen | Syrphidae | 3 |
| *Myathropa florea* L. | Syrphidae | 3 |
| *Parasyrphus punctulatus* Verrall | Syrphidae | 3 |
| *Platycheirus albimanus* Fabricius | Syrphidae | 3 |
| *Platycheirus clypeatus* Meigen | Syrphidae | 3 |
| *Platycheirus manicatus* Meigen | Syrphidae | 3 |
| *Platycheirus scutatus* Meigen | Syrphidae | 3 |
| *Scaeva albomaculata* Macquart | Syrphidae | 3 |
| *Syrphus ribesii* L. | Syrphidae | 3 |
| *Syrphus vitripennis* Meigen | Syrphidae | 3 |
| *Volucella pellucens* L. | Syrphidae | 3 |
| *Xanthandrus comtus* Harris | Syrphidae | 3 |
| *Echinomyia fera* L. | Tachinidae | 2* |
| *Siphona geniculata* Deg. | Tachinidae | 1 |
| Hymenoptera | | |
| *Apis mellifera* L. | Apidae | 3 |
| *Bombus terrestris* L. | Apidae | 3 |
| *Psithyrus* sp. | Apidae | 3 |
| 5 indet. spp. | Ichneumonidae | 1 |
| *Scolia hirta* Schr. | Scoliidae | 2* |
| *Dolichovespula norwegica* Fabricius | Vespidae | 3 |
| *Eumenes mediterranea* Krehb. | Vespidae | 2* |
| *Polistes gallica* L. | Vespidae | 2* |

**Table 1** *continued*

| Species | Family | Reference |
|---|---|---|
| *Vespa vulgaris* L. | Vespidae | 1, 3 |
| *Vespula germanica* Fabricius | Vespidae | 1, 2*, 3 |
| Lepidoptera | | |
| *Aglais urticae* L. | Nymphalidae | 4 |
| *Vanessa atalanta* L. | Nymphalidae | 4 |
| *Tortrix* sp. | Tortricidae | 1 |

1, Burkill & Willis in Knuth, Poll. II.
2, Knuth, Poll. II.
3, Data from national grid square TQ20; September–November 2000 & 2001 (Laura Kennison, undergraduate dissertation).
4, Tintagel, Cornwall; September 1999 (DJM, unpublished data).

**Table 2** Birds recorded as feeding on and therefore probably dispersing ivy. Based on British data unless indicated (*) as being a European observation

| Common name | Species | Family | Reference |
|---|---|---|---|
| Collared dove | *Streptopelia decaocto* Frivaldsky | Columbidae | 1* |
| Woodpigeon | *Columba palumbus* L. | Columbidae | 2, 3 |
| Carrion crow | *Corvus corone* L. | Corvidae | 2* |
| Starling | *Sturnus vulgaris* L. | Sturnidae | 2 |
| Corn bunting | *Miliaria calandra* L. | Fringillidae | 3 |
| Blackcap | *Sylvia atricapilla* L. | Sylviidae | 2, 3 |
| Capercaillie | *Tetrao urogallus* L. | Phasianidae | 2* |
| Robin | *Erithacus rubecula* L. | Muscicapidae | 2 |
| Redwing | *Turdus iliacus* L. | Muscicapidae | 2 |
| Blackbird | *T. merula* L. | Muscicapidae | 2, 3 |
| Song thrush | *T. philomelos* Brehm | Muscicapidae | 2, 3 |
| Fieldfare | *T. pilaris* L. | Muscicapidae | 2 |
| Ring ouzel | *T. torquatus* L. | Muscicapidae | 2 |
| Mistle thrush | *T. viscivorus* L. | Muscicapidae | 2 |
| Waxwing | *Bombycilla garrulus* L. | Bombycillidae | 2* |
| Warblers | – | Sylviidae | 1* |
| Sparrows | – | Passeridae | 1* |

1, Grivet & Petit (2002).
2, Snow & Snow (1988).
3, Disp. Pl.

a significant part of the diet, with mainly foliage but some fruits taken also (Jackson 1980; Hélène Verheyden-Tixier, pers. comm.). However, roe deer show a distinct avoidance in the summer, or take very little (Jackson 1980; Tixier *et al.* 1997). Fallow deer (*Dama dama* L.) will also take ivy foliage in winter (Jackson 1980), and red deer (*Cervus elephas* L.) will supplement their diet with ivy in hard winters, and take lesser amounts in spring and summer (Coleman-Cooke, in Simmons & Dimbleby 1974; cf. Lloyd 1970; Allen 1974; Allen & Floyd 1988). Red and roe deer are capable of significantly reducing the biomass of ivy by grazing (González-Hernández & Silva-Pando 1996). Sheep relish ivy, sick beasts taking ivy leaves when refusing other forage (G.W. Metcalfe, pers. comm.) and sheep may severely restrict ivy colonization of grassland areas and woodland understorey (Hillegers 1989, cited in Bottema 2001). Pike & Godwin (1953) report evidence of ivy in the teeth of a rhinoceros from Clacton-on-Sea, Essex, from the last interglacial, but this probably represents *post mortem* deposition rather than herbivory. Ivy berries form an important food resource in late winter and early spring for many bird species (Table 2).

Gastropods reject both the leaves themselves and filter paper wetted with water-extracts of the leaves (Grime *et al.* 1970). However, nematodes (*Meloidogyne* sp.) are associated with the roots (reported from both Italy and the USA; Nemat. Cat.), and a wide range of arthropods is found to feed on ivy (Table 3). These arthropods in turn attract other species to the plant; the conopid fly *Leopoldius signatus* Wiedemann is commonly seen around ivy flowers in late summer, amongst the swarms of *Vespula* wasps it parasitizes (Smith 1969; Clements 1997). The predaceous bug *Empicoris vagabundus* (L.) has been found on ivy (Butler, Hem.-Het.), whilst ivy provides the preferred habitat of the ladybirds *Clitostethus arcuatus* Rossi and *Nephus quadrimaculatus* Herbst (which also breeds on ivy) and the preferred over-wintering site of *Halysia 16-guttata* L. (Coleopt. Handb.; Majerus 1994).

**Table 3** Species of insects and mites known to feed on ivy, arranged by order; based on British data

| Species | Family | Reference |
|---|---|---|
| Coleoptera | | |
| *Anobium inexspectatum* Lohse | Anobiidae | 1, 2 |
| *Anobium A. punctatum* (Degeer) | Anobiidae | 1 |
| *Ochina ptinoides* Marsham | Anobiidae | 1, 2 |
| *Grammoptera ruficornis* (F.) | Cerambycidae | 1 |
| *Pogonocherus hispidulus* (Piller & Mitterpacher) | Cerambycidae | 1 |
| *P. hispidus* (L.) | Cerambycidae | 1 |
| *Lamprosoma concolor* Sturm | Chrysomelidae | 1, 2 |
| *Acalles misellus* Boheman | Curculionidae | 1 |
| *Barypeithes araneiformis* (Schrank) | Curculionidae | 1 |
| *B. pellucidus* (Boheman) | Curculionidae | 1 |
| *Dryophthorus corticalis* (Paykull) | Curculionidae | 1 |
| *Liophloeus tessulatus* Müller, O.F. | Curculionidae | 1, 2 |
| *Rhyncolus lignarius* (Marsham) | Curculionidae | 1 |
| *Oncomera femorata* (F.) | Oedemeridae | 1 |
| *Kissophagus hederae* Schmitt | Scolytidae | 1, 2 |
| *Xyloterus domesticum* (L.) | Scolytidae | 1 |
| Hemiptera | | |
| *Siphoninus immaculata* Heeger | Aleyrodidae | 1, 3 |
| *Cardiastethus fasciiventris* (Garbiglietti) | Anthocoridae | 1 |
| *Anuraphis angelicae* Koch | Aphididae | 4 |
| *Aphis hederae* Kalt. | Aphididae | 1, 5 |
| *A. pseudohederae* sp. nov. | Aphididae | 5 |
| *A. rumicis* Linn. | Aphididae | 5 |
| *Rhopalosiphoninus waltoni* Theo. & Walt. | Aphididae | 6 |
| *Myzus persicae* (Sulzer) II | Aphididae | 1 |
| *Planchonia arabidis* Signoret | Asterolecaniidae | 1 |
| *Empoasca vitis* (Gothe) | Cicadellidae | 1 |
| *Ribautiana debilis* (Douglas) | Cicadellidae | 1 |
| *Zygina angusta* Lethierry | Cicadellidae | 1 |
| *Z. flammigera* (Geoffroy in Fourcroy) | Cicadellidae | 1 |
| *Coccus hesperidium* L. | Coccidae | 1, 7, 8 |
| *Eulecanium* (*Parthenolecanium*) *corni* Bouché | Coccidae | 1, 8 |
| *Lichtensia* (*Filippia*) *viburni* Signoret | Coccidae | 1, 7 |
| *Saissetia coffeae* (Walker) | Coccidae | 1 |
| *Aspidiotus hederae* Newstead. | Diaspididae | 1, 8 |
| *Chrysomphalus dictyospermi* (Morgan) | Diaspididae | 1 |
| *Dynaspidiotus britanicus* (Newstead) | Diaspididae | 1 |
| *Fiorinia fioriniae* (Targioni) | Diaspididae | 1 |
| *Hemiberlesia lataniae* (Signoret) | Diaspididae | 1 |
| *Selenaspidus articulatus* (Morgan) | Diaspididae | 1 |
| *Issus coleoptratus* (F.) | Issidae | 1 |
| *Orthops cervinus* Herrich-Schaeffer | Miridae | 1, 9 |
| *Pseudococcus* sp. | Pseudococcidae | 2 |
| *Derephysia foliacea* Fallén | Tingidae | 1, 9, 10 |
| Lepidoptera | | |
| *Eupoecilia ambiguella* (Hubner) | Cochylidae | 1 |
| *Abraxas grossulariata* (L.) | Geometridae | 1 |
| *Acasis viretata* (Hubner) | Geometridae | 1 |
| *Alcis repandata* (L.) | Geometridae | 1 |
| *Idaea seriata* (Schrank) | Geometridae | 1 |
| *I. trigeminata* (Haworth) | Geometridae | 1 |
| *I. vulpinaria* (Herrich-Schaffer) | Geometridae | 1 |
| *Ourapteryx sambucaria* (L.) | Geometridae | 1 |
| *Peribatodes rhomboidaria* (Denis & Schiffermuller) | Geometridae | 1 |
| *Lasiocampa quercus* (L.) | Lasiocampidae | 1 |
| *Herminia tarsipennalis* (Treitschke) | Noctuidae | 1 |
| *Melanchra persicariae* (L.) | Noctuidae | 1 |
| *Mormo maura* (L.) | Noctuidae | 1 |
| *Mythimna I-album* (L.) | Noctuidae | 1 |
| *Polymixis flavicincta* (Denis & Schiffermuller) | Noctuidae | 1 |
| *Xestia c-nigrum* (L.) | Noctuidae | 1 |
| *Vanessa atalanta* (L.) | Nymphalidae | 1 |
| *Clysia ambiguella* Hübn. | Phalloniidae | 11 |
| *Ephestia parasitella* Staudinger ssp. *unicolorella* Staudinger | Pyralidae | 1 |
| *Batodes* (*Ditula*) *angustiorana* Haw. | Tortricidae | 1, 11 |

**Table 3** *continued*

| Species | Family | Reference |
|---|---|---|
| *Cacoecimorpha pronubana* (Hubner) | Tortricidae | 1 |
| *Choristoneura hebenstreitella* (Muller) | Tortricidae | 1 |
| *Clepsis consimilana* (Hubner) | Tortricidae | 1 |
| *Lobesia botrana* (Denis & Schiffermuller) | Tortricidae | 1 |
| *Tortrix (Lozotaenia) forsterana* Fabr. | Tortricidae | 1, 11, 12 |
| *T. unifasciana* Dup. | Tortricidae | 11 |
| *Celastrina argiolus* L. | Lycaenidae | 1, 12 |
| Thysanoptera | | |
| *Dendrothrips eastopi* Pitkin & Palmer | Thripidae | 1 |
| Acarina | | |
| *Acaricalus hederae* (Keifer) | Eriophyidae | 1 |
| *Polyphagotarsonemus latus* (Banks) | Tarsonemidae | 1 |
| *Steneotarsonemus pallidus* (Banks) | Tarsonemidae | 1 |
| Prostigmata | | |
| *Bryobia kissophila* Eyndhoven | Tetranychoidea | 1 |
| *Tetranychus urticae* C.L.K. | Tetranychoidea | 13 |

1, Phytophagous insects database (from the Biological Records Centre, Monks Wood), though with the caveats outlined in Ward (1988).
2, Coleopt. Handb.
3, Mound, Aleyrodidae.
4, Theobald, Aphid 3.
5, Theobald, Aphid 2.
6, Theobald, Aphid 1.
7, Newstead, Coccidae.
8, Rose (1980).
9, Southwood & Leston, Land & Water Bugs.
10, Butler, Hem.-Het.
11, Ford, Lepidopt.
12, Meyrick, Lepidopt.
13, Osborne & Chase (1985).

Ivy was gathered as fodder in the Neolithic and Bronze Age, possibly even in the Mesolithic, and at least until the sixteenth century (Simmons & Dimbleby 1974; Grime *et al*. 1988).

### (B) PLANT PARASITES

Two parasitic plants are associated with ivy, *Orobanche hederae* (Orobanchaceae), the ivy broomrape (Fl. Br. Isl.) and *Osyris alba* (Santalaceae) (Benharrat *et al*. 1987). *Orobanche hederae* has a largely southerly and westerly distribution in England and Wales, with outliers in southern Scotland. In Northern Ireland, *O. hederae* is almost restricted to County Fermanagh, with only one site known from the Antrim Coast (National Museums and Galleries of Northern Ireland and Environment and Heritage Service, 2004), but is spread through much of Eire with a southerly and westerly concentration (Rumsey & Jury 1991). *Osyris alba* is a southern-European hemiparasite with a very wide host range.

### (C) PLANT DISEASES

A large number of fungi has been isolated from ivy, some pathogenic and others associated with the breakdown of dead leaves and stem fragments (Table 4).

The main diseases of horticulturally grown ivies are bacterial leaf spot caused by *Xanthomonas hederae* and *X. campestris* pv. *hedera*, and ivy leaf spot fungus *Colletotrichum trichellum* (Fr.) Duke (Rose 1980; Osborne & Chase 1985; Lopez Carbonell *et al*. 1998). There is also a rhabdovirus that causes ivy vein clearing virus (IVCV; Russo *et al*. 1979).

## X. History

*Hedera* fossils have been recorded from the Oligocene of Korea, and in Europe from the early mid Pontian (Miocene, *c*. 5.8 million years ago) of Bulgaria (Ivanov & Pencheva 2000). These finds support an inferred Tertiary origin for the genus, although chloroplast DNA phylogenies suggest that many of the species have a much shorter evolutionary history (Ackerfield & Wen 2003).

The pollen record for ivy is poor, as it is insect pollinated and a sparse pollen producer, but both fruits and pollen are recorded from the interglacials (Godwin 1975). Ivy was present in the UK in mixed deciduous woodland in the Pastonian Stage (Lower Pleistocene, *c*. 1 million years BP) with *Quercus*, *Carpinus*, *Ulmus*, *Pinus* and *Corylus*. In the Hoxnian Interglacial (400–367 kyr BP) it occurred in mixed oak wood with *Quercus*, *Corylus*, *Fraxinus*, *Alnus*, *Euonymus europaeus*, *Viburnum lantana*,

**Table 4** List of species of fungi (Ascomycota) associated with ivy, based on British data unless asterisked (*); nomenclature follows Index Fungorum (2004)

| Species | Order | Part affected | References |
|---|---|---|---|
| *Diaporthe hederae* Wehm., (1933) | Diaporthales | wood & bark | 1, 2 |
| *D. pulla* Nitschke (1870) | | wood & bark | 1, 2 |
| *Calospora undulata* (Berk. & Broome) Sacc., (1883) | | | 2 |
| *Diplodia hederae* Fuckel (1870) | Dothideales | shoots & leaves | 3 |
| *Guignardia philoprina* (Berk. & M.A. Curtis) Aa (1973) | | leaves | 1, 4 |
| *Melanconium hederae* Preuss | | on all parts | 1, 3 |
| *Metasphaeria hederae* (Sawada) Sacc., (1883) | | | 2 |
| *M. helicicola* (Desm.) Sacc., (1883) | | | 2 |
| *Phyllosticta hederacea* (Arcang.) Allesch. | | | 5 |
| *Trochila craterium* (DC.) Fr., (1849) | Helotiales | Leaves | 1, 3, 4, 6 |
| *Calonectria hederae* G. Arnaud ex C. Booth (1960) | Hypocreales | Leaves | 1 |
| *Nectria sinopica* (Fr.) Fr., (1849) | | Wood & bark | 1, 2, 6 |
| *N. coccinea* (Pers.) Fr., (1849) | | | 6 |
| *N. hederae* C. Booth (1959) | | Wood & bark | 1, 6 |
| *Aulographum hederae* Lib., (1834) | Microthyriales | Leaves | 1, 2, 6 |
| *Microthyrium ciliatum* var. *hederae* J.P. Ellis (1977) | | Leaves | 1 |
| *Cercospora hederae* Togashi & Katsuki (1952) | Mycosphaerellales | | 7* |
| *C. hedericola* (Heald & F.A. Wolf) U. Braun (1993) | | | 7* |
| *Mycosphaerella hedericola* (Desm.) Lindau (1897) | | Leaves | 1, 2, 4 |
| *Septoria hederae* Desm., (1843) | | Leaves | 1, 4 |
| *Colletotrichum helicis* (Desm.) Morgan-Jones (1971) | Phyllachorales | Leaves | 1, 3 |
| *C. trichellum* (Fr.) Duke (1928) | | Leaves | 1, 4, 8 |
| *Cytoplea hederae* (Desm.) Petr. & Syd., (1927) | Pleosporales | Leaves | 3 |
| *Coniothyrium olivaceum* var. *hederae* Sacc. | | | 3 |
| *Hendersonia sarmentorum* Westend., (1851) | | Dead twigs | 3 |
| *Lophiostoma angustilabrum* Pass., (1868) | Pleosporales | | 2 |
| *Phoma hedericola* (Durieu & Mont.) Boerema (1976) | | | 1, 5 |
| *Pseudospiropes nodosus* (Wallr.) M.B. Ellis (1971) | | Dead wood | 9 |
| *P. simplex* (Nees) M.B. Ellis (1971) | | Dead wood | 9 |
| *Hypoderma hederae* (T. Nees ex Mart.) De Not., (1847) | Rhytismatales | Leaves | 1, 2, 6, 10 |
| *Lophodermium hedericola* S. Ahmad (1971) | | Leaves | 1, 10 |
| *Sporoschisma juvenile* Boud., (1904) | Sordariales | Dead wood | 9 |
| *Peristomialis berkeleyi* Boud., (1907) | Trichotheliales | | 2 |
| *Coryneopsis microsticta* Grove (1932) | Xylariales | Branches | 3 |
| *Rosellinia mammiformis* (Pers.) Ces. & De Not. (1863) | | Dead stems | 1, 2, 6 |
| *Cheirospora botryospora* S. Hughes (1958) | *Incertae sedis* | Wood & bark | 1 |
| *Diplodia caespitosa* Berk. & Broome | | Dead branches | 3 |
| *Hypoderma hederae* (T. Nees ex Mart.) De Not., (1847) | | Dead leaves | 3 |
| *Microdiplodia hedericola* (Sacc.) Allesch., (1903) | | Dead leaves | 3 |
| *Mycothyridium lividum* (Pers.) Petr., (1962) | | | 2 |
| *Oncopodiella trigonella* (Sacc.) Rifai (1965) | | Wood & bark | 1 |
| *Sporidesmium altum* (Preuss) M.B. Ellis (1958) | | Dead wood | 9 |
| *S. cookei* (S. Hughes) M.B. Ellis (1958) | | Dead wood | 9 |
| *S. folliculatum* (Corda) E.W. Mason & S. Hughes (1953) | | Dead wood | 9 |
| *S. socium* M.B.Ellis (1958) | | Wood & bark | 1 |
| *Thyrsidium hedericola* Sacc. | | Twigs | 3 |
| *Xylohypha nigrescens* (Pers.) E.W. Mason (1960) | | Dead wood | 9 |

1, Ellis & Ellis (1997).
2, List Pyrenomyc.
3, Br. Stem and Leaf F. 2.
4, Br. para. Fungi.
5, Grimes, O'Connor & Cummins (1932) cited in Dennis (1946).
6, Br. Asco.
7, Braun (1993).
8, Rose (1980), Osborne & Chase (1985), Lopez Carbonell *et al.* (1998).
9, Dem. Hyphomyc.
10, Path. Fungi & Bact.

*V. opulus*, *Cornus sanguinea* and *Sambucus* spp.; at about the same time in Ireland (the Gortian Interglacial) ivy is recorded with *Betula*, *Pinus*, *Quercus*, *Ilex* and *Lonicera* (Ingrouille 1995). Molecular data suggest postglacial colonization by *Hedera* probably from Iberian, Italian and Balkan refugia, with the scarce pollen data also supporting a Greek refugium (Grivet & Petit 2002). Data from Scandinavia suggest that ivy extended about

100 km north of Oslo in the postglacial thermal maximum (*c.* 9–2.5 kyr BP) when winters were perhaps 2 °C warmer than today (Hafsten 1956; Dahl 1998). These data support Godwin's (1975) observations of increasingly high values in the later Boreal (9–7.5 kyr BP) and Atlantic period (7.5–5 kyr BP), and of the highest values recorded being from the Sub-atlantic period. During the mid-Holocene (5–6 kyr BP) the UK range was less extensive than at present, neither extending as far north, particularly in the west, nor as far south as at the present, owing to cooler summers (Huntley & Birks 1983; Ingrouille 1995). The earliest record of ivy from the historical period is in William Turner's *Libellus de re Herbaria Novus* (1538, First Rec.).

## Acknowledgements

## References

Ackerfield, J. & Wen, J. (2002) A morphometric analysis of *Hedera* L. (the ivy genus, Araliaceae) and its taxonomic implications. *Adansonia*, **24**, 197–212.

Ackerfield, J. & Wen, J. (2003) Evolution of *Hedera* (the ivy genus, Araliaceae): insights from chloroplast DNA data. *International Journal of Plant Sciences*, **164**, 593–602.

Allen, N.V. (1974) *The Exmoor Handbook and Gazetteer*, 3rd edn. The Exmoor Press, Dulverton, UK.

Allen, N. & Floyd, G. (1988) Exmoor's wild red deer. *Exmoor Review*, **29**, 35–45.

Badre, B., Nobelis, P. & Trémolières, M. (1998) Quantitative study and modelling of the litter decomposition in a European alluvial forest. Is there an influence of overstorey tree species on the decomposition of ivy litter (*Hedera helix* L.)? *Acta Oecologia*, **19**, 491–500.

Bailey, L.H. & Bailey, E.Z. (1976) *Hortus Third: A Concise Dictionary of Plants Cultivated in the United States and Canada*. Macmillan, New York, USA.

Baldini, E., Facini, O., Nerozzi, F., Rossi, F. & Rotondi, A. (1997) Leaf characteristics and optical properties of different woody species. *Trees*, **12**, 73–81.

Bannister, P. (1976) *Introduction to Physiological Plant Ecology*. Blackwell Scientific Publications, Oxford, UK.

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

Bauer, H. & Bauer, U. (1980) Photosynthesis in leaves of the juvenile and adult phase of ivy (*Hedera helix*). *Physiologia Plantarum*, **49**, 366–372.

Bauer, H. & Kofler, R. (1987) Photosynthesis in frost-hardened and frost-stressed leaves of *Hedera helix* L. *Plant, Cell and Environment*, **10**, 339–346.

Bauer, H., Pamer, R., Perathoner, C. & Loidolt-Nagele, M. (1996) Photosynthetic depression in leaves of frost-hardened ivy is not caused by feedback inhibition via assimilate accumulation. *Journal of Plant Physiology*, **149**, 51–56.

Bauer, H. & Thöni, W. (1988) Photosynthetic light acclimation in fully developed leaves of the juvenile and adult life phases of *Hedera helix*. *Physiologia Plantarum*, **73**, 31–37.

Beckstrom-Sternberg, S.M. & Duke, J.A. (1994) *The Phytochemical Database*. ACEDB, Version 4.3 – data version July 1994 [cited 28 January 1999]. http://probe.nal.usda.gov:8300/cgi-bin/browse/phytochemdb.

Benharrat, H., Renaudin, S., Rey, L. & Thalouarn, P. (1987) Sur la différenciation des tracheides dans les haustoriums d'*Osyris alba* parasitant *Hedera helix*. *Canadian Journal of Botany*, **65**, 1746–1755.

Bottema, S. (2001) A note of the pollen representation of ivy (*Hedera helix* L.). *Review of Palaeobotany and Palynology*, **117**, 159–166.

Braun, U. (1993) Taxonomic notes on some species of the *Cercospora* complex (III). *Mycotaxon*, **48**, 275–298.

California Exotic Plant Pest Council (1999) *List A-1 Most Invasive Wildland Pest Plants: Widespread*. [cited 28 January 1999]. http://www.igc.org/ceppc/worst.html.

Carter, G.A. & Teramura, A.H. (1988) Vine photosynthesis and relationships to climbing mechanics in a forest understory. *American Journal of Botany*, **75**, 1011–1018.

Chandler, P., ed. (1998) A check list of British insects: Diptera. *Handbooks for the Identification of British Insects*, **12** (1).

Clark, J.R. (1983) Age-related changes in trees. *Journal of Arboriculture*, **9**, 201–205.

Clements, D.K. (1997) The enemy within: conopid flies as parasitoids of bees and wasps in Britain. *British Wildlife*, **8**, 310–315.

Clergeau, P. (1992) The effect of birds on seed germination of fleshy-fruited plants in temperate farmland. *Acta Œcologia*, **13**, 679–686.

Cooper, M.R. & Johnson, A.W. (1984) *Poisonous Plants in Britain and Their Effects on Animals and Man*. Ministry of Agriculture, Fisheries and Food Reference Book 161. Her Majesty's Stationery Office, London, UK.

Dahl, E. (1998) *The Phytogeography of Northern Europe*. Cambridge University Press, Cambridge, UK.

Davis, R.E., Bilderback, T.E. & Fantz, P.R. (1992) Arborescent 'Treetop' English ivy. *Hortscience*, **27**, 279–280.

Dennis, R.W.G. (1946) Notes on some British fungi ascribed to *Phoma* and related genera. *Transactions of the British Mycological Society*, **29**, 11–42.

Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge, UK.

Ellis, M.B. & Ellis, J.P. (1997) *Microfungi on Land Plants*. Richmond, Slough, UK.

Fægri, K. & van der Pijl, L. (1979) *The Principles of Pollination Ecology*, 3rd edn. Pergamon Press, Oxford, UK.

Fischer, A. & Feller, U. (1994) Seasonal changes in the pattern of assimilatory enzymes and the proteolytic activities in leaves of juvenile ivy. *Annals of Botany*, **74**, 389–396.

Fitton, M.G., de Graham, M.W.R.V., Boucek, Z.R.J., Ferguson, N.D.M., Huddleston, T., Quinlan, J. & Richards, O.W. (1978) A check list of British insects: Hymenoptera. *Handbooks for the Identification of British Insects*, **11**(4).

Forsyth, A.A. (1968) *British Poisonous Plants*, 2nd edn. Her Majesty's. Stationery Office, London, UK.

Frohne, D. & Pfänder, H.J. (1984) *A Colour Atlas of Poisonous Plants*. Wolfe, London, UK.

Fröman, I. (1944) De senkvartära strandförskjutningarna som växtgeografisk faktor i belysning av murgrönans geografi i Skandinavien-Baltikum. *Geologiska Föreningens i Stockholm Förhandlingar*, **66**, 655–681.

Fryer, J.D. & Makepeace, R.J. (1978) *Weed Control Handbook*, Vol. II *Recommendations*, 8th edn. Blackwell Scientific Publications, Oxford, UK.

García, M., Fernández, E., Navarro, J.A., del Pozo, M.D. & de Corrès, L.F. (1995) Allergic contact dermatitis from *Hedera helix* L. *Contact Dermatitis*, **33**, 133–134.

Gibbs, R.D. (1974) *Chemotaxonomy of Flowering Plants*, Vol. III. McGill-Queens University Press, Montreal, Canada.

Godwin, H. (1975) *The History of the British Flora: A Factual Basis for Phytogeography*, 2nd edn. Cambridge University Press, Cambridge, UK.

González-Hernández, M.P. & Silva-Pando, F.J. (1996) Grazing effects of ungulates in a Galician oak forest (northwest Spain). *Forest Ecology and Management*, **88**, 65–70.

González-Hernández, M.P. & Silva-Pando, F.J. (1999) Nutritional attributes of understorey plants known as components of deer diets. *Journal of Range Management*, **52**, 132–138.

Grime, J.P., Blythe, G.M. & Thornton, J.D. (1970) Food selection by the snail *Cepaea nemoralis* L. *Animal Populations in Relation to their Food Resources* (ed. A. Watson), pp. 73–99. Blackwell Scientific, Oxford, UK.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology: A Functional Approach to Common British Species*. Unwin-Hyman, London, UK.

Grivet, D. & Petit, R.J. (2002) Phylogeography of the common ivy (*Hedera* sp.) in Europe: genetic differentiation through space and time. *Molecular Ecology*, **11**, 1351–1362.

Hafsten, U. (1956) Pollen-analytic investigations on the late Quaternary development in the inner Oslofjord area. *Universitetet i Bergen, Årbok 1956. Naturvitenskapelig Rekke*, **8**, 3–161.

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

Herrera, C.M. (1987) Vertebrate-dispersed plants on the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs*, **57**, 305–311.

Hoflacher, H. & Bauer, H. (1982) Light acclimation in leaves of the juvenile and adult life phases of ivy (*Hedera helix*). *Physiologia Plantarum*, **56**, 177–182.

Holm, D. (1989) Thermal improvement by means of leaf cover on external walls – a simulation model. *Energy and Buildings*, **14**, 19–30.

Horne, J.M. (1952) Ivy as a forest weed. *Scottish Forestry*, **6**, 86–87.

Hostettmann, K. (1980) Saponins with molluscicidal activity from *Hedera helix* L. *Helvetica Chimica Acta*, **63**, 606–609.

Hubrecht, F. (1988) Propriétés antiappétantes et actions insecticides d'extraits d'*Hedera helix* L. *Annales de la Société Royale Zoologique de Belgique*, **118**, 85.

Huntley, B. & Birks, H.J.B. (1983) *An Atlas of Past and Present Pollen Maps of Europe: 0–13 000 Years Ago*. Cambridge University Press, Cambridge, UK.

Index Fungorum (2004) *Index Fungorum*. Custodians CABI Bioscience, CBS and Landcare Research. [cited 8 November 2004]. http://www.indexfungorum.org.

Ingrouille, M. (1995) *Historical Ecology of the British Flora*. Chapman & Hall, London, UK.

Ivanov, D. & Pencheva, E. (2000) New palynological data on the Late Miocene flora and vegetation in Gotse-Delchev Basin (Southwestern Bulgaria). *Review of the Bulgarian Geological Society*, **61**, 39–46.

Iversen, J. (1944) *Viscum*, *Hedera* and *Ilex* as climatic indicators. *Geologiska Föreningers Stockholm Förhandlinger*, **66**, 463–483.

Jackson, J. (1980) The annual diet of the Roe deer (*Capreolus capreolus*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*, **192**, 71–83.

Kjellson, G. (1992) Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography*, **15**, 86–100.

Kollmann, J. & Grubb, P.J. (1999) Recruitment of fleshy-fruited species under different shrub species: control by under-canopy environment. *Ecological Research*, **14**, 63–74.

Krajewska, A. (1981) Badania fitochemiczne ziela, kwiatów oraz owoców bluszczu pospolitego (*Hedera helix* L.). *Herba Polonica*, **27**, 303–309.

Lloyd, E.R. (1970) *The Wild Red Deer of Exmoor*. Exmoor Press, Dulverton, UK.

Lopez Carbonell, M., Moret, A. & Nadal, M. (1998) Changes in cell ultrastructure and zeatin riboside concentrations in *Hedera helix*, *Pelargonium zonale*, *Prunus avium*, and *Rubus ulmifolius* leaves infected by fungi. *Plant Disease*, **82**, 914–918.

Mabberley, D.J. (1997) *The Plant-Book*. Cambridge University Press, Cambridge, UK.

Mahran, G.H., Hilal, S.H. & el-Alfy, T.S. (1975) The isolation and characterisation of emetine alkaloid from *Hedera helix* L. *Planta Medica*, **27**, 127–132.

Majerus, M.E.N. (1994) *Ladybirds*. Harper Collins, London, UK.

McAllister, H. (1981) New work on ivies. *International Dendrological Society Year Book*, **1981**, 106–109.

McAllister, H.A. & Rutherford, A. (1990) *Hedera helix* L. and *H. hibernica* (Kirchner) Bean (Araliaceae) in the British Isles. *Watsonia*, **18**, 7–15.

Metcalfe, C.R. & Chalk, L. (1957) *Anatomy of the Dicotyledons*, Vol. II. Oxford University Press, Oxford, UK.

Mitchell, A.F. (1975) *Three Forest Climbers*. Forestry Commission Forest Record 102. Her Majesty's Stationery Office, London, UK.

Muller, F.M. (1978) *Seedlings of the North Western European Lowland*. Junk, The Hague, the Netherlands.

National Museums and Galleries of Northern Ireland and Environment and Heritage Service (2004) *Orobanche hederae*. [CITED 11 November 2004]. http://www.habitas.org.uk/flora/species.asp?item=4180.

Oberhuber, W. & Bauer, H. (1991) Photoinhibition of photosynthesis under natural conditions in ivy (*Hedera helix* L.) growing in an understory of deciduous species. *Planta*, **185**, 545–553.

Obeso, J.R. & Herrera, C.M. (1994) Inter- and intraspecific variation in fruit traits in co-occurring vertebrate-dispersed plants. *International Journal of Plant Sciences*, **155**, 382–387.

Osborne, L.S. & Chase, A.R. (1985) Susceptibility of cultivars of English ivy to two-spotted spider mite and *Xanthomonas* leaf spot. *Hortscience*, **20**, 269–271.

Parker, J. (1962) Relationships among cold hardiness, water-soluble protein, anthocyanins and free sugars in *Hedera helix* L. *Plant Physiology*, **37**, 809–813.

Pike, K. & Godwin, H. (1953) The interglacial at Clacton-on-Sea. *Essex Quarterly Journal of the Geological Society of London*, **108** (for 1952), 261–272.

Poethig, R.S. (1990) Phase change and the regulation of shoot morphogenesis in plants. *Science*, **250**, 923–930.

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

Preston, C.D., Pearman, D.A. & Dines, T.D. (2002) *New Atlas of the British and Irish Flora*. Oxford University Press, Oxford.

Rackham, O. (1990) *Trees and Woodland in the British Landscape*, 2nd edn. Dent, London, UK.

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

Rodwell, J.S., ed. (1992) *British Plant Communities*, Vol. 3. *Grasslands and Montane Communities*. Cambridge University Press, Cambridge, UK.

Rodwell, J.S., ed. (2000) *British Plant Communities*, Vol. 5. *Maritime Communities and Vegetation of Open Habitats*. Cambridge University Press, Cambridge, UK.

Rogler, C.E. & Hackett, W.P. (1975) Phase change in *Hedera helix*: induction of the mature to juvenile phase change by gibberellin A₃. *Physiologia Plantarum*, **34**, 141–147.

Rose, P.Q. (1980) *Ivies*. Blandford Press, Poole, UK.

Rumsey, F.J. & Jury, S.L. (1991) An account of *Orobanche* L. in Britain and Ireland. *Watsonia*, **18**, 257–295.

Russo, M., Castellano, M.A. & Martelli, G.P. (1979) Rhabdovirus-like particles in English ivy (*Hedera helix*) and ivy-leafed geranium (*Pelargonium peltatum*). *Phytopathologische Zeitschrift*, **96**, 122–131.

Sack, L. (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos*, **107**, 110–127.

Sack, L., Cowan, P.D., Jaikumar, N.J. & Holbrook, N.M. (2003a) The 'hydrology' of leaves: coordination of structure and function in temperate woody species. *Plant, Cell and Environment*, **26**, 1343–1356.

Sack, L. & Grubb, P.J. (2002) The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. *Oecologia*, **131**, 175–185.

Sack, L., Grubb, P.J. & Marañón, T. (2003b) The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecology*, **168**, 139–163.

Schäffner, K.-H. & Nagl, W. (1979) Differential DNA replication involved in transition from juvenile to adult phase in *Hedera helix* (Araliaceae). *Plant Systematics and Evolution*, **2** (Suppl.), 105–110.

Schnitzler, A. (1995) Community ecology of arboreal lianas in gallery forests of the Rhine valley, France. *Acta Oecologia*, **16**, 219–236.

Senser, M. & Beck, E. (1984) Correlation of chloroplast ultrastructure and membrane lipid composition to the different degrees of frost resistance achieved in leaves of spinach, ivy and spruce. *Journal of Plant Physiology*, **117**, 41–55.

Simmons, I.G. & Dimbleby, G.W. (1974) The possible role of ivy (*Hedera helix* L.) in the Mesolithic economy of Western Europe. *Journal of Archaeological Science*, **1**, 291–296.

Sinott, E.W. (1960) *Plant Morphogenesis*. McGraw-Hill, New York, USA.

Smith, K.G.V. (1969) A check list of British insects: Diptera: Conopidae. *Handbooks for the Identification of British Insects*, **10**(3). Royal Entomological Society, London.

Snow, B. & Snow, D. (1988) *Birds and Berries: A Study of an Ecological Interaction*. Poyser, Calton, UK.

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

Street, H.E. & Öpik, H. (1984) *The Physiology of Flowering Plants: Their Growth and Development*, 3rd edn. Edward Arnold, London, UK.

Swearingen, J.M. & Diedrich, S. (2000) *English Ivy*. Plant Conservation Alliance, Alien Plant Working Group – updated 4 December 2000 [cited 9 November 2004]. http://www.nps.gov/plants/alien/fact/hehe1.htm.

Thomas, L.K. Jr (1998) Topographic alterations, forest structure, and invasion by English ivy (*Hedera helix* L.) in the Rock Creek Floodplain, Washington, D.C. *Natural Areas Journal*, **18**, 164–168.

Tixier, H., Duncan, P., Scehovic, J., Yani, A., Gleizes, M. & Lila, M. (1997) Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. *Journal of Zoology, London*, **242**, 229–245.

Trémolières, M., Carbiener, R., Exinger, A. & Turlot, J.C. (1988) Un exemple d'interaction non competitive entre espèces ligneuses: le cas du lierre arborescent (*Hedera helix* L.) dans la forêt alluviale. *Acta Œcologia*, **9**, 187–209.

Turton, P.H.J. (1925) Poisoning by ivy. *British Medical Journal*, **ii**, 294.

UK Phenology Network (2001) UK Phenology Network [online] cited 06 June 2001. *Trends in Ivy First Flowering for England/Scotland/Wales/Northern Ireland from 1891 to 1999*. http://www.woodland-trust.org.uk/phenology/.

Utah Bureau of Land Management (2001) *Fire Resistant Plants*. Utah Fire Management Statewide Fire Assessment – updated 3 July 2001 [cited 9 November 2004]. http://www.ut.blm.gov/fire/Assessment/fireresistantplants.html#3.

Vargas, P., McAllister, H.A., Morton, C., Jury, S.L. & Wilkinson, M.J. (1999) Polyploid speciation in *Hedera* (Araliaceae): phylogenetic and biogeographic insights based on chromosome counts and ITS sequences. *Plant Systematics and Evolution*, **219**, 165–179.

Wallerstein, I. & Hackett, W.P. (1989) Inflorescence induction and initiation in *Hedera helix*. *Israel Journal of Botany*, **38**, 71–83.

Ward, L.K. (1988) The validity and interpretation of insect foodplant records. *British Journal of Entomology and Natural History*, **1**, 153–162.

Wareing, P.F. & Frydman, V.M. (1976) General aspects of phase change, with special reference to *Hedera helix* L. *Acta Horticulturae*, **56**, 57–69.

Warr, S.J. (1991) *Woodland ground flora and seed banks in South-West England*. PhD Thesis, Polytechnic South West, Plymouth, UK.

Zimmerman, R.H., Hackett, W.P. & Pharis, R.P. (1985) Hormonal aspects of the phase change and precocious flowering. Encyclopedia of plant physiology new series, Vol. 11 *Hormonal Regulation of Development III: Role of Environmental Factors* (eds R.P. Pharis. & D.M. Reid), pp. 79–115. Springer-Verlag, Berlin, Germany.