

Sambucus nigra L.

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Deciduous shrub or more rarely a small tree to 10 m, often with straight, vigorous erect shoots from the base; branches often arching. Bark brownish-grey, deeply furrowed, corky. Branches containing a white, porous pith. Twigs stout, greyish, with prominent lenticels. Leaves pinnate; leaflets 3–(5–7)–9, 3–9 cm, ovate, ovate-lanceolate or ovate-elliptic; acuminate; serrate; sparingly hairy on veins beneath. Lower pair of leaflets with short stalk (4–5 mm), other leaflets sessile. Petiole 3–4 cm, deeply grooved on the adaxial surface; stipules 0 or very small and subulate. Axillary buds triangular, reddish, 2–3 mm. Foliage and young shoots foetid. Stalk-like extrafloral nectaries (5–10 mm × 1 mm) occur at the base of leaves and leaflets. Inflorescence flat-topped, 10–20 cm diameter, corymbose with 5 primary rays. Flowers 5-merous, actinomorphic; calyx limb very small; corolla rotate with short tube and flat spreading limb; 5 mm diameter, cream-white; fragrant. Anthers extrorse, cream. Style short, with 3–5 stigmas. Fruit a drupe, 6–8 mm, globose, black, rarely greenish, containing 3–5 compressed seeds (for seed sizes and weights, see section VIII(C)). Pollen grains pale yellow, ellipsoidal, densely tuberculated, 31 × 15–16 µm (Knuth Poll. II).

Sambucus (Caprifoliaceae) is a genus of approximately 20 temperate and subtropical species of small trees, shrubs and herbs (Mabberley 1997). Bolli (1994) recognizes only nine, regarding *S. maderensis* Lowe, *S. canadensis* L., *S. palmensis* Link., *S. cerulea* Raf. and *S. peruviana* Humboldt as subspecies of *S. nigra*.

A large number of variants are known in horticulture (Bean 1951). Two forms have repeatedly been recorded as naturalized in Britain. The green-berried form *viridis*, also known as *fructo-albo*, *leucocarpa* and *chlorocarpa*, has been seen by the authors on Fleam Dyke, Cambridgeshire, in 1985 and again in 2001 and was recorded near Sheffield by Ardron & Rotherham (1984). A variety with deeply dissected leaflets (var. *laciniata*) is noted in a number of local floras (e.g. Wolley-Dod 1937; Lousley 1976). The inheritance of

the finely divided leaf character in *Sambucus nigra* was shown to be governed by a single recessive gene by Tobutt (1992). A similar genetic basis was found for the finely divided leaves of *Sambucus canadensis* (var. *acutiloba*) (Way 1965). Crosses were made among 'Aurea', 'Guincho Purple' and 'Laciniata' varieties and between two first-generation selections of *S. nigra*. Segregations showed that dominant genes were responsible for red and yellow leaf colour (Tobutt 1992).

Elderberries are grown on a commercial scale in Denmark as a colourant in juices and home wine kits (Kaack 1990). The selection of four new varieties of *S. nigra* on the basis of bush yield, anthocyanin content, number of upright shoots and flavour was described by Kaack (1989).

Sambucus nigra is native and widespread in the British Isles and continental Europe. It is predominantly a shrub of open areas and woodland edges and is associated with eutrophic and disturbed soils.

I. Geographical and altitudinal distribution

Sambucus nigra is found throughout the British Isles except in parts of northern Scotland (Fig. 1). It does, however, grow in Shetland as an outcast on rubbish tips, and as a garden plant (Scott & Palmer 1987). It also grows in Orkney, on cultivated ground (Bullard 1995). The altitudinal limit given in Fl. Br. Isl. is 460 m. However, Halliday (1997) gives the limit in Cumbria as 470 m. Other regional limits (Alt. Range Br. Pl.) are: 380 m in W. Yorkshire, 410 m in Swaledale (N. Yorkshire) and the Forest of Clun (Shropshire), 440 m on Tal-y-Fan (N. Wales), 310 m in Kerry (W. Ireland) and 350 m in Co. Dublin.

Sambucus nigra occurs throughout western Europe (Fig. 2). Isolated populations occur as far north as 63° N latitude in western Norway (Atl. N.W. Eur.; Godw. Hist.; Lid 1979; Hultén & Fries 1986) and as far as 61° N in Sweden (Atl. N.W. Eur.; Lid 1979; Hultén & Fries 1986). It is not now considered native in Norway but has probably been cultivated since the Middle Ages and was well established by the 1870s (Fremstad & Elven 1999). Continuous populations are restricted to the southern coast of Norway and the western coast of Sweden (Vergl. Chor. III). East of Lithuania, the northern limit is approximately 55° N.

The precise limit of *S. nigra* in southern Europe differs between the maps of Vergl. Chor. III and Hultén

*Abbreviated references are used for many standard works: see *Journal of Ecology* (1975), **63**, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and Stace (1997) for British species.

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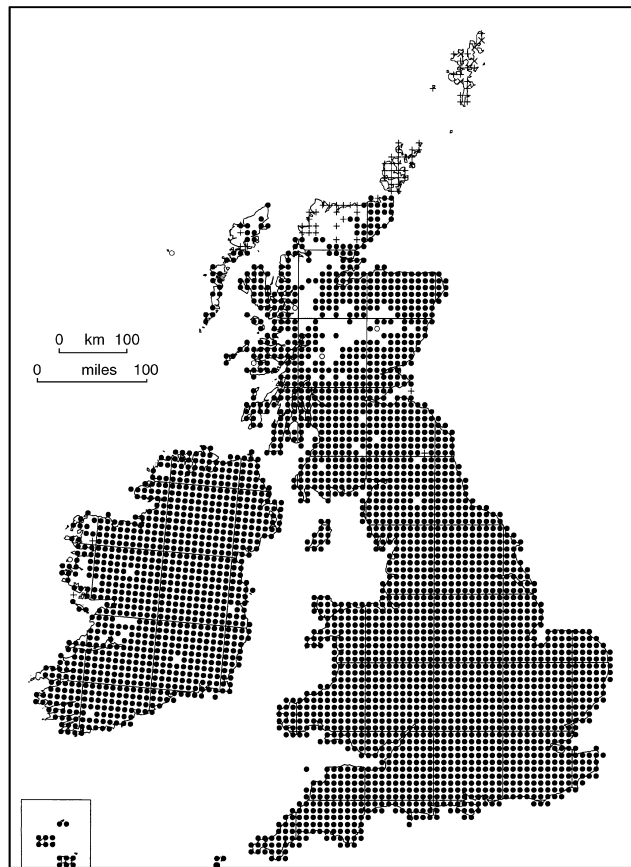


Fig. 1 The distribution of *Sambucus nigra* in the British Isles. Native: (○) pre-1950; (●) 1950 onwards; introduced: (×) pre-1950, (+) 1950 onwards. Each dot represents at least one record in a 10-km square of the National Grid. Mapped by H. R. Arnold, Centre for Ecology and Hydrology, Monks Wood, using A. Morton's DMAP program, mainly from records made by members of the Botanical Society of the British Isles.

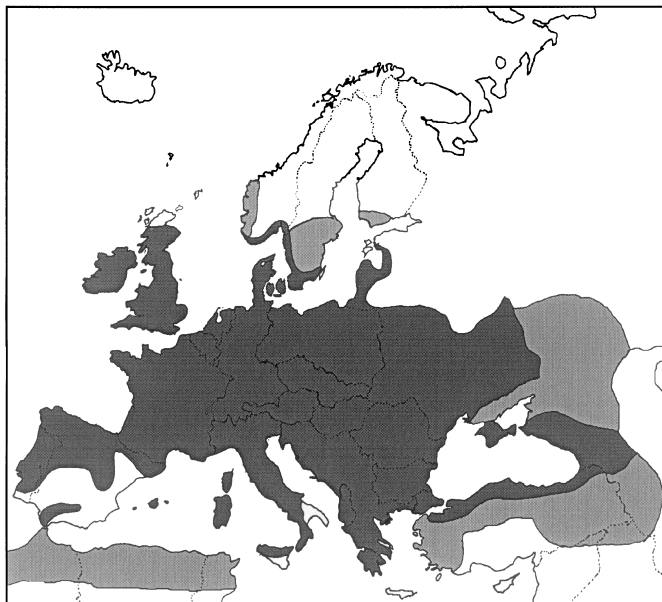


Fig. 2 The native distribution of *Sambucus nigra* in Europe. Compiled from maps in Vergl. Chor. III, Hultén & Fries (1986) and Atl. N.W. Eur. The dark shaded areas represent its continuous distribution. Isolated populations are enclosed within the light shaded regions.

& Fries (1986). The populations in the Atlas Mountains of Morocco, Algeria and Tunisia are thought to be introduced as well as that in the Azores (Vergl. Chor. III). *Sambucus nigra* is present in the northern and

western part of the Iberian peninsula, in Sicily and mainland Greece but is absent from Crete. It occurs sporadically in western and eastern Turkey, particularly in the northern coastal strip. The eastern limit of

its distribution is approximately 55° E. In mountainous regions, *S. nigra* is absent from the higher altitudes, such as above 1500 m in the Alps, 900 m in the Tatra mountains and 2200 m in Morocco (Vergl. Chor. III). It is classified as European Temperate by Preston & Hill (1997).

Sambucus nigra has been introduced into various parts of the world including E. Asia, N. America, New Zealand and the southern part of Australia (Hultén & Fries 1986).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

The distribution limit of *Sambucus nigra* in north-eastern Scotland, the Southern Uplands of Scotland and Upper Teesdale corresponds to a mean October temperature below 7.2 °C (Lennon & Turner 1995). The northern limit of *S. nigra* in Scandinavia, and the eastern limit in Europe, also correspond to approximately this temperature (Leemans & Cramer 1991). A limit related to low October temperatures may indicate that the seeds are unable to mature during the shorter growing season at these high latitudes and altitudes. This is supported by the fact that *S. nigra* does not set seed in Orkney (Bullard 1979) where it grows only where cultivated. The southern limit in Europe and North Africa corresponds approximately to a mean October temperature of 15 °C (Leemans & Cramer 1991).

Although it grows in Shetland, its foliage is often blackened by autumn gales (Scott & Palmer 1987).

Elder occurred at 3% of stations on the Pembrokeshire Coast Path in a survey (Gulliver 1992) of exposed locations (excluding those in more sheltered areas such as bays and inlets). Elder was considered to have moderate to low tolerance to salt-laden winds, in comparison with *Prunus spinosa* (highly tolerant, present at 17.3% of stations) and *Crataegus monogyna* (moderately tolerant, present at 6.8% of stations).

Young plants were slightly more frequent on south-facing than north-facing slopes in the Sheffield region (Grime *et al.* 1988).

(B) SUBSTRATUM

Sambucus nigra is characteristic of disturbed, base-rich and nitrogen-rich soils (Fl. Br. Isl.), and of phosphate-rich soils (Rackham 1986). High levels of available phosphate, available potassium and mineralizable nitrogen were observed in a series of soils from *S. nigra* sites (Table 1). The highest value of mineralizable nitrogen was recorded from a disused chalk quarry in Lincolnshire (sites 1 and 2) where rabbit grazing was evident. Other high levels were observed on a waterlogged soil on a stabilized flood plain (site 5), a domestic garden (site 8) and a scrubland area with a large elder population in a site with demolished buildings (site 11). Sites with the highest levels of available phosphate were the garden (site 8) and a mature, unmanaged hedgerow (site 7). Particularly notable were two sites on a sandy bank of the River Tyne (sites 3 and 4). These had low levels of the three major nutrients, although site 4 had higher levels than site 3, as expected because it was slightly further inland and

Table 1 Physical and chemical characteristics of soils from *Sambucus nigra* sites in England. Soils were collected in April and May 2001, from 0–15 cm depth and 30 cm from a bush. pH was measured on fresh soil (first value) and on the air-dried 2 mm sieved fraction (value in parentheses), using a glass electrode in a 1 : 1 v/v mixture of soil and distilled water. All other determinations were made on the air-dried 2 mm sieved fraction and are means of two replicates. Loss on ignition was measured by heating oven-dried soil at 375 °C for 16 h and expressed as percentage of oven-dried soil (2 mm fraction dried at 105 °C overnight). Available potassium was extracted with pH 7.0 ammonium acetate and estimated by flame photometry (Rowell 1994). Available phosphate was extracted in sodium bicarbonate (Olsen's method) and determined by a phosphomolybdate method (Rowell 1994). Mineralizable nitrogen was extracted in 4 M potassium chloride after anaerobic incubation for 7 days at 40 °C (Rowell 1994) and was determined as ammonia by titration after distillation with magnesium oxide (Chem. Anal.)

Site no.	Location	National Grid Ref.	Habitat	pH	Loss on ignition (%)	Available K (µg g ⁻¹)	Available P (µg g ⁻¹)	Mineralizable N (µg g ⁻¹)
1	Red Hill, Lincs.	TF264806	Chalk quarry	8.0 (7.5)	7.1	581.7	20.5	144.0
2	Red Hill, Lincs.	TF264806	Chalk quarry	7.4 (7.3)	14.8	577.0	27.8	354.0
3	Ovingham, Northbd.	NZ086637	Sandy flood-plain	7.6 (6.4)	1.2	24.0	*	20.0
4	Ovingham, Northbd.	NZ087638	Sandy flood-plain	7.8 (6.8)	4.0	53.5	7.1	46.8
5	Ovingham, Northbd.	NZ090640	Stabilized flood plain	7.7 (6.9)	7.5	34.8	14.9	124.8
6	Low Prudhoe, Northbd.	NZ092639	Solvay process waste	8.7 (7.6)	5.4	200.7	*	86.6
7	Compton, Wolverhampton	SO888988	Hedgerow	4.5 (4.4)	14.0	490.0	192.1	39.2
8	Wolverhampton	SO935006	Garden	6.8 (6.5)	14.4	610.0	87.6	170.3
9	Stourton, Staffs.	SO853854	Woodland margin	4.2 (4.0)	16.8	158.1	62.9	18.5
10	Ashwood, Staffs.	SO872884	Hedgerow	6.5 (6.6)	10.1	350.0	28.8	114.6
11	Tenbury Wells, Herefs.	SO616687	Scrubland	7.0 (6.6)	10.1	340.5	31.3	179.7

*Not detectable.

more stable. Indeed, available phosphate was undetectable in site 3. Presumably, plants here derive their nutrition largely from periodic flooding of the river which brings dissolved nutrients and vegetable material. Generally, levels of available potassium were high, ranging from 24.0 to 610 $\mu\text{g g}^{-1}$. Mean levels of the three nutrients with their associated standard errors were, for all sites; mineralizable N $118 \pm 29.3 \mu\text{g g}^{-1}$, available P $43 \pm 16.9 \mu\text{g g}^{-1}$ and K $310.9 \pm 69.3 \mu\text{g g}^{-1}$. Mean levels for all sites except 3 and 4 were mineralizable N $136.9 \pm 32.7 \mu\text{g g}^{-1}$, available P $51.8 \pm 19.6 \mu\text{g g}^{-1}$ and available K $371.4 \pm 69.4 \mu\text{g g}^{-1}$.

Sodium contents of soils within 30 cm of elder bushes in two coastal sites were measured by flame photometry after aqueous extraction of the 2 mm fraction of air-dried soils for one hour. Values were 644 $\mu\text{g g}^{-1}$ from Middle Head, Mumbles, Swansea (NG ref. SS632872), for a northerly facing seaward slope, susceptible to some sea spray, and 736 $\mu\text{g g}^{-1}$ from Penclawdd, Gower (NG ref. SS547959), for a site c. 3 m above a tidal river bank, in an area which would occasionally be flooded with brackish water. These values suggest at least some degree of tolerance of saline conditions. See also the extremely high soil sodium values associated with industrial waste in Germany (section IV). *Sambucus nigra* exhibited lime chlorosis in six sites surveyed by Grime & Hutchinson (1967).

In the Elbe valley above Hamburg, *S. nigra* grew in soils with mineralizable nitrogen values of between 12.3 and 16 mg of N per 100 cm^3 of soil (total of nitrate and ammonium forms) after the soils had been incubated for 8 weeks at 30 °C (Meyer 1957). To compare these values with the present analyses, bulk densities were estimated from loss on ignition using the relationship of Jeffrey (1970). The mean mineralizable nitrogen of all 11 samples was 9.5 mg per 100 cm^3 of soil. The range of values was 1.2–24.4 mg per 100 cm^3 , consistent with a wide range of habitats.

In submontane broadleaved woodland and scrub in Central Europe, *S. nigra* grows on slightly acid to nearly neutral soils, which are damp to slightly wet (Ellenberg 1988).

Ellenberg's indicator values for British plants assigned to *S. nigra* by Hill *et al.* (1999) were 6 for L (light level: tolerant of partial shade), 5 for F (moisture: mainly on fresh soils of average dampness), 7 for R (soil pH: indicator of weakly acid to weakly basic), 7 for N (nitrogen and general soil fertility level: often found in richly fertile places), and 0 for S (salt tolerance: absent from saline sites). The corresponding levels for Central European *S. nigra* (Ellenberg *et al.* 1991) were L 7, F 5, R value not given, N 9, and S 0. Field observations and the sodium content of soils in the vicinity of coastal elder bushes suggest that *S. nigra* is tolerant of mildly saline conditions.

Experiments on leaf litter decomposition rates were undertaken by Bockock (1964) in which fallen leaves of several species were put in mesh bags, placed on soil and weighed after 27 days. On a mull soil, only 8% of

the dry matter of *S. nigra* leaves and 25% of the original number of leaflets remained. On a moder soil, 24% of the dry matter was left, as was 57% of the leaflets. The total nitrogen content remaining after 27 days was 3% of the original on the mull soil and 22% on the moder. These decomposition rates were the most rapid of all the species tested, the only species with similar rates being *Urtica dioica*. The total nitrogen content of the freshly fallen leaves was 2.94% of dry matter and was among the highest of the species measured.

Similar experiments were carried out by Cornelissen (1996) in which coarse- and fine-mesh bags of leaves from individual species were buried in litter mixture for 8 or 20 weeks. For *S. nigra*, the decomposition rate (expressed as percentage dry weight loss) in fine bags over 8 weeks was 48.6 ± 1.12 ; in coarse bags over 8 weeks, 92.2 ± 7.78 ; in fine bags over 20 weeks, 76 ± 2.59 and in coarse bags over 20 weeks, 100. The decomposition rates were high compared with the majority of species. Both Bockock's and Cornelissen's results demonstrate the extremely rapid decomposition of elder leaves under nearly natural conditions.

III. Communities

As noted in section II (B), *Sambucus nigra* is associated with moderately to highly eutrophic soils. These are often soils subjected to disturbance either naturally as on floodplain terraces and woodland margins, or anthropogenically as in hedgerows, derelict gardens, farmyards and post-industrial wasteland. *Sambucus nigra* tends to be found in open or woodland edge situations. It sometimes occurs under deep shade in woodland but such bushes are often spindly and may often be survivors of former more open conditions.

The communities in which *S. nigra* is found in Great Britain are listed below within the framework of the National Vegetation Classification (NVC).

Sambucus nigra is an important component of *Crataegus monogyna*–*Hedera helix* scrub (NVC code W21) (Rodwell 1991). This community encompasses several of the most characteristic habitats of *S. nigra*, including hedges, derelict agricultural and post-industrial land, and is widespread throughout the British lowlands. *Crataegus monogyna* is the most frequent of the spinose shrubs in this community, followed in frequency by *Rubus fruticosus* agg. and many species of *Rosa*. *Sambucus nigra* is associated particularly with the *Hedera helix*–*Urtica dioica* and the *Mercurialis perennis* subcommunities on more mesotrophic soils and on man-made or fragmentary soils on derelict land where it is often accompanied by *Buddleja davidii*. In the *Brachypodium sylvaticum* and *Viburnum lantana* subcommunities, *S. nigra* is characteristic of locally enriched areas around rabbit warrens on the chalk. Elder is relatively abundant in species-poor hedges and its representation increases very little in species-rich hedges. This is in accord with its ability to colonize disturbed habitats quickly, and with its short life

span (Pollard *et al.* 1974). It is unlikely that elder would be planted in hedges and its appearance is a result of its ability to plug gaps, usually (one presumes) by bird-deposited seed.

Scattered shrubs of *Sambucus nigra* and *Crataegus monogyna* are present in the *Pteridium aquilinum*–*Rubus fruticosus* underscrub (W25), particularly in the *Hyacinthoides non-scripta* subcommunity. This community is dominated by the two constant species, *Pteridium aquilinum* and *Rubus fruticosus*, and commonly results from woodland clearance in agricultural or heath landscapes. The *Hyacinthoides non-scripta* subcommunity is widespread throughout lowland Britain, is most often found in woodland rides and clearings within wood-pasture and often dominates coastal cliff slopes in the south-west.

Sambucus nigra and other shrubs are a sparse component of *Rubus fruticosus*–*Holcus lanatus* underscrub (W24), a widespread community of the British lowlands, typical of abandoned and neglected arable, pasture and gardens.

Sambucus nigra can be prominent in patches, particularly in the more disturbed and enriched areas of *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* woodland (W10). It tends to be more frequent in the north-west, associated with *Fraxinus excelsior*, *Ulmus glabra* and *Acer pseudoplatanus*. It is commoner in the *Acer pseudoplatanus*–*Oxalis acetosella* subcommunity which is restricted to the upland margins of Wales, northern England and Scotland.

In the *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* woodland (W8), *S. nigra* occurs throughout in patches and is locally abundant in more eutrophic conditions. It is more common where older stands have been disturbed or enriched. In the *Geranium robertianum* subcommunity, restricted to the north and west of England, *S. nigra* occurs in a higher frequency throughout, a result perhaps of the higher rate of nutrient turnover that occurs in these better aerated soils. This is in contrast to the stands in the south-east where *S. nigra* is very much an indicator of local enrichment and disturbance.

Alnus glutinosa–*Urtica dioica* woodland (W6) is a community of eutrophic moist soils dominated by *Alnus glutinosa*, *Salix* spp. and *Betula pubescens*. Scattered bushes of elder dominate the shrub layer in the *S. nigra* subcommunity, which is particularly characteristic of sites of substantial deposition of mineral matter, such as on alluvial terraces or where enriched waters have flooded fen peats. Although moist enough for *Alnus glutinosa* to remain the dominant in all but the driest stands, the soils are in the most part dry towards the surface in the summer. This community is widespread but local throughout the lowlands.

Sambucus nigra is one of the common elements of the shrub layer of *Fagus sylvatica*–*Mercurialis perennis* woodland (W12) along with *Corylus avellana*, *Crataegus monogyna*, *Acer campestre* and *Ilex aquifolium*. *Fagus sylvatica* is always the most abundant tree. This is a

community of base-rich calcareous soils on the limestone scarps of south-east England.

Where fires have occurred in mesophytic or calcicolous woodland, on railway embankments or derelict land, the *Acer pseudoplatanus*–*Sambucus nigra* subcommunity of the *Epilobium (Chamerion) angustifolium* community (OV27) often occurs (Rodwell 2000). This community is overwhelmingly dominated by *Chamerion angustifolium*, *Rubus fruticosus* and *Pteridium aquilinum*, and the woody species usually present are *S. nigra*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Fagus sylvatica* and *Ulmus glabra*. This community is widely distributed throughout the British lowlands.

Alnus glutinosa–*Fraxinus excelsior*–*Lysimachia nemorum* woodland (W7) has a somewhat open canopy with *Alnus glutinosa* as the only constant tree. *Sambucus nigra* is most frequent in the *Urtica dioica* subcommunity where *Fraxinus* can be frequent. The understorey consists of *S. nigra*, *Salix cinerea* and saplings of *Acer pseudoplatanus*. The *Urtica dioica* subcommunity has eutrophic soils enriched by repeated deposition of material by flooding or flushing, but typically not so enriched as in W6 *Alnus*–*Urtica* woodland. This community has a wide but local distribution throughout the upland fringes of the north and west as well as the wetter parts of southern England.

Sambucus nigra occurs sparsely and at low frequency in *Fraxinus excelsior*–*Sorbus aucuparia*–*Mercurialis perennis* woodland (W9), found in the wetter and cooler parts of Wales, west Scotland and north-west England.

Sambucus nigra forms only a sparse and occasional component of the shrub layer of *Fagus sylvatica*–*Rubus fruticosus* woodland (W14), a type of beech wood confined to southern England, particularly well represented in the Chilterns and the New Forest. Elder is one of the few shrubs to be found in *Taxus baccata* woodland (W13), a community largely restricted to the chalk of the North and South Downs. Here the shrubs almost always reflect past association with rabbits.

Hippophaë rhamnoides dune scrub (SD18) is a community of less mobile sand dunes around the coasts of Britain, being particularly well established on the east coast and has become naturalized in scattered localities between Devon and Cromarty (Rodwell 2000). *Hippophaë rhamnoides* is the dominant and the only constant species in this community. *Sambucus nigra* occurs in the more mature and denser *H. rhamnoides* stands, where it reflects the more nitrogenous soils which may be the result of nitrogen fixation by the root nodules of *H. rhamnoides* (Pearson & Rogers 1962).

A provisional phytosociological catalogue of Irish vegetation (White & Doyle 1982) indicates communities in which *S. nigra* is a characteristic species. *Polystichum viridis* is an association of damp walls, paths, canal banks and drains on nitrate- and phosphate-rich substrates. Diagnostic species include *Phyllitis scolopendrium* and *Sagina procumbens*. *Sambucus nigra* and *Buddleja davidii* often occur here.

The association *Salicetum albo-fragilis* is a community of riversides, marshy woodland edges, ditches and hedges (White & Doyle 1982). Elder occurred in fewer than 20% of samples of this community (Kelly & Iremonger 1997).

The class *Rhamno-Prunetea* is a woodland margin and hedgerow vegetation of bushes and shrubs interspersed with climbers. The class character species are *Rubus* spp., *Sambucus nigra* and *Ribes uva-crispa*. The association *Primulo-Crataegetum*, of this class, has the diagnostic species *Crataegus monogyna*, *C. laevigata*, *Rubus* spp., *Prunus spinosa*, *Rosa canina*, *Rhamnus cathartica* and *Ligustrum vulgare*. Many hedgerows can be ascribed to this association (White & Doyle 1982), and a map of hedges with *Crataegus*, *Prunus spinosa*, *Fraxinus* and *Sambucus* is given by O'Sullivan & Moore (1979). These are largely distributed throughout the southern part of Ireland from Meath southwards and as far west as Tipperary. Another group of hedgerow communities is included in the alliance *Sambuco-Salicion capreae*, with the diagnostic species *Sambucus nigra*, *Salix caprea*, *Rubus idaeus* and *R. nes-sensis* (White & Doyle 1982). The alliance *Alno-padion* encompasses species-rich alder woods. The presence of *S. nigra* and other nitrophilous species distinguishes this alliance from the *Carpinion betuli* alliance (White & Doyle 1982). *Corylo-Fraxinetum* is an association of the alliance *Alno-padion*. This is a community of base-rich free-draining soils over limestone. Of 41 samples of this type of woodland, *S. nigra* occurred in only 2 (Kelly & Kirby 1982).

Sambucus nigra was present in fewer than 20% of stands of *Betuletum pubescentis*, a community of deep acid peat relatively well-drained in the upper layers (Kelly & Iremonger 1997). It corresponds with the *Dryopteris dilatata-Rubus fruticosus* subcommunity of the NVC W4 (*Betula pubescens-Molinia caerulea* woodland) (Rodwell 1991).

The vegetation of Central Europe is described in great detail by Ellenberg (1988) from which the following account is summarized.

Sambucus nigra is a variable component of brown-mull beech woods (suballiance *Galio odorati-Fagion*), the commonest type of beech wood in Central Europe whose soils range from rich to poor brown mulls. These woods typically have a high, dense canopy and do not normally have a well developed shrub layer.

Mixed woodland rich in sycamore and ash is a widespread community type. Fertile soils are dominated by *Acer pseudoplatanus*, *A. platanoides*, *Tilia platyphyllos*, *Ulmus glabra* and *Fraxinus excelsior*. These are in deep, damp soils on or at the foot of slopes. *Sambucus nigra* is often here associated with *Urtica dioica*, *Aegopodium podagraria*, *Silene dioica* and *Impatiens noli-tangere* on soils rich in bases and nutrients, especially nitrate.

Oak-hornbeam woods are a community of relatively dry climatic areas from Würzburg in the west as far as the central and eastern plains of Poland. *Sambucus nigra* is a variable component of the variants

of *Stitchwort-Oak-Hornbeam* and *Bedstraw-Oak-Hornbeam* woods with damper soils.

In river valleys of the lowland regions throughout Central Europe, woodlands of various mixtures of willow, poplar, elm and oak are the characteristic communities of flood plains. Elder is commonly found in many of these communities. On flood plains in the alpine coniferous region, grey alder (*Alnus incana*) woodlands predominate. *Sambucus nigra* is among the species here which can tolerate wet conditions.

Another vegetation type with a Central European distribution is the *Robinia pseudacacia-Sambucus nigra* association of which three regional variants are described by Klauck (1988). The Western variant, found in the Rhine and Saar Valleys, Vosges and Lorraine has *Acer pseudoplatanus*, *Carpinus betulus*, *Fraxinus excelsior* and *Quercus petraea* as its major constant tree species. The Central European variant, whose major constant trees are *Acer pseudoplatanus* and *Prunus serotina*, is distributed principally in north-eastern Germany. The eastern variant, centred on the Czech Republic, Slovakia and Hungary, has the constant tree species *Crataegus curvisepala*.

Many species of bryophytes and lichens are epiphytic on *Sambucus nigra* with *Cryphaea heteromalla* (Hedw.) Mohr, *Zygodon viridissimus* (Dicks.) R. Br. and *Orthotrichum affine* Brid. being particularly abundant (Watson 1981). In a transect survey of epiphytic bryophytes across southern Britain, *Sambucus nigra* held 17% of all epiphyte records, and was the species which accounted for the second greatest number of records, exceeded only by *Fraxinus excelsior* (Bates *et al.* 1997). It also has a distinctive lichen flora, with *Xanthoria parietina* (L.) Th. Fr. and *Physcia aipolia* (Ehrh. ex Humb.) Fűrnr. being particularly characteristic. This epiphyte richness is probably due to the fact that elder bark has one of the highest water-holding capacities of any tree or shrub measured; between 371% and 465% of dry weight (Barkman 1958). Its bark is moderately acidic: pH between 5.7 and 7 (Barkman 1958).

IV. Response to biotic factors

ESTABLISHMENT

Elder will not establish where there is a turf. For example, grazing of chalk grassland at Ramsdean Down (Hampshire) may have kept the turf intact. Only after sheep grazing was discontinued around 1914 did the effect of rabbit scraping and frost begin the break-up of the turf. By 1940 a full invasion of elder had occurred (Hope-Simpson 1941). *Sambucus nigra* is, however, capable of establishing in a closed shrub canopy (Gilbert 1991), partially as a result of leafing earlier than most tree and shrub species. A study of the population dynamics of seven woody species in the Voorne dunes (near Rotterdam) showed that *S. nigra* was the only species to show a population curve without discontinuities. Most of the species showed a lack of recruitment

in the 1960s and 1970s; in contrast *S. nigra* showed a continuous curve, which was very nearly linear when the numbers of individuals were plotted on a logarithmic scale (van der Maarel *et al.* 1985). This indicates a continuous recruitment of *S. nigra* seedlings, and that mortality was independent of age.

Sambucus nigra was an occasional weed of winter cereals, probably brought to the field by birds. It grew better in plots treated by reduced cultivation and by direct drilling (Pollard & Cussans 1976, 1981).

CONTROL

Sambucus nigra often invades hedges and is often regarded as undesirable (Marshall 1989). It was consistently controlled by 2,4,5-T and ammonium sulphamate (Fryer & Makepeace 1978). In trials in which 2-year-old seedlings of *S. nigra* were grown in pots and treated in June with half and full recommended rates of 15 herbicides and three plant growth regulators, Marshall (1989) noted that all plants treated with mecoprop, fluroxypyr and full rates of clopyralid and glyphosate were killed. Four months after application, vigour was reduced by the broad-leaved weed herbicides 2,4-D, fluroxypyr, ioxynil + bromoxynil and clopyralid, by glyphosate and by the highest rate of the plant growth regulator mefluidide.

TOXICITY AND PALATABILITY

Sambucus nigra leaves contain cyanogenic glycosides (see section VI(F)) from which hydrogen cyanide is released by enzyme action. Although *S. nigra* is not generally considered poisonous, isolated cases of poisoning in animals and man have been reported after eating the bark, leaves, berries, roots and stems (Cooper & Johnson 1984). Two individuals of Jardine's Parrot died as a result of poisoning by elder leaves (Griess *et al.* 1998); these authors review the literature on the toxicity of elder and the cyanogenic glycosides, sambunigrin, zierin and holocalin. The numbers of insect species reported on elder is low compared with other woody species (see section IX(A)), and the presence of cyanogenic glycosides may in part explain this. The leaves, however, can be relatively palatable as shown by Edwards *et al.* (1986) who observed that 272 mg of undamaged *S. nigra* leaf material was eaten by the larvae of *Spodoptera littoralis* (Boisd.) over a 48-h period. This was a relatively high palatability in an experiment in which the lowest was shown by *Populus tremula* (42 mg) and the highest by *Tilia × vulgaris* (420 mg). Leaves damaged by punching 1 mm² holes at 5 mm intervals were less palatable to the larvae than undamaged leaves collected from a different part of the canopy (Edwards *et al.* 1986). This effect was apparent when the leaves were removed for testing 14 days after damage, but not 2 days after damage. A similar pattern was observed when leaves adjacent to damaged leaves were tested. The bark contains many toxic lectins and

ribosome-inactivating proteins (see section VI(F)). Toxic type 2 ribosome-inactivating proteins account for around 80% of the total bark protein (Van Damme *et al.* 1997b). Clearly, many defensive compounds are present in the various tissues of elder. These have a role to play in the complex interactions between plant and herbivore which are increasingly being uncovered (Schultz 2002).

Rabbits are generally acknowledged to find elder unpalatable (Tansley, Br. Isl.; Fl. Br. Isl.; Gulliver 1992). However, a study of the relative palatability to deer of 16 trees and shrubs in a deciduous forest in southern Poland (Bobek *et al.* 1979) showed that *S. nigra* was one of the three most palatable species in the three types of forest studied.

RESPONSE TO POLLUTION

Sambucus nigra was resistant to severe pollution from a phosphate fertilizer factory in Germany. Soil pH was raised from 6.5–7.5 to 8.0–9.0, soil fluoride increased to 200 p.p.m. above normal levels and soil sodium content was more than 500 mg per 100 g soil (Heinrich & Schaller 1987). *Sambucus nigra* had low sensitivity to periodic exposures to ozone (0.2 p.p.m. for 5 h) throughout the growing season of 1976 (Davis *et al.* 1981). It was also very resistant to damage by gas and dust from a Polish copper smelter. The soil pH was 4.9, the concentration of copper 1240 p.p.m and lead 430 p.p.m. and the gaseous emission from the smelter was rich in sulphur dioxide. After 5 years of observations, 54.4% of *S. nigra* trees had survived. The mean leaf injury rate for *S. nigra* was 9%, the second lowest rate from 31 species (Rachwal 1983).

Sambucus nigra pollen is very sensitive to the acidity of the germination medium. In tests devised to simulate acid fog or mist, Paoletti & Bellani (1990) incubated fresh pollen in a standard medium with added acids to adjust the pH. Reduction in pollen germination percentages and pollen tube lengths were measured. Reduction in both was 10% at pH 5.0. At pH 4.0, germination had fallen by 87% and tube growth by 91%. These are averages over the six different acid treatments at each pH. At pH 3.0 no germination or growth occurred. Pure sulphuric acid was more damaging than pure nitric acid, but a ratio of two parts sulphuric to one part nitric acid caused the greatest reduction in the two variables.

V. Response to environment

(A) GREGARIOUSNESS

Sambucus nigra commonly invades hedgerows and pockets of eutrophic soils in urban habitats, although it rarely dominates. It often occurs in woodland margins and can reach ages of at least 25 years and quite high numbers in such situations. Large more-or-less even-aged stands of elder often occur where it has colonized

open areas such as abandoned farmyards and other areas on enriched soils, such as an extensive stand covering several hectares on the banks of the River Severn at Preston Montford, Shropshire. It can form thickets on the chalk downs (Wolley-Dod 1937), as on dumps of top-soil removed for quarrying.

Sambucus nigra accounted for 10% of the total number of trees in a survey of riparian communities in East Anglia (Mason & Macdonald 1990). Surveys of 50 1-km stretches of river showed that *S. nigra* had a mean density of 7.3 shrubs km⁻¹ and that 62.8% of the *S. nigra* plants were saplings. The majority of river stretches had between 1 and 10 elder plants km⁻¹ (62%); 16% of stretches had less than 1 plant km⁻¹, 10% had 10–20 plants km⁻¹, 10% had 20–30 plants km⁻¹ and 2% had 30–40 plants km⁻¹.

(B) PERFORMANCE IN VARIOUS HABITATS

A number of measures relating to the growth and leaf attributes of the seedling were recorded by Cornelissen *et al.* (1996). The values are based on 28 seedlings grown from seed from the Sheffield region. Seedlings were grown in a 14-h day regime with fluctuating day/night temperatures of 20–22 °C/15–17 °C, with 135 μmol m⁻² s⁻¹ of photosynthetically active radiation. The mean relative growth rate (RGR) of seedlings was 0.139 ± 0.0039 day⁻¹. Other leaf growth values measured were: leaf area ratio *sensu stricto* 17.4 ± 0.70 mm² mg⁻¹, leaf area ratio (using area of leaves plus leafy cotyledons) 19.03 ± 0.6 mm² mg⁻¹, leaf weight fraction *sensu stricto* 0.527 ± 0.014, leaf weight fraction (using leaves plus leafy cotyledons) 0.601 ± 0.009, specific leaf area 33.01 ± 1.08 mm² mg⁻¹, leaf saturated (turgid) weight/leaf dry weight 5.98 ± 0.17 and specific saturated leaf area 5.54 ± 0.17 mm² mg⁻¹.

Measurements were carried out on *Sambucus nigra* bushes on the Island of Hiddensee (off the north coast of Germany, 54°31' N, 13°8' E) which has particularly variable wind speeds (Steubing 1962). The specific leaf area on the windward side of a bush was 3.98 mm² mg⁻¹ and on the leeward side 4.31 mm² mg⁻¹. Measurements of specific leaf area (SLA) are summarized in Table 2. The specific leaf area of seedlings was very similar to that of mature bushes. Most bushes had a saturated

SLA of about 5 mm² mg⁻¹. The major exception to this was the bush at Ashwood, Staffordshire, in a clipped hedge in which the sampled leaves were very large and thick.

Elder growing on brick rubble had a mean height increment of 37 cm year⁻¹ (mean of 25 shrubs) (Gilbert 1991). A plant growing in a semi-shaded position in a garden in Wolverhampton had a mean annual radial increment of 4.0 mm.

(C) EFFECTS OF FROST, DROUGHT, ETC.

The loss of 85% of the water content of leaves led to the death of half the leaves and loss of 68% of fresh weight (Levitt 1980). *Sambucus nigra* is very susceptible to embolism and loss of conductivity in the xylem vessels but can refill the vessels and restore conductivity during periods of rain (Vogt 2001).

Bud-break may occur during warmer spells in winter, but leaves are often subsequently killed by severe frosts (Grime *et al.* 1988). Shoots which arise late in the growing season are often killed by cold winter weather (Metcalf 1948).

VI. Structure and physiology

(A) MORPHOLOGY

Young plants of *Sambucus nigra* have numerous branches arising from the base. Many of these branches subsequently branch again and form new shoots. However, new shoots may arise from the base, a form of growth induced by low temperatures (Barnola 1972) (see section VI(E)). After an age of 20–30 years, basal regeneration often stops and a single trunk becomes dominant (Bolli 1994).

The adaxial surface of the leaf is devoid of stomata. The stomatal density on the abaxial surface was reported by Weiss (1865) as 91 mm⁻². Stomatal densities of *S. nigra* leaves from around Berlin were given by Schramm (1912): juvenile plant, primary sun leaves (77 mm⁻²); juvenile plant, secondary sun leaves (138 mm⁻²); mature plant, sun leaves (165 mm⁻²); mature plant, shade leaves (71 mm⁻²). Recent estimates (means of five measurements) from single leaves of three plants, by

Table 2 Measurements of specific leaf area from *Sambucus nigra* bushes, with standard errors

Site	Specific leaf area (mm ² mg ⁻¹)		Reference
	Dry	Saturated	
North Yorkshire		5.1	Kovář <i>et al.</i> (1996)
South Yorkshire	33.01 ± 1.08	5.54 ± 0.17	Cornelissen <i>et al.</i> (1996)
Ashwood, Staffordshire	16.6 ± 0.7	3.3 ± 0.1	This study
Wolverhampton	26.8 ± 2.0	5.5 ± 0.2	This study
Wolverhampton	25.2 ± 0.9	5.2 ± 0.1	This study
Estonia	18.1		Niinemets (1996)
North Germany		4.15	Steubing (1962)
North-west Italy	23.8 ± 1.7		Salleo <i>et al.</i> (1997)

the present authors, were 56 mm^{-2} (semi-shaded sapling, Wolverhampton), 28 mm^{-2} (deeply shaded bush in woodland, Long Ashton, Bristol) and 59 mm^{-2} (bush on edge of woodland, Long Ashton, Bristol). Clearly, stomatal densities are very variable, although they are evidently smaller in shaded leaves.

In a survey of 60 tree and shrub species in Estonia, Niinemets (1996) found that leaf dry weight per projected surface area (LWA) was higher in shrubs with a high light demand. The mean area of the leaf (or leaflet in the case of *S. nigra* and other shrubs with compound leaves) (*S*) was negatively correlated with LWA. Increasing LWA would increase the load on the petiole. Thus decreasing *S* with increasing LWA may indicate an adaptive modification, avoiding the higher costs of leaf support. The values for *S. nigra* of LWA ($55.2 \pm 5.7 \text{ g m}^{-2}$) and *S* ($6.0 \pm 1.2 \text{ cm}^2$) were approximately in the middle of the range for shrubs.

A comparative study of the leaf anatomy of *S. nigra* and *S. racemosa* (Filipescu & Moțiu 1984) highlights similarities and differences between these species. In the petiole, the collenchyma immediately below the epidermis is continuous in *S. racemosa* but is organized in discrete, thick segments in *S. nigra*. The number of cells containing oxalic acid crystals is greater in the abaxial parenchyma particularly at the base of the petiole in *S. nigra*, whereas in *S. racemosa* they are principally in the central parenchyma at the median and basal levels in the petiole. *Sambucus nigra* also had mechanical cells associated with the vascular bundles and tannin-containing cells in the parenchyma, both of which were absent in *S. racemosa*. Tannin-containing cells were observed by Szuleta (1937) in the pith of *S. nigra*. Occasional stomata were present on the adaxial surface of the petiole of *S. nigra*, particularly on the side of the prominent groove (Filipescu & Moțiu 1984). Unicellular hairs, long in *S. nigra* and short in *S. racemosa*, were scattered on the epidermis. On the upper (adaxial) surface of the lamina of *S. nigra*, Filipescu & Moțiu (1984) observed that the epidermal cells were polygonal and that those on the lower (abaxial) surface had sinuous margins; in *S. racemosa*, epidermal cells on both surfaces were sinuous. The present authors have observed, in a single plant in the West Midlands, that the cell margins on the upper leaf surface were considerably less sinuous than those on the lower surface. Air spaces between the parenchymatous cells were larger in *S. racemosa* than in *S. nigra*.

Stalk-like extrafloral nectaries reaching up to 10 mm long occur in the nodal regions of the stem between the bases of the leaves, and also at the bases of leaflets (Fahn 1987). They were commoner on the leaves near the inflorescences and absent from the lower leaves.

Stipules are absent on the first two pairs of leaves which develop from hibernated buds in spring (Neubauer 1977) and are also lacking in late developed leaves on long shoots at the end of summer as well as on leaves closely below inflorescences (Neubauer 1977).

Very large leaves with an unusual morphology may grow from the top of cut hedgerow bushes. These often have an extra pair of small leaflets between one pair of leaflets and the next, in places where extrafloral nectaries often occur. There is a range of morphology of these small leaflets.

Plank (1976a) provided a comprehensive account of the anatomy of *S. nigra* wood. The wood of stem and root are histologically similar. Living fibres are predominant and the vessels are diffuse-porous and of small diameter, although the vessels in the roots are larger ($85 \pm 55 \mu\text{m}$) than those in the stem wood ($40 \pm 20 \mu\text{m}$). *Sambucus nigra* forms heartwood after 6–10 years (Plank 1976a). The variation in nuclear dimensions and DNA content of cells in the sapwood was discussed by Plank (1976b). The largest nuclei in the stem appeared in March and in the roots in May.

Micrographs and descriptions of the anatomy of the root of *Sambucus nigra* are given by Cutler *et al.* (1987), and of the stem wood by Metcalfe (1948).

(B) MYCORRHIZA

Vesicular-arbuscular mycorrhizas have been recorded in the British Isles (Harley & Harley 1987). They were recorded in Poland in Domaszyn near Wrocław, by Truszkowska (1953) and reported as rare in the beech forests near Szczecin, by Dominik (1957). Mycorrhizas were not observed on *S. nigra* in a study of post-war ruins in the city of Wrocław (Frydman 1957). No ectotrophic mycorrhizal fungal associates of *Sambucus* were reported by Trappe (1962).

(C) PERENNATION: REPRODUCTION

Microphanerophyte. Overwintering bushes are usually completely leafless although this species can break leaf in midwinter in the south of England (Edlin & Nimmo 1956; Grime *et al.* 1988). All plants are usually stripped of berries by birds by early November.

The oldest plant recorded in a population on a dune system in the Netherlands, on which grazing had ceased in the nineteenth century, was 44 years old (van der Maarel *et al.* 1985). Elders with 23 annual rings (from a canalside woodland edge in Staffordshire) and 25 rings (from a roadside verge in south Northumberland) were recorded by the authors.

Elder usually flowers in its third or fourth year, rarely in its second (Bolli 1994). The first crop of fruit was taken from 4-year-old bushes (Kaack 1988). Most shrubs produce copious amounts of fruit and viable seed every year (see section VIII(C)), the exception being shrubs growing in deep shade inside woodland which may produce few or no flowers.

Shoots grow readily from cut and burned stumps (Metcalfe 1948). Adventitious roots began to emerge about 9 days after *S. nigra* shoot cuttings were taken, and ceased to emerge after about 25 days (Wilson & Wilson 1977). Roots were confined to the basal 1 cm of

the cutting. If this region was cut off repeatedly after roots had developed, the mean number of roots growing on each subsequent occasion declined (from 38.0 to 32.4 to 31.6). When roots were continuously removed as they emerged, new roots continued to emerge until the end of the experiment. The authors concluded that the rate of root initiation falls in proportion to the number of roots already present. Wilson & Wilson (1977) also noted that *S. nigra* cuttings will not root unless leaves are present.

Root cuttings of *S. nigra* did not produce any shoots during the course of a 15-month experiment. Only *S. nigra* and *S. racemosa* produced no shoots among a total of 11 species of shrubs (Göttsche 1978).

(D) CHROMOSOMES

Chromosome number $2n = 36$ from a plant in Leicestershire (Hollingsworth *et al.* 1992). Other counts from non-British material agree (Tischler 1950; Hounsell 1968; Ourecky 1970; Benko-Iseppon & Morawetz 1993). The chromosomes vary in length from 3.5 to 6.5 μm ; there are 4 metacentric, 5 submetacentric and 6 acrocentric, 1 telocentric and 2 satellited pairs of which one is submetacentric and the other acrocentric (Benko-Iseppon & Morawetz 1993). However, only one satellited pair was noted by Hounsell (1968) who reported the longest pair as 7.9 μm and the shortest as 3.5 μm . A composite karyotype was constructed for seven species of *Sambucus* with $2n = 36$ (including *S. nigra*) by Ourecky (1970) which was similar, but only one satellited pair was noted. The difference may have been due to a higher degree of chromatin condensation. Cold-induced regions in the chromosomes of *S. nigra* were reported by Benko-Iseppon & Morawetz (1993). The 2C nuclear DNA amount was recorded as 3.1 pg by Grime *et al.* (1988).

(E) PHYSIOLOGICAL DATA

Nutrition

In a pot experiment run for 50 days (Pigott & Taylor 1964) with nine replicates, *Sambucus nigra* responded positively to the addition of phosphorus to soil, but growth was not significantly affected by the addition of nitrogen alone. In control pots, on a soil from Buff Wood, Cambridgeshire, the dry weight was 96 ± 20 mg. With addition of calcium dihydrogen orthophosphate alone the dry weight was 264 ± 25 mg and with addition of ammonium nitrate alone it was 86 ± 1 mg.

A study of the effects of rhizospheric bicarbonate on uptake, root assimilation, shoot allocation of nitrate and growth rate, was carried out by Wanek & Popp (2000), in order to test the hypothesis that increased levels of root-available inorganic carbon would stimulate growth. Clonal saplings of elder were grown hydroponically for 35 days in a nutrient solution containing 0, 0.5 and 1 mM potassium bicarbonate.

Neither net nitrate uptake nor carbon isotope discrimination showed any significant relationship with level of bicarbonate. Elder plants exhibited significant increases in root nitrate reduction (from 44% to 66%), and in root nitrate accumulation (from 6% to 25%) when subjected to 1 mM bicarbonate. The translocation of nitrate to shoots decreased from 50% to 8% of net nitrate uptake. The increase in relative growth rates, 7%, was not significant.

Very high levels of nitrate reductase activity (4.7 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight) were found in *S. nigra* leaves in March when the leaves expanded, consistent with the high rate of nitrate utilization of a nitrophilous species (Clough *et al.* 1989). This was followed by a swift fall to 1.4 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight in April, a rise to 2.9 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight in late May and a subsequent steady decline to around 0.72 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight in late September. The authors speculate that the initial high activity was because of high light availability for photosynthesis due to the lack of a canopy of other species, as elder is one of the earliest woody plants in leaf. Further studies of nitrogen reductase activity by Pearson & Ji (1994) showed that it remained high from late April to late May (12.5 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight) and then declined steadily to 0.36 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight by the last sampling date. These levels of nitrate reductase activity were approximately a factor of 10 higher than those in *Aesculus hippocastanum* and a factor of 100 higher than those in *Carpinus betulus* and *Quercus petraea*. Glutamine synthetase in *S. nigra* leaves was present in two isoforms: GS₂ (the chloroplastic isoform) was present at high level (125 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight) at the earliest sampling date (27 May) and fell to 4 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight by the last sampling date (11 November). Meanwhile GS₁ (the cytosolic isoform) started at zero on 27 May and rose to 17 $\mu\text{mol h}^{-1} \text{g}^{-1}$ fresh weight by 11 November. This supports the idea that GS₁ has an important role in the mobilization of nitrogen for translocation or storage. The two isoforms of GS were further characterized by Woodall *et al.* (1996).

Ammonium, nitrate and pH levels were higher in *S. nigra* leaves than in other hedgerow species in a survey of hedges in North Yorkshire (Kovář *et al.* 1996). Measurements made on 10 g of fresh material were pH 6.21, ammonium 10.0 p.p.m. and nitrate 75.6 p.p.m. The concentration of total nitrogen was 3.81% and of phosphorus 0.307% in samples of *S. nigra* leaves from around Salamanca in western Spain (Escudero *et al.* 1992).

Allen (1989) gives the following values for chemical composition of *S. nigra* leaves: N 2.2, K 1.9, P 0.17, Ca 0.70, Mg 0.28 and Na 0.02% dry weight and Fe 150, Mn 100, Zn 30 and Cu 8 $\mu\text{g g}^{-1}$ dry weight.

Growth and development

Barnola (1972) examined the nature of apical and basal dominance and their role in determining the shape of *S.*

nigra bushes. Young plants grown from seed were placed in growth chambers under different conditions. Those kept at 25 °C under 16-h days or continuous light demonstrated rapid growth with periods of intense growth alternating with short periods of slower growth, but there was no basal growth. When the apex was removed, it was the most apical nodes which developed. Plants grown at 25 °C in a day period and 12 °C in a night period, either under long (16 h) or short (8 h) days, grew more slowly than the plants kept at constant temperature. After several months all the plants showed some growth from basal nodes. The cool nights induced the type of growth seen in naturally grown bushes. The fixation of basal growth was observed when plants which were grown at 25 °C in long days were transferred to 12 °C under long days. If this period at 12 °C exceeded 4 weeks, the plants continued basal growth indefinitely after they were returned to 25 °C. If, however, the period at 12 °C was less than 4 weeks, basal growth ceased after returning the plants to 25 °C. Complementary experiments on branches and excised buds from different parts of branches and in different months were also carried out. Buds were excised in September from the lower, middle and upper parts of a current year's branch and incubated at a range of temperatures for 30 days. At all temperatures less than 25 °C, a much greater proportion of buds from the lower region burst than from the middle and upper regions. At 15 °C (the maximum difference), 19/20 buds burst from the lower and 3/20 from the upper region. The difference between the growth of *in situ* buds on removed branches from the basal part of the shoot and those from the upper part increased after December and was double by April.

Sambucus nigra is unusual in that after the removal of apical dominance, by excising the apical bud, the rate of elongation of distal axillary buds does not increase until 10 days later. It is not until 3 weeks after excision of the apical bud that the rate of initiation of bud primordia increases (Champagnat *et al.* 1979).

Fruit ripening

Physiological changes during fruit ripening of four cultivars 'Samdal', 'Sampo', 'Samidan' and 'Samyl' were monitored by Kaack (1990). Titratable acid content declined in all four cultivars as ripening progressed. Anthocyanin and soluble solids contents increased.

Changes in amino acid concentration and composition during the ripening and senescence of *S. nigra* fruit were followed by Künsch & Temperli (1978). The ripening period was characterized by a steady decrease of total (bound and free) amino acid content from 2.02 g N per 100 g dry weight in green fruit to 1.28 g N per 100 g dry weight in ripe fruit. Total free amino acid content declined initially and then rose to maturity. This was due primarily to increases in leucine, tyrosine and phenylalanine, the predominant free amino acids in

the fully developed fruit. Senescence was characterized by a marked increase in all levels of free amino acids and a slight decrease in levels of the bound amino acids.

Response to shade

Photosynthetic measurements were made on glasshouse-grown seedlings of *Sambucus nigra* (Kollmann & Reiner 1996) with relative humidity at a constant 60%, vapour pressure deficit 5 g m⁻³ at 15 °C and 9 g m⁻³ at 25 °C. Illumination was provided by fluorescent lamps. *Sambucus nigra* was shown to be relatively light demanding, with high light compensation points (13.7 µmol m⁻² s⁻¹ at 15 °C and 17.9 µmol m⁻² s⁻¹ at 25 °C); moderately high photosynthetic capacities (11.6 ± 0.6 µmol CO₂ m⁻² s⁻¹ at 15 °C and the corresponding saturating irradiance 491 µmol m⁻² s⁻¹ and 12.5 ± 1.3 µmol CO₂ m⁻² s⁻¹ at 25 °C and the corresponding saturating irradiance 444 µmol m⁻² s⁻¹); and high dark respiration (-0.63 ± 0.06 µmol CO₂ m⁻² s⁻¹ at 15 °C and -1.28 ± 0.07 µmol CO₂ m⁻² s⁻¹ at 25 °C). However, quantum efficiency near saturated photosynthesis was rather high (24 µmol CO₂ mol⁻¹ at 15 °C and 28 µmol CO₂ mol⁻¹ at 25 °C). Thus, from these measurements, *S. nigra* had a low shade tolerance but its response to light was surprisingly high.

Water relations

Leaves reached their vital resistance limit (10% leaf area necrotic) at approximately 50% leaf water saturation deficit (LWSP). Lethal limit (50% leaf area necrotic) was reached at 70% LWSP. In early summer, the leaves needed 14 h to reach the vital resistance limit. This time was reduced with the progressing season (Linnenbrink *et al.* 1992). Differences in osmotic potentials between north- and south-facing leaves increased during the season (Linnenbrink *et al.* 1992).

The degree of sclerophylly of *Sambucus nigra* leaves, estimated as the ratio of leaf dry weight to surface area, was 0.42 ± 0.03 g dm⁻² for 50 leaves (Salleo *et al.* 1997). Leaf water potential at the turgor loss point was -1.02 ± 0.05 MPa; leaf water potential at full turgor was -0.77 ± 0.03 MPa and the bulk modulus of elasticity at full turgor was 7.4 ± 0.41 MPa. The relative water loss at the turgor loss point was high at 25%. The characteristic rehydration time was calculated as 7.00 ± 0.48 minutes. Recovery of water content of approximately 83% was achieved in 7 minutes; full recovery took a further 43 minutes. A comparison was made between leaf relative water deficit and leaf water potential values recorded both during leaf dehydration in a pressure chamber and rehydration, as measured by weight difference. This showed a significant hysteresis between the two curves which indicates that a residual water loss persisted during re-hydration, compared to leaf dehydration. The refilling of the cavitated apoplast (the xylem and mechanical tissue) lagged behind the

filling of the other tissues. This volume refilled only very close to full turgor (Salleo *et al.* 1997).

Sambucus nigra was considered to be very vulnerable to cavitation (Vogt 2001). A water potential of -2.2 MPa led to 90% loss of conductivity. Measurements of stem water potentials during the course of three seasons showed that the water potential was never more negative than -1.7 MPa. However, the fact that conductivity loss exceeded 40% several times showed that embolism did occur, but that xylem vessels refilled on rainy days. *Sambucus nigra* maintained stem water potential by reducing leaf conductance soon after the onset of drought, by closing stomata (Vogt & Löscher 1999).

Saturation deficit was observed to be higher on the windward side of *S. nigra* bushes than on the leeward side. These bushes were in northern Germany, see section V(B) (Steubing 1962). The maximum difference reported was 10% on the windward side and 7% on the leeward side, at a wind speed of 9 m s^{-1} . Slight differences were observed in transpiration rate between leeward and windward sides, the highest recorded being $38.2 \text{ mg g}^{-1} \text{ minute}^{-1}$ in still conditions, and the lowest $4.9 \text{ mg g}^{-1} \text{ minute}^{-1}$ at a windspeed of 12.2 m s^{-1} . The mean transpiration rate was $12.7 \text{ mg g}^{-1} \text{ minute}^{-1}$ ($n = 30$).

Sambucus nigra cannot be considered a drought-tolerant species, but is able to recover from short periods of water shortage (at least up to three weeks).

(F) BIOCHEMICAL DATA

Cyanogenic glycosides

Many cyanogenic glycosides have been reported from *S. nigra* of which the most commonly noted is sambunigrin (Bourquelot & Danjou 1905; Jensen & Nielsen 1973). These authors also observed prunasin and the *m*-hydroxysubstituted glucosides zierin and holocalin. The latter two were observed in two out of six collections of Danish material. Sambunigrin was found in all six collections. All collections made in September contained holocalin, exclusively or with zierin, and the sambunigrin contents were low. Collections in southern Italy (Dellagrecia *et al.* 2000a) yielded sambunigrin, prunasin, holocalin and its acetyl derivative, as well as a new glycoside, 2*S*- β -D-apio-D-furanosyl-(1 \rightarrow 2)- β -D-glucopyranosylmandelonitrile. Sambunigrin and prunasin were phytotoxic, as shown by *Raphanus sativus* and *Lactuca sativa* bioassays (Dellagrecia *et al.* 2000b). Three cyanohydrins were isolated from southern Italian material (Dellagrecia *et al.* 2000b) which had a slight stimulant effect on the bioassay species, suggesting that they were involved in the detoxification of the plant. An iridoid glucoside, morroniside, was isolated from young shoots collected in April (from a Danish collection), but was not detected in fully developed leaves or green fruits (Jensen & Nielsen 1974).

Aroma compounds of fruit, flower and leaf

Fourteen new compounds were found in distillates of elderberries and several elderberry products (juice, stewed fruit and wine) (Mikova *et al.* 1984). Two of these were ketones (methyl vinyl ketone and damascenone) and 12 were methyl and ethyl esters of higher fatty acids (myristic, palmitic, palmitoleic, stearic, oleic, linoleic and linolenic).

Eberhardt & Pfannhauser (1985), using steam distillation followed by gas chromatography/mass spectroscopy (GC/MS), isolated aroma compounds from elderberries. The main compounds were hexenal, hexenol, hexanol, linalool, hotrienol, phenylacetaldehyde, damascenone and linalool oxide. Unripe berries lacked hexenol and hexanol and had less phenylacetaldehyde than ripe berries. Forty aroma compounds from elderberry juice were identified by Jensen *et al.* (2000). These were separated by GC/MS and their odours characterized by a sniffing panel. The characteristic odour of elderberries was due to dihydroedulan and β -damascenone. Fruity odours were contributed by aliphatic alcohols and aldehydes and aromatic esters. The odours associated with elderflowers (although present here in the fruit), were due to 1-nonanol, nerol oxide and (Z)- and (E)-Rose oxide (4-methyl-2-(2-methyl-1-propenyl) tetrahydro-2H-pyran). Other flower odours were associated with hotrienol, linalool and α -terpineol. Fresh and grassy odours were due to 1-hexanal (E)-2-hexen-1-al (Z)-3-hexen-1-ol (E)-2-hexen-1-ol and (E)-2-octen-1-al. The aroma of mushrooms was a result of the presence of 1-octen-3-ol and 1-octen-3-one.

Extractions from elderflowers (Eberhardt & Pfannhauser 1985) showed the presence of the following aroma compounds: two pyranoid and two furanoid forms of linalool oxide, hotrienol and linalool. A GC/MS analysis of the aroma compounds of elder flower syrup coupled with a panel sniffing test, by Jørgensen *et al.* (2000), showed that *cis*-Rose oxide, nerol oxide, hotrienol and nonanal contributed to the elderflower odour. Other floral odours were associated with linalool, α -terpineol, 4-methyl-3-penten-2-one and (Z)- β -ocimene. Fruity odours were associated with pentanal, heptanal and β -damascenone. Fresh and grassy odours were due to hexenal and (Z)-3-hexenol.

Extracts of dry elder flowers were analysed by Toulemonde & Richard (1983) resulting in a total of 79 compounds: 16 hydrocarbons, 11 ethers and oxides, 7 ketones, 7 aldehydes, 16 alcohols, 6 esters and 16 acids.

An analysis of the constituents of fragrance of *S. nigra* growing in south-west France by Joulain (1987) yielded 3,7-dimethyloctadi-1,6-ene-3,5-diol (5-hydroxylinalol), valine methyl ester (0.3%), isoleucine methyl ester (7%), the acetaldehyde-(0.15%), butanal-(0.1%) and acetone-imines (0.15%) of isoleucine methyl ester.

Leaf volatiles from intact branches were collected from *S. nigra* as well as from other species in southern Sweden in June and August (Zhang *et al.* 1999). Samples taken on June 9 yielded 24 chemical species, but on

August 4, only 11 compounds were detected. One constituent (Z)-3-hexen-1-ol, present only in the June samples, was detected by an electrophysiological assay of an antenna of the spruce-bark beetle *Ips typographus*, of which *S. nigra* is not a host. The authors suggest that the beetle uses such signals to avoid prolonged searching in areas dominated by non-host trees.

Lectins and ribosome inactivating proteins

Lectins are glycoproteins with sugar binding sites, which bind reversibly with specific sugars. Type 1 ribosome inactivating proteins (RIPs) are enzymes with glycosidase ribosomal inactivating ability. Type 2 RIPs consist of two structurally and functionally different polypeptides. The A chain has similar structure and function to a type 1 RIP and the B chain has the carbohydrate activity typical of lectins. The B chain, through lectin–receptor interaction, allows the A chain to enter the cytoplasm and kill the cell (Van Damme *et al.* 1997b).

The lectin SNA-I was isolated from *S. nigra* bark by Broekaert *et al.* (1984) which bound most strongly with sialic acid, making it unique amongst plant lectins (Shibuya *et al.* 1987). It accounted for about 5% of the protein in the tissue and was the first lectin isolated from a species in the Caprifoliaceae. The lectin was demonstrated by Greenwood *et al.* (1986) to be located in protein bodies in the phloem parenchyma. The level of the lectin in bark was very much lower in summer than in winter, seen as evidence that it acts as a storage protein. Also the disappearance of the lectin during the summer decreases as a function of the age of the bark. The lectin accumulates more rapidly in the proximal than in the distal internodes (Nsimba-Lubaki & Peumans 1986). SNA-I was also shown to be a type 2 RIP (Van Damme *et al.* 1996b). Subsequently a variant of this was found (SNA-I') which differs only slightly (Van Damme *et al.* 1997a). A second bark lectin (SNA-II) which was specific for 2-acetamido-2-deoxy-D-galactose was isolated by Kaku *et al.* (1990). SNA-I and SNA-II are present in comparable quantities; each represents 30–40% of the total bark protein in the winter (W.J. Peumans, personal communication). A further bark type 2 RIP (basic nigrin b) was isolated by de Benito *et al.* (1997). A type 2 ribosome-inactivating protein, nigrin-b, was isolated from *S. nigra* bark by Girbés *et al.* (1993) and was further characterized by Battelli *et al.* (1997). This protein was shown to have a high amino acid sequence homology with the lectin SNA-II. Since it exhibits the carbohydrate binding properties of lectins, it is also referred to as SNA-V (Van Damme *et al.* 1996a). The presence of further type 2 RIPs in elder bark was deduced by Citores *et al.* (1994). Similarly, a bark protein (SNLRP) was found which had a truncated B chain but it was very similar in amino acid sequence to SNA-I (Van Damme *et al.* 1997c).

Lectins and type 2 RIPs have also been isolated from the seed and fruit. The lectin SNA-III was isolated

from *S. nigra* fruits by Mach *et al.* (1991) and consisted of two isoforms. This was subsequently found to be a type 2 RIP and named nigrin-f (Citores *et al.* 1996; Girbés *et al.* 1996). A similar lectin was isolated from dried seeds by Peumans *et al.* (1991) and was independently designated SNA-III. These two lectins are distinct and the fruit lectin was subsequently renamed SNA-IV (Mach *et al.* 1996). In structure, specificity and serologically, SNA-II and SNA-III are similar and very different from SNA-I (Peumans *et al.* 1991). Likewise, SNA-II and SNA-IV are similar, and both are very different from SNA-I (Mach *et al.* 1991). The fruit lectin SNA-IV was further characterized by Mach *et al.* (1996), who found that it occurred in several isoforms. Two type 1 RIPs were found in elderberries (de Benito *et al.* 1998), one of which, nigrin-f1, is found in both green and mature fruits, and the other, nigrin-f2, is found only in mature fruits.

The major protein of *S. nigra* fruit, SNA-IVf, is identical in its amino-acid sequence to the toxic RIP SNA-Vf, except that it has a truncated A chain, thus rendering it non-toxic. In fruits, SNA-Vf accounts for only 3% of the total protein. Further work (Peumans *et al.* 1998) has provided more evidence that type 2 RIP genes give rise to complex mixtures of type 2 RIPs and lectins. Two lectins were discovered which were composed of truncated B chains of type 2 RIPs. A chitin-binding lectin (SN-HLPf) was found in fruits (Van Damme *et al.* 1999), which had very little antifungal activity, as has been associated with proteins of this type in other species.

Bark lectins have been isolated from other species of *Sambucus*, for example *S. sieboldiana* (Tazaki & Shibuya 1989), *S. canadensis* (Shibuya *et al.* (1989), *S. ebulus* and *S. racemosa* (Nsimba-Lubaki *et al.* 1986). Lectins, through their carbohydrate binding properties, have many applications in physiology and medicine (see section X(B)).

Evidently both bark and fruit contain very complex mixtures of lectins and RIPs, some toxic and some not. While some are likely to be connected with defence and deterrence against predators and disease, the function of others is far from clear.

Others

The flavonoid rutin (3-rhamnoglucoside) is known from numerous plant species and was isolated from the flowers of *S. nigra* as a particularly pure preparation (Davidek 1961).

Triterpenoids have been reported from the bark of *S. nigra* (Huneck & Snatzke 1965): the methylester of ursolic acid, betulin, α -amyrin and β -sitosterin. Triterpenoids found in leaves by Inoue & Sato (1975) were α - and β -amyrin, ursolic acid and oleanolic acid.

A comparative study of the monomeric composition of suberins from the cork layers of 16 higher plants (Holloway 1983) showed that *S. nigra* had no monomers longer than C₂₆ in its suberins.

Chemical analyses of the pollen of 58 plant species (Knight *et al.* 1972) showed the following results for *S. nigra*: cation exchange capacity 24 mequiv 100 g⁻¹ dry matter, uronic acids 50, K 30, Na 1, Ca 11, Mg 23, total cations 65, N 428, P 37, S 22 mequiv 100 g⁻¹ dry matter, Fe 287 p.p.m. and ash 5.2%. Of these, UA, N and P were towards the high end of the range whereas the value for Na was particularly low.

The variability and genetic linkage of seven enzyme systems were analysed with polyacrylamide gel electrophoresis using progenies from three crosses between *S. nigra* cultivars (Boskovic & Tobutt 1992). A total of 17 loci were deduced from the bands of esterase, glutamate oxaloacetate transaminase, peroxidase, phosphoglucomutase and 6-phosphogluconate dehydrogenase (6Pgd). No variation was observed in glucose-6-phosphate isomerase and leucine aminopeptidase. Tight linkage was observed between two esterase loci and between an esterase and a 6Pgd locus. None of the loci were closely linked with the dominant genes for red and yellow leaf.

VII. Phenology

Leaves usually emerge in February or March, and flowers in May or June. Fruits start to develop in July, ripen during August and are fully ripe by early September. Bud-break may occur during warmer spells in winter (Grime *et al.* 1988). The leaf longevity, calculated from life tables based on numbers of leaves in each age class, was 196 days (Escudero *et al.* 1992).

The range of first appearance of seven phenological events is shown in Fig. 3. These were derived from a series of observations made by Frederick Lowe at Tenbury, Worcestershire between 1915 and 1931 as part of a national phenological observation network organized by the Royal Meteorological Society (Clark & Adames 1916–21; Clark *et al.* 1922–23; Clark *et al.* 1924–27; Clark *et al.* 1928–32). Other data on the dates of first flowering were provided by R.S.R. Fitter from observations in England, Scotland and Wales between 1953 and 1996. Dates of first flowering in Central England in this data series were between April 30 and June 27 (Fig. 3) and in Scotland between June 4 and June 14.

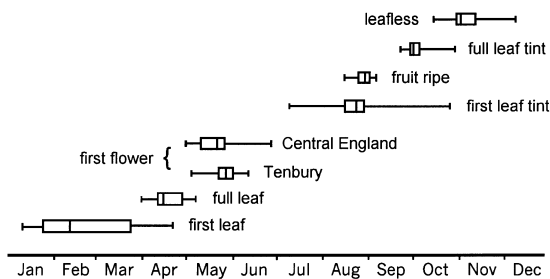


Fig. 3 First dates of occurrence of phenological events. Box and whisker plots in which the left end of the box shows the lower quartile, the central line the median and the right end of the box the upper quartile. The whiskers show the lower and upper ranges.

The data provided by R.S.R. Fitter were a part of those discussed by Fitter *et al.* (1995) in which positive relationships were observed between first flowering dates and monthly mean temperatures for 243 species of flowering plants. We have analysed the phenological observations of Fitter and those of Lowe in relation to monthly mean central England temperatures (CET) (originated by Manley (1974), updated by Parker *et al.* (1992) and now updated by the Hadley Centre (<http://www.cru.uea.ac.uk/~mikeh/datasets/uk/cet.htm>)). We have included only those observations of Fitter which are in central England. These analyses are multiple regressions of flowering date on monthly mean CETs. We have carried out analogous analyses with the first leafing dates recorded by Lowe (Table 3), and also of the two data sets combined. The mean date of first flowering shown by this combined data set was 23 May.

It is instructive to compare the results of the analyses of first leafing dates to those of Sparks *et al.* (2000). This was a similar analysis carried out on mean British Isles first flowering dates taken from the Royal Meteorological Society network. The data used for *S. nigra* were from 1929 to 1948. These authors found a very strong relationship with March and April mean temperatures ($R^2 = 0.901, n = 20, P < 0.001$). This contrasts with the present results where the strongest influence is March temperature. The mean date of first flowering in the study by Sparks *et al.* (2000) is June 4, later than our mean (23 May). Our data have a strong southern

Table 3 Results from multiple linear regression of first flowering and first leafing dates of *Sambucus nigra* on monthly Central England temperatures. The regression coefficients are given next to the months. R^2 (the proportion of variance accounted for by the regression), n (number of observations) and P (the probability that this degree of association could be exceeded by chance alone) are also shown

	Tenbury 1915–1931	First flowering Central England 1953–1996	Both 1915–1996	First leafing Tenbury 1915–1931
November		-2.4	-1.8	
February		-1.7	-1.6	-12.0
March	-4.6	-4.5	-4.2	
R^2	0.44	0.55	0.53	0.62
n	17	37	54	15
P	0.004	<0.00001	<0.00001	0.0005

central English bias, compared with the British Isles data of Sparks *et al.* (2000), and this probably accounts for the later mean date of Sparks's data and for the influence of April temperature.

We also demonstrated a significant relationship between mean February temperature and the date of first leafing in the Tenbury data set (Table 3). Murray *et al.* (1989) demonstrated that with 144 chill days (below 5 °C), the thermal time required for budburst of *Sambucus nigra* was 60 day °C > 5 °C. If the number of chill days was reduced to 56, the thermal time required for budburst was 180 day °C > 5 °C. This was similar to the requirements of *Rosa rugosa*, *Salix viminalis*, *Larix decidua* and *Prunus avium*.

Data relating to phenological events in mainland Europe were obtained from the International Phenological Gardens (IPG) network and are presented here by permission of F.-M. Chmielewski. The IPG network was founded in 1957 and established gardens across Europe which grew clonal material from a number of woody species, avoiding genetic variability in dates of phenological events (Chmielewski & Rötzer 2001). The variation in dates of first leafing (Fig. 4b) and first flowering (Fig. 4c) is summarized for a region covering northern and Central Europe. Particularly notable is the lateness of first leafing at Freyung (23 days later than the European average) and first flowering (13 days later than the average). This is attributable to the altitude of this station (956 m) compared with its nearest neighbours Freising (460 m) and Munich (540 m). Sarajevo (1000 m), in spite of being at almost the same altitude, has an earlier first flowering date because it is approximately 500 km further south. The main difference between the UK phenological data (represented by the Tenbury study) and the European data are in the dates of first leafing. The range in the European data (Fig. 4d) is from 20 March to 28 April, and in the UK data 15 January to 21 April, the median being much later for mainland Europe (4 April) compared with Tenbury (11 February). This will be the result of more oceanic winters and earlier springs in Britain compared with Central Europe.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Homogamous or protogynous (Knuth, Poll. II). Koncalová *et al.* (1983) gave a value for self-compatibility as 1.22% of buds. They do not state whether this refers to pollination of single flowers by their own pollen, or pollination by other flowers within the same bush, but the former seems more likely. Experiments by Bolli (1994) suggested that pollen did not normally travel beyond neighbouring flowers and that most fertilization was effected by pollen from the same individual but from different flowers or inflorescences. Bolli (1994) found that when freshly opened flowers were pollinated with pollen from another inflorescence from

the same bush, more pollen tubes germinated than when pollen from another bush was used.

The flowers are nectarless but have a strong odour (see section VI(F) for biochemical analyses of the odour compounds). This may deter some visitors, but may attract others. The flowers are visited by beetles, particularly longhorn beetles (Bolli 1994) and flies. Honeybees have been observed searching for pollen (Wade *et al.* 1994). The beetle *Cerambyx scopolii* Füssly (Coleoptera: Cerambycidae) frequents flowers of *S. nigra*, Rosaceae and Umbellifers (Hickin 1963). A number of flies, Hymenoptera and beetles are mentioned (Knuth, Poll. II) from various parts of Europe as visiting the flowers to eat the flowers or pollen.

(B) HYBRIDS

Natural *Sambucus* hybrids are very rare, the hybrid between *S. nigra* and *S. racemosa* L. having been reported twice in Denmark and in 1940 in Jutland (Böcher 1941), in 1943 in North Zealand (Winge 1944) and in southern Sweden (Nilsson 1987). *Sambucus racemosa* normally flowers several weeks before *S. nigra* but Winge (1944) procured precocious flowers from a plant of *S. nigra* and was thus able to pollinate it with *S. racemosa* pollen, from which he obtained 10 F₁ hybrids. These hybrids were sterile. Of about 15 000 fruits sown, none germinated. Likewise, 10 plants were produced from the cross *S. nigra* × *S. racemosa* by Koncalová *et al.* (1983) which developed fruits but no viable seed. The reciprocal cross *S. racemosa* × *S. nigra* resulted in the development of fruits but no germinable seeds (Koncalová *et al.* 1983). The F₁ hybrid plants *S. nigra* × *S. racemosa* were intermediate between the parent species in a number of characters (Winge 1944): flowering date; inflorescence form (racemose in *S. racemosa* and corymbose in *S. nigra*); flower size (small and greenish in *S. racemosa* and large and white in *S. nigra*); fruit colour (reddish in *S. racemosa* and black in *S. nigra*, and described as 'dirty brownish-red' in the hybrid); odour (similar to that of *S. nigra* but less pronounced); the pith in the branches (orange-brown in *S. racemosa* and white in *S. nigra*). The natural hybrid *S. nigra* × *S. racemosa* observed by Nilsson (1987) was also intermediate in the same characters and had poor pollen stainability (0.5% from 400 grains). The author stated that 6 out of 40 investigated seeds had oily contents and seemed viable.

Four hybrid plants resulted from the cross *S. nigra* × *S. ebulus* L.; the reciprocal cross produced seed but no progeny (Koncalová *et al.* 1983). Seed set was obtained from the cross *S. canadensis* × *S. nigra* (Chia 1975). From 3 crosses, one produced 63 seeds and 2 seedlings, one produced 43 seeds and no seedlings, and one was sterile. The cross *S. cerulea* × *S. nigra* produced 58 seeds and 8 seedlings (Chia 1975).

No hybrids have been reported from Britain, although *S. racemosa* does occur sporadically, particularly in eastern Scotland (Atl. Br. Fl.).

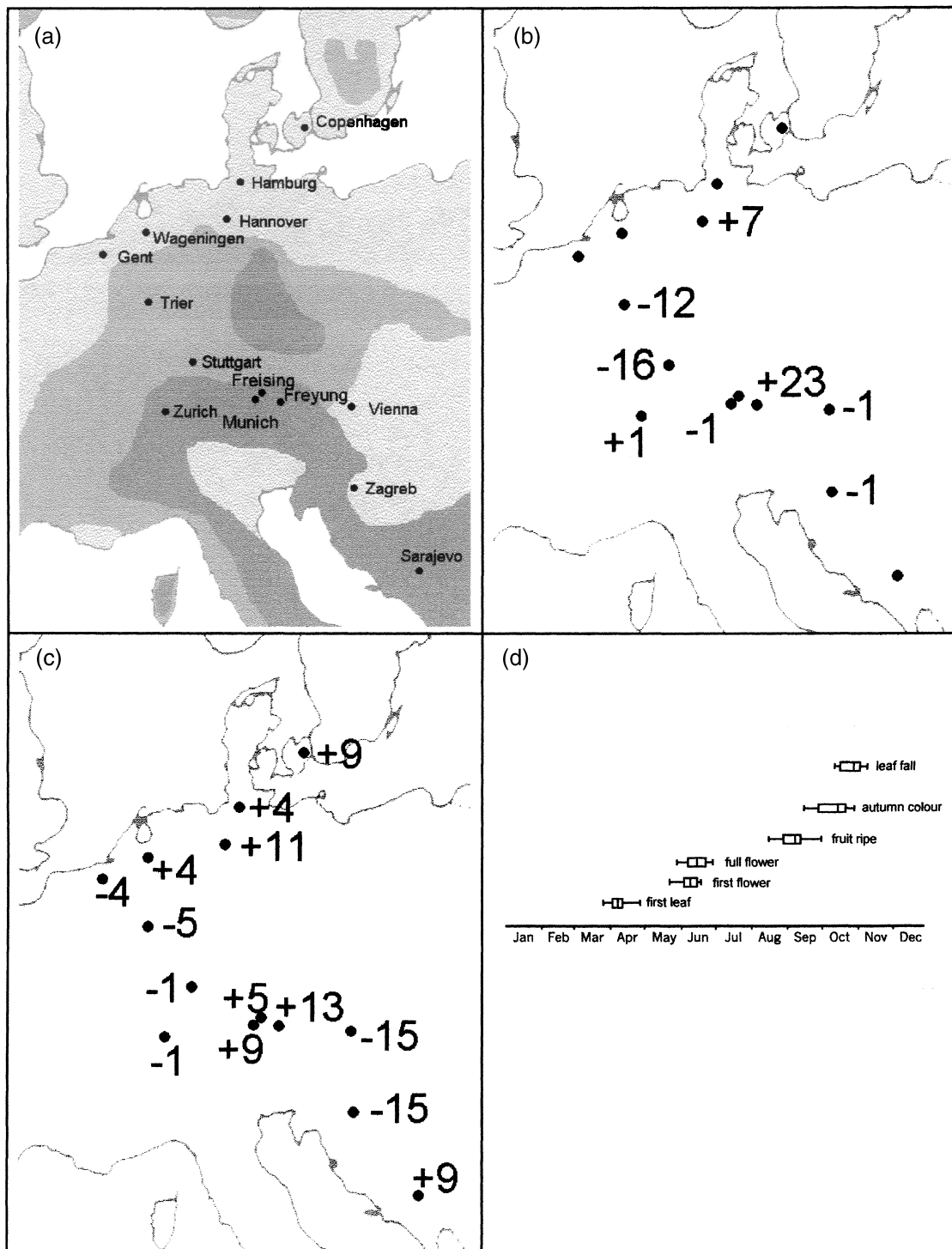


Fig. 4 European phenological data from the International Phenological Gardens. (a) Phenological gardens. Shading indicates approximate altitude; light shading 0–200 m; medium shading 200–500 m; heavy shading above 500 m. (b) Mean dates of first leafing at each station, given as the deviation in days from the overall mean for all stations (5 April). The data are for periods between 6 and 22 years. (c) Mean dates of first flowering, expressed as in (b). Overall mean date 4 June. The data are for periods between 14 and 31 years. (d) First dates of occurrence of phenological events. Box and whisker plots in which the left end of the box shows the lower quartile, the central line the median and the right end of the box the upper quartile. The whiskers show the lower and upper ranges.

(C) SEED PRODUCTION AND DISPERSAL

Fruit and seed may be formed in the absence of pollination (Bolli 1994) and seeds without embryos can be detected (Table 4). Low set of fruit occurs particularly

in deeply shaded trees, but can also result from unfavourable weather conditions during anthesis (Bolli 1994). Corymbs in bushes under these conditions are often very sparse, many of the fruits having aborted early in development.

Table 4 Dimensions (mm) and weights (mg) of fruits and seeds of *Sambucus nigra*. Each collection is from a single bush (unknown for collection 14). Seed dimensions are the means of ten filled seeds. Seed weights are the means of between 4 and 89 seeds. Percentages of filled seed are the means of between 30 and 100 seeds. The weights of fruits are the means of 10 and fruit measurements the means of five ripe fruits

Coll. no.	Year	Fresh weights (mg)		Fruit size (mm)		Seed dimensions (mm)			Percentage filled	Dry weight (mg)	
		Fruit	Pulp	Length	Width	Length	Width	Thickness		Filled	Empty
1	1993					3.0	1.9	0.8	89	2.5	1.2
2	1993					3.8	1.6	0.7	89	2.7	1.4
3	1995					3.3	1.6	0.5	50	4.0	1.6
4	1995					3.3	2.0	0.8	58	3.2	1.3
5	1995					3.4	1.8	0.7	45	3.7	1.9
6	1996	80.5	74.2	4.2	4.4	2.7	1.2	0.4	68	1.9	0.7
7	1996	94.0	85.0	–	–	2.8	1.1	0.3	35	1.9	0.8
8	1996	144.0	129.7	5.4	5.2	3.5	1.6	0.8	69	3.4	1.5
9	1996	161.7	150.9	–	–	3.7	1.5	0.4	52	3.0	1.3
10	1996	110.5	100.4	5.7	4.8	3.5	1.2	0.4	74	2.7	1.3
11	1996	71.8	61.2	4.6	3.9	3.4	1.2	0.5	50	2.9	1.2
12	1993					3.1	1.8	0.7	82	3.6	1.5
13	1993					4.7	1.8	0.8	88	4.9	2.0
14	1992					2.8	1.5	0.6	64	2.0	1.5
Mean		110.4	100.2	5.0	4.6	3.4	1.6	0.6	65	3.0	1.4

1. Teversham Fen, Cambs. (TL5058), 2. Narborough, Norfolk (TF7412), 3. Allerton, Yorks (SE4058), 4. Aysgarth, Yorks. (SE0188), 5. Pensnett, W. Midlands (SO9189), 6. Hay on Wye (SO2445), 7. Tilstock, Shropshire (SJ5638), 8. Stanhope, Co. Durham (NY9838), 9. Caton, Lancs. (SD5264), 10. Wednesfield, Wolverhampton (SJ9300), 11. Compton, Wolverhampton (SO8999), 12. Cormède, South central France (45°49' N, 3°14' E), 13. Pont du Château, South central France (45°48' N, 3°15' E), 14. Kosické, Slovakia (48°42' N, 21°10' E).

Mean seed weights from the Sheffield region were reported by Grime *et al.* (1988) as 1.9 mg and by Cornelissen *et al.* (1996) as 3.44 mg. Weights and sizes of seeds from a number of sites are shown in Table 4. The mean weight for filled seeds (seeds containing embryos) for all sites was 3.0 mg (1.9–4.9) and for British sites 2.9 mg (1.9–4.0). A mean weight of 4.2 mg (mean of 1000 air-dried seeds, 8.5% water content) was reported by Tytkowski (1982) for seed collected from Kornik, Poland. Jinadasa (2000) recorded a mean weight ($n = 3500$) of 2.3 mg from New Zealand.

The mean weight of fruits from 20 British sites (10 fruits per bush, 1 bush per site) was 117.9 mg (66.6–182) (some shown in Table 4). The mean weight of pulp per fruit was 107.5 mg (57–169.3). A mean weight of the fruit in Spain was 43.4 mg (Herrera 1987), and Sorensen (1981) reported a mean of 55 mg pulp per fruit from an Oxfordshire wood. The weight of fruits from Galicia, Spain was reported by Romero Rodriguez *et al.* (1992) as 100–130 mg.

The mean total weights of fruit in a number of experimental plots in which nitrogen level (between 100 and 400 kg N ha⁻¹) and planting density were varied were 3.68, 7.36 and 12.04 kg per bush for 4-, 5- and 6-year-old bushes, respectively (Kaack 1988). Assuming that the weight of a single fruit is 0.12 g (Romero Rodriguez *et al.* 1992), estimates of the approximate numbers of fruits per bush are 30 700, 61 400 and 100 300 for 4-, 5- and 6-year-old bushes, respectively.

The seeds of *S. nigra* are dispersed by birds which either regurgitate or defecate the seeds after ingesting the fruit. A negative exponential distribution of seeds

with distance from a bush was observed by Debussche & Isenmann (1994) in which 1 seed m⁻² was observed 175 m from the bush and 12 seeds m⁻² 115 m from the bush. Birds known to eat elderberries are listed in section IX.

Three analyses are available of the nutritive quality of elder fruit pulp; these are summarized in Table 5. The first (Herrera 1987) is based on a sample of 20–40 fruits collected in Spain. Sorensen (1981) reported analyses of material from Wytham Wood, Oxfordshire. Romero Rodriguez *et al.* (1992) analysed material from Galicia, north-west Spain. These latter authors also measured the concentrations of a number of components, expressed here in mg 100 g⁻¹ dried pulp: vitamin C 117–141, sodium 40.1–52.1, potassium 57.5–2137, calcium 127–139, magnesium 144–158, iron 8.1–8.7, copper 0.5–1.1, zinc 1.6, manganese 1.1 and phosphate 294–319. Snow & Snow (1988) estimated the energy yield of the dried pulp using standard conversion factors for lipid, protein and carbohydrate, as 3.35 kcal g⁻¹ dry pulp (14.0 kJ g⁻¹) and 0.38 kcal g⁻¹ of whole fruit (1.59 kJ g⁻¹).

(D) VIABILITY OF SEEDS: GERMINATION

A series of experiments on the germination of *S. nigra* seed, particularly in relation to ingestion by birds was carried out by Clergeau (1992) in Brittany. The germination percentage of fresh intact fruits was 12.5% ($n = 6120$ fruits); that of dried intact fruits was 2.0% ($n = 5100$ fruits). Seeds manually removed from the pulp had a considerably higher germination rate of 62.5% ($n = 8160$ seeds). Seeds which had been ingested

Table 5 Chemical composition of *Sambucus nigra* fruit pulp from three sources. These are expressed as percentages of the weight of dried pulp, except for the water content

Constituent	Herrera (1987)	Sorensen (1981)	Romero Rodriguez <i>et al.</i> (1992)
Water	81.6*	76.4 ± 0.76	81.0–82.2
Protein	18	9.8 ± 0.11	10.2–11.5
Lipids	3.3	3.3 ± 0.63	0.42–0.53
Non-structural carbohydrates	52.7		
Soluble carbohydrates		2.3 ± 0.04	
Glucose			16.3–22.1
Fructose			12.7–15.4
Sucrose			0.4–1.0
Neutral-detergent fibre			33.1–39.3
Acid-detergent fibre	20.5		
Citric acid			0.26–0.47
Malic acid			0.63–1.17
Ash	5.5		4.5–4.9

*Water content of the pulp and seed.

by birds had intermediate percentages of germination: 42.8% ($n = 8160$ seeds) when the seeds were defecated and 36.3% ($n = 487$ seeds) when regurgitated. The treatments also had different effects on the mean time from sowing to germination. Fresh and dried intact fruits had the longest period (41 weeks and 43 weeks, respectively). Seeds with pulp removed had a reduced mean time to germination of 38.2 weeks, and seeds which had been ingested had a still shorter time (36.6 weeks for defecated and 30.5 for regurgitated seeds). These experiments were carried out under conditions intended to simulate natural temperature changes; 8 weeks at 15 °C, 10 weeks at 0 °C, observation period starting, 18 weeks at 13 °C, 8 weeks at 18 °C, 10 weeks at 0 °C and 16 weeks at 13 °C. The period of 15 °C was intended to simulate autumn, 0 °C to simulate winter, 13 °C to simulate spring and 18 °C to simulate summer.

Cold treatment for a whole winter was found by Kinzel (1920) to be necessary to allow any germination. Even after two winters, only 39% of the seed had germinated. The effects of pre-stratification warming were investigated in a series of experiments by Tylkowski (1982) with filled seeds from Kornik, Poland, which had been stored for 15 months in sealed bottles at –3 °C. Of seeds which were kept at 3 °C, 24% germinated, and germination started between the 16th and 17th week. After 26 weeks the temperature was increased to 15 °C in a subsample with only a very slight rise in percentage germination. When the 3 °C stratification was preceded by periods at 10 °C, the percentage germination increased slightly but the time from sowing to germination remained the same, 17 weeks after the onset of the 10 °C treatment. When stratification was preceded by higher temperatures (15°, 20° and 25 °C), the germination percentage increased (Fig. 5). However, the period of higher temperature treatment (3, 6 or 9 weeks) had no effect on the percentage germination and the period required for germination remained the same (14–16 weeks after the onset of stratification) whatever the temperature

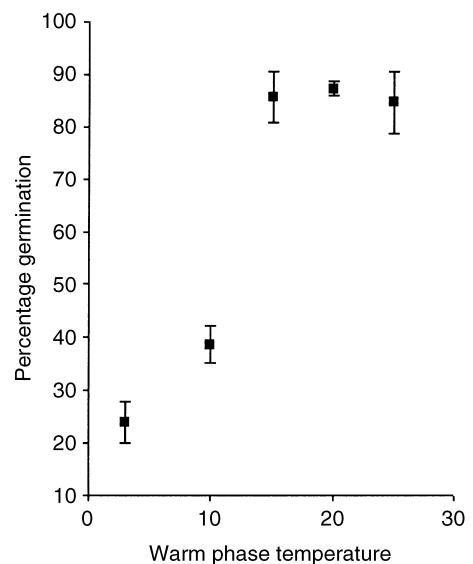


Fig. 5 Maximal seed germination percentage at 3 °C after warm phases of 10 °C, 15 °C, 20 °C and 25 °C and no warm phase (3 °C). Each value is the mean of three warm phase periods (3, 6 and 9 weeks). Data were provided by T. Tylkowski.

treatment. In all the pre-stratification temperature treatments, if the temperature was raised to 15 °C at the onset of germination, the time to maximum germination was reduced from 7 to 3 weeks although the final percentage of germination did not change significantly. In similar experiments carried out by Jinadasa (2000) on New Zealand material, only 3% germination occurred in seeds which were subjected only to stratification at 4 °C (compared with 24% found by Tylkowski). With a high temperature of 20 °C for 2 weeks followed by stratification at 4 °C, only 10% germination was attained, and with 8 weeks' treatment at 20 °C, 60% germination was observed. With 8 weeks at 15 °C, only 30% germination was found. So, not only was the maximum germination at 15 °C and 20 °C lower than that observed by Tylkowski (Fig. 5), but there was a significant difference between the germination

percentage after 4 weeks and 8 weeks, a difference which Tylkowski did not observe. Jinadasa also noted no difference in germination percentage in any treatment when seeds were subjected to a second high temperature period. The effect of seed storage prior to the experiments cannot be ruled out as a possible reason for the difference. Tylkowski's seeds were air-dried and stored at -3°C for 15 months whereas Jinadasa's seeds were stored dry at 3°C for 3 months. Clergeau's seeds were put into germination conditions on the day of collection. Other possibilities are that there are significant differences between populations in the depth of dormancy or germination speed. The consensus from the three sets of experiments is that elder seeds require between 13 and 36 weeks between sowing and germination.

No effect was found in percentage of germination as a result of scarification (Jinadasa 2000). The depth of soil covering stratified seeds significantly affected the percentage of emergence; 43% of seed on the surface germinated, 32% at 1 cm, 22% at 3 cm, 5% at 5 cm and none at 7 cm and 10 cm (Jinadasa 2000). The effect of water stress on seed germination percentage was studied by Jinadasa (2000). Stratified seeds were placed at 0.5 cm depth in soil which was watered at different daily rates. Other soil trays were used to estimate water contents of the different watering regimes. The percentages of germination observed were 15.3% (soil water content (SWC) 34%), 5.3% (SWC 29%), 1.6% (SWC 24%) and no germination at SWC 19%.

Elder seeds had a mean viability (determined by tetrazolium testing) of 84% when fresh. Viability declined very little over a 2-year period whether at room temperature or at 5°C in sealed polythene bags after which the mean viability was 80% (Jinadasa 2000).

In a study of soil seed banks in neglected coppice woods in Essex and Suffolk, Brown & Oosterhuis (1981) collected 27 samples from five woods. A total of 11 *Sambucus nigra* seeds germinated from these samples; *S. nigra* seeds germinated in 28% of the samples from three of the woods.

Seeds from archaeological sites in Denmark were germinated by Ødum (1965). Seeds were collected, with careful precautions against contamination, and germinated in mineral soil sterilized in ethanol for 10 days. Seven *Sambucus nigra* seeds germinated from samples ranging from 160 to 560 years old. The possibility always exists in such observations that seeds could be moved downwards in the soil by biological or physical agents.

(E) SEEDLING MORPHOLOGY

Germination epigeal. At the two leaf stage: cotyledons 2, lamina oblong-ovate, 8–15 mm long, glabrous, tip rounded-truncate, base cuneate; petiole 3–6 mm, channelled above, glabrous, \pm sheathed at base. Hypocotyl glabrous, 1.5–3 cm long. Leaves opposite, 1–3 cm. Epicotyl 0–1 mm. Leaves opposite, first pair entire, 9–18 mm, cordate or ovate, coarsely dentate

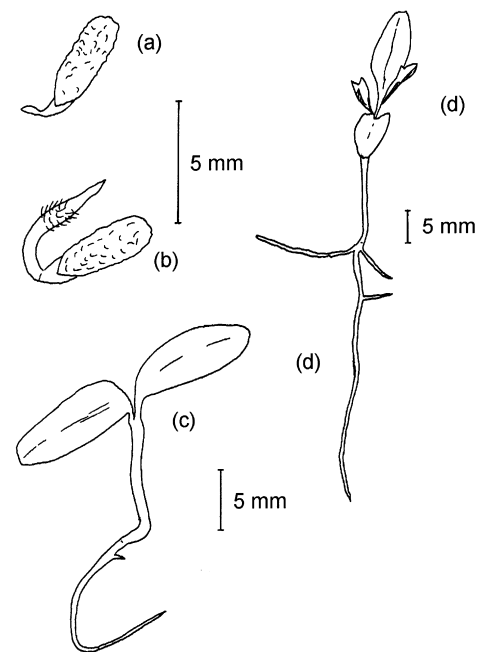


Fig. 6 Drawings of the developing seedling of *Sambucus nigra* at different numbers of days after germination. (a) 4 days, (b) 8 days, (c) 12 days, and (d) 32 days.

with unicellular hairs; petiole 3–18 mm, glabrous, \pm sheathed at base. The first pair of true leaves does not have stipules (Neubauer 1977). A drawing of the seedling with two true leaves is given by Muller (1978) and a drawing showing four true leaves by Csapody (1968). In the population of seedlings from which the present drawings (Fig. 6) were made (Hay on Wye, Herefordshire), both of the second pair of true leaves were entire and only the third pair was pinnately trifoliate; the same situation was described by Lubbock (1892). In the drawing by Csapody (1968), one of the second pair has two leaflets and the other has three. According to Bolli (1994), the second leaf pair has three leaflets. Evidently, the first appearance of the trifoliate leaf differs between populations or individuals.

The vascular supply to the cotyledon petioles consists of a single strand. The first true leaves have three, later leaves five and fully developed leaves no more than nine bundles (Neubauer 1977).

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Aves

Wood pigeons (*Columba palumbus* L.) occasionally eat both leaves and fruits of elder (Colquhoun 1951) and usually eat the seed rather than dispersing it (Snow & Snow 1988). Other birds observed by Snow & Snow (1988) over a four-year period in Buckinghamshire to ingest the seed were bullfinch (*Pyrrhula pyrrhula* (L.)), blue tit (*Parus caeruleus* L.) and, taking much less fruit, collared dove (*Streptopelia decaocta* (Frisvaldszky)), great

Table 6 Numbers of species and individuals of insects recorded from *Sambucus nigra*

	Number of species		Number of individuals Ward (1977)
	Present list	Duffey <i>et al.</i> (1974)	
Lepidoptera	12	7	22
Hemiptera–Heteroptera	2	1	6
Hemiptera–Homoptera	2	4	54
Hymenoptera–Symphyta	4	2	1
Coleoptera	6	1	16
Thysanoptera	5	1	2
Diptera–Cecidomyiidae	4	2	
Diptera–Agromyzidae	1	1	

tit (*Parus major* L.) and marsh tit (*Parus palustris* L.). In the same study, the following species were major pulp eaters and dispersers of seed: starling (*Sturnus vulgaris* L.), song thrush (*Turdus philomelos* Brehm), blackbird (*Turdus merula* L.), blackcap (*Sylvia atricapilla* L.) and robin (*Erithacus rubecula* L.). Birds taking much less fruit were: magpie (*Pica pica* L.), garden warbler (*Sylvia borin* (Boddaert)), lesser whitethroat (*Sylvia curruca* (L.)), mistle thrush (*Turdus viscivorus* L.), spotted flycatcher (*Muscicapa striata* Pallas), jay (*Garrulus glandarius* L.), common whitethroat (*Sylvia communis* Latham), redwing (*Turdus iliacus* L.), fieldfare (*Turdus pilaris* L.), carrion crow (*Corvus corone* L.) and moorhen (*Gallinula chloropus* L.). Chaffinches (*Fringilla coelebs* L.) were also reported as eating berries (Disp. Pl.). Elder berries were eaten by a greater number of species than any other fruit, which Snow & Snow (1988) ascribed partly to their abundance, early ripening and ease of plucking. *Sambucus nigra* fruits were one of more than 60 species recorded as being foraged by various species of waterfowl (Gillham 1970).

Studies of the feeding patterns of migrating blackcaps in Lincolnshire showed that, by eating elderberries, these birds could obtain 75–90% of their daily energy requirements in 10% of the hours available for feeding (Boddy 1991). For data on the nutrient contents of berries see section VIII(C). The importance of bird ingestion of seeds on germination is discussed in section VIII(D).

Acari

Eriophyidae. *Epitrimerus trilobus* Nalepa causes the leaf margins to be rolled upwards to form a pouch (Swanton 1912; Winter 1983; Stubbs 1986) and is widely distributed (Alford 1991).

Insecta

The number of species of phytophagous insects associated with various shrubs and small trees was reported by Duffey *et al.* (1974). A total of 19 species was recorded on *Sambucus nigra*. This was a relatively small number; the only other shrubs with the same or fewer phytophagous insects were *Buxus sempervirens*

(4), *Cornus sanguinea* (18), *Clematis vitalba* (18), *Euonymus europaeus* (19), *Ilex aquifolium* (13), *Taxus baccata* (6) and *Viburnum* spp. (17) (Table 6). In a comparison of the invertebrate fauna of six shrub species, Ward (1977) showed that relatively small numbers of individuals were found on *S. nigra* compared with the other species (Table 6). The samples were all taken from Aston Rowant National Nature Reserve in Oxfordshire (NG ref. SU7198). The shrubs were beaten at regular intervals between April and October, during which time seven collections were made. The total number of individuals of phytophagous insects observed on each species were *Sambucus nigra* 95, *Juniperus communis* 415, *Viburnum lantana* 1799, *Rosa canina* agg. 454, *Cornus sanguinea* 145 and *Ligustrum vulgare* 106. The number of individuals of species classed as predators and parasites on *S. nigra* was 146, the range for the numbers of individuals on other plant species being 136–777. For invertebrates of other habitats, 209 were found on *S. nigra*, and the range for other plant species was 98–430.

Thysanoptera

Aeolothripidae. *Aeolothrips melaleucus* Bagnall is found on the flowers of *S. nigra*, *Quercus* spp., and other trees in southern England; it is predatory on thrips and other small arthropods but is not common (Mound *et al.* 1976).

Thripidae. *Thrips sambuci* Uzel is found in flowers of *S. nigra* (Pitkin 1976) and is widespread in England and Scotland (Mound *et al.* 1976). Larvae and adults of *Thrips major* Uzel, larvae of *Taeniothrips atratus* Haliday and adults of *Taeniothrips vulgatissimus* Haliday were found on elder flowers in Sussex (Ward 1973).

Hemiptera–Homoptera

Aphididae. *Aphis sambuci* L. (Davidson 1925; Winter 1983; Alford 1991) is widespread in Britain. It forms dense colonies in spring on young elder shoots and overwinters on the roots and as eggs. During the summer it lives on elder and on secondary hosts (Stroyan 1984).

Diaspididae. *Chionaspis salicis* (L.) was collected by L.K. Ward in 1981 (Phytophagous Insects Database).

Hemiptera–Heteroptera

Miridae. Eggs of *Lygocoris pabulinus* (L.) are laid on elder and other herbaceous and shrubby plants and are common and widespread in the British Isles (Southwood & Leston, *Land and Water Bugs*). Elder is unusual in that it can serve as a single host throughout the year, whereas this insect usually has different hosts for the winter and summer parts of its life cycle.

Aneuridae. *Aneurus avenius* (Dufour) is found under dead bark of *S. nigra* and other trees and shrubs south of a line from Cambridge to Gloucester (Southwood & Leston, *Land and Water Bugs*).

Lepidoptera

Tortricidae. *Choristoneura hebenstreitella* (Müller) is widespread on elder and other trees and bushes where the larvae feed in spun or rolled leaves in the spring (Bradley *et al.* 1973).

Pyrilidae. *Udea prunalis* (Denis & Schiffmüller) is common throughout Great Britain and Ireland and feeds on a variety of hedgerow shrubs and herbs including elder. It feeds on the undersides of leaves and hibernates in a silken cocoon (Beirne 1952; Goater 1986). *Udea olivialis* (Denis & Schiffmüller) is common and widespread in mainland Britain and Ireland. It feeds on elder and many herbs and shrubs in spun leaves or the turned down edge of a leaf and pupates in a web on a spun leaf (Beirne 1952).

Phlyctaenia coronata (Hufnagel) feeds only on elder. It is common in England south of Durham and Lancashire and in Wales and Ireland. It feeds in August and September and spins webs from where it emerges and feeds at night. It hibernates in a silken cocoon on bark or fallen leaves and pupates in this cocoon in the spring (Beirne 1952; Emmet 1979; Winter 1983; Goater 1986).

Saturniidae. *Saturnia pavonia* (L.) (emperor moth) has a very broad range of food plants, but will eat elder in confinement (Allan 1949).

Geometridae. *Ourapteryx sambucaria* (L.) (swallow-tailed moth) is widespread throughout Britain and feeds on elder and other shrubs (Allan 1949; South 1961; Winter 1983). It has greyish-brown twig-like larvae (Alford 1991).

Eupithecia tripunctaria Herrich-Schaffer (white-spotted pug) is widely distributed in England, South Wales, southern Scotland and Ireland. It feeds on hogweed and related plants as well as elder (Carter 1994). Larvae were reported as being commonly found in summer feeding on elder flowers in Oxfordshire

(Corley 1984). Both *E. tripunctaria* and *E. exiguata* Hübner (mottled pug) were found feeding on elder berries (Corley 1984).

Apeira syringaria (L.) (lilac beauty moth) is found on *S. nigra* and other shrubs (Winter 1983). The larvae hibernate and complete their development in the following spring, pupate in June and hatch in June and July (Alford 1991).

Lymantriidae. *Euproctis chryorrhoea* (L.) (brown-tail moth) may attack and defoliate elder in some years. The larvae construct silken tents (Alford 1991).

Arctiidae. *Spilosoma lubricipeda* (L.) (white ermine moth) and *S. luteum* Hufn. (buff ermine moth) were found by West (1984) on *S. nigra* and several species of climbers.

Noctuidae. *Gortyna flavago* (Denis & Schiffmüller) (frosted orange moth) occurs throughout England, Wales and eastern Scotland and its larvae have been found feeding in the stems of elder as well as many herbaceous plants (Allan 1949; South 1961; Alford 1991).

Melanchra persicariae (L.) (dot moth) is polyphagous but feeds on elder (Bretherton *et al.* 1979; M.F.V. Corley personal communication; West 1984; Carter 1994). It is distributed throughout England, particularly in the south and is local in Ireland and Wales (Bretherton *et al.* 1979). *Diataraxia oleracea* L. (bright-line brown-eye moth) was observed by West (1984) on elder and a number of species of climbers.

Coleoptera

Anobiidae. *Anobium punctatum* (Degeer) and *Ptilinus pectinicornis* (L.) were observed in an elder on an area of exposed heartwood (Hickin 1963).

Apionidae. *Sambucus nigra* was a minor food plant of *Apion vorax* Herbst in woodland around Rothamsted (Cockbain *et al.* 1982).

Cerambycidae. The larvae of *Pogonocherus hispidulus* (Piller & Mitterpacher) feed in the cambium and bore into the sapwood of elder and other trees. The adults emerge in April or May. Local but recorded in England, Scotland and Wales (Hickin 1963).

Larvae of *Saperda scalaris* (L.) feed in the cambium of several tree species including *S. nigra*. The adults feed on leaves, eating along the veins (Hickin 1963).

Grammoptera ruficornis (F.) feeds on the outer sapwood of elder among a wide range of host species (Hickin 1963).

Hymenoptera

Tenthredinidae. *Macrophya ribis* (Schrank) larvae feed on *S. nigra* in England north to Yorkshire and Cheshire, locally abundant in the south (Benson, Symphyta).

M. albicincta (Schrank) larvae usually feed on *S. nigra*, and sometimes on *Valeriana officinalis*. It is common throughout the whole of Britain from Cornwall to Sutherland (Benson, Symphyta).

Eulophidae. The parasitic Hymenoptera *Sympiesis acalle* (Walk.) and *Aprostocetus bruzzonis* (Masi) were observed in South Wales feeding on the surface of the gynoecium, possibly on gynoecial tissue or pollen grains (Jervis *et al.* 1993).

Diptera

Agromyzidae. Larvae of *Liriomyza amoena* (Meigen) initially form irregular linear mines which later develop into conspicuous blotches. It is common in the south, also reported in Westmorland, Co. Wexford, Dublin, New Ross (Spencer, Agromyzidae) and Warwickshire (Robbins 1983).

Cecidomyiidae. The following four species are associated with closed, swollen flowers (Barnes, Gall Midges). *Arnoldiola sambuci* (Kieffer) was found in Dorset (Bagnall & Heslop Harrison 1921). *Contarinia sambuci* (Kaltenbach) and *Asphondylia* sp. were recorded in Northumberland (Bagnall & Heslop Harrison 1922). *Placochela nigripes* (F. Loew.) was reported in Northumberland (Bagnall & Heslop Harrison 1922), in Surrey and Kent (Niblett 1941) and in East Sussex (Grasswitz 1999).

(B) AND (C) PLANT PARASITES AND DISEASES

Fungi

Basidiomycotina. The Jew's ear fungus, *Auricularia auricula-judae* (L. ex Fr.) Schröt occurs commonly on dead branches and old elders (Peace 1962). Although this species predominantly occurs on elder, it was recorded on an additional seven species in Northumberland and Durham: *S. nigra* accounted for 62% of records, *Acer pseudoplatanus* for 20% and *Ulmus glabra* for 9% (Fenwick 1998).

Ascomycotina (including anamorphic genera). Leaf spots are produced by *Cercospora depazeoides* (Desm.) Sacc. (Peace 1962; Ellis & Ellis 1985), *Ramularia sambucina* Sacc. (Peace 1962; Ellis & Ellis 1985) and *Phyllosticta sambucicola* Kalchbr. (Peace 1962).

A study of corymb wilt in Austrian elder orchards (Steffek & Altenburger 2000) showed that, in all strongly infected bushes, the endophytic *Graphium* spp., *Acremonium* spp. and *Verticillium* spp. predominated. In the uninfected bushes, no *Graphium* spp. were isolated, but *Acremonium* spp. and *Verticillium tenerum* were sometimes found.

Fungi found on dead wood are *Sporidesmium altum* (Preuss) M.B. Ellis which stains wood green, *S. aturbinatum* (Hughes) M.B. Ellis, *S. cookei* (Hughes) M.B.

Ellis, *S. leptosporum* (Sacc. & Roum.) Hughes which is especially common on elder, *Diaporthe circumscripta* (Fr. ex Mont.) Othex Fuckel, *Dothidea sambuci* (Pers.) Fr., *Balanium stygium* Wallr., *Ascochyta deformis* (Karst.) Grove and *Phoma sambuciphila* Oudem. (Ellis & Ellis 1985).

Viruses

Golden elderberry virus was isolated from all nine examined bushes of golden elder (*Sambucus nigra aurea*). This virus was a 30-nm diameter spherical particle and infected 44 out of 55 herbaceous hosts. It was serologically unrelated to 14 other spherical viruses (Hansen & Stace-Smith 1971). Viruses recorded on *Sambucus* spp. are: cucumber mosaic, Arabis mosaic, tomato black ring, cherry leaf roll, strawberry latent ringspot, tobacco ringspot, tobacco mosaic, tomato ringspot, elderberry latent and elderberry carlavirus (Schimanski 1982). Yellow net, a yellow-pale green colour in veins of some leaves could be caused by a number of viral agents: Arabis mosaic, tomato black ring, cherry leaf roll, strawberry latent ringspot and golden elderberry (Cooper 1979).

X. History

(A) PALAEOBOTANY

Present in the middle substages of Hoxnian and Ipswichian interglacials. In the former it attained 2–5% of the total tree pollen at Birmingham. The earliest Flandrian record is from the Dogger Bank. It is present in zone VIIa but is not frequent until VIIb and VIII. Throughout the Flandrian the records are strongly associated with archaeological sites: Mesolithic 2, Neolithic 3, Bronze Age 6, Iron Age 6, Roman 8, Anglo Saxon and later 4 (Godw. Hist.). There is little evidence that *S. nigra* survived through glacial periods.

(B) SOCIOECOLOGY

The present economic use and future potential of the flower and fruit crop of elder in Britain are discussed by Prendergast & Dennis (1997) who note that around 15 million litres of natural-flavoured elder-based drinks (mostly elderflower cordial) were consumed in 1995 in the UK. This was a 500% increase over 1991. Most of the material used was picked from naturally occurring bushes within a few kilometres of the processing plants, leading the authors to speculate on the future impacts on wild populations.

Elders are grown on a commercial scale in many European countries. The fruits are used for colouring fruit juices and for making elderberry wine and jelly. The flowers are used for elderflower cordial and wine. For a review of the uses of elder in continental Europe, see Treptow (1985).

The pith from elder stems has long been used as a support for hand-sectioning of biological specimens and in fine cleaning of engineering materials. Collection and preparation of elder pith are discussed by Metcalfe (1948). Smith & Secoy (1981) review many historical references to the use of bruised elder leaves or infusions of elder leaves to control various domestic and agricultural pests. Elder has had a long tradition of use in folk remedies and herbalism (Grieve 1985). The bark has strong purgative and diuretic properties and was used in epilepsy. The leaves were used in various preparations to treat bruises and sprains, wounds, eye inflammations and headache. The flowers were used to treat bronchial and pulmonary conditions, tumours and boils. There is much folklore associated with elder, including its value as a protector of people and livestock, the dangers of burning and cutting the wood and links with witchcraft (Grigson 1958; Grieve 1985).

Further investigations of some potential therapeutic uses have been carried out. An aqueous extract of *S. nigra* flowers was found to be effective in stimulating insulin secretion in *in vitro* experiments on mouse abdominal muscle. The extract also enhanced muscle glucose uptake and metabolism (Gray *et al.* 2000). Spray-dried elderberry juice, containing high amounts of anthocyanin glucosides, showed *in-vitro* antioxidant protection from copper-induced oxidation of low-density lipoproteins. This preparation may have potential value as a dietary supplement for moderating the risk of atherosclerosis (Abuja *et al.* 1998).

Sambucus nigra agglutinin (SNA-I) is a lectin, a large class of plant glycoproteins with sugar binding sites, which bind reversibly with specific sugars (see section VI(F) for more detail). SNA-I is unique among lectins in recognizing sialic acid residues, and this has made it invaluable as a probe to detect cell-surface sugars, enzymes and immunoglobulins, and has led to many uses in medicine and physiology. These include studies in the development of cancers (Vierbuchen *et al.* 1995; Fernandez-Rodriguez *et al.* 2000); in the understanding of immunological (Basset *et al.* 2000) and allergic disorders (Ueno *et al.* 1997); in the study of the cell surfaces of normal tissues, for instance the human retina (Kivela 1990), rat kidney and liver (Schmauser *et al.* 1999); in comparison of the surface properties of normal and diseased tissues (Babal *et al.* 1996) and used to facilitate gene transfer into epithelial cells (Yin & Cheng 1994). Lectins can induce allergic responses when present in human diets (Haas *et al.* 1999). These and other applications of plant lectins are reviewed by Singh *et al.* (1999) and Kennedy *et al.* (1995).

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