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## *Viburnum lantana* L. and *Viburnum opulus* L. (*V. lobatum* Lam., *Opulus vulgaris* Borkh.)

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*Viburnum lantana* (Sectio *Viburnum*). Traditionally placed in Caprifoliaceae, but now in Adoxaceae (Stevens 2002). A shrub up to 4(–6) m tall, with a dense growth form partly caused by adventitious shoots and rooting of branches in close contact to the ground. Despite the common name ‘wayfaring tree’ it seldom forms a single main trunk, but is usually much branched from near the base. Twigs terete with few lenticels, grey-brown with dense stellate hairs in their first year, but less hairy and sometimes glabrous by the second year; pith solid, white. Older branches smooth-barked, reddish-brown, may still be somewhat hairy. Fine roots on mature plants mid-brown, 0.3–0.5 mm wide (5 mm back from apex); rootlets 10–15 mm long commonly have 3–4 branches; on longer rootlets (up to 60 mm) there is a dense array of much branched laterals. The species is deciduous when adult but tends to be evergreen as a juvenile (first post-cotyledonary leaves on seedlings may last at least 2 years).

Leaves opposite, exstipulate; petiole (0.5–)1–3(–4) cm long, flattened above, and on the largest leaves with a groove (< 1 mm deep) along its whole length, most densely hairy on the edges of the groove; without glands. Lamina ovate or elongate-ovate, usually acute, slightly cordate at base (3–)4–14(–16) × (2–)3–9(–12) cm and serrulate (rarely crenulate); rugose, dark green and nearly hairless above. In the type variety (*lantana*) the undersides of the leaves appear whitish grey as they carry dense stellate hairs, smaller on the veins than between them. Winter-buds naked (i.e. without differentiated bud scales) but covered by dense stellate hairs; flower buds at least partly covered by bracts.

Inflorescences terminal, flat-topped, umbel-like compound cymes 6–10 cm across, with a hairy stalk 10–20(–25) mm above the pair of leaves or shoot junction below; primary axes of compound cyme one central and usually six lateral (up to seven), 15–25 mm long; two to five secondary axes, 6–15 mm long; and one to five tertiary axes, 5–10 mm long, each with 1–4

flowers. All flowers are fertile and of similar size and form, with an unpleasant smell; they have almost no pedicel but two small bracts. Calyx reduced to five very small teeth, about 0.5 mm long. Corolla creamy-white, rotate, funnel-shaped (3–5 mm long and about 4–8 mm wide at the mouth) with five spreading lobes, lobes twice as long as the tube. The five stamens only slightly longer than the corolla; yellow anthers open toward the centre of the flower. Stigma three-lobed. Ovary inferior, one-celled with a single pendent ovule; two carpels remain undeveloped.

Fruit a strongly flattened oval drupe, with a shiny skin and scattered stellate hairs, 7–11 mm long, 5–8 mm wide and 4–7 mm thick, ripening yellow-green, red, then black. Stone single, flat, leathery, with four ventral and three dorsal ribs, up to 8–8.5 × 5.5–6.5 × 1.5 mm; mean dry mass 35 mg (Lee *et al.* 1991) to 44 mg (Rep. Capac.).

Two varieties occur naturally in Britain: var. *lantana* and var. *glabratum* Chab. (= var. *viride* Kern.). The latter is distinguished by having at anthesis stellate hairs only on the undersides of the leaf veins, and these hairs dropping later so that the underside of the leaf looks green (Chabert 1884); in Britain it seems to be confined to the south-west of England and Wales, east to the Isle of Wight (P. D. Sell & G. Murrell, pers. comm.). Druce (1926) recorded var. *viride* from Buckinghamshire, but we have seen no specimen. Hegi (1926) described f. *cuspidatum* L. et K. Rechinger from Austria; it has acuminate leaves. Cultivars are ‘Aureum’, ‘Rugosum’, ‘Variegatum’, ‘Versicolor’ and ‘Xanthocarpum’ (Krüssmann 1962). See VIII (B) for hybrids commonly planted as ‘*V. lantana*’.

*Viburnum opulus* (Sectio *Opulus*). A deciduous shrub up to 4 m tall; it frequently forms adventitious roots and new vertical shoots on branches close to the ground. Branching pattern is close to a long/short shoot system. Twigs slightly 4–5-angled with few lenticels, glabrous, bright green in their first year, later yellow-grey; pith solid, white. Older branches striped grey and reddish-brown. Fine roots on mature plants mid-brown, c. 1 mm wide (5 mm back from apex); rootlets 10–15 mm long commonly have only one branch. Longer rootlets (< 60 mm long) have unbranched laterals < 12 mm long at intervals of 3–10 mm.

\*Abbreviated references are used for standard works; see *Journal of Ecology* (1975), 63, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and, where different, Stace (1997).

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Leaves opposite, stipulate, petiole 1–2(–3) cm long. Lamina with 3(–5) acuminate, irregularly and shallowly dentate lobes (2–)4–9(–13) × (2–)3–8(–12) cm; fresh green and glabrous on the upper side, sparingly pubescent or glabrescent beneath – in particular, hairs occur near the origins of lateral veins close to the midrib. Petiole always with a shallow groove on the upper side all along it. Stipules pale green, parallel-sided but acute-tipped (subulate), fused with the petiole and diverging from it 1–3(–5) mm above the leaf base, 2–5(–10) mm long and 0.2–0.7 mm wide. Extrafloral nectaries variable with a size of 0.5–1 mm; on some leaves up to five pairs and/or extending onto the edge of the lamina. Often nectaries in a ‘pair’ offset along the petiole. The number of nectaries per leaf is not simply related to lamina area (comparing whole shrubs) but is generally smaller on shade leaves than on sun leaves. For the limited activity of the nectaries see VI (E). Occasionally stipules arising a few mm above the axil end in a small nectary; Goebel (1922; p. 1426) argued that the ‘stipules’ are actually reduced extrafloral nectaries. Buds shortly stalked (< 1 mm) with one to two pairs of scales, the outer pair partly fused, red-brown, usually glabrous, the inner pair even more fused, green with a three-lobed tip. Basal long shoots have long-lived terminal buds, which are six-sided; their scales are particularly distinct as rudimentary leaf bases. Flower buds rounder than vegetative ones.

Inflorescences terminal, on glabrous or shortly glandular stalks 1–4 cm long above the highest pair of leaves, flat-topped, umbel-like compound cymes 5–10 cm across; laxer than in *V. lantana*, and the flowers of unequal size, there being a single row of much larger outer flowers which are sterile and on longer peduncles (< 4 cm). Flowers with an unpleasant, rather sickly smell. Primary axes of compound cyme are one central and usually six lateral (only two to three in shade) and 6–20 mm long; secondary axes four to seven, 3–8 mm long, each carrying one to five flowers. Flowers epigynous with five-lobed calyx and corolla. Corolla of inner flowers yellowish-white, bell-shaped, 4–7 mm in diameter and 2–3 mm long. The stamens twice as long as the corolla; anthers yellow, opening toward the centre of the flower; stigma three-lobed. Corolla of the outer flowers white, flat (9–)15–20(–25) mm in diameter with five egg-shaped petals (one may be slightly larger). These flowers have reduced anthers and carpels, but the small, five-lobed calyx is identical in the two flower types.

Fruit a subglobose drupe, 8–10 mm long, 8–10 mm wide and 7–9 mm thick; after ripening translucent red; flesh more watery than in *V. lantana*, and smell unpleasant, rather sickly. Stone single, flat, leathery, not ridged as in *V. lantana*, 8.5 × 8 × 2 mm; mean dry mass 26 mg (Lee *et al.* 1991) to 46 mg (Rep. Capac.).

Staszkiwicz & Białobrzaska (1997) analysed variation in leaf and fruit morphology of *V. opulus* in Poland. Twelve leaf characters were measured in 14 populations and five fruit characters in eight populations. The authors found no significant difference between leaves

from flowering shoots and those from sterile long shoots, but leaf form changed from the base to the top of long shoots and there was considerable variation between populations. The cultivar ‘Roseum’ (‘snowball tree’), with a more globose compound cyme and only sterile enlarged white flowers, is very widely grown; less common cultivars are ‘Aureum’, ‘Compactum’, ‘Fructuluteo’, ‘Nanum’, ‘Notcutt’s Variety’, ‘Park Harvest’ and ‘Xanthocarpum’ (Krüssmann 1962; Bean 1980).

### I. Geographical and altitudinal distribution

*Viburnum lantana* is almost confined to Europe, and *V. opulus* mainly European, but related taxa are found in the temperate zone of East Asia, which is the centre of diversity of the section *Viburnum*, and in North America, which is the centre of diversity of the section *Opulus*. Naked overwintering buds in *V. lantana* and development of flower buds early in autumn suggest that the plant is suited to relatively mild climates, but compared with *V. rhytidophyllum* Hemsl. ex Forbes & Hemsl. from south-western China, which has larger, evergreen leaves and is often cultivated in gardens in north-western and central Europe, *V. lantana* may perhaps be more suited to climatic conditions in these areas where there are few native broad-leaved evergreens. Both *V. lantana* and *V. opulus* are typically found in scrub, woods and hedges, the former on calcareous soils and the latter especially on damp soils.

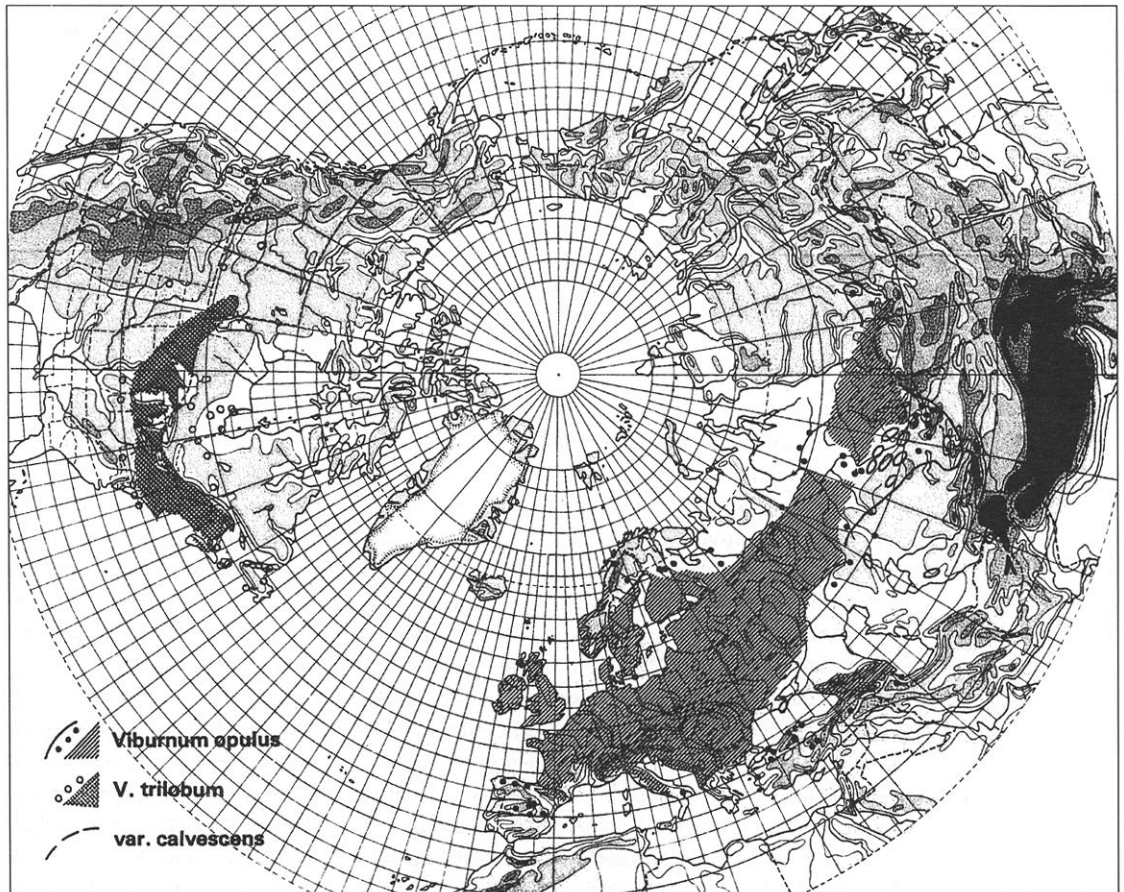
*Viburnum lantana* is found in western, central and southern Europe (Fig. 1a); the range is similar to that of *Ligustrum vulgare* and can be characterized as ‘European temperate’ *sensu* Preston & Hill (1997). Around the Mediterranean it occurs only in some of the more humid mountain ranges (e.g. Abruzzo, Andalusian Highlands, Central Atlas, Kroumerie (Tunisia) and Peloponnese; Herrera 1987; Meusel & Jäger 1992). It occurs further north (as a native) in the British Isles than in central Europe (Fig. 1a); it reaches Belgium, but not the Netherlands, and in Germany it is confined to the southern half (Haeupler & Schönfelder 1988). It ranges from northern Spain to central Ukraine, and is found in northern Asia Minor (Meusel & Jäger 1992). In Russia, *V. lantana* is found only in the south-western parts (the Crimea) and in Georgia only in the Caucasus mountains. The south-eastern limit is in northern Iran (Meusel & Jäger 1992). The north-eastern border is the River Dneiper (‘Dnjepr’), except in its lower parts. However, in cultivation the species fruits even in St. Petersburg (Köppen 1888). In Africa, *V. lantana* occurs in Morocco and Algeria (very rare in both). The species has also been introduced to north-eastern USA (Fernald 1950). In New Zealand, the plant (often used as a rootstock for other *Viburnum* spp.) persists in former gardens, but has not become naturalized in the way that *V. tinus* has (Webb *et al.* 1988).

*Viburnum lantana* is widespread in southern England (becoming rarer northwards to Nottingham and Derby) and in southern Wales (Fig. 2a). In places northwards to

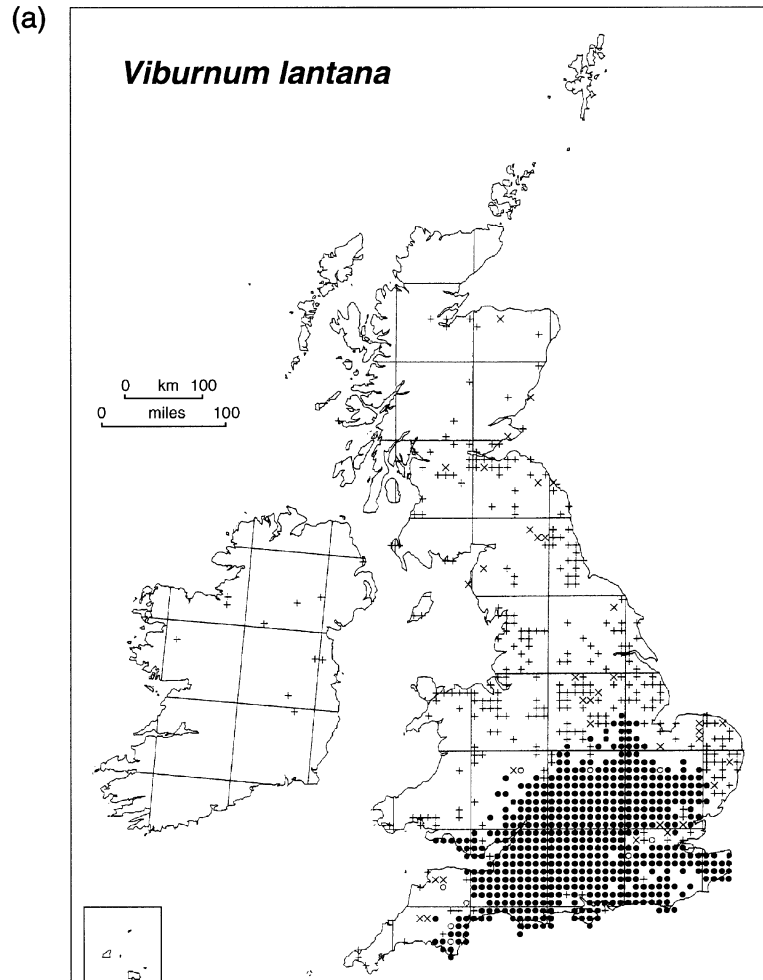
(a)



(b)



**Fig. 1** World distributions of (a) *Viburnum lantana* and (b) *V. opulus*. Closely related taxa of *V. opulus* are *V. opulus* var. *calvescens* (= *V. sargentii* Koehne) in East Asia, and *V. trilobum* Marsh. in North America (●, outlying occurrences; *V. lantana* modified after Meusel & Jäger 1992; *V. opulus* after Hultén & Fries 1986, with permission).



**Fig. 2** Distributions in the British Isles of (a) *Viburnum lantana* and (b) *V. opulus* (see over). Each symbol represents at least one record in a 10-km square of the National Grid. Native: (○) pre-1950, (●) 1950 onwards; introduced: (×) pre-1950, (+) 1950 onwards. Mapped by H. R. Arnold, Biological Records Centre, using Alan Morton's DMAP program, mainly from records collected by members of the Botanical Society of the British Isles.

Moray and in Ireland it is introduced. In recent decades the area of distribution in Germany has been enlarged by planting in hedgerows and on road banks (see, e.g. Trautmann 1976; Reif & Aulig 1990); *V. lantana* is now locally naturalized in some areas of northern Germany (Benkert *et al.* 1998), and even in southern Sweden (Anderberg 1998).

*Viburnum opulus* has a distribution range that is eurasiatic and suboceanic, and markedly different from that of *V. lantana* (Fig. 1b; 'circumpolar temperate' *sensu* Preston & Hill 1997). The species is widespread in western, central, eastern and north-eastern Europe, and extends eastward across Asia. In general it is missing in the area around the Mediterranean Sea, and rare in submediterranean areas, but it extends northward to the boreal zone, much as seen in the closely related *V. sargentii* Koehne of East Asia and *V. trilobum* Marsh. of North America. It is widespread in Scandinavia, although it is limited to the southern boreal zone (Dierssen 1996): in Norway up to 67° latitude, in Sweden rare north of Helsingland (62°) although some individuals are found up to Norrbotten, close to the

polar circle (66.5°, Anderberg 1998); in Finland probably up to 64°, and in northern Russia to about 60° (Köppen 1888). Köppen (1888) suggested that the northern border of *V. opulus* in Russia is correlated with a mean temperature of 8.5 °C in September. The southern border in Russia coincides with the northern margin of the steppe – here the species is present only in sufficiently moist habitats, e.g. in gorges and on northern slopes in the Crimea (Köppen 1888). The species has been introduced to north-eastern USA (Krannitz & Maun 1991b; references therein). It occasionally escapes from cultivation in Victoria, Australia (Ewart 1930), but apparently not in New Zealand (Webb *et al.* 1988).

*Viburnum opulus* is common in England, Wales and Ireland, and less common in Scotland but it extends to Caithness (Fig. 2b).

Both *V. lantana* and *V. opulus* are primarily lowland species north of the Mediterranean region. No value is given in Alt. Range Br. Pl. for the upper altitudinal limit of *V. lantana* in Britain; probably its highest occurrences are in the Marlborough Downs in Wiltshire at *c.* 285 m. The limit is 1450 m in the northern

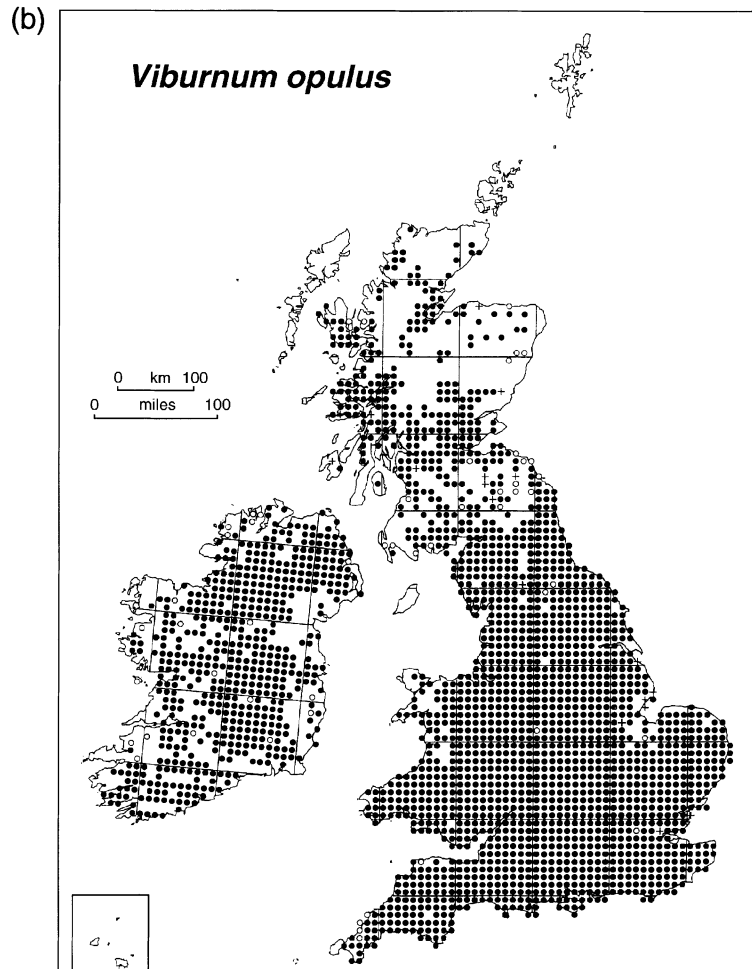


Fig. 2 continued

Alps, 1600–1700 m in the central Alps (Engadin), and 1450–1800 m in Morocco (Meusel & Jäger 1992). Chabert (1884) reported var. *glabratum* occurring at 1800–2000 m in Savoie. In northern Greece *V. lantana* is found most often from (800–)1000 to 1700–1850 m, but its highest locality in the Gramos Mts is at about 2100–2150 m (Boratyński *et al.* 1992).

For *V. opulus* the upper limit is 320 m in Britain (Alt. Range Br. Pl.). In hedgerows of eastern Bavaria, Reif (1983) found the highest abundance of *V. opulus* between 500 and 550 m, and few plants below 450 m or above 700 m. In the Alps the altitudinal limit of *V. opulus* is lower than for *V. lantana*, i.e. 1270 m in the northern Alps and about 1400 m (1700 m, Schütt *et al.* 1994) in the central Alps (Valais). This observation is surprising because a species with a more northern distribution would be expected to have higher altitudinal limits. In the Caucasus it occurs at 1000–2300 m (Köppen 1888).

## II. Habitat

### (A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Although *V. lantana* is the most demanding of the British tall-shrub species in respect of summer warmth,

as judged by its northern limit, it is present on all slopes, at least in southern England, e.g. in the Chiltern Hills. In south-western Germany it was also not found to be favoured by south-facing sides of hedgerows or scrublands (Bronner 1986; Kollmann 1992).

*Viburnum lantana* persists as a seedling in considerable shade, e.g. under a diffuse site factor *sensu* Anderson (1964) of 1–2% in a long-term garden experiment in Cambridge University Botanic Garden (Kollmann & Grubb 1999), but appears to be very light-demanding for onward growth. Kollmann (1997) has argued that in the primeval landscape it was primarily an edge-species rather than a plant of gaps in the forest. It is now found as a flowering adult in fully open to moderately shaded habitats, as in scrub, and the edges of woods or inside woods opened periodically by coppicing.

*Viburnum opulus* is found at sites with lower temperatures than those of *V. lantana* in both summer and winter, and is associated with more shaded habitats. It occurs as healthy, non-flowering bushes in considerable shade in woods, but in the primeval landscape it might still have reached its maximum abundance and optimal reproduction close to forest edges in riverine landscapes or around lakes and mires (Kollmann 1997). In central Europe, it is found more often inside forests or shrublands, i.e. less exposed to direct sunlight

(Ellenberg 1988), and within hedgerows it indicates moist conditions (Richert 1996). In transects through hedgerows, Küppers (1984) found it in the central to lateral parts of the canopy, but absent from the understorey. In a study on hedgerows in northern Germany, *V. opulus* was found to be more frequent on the western and southern sides of hedges (Weber 1975).

#### (B) SUBSTRATUM

In Britain, *V. lantana* is most abundant on freely draining soils, usually derived from chalk or limestone (Oolitic and Magnesian, also Carboniferous in the south and in Denbighshire but not in Derbyshire – see Clapham 1969). It sometimes occurs on soils derived from shallow drift deposits (clay or silt) over chalk or limestone (Grubb *et al.* 1969; Duffey *et al.* 1974). The soils are base-rich and  $\text{pH}_{\text{H}_2\text{O}}$  is most often  $> 7$  but occasionally as low as 5. Rarely it is found on soils derived from andesite, e.g. at Moons Hill in the Mendip region (Nat. Grid ref. ST 648455;  $\text{pH}_{\text{H}_2\text{O}}$  4.9–6.1 at 0–5 cm). The soils on the harder limestones can be very dry in summer. The species is also found occasionally on soils which are liable to severe drying in summer but which suffer a degree of waterlogging in spring, e.g. in woods on boulder clay soils in Cambridgeshire ( $\text{pH}$  5–7), but is absent from soils commonly waterlogged throughout the year, e.g. those of alder woods or scrub on partly dried-out fens such as Wicken Fen in Cambridgeshire. The soils vary widely in availability of N and P, but the species is most dominant on soils rich in both, notably on former rabbit warrens on steep chalk slopes (see III), and the species is more strongly responsive to extra N and P than most British tall-shrub species (see VI (E)). In central Europe also the species is found chiefly on calcareous substrates, and it is missing in mountain ranges with silicate bedrock (Haeupler & Schönfelder 1988; Seybold *et al.* 1996).

*Viburnum opulus* occurs rather rarely on soils which never experience very wet conditions, e.g. on oolitic limestone at Castor Hanglands NNR in Northamptonshire (Duffey *et al.* 1974), and on chalk and sands in Cambridgeshire (Perring *et al.* 1964). Typically it occurs on soils that are usually wet for at least part of the year. These soils include some where summer drying can be severe, e.g. in woods on boulder clay soils in Cambridgeshire, where the species is one of the first to wilt in a dry spell. Its distribution extends to soils that are peaty and waterlogged through most of the profile all year, e.g. in alder woods. The upper pH limit is as for *V. lantana*, and thus the species is missing from coastal salt-enriched soils, but the lower limit is significantly lower – about 4.3. It is not found on mor humus. In northern Germany the species is frequent on moraines from the last glaciation, it is rarer on sandy deposits of the previous glaciation, and it is almost absent from the marshland close to the North Sea (Raabe *et al.* 1987). For both *V. lantana* and *V. opulus*, the soil tolerance in central Europe is similar to that seen in Britain (Oberdorfer 2001).

### III. Communities

The occurrence of *V. lantana* and *V. opulus* in communities in Britain is described following the National Vegetation Classification (Rodwell 1991). *Viburnum lantana* is a frequent member of chalk scrub and of wood margins. The species is found most often in the *Viburnum lantana* subcommunity of the *Crataegus monogyna*–*Hedera helix* scrub community (W21) of Rodwell (1991), where it attains constancy class V, and is associated with other ‘calicolous shrubs’ (*Cornus sanguinea*, *Euonymus europaeus*, *Ligustrum vulgare* and *Rhamnus cathartica*), *Juniperus communis*, *Prunus spinosa*, various *Rosa* spp., *Rubus fruticosus* agg. and sometimes *Corylus avellana* – also several climbers apart from *Hedera helix*: *Bryonia dioica*, *Clematis vitalba*, *Lonicera periclymenum* and *Tamus communis*. The field layer is not especially distinctive (Rodwell 1991). At the northern edge of the range of this subcommunity, in Derbyshire, *V. lantana* is sparse, and the dominant is *Corylus avellana*. Occasionally, *V. lantana* is found in other subcommunities of the *Crataegus monogyna*–*Hedera helix* community (constancy I).

Woods in which *V. lantana* is found are assigned to the *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* (W8), *Fagus sylvatica*–*Mercurialis perennis* (W12) and *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* (W10) communities. For all three communities, Rodwell (1991) reported a constancy value of only I, and the species is confined to base-rich facies of W10. In W8 and W12, the herb layer is much better developed than in the scrub communities, and besides *Mercurialis perennis* includes *Circaea lutetiana*, *Geum urbanum*, *Hyacinthoides non-scripta*, *Viola reichenbachiana* and *Viola riviniana* among many other species. Most of the shrub species associated with *V. lantana* in scrub (not *Juniperus communis*), and all the climbers found there, are also found in woods. Interestingly *V. lantana* is not reported for the *Taxus baccata* community (W13), characteristic of shallow rendzinas on steep chalk slopes.

In central Europe, *V. lantana* is commonest in scrub communities at well-lit forest margins and in hedgerows, often together with *Cornus sanguinea* and *Ligustrum vulgare* (a ‘Mantel’ species *sensu* Ellenberg 1988). Like *Berberis vulgaris* and *Ligustrum vulgare*, it is used as a character species of the alliance Berberidion (Weber 1999), and it is most frequent in the association Pruno-Ligustretum (Oberdorfer 1992, 2001). The species is notably absent from scrub communities of the order Sambucetalia racemosae which are typical for forest gaps and clear cuts; it is also missing from the alliance Pruno-Rubion radulae which is prominent in north-western Germany on slightly acidic soils (Weber 1999). *Viburnum lantana* is also found in light oak and pine forests (*Quercion pubescenti-petraeae* and *Erico-Pinion*), more rarely in rather lightly shading beech and mixed deciduous forest communities (*Carici-Fagetum*, *Galio-Fagetum* and *Galio-Carpinetum*), or montane



silver fir-spruce forest (Galio-Abietenion; Ellenberg 1988). Sometimes suppressed individuals are found in mature deciduous forest, surviving from periods of more open canopy conditions (Von Rochow 1951).

In western Ukraine, *V. lantana* is common in 'mixed oak woods' with an upper tree canopy of *Quercus robur*, *Acer platanoides*, *A. pseudoplatanus*, *Fraxinus excelsior* and *Ulmus glabra*, a lower canopy of *Carpinus betulus*, and a suppressed shrub layer of *V. lantana*, *Corylus avellana* and *Euonymus verrucosus* (Walter 1974). At its eastern limit close to the steppe, the species is found in gorge forests. *Viburnum lantana* does not extend as far east as *Crataegus monogyna* or (especially) *Prunus spinosa* in scrub-forest remnants in the steppe landscape (Hultén & Fries 1986). Also, *V. lantana* is not listed for the 'thorn bush mixed forest' at the southern edge of the 'Waldsteppe' zone in Moldova where the major shrubs among the dwarf gnarled oaks are *Crataegus monogyna*, *Prunus spinosa* and *Rosa* spp. (Walter 1974).

In the Balkans, *V. lantana* is found in a broad diversity of fairly dry forest types (alliances Carpinion, Fagion illyricum, Ostryo-Carpinion orientalis, Orno-Ericion, Ostryo-Fagion, Quercion frainetto, Quercion pubescentis and Fago-Colurnium; Horvat *et al.* 1974), including communities close to the dry margin of forest growth (e.g. the *Quercus virgiliana-Quercus pubescens-Carpinus orientalis* community). As in central Europe, the species is common in scrubland communities, for example the Corno-Ligustretum. These scrublands constitute the only community type in which the two *Viburnum* species co-occur, and they do so only rarely.

In Britain, *Viburnum lantana* is a locally dominant invader of former rabbit warrens on the steep slopes of valleys in the chalk, e.g. at the Devil's Dyke near Brighton (TQ 265110) and Deep Deene near Alfriston (TQ 542023), but it is rare on ex-arable land; in continental Europe, it is perhaps more common as an invader in orchards and vineyards (Knapp & Reichhoff 1975; Wolf 1980; Sendtko 1999), but it comes late in the successional sequence (e.g. Schmidt 1983). *Viburnum lantana* is rarely seen invading derelict grassland where *Juniperus communis*, *Crataegus monogyna*, *Prunus spinosa* and *Rosa canina* are more effective (Tansley 1922; Kienzle 1984; Kollmann 1992; Schreiber 1997). However, during the development of scrub on abandoned grasslands there can be a steady increase in abundance of *V. lantana* with scrub size and age (Kollmann 1994). Willems (1978) reported that *V. lantana* and *Cornus sanguinea* were common invaders of continuous turf on chalk in southern England, following cessation of grazing, but that observation is not consistent with our experience.

*Viburnum opulus* is quite different from *V. lantana* in the spectrum of communities in which it is found, and it has a wider range. First, it is found in carr, with a frequency value of I, in the *Salix cinerea-Betula pubescens-Phragmites australis* (W2), *Alnus glutinosa-Carex paniculata* (W5) and *Alnus glutinosa-Urtica dioica*

(W6) communities of Rodwell (1991), but it is absent from the yet more waterlogged *Salix cinerea-Galium palustre* (W1) and *Salix pentandra-Carex rostrata* (W3) communities, and from the *Betula pubescens-Molinia caerulea* community (W4) of more northern, highly acidic soils. In carr, other shrubs also have mostly low constancy values: *Corylus avellana*, *Crataegus monogyna*, *Frangula alnus*, *Prunus spinosa*, *Rhamnus cathartica*, *Ribes nigrum*, *R. rubrum* and *Rosa canina*. Tall herbs are abundant, especially in W2 and W4, notably *Eupatorium cannabinum*, *Filipendula ulmaria*, *Lysimachia vulgaris* and *Lythrum salicaria*. The scrambler *Solanum dulcamara* is often common, and the climber *Humulus lupulus* is occasional.

On the uplands, *V. opulus* is a species of low constancy (I) in woods on base-rich soils which are moist for most of the year (*Fraxinus excelsior-Acer campestre-Mercurialis perennis* community, W8) and in the equivalent community on base-poor brown soils (*Quercus robur-Pteridium aquilinum-Rubus fruticosus*, W10) but not in that on extremely acidic soils (*Quercus* spp.-*Betula* spp.-*Deschampsia flexuosa*, W16). Only in the very local *Teucrium scorodonia* subcommunity of the *Fraxinus-Acer-Mercurialis* community, found chiefly in west-central England, does *V. opulus* attain a constancy value of III. The major herbs on the base-rich soils are listed above in connection with *V. lantana*; on the base-poor soils forb cover may be sparse, but the bracken fern and grasses often have high cover. *Viburnum opulus* is present in the beech equivalent of the *Fraxinus-Acer-Mercurialis* community (the *Fagus sylvatica-Mercurialis perennis* community, W12) but is not recorded from beechwoods on moderately acidic soils (*Fagus sylvatica-Rubus fruticosus* community, W14) or the beechwoods on strongly acidic soils (*Fagus sylvatica-Deschampsia flexuosa* community, W15). It is also not recorded for the northern equivalents of W8 and W10 (the *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* community, W9, and the *Quercus petraea-Betula pubescens-Oxalis acetosella* community, W11), despite these communities being found within its geographical range.

Rodwell (1991) does not record *V. opulus* from the *Crataegus monogyna-Hedera helix* community (W21), but it does occur rarely. In this community, in W8, W12 and the more base-rich facies of W10, it overlaps the range of *V. lantana*.

In central Europe, *V. opulus* is present in a wider range of communities than *V. lantana* as found by Reif (1983) for hedgerows in northern Bavaria. It is found along the margins of floodplains and lakes; here it is a character species of the scrub community *Salici-Viburnetum opuli*, and more rarely it occurs in other scrub communities within the alliances Berberidion and Pruno-Rubion radulae (Weber 1999). It is also present in moist forest communities of the alliance Alno-Ulmion (e.g. Pruno-Fraxinetum and Alnetum incanae, often with *Rubus caesius*), in drier variants of alder swamps (*Caricelongatae-Alnetum*), in oak-hornbeam



communities (Stellario-Carpinetum), lime-hornbeam forests (Tilio-Carpinetum), and even in moist beech forests (Fagion; Ellenberg 1988). It occurs in hedgerows, chiefly those on moist soils (Carpino-Prunio, Salicion cinereae; Richert 1996; Weber 1999), and this is the habitat in which it sometimes occurs together with *V. lantana* (Reif 1983). *Viburnum opulus* is rarely found in recent plantations (Pfadenhauer & Wirth 1988; Reif & Aulig 1990), indeed in < 1% in the latter study.

In northern Europe, where the climate is moister, *V. opulus* occurs in a range of forest communities on less reliably moist soils (Dierssen 1996): Scots pine forests (Pulsatillo-Pinetea, e.g. Melica-Pinetum and Saniculo-Pinetum), oak forests (Quercion robori-petraeae) and lime-maple forests (Tilio-Acerion) as well as grey alder forests (Alnion incanae). In a descriptive study in southern Sweden, *V. opulus* was associated with dense forest edges, wide hedgerows and hedgerows with a high forest cover nearby (Herlin & Fry 2000). However, there was no significant difference in overall frequency in forest edges vs. hedgerows, and *V. opulus* was the rarest among 12 animal-dispersed woody species.

In eastern Europe, *V. opulus* occurs in Quercio-Carpinetum and in moist mixed pine forests, but also in moist forest islands with *Populus tremula* and *Quercus robur* in the steppe landscape (Walter 1974). Between the two mountain ranges of the Caucasus, *V. opulus* is found in alder swamps with *Alnus barbata*, but it is also listed for montane beech forests; in central Asia the species grows in subalpine *Pinus sibirica* forests of the central Altai mountains (1400–2200 m; Walter 1974).

In the Balkans, *V. opulus* occurs in moist to wet floodplain forests of the alliances Salicion albae, Alnion glutinosae, Alno-Ulmion and Carpinion, including the associations Populetum nigro-albae, Carici-Alnetum glutinosae, Genisto-Quercetum roboris, Leucojo-Fraxinetum parvifoliae, Querco-Ulmetum moesiaticum, Pruno-Fraxinetum and Querco-Carpinetum betuli. However, the species is also found in scrublands, e.g. Corno-Ligustretum illyricum, and in riverine forests of the montane zone, e.g. Pino-Betuletum pubescentis and Oxali-Alnetum incanae (Horvat *et al.* 1974).

In Britain, *V. opulus* commonly invades wet meadows and mown fens which have become derelict (Duffey *et al.* 1974). The same is observed in south-western Germany, although along a transect from old scrub to recently abandoned wet meadows, the species was absent from the latter (Kollmann 1994). Like *V. lantana*, it is a late invader of abandoned grassland or old-fields (see, e.g., Schmidt 1983; Bakker *et al.* 1996).

#### IV. Response to biotic factors

Both species regrow very well on cutting (Beckett & Beckett 1979). *Viburnum lantana* is highly unpalatable to deer and rabbits, while *V. opulus* can be palatable to deer and moderately palatable to rabbits (see IX (A)). The ability of *V. lantana* to invade rabbit warrens

depends partly on unpalatability, and partly on ability to regrow after being eaten. Possibly its name 'wayfaring tree' reflects its frequent occurrence in the past on the edges of tracks, enriched by the faeces of stock. In an unpublished outdoor experiment done over two growing seasons by W. G. Lee and P. J. Grubb, testing the sensitivity of seedlings of tall-shrub species to root competition from frequently cut *Festuca rubra*, *V. lantana* proved to be markedly more sensitive than *Cornus sanguinea* and *Rhamnus cathartica* (59% reduction in shoot length of the second year vs. 30% and 17%).

#### V. Responses to the environment

##### (A) GREGARIOUSNESS

Both *Viburnum* species typically occur as isolated individuals, though *V. opulus* can spread widely by layering. Both species occur less commonly in groups; they rarely become locally dominant, for example in scrub vegetation (Kollmann 1994). In the Netherlands, density of *V. opulus* was found to be negatively related to the area of isolated oak forests, and the chance that a forest was occupied by *V. opulus* increased with increasing perimeter of the woodlots (Van Ruremonde & Kalkhoven 1991).

##### (B) PERFORMANCE IN VARIOUS HABITATS

No information found.

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

Hard frosts are not recorded as causing obvious damage to shoots of either species in southern Britain, but clones of *V. opulus* can differ in their hardiness to frost, and this fact has consequences for landscape gardening, e.g. in northern Scandinavia (Juhanoja *et al.* 1998). The freezing point of the sap of buds and leaves of *V. lantana* and *V. opulus*, and of eight other shrub species was determined by W. G. Lee (unpubl. data) in 1984–85 ( $n = 10$  for all species and occasions). The mean freezing points of the sap of winter buds of *V. lantana* and *V. opulus* were  $-9.6\text{ }^{\circ}\text{C}$  and  $-7.0\text{ }^{\circ}\text{C}$  (cf.  $-6.3\text{ }^{\circ}\text{C}$  to  $-9.4\text{ }^{\circ}\text{C}$  for most other shrub species,  $-9.8\text{ }^{\circ}\text{C}$  for *Juniperus communis*, and  $-10.1\text{ }^{\circ}\text{C}$  for *Rhamnus cathartica*). The mean freezing points of the sap of spring leaves were  $-5.2\text{ }^{\circ}\text{C}$  and  $-5.5\text{ }^{\circ}\text{C}$  for *V. lantana* and *V. opulus*, to be compared with  $-6.1\text{ }^{\circ}\text{C}$  to  $-9.6\text{ }^{\circ}\text{C}$  for other dicotyledons and  $-11.3\text{ }^{\circ}\text{C}$  for *J. communis*. The mean values for summer leaves in 1984 and 1985 were  $-3.5\text{ }^{\circ}\text{C}$  and  $-2.9\text{ }^{\circ}\text{C}$  for *V. lantana* and *V. opulus*, respectively. These values may be compared with the range of  $-3.8\text{ }^{\circ}\text{C}$  to  $-5.8\text{ }^{\circ}\text{C}$  found for seven other dicotyledonous shrubs, and  $-8.2\text{ }^{\circ}\text{C}$  for *J. communis*. Overall, there is little evidence that *V. lantana* or *V. opulus* should be more sensitive to frost than other tall-shrub

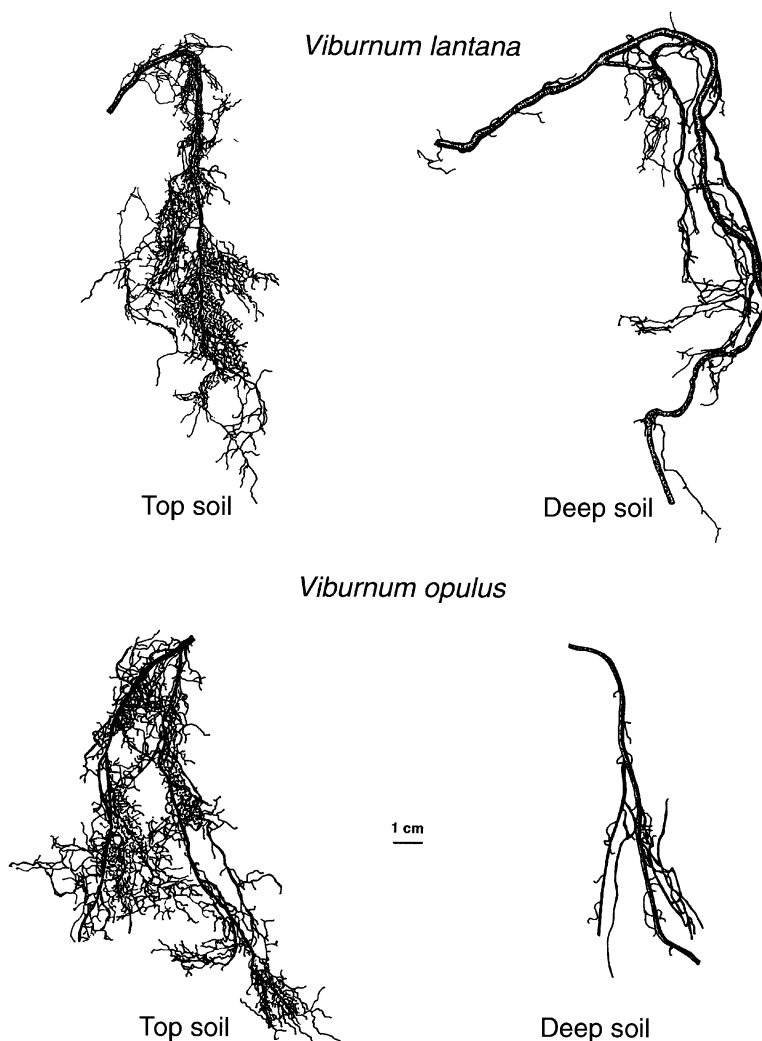
species in western Europe, but it is just possible that they are significantly more sensitive in spring.

On clayey soils in Cambridgeshire, *V. opulus* readily wilts in dry spells, and *V. lantana* wilts similarly markedly in very dry summers; at Buff Wood (Cambridgeshire, TL 283503) there was extensive die-back in 1989–90 of shoots of *V. opulus* which wilted early and severely in the dry summer of 1989, whereas little damage was observed on shoots of *V. lantana*. In dry years, when *V. lantana* wilts strongly on clayey soils, it does not do so on well-drained chalk-derived soils; the explanation is probably partly the large reservoir of ‘available’ water in chalk-derived soils (Smith 1980), and possibly partly shallow-rooting of adults on clayey soils which are liable to periodic waterlogging, particularly in winter and spring. Certainly, seedlings of *V. lantana* in waterlogged pots have roots confined to the surface few cm in a way not seen in other British tall-shrub species (P. J. Grubb, pers. observ.), but see VI (A) regarding the depth of rooting of adult shrubs. A similar but less extreme sensitivity of rooting to waterlogged soil was recorded for *Cornus sanguinea* (Kollmann & Grubb 2001).

## VI. Structure and physiology

### (A) MORPHOLOGY

The root systems of one adult *V. lantana* and two *V. opulus*, grown at the edges of the plot described by Grubb *et al.* (1999) and 17 years old, were excavated. There was c. 50 cm of long-cultivated humus-enriched soil with a good tilth (‘top soil’) over very dense, somewhat stony calcareous clay subsoil (‘deep soil’; Fig. 3). The roots spread very little beyond the crowns (cf. *Cotoneaster lacteus* W.W. Smith in a nearby hedge which made much wider-running major roots). Neither species had a taproot, and both produced numerous major roots descending gently and branching little (apart from fine laterals) while growing mostly at a depth of 10–20 cm; those of *V. lantana* were 7–12 mm in diameter 30 cm from the crown, and those of *V. opulus* 10–12 mm. One *V. opulus* produced an asymmetric system with one long spreading root 25 mm in diameter at 30 cm from the crown. Both species had the very plentiful fine roots concentrated in the top 20 cm of the



**Fig. 3** Root structure of *Viburnum lantana* and *V. opulus* in top soil and deep soil in a common garden experiment over 17 years (for more details of the experiment see Grubb *et al.* 1999 and main text).

profile, supporting the notion of Bartels (1993). However, both also produced roots which penetrated far into the dense clayey subsoil, to a depth of 100 cm in *V. lantana*, and to 106 and > 90 cm in *V. opulus*. Most of the descending roots of *V. lantana* were c. 2.5 mm in diameter where they entered the clayey subsoil but some were of 1.5–2.0 mm; those of *V. opulus* were mostly 1.5–2.5 mm in diameter where they entered the subsoil, but a few were of 4 mm. The roots in the subsoil, apparently not described before, branched at very acute angles, seeming to exploit slight cracks in the clay, and the finer parts were thicker and much less branched than the fine roots in the topsoil (Fig. 3). However, there were no clear anatomical differences in root structure (e.g. with respect to intercellular air spaces) between roots from the top soil and from the deep soil in the two *Viburnum* species (J. Kollmann, pers. observ.). The deep rooting into very dense and presumably often anaerobic subsoil by *V. lantana* is surprising in view of the sensitivity of its seedlings to waterlogging (see V(C)).

The fact that the fine roots are thicker and less densely branched in *V. opulus* than in *V. lantana* is consistent with the general trend, seen especially clearly in the tropics, for plants of wetter-climate forests to have thicker and less densely branched roots than those of drier forests (cf. Coomes & Grubb 2000).

In the experiment of Grubb *et al.* (1999), wood density for stems of 1–2 cm diameter was higher in *V. lantana* (0.63 g cm<sup>-3</sup>; cf. 0.84 g cm<sup>-3</sup> given by Schütt *et al.* 1994) than in *V. opulus* (0.54 g cm<sup>-3</sup>), and the two species spanned the full range of other European tall-shrub species. Wood of both *Viburnum* species has distinct heartwood; it is diffuse-porous and rays are conspicuously heterogeneous (Schweingruber 1990). In transverse section, the pores are relatively small and generally solitary. The growth ring boundaries are indistinct, but marked by 2–3 rows of tangentially flattened ground tissue cells in the late wood. The parenchyma is apotracheal and diffuse. In tangential section the rays are generally uni- to biseriate, rarely triseriate with biseriate rays 8–15 cells high. *Viburnum lantana* can be differentiated from *V. opulus* by the presence of spiral thickenings in the fibre-tracheids. More information and figures are given by Schweingruber (1990). In a survey of stem anatomy and growth in seedlings of a wide range of woody species, *V. opulus* had average values in diameter of the 10 widest xylem conduits (16.0 µm) and percentage of xylem tissue occupied by cell wall material (46%; Castro-Díez *et al.* 1998); growth conditions were as for Castro-Díez *et al.* (2000). Considered across species, the mean diameter of the widest xylem conduits and the percentage of xylem tissue not occupied by wall were positively cor-related with seedling relative growth rate. No comparable data are available for *V. lantana*.

After 12 years in a common garden experiment in eastern England, on clayey soil derived from riverine deposits, subject to strong drying out in drought years, *V. lantana* had fewer main stems than *V. opulus*: the mean numbers of stems per plant were 7 and 16, respec-

tively (basal areas 98 cm<sup>2</sup> and 139 cm<sup>2</sup>). This was true even though the mean heights were very similar (3.1 m and 3.3 m). Branching of the shoots of both species is pseudo-dichotomous because the leaves are opposite and, after the terminal bud has developed into an inflorescence, the two lateral buds develop into new leading shoots (Jessen & Mentz 1940; Schulz 1999).

The mean values for leaf dry mass per unit area (LMA) of mature leaves on lightly shaded mature individuals of *V. lantana* and *V. opulus* in Buff Wood, Cambridgeshire (TL 283503) in June–July 1985 were found by W. G. Lee (unpubl. data) to be c. 40 g m<sup>-2</sup> and c. 36 g m<sup>-2</sup>, respectively. At that time, six other tall-shrub species nearby gave values of 33–50 g m<sup>-2</sup>. The LMA values for these plants were determined at monthly intervals from April to October; in *V. lantana* and *V. opulus* it decreased between April and June–July (starting from c. 50 g m<sup>-2</sup> and c. 43 g m<sup>-2</sup>, respectively), while the mean thickness of the leaf declined (certainly true in *V. lantana* where the young leaf is dominated by a thick midrib) and/or dry mass per unit volume declined. The same trend was found for *Cornus sanguinea* and *Ligustrum vulgare*, but four other species (*Crataegus monogyna*, *Euonymus europaeus*, *Prunus spinosa* and *Rosa canina*) showed the reverse trend in LMA, indicating that the mean thickness of the leaf increased and/or the dry mass per unit volume increased.

J. H. C. Cornelissen (pers. comm.) found specific leaf area (SLA) values of 54–76 g m<sup>-2</sup> for unshaded mature leaves of adult plants of *V. opulus* in central England. They had a mean stomatal density of 126 mm<sup>-2</sup> on the lower surface. In using plant material from the experimental shrub plot described by Grubb *et al.* (1999), we found mean stomatal densities of 127 ± 18 mm<sup>-2</sup> on the lower surface in sun leaves of *V. opulus* and 65 ± 16 mm<sup>-2</sup> for shade leaves. In *V. lantana* there were 145 ± 46 mm<sup>-2</sup> stomata in sun leaves and 65 ± 25 mm<sup>-2</sup> in shade leaves (means ± SD, five measurements on three leaves, respectively). No stomata were found on the upper leaf surface in both species.

In a comparison of 3–4 replicate seedlings of 29 native European temperate trees and shrubs grown in growth chambers under about 19% daylight, Castro-Díez *et al.* (2000) found that leaves of *V. opulus* were relatively thin (105 µm; range of all species 95–257 µm) but had a relatively high leaf mass per unit area (LMA, 44 g m<sup>-2</sup>; 18–54 g m<sup>-2</sup>). In this study lamina thickness and LMA were independent; seed was from Cressbrook Dale, Peak District (J. H. C. Cornelissen, pers. comm.). Castro-Díez *et al.* (2000) did not study *V. lantana*.

#### (B) MYCORRHIZA

Both species have vesicular-arbuscular mycorrhiza (Harley & Harley 1987).

#### (C) PERENNATION: REPRODUCTION

In a long-term garden experiment on the growth of fleshy-fruited species (Grubb *et al.* 1999), the individuals of

*V. lantana* produced flowers after 5–6 years, while *V. opulus* flowered after 4–5 years, and the trees *Crataegus monogyna* and *Sorbus aria* only after 11–12 years. Only minor differences were observed between two provenances of the *Viburnum* species. Schopmeyer (1974) reported first flowering of *V. opulus* after 3–5 years. Hegi (1926) recorded a maximal age of 50 years for *V. opulus*. In cultivation, the two *Viburnum* spp. are generally grown from seed, but rooting of cuttings is also possible (Schütt *et al.* 1994).

#### (D) CHROMOSOMES

$2n = 18$  for both species (Tischler 1950).

#### (E) PHYSIOLOGICAL DATA

##### *Growth rates of seedlings and responses to shade, nutrient supply and soil drying*

Grubb *et al.* (1996) found that the maximum relative growth rate (RGR) values of seedlings of *V. lantana* and *V. opulus* in their first season are relatively low, when compared with those of other northern European tall-shrub species, and this fact is consistent with their relatively large embryo-cum-endosperm dry mass values. In a study on seedling growth, allocation and leaf attributes of about 40 deciduous woody species from the temperate zone in solution culture in sand within controlled-environment cabinets under about 19% daylight (Cornelissen *et al.* 1996), *V. opulus* had values for RGR ( $0.077 \text{ day}^{-1}$ ), leaf area ratio (LAR,  $14.1 \text{ mm}^2 \text{ mg}^{-1}$ ) and SLA ( $22.6 \text{ mm}^2 \text{ mg}^{-1}$ ) which were fairly near to the mean of all deciduous species (RGR,  $0.101 \text{ day}^{-1}$ ; LAR,  $15.9 \text{ mm}^2 \text{ mg}^{-1}$ ; SLA,  $30.6 \text{ mm}^2 \text{ mg}^{-1}$ ). However, these results were markedly different from those found for seedlings under 11% daylight on scrubland soil by Grubb *et al.* (1996), i.e. RGR,  $0.026 \text{ day}^{-1}$ ; LAR,  $22.6 \text{ mm}^2 \text{ mg}^{-1}$ ; and SLA,  $51.3 \text{ mm}^2 \text{ mg}^{-1}$ . The mean density of stomata on the lower leaf surface was markedly higher in the seedlings of Cornelissen *et al.* (1996) than in mature leaves of the species ( $151 \text{ mm}^{-2}$  vs.  $126 \text{ mm}^{-2}$ ; see VI (A)).

Grubb *et al.* (1996) found seedlings of both *Viburnum* spp. species to have a high potential for survival in deep shade. Plants were grown on two chalk-derived soils, one from under *Bromopsis erecta* and low in available N and P, and another from under *Crataegus monogyna* and high in available N and P. Survival over one summer in 0.3% daylight was 90–100% on the grassland soil, but only 30–40% on the scrub soil. The rates of growth were less affected by shade (0.3–11% daylight vs. 66% daylight) than those of most other tall-shrub species studied. Uniquely among the 10 shrub species tested, *V. opulus* yielded more in 11% daylight than in 66%; its mature lamina size was also largest in the 11% treatment, whereas *V. lantana* had its largest leaves in the 66% treatment. The RGR of *V. lantana* was more responsive to the increased nutrient supply in scrub soil as

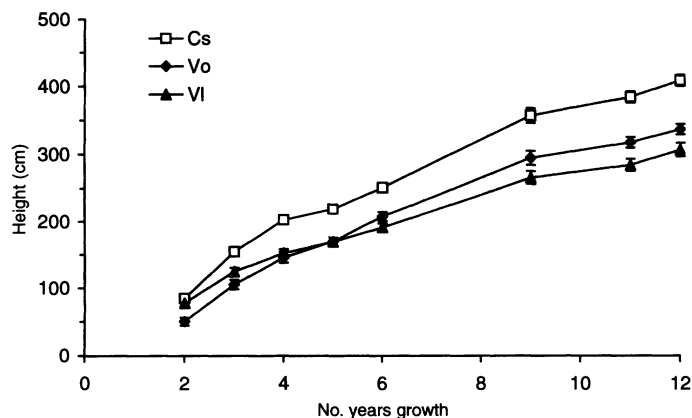
opposed to grassland soil than that of any other species tested. In 11% daylight the extent of increase in RGR of *V. opulus* was similar to that found for *Rosa canina*.

In the same study, shading led to a reduction of the root mass fraction (RMF) of *V. opulus* and all other tall-shrub species tested except *V. lantana*. Shading increased the leaf mass fraction (LMF) of *V. opulus* but not that of *V. lantana*, and caused a greater increase in the SLA of *V. opulus* than in that of *V. lantana*. Grubb *et al.* (1996) suggested that these distinctions in the responses of RMF, LMF and SLA may facilitate establishment of *V. lantana* in dry shade.

Sack & Grubb (2002), using a new experimental technique which truly separates shade and drought effects, found that there was no interaction of these effects on seedling RGR in *V. lantana*, *V. opulus* or *V. tinus*. They found that for all species RGR in 3–4% daylight (neutral shade) was reduced to 56–73% of that in 30–40% daylight, but that – as expected from their field distributions – sensitivity of RGR to soil-drying decreased in the order *V. opulus* > *V. lantana* > *V. tinus* (the last being found naturally in Mediterranean sclerophyll communities). Indeed, *V. tinus* showed no sensitivity to the degree of soil drying which reduced the growth of *V. opulus* and *V. lantana* significantly. Incidentally, the same study showed that whereas the RGR of *Hedera helix* was reduced considerably when the plant was grown in green shade as opposed to neutral shade at 3–4% daylight, that was not true of any of the three *Viburnum* spp. tested.

Kollmann & Grubb (1999) reported rates of survival for first-year seedlings and pre-established seedlings in deep shade under a mixture of shrub species in a long-term garden experiment over the period April–September in 1995, when August was exceptionally hot and dry. For first-year seedlings of *V. lantana* ( $n = 102$ ) the rate of survival was 18%, near to the mean of 22% for the 13 species with most abundant seedlings, but half that of *Hedera helix* – the species accumulating most seedlings over a decade. As expected, the survival rate of *V. opulus* ( $n = 62$ ) was lower; in fact it was zero (not 24% as reported, in error, by Kollmann & Grubb 1999). For pre-established seedlings the rates of survival produced a similar picture: *V. lantana* ( $n = 502$ ) 75%, and *V. opulus* ( $n = 13$ ) 62%. For *Hedera*, survival of pre-established seedlings was significantly greater in 1995 under species which dried the soil less during that very dry summer (Kollmann & Grubb 1999); this result is compatible with the idea that differences in survival of the two *Viburnum* spp. in deep shade in the field are commonly more dependent on tolerance of soil-desiccation than tolerance of shade.

Seedlings of *V. lantana* grown in deep tubes of chalkland soil, which were accidentally but persistently waterlogged, grew extremely shallow roots and discoloured shoots while those of *Cornus sanguinea*, *Crataegus monogyna*, *Ligustrum vulgare*, *Rhamnus cathartica* and *Rosa canina* appeared unaffected (W. G. Lee & P. J. Grubb, unpubl. data); *V. opulus* was not included in that experiment. In a further experiment, seedlings of both species were



**Fig. 4** The heights attained by *Viburnum lantana* (VI), *V. opulus* (Vo) and the comparator species *Cornus sanguinea* (Cs) in a common garden experiment over 12 years (means  $\pm$  SE, after Grubb *et al.* 1999).

grown in pots of chalk grassland soil in a controlled-environment cabinet and subjected to waterlogging; those of *V. lantana* soon showed epinasty (leaves not wilted but strongly curled downward with the lamina firmly rolled upward) like those of *Cornus sanguinea*, but those of *V. opulus*, *Crataegus monogyna*, *Euonymus europaeus* and *Rhamnus cathartica* did not do so, while those of *Ligustrum vulgare* and *Rosa canina* did so only marginally (W. G. Lee & P. J. Grubb, unpubl. data). The leaves of *V. lantana* turned brilliant crimson in colour, while those of *V. opulus* became suffused with pink.

#### Growth rates of saplings

In a common garden plot with both *Viburnum* species and nine other fleshy-fruited tall-shrub species, the rates of sapling height growth remained constant for some years, though after 9 years most rates began to decline (Fig. 4). Canopy diameter was always strongly correlated with plant height. The mean heights of *V. lantana* and *V. opulus* after 12 years (3.1 m and 3.3 m, respectively) were lower than for any of the other shrubs tested except the slow-growing *Juniperus communis*. Unfortunately, the *Viburnum* spp. were not included in the important study of Küppers (1985) who found that the competitive ability of shrub species in hedgerows was more closely related to patterns of allocation than to either net photosynthesis or water use efficiency.

#### Responses of adult plants to drought and ozone

The two *Viburnum* spp., like *Cornus sanguinea* (Kollmann & Grubb 2001), wilt strongly during drought, but – in contrast to *Crataegus monogyna*, *Prunus spinosa* and *Rosa canina* – they do not show premature yellowing and abscission of the older leaves. At the end of August 1989, following a sustained drought, adult leaves of lightly shaded plants of *V. lantana* and *V. opulus* ( $n = 6$ ) on boulder clay soil at Buff Wood in Cambridgeshire had mean relative water concentrations of 52% and 59% (at saturation the water concentration values were 74% and 68%). At this stage in life, the key

difference between the species seems not to be in the degree of leaf drying sustained, but the resistance of the buds to desiccation; several plants of *V. opulus* showed considerable die-back by the next summer, while plants of *V. lantana* which had seemed similarly strongly wilted showed no twig- or branch-death the next year.

Gas exchange and ozone-induced foliar injury were intensively measured in summer on leaves of *V. lantana* and 12 other deciduous woody species in forests of southern Switzerland (Skelly *et al.* 1998; Zhang *et al.* 2001). Plants were grown in open plots, in open-top chambers receiving carbon-filtered air, and in open-top chambers receiving non-filtered air. Significant variation in the effects of ozone on gas exchange was detected among species with a reduction of average net photosynthesis and average stomatal conductance under ozone treatment by a factor of two. *Viburnum lantana* was among the most sensitive species, and the most to least symptomatic species grown within open-plots ranked *Prunus serotina* > *Salix viminalis* > *Viburnum lantana* > *Rhamnus cathartica* > *Betula pendula* > *Sambucus racemosa* > *Morus nigra* > *Prunus avium* > *Fraxinus excelsior* > *Frangula alnus* > *Alnus viridis* > *Fagus sylvatica* > *Acer pseudoplatanus* (VanderHeyden *et al.* 2001).

#### Differences between sun and shade leaves

The most strongly shaded leaves of *V. lantana* are dimorphic, i.e. some are very small relative to sun leaves and others larger in area than most sun leaves. In contrast, *V. opulus* has only smaller leaves in the shade, the condition found in most tree and shrub species which show a significant difference between the two leaf types (R. Atkinson & S. Relf, pers. comm.).

Papavassiliou (1991) made a critical study of photographed leaves on plants of *V. opulus* grown in the long-term garden experiment described by Grubb *et al.* (1999), and showed that during senescence there was a significant decrease in dry mass in both sun and shade leaves, but generally no significant change in leaf area. The percentage decrease in dry mass was not

**Table 1** Concentrations of major nutrients in sun and shade leaves of *Viburnum opulus*, including results of a one-factor ANOVA (\*,  $P < 0.05$ ; means  $\pm$  SE;  $n = 8$ , for potassium  $n = 7$ ). Observations by Papavassiliou (1991) in eastern England

	Nutrient concentrations (mg g <sup>-1</sup> dry mass)		
	N	P	K
Sun leaves	11.1 $\pm$ 0.33	1.13 $\pm$ 0.14	15.7 $\pm$ 1.4
Shade leaves	9.8 $\pm$ 0.36	1.60 $\pm$ 0.15	19.1 $\pm$ 0.49
<i>P</i>	*	*	*

significantly different between sun and shade leaves, but varied appreciably between individual plants ( $n = 4$ ): sun leaf means 7–22% (overall mean 15%) and shade leaf means 14–25% (overall mean 20%). Senescence and leaf fall occurred much earlier in shade leaves; half of those marked had fallen within 14 days of the first falling (during heavy winds or strong rainfall) while few sun leaves fell until 28 days after the first fell. Shade leaves showed a greater tendency to be pendent (wilted) during senescence. Also shade leaves turned yellow in autumn while the sun leaves turned purple-red, suggesting a greater availability of sugars in the sun leaves for manufacture of anthocyanins. In the same study no significant difference was found between sun and shade leaves in the percentage of N or P lost (and apparently resorbed) from the leaves during senescence. The mean value for N was 36%, and for P 22%.

Before senescence there were significant differences between the sun and shade leaves in the concentrations of major nutrients (Table 1). The absolute concentrations reported in this study are possibly low compared with those generally found in the wild; parallel work with *Cornus sanguinea* found a mean concentration of 13 mg g<sup>-1</sup> for N in plants in the garden bed, to be compared with 15–25 mg g<sup>-1</sup> reported by Mwalukomo (1987) for plants in the wild. On the other hand, Cornelissen *et al.* (1997) reported values for N of 13.8 mg g<sup>-1</sup> (P, 2.02 mg g<sup>-1</sup>; K, 12.5 mg g<sup>-1</sup>) for seedlings of *V. opulus* in solution culture in sand within controlled-environment cabinets under about 19% daylight. These nutrient values were lower than the grand means for 45 deciduous woody species (N, 25.2 mg g<sup>-1</sup>; P, 3.04 mg g<sup>-1</sup>; K, 18.1 mg g<sup>-1</sup>). Decomposition of fallen leaves was found by Cornelissen (1996) to be faster in *V. opulus* than in *V. lantana*; the rates of the latter species were close to the grand mean of 57 deciduous woody species in Europe, while the rates for *V. opulus* were similar to those found for *Cornus sanguinea*, *Fraxinus excelsior* and *Ulmus glabra*. Schütt *et al.* (1994) suggested that fast decomposition in these species is a result of relatively high protein concentrations in the newly fallen leaves, but leaf structure and low concentrations of inhibitory substances may be equally important (Grime *et al.* 1996; Cornelissen *et al.* 1999).

The lesser development (and occasional lack) of extrafloral nectaries on shaded leaves parallels the lack

of stinging hairs on deeply shaded seedlings of *Urtica dioica*, the lack of spines on deeply shaded seedlings of *Ilex aquifolium* (P. J. Grubb & L. Sack, pers. obs.), and the smaller accumulation of phenolics in shaded leaves of at least some tropical trees (Waterman & Mole 1989).

#### Functioning of the extrafloral nectaries

We have never seen nectar or ants on the extrafloral nectaries of *V. opulus* in the field, and we have repeatedly failed to provoke accumulation of nectar on nectaries of shoots collected in summer and kept overnight in a warm, water-saturated atmosphere. In both respects, *V. opulus* differs from *Prunus avium* and *Sambucus nigra*. However, some of the nectaries on shoots collected in spring 2002 from the plot described by Grubb *et al.* (1999) did produce nectar – enough to form hemispheres of solution. Shoots collected on 1 April (leaf blades 10–30 mm across) and 15 April (leaf blades 25–45 mm across) and kept in a damp atmosphere overnight showed what seemed to be nectar production on about half of the leaves, and clear drops of nectar on 10–20% of nectaries. Only 3/40 leaves on shoots collected on 8 May made nectar, and 4/5 nectaries on the responsive leaves. Only 3/36 leaves on shoots collected on 23 May gave a positive result, and only 5/15 nectaries on those leaves. On 21 June, 36 leaves were collected with a total of 81 extrafloral nectaries; kept overnight as before only one extrafloral nectary secreted nectar on each of two leaves.

#### (F) BIOCHEMICAL DATA

The bark of both *Viburnum* spp. was used to treat various diseases (Hegi 1926), and some compounds with pharmacological potential have been found in the bark and the leaves, i.e. the bitter resin viburnin,  $\alpha$ - and  $\beta$ -amyryn, oxalates, and the glycosides astragalin and paeonosid (Frohne & Pfänder 1987; Roth *et al.* 1994).

Beckett & Beckett (1979) recorded that fruits of *V. opulus* are mildly poisonous to humans when raw, but not after cooking, while raw fruits of *V. lantana* are merely unpleasant to humans. Schopmeyer (1974) referred to use of *V. opulus* fruits as food for humans (see also X). The fruit flesh of both species contains calcium oxalate crystals, and fruits of *V. opulus* valeric acid (Hegnauer 1973; p. 657). A detailed analysis of the lipid compounds of seeds of *V. opulus* was made by Yunusova *et al.* (1998) and Karimova *et al.* (2000). Recently various water-soluble polysaccharides with physiological activity have been isolated from fruit flesh of *V. opulus* (Ovodova *et al.* 2000), but their physiological relevance for palatability of the fruits is not yet clear.

#### VII. Phenology

Beckett & Beckett (1979) recorded that in Britain leaves of both species open in April, that leaves of *V. lantana*

may turn reddish in September and are abscised in October, and those of *V. opulus* regularly turn red in September to October and are abscised in October to November. Sylvia Papavassiliou (pers. comm.) found the same for abscission of *V. opulus*, and Küppers (1984) reported a similar phenological timing in central Europe. In eastern Europe (about 300 km west from Moscow), the growing season of *V. opulus* seems to be shorter, because leaves are developed first in mid-May and leaf abscission is already finished in late October (Karpov 1973 in Walter 1974).

In Britain, *V. lantana* flowers from late April to June, and *V. opulus* in June to July (Fl. Br. Isl.; Beckett & Beckett 1979; Snow & Snow 1988). In continental Europe, the flowering times are similar, and show only little delay in the areas with cooler, later springs (Küppers 1984; Englund 1993b; J. Kollmann, unpubl. data). Even in central Sweden, flowering of *V. opulus* occurs in the second half of June (Eriksson & Ehrlén 1991). In 2002, after an exceptionally mild winter, *V. lantana* in Cambridgeshire began to open its flowers in the first or second week of April.

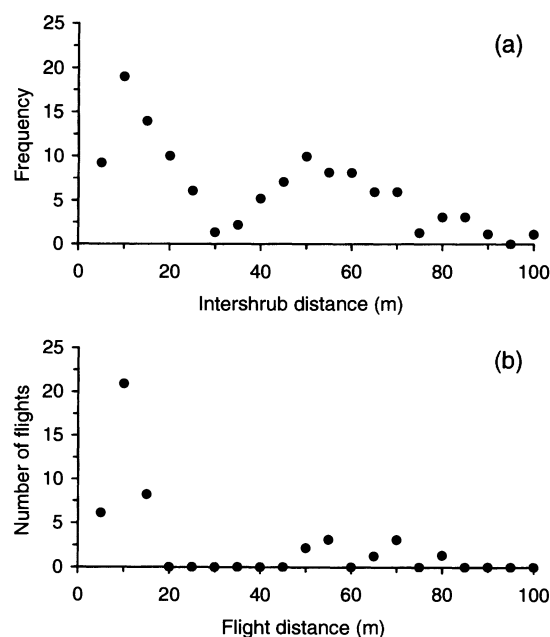
In the British Isles, *V. lantana* fruits from late July to September (Fl. Br. Isl.). Snow & Snow (1988) found that around Aylesbury in southern England there was up to 3 weeks variation between individuals. In southern France and south-western Germany, most fruits ripen in August, few in late July and some remain in September (Debussche & Isenmann 1987; Kollmann 1994, 1996). There is little overlap between the fruiting seasons of the two *Viburnum* species; *V. opulus* fruits ripen in western, central and northern Europe in September to November (Fl. Br. Isl.; Küppers 1984; Eriksson & Ehrlén 1991; Kollmann 1994; Kollmann & Pirl 1995; Pirl 2000). Thus, *V. lantana* belongs to the group of summer-fruiting species including *Rubus fruticosus* agg. and *Sambucus nigra*, while *V. opulus* belongs to the autumn-fruiting group including *Crataegus monogyna* and *Ligustrum vulgare* (cf. Stiles 1980; Herrera 1987; Eriksson & Ehrlén 1991). Fruits of *V. lantana* are commonly all taken by mid-September, but those of *V. opulus* remain on the shrubs for a long time in autumn and winter after apparently becoming ripe (see VIII (C)).

## VIII. Floral and seed characters

### (A) FLORAL BIOLOGY

In flowers of the two *Viburnum* species both selfing and insect pollination have been observed (Fl. Br. Isl.). In *V. lantana* only little nectar is offered, and the flowers seem to be attractive mainly to pollen-gathering insects such as beetles and honeybees, although wild bees are occasional visitors, and Westrich (1989) in an extensive study in south-western Germany noted only *Andrena fulva*. In *V. lantana* selfing seems to be possible because the anthers are placed directly above the stigma.

In *V. opulus* pollination by hoverflies and beetles (leading to outbreeding) prevails, whereas selfing



**Fig. 5** Distribution of distances between individual *V. opulus* plants and of recorded flights by *Cetonia* beetles. (a) Distances between all 16 flowering shrubs, and (b) actual distances of moves made by 45 beetles (after Englund 1993b).

seems to be rare (Schütt *et al.* 1994). Müller (1873; p. 364) listed the Syrphidae *Eristalis arbustorum* L., *E. nemorum* L., *E. sepulcralis* L., *E. tenax* L., *Helophilus florens* L. and *H. pendulus* L., as well as the Tachinidae *Echinomyia fera* L., the Halictidae *Halictus sexnotus* K. Psd., and the Nitidulidae *Meligethes* spp. and the Scarabaeidae *Phyllopertha horticola* L. The insects take up some of the scarce nectar offered at the surface of the carpels. However, in a comprehensive survey of insect visitors on flowers of *V. opulus* in southern Canada, where this species is introduced, Krannitz & Maun (1991a) found 49 species of insects, ranging across five orders: Syrphidae (hoverflies), Halictidae and Andrenidae (native solitary bees) were the families with the most species carrying large loads of pollen of *V. opulus*. Plant bugs moved infrequently between plants, and therefore did not pollinate many individuals. Non-syrphid flies and beetles carried minimal amounts of pollen. The authors concluded that solitary bees are particularly effective pollinators. This result contrasts with that of Englund (1993b) who investigated over 4 years movement patterns of *Cetonia* beetles (Scarabaeidae), the most important pollinators of *V. opulus* in central Sweden. Beetles were marked individually, and tracked throughout their visits to flowering individuals. Beetle abundance differed greatly between study years. The beetles showed fidelity to individual shrubs but did perform frequent interplant flights (Fig. 5). *Viburnum opulus* was preferred to other plants flowering at the same time. Individuals in unshaded locations with large numbers of inflorescences and flowers per inflorescence were preferred. On average, beetles flew four times the horizontal



nearest-neighbour distance between flowering individuals (c. 18 m), leading to relatively long-distance pollen dispersal.

In a second study, Krannitz & Maun (1991b) investigated the effects of the floral display in *V. opulus* on fruit initiation and maturation. The size of the floral display was manipulated by planting individuals alone and in groups of 5 or 10 in 1985, and 2 or 6 in 1986. At the level of the individuals, the attractiveness of the inflorescence was altered by leaving 0, 4 or all sterile flowers in 1985, and 0 or all in 1986. Removal of sterile flowers did not lead to a significant reduction in fruit initiation or maturation, whereas the plant-grouping treatment had a significant effect in 1985 (not in 1986). The number and proportion of fruits initiated per plant were higher in larger groups of plants; 6.9%, 15% and 23% fruits produced per plant, respectively, for those alone and those in groups of 5 and 10 plants. Higher rainfall in 1986 might have been the reason for an overall higher production of fruits (32% vs. 11%) which could have over-ridden any effect of group size. Very few fruits were initiated when insects were excluded by bagging inflorescences (0.03% of the flowers per inflorescence). Self-pollination resulted in some fruit initiation (1.9%), but significantly more fruits were initiated from hand cross-pollination (84%) and from natural exposure to pollinators (18%). The effect of hand pollination indicates pollen limitation in this study.

#### (B) HYBRIDS

No hybrid is recorded for either species by Hyb. Br. Isl. or Heß *et al.* (1980), but  $\times$  *rhytidophylloides* J.V. Suringar (*V. lantana*  $\times$  *V. rhytidophyllum* Hemsl. ex Forbes & Hemsl., which is widely cultivated) has been recorded at two sites in Kent (Clement & Foster 1994) and three sites in Surrey: Banstead Downs, 51/253608; Long Hill, 41/886458; and Tilford Common, 41/874425 (A. C. Leslie, pers. comm.). Peter D. Sell (pers. comm.) has found that this hybrid is commonly being planted as '*V. lantana*' in new woods around Cambridge, and we suspect that the same is happening more widely. He has suggested that var. *rugosum* Lange of

*V. lantana* may perhaps be a back-cross between *V.  $\times$  rhytidophylloides* and *V. lantana*.

#### (C) SEED PRODUCTION AND DISPERSAL

##### *Fruit and seed form and contents*

For both species there is appreciable variation in the mean values for characteristics of the fruits that are relevant to dispersal. For *V. lantana* mean fruit lengths of 9.1 mm and 8.8 mm, respectively, have been recorded from southern England (Snow & Snow 1988) and Spain (Herrera 1987). For *V. opulus* mean lengths of 9.3 mm, 9.0 mm and 10.2 mm, respectively, have been recorded from central Sweden (Englund 1993a), southern England (Snow & Snow 1988) and Spain (Herrera 1987). These fruits are slightly above the modal size found by Herrera (1987) for 111 fleshy-fruited species in Spain, and only marginally acceptable to smaller passerines, notably the warblers.

Recorded variation in fruit mass values is greater. For *V. lantana* mean fruit fresh mass values of 280 mg and 250 mg were recorded from southern England (Snow & Snow 1988; Lee *et al.* 1991), and 160 mg from Spain (Herrera 1987). For *V. opulus*, values of 380 mg and 460 mg were observed in southern England (Snow & Snow 1988; Lee *et al.* 1991) and those of 494 mg and 480 mg in central Sweden (Eriksson & Ehrlén 1991; Englund 1993a). A value of 370 mg was found in Switzerland by Müller-Schneider (1986). In southern England the percentage of the fruit fresh mass in 'seed' (stone) was 25% and 14% for *V. lantana* and *V. opulus*, respectively (Lee *et al.* 1991); mean dry mass values for the stone were 35 mg and 26 mg, respectively – much lower than the values of 44 mg and 46 mg reported by Salisbury (Rep. Capac.). Cornelissen *et al.* (1996) recorded 21 mg for seeds of *V. opulus* from central England, and Eriksson & Ehrlén (1991) recorded 30 mg in central Sweden. The mean dry mass value for the embryo-cum-endosperm fraction (EEF) in the collections of Lee *et al.* (1991) was 17 mg for both species. Kollmann *et al.* (1998) reported from south-western Germany virtually the same mean dry mass for the

**Table 2** Allocation of biomass (a) and nitrogen (b) in fruits of *Viburnum lantana* and *V. opulus* in samples from southern England ('coat', fibrous coat of the stone; EEF, embryo-cum-endosperm fraction; WC, water content; after Lee *et al.* 1991)

(a)	Dry mass per fruit (mg)				Allocation (%)			Stone (mg)	Pulp WC (%)
	Total	Pulp	Coat	EEF	Pulp	Coat	EEF		
<i>V. lantana</i>	69.9	34.8	18.4	16.8	49.7	26.3	24.0	35.2	81.5
<i>V. opulus</i>	68.3	42.3	9.2	16.8	61.9	13.4	24.7	25.9	89.2

(b)	N concentration (mg g <sup>-1</sup> )		Content (µg per fruit)		Allocation (%)	
	Pulp	EEF	Pulp	EEF	Pulp	EEF
<i>V. lantana</i>	7.0	25.9	243	435	34.3	61.3
<i>V. opulus</i>	5.8	25.6	245	428	35.4	61.8

stone of *V. lantana* as Lee *et al.* (1991) in England (36 mg) and a somewhat higher value for the EEF (22 mg). The mean dry mass value for the stone of *V. lantana* in Spain (32 mg; Herrera 1987) was also close to that recorded in England by Lee *et al.* (1991). Snow & Snow (1988) reported mean 'seed weights' of 59 mg and 55 mg for *V. lantana* and *V. opulus*, respectively; we assume these are fresh mass values (cf. 62 mg and 65 mg in the samples of Lee *et al.* 1991). The allocation pattern in fruits of the two *Viburnum* species is different, although total dry mass and EEF are similar (Table 2a). In *V. lantana* the allocation to the fibrous coat of the stone is higher and that to the pulp fraction lower.

Lee *et al.* (1991) found the nitrogen concentration in the EEF was 26 mg g<sup>-1</sup> in both species (cf. 25 mg g<sup>-1</sup> in *V. lantana* of Kollmann *et al.* 1998), and in the seed coat (testa plus endocarp) 2 mg g<sup>-1</sup> in both species (Table 2b). The concentration in the EEF was lower than found for 6/7 other tall-shrub species studied by Lee *et al.* (1991), and lower than found for 10/12 of other species studied by Kollmann *et al.* (1998); in both studies the species with the lowest concentration was *Ligustrum vulgare* (21–22 mg g<sup>-1</sup>).

The mean water concentration in the flesh has been found to be consistently lower in *V. lantana* than in *V. opulus*: 77% vs. 84% and 82% vs. 89% in southern England (Snow & Snow 1988; Lee *et al.* 1991, respectively), and 63% vs. 78% in Spain (Herrera 1987). Debussche & Isenmann (1987) recorded a value of 78% for *V. lantana* in southern France; Eriksson & Ehrlén (1991) found 88% for *V. opulus* in Sweden. The mean for 111 species in Spain was 71% (Herrera 1987). The nitrogen concentrations of the flesh in southern England were 7.0 mg g<sup>-1</sup> and 5.8 mg g<sup>-1</sup> dry mass in *V. lantana* and *V. opulus*, respectively (say 4.4% and 3.6% protein); the protein concentrations of the two species recorded in Spain were much lower (1.7% and 1.0%; Herrera 1987). In Spain the lipid concentrations were higher in *V. opulus* than in *V. lantana* (Table 3). In southern France the protein and lipid concentrations for *V. lantana* were both 2% (Debussche & Isenmann 1987); Eriksson & Ehrlén (1991) found lipid concentration to be 1.3% for *V. opulus* in Sweden. The values for protein were the lowest among both the 111 species sampled in Spain and the nine species sampled in Britain. The lipid values were well below the mean of 6.9%. In contrast, Herrera (1987) found that the fibre content of *V. lantana* flesh was well above the mean (26% vs. 16%) while that for

*V. opulus* was low (8.4%). The concentration of non-structural carbohydrates in *V. lantana* flesh was equal to the mean (Table 3), but considerably higher in *V. opulus*.

Herrera (1987) found similar concentrations of most mineral elements in the flesh of the two species, except for higher concentrations of Cu and Zn for *V. lantana*, and a higher Fe concentration for *V. opulus*.

### Dispersal

Both species are dispersed by frugivorous birds, but the fruits of *V. lantana* seem to be much more attractive to them. This species produces fruit earlier (see VII) and has a bicoloured display with a mixture of red and (fully ripe) black fruits while the unripe fruits are yellowish-green, but the key difference in attractiveness appears to relate to the chemistry of the flesh (see below).

*Viburnum lantana* is fairly attractive to passerine birds in late summer, but less so than *Sambucus nigra* (Snow & Snow 1988). Therefore, its seeds are widely dispersed but mainly to other shrubs and isolated trees (Kollmann 1994). However, because the shrub is typically not very abundant at a local scale, and produces a smaller crop than other fleshy-fruited species, total densities of dispersed seed are relatively low (Kollmann 1996). The birds taking *V. lantana* in southern England were found by Snow & Snow (1988) to be in the thrush and warbler families: *Turdus merula* > *Erithacus rubecula* > *Sylvia atricapilla* > *S. curruca* > *T. philomelos* > *S. borin* (order in decreasing frequency of fruit consumption). The first three species were found by Fuentes (1994) to be also the most frequent consumers in north-western Spain. For various European regions, Schuster (1930) and Müller-Schneider (1986) additionally listed *Bombycilla garrulus*, *Turdus iliacus*, *T. pilaris*, *T. torquatus* and *T. viscivorus*. In a large survey on 25 dispersers of 64 fleshy-fruited species in southern France, Debussche & Isenmann (1989) reported only two carnivorous mammals, the stone marten (*Martes foina*) and red fox (*Vulpes vulpes*), dispersing seed of *V. lantana*. Herrera (1989) failed to find seed of *V. lantana* in faeces of stone marten, red fox and badger (*Meles meles*). Maybe the 'design' of these fruits is not suitable for seed-disperser mammals (but see contrasting findings by Hernández 2001). Feeding on this species declines as soon as other fruits of more attractive species become available in September and October. Thus, many fruits – especially those of late-fruited

**Table 3** Constituents of the pulp of fruits of *Viburnum lantana* and *V. opulus* in Spain (Herrera 1987) and the energy content of whole fresh fruits in England (\*Snow & Snow 1988)

	Lipids (% dry pulp)	Protein (% dry pulp)	Soluble carbohydrate (% dry pulp)	Energy dry pulp (kcal g <sup>-1</sup> dry pulp)	Energy whole fruit (kcal g <sup>-1</sup> fresh fruit)*
<i>V. lantana</i>	2.6	1.69	66.9	3.0	0.54
<i>V. opulus</i>	4.2	0.98	82.9	3.8	0.52

individuals – are not taken and remain dried up on the shrubs (Snow & Snow 1988). Relatively few seeds are destroyed on the parent shrub by seed predators, mainly by bullfinches (*Pyrrhula pyrrhula*) in winter.

For *V. opulus* in southern England, Snow & Snow (1988) observed fruit consumption in December by *Turdus philomelos* > *T. merula* > *T. viscivorus* > *Erithacus rubecula* > *T. iliacus* > *Sylvia atricapilla* (decreasing fruit consumption). The same authors list *Pyrrhula pyrrhula* as most important predator of seeds still on the bush. *Viburnum opulus* is also dispersed by red foxes (*Vulpes vulpes*, Turcek 1967), and by *Bombycilla garrulus*, *Turdus pilaris* and *T. torquatus* (Schuster 1930; Müller-Schneider 1986). Fruits of *V. opulus* are unattractive to most birds (Hegi 1926). Müller-Schneider (1983) reported from central Switzerland that the fruits persist on the plant in winter and are consumed by birds only under really adverse weather conditions. The same was found near Munich by Zedler (1954), who also reported that eventually many fruits shrivelled and fell to the ground, where the seeds were eaten by mice. One possible partial explanation of the low attractiveness to birds might be the fact that they are still firmly attached to their stalks and are pluckable by birds only with difficulty until the end of November (Snow & Snow 1988; Englund 1993a). However, some over-ripe fruits remain on the shrubs even until next spring, and there are few signs of shrivelling during the winter or infestation by insects or microorganisms (Englund 1993a). Similarly, the fruits of *Viburnum dilatatum* in Japan have a low rate, and late time, of removal (Kominami 1987), also those of *V. acerifolium*, *V. lentago* and *V. prunifolium* in North America (Schopmeyer 1974). Jones & Wheelwright (1987) studied the reasons for the low rate of consumption of *V. opulus* fruits during winter in North America, and concluded that the very low pH of the sap (2.8) and the content of chlorogenic acid might render the fruits unpalatable as well as repelling pathogens. The fruits did not become more palatable during winter even though the sugar content increased. Sorensen (1983) found that caged *Turdus merula* and *T. philomelos* rejected artificial 'dough fruits' when flavoured with the juice of *V. opulus* but not when flavoured with other fleshy-fruited species. One reason might be the valeric acid in the fruits of *V. opulus*. A recent study on frugivory of *V. opulus* comes from central New York (Witmer 2001). Here again the fruits of *V. opulus* ripen in autumn and remain uneaten throughout the winter months but were often completely consumed in April and May, almost exclusively by cedar waxwings (*Bombycilla cedrorum*). Sugar solute concentration of fruit pulp increased over the winter season through dehydration. When wild cedar waxwings were presented with early season and remnant late-season fruits, they strongly preferred early season fruits. This result demonstrated that springtime consumption of fruits of *V. opulus* is not caused by chemical changes in the pulp during winter. Cedar waxwings often fed intermittently on the male catkins of eastern cotton-

woods (*Populus deltoides*) when eating *V. opulus* fruits. Feeding experiments with captive waxwings showed that birds lost body mass on either *V. opulus* fruits or *P. deltoides* catkins alone, but maintained or gained body mass when offered both foods simultaneously due to the combination of fruit sugars and protein from pollen. Apparently, a low nitrogen : carbohydrate ratio and secondary, acidic compounds of *V. opulus* fruits created a short-term demand for supplemental protein in birds feeding on fruits of this species.

Both *Viburnum* species may benefit from secondary dispersal by other passerine birds and small mammals who hoard these seeds and lose (i.e. disperse) at least some of them. Englund (1993a) investigated fruit removal, seed predation and dispersal in *V. opulus* for 2 years in central Sweden. The fruit crop was ripe in September but mainly removed during November to December. Large infructescences were located in the upper parts of the shrubs and had the slowest removal rates. The most important seed predators were bullfinches (73% removal) and bank voles (*Clethrionomys glareolus*, 26%). Possibly, the rodents occasionally acted as dispersal agents through forgotten fruits. The rate of seed predation was very high (c. 99%). Legitimate seed dispersers, i.e. waxwing (*Bombycilla garrulus*) and thrushes (*Turdus* spp.), removed only a minute fraction of the fruit crop (0.3%), and fallow deer (*Dama dama*) contributed only infrequently to fruit removal. The legitimate dispersers preferred other fruits (e.g. *Sorbus aucuparia*) to those of *V. opulus*; they switched to *V. opulus* when other fruit resources had been depleted. However, there might be sporadic massive seed dispersal by waxwings in certain favourable years.

#### Seed production

The values for seed production reported by Kollmann (1996) and Pirl (2000) for *V. lantana* (6 seed m<sup>-2</sup> year<sup>-1</sup>) and *V. opulus* (9 seed m<sup>-2</sup> year<sup>-1</sup>) in central European scrub communities are modest compared with those reported by them for other species in the same communities, e.g. *Cornus sanguinea* (122 seed m<sup>-2</sup> year<sup>-1</sup>), *Crataegus monogyna* (260 seed m<sup>-2</sup> year<sup>-1</sup>), *Frangula alnus* (165 seed m<sup>-2</sup> year<sup>-1</sup>) and *Sambucus nigra* (275 seed m<sup>-2</sup> year<sup>-1</sup>). However, seed production was estimated on the basis of seed rain records and the calculations may partly reflect differences in species abundance. We have no precise information on annual variation in seed production and possible masting events, as suggested by Herrera (1998) for fleshy-fruited species in southern Spain, among them *V. tinus*. However, our impression is that there is a relatively modest variation from year to year, except that in strong drought years the crop may fail, at least on clayey soils, as in 1995 in the long-term experiment of Grubb *et al.* (1999).

The number of fruits per infructescence seems to be slightly larger generally in *V. lantana* than in *V. opulus*, say 15–30 vs. 10–25 on well-lit shoots; exceptionally the number reaches 60–120 on *V. lantana* but rarely > 75 on

*V. opulus*. On the most strongly shaded flowering shoots of both species the number of fruits per infructescence is 1–10.

#### Natural levels of recruitment

In successional scrub developed on calcareous grassland in south-western Germany, natural levels of seedling recruitment in *V. lantana* were rather low (0.2 seedlings m<sup>-2</sup>) corresponding to the sparse seed rain (see above; Kollmann 1996). Seedlings of *V. lantana* amounted to 1–2% of all fleshy-fruited species. Seedlings of this species were less abundant than those of *Rosa canina*, *Cornus sanguinea*, *Crataegus monogyna* and *Ligustrum vulgare*, but more abundant than those of *Berberis vulgaris*, *Euonymus europaeus* and *Sambucus nigra*. Survival rates after 5 months were about 35%, and lower than those of the more abundant shrub species in the same study (41–61%), except *Cornus sanguinea* (36%).

In a long-term common garden experiment on regeneration of fleshy-fruited species under various species in a continuous patch of scrub, seedlings of *V. lantana* had fairly high densities (3.7 m<sup>-2</sup>), whereas *V. opulus* (0.5 m<sup>-2</sup>) ranked low among the nine planted tall-shrub species and nine invading fleshy-fruited species (Kollmann & Grubb 1999). The greater recruitment of *V. lantana* than of *V. opulus* in this experiment fits with the fact that seedlings of species with at least partly winter-green leaves were particularly common (*Hedera helix* > *V. lantana* > *Ligustrum vulgare* > *Ilex aquifolium*). Seedling survival of both species was lower under conspecific shrubs, in accordance with the Janzen–Connell hypothesis (Janzen 1970; Connell 1971). In a related glasshouse experiment of Finkelstein (1999), the rates of growth of seedlings of four shrub species were determined on soil cores (including the roots) from under mature individuals of the same species in the long-term garden experiment. The mean RGR value for *V. lantana* was significantly higher on soil from under *Cornus sanguinea* or *Crataegus monogyna* than on soil from under *Rosa canina* or *V. lantana*. In three out of five cases seedlings had their lowest RGR values on soil from under *V. lantana*. The differentially inhibitory effect on seedling growth may reflect differences in rooting density, species-specific nutrient-exploitation, soil pathogens or autotoxic effects.

In the long-term garden experiment described by Kollmann & Grubb (1999), the mean number of seedlings of all fleshy-fruited species accumulating under *V. lantana* was smaller than that under *V. opulus* (9 vs. 20 seedlings m<sup>-2</sup>). The mean diffuse site factor *sensu* Anderson (1964) under the two species in mid-summer was very similar (1.08% and 0.99%, respectively). However, in the strong drought of August 1995, the topsoil dried to a greater extent under *V. lantana* than under *V. opulus* (down to c. 7.0% dry mass as opposed to 8.0%). The idea that greater drying of the soil limits recruitment is consistent with the fact that the number

of accumulated seedlings of *Hedera helix* (the most abundant recruit) was related – across all species – to the water content left in that dry August, and not to the diffuse site factor.

#### (D) VIABILITY OF SEED: GERMINATION

Most fleshy-fruited shrubs have no persistent seed bank, and several authors have observed few or no viable seeds of these species in soil samples (Thompson *et al.* 1997). For example, Kollmann & Staub (1995) found no seeds of *V. lantana* in soil from c. 10-year shrub on abandoned calcareous grassland in south-western Germany, although fruiting shrubs of the species were present in the study patch; similar results were reported by Poschlod *et al.* (1991) and Dutoit & Alard (1995) for comparable habitat types. Kollmann (1996) found also no dormant seeds of *V. lantana* in c. 50-year mixed shrub, although about 6 seeds m<sup>-2</sup> year<sup>-1</sup> were recorded in the seed rain; this result was in stark contrast to that for certain other fleshy-fruited species, e.g. *Rosa canina* or *Sambucus nigra*, which had high densities both in seed rain and in the soil seed bank. A similar lack of viable seeds in soil samples of wetlands was reported for *V. opulus* by Van der Valk & Verhoeven (1988).

Baskin & Baskin (1998) classified *V. opulus* (and six other *Viburnum* spp.) as having seeds with a ‘deep simple epicotyl morphophysiological dormancy’ based on research of Giersbach (1937). In these species the radicle emerges in autumn and the shoot in the following spring—a sequence that might be interpreted as an adaptation to a temperate climate; such epicotyl dormancy is not found in *Viburnum* spp. in the southern USA (Schopmeyer 1974). Gibberellic acid can be used to substitute for 2–3 months of cold stratification in breaking epicotyl dormancy (Fedec & Knowles 1973), and there is some evidence that the inhibition of shoot growth is controlled by the cotyledons and not by the epicotyl *per se* (Knowles & Zahlik 1958). Germination of *V. lantana* and *V. opulus* occurs mostly in the first spring after fruiting with few additional seedlings in the second spring (Beckett & Beckett 1979; Lee *et al.* 1991; Kollmann 1994). A lack of emerging seedlings in the first spring and germination in years 2 and 3 (as in Schütt *et al.* 1994; Pirl 2000) may be caused by storage conditions of the seeds. The results of Kollmann (1996) support the view that seeds of *V. lantana* are viable for < 2 years, as also described by Kinzel (1926) and Krüssmann (1997).

In the experimental scrub plot used by Kollmann & Grubb (1999), most seedlings of *V. opulus* emerged in April (52 of 66) and most of *V. lantana* in May (44 of 84), whereas no germination was observed in March (except one *V. opulus*), July and August (J. Kollmann, unpubl. data). Muller (1978) describes germination of *V. lantana* in early summer to autumn, which does not accord with our experience, and that of *V. opulus* in spring–early summer. Germination rates of *V. lantana*

**Table 4** Phytophagous insects and mites recorded as occurring on *Viburnum lantana* and *V. opulus*, ordered alphabetically; symbols explained in footnotes

Insect or mite	Host plant	Feeding habit	Status	Reference
<b>ACARINA</b>				
<b>Eriophyidae</b>				
<i>Eriophyes viburni</i> (Nalepa)	VI/Vo	Galling	–	3, 12, 20, 25, 27
<i>Vasates oblongus</i> (Nalepa)	VI	Galling	–	12, 20
<b>COLEOPTERA</b>				
<b>Chrysomelidae</b>				
<i>Orsodacne cerasi</i> (L.)	V*	Mining	Pest	10, 11
<i>Pyrrhalta viburni</i> (Paykull)	VI/Vo	–	–	10, 22, 34
<b>Curculionidae</b>				
<i>Phyllobius pyri</i> (L.)	Vo*	–	Pest	23
<i>Rhynchaenus lonicerae</i> (Herbst)	V	Mining	Extinct	29
<b>Scarabaeidae</b>				
<i>Trichius fasciatus</i> (L.)	VI/Vo	–	Rare	21
<b>DIPTERA</b>				
<b>Cecidomyiidae</b>				
<i>Contarinia sambuci</i> (Kaltenbach)	VI/Vo	Galling	–	2, 4, 8
<i>Contarinia viburnorum</i> Kieffer	VI/Vo	Galling	–	4, 9
<i>Phlyctidobia solmsi</i> (Kieffer)	VI	Galling	–	9, 26
<i>Syndiplosis lonicearum</i> F. Loew.	VI	Galling	–	2
<b>HETEROPTERA</b>				
<b>Aneuridae</b>				
<i>Aneurus avenius</i> (Dufour)	VI*	–	–	32
<b>HOMOPTERA</b>				
<b>Aphididae</b>				
<i>Aphis citricola</i> van der Goot	V*	–	Introd. pest	13
<i>Aphis fabae</i> Scopoli I	VI/Vo	Rolling	Pest	7, 13, 24, 33
<i>Aphis lantanae</i> Koch, C.L.	VI	Rolling	–	7, 33
<i>Aphis viburni</i> Scopoli	VI/Vo	Rolling	–	7, 33
<i>Aulacorthum solani</i> (Kaltenbach)	V*	–	Pest	7
<i>Ceruraphis eriophori</i> (Walker) I	VI/Vo	Rolling	–	7
<i>Myzus ornatus</i> Laing	V*	–	Pest	7
<i>Myzus persicae</i> (Sulzer) II	Vo*	–	Pest	7
<b>Cicadellidae</b>				
<i>Edwardsiana prunicola</i> (Edwards, J.)	VI	–	–	18
<i>Idiodonus cruentatus</i> (Panzer)	V	–	–	30
<b>Diaspididae</b>				
<i>Chionaspis salicis</i> (L.)	V*	–	Pest	31
<i>Dynaspidiotus britannicus</i> (Newstead)	V	–	Pest	31
<b>Psyllidae</b>				
<i>Psylla viburni</i> Low	VI	–	–	15
<b>HYMENOPTERA</b>				
<b>Cephididae</b>				
<i>Janus luteipes</i> (Lepelletier)	V	Mining	–	5, 17
<b>Tenthredinidae</b>				
<i>Tenthredo livida</i> L.	Vo*	–	–	6, 19
<i>Tenthredo vespa</i> Retzius	V*	–	–	6, 19
<b>LEPIDOPTERA</b>				
<b>Coleophoridae</b>				
<i>Coleophora ahenella</i> Heinemann	V	–	–	14
<b>Geometridae</b>				
<i>Acasis viretata</i> (Hubner)	Vo	Webbing	–	1
<b>Gracillariidae</b>				
<i>Phyllomorcyter lantanella</i> (Schrank)	VI/Vo	Mining	–	14
<b>Lycaenidae</b>				
<i>Strymonidia pruni</i> (L.)	VI	–	Rare	16
<b>Noctuidae</b>				
<i>Brachionycha nubeculosa</i> (Esper)	Vo	–	Rare	1
<i>Brachionycha sphinx</i> (Hufnagel)	VI	–	–	1, 28
<i>Orthostia cerasi</i> (F.)	Vo*	Webbing	–	1, 28
<b>Pyralidae</b>				
<i>Phlyctaenia coronata</i> (Hufnagel)	V	Webbing	–	14

Table 4 Continued

Insect or mite	Host plant	Feeding habit	Status	Reference
Sesiidae				
<i>Synanthedon anthraciniformis</i> (Esper)	VI	Mining	–	28
Sphingidae				
<i>Sphinx ligustri</i> L.	VI/Vo	–	Migrant	1
Tortricidae				
<i>Acleris schalleriana</i> (L.)	VI/Vo	–	–	14
<i>Lobesia botrana</i> (Denis & Schifferm.)	V	–	–	14

VI, *Viburnum lantana*; Vo, *Viburnum opulus*; V, *Viburnum* spp.; \*, polyphagous; –, no information available.

Reference source (complete references are provided in the bibliography):

- |                                     |                              |  |
|-------------------------------------|------------------------------|--|
| 1. Allan (1949)                     | 13. Eastop (1981)            | 25. Niblett (1934)                               |
| 2. Bagnall & Heslop Harrison (1921) | 14. Emmet (1979)             | 26. Niblett (1941)                               |
| 3. Bagnall & Heslop Harrison (1928) | 15. Hodkinson & White (1979) | 27. Niblett (1959)                               |
| 4. Barnes, Gall Midges (1948)       | 16. Howarth (1973)           | 28. Noble (1975)                                 |
| 5. Benson, Symphyta (1951)          | 17. Klausnitzer (1978)       | 29. Read (1987)                                  |
| 6. Benson, Symphyta (1952)          | 18. Le Quesne & Payne (1981) | 30. Ribaut (1952)                                |
| 7. Börner, Aphides (1952)           | 19. Lorenz & Kraus (1957)    | 31. Schmutterer (1959)                           |
| 8. Buhr, Gallen (1964)              | 20. Massee (1965)            | 32. Southwood & Leston, Land & Water Bugs (1959) |
| 9. Buhr, Gallen (1965)              | 21. Miles (1982)             | 33. Stroyan (1984)                               |
| 10. Cox (1976)                      | 22. Mohr (1966)              | 34. Walsh & Dibb (1954)                          |
| 11. Cox (1981)                      | 23. Morris (1981)            |  |
| 12. Davis <i>et al.</i> (1982)      | 24. Müller (1982)            |  |

are high compared to those of other European tall-shrub species. Schopmeyer (1974) recorded 100% in the first spring, and Beckett & Beckett (1979) 80–90%, although they found that seeds allowed to dry out during summer germinated mostly in the second spring. Schopmeyer (1974) reported that cleaned seeds gave a higher percentage than dried fruits. For a population in south-western Germany Kollmann (1996) found 68% germination in darkness (two trays with a total of 140 seeds on blotting paper). Pirl (2000) observed 55% germination for *V. opulus* in flower pots with a sand-soil mixture in an unshaded common garden experiment (1.5 cm seeding depth); this is close to the 60% given by Schütt *et al.* (1994). Beckett & Beckett (1979) reported that the germination of *V. opulus* is erratic, and the percentage is rarely as high as for *V. lantana*.

Germination of *V. lantana* appears not be influenced by the red : far-red ratio. When seeds were sown into a short sward of *Festuca rubra* the timing of germination was essentially the same as on bare ground, while that of *Ligustrum vulgare* in the same experiment was strongly delayed under the grass sward (P. J. Grubb & W. G. Lee, unpubl. data).

#### (E) SEEDLING MORPHOLOGY

Seedlings of both species have a 2.5–3.0 cm long hypocotyl which is glabrous, woody and dark-brown (Fig. 6). There are two glabrous, herbaceous cotyledons with a petiole of 2–3 mm length in *V. lantana* (1 mm in *V. opulus*). In *V. lantana* the cotyledons are ovate to rounded-cuneate and about 16–21 mm long; in *V. opulus* they are elliptically lanceolate and slightly shorter (11–15 mm long). The epicotyl in *V. lantana* has many stellate hairs and is shorter (3–5 mm) than in

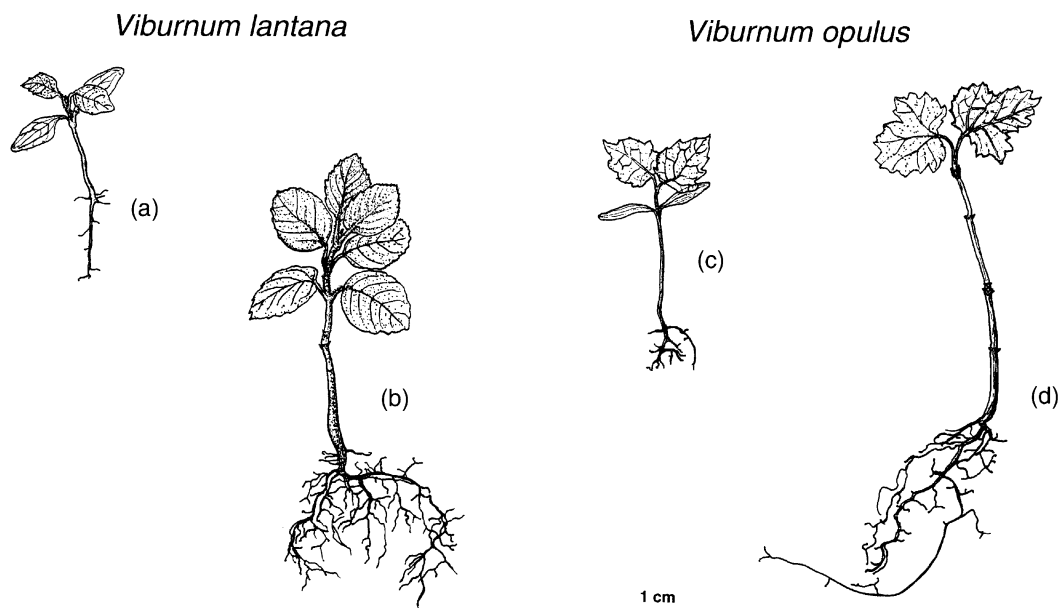
*V. opulus* (5–15 mm), but the degree of hairiness and the length of the epicotyl may vary depending on light climate and soil conditions. The first post-cotyledonary leaves are opposite with a petiole of 1.5–2.0 mm in *V. lantana* and 7–9 mm in *V. opulus*. In *V. lantana* they are ovate-oblong, slightly dentate and rounded at the base (9–13 mm long). In *V. opulus* they are ovate with a rounded-truncate base and 15–25 mm long with short unicellular hairs, coarsely serrate-lobate, but without nectaries. From an early stage the seedlings have a lignified main root with unbranched laterals. Under some conditions, seedlings of *V. opulus* with 2–4 post-cotyledonary leaves can have densely branched roots (Sylvén 1906).

## IX. Herbivory and disease

### (A) ANIMAL FEEDERS OR PARASITES

#### *Insecta*

Ten species of phytophagous insects have been observed on *V. lantana* but not *V. opulus*, and six on *V. opulus* but not *V. lantana*, while a further 24 have been observed on both species (Table 4). In a study by Duffey *et al.* (1974) the two *Viburnum* spp. sustained relatively low numbers (17) of phytophagous insect species in comparing 21 genera of woody plants in Britain (on average 58 species; 107, *Corylus avellana*; 230, *Crataegus* spp.; 157, *Prunus* spp.). In this compilation only *Ilex aquifolium* (13), *Taxus baccata* (6) and *Buxus sempervirens* (4) had fewer associated insects. However, the genus *Viburnum* stands out among the British tall-shrub species for its propensity to suffer heavy defoliation by one insect; the leaf outlines remain while holes 3–6 mm across are made in the lamina.



**Fig. 6** Morphology of 1st-year (a, c) and 3rd-year (b, d) seedlings of *Viburnum lantana* and *V. opulus* (age based on year rings, J. Kollmann, pers. observ.). The seedlings of *V. opulus* showed no signs of extrafloral nectaries.

Remarkably the same flea-beetle (*Pyrrhalta viburni* (Paykull), Chrysomelidae) is responsible on both *Viburnum* spp., despite the marked differences in colour and surface-texture of their leaves. *Pyrrhalta viburni* is also a serious pest on *V. opulus* in North America (Johnson & Lyon 1991). As far as known, *P. viburni* limits its feeding to *Viburnum* species, but it appears to have preferences within this genus for *V. dentatum*, *V. opulus* and *V. rafinesquianum*. Both larvae and adults devour the leaves and give them a tattered appearance at first, but larvae in dense populations eat all of the leaf except the major veins. In addition, Johnson & Lyon (1991) mentioned mealybugs of the genus *Pseudococcus* as causing damage on *V. opulus*. Serious plant injuries on wild and cultivated varieties of *V. opulus* are caused by the snowball aphid, *Aphis viburni* Scop. (= *Neoceruraphis* (= *Aphis*) *viburnicola* (Gillette)); damage on *V. lantana* seems to be less severe (Schütt *et al.* 1994). *Viburnum* is the host on which the aphid overwinters, because it is on the twigs and buds of the shrubs that the aphid lays its eggs in the autumn. The eggs hatch at the time the buds open in spring. Within 3 weeks of bud break the *Viburnum* leaves are grossly misshapen; sometimes even the petiole is bent. In contrast, *Aphis viburniphila* Patch, has a year-round association with the plant, but this species causes no leaf deformation. Injury of the foliage by the bean aphid, *Aphis fabae* Scopoli, has also been reported for *V. opulus* (Johnson & Lyon 1991; Douglas 1997).

In central Europe, herbivory on *V. lantana* has been observed for polyphagous caterpillars of one butterfly (*Callophrys rubi*) and six moth species (*Angerona prunaria*, *Hemitea aestivaria*, *Lasiocampa quercus*, *Saturnia pavonia*, *Xestia baja* and *Zeuzera pyrina*; FloraWeb 2001). Various food-chains on four resources provided by *V. lantana* (leaves, sap, pollen and fruit) were

reported by Side (1955) who noted many insects associated with *V. lantana* in addition to those given in Table 4. Insect herbivory on adult shrubs of *V. lantana* was studied by Jackson *et al.* (1999) in south-western Germany, where no damage by *Pyrrhalta* was noted, and rates of herbivory were compared with those for seven other European tall-shrub species. The prevalent herbivores in this study were the lepidopteran larvae *Ectropis bistortata*, *Croesia bergmanniana* and *Yponomeuta padellus*. *Viburnum lantana*, *Euonymus europaeus*, *Prunus spinosa* and *Rosa canina* had the highest losses of leaf area, and herbivory was markedly lower in *Cornus sanguinea*, *Ligustrum vulgare* and *Lonicera xylosteum*. In most species, loss rates were very low in the folded or rolled young leaf stage, highest in the unfolded or unrolled expanding leaf stage, and lower again in the mature stage, but measurements at the different stages were not made for *V. lantana*. Folded, very young leaves of *V. lantana* are expected to be unattractive to herbivorous insects because of the dense covering of stellate hairs, low specific leaf area ( $22 \text{ cm}^2 \text{ g}^{-1}$ , compared with  $105 \text{ cm}^2 \text{ g}^{-1}$  in the unfolded expanding stage) and low water concentration (56% of dry mass, the lowest value among 11 tall-shrub species; Jackson *et al.* 1999). The high rates of area loss by mature leaves of *V. lantana* almost certainly result from ineffective control of the herbivores by predators, parasitoids and diseases. The values given by Jackson *et al.* (1999) for specific leaf area of mature leaves ( $123 \text{ cm}^2 \text{ g}^{-1}$ ), water concentration (60%) and nitrogen concentration ( $28 \text{ mg g}^{-1}$ ) were mostly lower than, or the same as, those found for 10 other fleshy-fruited tall-shrub species.

In central Europe, herbivory on *V. opulus* has been observed for polyphagous caterpillars of one butterfly (*Euphydryas maturna*) and two moth species (*Euplexia lucipara* and *Herminia grisealis*); also nectar feeding by



*Euphydryas maturna* and by the moth *Scoliopteryx libatrix* (FloraWeb 2001). Losses of leaf area to herbivorous insects were observed for *V. opulus* from mid-June to mid-August by Küppers (1984).

### Mammalia

In a survey of herbivory by roe deer (*Capreolus capreolus* L.) in forests of the Swiss midland, Klötzli (1965) found that *V. lantana* was among the least attractive plants; browsing was observed only in late spring and only in 1–40% of the sample plots at a number of different sites. In contrast, *V. opulus* ranked highly as a preferred food plant, and browsing was found in 40–100% of plots at different sites; herbivory was most frequent in summer. Also Schütt *et al.* (1994) ranked *V. opulus* higher than *V. lantana* with respect to browsing by roe deer in Romania.

In a garden experiment involving nine tall-shrub species and two tree species, *V. lantana* proved to be one of the species least palatable to rabbits (*Oryctolagus cuniculus* L.) while *V. opulus* gave inconsistent results but tended to be more palatable (Grubb *et al.* 1999).

For *V. lantana* some information about rates of post-dispersal seed predation is available. In extensive soil samples under scrub in calcareous grasslands among 10 559 seeds of 17 fleshy-fruited species only four seeds of *V. lantana* were found and these had been destroyed by rodents (Kollmann 1994). There were clear differences between species in the extent of predation, e.g. 87% for *Prunus avium* ( $n = 71$ ) and only 59% for *Crataegus laevigata* ( $n = 770$ ). In the experiments of Kollmann *et al.* (1998) in southern England and south-western Germany, *V. lantana* ranked third among 12 fleshy-fruited woody species in terms of attractiveness to rodent seed predators. The main predators were yellow-necked mouse (*Apodemus flavicollis* Melch.), wood mouse (*A. sylvaticus* L.) and bank vole (*Clethrionomys glareolus* Schreber). One possibly important trait which correlated with attractiveness to rodents was seed viability: 100% in *V. lantana* and the two most-preferred species compared with 53–90% for

most of the other nine species. Another decisive factor might have been the proportion of total seed dry mass in the wall ( $39 \pm 0.6\%$ , means  $\pm$  SE;  $n = 30$ ) which is a measure of the relatively modest physical protection of the seed. This proportion was lower in *V. lantana* than in eight other fleshy-fruited species, among them the less attractive *Crataegus laevigata* ( $82 \pm 0.7\%$ ), *Sambucus nigra* ( $62 \pm 3.3\%$ ) and *Cornus sanguinea* ( $82 \pm 1.4\%$ ). Variation in seed mass did not explain the preferences of the rodents. *Viburnum opulus* was not included in this study. However, *Viburnum* species generally seem to be particularly attractive to rodent seed predators, as also observed by Meiners & Stiles (1997) in a comparison of *V. dentatum* with eight other woody species in old-fields in New Jersey.

### (B) AND (C) PLANT PARASITES AND DISEASES

A list of eight fungal parasites and saprophytes on the two *Viburnum* species is given in Table 5, based on Ellis & Ellis (1985). Most fungal diseases have been observed on *V. opulus* (5), only one on *V. lantana*, and two on both. Schütt *et al.* (1994) noted that various leaf spot diseases were found on *V. opulus* due to fungal pathogens (e.g. *Ascochyta*, *Cercospora* and *Phyllosticta*), including mildew in humid shaded habitats. The same authors report that *V. lantana* can be infected by *Ascochyta viburni* (Roum) Sacc. and *Septoria viburni* West.

### X. History

The Adoxaceae-Caprifoliaceae complex (18 genera, about 400 species) is of Laurasian origin. The oldest genus is probably *Viburnum* (Mai 1995). Leaves of this genus were already present in the Middle Cretaceous period, and seeds of *V. opulus* have been found in Europe since the Upper Miocene. Fossil records for both *Viburnum* species exist from interglacial deposits in Britain and Switzerland (Godwin 1956; Ingrouille 1995; Burga & Perret 1998).

**Table 5** Fungal parasites and saprophytes on *Viburnum lantana* and *V. opulus* (from Ellis & Ellis 1985)

Host	Parasite or saprophyte	Organ	Symptoms	Time period
<i>V. lantana</i>	<i>Diplodia lantanae</i> Fuckel	Dead branches	–	–
<i>V. opulus</i>	<i>Ascochyta viburni</i> Sacc.	Living leaves	Pale spots (< 1 cm) with purplish borders	Aug–Sept
	<i>Diaporthe beckhausii</i> Nitschke	Dead twigs	–	Jan
	<i>Microsphaera viburni</i> (Duby) Blumer	Powdery mildew on leaves	Leaves redden and tend to fall	–
	<i>Stigmata tinea</i> (Sacc.) M.B. Ellis	Leaves	Large, often angular, dark brown spots (visible on both leaf surfaces but colonies mostly hypophyllous)	–
	<i>Valsa opalina</i> Sacc. & Syd.	Dead branches	–	–
<i>V. lantana</i> and	<i>Cytospora lantanae</i> Bres.	Dead twigs	–	Jan–May
<i>V. opulus</i>	<i>Phomopsis tinea</i> (Sacc.) Died.	Dead branches	–	Apr–May

–, no information available.

After the last glacial period, *V. lantana* and *V. opulus* recolonized central Europe when the climate became sufficiently warm. In the Swiss lowlands, pollen records of both species are found from 12 000 to 11 000 years BP ('Alleröd'/'Younger Dryas'; Burga & Perret 1998). Unfortunately, pollen from the two species has often not been differentiated, although there are clear differences in pollen morphology (Maciejewska 1997). In England, *V. opulus* has not been identified in the postglacial period before Neolithic time. In south-western Germany, the first records of *V. lantana* and *V. opulus* date back to about 6000 years BP (Rösch 1985).

Seeds of *V. opulus* are found in many Mesolithic and Neolithic settlements, for example in late Mesolithic (Ertebølle) coastal settlements in central Denmark (5600–4000 BC; Kubiak-Martens 1999) and southern Sweden (Regnell *et al.* 1995), and the fruits of both *Viburnum* species might have been collected as wild food (Schoch *et al.* 1988). Today, fruit juice of *V. opulus* is still a traditional drink in the mid-Anatolian region of Turkey (Soylak *et al.* 2002). The Latin word *lentare* means bending, and the young flexible twigs of *V. lantana* were used for binding of sheafs and wicker-work (Hegi 1926).

*Viburnum lantana* seems to be more or less stable in abundance in central and north-western Europe, but may decrease locally where open vegetation of dry land is turned into forest or vineyards. However, any reduction in abundance is set off by the species being frequently planted (Reif & Aulig 1990; Starkmann & Tenbergen 1994). *Viburnum opulus* also seems to be generally stable in abundance; it may even show a net increase as a result of invasion of fallow wetlands and planting on the uplands.

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