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Heracleum mantegazzianum Sommier & Levier

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Biennial or perennial monocarpic herb. Root pale yellow, bruising brown and exuding a sickly yellow sap from the cut surface; tap-root, 45–60 cm, initially narrow, becoming thicker and more divided with age, the crown reaching up to 15 cm in diameter at flowering. Lateral branches spreading horizontally or spirally from the often multiple tap-root; laterals suppressed in dense stands. The exocortex of the main root contractile from the first seedling leaf stage, the crown of adult plants ultimately positioned 8–12 cm below ground level, deeper where sediments have accumulated after flooding. Older plants develop a solid stem-like stock, with old leaf scars, between the true root and the stem base. Stem single, annual, up to 10 cm thick at base and 200–500 cm tall, hollow, ridged, with purple blotches decreasing towards the top. Stem and petioles clothed with pustulate bristles, dense in the young state, more sparse after elongation. Leaves alternate, lower up to 250–300 cm, blades ternately or pinnately divided to a varying extent, coarsely and irregularly deeply lobed: lobes and larger teeth long-acuminate, usually puberulent below and more or less glabrous above; petiole stout, fleshy, hollow, more or less hairy, shortly sheathing at the base. Upper leaves progressively smaller, with a greatly inflated sheathing petiole to almost sessile, becoming increasingly bracteate higher up the stem.

Flowers in compound umbels up to 80 cm across with 50–150 somewhat unequal hairy rays (15–40 cm). Rays shortest in the centre and longest at the edge of the umbel bringing all secondary umbels to a similar subspherical plane. Central ray vertical and distinct in main and branch terminal umbels, the remainder progressively curved centrifugally. Compound umbels on a short stem-like hollow peduncle, subtended by bracts. The terminal umbel is largest and hermaphrodite, surrounded by up to eight satellite umbels on elongated curving stalks raising them up to 40 cm above the level of the terminal umbel. Additional terminal umbels may be borne on the main

axillary branches which develop from the base of the main stem upwards; however, other umbels can develop from any of the remaining leaf or bract axils, especially on large vigorous plants or where the growth point of the main stem becomes damaged. Under stress, umbels may be degenerate and sterile.

Umbels mature in sequence, the lower umbels smaller and sometimes male. Bracts usually several, linear or ovate and long acuminate; bracteoles linear, caducous. Pedicels 10–20 mm, hairy.

Flowers white or rarely pinkish, sepals triangular, calyx teeth prominent, acute. Petals up to 12 mm, outer petals radiating, styles with enlarged base forming the stylopodium. Styles about three times the length of the stylopodium, divergent or somewhat recurved. Stigma capitate. Pollen grains range from 56 to 77 μm long (Grace & Nelson 1981). Fruit elliptical 6–18 mm long, 4–10 mm wide, typically 15 mm long, 8 mm wide in large fruits, 8 mm long, 6 mm wide in small fruits, e.g. from the satellite inflorescences. Fruits usually glabrous to villous, dorsally much compressed; commissure broad. The fruit splits into two winged mericarps. Mericarp with slender, low dorsal ridges and rather broadly winged lateral ridges; the wings are flat and closely appressed to one another; carphophore present. The mericarp has three to five, usually four, conspicuous solitary claviform vittae (oil ducts), dark brown on the outer wall, approximately two-thirds as long as the mericarp and usually 0.5–1.0 mm wide at the lower end (Tutin 1980) and two smaller vittae on the inner wall. The endosperm is oily and mature fruits have a strong resinous smell.

Meriarp mass variable, ranging from a mean dry weight of 5.7 mg (Grime *et al.* 1981) to 11.9–12.7 mg dry weight from a population in Sheffield (J. Hodgson personal communication), 16.5 mg the average dry weight in a population in the Lea Valley, London (range 4.6–23.2 mg) to 18.2 mg the average weight from a terminal umbel of a plant in west Scotland. The seed size and weight depend on the vigour of the plant and hierarchy of the umbel and are normally largest in the terminal umbel. Size and weight, but not necessarily viability, are reduced in the satellite and lower order umbels and in those late developing. The cotyledons are abruptly contracted into a petiole.

*Abbreviated references are used for many standard works: see *Journal of Ecology* (1975), 63, 335–344. Nomenclature of vascular plants follows *Flora Europaea* and, where different, Stace (1991).

No subspecies of *H. mantegazzianum* have been recognized in the British Isles. The type species is described by Sommier & Levier (1895). The more descriptive names, *H. giganteum* Fischer ex Hornem. and *H. villosum* Fischer ex Sprengel, are considered synonyms of *H. mantegazzianum* (Dallman 1943), as is *H. asperum* Bieb. (Nelson 1991). Clement & Foster (1994) quote other binomials used in British works for *H. mantegazzianum*. These include *H. persicum* Desf. ex Fischer, *H. stevenii* Manden and *H. sibiricum* Sphalm and they also suggest *H. lehmannianum* Bunge, most of the records being referable to *H. mantegazzianum*. *Heracleum persicum* has been reported from Cheltenham, Aldeburgh, Usk, Cambridge and Edinburgh and plants thought to be *H. stevenii* from Wateringbury (W. Kent) (Clement & Foster 1994). Some confusion exists in the earlier literature between similar related species of *Heracleum* (Wellendorf 1967; Wyse Jackson 1989), particularly among naturalized plants and further investigation is required. All British and Irish material seen accords with type *H. mantegazzianum*. Common names include giant cow parsnip, wild rhubarb, cartwheel flower, Riesen-Bärenklau, Jätteloken, Kaempe-bjørneklo, La Grande Berce du Caucase and Siberian cow parsnip.

Heracleum mantegazzianum is an alien species naturalized throughout much of the British Isles (Fig. 1), forming dominant stands where it occurs locally.

I. Geographical and altitudinal distribution

Heracleum mantegazzianum is native to the Caucasus, south-west Asia (Mandenova 1950) and is becoming naturalized throughout Central Russia and Europe with a continuing increase in its distribution, being found in Austria, Belgium, British Isles, Czech Republic, Denmark, Finland, France, Germany, Holland, Hungary, Ireland, Italy, Liechtenstein, Norway, Slovakia, Sweden and Switzerland. Outside Europe, it is found in Canada and the United States where it is known as giant cow parsnip (Fl. Eur. 2; Morton 1978; Berenbaum 1981; Lhoest & Lejeune 1987; Pira *et al.* 1989). A giant hogweed, the Tromsø palm, reported from Tromsø, Norway (68°N) is not now considered to be *H. mantegazzianum* but is likely to be another, undetermined, species from southern Russia (Jørgensen 1992).

Heracleum mantegazzianum has spread throughout the British Isles, extending from the south coast of England to Shetland in the north of Scotland (Clegg & Grace 1974). It has been recorded in 119 out of the 153 vice-counties of the British Isles, being distributed mainly in south-eastern England and south-west and eastern Scotland (Fig. 1). In the British Isles it is essentially a lowland species and has been recorded from sea level up to an altitude of 213 m on the river Don, Aberdeenshire and at 170 m in western Scotland (H. Arnold, Biological Records Centre, Monks Wood).

From central Europe, *H. mantegazzianum* is recorded up to an altitude of 1850 m (Hegi Fl., ed. 1. 5) and Pysek (1991) records an altitudinal range of 150–1279 m in the Czech Republic.

In Sweden *H. mantegazzianum* occurs throughout the entire country (Lündström 1984). It appears to be spreading rapidly in south Norway and occurs on all soil types in Denmark, including the sandy soils in western Jutland (Lundström 1984).

Heracleum mantegazzianum was recorded from Canada probably as early as the late 1940s in Ontario, by 1944 from Vancouver and by the 1970s from British Columbia (Dawe & White 1979) at which time it was spreading rapidly in Ontario (Morton 1978). It has also been recorded from Seattle in America since 1953 (Morton 1975) and more recently from Tompkins County, New York (Berenbaum 1981) and Michigan (Case & Beaman 1992).

The spread of *H. mantegazzianum* in the British Isles has been very rapid, particularly during the last 20–30 years (Fig. 2). In the Czech Republic, spread was considered to be exponential following an initial colonization up the river valleys with subsequent establishment in the general countryside (Pysek 1991). A similar pattern of invasion was suggested for the British Isles. Recent surveys in Scotland (Neiland *et al.* 1987; Tiley & Philp 1992; Gibson *et al.* 1995) indicate an increase in number of sites and consolidation of major infestations with new primary colonization away from water courses.

II. Habitat

Characteristically an invasive species of river banks, streams, damp places and waste ground. Many infestations can be traced to an original introduction into a Victorian garden from which it escaped (Tiley & Philp 1994). Secondary spread readily occurs onto roadsides, railway embankments, cemeteries, and refuse tips. Human activity such as the collection of fruiting heads also contributes to spread (Lundström 1984).

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

In its native habitat (western Caucasus) *H. mantegazzianum* occurs in forest edges and glades, often at stream sides in montane areas with annual rainfall between 1000 and 2000 mm (Pysek 1991; Ochsmann 1992). Here the climate is typically continental, with hot summers and cold winters, tempered somewhat by the forest and upland environment, giving humid conditions (Mandenova 1950).

In Europe, it was introduced into gardens and parks, from which primary colonization has been along watercourses (Clegg & Grace 1974; Neiland 1986; Pysek 1991, 1994; J. M. Caffrey, unpublished). Later spread has occurred to waste places such as

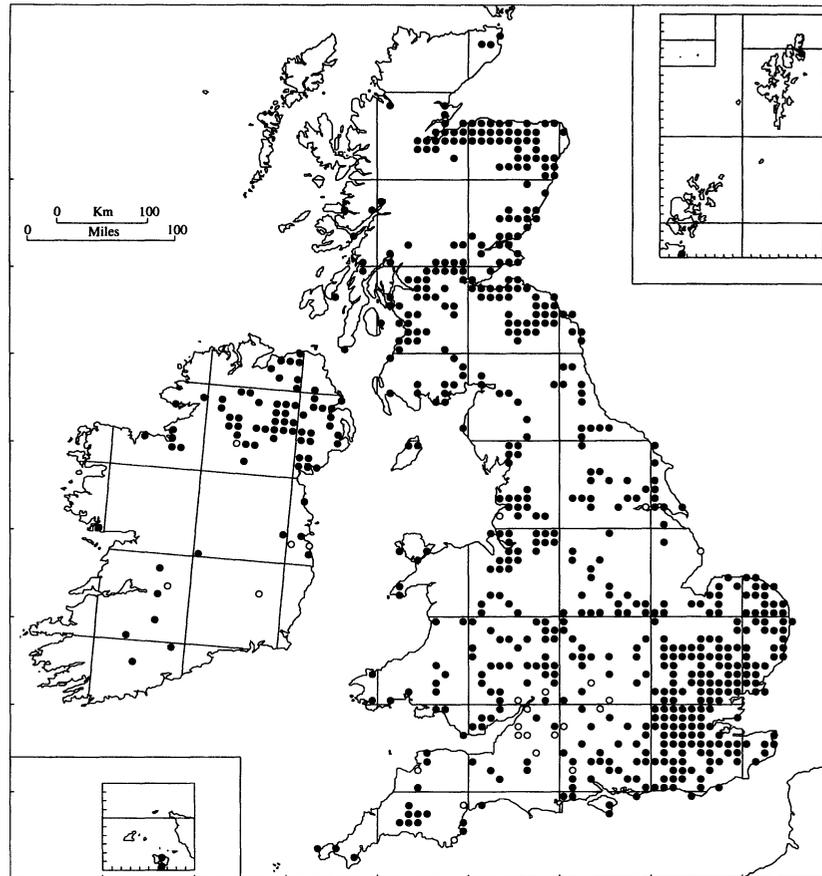


Fig. 1 The distribution of *Heracleum mantegazzianum* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (○) Pre-1950; (●) 1950 onwards. Mapped by the Environmental Information Centre, Institute of Terrestrial Ecology.

roadsides, hedgerows and disused farmland (Williamson & Forbes 1982; Pysek 1994).

Distribution in the British Isles and Ireland indicates a preponderance in lowland sites and urbanized areas, with a bias towards the east (Fig. 1). This may be a result of greater human influence, as in the Czech Republic (Pysek 1994), with spread from initial sites of introduction. As recently as 1992 *H. mantegazzianum* was on sale in garden nurseries. *Heracleum mantegazzianum* is generally of local distribution especially in suitable, usually riverside, habitats. It normally occurs in relatively sheltered sites, frequently to the leeward of prevailing winds, though plants also grow on south-facing cliffs on the south coast (W. E. Sterland, personal communication). It appears to be particularly well adapted to the cooler, moist maritime climate of Scotland and Ireland and is a widespread and noxious weed where soil moisture is maintained throughout the year (Tiley 1996). In Scotland, densely wooded areas and steep rocky banks are free of the plant (Tiley & Philp 1994). In Ireland *H. mantegazzianum* is well established and grows on a range of gradients from low-lying mud flats to steep bank sides, being rarely recorded from lake shores and canal banks. It is rare in tilled, landscaped or grazed habitats and is best suited to undis-

turbed or unmanaged sites, being most prolific along the banks of rivers and streams (Caffrey 1994).

Pysek (1994) studied the role of recipient habitat on the spread of *H. mantegazzianum* in the Czech Republic. Records of 378 localities reported in the Czech Republic in 1990 were analysed for habitat type; 42.8% occurred in linear habitats such as ponds, valleys, river banks, road verges and railway tracks, 41.5% occurred in man-made, disturbed habitats including rubbish dumps, parks and gardens and other urban areas and 15.7% occurred in seminatural habitats such as scrub, meadows and forests. The plant was most frequently reported from urban areas and road verges. The total number of localities increased exponentially from 1947 to 1990, the rate of expansion being greatest, though not significantly so, in roads and urban areas. Seminatural and less disturbed sites tended to show a lower expansion rate. Pysek (1994) concluded that recent expansion had been similar in each of the habitat types invaded and that the recipient habitat was less important than expected. The spread of *H. mantegazzianum* was found to be exponential in the Czech Republic regardless of habitat once a colony had become established.

Establishment is possible in a range of habitats and a variety of substrates, providing there is sufficient

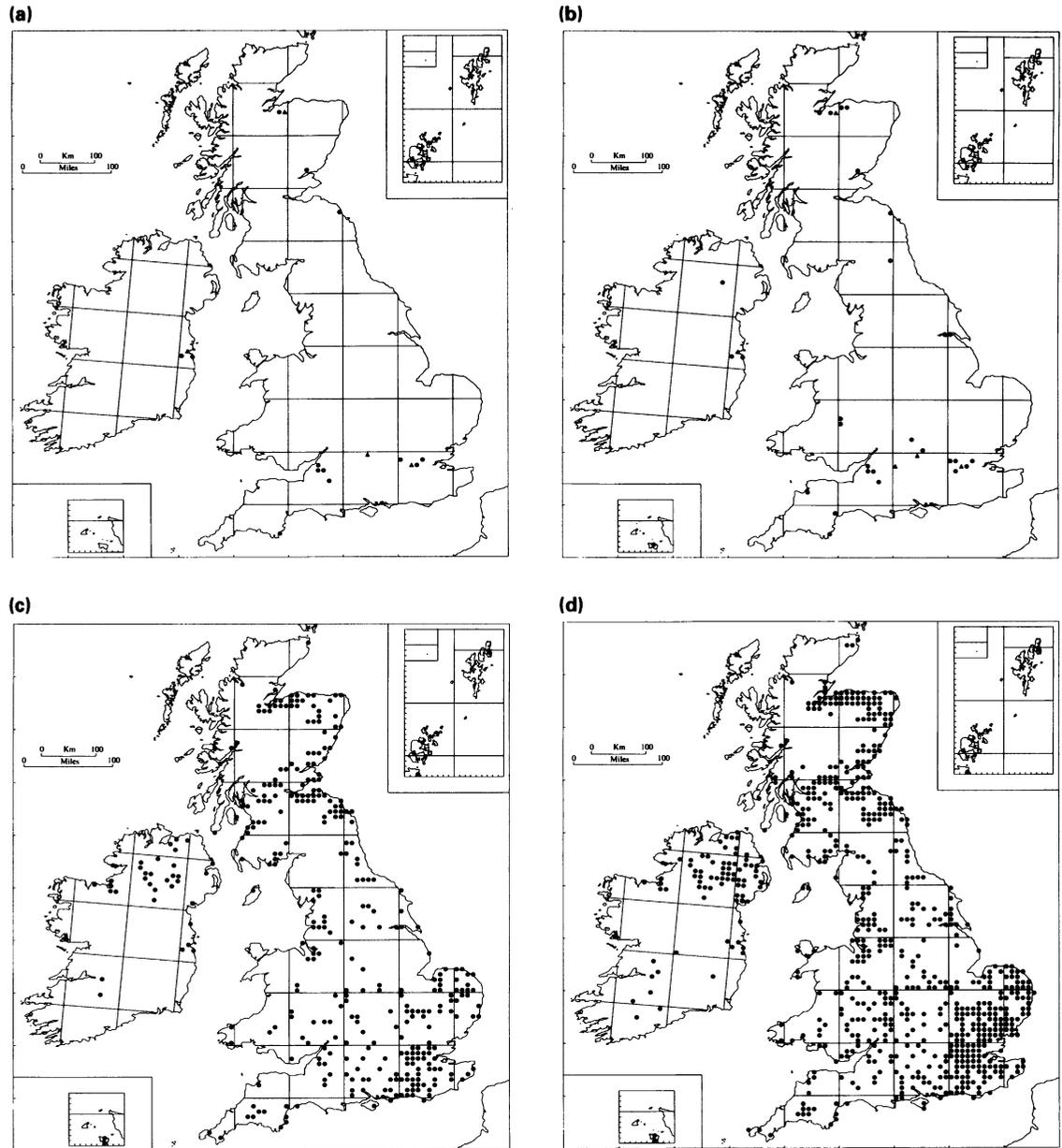


Fig. 2 The spread of *Heracleum mantegazzianum* in the British Isles. All records (a) up to 1920, (▲) introduced; (b) up to 1940, (▲) introduced; (c) up to 1970; (d) up to 1995. Mapped by the Environmental Information Centre, Institute of Terrestrial Ecology.

moisture at the seedling stage (Neiland 1986; Ochsmann 1992; Tiley & Philp 1994; J. M. Caffrey, unpublished). Sampson (1994) found that among 150 sites, the river bank was the most frequent habitat, followed by roadsides and wasteland. One cliff top and five woodland sites were recorded. In a survey in Scotland, Neiland (1986) found that *H. mantegazzianum* was most likely to colonize riverbanks and riverside woodlands though it was also common around derelict buildings, rubbish dumps and other waste sites, on roadsides and railway tracks and also in gardens. Grazing and arable land were least often colonized though young plants survived mowing in a rosette form in a riverside football pitch. In Germany, Ochsmann (1992) found that *H. mantegazzianum* occurred most frequently on ruderal sites and wet areas.

Heracleum mantegazzianum appears to grow best in more northerly and temperate areas, e.g. British Isles, Denmark, Sweden and Germany (Ochsmann 1992; Pysek 1994), possibly relating to moisture requirements for establishment. In warmer climates, it is favoured by semishaded habitats. Incidence of frost and cold is not limiting and the deep-rooting habit confers resistance to moderate summer drought.

In Britain and elsewhere, numerous examples exist of habitat suitable for the growth of *H. mantegazzianum* which have not been colonized owing to lack of local seed source. The uplands of Britain are generally free of the plant, possibly due to the absence of seed and less favourable growing conditions, although occasional plants are recorded. It is not known if acid soil pH inhibits establishment of *H.*

mantegazzianum. Roadside and waste places are frequently of higher pH than the surrounding countryside owing to deposits of rubble, salt and building materials.

In the Czech Republic, Pysek (1994) found a pronounced shift towards lower elevation with 28.5% of records >600 m above sea level in 1970 and 14.7% in 1990. He also found a strong tendency for *H. mantegazzianum* to be absent from the warmest climatic regions, being favoured by cooler, more humid areas.

(B) SUBSTRATUM

Along river banks *H. mantegazzianum* is most frequent on recent sandy and silty deposits. Floating seeds come to rest after dispersal by water and find a niche in this disturbed habitat. Seeds also germinate well in surface organic matter and detritus, for example, in woodland. Occurrences on moist or waterlogged soils, loams, heavy clays, among rocks, in pavements, or on rubbish tips are as much a result of local seed dispersal as of substratum type. Sufficient depth of soil or crevice size is required to allow the development of the tap-root, for example, beneath tarmac, paving stones or on rotting wood, particularly from the second year onwards. *Heracleum mantegazzianum* is tolerant of permanently moist soil, waterlogging and winter flooding associated with the riverside habitat, but once established also thrives on drier, well-drained sites.

In Scotland soils associated with colonies of *H. mantegazzianum* are of largely neutral – alkaline pH. Clegg & Grace (1974) found all but two out of 23 samples with pH > 7.0, range 5.0–8.5. Neiland (1986), also working in Scotland, reported pH ranging from 5.1 to 7.2 and Ochsmann (1992) found soil pH of sites in Germany to be predominantly above 6.0, with the greatest frequency between 7.4 and 7.8. Organic matter content of 3.1–8.7% was reported by Clegg & Grace (1974) and of 3.9–15.5% by Neiland (1986). Values for pH, organic matter, P, K, Mg and Ca for

soil samples from sites in the west of Scotland are given in Table 1; pH values are mostly above 6.0, organic matter is frequently low on sandy river banks but higher on rubbish tips. Phosphorus levels vary from high to very low, potassium and magnesium levels are generally medium to high and calcium levels are high. Neiland (1986) analysed soil samples from 10 sites in Scotland and found a variable range of concentrations (given in m-equivalent of exchangeable cations 100 g⁻¹ dry soil) for phosphorus 1–99, potassium 0.12–2.69, magnesium 0.73–3.51, calcium 5.1–28.7 and sodium 0.25–1.4. Neiland obtained a positive correlation of plant height with soil potassium and calcium levels along a 150 m transect.

Plants showing obvious signs of nutrient deficiency are rarely seen, though the leaf blades generally lose their dark green colour as temperature rises in the summer.

Habitats of *H. mantegazzianum* in the Edinburgh area exhibited a range of soil textures from clay loams to sands (Clegg & Grace 1974); a similar range of soil textures from gravels, sands, loams, silty loams to clays was observed by Neiland (1986). Wasteland and roadside sites frequently contain coarse or gravelly substrata or may be overlain with organic debris.

The occurrence of plants among a *Leymus arenarius* community on foredunes in Scotland and on cliffs on the south coast of England within reach of sea spray indicate tolerance to salt. Cwiklinski (1973) also successfully germinated and grew plants on the seashore.

III. Communities

Heracleum mantegazzianum is an invasive species capable of establishment and seeding in a range of habitats and communities. It is, however, most frequent as a colonizer of open ruderal communities, disturbed habitats or bare ground, especially in riparian habitats where it is a highly competitive ruderal. It can also invade closed communities such as grassland

Table 1 Chemical characteristics of soil sampled from *H. mantegazzianum* sites in west Scotland. Soils sampled at 0–15 cm depth and < 2 mm fraction analysed. Dried soils extracted with acetic acid and minerals determined by atomic absorption spectrophotometer. P determined by ammonium molybdate method. Loss on ignition determined after heating at 680 °C

Location	National Grid ref.	Habitat	pH	Loss on ignition (%)	Concentration (mg L ⁻¹)			
					P	K	Mg	Ca
Crianlarich, Perth	NN 385283	Roadside	7.1	7.3	26	120	224	2304
Failford, Ayrshire	NS 457263	Streamside	6.0	6.7	2	168	176	1248
Catrine, Ayrshire	NS 528248	Streamside	6.6	5.9	27	200	140	1520
Catrine, Ayrshire	NS 545247	Roadside	6.9	14.0	83	220	264	3200
Drongan, Ayrshire	NS 446198	Streamside	6.3	12.8	23	220	280	2088
Stair, Ayrshire	NS 434233	Riverbank	6.9	4.6	44	144	200	1624
Annbank, Ayrshire	NS 408228	Rubbish dump	7.7	13.4	141	356	296	10160
Annbank, Ayrshire	NS 408227	Riverbank	7.1	3.5	40	84	200	1512
Auchincruive, Ayrshire	NS 225385	Riverbank	6.3	8.1	21	376	216	1408
Ayr, Ayrshire	NS 363209	Rubbish dump	7.6	15.5	329	400	288	8000

especially when under a low management regime. Vegetation surveys at 11 sites round the country, including nine by the Unit of Comparative Plant Ecology (J. Hodgson, personal communication) found *H. mantegazzianum* growing with 64 other species at sites varying from shaded to open and from limestone to acidic heath. Only 17 species were found at two or more sites; these are listed below (figures in brackets refer to the number of sites where the species was present): *Urtica dioica* (8), *Galium aparine* (8), *Poa trivialis* (7), *Arrhenatherum elatius* (6), *Elytrigia repens* (4), *Lamium album* (3), *Ranunculus ficaria* (3), *R. repens* (3), *Cirsium vulgare* (3), *Rumex obtusifolius* (2), *Anthriscus sylvestris* (2), *Dactylis glomerata* (2), *Rubus fruticosus* (2), *Heracleum sphondylium* (2), *Agrostis stolonifera* (2), *Holcus lanatus* (2) and *Glechoma hederacea* (2).

In southern Scotland *H. mantegazzianum* was found to invade two main riparian community types: grassland and woodland (Gibson *et al.* 1995). In the grassland sites, *H. mantegazzianum* was associated with *Allium ursinum*, *Petasites hybridus*, *Poa trivialis*, *Symphytum officinale*, and *Urtica dioica* although the cover of these species was sparse. The community was rank, species-poor, showing some affinity to MG1b, *Arrhenatherum elatius* grassland – *Urtica dioica* sub-community (Rodwell 1992), but also strongly resembling a *Petasites hybridus* – *Urtica dioica* inundation weed community (Rodwell 1995). Gibson *et al.* (1995) found that *H. mantegazzianum* in a grassland area was accompanied by an increase in plant diversity owing to a shading effect on the grass species (Table 2b) whereas, in woodland habitats, the combined canopies of *H. mantegazzianum* and the tree cover were noticeably detrimental to both species diversity and cover (Table 2a). The alien *Tolmeia menziesii* was locally abundant. The main plant species associated with *H. mantegazzianum* on the banks of the River Allan in Stirling district were: *Arctium minus*, *Cirsium arvense*, *C. vulgare*, *Fallopia japonica*, *Galium aparine*, *Holcus lanatus*, *Lapsana communis*, *Polygonum convolvulus*, *Ranunculus repens*, *Rumex obtusifolius* and *Urtica dioica* (Neiland 1986). On alluvial or fluvial sites *H. mantegazzianum* was observed in mixed riparian communities whereas on drier, disturbed ground away from water it became entirely dominant (Clegg & Grace 1974).

Caffrey (1994) noted *Anthriscus sylvestris*, *Hedera helix*, *Heracleum sphondylium*, *Ranunculus ficaria*, *Rumex* spp. and grass species in the associated vegetation at sites in Ireland.

In Denmark, Vogt Andersen (1994) traced the increase in plant diversity and species abundance in an *H. mantegazzianum*-infested area following grazing by sheep. The vegetation changed from a deeply shaded community to an open grassland, rich in short growing grasses and herbs together with common weed species. Before imposition of grazing, the main species were *Angelica sylvestris*, *Carex* spp., *Cirsium*

Table 2 Species showing differential frequencies of occurrence in adjacent 2 m × 2 m quadrats with and without *Heracleum mantegazzianum*. (a) Frequency lowered when *H. mantegazzianum* present, (b) frequency increased when *H. mantegazzianum* present (Gibson *et al.* 1995)

	% frequency (means of two sites)	
	<i>H. mantegazzianum</i> present	absent
(a) Decreased occurrence		
Grassland sites		
<i>Arrhenatherum elatius</i>	2.5	43.7
<i>Cirsium arvense</i>	0	48.7
<i>Holcus lanatus</i>	5.0	23.7
<i>Symphytum officinale</i>	16.3	61.3
Woodland sites		
<i>Chrysosplenium oppositifolium</i>	2.5	40.0
<i>Galium aparine</i>	1.3	37.5
<i>Geranium robertianum</i>	2.3	22.5
<i>Hedera helix</i>	10.0	22.5
<i>Holcus lanatus</i>	0	21.3
<i>Poa trivialis</i>	2.5	25.0
<i>Ranunculus ficaria</i>	17.0	50.0
<i>R. repens</i>	3.8	30.0
<i>Rubus fruticosus</i> agg.	1.3	23.7
(b) Increased occurrence		
Grassland sites		
<i>Agrostis stolonifera</i>	12.5	5.0
<i>Allium ursinum</i>	27.5	0
<i>Geum urbanum</i>	6.3	0
<i>Glechoma hederacea</i>	12.5	0
<i>Mercurialis perennis</i>	6.3	0
<i>Petasites hybridus</i>	23.7	0
<i>Poa trivialis</i>	28.7	11.3
<i>Ranunculus ficaria</i>	7.5	2.5
<i>Silene dioica</i>	7.5	1.3
<i>Urtica dioica</i>	26.3	3.8

arvense, *C. vulgare*, *Deschampsia cespitosa*, *Epilobium parviflorum*, *Glechoma hederacea*, *Phragmites australis*, *Poa pratensis*, *Ranunculus ficaria*, *R. repens* and *Urtica dioica*.

Ochsmann (1992) working in Germany found *Cirsium arvense*, *Galium aparine*, *Glechoma hederacea*, *Poa* sp., *Ranunculus ficaria* and *Urtica dioica* to be commonly associated with *H. mantegazzianum*. The number of species in 91 *H. mantegazzianum* sites ranged from 6 to 51, the commonest frequency being 10–14 species.

Alliances of the continental classification where *H. mantegazzianum* frequently establishes include *Phalaridion*, *Calystegion*, *Calthion*, *Alopecurion* (degraded stands), *Agropyro-Rumicion crispis*, *Ulmion*, *Arrhenatherion* (degraded stages), *Trisetio-Polygonion* (degraded stages), *Aegopodion* and *Arction lappae*.

IV. Response to biotic factors

Heracleum mantegazzianum is the largest herbaceous plant in the European flora and is a highly competitive

species owing to its rapid and prolific growth (Pysek 1994). In the Czech Republic, many more sites result from human activity compared with natural colonization (Pysek 1994). Lundström & Darby (1994) also emphasize the anthropogenic influence contributing to its spread in Sweden. However, Caffrey (1994) noted its tendency to spread to unmanaged habitats.

Although conspicuous and attractive, *H. mantegazzianum* is now considered a noxious weed (Tiley 1996), and management consists largely of measures to control it. Methods of control were summarized by Dodd *et al.* (1994) and are included in many references (Rubow 1979; Neiland 1986; Bingham 1989; Tiley & Philp 1992; Department of Agriculture for Northern Ireland 1993; Caffrey 1994; Tiley 1996). Current control methods are grazing, mechanical cutting or other damage and chemical treatment.

1 Grazing: *H. mantegazzianum* is eaten by cattle, sheep, pigs and goats (Caffrey 1994; Tiley & Philp 1994). In fields lightly or rotationally grazed by cattle, sheep or goats, mature plants may escape lethal damage and progress to flowering and fruiting. Pig foraging, however, would eradicate plants through damage to their roots. In Denmark heavy grazing by sheep greatly reduced the plant and allowed the development of pasture grasses and herbs (Vogt Andersen 1994). Cessation of grazing led to a reassertion of dominance by *H. mantegazzianum*. Seven years after the introduction of sheep grazing (3 years at five sheep ha⁻¹, followed by 4 years at 10 sheep ha⁻¹) it was found to be eradicated and no viable seeds remained in the soil seed bank (Vogt Andersen & Calov 1996). The leaves are less acceptable to cattle and sheep than summer grass growth and are more likely to be eaten in the second half of the season when grass growth is reduced.

2 Mechanical: cutting of leaves is frequently used to reduce the above-ground growth of *H. mantegazzianum* both in its vegetative and flowering stages. This method is used to clear riverbanks, pathways and other sites of the prolific growth during late spring or summer. Cutting the vegetative plants above ground has only a cosmetic effect and does not lead to long-term control. Fresh leaf growth regenerates from the crown bud of the thick storage root within two weeks (Lundström 1984) and a tall canopy is soon re-established. Similar regrowth of axillary buds at the base of the plant occurs when flowering stems are cut above ground level. However, if the tap-root is chopped with a spade or mattock below the base of the stem (8–12 cm below ground level), this effectively kills the plant in both the vegetative or reproductive state (Tiley & Philp 1992; Tiley 1996). This treatment is obviously labour-demanding but suitable for small infestations or isolated plants.

J. M. Caffrey (unpublished) compared the effects of cutting flowering plants early in March and in May with uncut controls in Ireland. Cutting reduced plant

height and number of seeds produced, with severe effects from the May cut, which also produced smaller seed size. Flowering plants which were cut at different heights above ground at the end of June in Scotland had greatly reduced flower and seed production and those cut below ground did not flower (Table 3). Cutting the shoots will gradually reduce the reserves in the tap-root (Schuldes & Kübler 1991).

Pulling by hand, which requires glove protection, can eradicate occasional seedlings or very young plants (Dodd *et al.* 1994).

Ploughing effectively eradicates the plant from infested fields, though large roots are capable of regrowth in the following crop (Bingham 1989).

3 Chemical: in the United Kingdom, glyphosate, triclopyr and imazapyr are recommended for the control of *H. mantegazzianum*. Herbicides are effective only when applied appropriately and early in the season, otherwise the plants are not completely killed and can flower. Triclopyr produces knockdown and twisting of the foliage within a week of application (Davies & Richards 1985). Glyphosate is best applied early in the growing season (March–May). This herbicide when appropriately applied kills plants after 3 weeks (Williamson & Forbes 1982; Dodd *et al.* 1994). Imazapyr not only kills off any adult plants but also has a residual activity which prevents the germination of seedlings for several months. Leaf vigour is too low in the autumn for efficient herbicide action.

V. Response to environment

(A) GREGARIOUSNESS

In its initial colonization of a site, *H. mantegazzianum* frequently occurs as only a solitary plant. Subsequent flowering and seeding lead to a massive local dispersal of fruits from which a group of plants is established with potential for progressive expansion. Field surveys (Neiland 1986; Ochsmann 1992) indicate that *H. mantegazzianum* occurs most frequently in small groups of plants (< 50). Neiland (1986) counted plant numbers in small-sized groups and estimated numbers when above 50. Other surveys have used 10 or 20 as the count limit. Occasional large colonies containing > 2000 plants have been recorded, excluding seedlings (Ochsmann 1992), areas up to 1 ha and over 1 km of linear river bank habitat have been recorded in Scotland (Tiley & Philp 1992). Seedbank populations up to 2664 m⁻² were recorded in the soil by Ochsmann (1992). In early spring a massive germination of seeds results in high densities of seedlings; 400 first leaf stage seedlings m⁻² were recorded in Scotland, falling to 33 m⁻² with full canopy cover of adjacent adult plants in mid-summer.

Severe competition among germinating seedlings limits the densities of established 1-year-old vegetative plants to *c.* 6–10 m⁻². Mature flowering specimens (3–4 years old) are commonly no more than *c.* 0.5–1.0

Table 3 Effect of cutting *Heracleum mantegazzianum* plants at different heights

Height of cutting (30 June 1994)	Sampled 14 August 1994 (means of 4 plants)		
	No. of branches	No. of terminal umbels	Dry weight of umbels (g)
15 cm below ground level	—	—	—
5 cm below ground level	0.8	—	—
0 cm at ground level	0.3	1	9.8
15 cm above ground level	9.8	3	36.0
50 cm above ground level	6.5	2.3	33.8
Inflorescence bud	4.8	3.3	83.5
Control	6.8	1	227.5
LSD at $P = 0.05$	4.21	1.08	53.7

m^{-2} , though sometimes interspersed with an understorey of successional nonflowering stages. Gibson *et al.* (1995) recorded 4–7 flowering stems m^{-2} with 5–19 vegetative plants m^{-2} within established stands of *H. mantegazzianum*. Among the small proportion of seedlings surviving, some suffer leaf die-back under the influence of shade, but have sufficient root reserves to survive the summer and recover in the autumn or in the following season.

Densities of plants in continuous stands appear to be determined by competition for available light in the early part of the growing season. In semishaded habitats resultant densities are lower than in open situations. Very rapid leaf growth rates quickly establish a hierarchical pattern in spring. Leaves from older plants with larger root reserves grow larger and more quickly, especially early in the season. Plant density affects leaf and root yield and root architecture such that the ratio of lateral:vertical root growth was higher and root size greater in isolated or widely spaced plants compared with high density populations (Table 4).

(B) PERFORMANCE IN DIFFERENT HABITATS

Heracleum mantegazzianum is cultivated for silage in Russia (Khodyrev *et al.* 1980) and has been suggested as a crop in Poland (Cwiklinski 1973). Biomass measurements in the west of Scotland indicate single plant yields, including root, of up to 6.75 kg dry

weight from open, unmanaged habitats. This is equivalent to a yield of 57 tonnes ha^{-1} dry weight and 306 tonnes ha^{-1} fresh weight. However, intraspecific competition reduces branch development and lower yields per plant are obtained from within stand samples. Leaf number, growth and chemical composition of plants in Moscow were studied by Ruskova (1973). Fresh weight yields in the first to fourth years were 9.2, 79.4, 93.6 and 53.7 tonnes ha^{-1} , respectively.

In flowering and fruiting plants dry matter is nearly equally distributed between inflorescences, leaves, stem and root. In vegetative plants, root dry matter becomes an increasingly higher proportion of total plant biomass (Table 5). Table 4 lists plant biomass after the second year of vegetative growth at different

Table 5 Distribution of dry matter (%) in *Heracleum mantegazzianum*

Distribution of dry matter (%)	Flowering plant early fruiting stage	2-year-old vegetative plant
Root	17	76
Stem	26	—
Petiole	9	6
Leaf blade	19	18
Inflorescence stalks, rays, pedicels	10	—
Fruits	19	—

Table 4 Effect of plant density on biomass yield of *Heracleum mantegazzianum* at the end of the second year of growth (vegetative plants)

Density	Yield (g dry weight m^{-2})				Ratio vertical/ lateral roots
	Petiole	Leaf blade	Leaf total	Root	
1 plant m^{-2}	57	174	231	753	0.82
4 plants m^{-2}	178	254	432	906	0.83
6.5 plants m^{-2}	138	228	366	1036	2.06
17.5 plants m^{-2}	273	453	706	2049	1.82
19.0 plants m^{-2}	126	181	307	1335	4.72
LSD at $P = 0.05$	80.1	123.4	249.0	98.0	

plant densities. Except at the two lower densities, a wide divergence in size developed as some plants showed a competitive ascendancy.

Dry matter partitioning and reproductive yields were measured on plants flowering in deeply and lightly shaded habitats (Table 6). Deeply shaded plants were not as tall, had less stem, leaf and root biomass, fewer fertile umbels and much lower umbel weights, fruit yields and numbers. Stem diameter, dry matter contents and leaf sizes were also lower. These data confirm field observations that light is a major factor influencing the performance of vegetative, reproductive and seedling plants of *H. mantegazzianum*. Notwithstanding its better growth in open sites, the species can establish and grow successfully in woodland, glade edges and partially shaded habitats (Gibson *et al.* 1995). The effect of soil fertility on *H. mantegazzianum* has been little studied, though Nieland (1986) obtained yield responses in pot-grown seedlings three weeks after adding NPK nutrient solution. *Heracleum mantegazzianum* grows with vigour on building sites, roadsides, rubbish dumps and other ruderal habitats with shallow or poor soil. Well developed flowering plants occur amongst dense grassland in hedgerows or on riverbanks where severe competition for nitrogen would be expected.

(C) EFFECT OF FROST, DROUGHT, ETC.

All parts of the plant are resistant to frost, including exposed over-wintering roots, newly germinated seedlings, rosette buds and young leaf growth in spring. Overwintering roots and sprouting shoots have survived air temperatures to -17°C in Scotland. Lower temperatures or more prolonged frosts may occur in continental Europe and in the native habitat of *H. mantegazzianum*. Plants flowering late in September may fail to set seed, due possibly to poor pollination, pollen tube growth or fruit development. Early aut-

umn low temperatures can hasten leaf senescence. Periods of low temperature are considered necessary to break seed dormancy and may be required to induce flowering (Shumova 1972a).

In prolonged dry spells high summer temperatures can induce temporary flaccidity of the leaf blades and whole plant size may be reduced. Plants are shorter and smaller where rooting is restricted, e.g. shallow soils, roadsides, rocky substrates, or when the plants have been cut, damaged or affected by herbicides.

The branched tap-root is tolerant of poorly drained or marshy areas in which *H. mantegazzianum* appears to thrive, though it does not occur on permanently submerged ground. Both vegetative and flowering plants withstand and recover from temporary river-bank flooding in summer. In winter, flood water can detach and transport stem skeletons and disperse fruits. The much divided leaves are moderately resistant to wind but unseasonal gales can lead to laceration of the larger leaves and snapping of the petiolar veins. On exposed sites and roadsides, wind or vehicle slip streams can cause browning of the leaf tips and edges. Leaf and shoot growth is generally more compact in such exposed sites, though the well anchored flower stems remain erect until they decay in winter. Wind is a primary means of seed dispersal in autumn.

VI. Structure and physiology

(A) MORPHOLOGY

In the first year the seedling develops a single leaf or a rosette of two to four leaves which may reach a width of up to 0.5 m or more (Williamson & Forbes 1982). The root is initially a deep (45–60 cm), narrow, tap-root. The upper part thickens early as root reserves accumulate, becoming contractile with surface annular wrinkling. During summer, multiple

Table 6 Effect of shade on plant size and flowering in *Heracleum mantegazzianum*. Means of five plants sampled (a) in the deep shade of the summer deciduous tree canopy and (b) in the open in light shade. PAR measurements were taken at 1 m above ground level in summer when *H. mantegazzianum* was fully grown and at the late flowering/early fruiting stage

	(a) Deep shade	(b) Light shade	LSD at $P = 0.05$
PAR values, % ambient	12.6	38.9	
Overall height (m)	2.91	3.45	0.074
Dry weight (g)			
Root	121	355	152.8
Stem	129	486	96.4
Leaf	58	115	104.3
Umbels, total	132	401	217.5
Umbel characteristics			
Height \times diameter (cm) of terminal umbel	18 \times 68	23 \times 75	2.2 \times 4.5
Number of rays on terminal umbel	105	135	17.4
Fresh weight (kg) of terminal umbel	0.48	1.01	0.114
Number of satellite umbels	4.8*	6.6	1.17
Total number of fertile rays	58	759	511.5
Fresh weight (g) of satellite umbels	96	771	310.4

*All satellites in the shade sterile except for one plant.

(2–5), often curved, branches develop (Fig. 3). The largest root branches grow vertically or subvertically with finer horizontal branches which extend laterally or in a circular fashion in the upper soil layers depending on root competition. In subsequent years the crown of the root progressively enlarges (up to 15 cm diameter at flowering), becomes lignified and is surmounted by a solid stem stock bearing the scars of former leaves. In the dormant overwintering state, this bears a single large terminal bud ensheathed by the broad petiolar bases of diminutive leaves. At the onset of growth these develop progressively larger petioles and leaf blades, culminating in an inflorescence-bearing stem in reproductive plants. Vigorously growing vegetative plants may bear three to four green leaves which are replaced during the growing season. Satsiperova (1977) reported that the transition from vegetative to reproductive phase in all hogweed species is accompanied by an increase in subdivision of the leaf blade. This has also been noted by Ochsmann (1992). Plants under stress, such as those in shade or in competition with grasses, commonly bear only one leaf for several years until sufficient root reserves have accumulated to support a rosette. Flowering plants may bear four to six stem leaves in addition to three to four large basal leaves.

In the architecture of the umbel, especially the large terminals, the outermost rays are longest, often growing downwards before curving upwards at their extremities to bring the secondary umbel to the periphery of the inflorescence. Rays become progressively shorter and more erect towards the centre of the umbel, which is sometimes marked by a shorter, thicker central ray. Flower-bearing pedicels within

each secondary umbel reflect the length distribution of the rays, with the longest pedicels curved and pointing outwards and the inner shortest and erect. Mean pedicel length declines from the periphery of the primary umbel inwards. The floral surface of each compound umbel is subhemispherical, presenting a conspicuous, cauliflower-like, white structure to visiting insects. Number, size and weight of the inflorescence rays correlate with each other, with umbel size of the same order and with overall plant size. Field observations indicate that threshold root size is important in the initiation of flowering, as in *H. sphondylium* (Shepard 1991).

Shumova (1972b) studied the morphology of the juvenile (vegetative) phases in Moscow, tracing the lengthening of successive leaves over time during 2 years of vegetative growth. Six leaves appeared during April–May, four of these senescing in May and June and two in September. A second period of growth in July and August produced three new leaves which remained green into winter. At the end of the third year the dormant crown bore a main and several side shoot buds. The morphogenesis of the main flowering stem was also studied (Shumova 1973). *Heracleum mantegazzianum* was found to be polycarpic in Russia, exhibiting die-back of the shoot only, not monocarpic as in the British and European forms.

Mean values of stomatal density are given by Arora *et al.* (1982). For a sample size of 18, the figures were 491 mm^{-2} (range 245–737) on the lower surface and 75 mm^{-2} (range 26–124) on the upper surface. Stomata are mesoperigenous, anomocytic (Guyot 1971).

(B) MYCORRHIZA

Mycorrhizas have not been recorded (Harley & Harley 1987).

(C) PERENNATION: REPRODUCTION

Heracleum mantegazzianum is a herbaceous perennial with deciduous leaves and classed as a hemicryptophyte. The above-ground vegetation dies back each autumn until the third or fourth year when the plant flowers and seed is set, after which the whole plant dies though in Russia Shumova (1973) reported perennality after flowering. Observations on cultivated material by Stewart & Grace (1984) showed that the plant can flower in its second, third, fourth or fifth year, but that most flowered in their third year. Reproduction is entirely by seed which is vital for the perpetuation of plants within a stand. If the plant is damaged before flowering has finished, the crown can either quickly regenerate new leaves and shoots with flower heads or produce weak flowering stems in the following year. There is a limited possibility of the gross removal of overwintering tap-roots from eroded river banks by water flow and also in

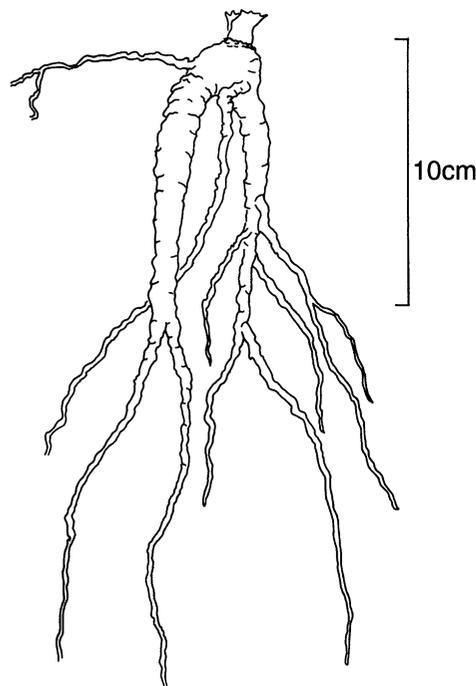


Fig. 3 Root of *Heracleum mantegazzianum* after 1 year's growth.

transported soil. There are no reports of reproduction by vegetative means.

(D) CHROMOSOMES

For *Heracleum mantegazzianum*, in common with other *Heracleum* species, $2n = 22$ (Tutin 1980; Wiemark *et al.* 1979).

(E) PHYSIOLOGICAL DATA

A number of microscopical studies has been conducted on the sieve tube elements of *H. mantegazzianum*. Lee *et al.* (1971) reported that these are 175–350 μm in length, and 15–30 μm in diameter, with a cell wall thickness of 3–5 μm and sieve plate 1–2 μm thick containing about 140 pores of 0.4 μm in diameter.

The phloem is relatively easily separated from the vascular bundles of the petioles of actively growing plants and can be examined *in situ* (Barclay & Johnson 1982). Fensom *et al.* (1968) reported a method for the observation of transport phenomena in the functioning phloem, where they observed protoplasmic streaming and vibratory movement. The large sieve tubes of both *H. mantegazzianum* and *H. sphondylium* have been the subject of several studies on phloem transport. Lee *et al.* (1971) detected rapidly moving distinctive marker particles in the phloem of *H. mantegazzianum* and *H. sphondylium* which Barclay *et al.* (1977) concluded were starch grains released from ruptured plastids. The random motion of these particles was studied by Barclay & Johnson (1982) who concluded that a less than expected movement indicated a higher than normal viscosity of sieve tube contents. A re-analysis of the data by Murphy (1986) showed that Barclay & Johnson had underestimated the Brownian motion of the particles and thus overestimated sieve tube viscosity. Murphy concluded that the latter was determined largely by the concentration of sucrose, usually about 24%.

Measurements made by Tyree & Fensom (1970) on phloem strands of *H. mantegazzianum* to elucidate the nature of the transport process did not suggest that either an electrokinetic or a pressure flow mechanism is the major motive 'force' for translocation in mature phloem.

Hart & Sabnis (1975) provided evidence of a filamentous component in plant extracts from the epidermis of the petiole. Its stability between pH 3 and 8.5 and in the presence of various chemicals and enzymes suggested a coherent, covalent structure. The filaments, of beaded appearance under electron microscopy, resembled similar structures from the phloem of *H. mantegazzianum* described as P-protein (Lee *et al.* 1971).

Stant (1973) studied the anatomy of stems and roots using electron microscopy. The primary xylem vessels in the stem are surrounded by parenchyma

cells and have spiral banded thickening. Smaller secondary xylem vessels are grouped in multiples supported by radial fibre cells. The vessel cell walls are thick with a warty inner face. The xylem in the roots is mainly secondary. Satsiperova & Filinkova (1978) concluded that stem anatomy was species-specific within the genus *Heracleum*. They observed that stem structure changed during development from a solid stem with V-shaped peripheral vascular bundles to a hollow stem with a circular arrangement.

(F) BIOCHEMICAL DATA

The chemistry of the Umbelliferae as a whole and of individual species is very complex, and further studies could shed light on taxonomic relationships (Hegnauer 1971; Heywood 1971). Biochemical studies in Russia have been used to support taxonomic grouping within the genus *Heracleum* (Satsiperova & Comissarenko 1978; Tkachenko 1987). A number of compounds are of general occurrence in the family but those specific to *H. mantegazzianum* include certain flavonoids (Harborne 1971), essential oils (Wellendorf 1967) and coumarins (Nielsen 1971).

Flavonoids

The anthocyanin pigment of the purple spots on the stem epidermis contain a cyanidin which can occur in the glucoside form: cyanidin 3-sambubioside (Harborne 1971).

Essential oils

Wellendorf (1967) studied the essential oil content of *Heracleum* species including *H. pubescens* Bieb., to which Danish plants of *H. mantegazzianum* were ascribed. Gas chromatographic analysis indicated that octyl acetate and octanol were the major essential oils in the fruits, together with ethyl butyrate, hexyl acetate and acetic acid. Gildemeister & Hoffmann (1961) had found octanol esters as the major constituent, together with esters of acetic, butyric, isobutyric and optically active isovaleric acids.

Coumarins

According to Nielsen (1971) the genus *Heracleum* contains only simple coumarins (e.g. umbelliferone) and furanocoumarins from the coumarin group of compounds. Only one dihydro furanocoumarin, hermandiol, and no dihydro pyranocoumarins have been isolated (Fischer *et al.* 1978). All *Heracleum* species examined contained linear furanocoumarins. In some references the equivalent term furocoumarin is used. The furanocoumarins are stored as biologically active aglycones, mainly in the oil channels or ducts in the leaves, stems, roots, flowers and seeds (Towers 1980).

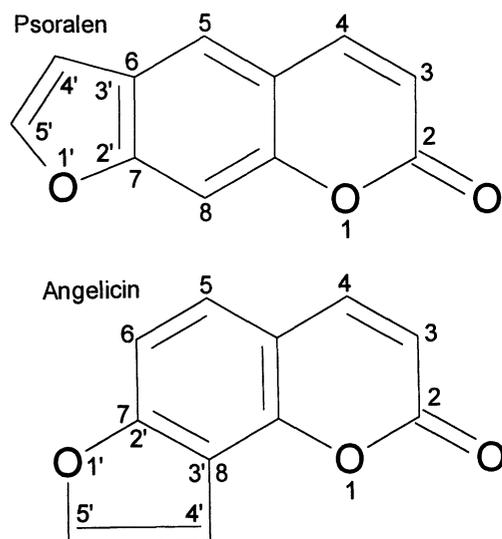
Molho *et al.* (1971) analysed 20 *Heracleum* species

Table 7 Occurrence of furanocoumarins in *Heracleum mantegazzianum*. Summarized from Mohlo *et al.* (1971), Musajo & Rodighiero (1962) and Pira *et al.* (1989)

	Root	Stem	Leaf	Fruits	Seeds
Linear furanocoumarins					
Bergapten*	•	•	•	•	
Columbianetin	•			•	
Imperatorin				•	•
Isopimpinellin	•	•	•	•	
Marmesin	•			•	
Psoralen*	•	•	•	•	
Xanthotoxin*		•	•	•	•
Angular furanocoumarins					
Angelicin			•	•	•
Byak-angelicol				•	
Isobergapten	•				•
Pimpinellin	•	•	•	•	•
Sphondin	•				

*Psoralen, Bergapten and Xanthotoxin are the most active in photosensitization of human skin (Musajo & Rodighiero 1962)

for furanocoumarins and discussed their phylogenetic significance in relation to biogenetic pathways. *Heracleum mantegazzianum* contains both linear and angular furanocoumarins, including the following: byak-angelicol, imperatorin, xanthotoxin, isopimpinellin, bergapten, angelicin, psoralen, columbianetin and marmesin (Table 7). The ratio of linear : angular furanocoumarin content is important in phytotoxic activity. The furan ring is at the 6,7 position on the benzene ring in the linear furanocoumarins, e.g. psoralen, whereas in the angular compounds, e.g. angelicin, it is at the 7,8 position creating an angular molecule (Fig. 4). Molho *et al.* (1971) found different results from material from three different sources and suggested that the giant hogweeds which have spread from botanic gardens

**Fig. 4** Chemical structure of furanocoumarins found in *Heracleum mantegazzianum*: psoralen, a linear furanocoumarin and angelicin, an angular furanocoumarin.

represent a group of species. Other furanocoumarins isolated from *H. mantegazzianum* are isobergapten, pimpinellin and sphondin.

Biological significance of furanocoumarins

Berenbaum (1981) surveyed furanocoumarin contents in relation to insect herbivory and plant habitat. Linear furanocoumarins are toxic to many generalist insect species owing to a cross-linking of the furan ring with the pyrimidine bases of DNA in the presence of UV light. However, they appear to enhance the growth and development of some Umbelliferae specialist-insects. Angular compounds lack this toxicity owing to a shift of the furan ring, but these can still interfere with growth and reproduction of some Umbelliferae specialists such as *Papilio polyxenes* (Fabricius) (black swallow tail) (Berenbaum 1981). Therefore the more complex the chemical constituents of a plant, the more specialized the insect fauna feeding on that species. Species in a high irradiance habitat (e.g. roadsides and waste areas) are more likely to produce furanocoumarins than, for example, species of woodland which were found to have no furanocoumarins. This is considered to be related to the limited value of furanocoumarins as a defence against insects in low light areas. Plants in habitats with a low nitrogen status were also found to have a low furanocoumarin content.

Furanocoumarins are antimicrobial both in the presence and absence of activating UV light and therefore may act as phytoalexins in some Umbelliferae, e.g. celery infected with *Sclerotinia* accumulates xanthotoxin (Ivie 1978). The angular furanocoumarins have antifungal and antimicrobial properties which may protect the root if it becomes damaged (Fischer *et al.* 1978). Extracts of *H. sphondylium* root containing pimpinellin, isopimpinellin, isobergapten and sphondin were found to be markedly fungitoxic to *Botrytis cinerea* and other fungi (Martin *et al.* 1966). This only partly explains the biological significance of photoactive compounds in the underground root (Towers 1980).

A number of furanocoumarin-containing plants (e.g. *Ammi majus*) have been shown to produce photosensitization in poultry, cattle and sheep (Ivie 1978). However, few cases of injury to animals eating *H. mantegazzianum* have been reported. Andrews *et al.* (1985) linked mouth ulceration of a pygmy goat to browsing of *H. mantegazzianum*. Skin and mouth injuries to sheep were then experimentally induced by sap from the plants. Dermatitis injury to a dog was reported by Hinterman (1962). Harwood (1985) reported vesication of the beaks and feet of one-week-old ducklings which had trampled among young plants. After three weeks the beaks were deformed and the feet darkly pigmented.

Cattle, sheep and goats are, however, frequently seen to browse *H. mantegazzianum* with impunity and

no apparent ill effects have been reported from countries where *H. mantegazzianum* is used for silage.

Phytophotodermatitis

Phytophotodermatitis in man was reviewed by Pathak (1974), the term having been proposed by Klüber (1942) to describe the reaction of human skin to contact with photosensitizing plants and subsequent solar irradiation. Many references point out the hazards of contact of humans with the plant in sunlight and with the cut material which remains active for several hours after cutting (Camm *et al.* 1976; Morton 1978; Rubow 1979; Lundström 1984; Wyse Jackson 1989). Drever & Hunter (1970) described phytophotodermatitis cases in children and adults from the Edinburgh area of Scotland. Symptoms appeared 24–48 h after contact and involved mild to severe erythematous reaction with or without vesicles or bullae, usually on the exposed parts of the body and following closely the pattern of contact between plant and skin. Dense postinflammatory hyperpigmentation is visible within 3–5 days and may persist for at least 6 years (Anon 1970). Knudsen & Kroon (1988) and Camm *et al.* (1976) carried out clinical trials using *H. mantegazzianum* sap confirming field observations. An extensive medical literature has built up on the dermatological aspects which is reviewed by Musajo & Rodighiero (1962), Pathak (1974) and Scott *et al.* (1976). Cases of injury from the plant are not always clinically recorded or recognized but local enquiries reveal that these occur regularly where *H. mantegazzianum* is present (G. E. D. Tiley & B. Philp, unpublished).

All sap-bearing parts of *H. mantegazzianum* are capable of producing this reaction. The threshold concentration ($10\text{--}100\ \mu\text{g mL}^{-1}$) of photoactive substances necessary to produce skin erythema was far exceeded during the main growing season (Knudsen 1983). There is evidence that high humidity and increased radiation increase the reaction (Knudsen & Kroon 1988). Pira *et al.* (1989) working in Italy & Knudsen (1983) in Denmark found the highest content of phototoxic substances in the leaves, the lowest in the stems and petioles with the root intermediate. Levels fluctuate during the growing season and content in the seeds increases into the winter.

The relationship between chemical composition and photodynamic properties of furanocoumarins was studied by Musajo & Rodighiero (1962). Long-wave UV radiation, particularly of wavelength 340–360 nm, is most effective in inducing cutaneous photosensitivity. Pathak & Krämer (1969) established that the chemical reaction involves cyclo-additive crosslinking between the 3,4 double bond of a linear furanocoumarin to the pyrimidine bases of epidermal DNA, thus inducing cellular damage. Only linear furanocoumarins which can intercalate with the DNA double helix are photoactive, particularly psoralen,

bergapten, xanthoxin and marmesin (Towers 1980). The increased pigmentation of skin was observed to be due to activation of melanocytic cells, increase in melanosomes and malpighian cells, changes in melanosome distribution and associated abnormal reactions (Pathak 1974). The mechanism may involve photoinduced gene depression to give increased melanocyte production, or alternatively induction of somatic mutation after photobinding of furanocoumarin to DNA (Scott *et al.* 1976). Research on the mechanism of furanocoumarin activity was reviewed by Rodighiero & Dall'Acqua (1976).

Clarke (1975) obtained mutagenesis of *Escherichia coli* bacteria with *H. mantegazzianum* sap under long-wave UV radiation. Photocarcinogenic studies with furanocoumarins indicate a range of results on skin cancer: induction, protection from or no results, depending on the wavelengths of UV light used (Ivie 1978). Scott *et al.* (1976) considered that the furanocoumarins are unlikely to be a genetic or carcinogenic hazard to humans.

VII. Phenology

The first year's growth from the seedling stage is generally slow. In the second and subsequent years, leaf growth is progressively larger (up to 1–2 m), more rapid and competitive.

Stem elongation in the final, flowering year is extremely rapid in the warmth of early summer after initial slower growth in the spring. Expansion of the terminal umbel array gives the main stem an overall height of 3–5 m.

The first signs of growth in vegetative plants are often visible in late December in mild winters by a greening and swelling of the crown buds. This is followed by a gradual development of almost sessile diminutive leaf blades with narrow leaf segments, giving place to more petiolate leaves in February/March, expanding to a spread of 50 cm or more. These form the basis of a rapidly expanding leaf array which develops during the warmer temperatures of April and May, resulting in an arching leaf rosette of 3–4 leaves 1–2 m high. Leaf number remains more or less constant through growth and replacement until shoot senescence in September–October. Occasionally 1–3 new basal leaves with distinctly narrow segments and low leaf area develop in late September/October which remain green until die-back at the onset of winter. These may be analogous to the autumn growth observed by Shumova (1972b). Ochsmann (1992) observed a seasonal dimorphism in the leaf blades in Germany. The blade segments of spring leaves were broader with higher surface area than the summer leaves which had longer, narrower segments.

The previous year's seedlings, which failed to develop to adult vegetative plants, are distinguished by the production of single small entire leaves in January/February (similar to Fig. 7d). If competitive con-

ditions allow, this may be followed in sequence by a simple ternate leaf, then 2–3 increasingly compound leaves.

Flowering occurs in the second year onwards from seedling establishment, depending on the vigour of previous vegetative growth (Pysek 1991; G. E. D. Tiley & B. Philp, unpublished). Seedlings germinating in the autumn may flower in the second growing season, i.e. after two winter periods (Tiley & Philp 1994). In an even-aged stand only the largest individuals flower, the remaining plants growing larger and flowering in subsequent years. A minimum storage root size may be required before flowering is initiated. Plants destined to flower possess broad crowns on well developed roots, are among the earliest to begin growth in December/January and have the largest spring leaf development, which is of a more erect habit than in vegetative plants. The increase in leaf blade subdivision noted by Satsiperova (1977) may also be apparent. Signs of stem and inflorescence development become visible in late April – early May within the growing apex of the shoot emerging from the bases of the petioles.

After gradual elongation in early May, there follows a period of rapid extension growth as temperature rises. A swollen terminal bud sheathed in bracts is visible by early June, from which emerges the first and largest (terminal) compound umbel. This is followed shortly by the satellite umbels arising from the base of the terminal umbel peduncle. The satellites grow on elongate branch stems, with two or more bracteate nodes, to produce a circle of umbels around the periphery of the terminal inflorescence and raised 10–40 cm above its level. The whole terminal inflorescence array can exceed 1.5 m in diameter (Fig. 5). Expansion of the main inflorescence occurs for 2–4 weeks accompanied by the final elongation of the stem. Within a flowering stand the general height of the terminal inflorescence arrays is noticeably very similar (Neiland 1986). Flowers in an umbel open sequentially from the periphery inwards over a period of a week or more, the rays and all other parts of the inflorescence enlarging continuously.

Axillary branches arising from the base of the main stem progressively produce their own terminal and lower order umbels from the top of the stem downwards.

Flowering in the United Kingdom extends from early June to August, with a peak in early July, followed by sequential ripening of seeds, beginning with the main terminal umbel, from July to September. Seed dispersal occurs from late August to mid-October (Kees & Krumrey 1983; Schuldes & Kübler 1990; Sampson 1990; Schwabe & Kratochwil 1991; Ochsmann 1992; G. E. D. Tiley & B. Philp, unpublished).

If the main stem is damaged by cutting, small, later flowering inflorescences are produced on short stems arising from axillary buds below the damaged part of the stem.

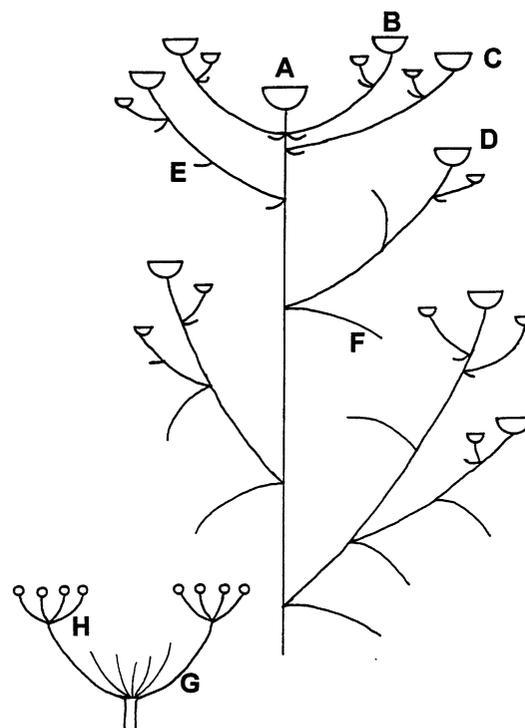


Fig. 5 Diagrammatic representation of inflorescence hierarchy, position and umbel structure in *Heracleum mantegazzianum*. (A) Terminal umbel; (B) satellite umbel; (C) sub-satellite umbel; (D) axillary branch terminal umbel; (E) bract; (F) Leaf; (G) ray of primary umbel; (H) pedicel with flower in secondary umbel.

After flowering and seed set the whole plant, including the root, normally dies. Flowering plants which are damaged or cut above the root may survive for one or more seasons.

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Reproduction is amphimictic. The flowers, contained in large umbels, are insect-pollinated and self-compatible. A list of insects caught on plants during June and July is given in Table 8 and indicates the relative amount of *H. mantegazzianum* pollen found on those insects (Grace & Nelson 1981). Flowers are hermaphrodite and protandrous; the anthers dehisce and pollen is shed before the stigma becomes receptive (Grace & Nelson 1981). Whilst there is complete protandry within an umbel, there is sometimes an overlap in staminate and pistillate phase between primary and secondary umbels making self-fertilization possible (Stewart & Grace 1984).

(B) HYBRIDS

Putative hybrids between *H. mantegazzianum* and *H. sphondylium* occur where the two grow in the same location (Stewart & Grace 1984), though their frequency at such sites is less than 0.1% (Grace & Nelson

Table 8 Flower-visiting insects caught on 15 plants sampled over five days during June and July, 1977 and the relative abundance of *H. mantegazzianum* pollen removed from them (Grace & Nelson 1981)

	Pollen abundance
Ephemeroptera	
<i>Ephemerella ignita</i> (Poda)	t
Hemiptera	
<i>Anthocoris</i> sp.	t
<i>Orthops campestris</i> (Linnaeus)	t
<i>Calocoris sexguttatus</i> (Fabricius)	t
Coleoptera	
<i>Rhagonycha fulva</i> (Scopoli)	***
<i>Meligethes</i> sp.	t
<i>Antherophagus nigricornis</i> (Fabricius)	t
<i>Anaspis</i> sp.	t
Trichoptera	
<i>Anthripsodes annulicornis</i> (Stephans)	t
Lepidoptera	
<i>Micropterix aruncella</i> (Scopoli)	t
<i>Ölethreutes lacunana</i> (Denis & Schiffermüller)	t
Hymenoptera	
<i>Dolichovespula norwegica</i> (Fabricius)	***
<i>Dolichovespula sylvestris</i> (Scopoli)	***
<i>Bombus lucorum</i> (Linnaeus)	***
<i>Psithyrus bohemicus</i> (Seidl)	***
<i>Apis mellifera</i> Linnaeus	***
Diptera	
<i>Simulium</i> sp.	t
<i>Empis albinervis</i> (Meigen)	t
<i>Phora aterrima</i> (Fabricius)	t
Syrphid	**
<i>Episyrphus balteatus</i> (Degeer)	*
<i>Eristalis arbustorum</i> (Linnaeus)	**
<i>Eristalis horticola</i> (Degeer)	***
<i>Eristalis intricarius</i> (Linnaeus)	**
<i>Myathropa florea</i> (Linnaeus)	***
<i>Psila pallida</i> (Fallén)	t
<i>Sepsis cynipsea</i> (Linnaeus)	t
<i>Palloptera arcuata</i> (Fabricius)	t
<i>Sarcophaga subvicina</i> Rohdendorf	*
<i>Lucilia illustris</i> (Meigen)	**
<i>Scatophaga stercoraria</i> (Linnaeus)	t
<i>Paregle radicum</i> (Linnaeus)	t
<i>Nupedia infirma</i> (Meigen)	t
<i>Morellia hortorum</i> (Fallén)	*
<i>Thricops nigrifrons</i> (Robineau-Desvoidy)	*
<i>Hydrotaea irritans</i> (Fallén)	t

Pollen abundance expressed on a relative scale
 *** > ** > * > t, where t = trace.

1981) and there are no records of hybrids outside Britain and Ireland (McClintock 1975). Wiemark *et al.* (1979) found no more than 15% seed set when *H. mantegazzianum* was the maternal plant compared to a 50% seed set when *H. sphondylium* was the maternal plant. The hybrids are morphologically intermediate between the parents (McClintock 1975) and can be identified as such by the pollen and length of trichomes on the leaf surface (Arora *et al.* 1982). Wiemark *et al.* (1979) studied male meiosis in *H. mantegazzianum*, *H. sphondylium* and the hybrid, and found

the hybrid virtually sterile. Hybrids have a low fertility owing to an abnormality at male meiosis causing a reduction in pollen fertility (Arora *et al.* 1982). Grace & Nelson (1981) studied insects at a hybrid site; 54 species were caught on *H. sphondylium* and 48 from *H. mantegazzianum*. However, only 23 species were common to both and very few insects carried both types of pollen. They concluded that the selective foraging behaviour of insects reduces the likelihood of cross-pollination and therefore hybridization.

(C) SEED PRODUCTION AND DISPERSAL

Heracleum mantegazzianum is typically monocarpic in the British Isles and is characterized by a massive production of flowers from a single plant. The main terminal umbel produces up to c.120 rays, each with a secondary umbel bearing 40–90 flowers (G. E. D. Tiley & B. Philp, unpublished). Together with the satellite umbels on the main stem and inflorescences on the axillary and side branches, a total of more than 80 000 flowers can occur on a single plant. Each flower produces two mericarp fruits thus giving a potential seed production of over 100 000 per plant. There is a wide range in estimated numbers of seeds produced per plant including 5000 (Pysek 1991), 1500–18 000 (Neiland 1986), 27 000 (Brondegaard 1990), 1000–29 000 (Ochsmann 1992), <20 000 (Sommier & Levier 1895). Flower counts from the terminal umbels and estimates from the satellite and axillary umbels of single large plants in west Scotland are given in Table 9. Additional counts confirm that the main inflorescence array (terminal and satellite umbels) on a vigorous plant can produce over 50 000 seeds.

J. M. Caffrey (personal communication) recorded seed counts per plant ranging from 1500 to 108 000 in Ireland. The largest and best quality seeds are produced by the peripheral rays on the highest order umbels. Apical dominance ensures that the main reproductive effort of the plant is concentrated into the terminal and satellite umbels and this progressively limits the development and setting of later flowering and lower order umbels. This is more pronounced in plants which are smaller, in shade or under stress. Similarly, if the stem is damaged, interrupting the progress of the main umbels to seed set, the plant resources become diverted to progressively lower order inflorescences which are then more likely to mature and set viable seeds, albeit of smaller size.

Maturation of fruits occurs centripetally in the compound umbel.

When dry, the mericarps separate, suspended from the carpophore (Fig. 6), and become detached by gravity, under the influence of wind or animals brushing by the standing stems. The bulk of the seeds fall within short distances of the parent plant. Neiland *et al.* (1987) released seeds from a height of 2 m and found that these travelled over 2 m in wind speeds of

Table 9 Flower production in *Heracleum mantegazzianum*. Flower and umbel numbers on single large flowering plants, July 1992 and 1993

Umbel type	No. of umbels	Mean no. of rays per umbel	No. of flowers per ray	Total no. of flowers
			mean \pm SD (range)	
July 1992				
Terminal	1	122	57.8 \pm 0.53 (44–74)	7564
Satellite	5	69.8	50.5 \pm 0.48 (30–66)	17 625*
Axillary	14	80.6	49.9 \pm 0.46 (26–76)	56 330*
Totals	20	1599	–	81 519*
July 1993				
Terminal	1	120	67.4 \pm 0.31 (37–113)	8088
Satellite	6	87.2	52.6 \pm 1.34 (27–74)	24 510*
Axillary	14	59.6	34.9 \pm 0.81 (9–56)	29 164*
Totals	21	1478	–	61 762*

*estimated

3 m s⁻¹ and over 10 m in winds of 14 m s⁻¹. Testing seed dispersal from a height of 0.69 m in a wind tunnel Clegg & Grace (1974) concluded that wind could be important in short distance dispersal. Ochsmann (1992) had similar results. Long-distance dispersal occurs naturally along water courses and flotation tests indicate that the fruits float in water for up to three days (Clegg & Grace 1974; Dawe & White 1979). While theoretically the seeds could be carried many kilometres, variation in water flow and turbulence, meanders and ebb-flow deposition can limit distribution distances. Caffrey (1994) observed that in areas infested with *H. mantegazzianum*, most seeds

and seedlings were found within 10 m of the colony and few more than 50 m away. There is no evidence of dispersal by birds (Neiland 1986) though isolated fruits may be carried on the feet of animals.

Anthropogenic dispersal includes the transport of seed heads for use in flower arrangements, e.g. on the roofs of cars in Sweden (Lundström 1984). Subsequent disposal of the flower heads in refuse leads to the spread on waste tips. The slip-streams of vehicles and trains are assumed to assist in wind dispersal of fruits along roads and railways. Transport of seed-laden soil in site works could also contribute to long-distance spread.

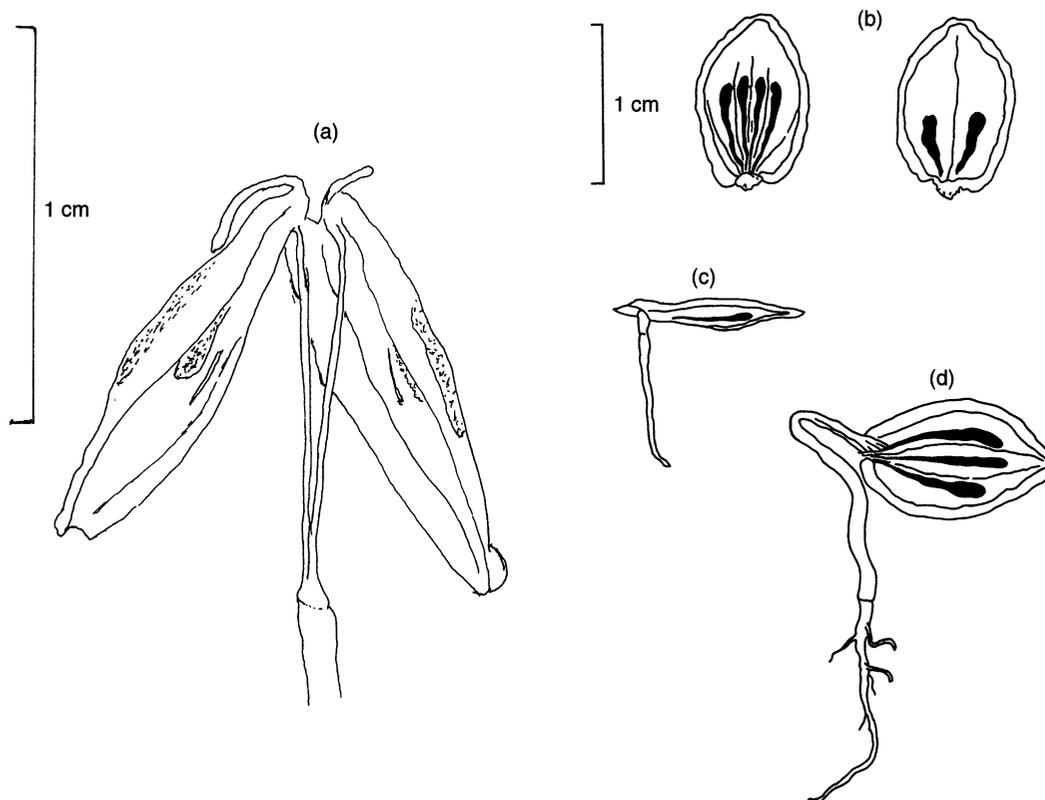


Fig. 6 (a) Mericarps splitting (after Ochsmann 1992); (b) external and internal sides of ripe mericarp; (c) lateral view of seed, 3 days after germination; (d) seedling 1 week after germination, cotyledons about to emerge.

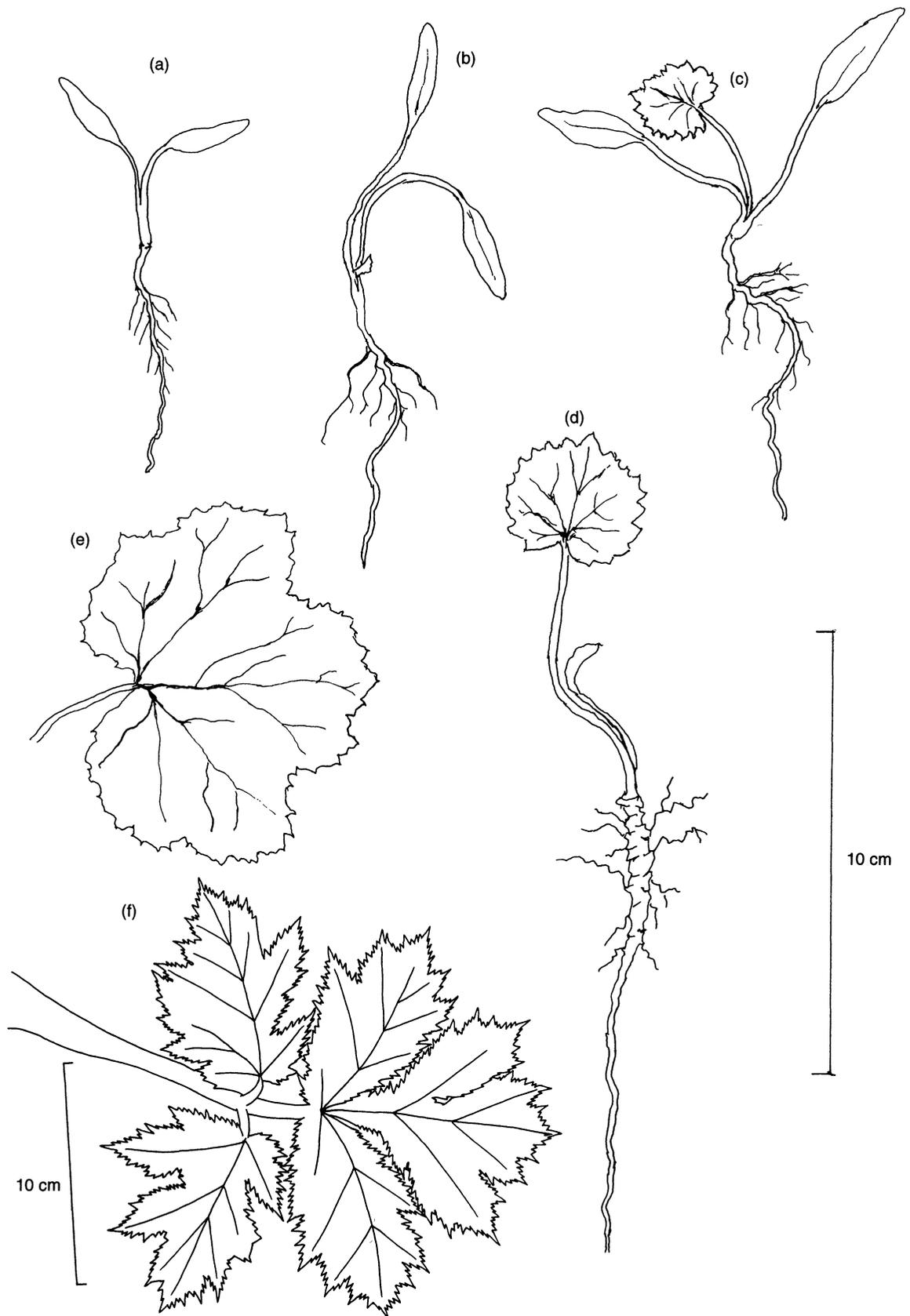


Fig. 7 Seedling development of *Heracleum mantegazzianum*. (a) Emerged seedling 4–5 weeks old; (b) seedling 6–8 weeks old, first true leaf emerging; (c) seedling 8–10 weeks old with primary leaf; (d) seedling at around 12 weeks, second leaf appearing, cotyledons senesced; (e) fully grown second leaf showing simple ternate shape; (f) adult leaf form, first compound leaf in spring (March).

(D) VIABILITY OF SEEDS: GERMINATION

Though there is a massive production and dispersal of seeds, a range of viability can be observed in the field. Under favourable conditions some germination of seeds will take place in the autumn (Cwiklinski 1973) and also sporadically in mild spells throughout the winter. Field observations indicate that most if not all shed seeds germinate in the following year, if conditions are suitable. This can be as early as January in mild conditions. Little germination occurs after March (G. E. D. Tiley & B. Philp, unpublished).

Evidence suggests that *H. mantegazzianum* seeds have a maturation requirement and germination pattern similar to *H. sphondylium* (Sheppard 1991). Seeds collected in the summer and autumn and dried artificially, followed by storage indoors, failed to germinate in the laboratory (G. E. D. Tiley & B. Philp, unpublished). This was also found by Cwiklinski (1973). Neiland (1986) too found that seeds dried before imposing several cold treatments failed to germinate. Experiments on seeds collected from the Lea Valley (UK) in July and stored at room temperature showed that germination occurred after 12 weeks at 5 °C in the dark, on moist filter paper. Seeds kept dry at 5 °C, seeds subjected to 24 h dark or 12 h dark/12 h light at room temperature all failed to germinate, indicating that a period of chilling and moisture are prerequisites for germination. Freezing the moistened seeds for one or six weeks, as suggested by Protsko & Gershunina (1990), did not induce germination. Seeds from the same umbels allowed to remain outdoors throughout the winter germinated strongly under both outdoor and laboratory conditions (G. E. D. Tiley & B. Philp, unpublished). Shumova (1972a) studied the dormancy of seeds and concluded that when the seeds are shed they are not mature, a long period of natural stratification being required during which seed development continued followed by germination. However, if the seeds were subjected to a rise in temperature during that period, development was interrupted and they failed to germinate until after another long period of stratification. Victorian gardeners were aware of the need to sow the seeds before the winter to achieve germination in the spring (Nelson 1991).

Protsko & Gershunina (1990) found that post-harvest dormancy of *Heracleum* seeds is not dependent on seed coat properties. Volatile and organic but not water-soluble inhibitors were extracted from the seeds. Dormancy was not broken by soaking in gibberellin and other hormone solutions of concentrations up to 100 mg L⁻¹. Gibberellin GK at 1 g L⁻¹ induced a weak germination. Cold stratification for six weeks induced germination up to 10–30%. Gibberellin GK treatment followed by six weeks of cold stratification increased germination up to 40%. The metabolic role of the furanocoumarin content of the seeds in dormancy is unknown.

Information on viability is fragmentary and conflicting, possibly because of a variable degree of maturation of the seed material and differences in harvesting and storage history on which reports are based. Lundström (1989) notes seed remaining viable for up to 15 years. Morton (1978) reports a viability period of up to seven years when seeds are kept dry at room temperature. In Scotland two-year-old seed was found to be viable albeit with very limited germination capacity (G. E. D. Tiley and B. Philp, unpublished). Seed stored dry, then placed outside for one year, germinated normally after the second winter. Vogt Andersen & Calov (1996) found no viable seeds in the soil seed bank where flowering and fruiting had been prevented for seven years.

Under field conditions germination and establishment are best in open vegetation with adequate light and moisture. Germination also takes place in more dense or shaded vegetation, in dead wood, rock crevices and roadsides. The petiole-like bases of the cotyledon elongate to raise the broadened tips towards the light (see Fig. 7). The petioles of the first and subsequent leaves also extend to lift the leaf blades upwards. Some laboratory tests indicate a light requirement for germination, though Stewart & Grace (1984) germinated hybrid (*H. mantegazzianum* × *H. sphondylium*) seed on agar plates in the dark at 3–4 °C. Lightly buried seeds germinate freely but the critical depth of seed burial is not known. Ochsmann (1992) observed better germination and seedling performance in wet conditions, though inundation was unfavourable. J. M. Caffrey (personal communication) reports low (1–23%) survival rates of germinating seedlings.

The moist habitats favouring *H. mantegazzianum*, such as riverbanks, may be partly related to a requirement for the seeds to remain moist after dispersal. However, permanently inundated seeds, both mature and immature, readily deteriorate and rot.

(E) SEEDLING MORPHOLOGY

As in *H. sphondylium* (Sheppard 1991) the cotyledons are panduriform, orientated and elevated by the extensile petioles which narrow to a sheathing base above a fleshy hypocotyl (Fig. 7a). The narrow taproot quickly penetrates deep into the substratum, producing lateral branches and soon thickening and contracting downwards. Under field conditions the cotyledons of germinating seedlings emerge in January–March; in mild conditions, these persist for several weeks before the appearance of the first foliage leaf in April (Fig. 7a–c). This is serrate and suborbicular, persistent for several weeks before the emergence and later replacement by the second foliage leaf, at which stage the cotyledons senesce. The second and later leaves are subternate, becoming progressively divided until the fifth and sixth leaves take on the adult deeply divided, serrate form (Fig. 7d–f).

Under shaded conditions, there is rarely more than one leaf present at any given stage, whereas vigorously growing plants in more open positions may develop a rosette of two to three leaves.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

Cattle, sheep, goats and pigs will graze *H. mantegazzianum* (Neiland *et al.* 1987; Lundström 1989; Tiley & Philp 1994; Vogt Andersen 1994). Damage caused by unidentified molluscs has been noted (Sampson 1990) and banded snails have also been recorded as nocturnal feeders on the leaves (Foster 1983).

Hardman & Ellis (1982) recorded *H. mantegazzianum* as a host for the carrot fly (*Psila rosae* (Fabricius)) and the parasitic fly *Chorebus gracilis* (Nees), but found no sign of root damage. Stewart & Grace (1984) refer to damage of *Heracleum* spp. by the larvae of *Depressaria pastinacella* (Duponchel 1838). Foster (1983) noted that the caterpillar *Depressaria daucella* (Denis & Schiffermüller 1775) and giant weevil *Liophloeus tessulatus* (Müller 1776),

which fed on the flowers and leaves, respectively, have pigmented skins, possibly as a protection against light-induced phytotoxicity.

L. K. Ward (personal communication) has records of *Phytomyza sphondylii* (Goureau), *Eupteryx aurata* (Linnaeus), *Trialeurodes vaporariorum* (Westwood) and *Phytomyza heracleana* (Hering) on the Phytophagous Insect Data Base; however, the last two species are European records rather than specific to the British Isles.

Sampson (1990) studied the potential for biological control; however, none of the organisms she recorded were shown to cause sufficient damage to reduce plant growth seriously or to prevent flowering and fruiting. Significant damage to the roots or other plant parts has not been observed in the field.

Insects on *H. mantegazzianum* recorded by Sampson (1990) are listed in Table 10.

(B,C) PLANT PARASITES AND DISEASES

Fungal pathogens: *H. mantegazzianum* is a host for *Sclerotinia sclerotiorum* (Lib.) de Bary (Gray & Noble 1965) and *Melanochaeta actearoae* (S. Hughes) E. Müller, Harr and Sulmont (Fowler *et al.* 1991).

Table 10 The main herbivorous insect species recorded on *H. mantegazzianum* by Sampson (1990)

	Abundance*	Part of plant affected
Hemiptera: Heteroptera		
<i>Orthops basalis</i> (Costa)	C&W	larvae and adults feed on young leaves, buds, unripe fruits
Hemiptera: Homoptera		
<i>Philaenus spumarius</i> (Linnaeus), spittle bug	C	sap sucker, leaf/stem
<i>Eupteryx aurata</i> (Linnaeus)	C	sap sucker, leaf
<i>Trioza apicalis</i> (Forster)		sap sucker, leaf
<i>Cavariella aegopodii</i> (Scopoli 1763)	C	sap sucker, flower
<i>C. pastinacae</i> (Linnaeus)	C	sap sucker, flower
<i>C. theobaldi</i> (Gillette & Bragg 1918)	C	sap sucker, flower
<i>Aphis</i> sp.	C&W	sap sucker, flower
<i>Paramyzus heraclei</i> (Börner 1933)		sap sucker, leaf/root
<i>Psila rosae</i> (Fabricius)		sap sucker, leaf
Thysanoptera		
<i>Thrips atratus</i> (Haliday)		flower
<i>T. vulgatissimus</i> (Haliday)		flower
Diptera: Acalyptera		
<i>Phytomyza sphondylii</i> (Goureau 1851)	C	larvae are leaf miners
<i>Euleia heraclei</i> (Linnaeus), the celery fly.	C&W	larvae are leaf miners
Lepidoptera		
<i>Epermenia chaerophyllella</i> (Goeze 1781)	C	larvae feed on the leaves
<i>Phaulernis dentella</i> (Zeller 1839)		leaf
<i>Depressaria pastinacella</i> (Duponchel 1838), parsnip web worm		larvae feed on flower heads
<i>Cydia aurana</i> (Fabricius 1775)		flower
<i>Agonopterix heracleana</i> (Linnaeus)	A	larvae feed on leaves
Coleoptera		
<i>Phaedon tumidulus</i> (Germar 1824)	C&W	larvae and adults feed on leaves
<i>Crepidodera ferruginea</i> (Scopoli)		leaf
<i>Meligethes</i> sp.		pollen chewer
<i>Byrrhus</i> sp.		pollen chewer

*C, common; C&W, common and widespread; A, abundant.

Phoma complanata Desm. has been recorded as being abundant on dead herbaceous stems of *H. giganteum* (Br. Stem and Leaf F. 1 & 2).

Powdery mildew (*Erysiphe heraclei* DC.) has been seen completely covering plants after humid dry weather conditions (Sampson 1990).

Unidentified soft rot in the roots has been noted (Sampson 1990).

Fischer *et al.* (1978) isolated *Trichoderma hamatum* (Bonord.) Bainier from the epidermis, a saprophytic *Erwinia* sp. and a phytopathogenic *Pseudomonas syringae*; the last caused putrefaction of the roots under certain conditions.

Aphid-transmitted virus diseases cause a distinctive, yellow mottling of the plant but have not been identified (Sampson 1990).

X. History

There is no evidence of *H. mantegazzianum* in Quaternary records; however, the pollen of *H. mantegazzianum* cannot (as yet) be distinguished from that of other *Heracleum* or *Pastinaca* species (K. D. Bennett, personal communication).

In the past 50 years the distribution of *H. mantegazzianum* in Britain has increased more than 40-fold. Although most sources date its arrival in Britain as 1893 (Briggs 1979) it was present as a colonist before this. The earliest county record is that from Cambridgeshire in 1828 (Perring *et al.* 1964). White (1912) refers to this 'ornamental alien' known about the Great Western Railway in the Bristol area for '50 years or more'. Wyse Jackson (1989) reports that a specimen was collected in Dublin before 1866. Stewart (1979) looking in the record books at Kew found references to seeds of *H. giganteum* as amongst those presented to the Royal Botanic Gardens at Kew from the Gorenki Botanic Gardens (Russia) in 1817 and seeds were circulating between the larger botanic gardens by the 1840s. Nelson (1991) quoting an advertisement from an Essex seed grower for seeds of *H. giganteum* in an Irish journal dated 1849 considers records of *H. asperum*, Siberian Cow Parsnip, made as early as 1835 in London, to be *H. mantegazzianum*. The same reference refers to seeds being distributed to Ireland and northern Norway at the same date 'because we do not know of a more suitable herbaceous plant . . . for a glade in a wood'.

Following its propagation in ornamental gardens, *H. mantegazzianum* has escaped and spread rapidly throughout Britain. Perring & Walters (1976) give nine pre-1930 records, by 1962 there were records from 170 of the 10 km squares and by 1972 reports from 100 additional 10 km squares, most of these in Scotland (Briggs 1979). A similar pattern of introduction, use as an ornamental plant, followed by escape to the wild and a recent rapid spread can be traced in other European countries (Pysek 1991).

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