The Biology of Invasive Alien Plants in Canada. 4. Heracleum mantegazzianum Sommier & Levier

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Page, N. A., Wall, R. E., Darbyshire, S. J. and Mulligan, G. A. 2006. The Biology of Invasive Alien Plants in Canada. 4. Heracleum mantegazzianum Sommier & Levier. Can. J. Plant Sci. 86: 569-589. Heracleum mantegazzianum (giant hogweed) is an invasive alien plant of management concern in southern Canada where it has escaped from horticulture and established and spread in natural, ruderal, and agricultural ecosystems. It poses a threat to natural ecosystems and human health, and is also a weed in agricultural and urban areas. It is a member of the Carrot family (Apiaceae) and is closely related to the native species Heracleum maximum Bartram (cow-parsnip). It is a monocarpic perennial, which generally flowers in its 3rd or 4th year. Large size, leaf shape, dark reddish pigments in patches on stems and petioles, and fruit characteristics readily distinguish H. mantegazzianum from other plants in Canada. It is increasingly common in riparian areas, floodplains, and forest edges in or near urban areas in southwestern British Columbia and southern Ontario. Based on herbarium specimens, H. mantegazzianum was first recorded in Ontario in 1949, British Columbia in 1964, Nova Scotia in 1980, Quebec in 1990, and New Brunswick in 2000. The development of dense stands of *H. mantegazzianum* can also reduce the richness of native plants. Contact with *H. mantegazzianum* can cause phytophotodermatitis, a serious skin inflammation caused by UV photo-activation of furanocoumarins present in the sap. Control methods include herbicide application, mechanical cutting, and animal grazing, but strategies to address seed dispersal and re-establishment from dormant seed must also be adopted. Widespread establishment in southern Canada suggests that eradication is unlikely. However, range expansion and rapid population growth can be prevented through strategic management including public education.

Key words: Giant hogweed, Heracleum mantegazzianum, Apiaceae, HERMZ, invasive plant, weed biology, furanocoumarins

Page, N. A., Wall, R. E., Darbyshire, S. J. et Mulligan, G. A. 2006. La biologie des plantes exotiques envahissantes au Canada. 4. Heracleum mantegazzianum Sommier & Levier, Can. J. Plant Sci. 86: 569–589. Heracleum mantegazzianum (berce du Caucase) est une espèce exotique envahissante qui préoccupe les producteurs du sud du Canada, car la plante s'est échappée des jardins pour coloniser les écosystèmes naturels, rudéraux et agricoles. En plus d'être une adventice dans les régions agricoles et urbaines, l'espèce s'avère une menace pour les écosystèmes naturels et la santé humaine. Membre de la famille de la carotte (Apiacées), la berce du Caucase est étroitement apparentée à l'espèce indigène Heracleum maximum Bartram (berce laineuse). Cette vivace monocarpienne fleurit habituellement la troisième ou la quatrième année. Il est facile de la distinguer des autres plantes à cause de sa grande taille, de la forme de ses feuilles, des taches rouge foncé sur la tige et les pétioles et des fruits très caractéristiques. On la trouve de plus en plus dans les habitats riverains, les plaines inondables et la lisière des forêts, ou à proximité des zones urbaines dans le sud-ouest de la Colombie-Britannique et le sud de l'Ontario. D'après les spécimens conservés dans les herbiers, H. mantegazzianum a été identifiée pour la première fois en 1949 en Ontario, en 1964 en Colombie-Britannique, en 1980 en Nouvelle-Écosse, en 1990 au Québec et en 2000 au Nouveau-Brunswick. Le développement de peuplements denses peut nuire à la diversité des espèces indigènes. Toucher la berce du Caucase entraîne parfois une phytophotodermatose, inflammation grave de la peau résultant de la photoactivation des furanocoumarines présentes dans la sève par les rayons ultraviolets. Les méthodes de lutte comprennent l'application d'herbicides, la coupe mécanique et la paissance, mais on devrait aussi adopter des stratégies pour empêcher la dispersion des semences et la germination des graines dormantes. La propagation de cette plante dans le sud du Canada laisse planer un doute sur la possibilité de son éradication. Néanmoins, on pourrait éviter l'expansion de son aire et ralentir la croissance de la population par des méthodes de gestion stratégiques comprenant la sensibilisation de la population.

Mots clés: Berce du Caucase, *Heracleum mantegazzianum*, Apiacées, HERMZ, plante envahissante, biologie des mauvaises herbes, furanocoumarines

1. Species Name and Taxonomic Relationships

Heracleum mantegazzianum Sommier & Levier (1895) — Synonyms: *H. grossheimii* Manden. — **giant hogweed** (Darbyshire et al. 2000); cartwheel-flower (Huxley 1992); giant cow-parsnip (Morton 1975, 1978); giant Russian hogweed (Epstein 1987); Siberian cow-parsnip (Dodd et al. 1994); wild rhubarb (Camm et al. 1976a); **berce du** **Caucase** (Darbyshire et al. 2000). Bayer code: HERMZ. Apiaceae (= Umbelliferae), carrot family (= parsley family), Apiacées (= Ombellifères).

The genus *Heracleum* encompasses about 70 species which are found mostly in north temperate regions, particularly central Asia (Mandenova 1951). Of the three species known in Canada, one is a widespread native species,

Heracleum maximum Bartram (= Heracleum lanatum Michx.), and two are introduced species, *H. mantegazzianum* and *H. sphondylium* L. The introduced *H. sphondylium* is rare in Canada from Newfoundland to Ontario (Morton 1978; Marie-Victorin 1997; Roland and Zinck 1998; Hinds 2000) and is not considered invasive. Giant hogweed, *H. mantegazzianum*, has been introduced in eastern Canada and British Columbia and has become an invasive plant of increasing management concern throughout its Canadian range. It is endemic to the Caucasus region of central Asia and is widespread in Europe and North America through purposeful or accidental human introduction.

There are several taxonomic uncertainties in the genus *Heracleum* caused by the variability of distinguishing characters. Although treated as separate species in the following key, the North America native *H. maximum* could not be distinguished from the highly variable Eurasian taxon *H. sphondylium* by Brummitt (1971). He proposed that the North American plants are best treated as *H. sphondylium* subsp. *montanum* (Gaudin) Briquet. The name *H. lanatum* Michx. was adopted by Cronquist et al. (1997) who were reluctant to apply the European name to our North American plants.

2. Description and Account of Variation

(a) Species Description — This description is based on characteristics of Canadian populations supplemented with published information (e.g., Tutin 1980; Tiley et al. 1996) and with measurements and observations on specimens from Canada. Definitions of specialized terms and detailed descriptions of morphological characteristics in the family Apiaceae are given by Kljuykov et al. (2004). The illustrations (Figs. 1A–1C) are based on plants from Canadian populations. Leaf epidermal characteristics are described by Arora et al. (1982) and pollen morphology by Cerceau-Larrival (1971).

Plants are monocarpic perennials or occasionally biennials. A large, hollow central stem develops from a rosette of basal leaves. Plants are typically 3-4 m tall during flowering, but range up to 5.5 m. The plant has a stout branching taproot up to 60 cm long and 15 cm in diameter at the crown. Stems are 4-10 (-15) cm wide, hollow and ridged (Fig. 1A). Stems and lower petioles are usually extensively blotched or spotted with reddish-purple pigments, and with pustulate-based hollow hairs, especially near the nodes (Fig. 2). Leaves are alternate. Lower leaves are $1-2.5 \text{ m} \log_{10}$ compound, divided to a varying extent but usually in three (ternate) or sometimes five (pinnate) segments (the lower ones usually with a short stalk), which are usually deeply lobed and coarsely and irregularly toothed. The leaves are usually pubescent beneath, particularly when young, and more or less glabrous above; petioles are stout, hollow and with a broad sheath at the base; upper stem leaves are smaller (sometimes not divided) with longer petioles and more inflated sheaths. Most parts of the plant, except the upper leaf surfaces, are covered with stiff whitish hairs (Fig. 2). The hairs are brittle and hollow. When fresh they are filled with a clear sap. The plant has a strong resinous or musty smell, particularly when the stem or leaves are brushed or broken.

The inflorescence is a large compound umbel composed of 4–12 flat-topped or broadly rounded units, the main ones are up to 80 cm wide and with 50–150 hairy umbel rays that are 15–40 cm long and terminate in smaller umbellets; the peduncle is as long as or longer than the rays (up to about 60 cm) and usually with spreading hairs; the terminal umbel contains hermaphrodite flowers and is surrounded by up to eight lateral umbels, which contain mostly male flowers. Flowers are whitish; sepals triangular; petals creamy white or rarely pinkish, up to about 1 cm long but irregular in size, the larger ones toward the outside of umbellets and deeply notched, the smaller ones toward the inside of umbellets are ovate and not notched; styles enlarged at the base (stylopodium). Flowers are lightly scented.

Fruits are dry schizocarps that consist of two strongly flattened mericarps (seeds), which are joined until ripening, 6–18 mm long, 4–10 mm wide, and 1 mm thick; mericarps are elliptical and emarginate at the apex, with slender, low dorsal ridges and broadly winged lateral ridges, the wings flat and closely appressed to one another, hairy on the outer face when young and becoming glabrous with age. Mericarps have 4–6 prominent abaxial oil tubes (vittae) about 3/4 as long as the fruit (Fig. 3), usually broadened (spatulate or clavate) and about 1 mm wide at the lower end; pedicels 10–20 mm, hairy; the persistent styles are divergent or somewhat recurved. Cotyledons are linear and narrowed to a distinct petiole. The first leaves are simple, rounded and more or less kidney-shaped with a crenulate margin (Fig. 4).

Chromosome counts of n = 11 and 2n = 22 were obtained from plants that were grown from seeds collected at Wakefield, Québec (reported here). Another gametophyte count of n = 11 was reported from plants cultivated at Portland, Oregon (Bell and Constance 1966). Wanscher (1932) counted n = 11 from material in cultivation at Copenhagen and Hindáková and Schwarzová (1987) counted 2n = 22 from material naturalized in Slovakia. The only count from plants growing in their native range in Georgia was 2n = 22 (Gagnidze and Chkheidze 1975).

(b) Distinguishing Features — Large size, leaf shape, dark reddish pigments in patches or spots on stems and petioles, and fruit characteristics readily distinguish *H. mantegazzianum* from other species of Apiaceae in Canada. Species of the genus Angelica are superficially similar, but both the native *A. atropurpurea* L. and the introduced *A. sylvestris* L. have twice pinnate principal leaves with the distinct leaflets toothed but not lobed.

Key to Heracleum species in Canada:

 Flowering stems 3–4 m tall (up to 5.5 m), usually with extensive reddish-purple blotching; principal leaves deeply lobed and toothed, 1–3 leaflets (1-ternate), the stalks of the lower leaflets usually less than 10 cm long; rays of main umbel more than 50; fruits elliptic to ovate, with oil tubes broadened towards the ends

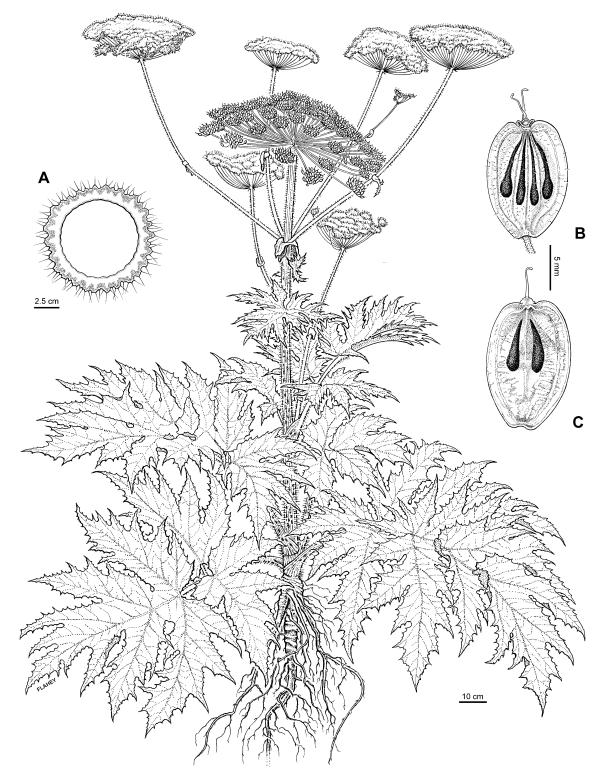


Fig. 1. *Heracleum mantegazzianum*: A. Cross section through stem; B. abaxial (outside) view of the schizocarp or fruit (note the two styles) showing four dark oil tubes; C. adaxial (inside) view of mericarp or seed (half of the schizocarp).

and extending 3/4 or more of the seed length (Figs. 1B and 3); introduced species in British Columbia and Eastern Canada......*H. mantegazzianum*

1. Flowering stems about 2 m tall (up to 3 m), usually with diffuse reddish-purple coloured blotches or spots; principal leaves with 3–5 leaflets (ternate to pinnate),



Fig. 2. Sheathing base of petiole surrounding the flowering stem. Note the long white hairs with pustulate reddish bases.

- 2. Plants with stiff hairs; principal leaves with 3–7 leaflets (once pinnate), the lower leaflets sessile

or with short stalks; fruits shallowly notched; uncommon and local introduced species in Eastern Canada*H. sphondylium*

(c) Intraspecific Variation — Little intra-specific variation has been detected in *H. mantegazzianum* and no subspecific taxa have been described. In a chromatographic study of 18 plants from a Scottish population, Weimarck et al. (1979) found only two phenotypes, as opposed to eight phenotypes in the native *H. sphondylium*, of which one was found in 94% of plants. Walker et al. (2003) used microsatellite DNA markers to assess genetic diversity in 13 *H. mantegazzianum* populations in three drainage catchments in Britain. They found that overall genetic variation was high, and that pop-

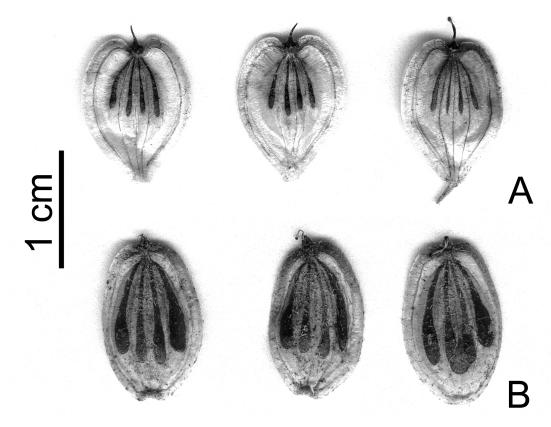


Fig. 3. Abaxial (outside) surface of Heracleum mericarps showing differences in oil tubes (vittae): A. H. maximum; B. H. mantegazzianum.

ulations from the same catchment were more similar, suggesting connections through waterborne dispersal.

3. Economic Importance and Environmental Impact

(a) Detrimental — Considered to be one of the most noxious invading plants in Europe (Pyšek et al. 1998), H. mantegazzianum poses a threat to natural ecosystems and human health, as well as being a weed in agricultural and urbanized areas. In Europe it has rapidly established in a variety of semi-natural and man-made ecosystems, particularly floodplains, riparian zones, forest edges, roadsides, meadows, open forest, and unmanaged urban areas (Williamson and Forbes 1982; Tiley and Philp 1992; Pyšek 1994; Pyšekand Prach 1994; Otte and Franke 1998). It often forms monospecific stands (Fig. 5) where its tall stems and large leaves effectively compete for light against other plants (Clegg and Grace 1974; Williamson and Forbes 1982; Pyšek 1991; Andersen 1994; Otte and Franke 1998). There is some evidence of allelopathy in Heracleum species (Junttila 1975, 1976), which may increase the detrimental impact of H. mantegazzianum on other plants. In general, *H. mantegazzianum* is believed to reduce diversity of native plant communities (Tiley and Philp 1992; Godefroid 1998), although there is little comprehensive research to assess this impact. It is especially invasive in riparian ecosystems, where new colonies can be established from waterborne seeds (Dawe and White 1979; Pyšek 1994). It can displace riparian vegetation and increase streambank erosion during the winter when *H. mantegazzianum* is senescent (Wright 1984; Tiley and Philp 1992, 1994; Dodd et al. 1994). Instability of river banks dominated by *H. mantegazzianum* in Great Britain and Ireland poses a serious threat to salmon spawning habitats (Caffrey 1999).

It is well known that H. mantegazzianum causes phytophotodermatitis, a serious skin inflammation resulting from the activation, under ultraviolet radiation, of compounds contained in the plant sap (Kuske 1940; Drever and Hunter 1970; Camm et al. 1976a). The major phytotoxic principles in Heracleum species are linear furanocoumarins or psoralens, mainly 5-methoxypsoralen and 8-methoxypsoralen (Pathak et al. 1967; Nielsen 1970; Molho et al. 1971; Pira et al. 1989). Toxicity is due to cross-linking of the furan ring with pyrimidine bases (thymine) of DNA in the presence of ultraviolet light at 315-400 nm. Furanocoumarininduced dermatitis typically consists of painful blisters that form within 48 h and become pigmented scars that can last as long as 6 yr, but more typically disappear after several months (Sommer and Jillson 1967; Morton 1978; Tiley et al. 1996). Long-term sensitivity of affected skin areas to sunlight may follow. Furanocoumarins may also be mutagenic (Igali et al. 1970; Townsend et al. 1971; Clarke 1974). Numerous cases of phytophotodermatitis attributable to contact with H. mantegazzianum have been documented by medical practitioners (Miescher and Burckhardt 1937; Jones and Russell 1968; Smellie 1968; Drever and Hunter 1970; Camm et al. 1976a; Mitchell and Rock 1978) and many

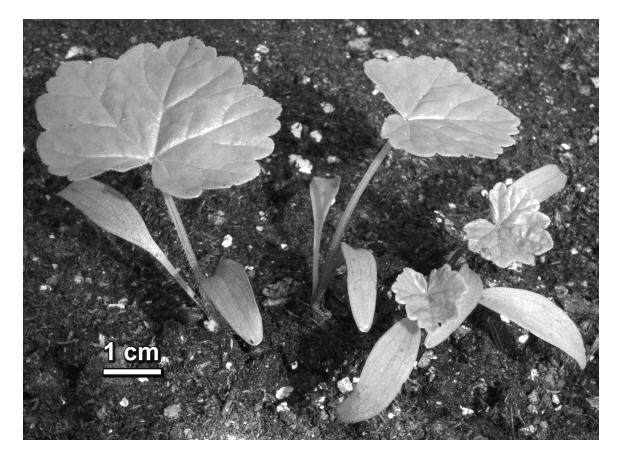


Fig. 4. Four seedlings of *Heracleum mantegazzianum* about 1 wk after emergence.

more have been reported by the public media (e.g., Kamermans 1977; Anonymous 2002; Leslie 2003; Dutton 2004). In addition, injuries to livestock and pets have been attributed to furanocoumarins in *H. mantegazzianum* (Hinterman 1962; Camm et al. 1976a; Andrews et al. 1985; Harwood 1985). However, Dickson (2001) noted that despite the widespread presence of *H. mantegazzianum* in Glasgow, Scotland, local dermatologists considered phytophotodermatitis to be an uncommon medical problem.

Although *H. mantegazzianum* is not commonly regarded as an agricultural weed, there is some concern about its establishment in pastures and field crops because of injuries to livestock. In Sweden it has been found to invade arable lands such as potato fields (Lundström 1984). Some of these concerns have been offset by reports of successful suppression of *H. mantegazzianum* through foraging by livestock (Andersen 1994; Tiley et al. 1996). It can also harbour pests and pathogens of agricultural crops (see Section 13).

There is a possibility of detrimental effects to *H. maximum* in Canada from hybridization with *H. mantegazzianum*. Occurring in a variety of habitats across North America, *H. maximum* will be increasingly in contact with *H. mantegazzianum* as the latter spreads. Although *H. maximum* flowering peaks 3–4 wk earlier than *H. mantegazzianum*, there is sufficient overlap in flowering times for cross-pollination to occur. In Europe, *H. mantegazzianum* is known to hybridize with *H. sphondylium* (see Section 9).

(b) *Beneficial* — The striking size and distinctive inflorescences make *H. mantegazzianum* an impressive ornamental plant for gardens (Mondoor 2001). Indeed, some of its rapid spread in Canada is likely caused by purposeful introductions for horticulture. As of 2005, it is still seen for sale in some Canadian nurseries (Darbyshire, personal observation). Its popularity as an ornamental plant has been identified as a major cause of its spread in central Europe (Pyšek 1991).

The flowers are nectar sources for honeybees (Grace and Nelson 1981; Bürki and Nentwig 1997) and the dried umbels are used for decorative purposes. In addition, the seeds are used as a spice (golpar) in Middle Eastern cooking (Westbrooks 1991), although five Heracleum species native to mountainous areas of Iran are traditionally the source of golpar. Both *H. mantegazzianum* and its close relative *H.* sosnowskyi Manden. have also been cultivated as forage plants in Eastern Europe (Nielsen et al. 2005). Nutrient concentrations were examined by Otte and Franke (1998) and compared favourably with other forages. Furanocoumarins gathered from plant sources (including *Heracleum* species) are used extensively in the treatment of leukodermia and in the preparation of sun-tan lotions (Devagiri et al. 1997). They have also been found to have potential as insect repellents as they suppress feeding and growth in some species (Klocke et al. 1989). Various compounds present in H. mantegazzianum, including furanocoumarins and glycosides,



Fig. 5. A large colony of Heracleum mantegazzianum growing in a roadside area in North Vancouver, BC.

have been investigated for their anti-bacterial and anti-fungal properties (Fischer et al. 1976, 1982).

(c) *Legislation* — There is no federal or provincial legislation preventing entry of *H. mantegazzianum* into Canada or designating it as a noxious weed (Darbyshire 2003). The District of Saanich on southern Vancouver Island, BC, recently designated it a noxious weed under a municipal bylaw (District of Saanich 2005). In Ontario, it is listed as a noxious weed in the bylaws of Grey (3379-92) and Huron (24-92) counties, where it is to be controlled on agricultural lands under section 10 of the Ontario Weed Control Act (M. Cowbrough, personal communication).

In the United States, *H. mantegazzianum* is listed under the Federal Noxious Weeds Act of 1974 whereby it must be reported and controlled when found and importation or interstate movement is illegal (Anonymous 1999). Washington State lists it as a Class A weed (Anonymous 2003a) and prohibits sale and transport of propagating materials (Hamel and Parsons 2001). In the United Kingdom, there is a ban on planting *H. mantegazzianum* under the 1981 Wildlife and Countryside Act (Anonymous 2005)

4. Geographical Distribution

The natural range of *H. mantegazzianum* is the subalpine zone of the western Caucasus Mountains of Georgia,

Azerbaijan, and southern Russia (Mandenova 1951; Otte and Franke 1998), where it is found in meadows, clearings, and forest edges between 1500 and 1850 m.

Since the 19th century, *H. mantegazzianu*m and a number of other Caucasus plants have been introduced to a variety of regions of both the northern and southern hemispheres, particularly Europe (Clegg and Grace 1974; Knapp and Hacker 1984; Pyšek 1991). Early range expansion of *H. mantegazzianum* appears to have begun in the early to mid-19th century when it was introduced to botanical gardens in the United Kingdom and continental Europe as an ornamental plant. Introduction to North America likely occurred during the first half of the 20th century.

In Canada, it is found from British Columbia to Newfoundland (Fig. 6A). In British Columbia, it is most prevalent on southeastern Vancouver Island, particularly the Parksville area, and in North and West Vancouver (Fig. 6B) (Page and Wall 2003). It is also widespread in southwestern Ontario, with most occurrences found east of Lake Huron (Fig. 6A). Localized populations are known in southern Quebec, New Brunswick, Cape Breton and eastern Newfoundland. It has been recorded in six US states, either in the northeast or Pacific northwest: Conneticut, Maine, Massachusetts, Michigan, New York, Pennsylvania, Oregon, and Washington (Kartesz 1999)

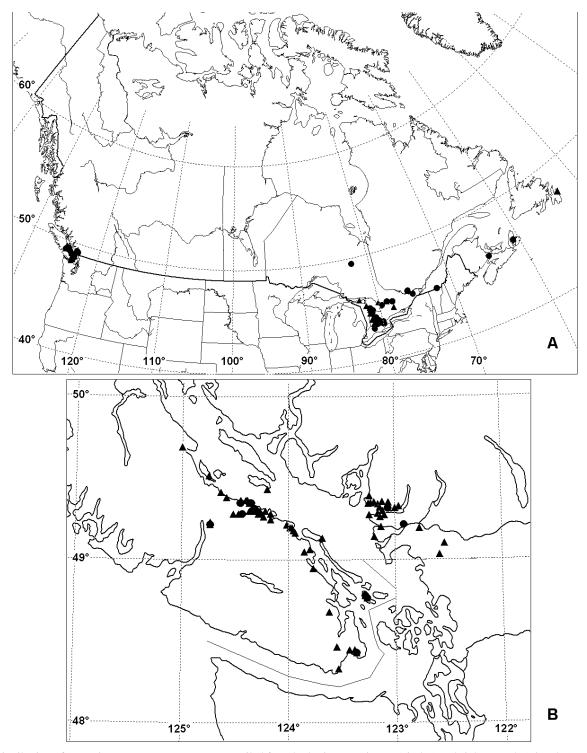


Fig. 6. Distribution of *Heracleum mantegazzianum* as compiled from herbarium specimens (circles) and sight records (triangles). Herbarium specimens examined from CAN, DAO, HAM, MICH, MTMG, NSPM, OAC, QUE, TRT, UBC, UNB, UWO and V (acronyms after Holmgren et al. 1990) A. Canadian distribution; B. Detail of distribution in southwestern British Columbia.

It has also been reported as established in Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Hungary, Iceland, Ireland, Italy, Latvia, Luxembough, the Netherlands, Norway, Poland, Slovakia, Sweden, Switzerland, and the United Kingdom (Brummitt 1968; Hindáková and Schwarzová 1987; Nielsen et al. 2005) and in New Zealand, mainly eastern South Island (Webb et al. 1988).

5. Habitat

(a) *Climatic Requirements* — Although it grows in a wide range of climatic conditions, H. mantegazzianum is most invasive in regions with cool, moist climates that are similar to its native habitat. In Canada, its distribution is primarily in developed areas and the limiting effects of climate on its range are unknown. It does, however, occur as far north as Kapuskasing, Ontario (Fig. 6A). In the Czech Republic, Pyšek et al. (1998) found that peak incidence of H. mantegazzianum was associated with January isotherms of 3°C, June isotherms of 7°C, and annual precipitation of 400-500 mm. January isotherm and density of human population were the factors most significantly correlated with H. mantegazzianum distribution. In the Scandinavian countries, H. mantegazzianum is found only in Denmark, southern Sweden and southern Norway (Nielsen et al. 2005). Based on the climates in which this species grows, it is readily apparent that overwintering plant parts (e.g., roots and stembud) can withstand cold conditions. Plants, including seedlings, are frost resistant (Godefroid 1998) and sprouting shoots have been observed to survive -17°C (Tiley et al. 1996). Its occurrence in northern Ontario (Fig. 6A) and its distribution in northern European countries (Nielsen et al. 2005) suggest it could be tolerant of the extremely cold, continental climates in Canada.

(b) Substratum — The prevalence of H. mantegazzianum in riparian zones, ditches, and forest edges suggest that it prefers moist, fertile soils, but this may be due largely to its tendency to spread along streams (Pyšek and Pyšek 1995; Tiley et al. 1996; Otte and Franke 1998). Large colonies are often found on sandy or silty deposits along watercourses where seeds come to rest (Morton 1978; McIlveen 2001), but seedlings may also become established in organic soils typical of woodlands. Deep soils are required for optimum growth, but plants may also thrive on drier, well-drained soils characteristic of roadsides and waste-ground (Godefroid 1998). Along French Creek on Vancouver Island, BC, initial establishment has been in alluvial soils along the stream, but there has been subsequent spread into adjacent woodlands and along road embankments (Wall, personal observation). This distribution pattern was also observed in North Vancouver, BC (Page, personal observation). Morton (1978) reported it growing in deep rich moist soils in semi-shade, mostly along rivers and streams, in Ontario. In eastern Ontario and western Québec, plants are frequently growing in sandy-gravel of road embankments and ditches (Darbyshire, personal observation).

In the United Kingdom, *H. mantegazzianum* has been found on a wide variety of soils ranging from clays to gravels, and from limestone to acid heath, but high organic matter (usually 3–9%) and high potassium and calcium levels are especially favourable (Clegg and Grace 1974). Tiley and Philp (1992) report occurrences on sandy soils in riparian and ruderal habitats. Soils supporting *H. mantegazzianum* are usually neutral to alkaline; a pH range from 5 to 9 has been reported in Scotland (Clegg and Grace 1974). Pyšek and Pyšek (1995) reported that it is not found in acidic habitats in the Czech Republic. Detailed soil analysis at a site in

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Germany by Otte and Franke (1998) also showed high organic matter (1.5–4.9% organic carbon) and slightly acidic pH (6.4–6.7). The presence of *H. mantegazzianum* on sea shores and oceanside cliffs with frequent salt spray, as well as roadside areas receiving de-icing salt, indicates that it is salt tolerant (Tiley et al. 1996; Godefroid 1998). Lundström (1984) also reported that it occurs in coastal sands in southern Sweden.

(c) Communities in which the Species Occurs - In Canada, H. mantegazzianum occurs in open and forested floodplains, alluvial gravel bars, roadside ditches and embankments, hedgerows, open forests, forest edges, marine shorelines, and old fields (Morton 1978; McIlveen 2001; herbarium specimen label data). The pattern of H. mantegazzianum distribution in Canada suggests that initial establishment is usually in disturbed, nonforested habitats such as roadsides (see Fig. 5), forest edges, and stream margins and from these foci it can invade open woodlands, grasslands or wet meadows. H. mantegazzianum does not thrive and spread in dense coniferous forests, grasslands, or sedge meadows where competition from the existing community may preclude seedling establishment or growth. It is also intolerant of wetlands subject to long periods of inundation. On alluvial or fluvial sites, H. mantegazzianum often grows in mixed communities with herbs and grasses, but it can become dominant on drier, disturbed sites.

In its native range, H. mantegazzianum occurs in subalpine meadows, ravines, along forest edges, and along streams (Mandenova 1951; Tiley et al. 1996; Otte and Franke 1998; Wittenberg et al. 2003). In regions where it has recently been introduced, it occurs mainly in riparian areas and near human habitations where it has been planted or has escaped from garden cultivation. Populations in Europe are frequently distributed along dispersal corridors, such as watercourses, roadsides and railways (Pyšek 1991; Otte and Franke 1998), although many types of communities have been colonized (Pyšek and Pyšek 1995) and its ecological range is still expanding (Caffrey 1999). A similar pattern was found in a survey around Edinburgh, Scotland (Clegg and Grace 1974), and in Belgium it grows principally along roads and railways and in waste ground and parks (Godefroid 1998). In regions where H. mantegazzianum has been present for many decades, it occurs in a broader range of habitats including riparian areas, roadsides, pastures, open woodlands, wetlands, landfills, urban parks, and urban gardens (Andersen 1994; Pyšek 1994; Tiley et al. 1996). Otte and Franke (1998) state that it is a plant of nitrophitic herbaceous perennial communities in central Europe where it occurs in a variety of sites including abandoned farmland, eutrophied forest edges, and transportation corridors in lowland and submontane regions. They analysed the plant communities at a number of sites in the Lahn Valley in central Germany and found that H. mantegazzianum formed a distinct community with Galium aparine L. and Urtica dioica L.

6. History

The introduction of *H. mantegazzianum* into Canada was probably as a result of escape from horticultural planting

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(Morton 1978), as it was in many parts of Europe. The earliest herbarium specimen of H. mantegazzianum in Canada was collected from Kemble, ON in 1949. The first widely distributed literature report of its occurrence in Canada was that of Morton (1975) which was based on his observations on a population at Tara, ON. Additional surveys by Morton (1978), after his initial discovery, indicated that it was widely spread in eight counties in southwestern Ontario. The earliest specimen from British Columbia was collected in 1964 near Parksville on southeastern Vancouver Island, although it may have been introduced to the province in the 1920s or 1930s (Merilees 1978; Dawe and White 1979; Merilees 1981). The first specimen from the Lower Fraser Valley in southwestern British Columbia was collected in 1974 from Mahon Park in the City of North Vancouver, BC. In other provinces the first collections were made at Baddeck, NS, in 1980; Stanstead, QC, in 1990; and, Sackville, NB, in 2000.

7. Growth and Development

(a) *Morphology* — Various morphological features in combination with its toxic properties make *H. mantegazzianum* very difficult to control. The sheer size of older rosettes and mature plants, as well as the usually dense growth, pose challenges for control practices. Large taproots store considerable below-ground resources that confer some protection against physical and chemical control measures. As well as providing energy reserves in the event of poor growing conditions, the large taproots are difficult to dig up and are resistant to energy depletion through repeated cutting of above-ground parts.

The large root reserves also allow plants in the vegetative growth stage to develop an extensive leaf canopy elevated on long petioles early in the growing season. This facilitates competition with other herbaceous species and results in high productivity. In Germany, Otte and Franke (1998) calculated the total biomass production at 947 t ha⁻¹ and the above-ground biomass at 710 t ha⁻¹.

All parts of the plant contain toxic furanocoumarins (see Section 3a), which is a hazard for those attempting vegetation management. The lower parts of the hollow stems and petioles may be partly filled with fluid containing furanocoumarins, sometimes in considerable volumes (Darbyshire, personal observation). Mechanically cutting the plant risks splashing or volatilizing sap and fluids, putting workers at high risk. The hollow hairs, often abundant on the stems around the nodes and on the lower petioles (Fig. 2), also contain sap. These brittle hairs may penetrate and break off in skin causing physical irritation (Morton 1978), as well as facilitating delivery and penetration of furanocoumarins.

(b) *Perennation* — *H. mantegazzianum* is a monocarpic perennial or occasional biennial. In Germany, plants may flower in the second year, but usually mature after 3 or more years (Otte and Franke 1998). Above-ground plant parts annually die back to the taproot each autumn until the year that flowering occurs, after which the whole plant senesces. Plants may flower in the 2nd, 3rd, 4th or 5th years but most flower in the 4th year in Ontario (Morton 1978) and the 3rd

year in the United Kingdom (Stewart and Grace 1984; Tiley et al. 1996).

There may occasionally be continued growth after flowering, and Morton (1978) reported that some plants produce new crowns after flowering. Similarly, a second flowering stem is usually produced if the main stem is cut or damaged before the flowers open (Stewart and Grace 1984; Dodd et al. 1994).

(c) *Physiological Data* — Since the phloem of *H. mantegazzianum* is easily separated from the vascular bundles, it has been used extensively in studies of translocation. Fensom et al. (1968) estimated a streaming rate of about 1 cm h⁻¹. Other studies have been conducted, mainly at Mount Alliston University in Sackville NB, using *H. mantegazzianum* as a research tool to elucidate the underlying forces governing mass flow (Tyree and Fensom 1970; Spanner 1970), determine the nature of particles observed in phloem (Lee et al. 1971; Hart and Sabnis 1975; Barclay et al. 1977; Murphy 1986), and gain further insight into energy transfers in active phloem (Ezeala et al. 1974).

The chemistry of *H. mantegazzianum* is well studied because of its production of complex secondary compounds, particularly furanocoumarins (Murray 2002), but also flavonoids (Harborne 1971), glycosides (Fischer et al. 1982), and essential oils (Jain 1969). A considerable amount of information is summarized in the comparative phytochemistry study by Carbonnier et al. (1982). Furanocoumarin chemistry and content vary between plant parts and growth stages. Both Knudsen (1983) using material from Denmark and Pira et al. (1989) using material from Italy found maximum levels in the fruit, with intermediate levels in the leaves, followed by the roots, and the lowest levels in the stem. Psoralen was the predominant furanocoumarin in the leaves and bergapten in the fruit (Pira et al. 1989). Furanocoumarin levels peaked in spring and early summer and declined in late summer and autumn. Glowniak et al. (2003) isolated bergapten, xanthotoxin, isopimpinellin, imperitorin, pimpinellin from the fruits of H. mantegazzianum collected in Poland. Analysis by Dragan et al. (1999) of material collected in France found the same compounds, as well as byakangelicol.

(d) *Phenology* — First year growth is usually slow, and the seedling initially develops a single leaf or a rosette of four small, sessile leaves in early spring (Fig. 4). These are followed by larger, more petiolate leaves. A narrow taproot, 45–60 cm deep, develops quickly and the upper part of the root thickens as food reserves accumulate. In the juvenile vegetative growth stages, photosynthetic production is preferentially directed to the taproot for storage, and the root to shoot dry mass ratio is about 1.4:1 (Otte and Franke 1998). The root over-winters with large terminal buds that form the next year's shoots.

In the second and subsequent years, growth may begin as early as late December in regions with mild winters such as coastal British Columbia. Vegetative growth begins as a greening and swelling of buds on the root crown. By April or May, plants may be 1–2 m high with three to four leaves. Lower leaves senesce, resulting in a fairly constant leaf number until die-back in September or October. Occasionally, 1–3 basal leaves develop in late September or October and remain green into the winter. Spring leaves are broader with more surface area, while summer leaves are longer, with narrower segments (Tiley et al. 1996; Willis and Hulme 2002).

Plants destined to flower in the ensuing year have a certain threshold root size, have woody secondary thickening of the roots, are the earliest to begin growth, and have the largest spring leaf development. In an even-aged stand, only the largest plants flower and these plants usually possess three to four large basal leaves plus four to six stem leaves. In early June, flowering plants form a swollen terminal bud, which encloses the terminal umbel. Secondary umbels form later and may not develop fully unless the terminal umbel is damaged (Tiley et al. 1996). Flowering occurs over a 5–6 wk period between June and August (Mandenova 1951; Morton 1978; Otte and Franke 1998). The fruits mature and dry over August and September, and split into two mericarps when ripe. These usually detach over autumn and winter but are sometimes retained until the following year.

Detailed studies on the growth and phenology of *H. mantegazzianum* in Germany were undertaken by Otte and Franke (1998) and in Ireland by Caffrey (1999). Otte and Franke (1998) described four development phases in plants flowering that year in central Germany: (i) vegetative development (10 wk: Mar. 01–May 10); (ii) flowering (8 wk: May 10–Jul. 03); (iii) fruiting (5 wk: Jul. 03–Aug. 10); and, (iv) release of mericarps (>4 wk: after Aug. 10). Caffrey (1999) found similar growth and flowering patterns in Irish populations: plants emerged in early February, grew vegetatively until early May when flowering began, flowering peaked in late June, and most seeds had ripened and dispersed by the end of August.

(e) *Mycorrhiza* — No records of mycorrhiza on *H. mantegezzianum* have been reported. In Germany, Kühn et al. (1991) surveyed a field abandoned from maize production for the presence of mycorrhizal relationships. Although *H. mantegazzianum* was not present, they reported that *H. sphondylium* was occasionally infected with mycorrhizal fungi.

8. Reproduction

(a) *Floral Biology* — *H. mantegazzianum* produces a large numbers of hermaphrodite flowers on upright umbels. Flowers mature in a centripetal sequence and the primary terminal umbel matures first (Stewart and Grace 1984; Tiley et al. 1996). Secondary or tertiary umbels, some of which are staminate, may only mature if the terminal umbel is destroyed (Tiley et al. 1996). Stamens mature and dehisce before the pistils are receptive, although self-pollination is possible between flowers in umbels at different stages of maturity on the same plant (Weimarck et al. 1979; Stewart and Grace 1984). In the staminate phase, flowers of an umbel open over a 5-d period, the stamens lasting for about

a day, after which a period of 1-3 d usually elapses before all the stigmas across the umbel become receptive on the same day (Stewart and Grace 1984).

There is little information on insect pollinators of *H. mantegazzianum*; however, like most Apiaceae, it attracts a wide range of unspecialized pollinators. A long list of coleopteran, dipteran and hymenopteran visitors is given for the European *H. sphondylium* by Knuth (1908). Grace and Nelson (1981) found that *H. sphondylium* and *H. mantegazzianum* had attracted distinct insect faunas in areas of sympatry in Scotland. They list 48 species of insects caught on *H. mantegazzianum*, but found significant amounts of pollen on only 16 taxa (10 diptera, five hymenoptera and one coleopteran). Otte and Franke (1998) report that pollination in central Europe is primarily by beetles (Coleoptera).

(b) Seed Production and Dispersal — The large inflorescence of *H. mantegazzianum* produces prodigious amounts of seed. In central Europe, each of the several large umbels may produce 5000 to 6500 seeds (Pyšek 1991; Otte and Franke 1998). In the Czech Republic, Pyšek and Pyšek (1995) reported that up to 107 000 seeds may be produced by a single plant. Tiley and Philp (1994) estimated 60 000 flowers (producing up to 120 000 seeds) on one large plant examined in Scotland. Otte and Franke (1998), however, observed that not all flowers in secondary and tertiary umbels on plants growing in Germany produced viable seeds and that seeds in these umbels are lighter and smaller than those of the primary umbels.

Plants from Scotland studied by Weimarck et al. (1979) showed a seed set of 84% and pollen stainability (cotton blue) of 91%. In their artificial pollination experiments, Stewart and Grace (1984) found that mean seed set was minimal when flowers within a single umbel were used (1%), but 68% when flowers between different umbels on the same plant were used. Mean seed set in flowers between different cross-pollinated plants was 64% (range 47–85%). Germination after 22 wk at 2°C stratification was less for seed from self-pollinated than cross-pollinated flowers, 27% versus 59%, respectively.

The fruit splits into two flat and winged mericarps each up to 20 mg in weight and possessing distinctive oil tubes (Figs. 1B, 1C, and 3). The light, buoyant fruit may be waterborne for long distances and also carried short distances by strong air currents (Tiley et al. 1996). Dispersal occurs by direct seed fall within the immediate vicinity of mature plants, by wind, by water along streams, ditches, or road margins, and by direct human transport (Otte and Franke 1998; Dawson and Holland 1999). Otte and Franke (1998) found that the 75% of seeds fell within 120 cm of the mother plant. Several authors have mentioned that seeds may be dispersed by wind (e.g., Lundström 1990; Godefroid 1998). Although the seeds are flat with winged margins, experiments on wind dispersal suggest that this is not a very effective means of dispersal since seeds released from a height of 0.69 m, at wind speeds of 0.6–5.5 m s⁻¹, traveled less than 1 m from the release point (Clegg and Grace 1974). Otte and Franke (1998) noted that the maximum dispersal distance by wind was 8–10 m. Wind currents from fast moving vehicles may contribute to the dispersal of seed along highways and railroads (Clegg and Grace 1974). The first reported population in Michigan (Case and Beaman 1992) occurred in a very isolated locality that was clearly not a deliberate planting. Its long distance dispersal to the reported location could not be explained by the discoverers.

Since seeds can float for up to 3 d (Morton 1978), water is a major agent of local and long distance seed dispersal (Pyšek and Prach 1994; Walker et al. 2003). Floatation experiments in Scotland showed that seeds would remain afloat for 1.5–2 d in turbulent water and 3 d in calm water (Clegg and Grace 1974). At a modest flow rate of 0.1 m s⁻¹, seeds would be able to travel 10 km or more. Movement of seed-contaminated soil by humans is an important dispersal mechanism in North Vancouver, BC (Page, personal observation). Movement of young plants or seeds for horticultural plantings is also a source of new populations. No evidence has been found of significant transport by birds, mammals, or insects (Otte and Franke 1998).

(c) Seed Banks, Seed Viability and Germination — A seed bank study at seven sites in the Czech Republic by Krinke et al. (2005) found that the numbers of seeds in the seed bank was directly related to plant density and that the numbers and proportion of viable seeds at any one site varied between years. Pooled results showed a mean total soil seed population per m² of 6719 ± 4119 in autumn, 4907 ± 2278 in spring and 1301 ± 1036 in summer, 95% of which were present in the upper 5 cm. However, the population of viable seeds was 3759 ± 2906 , 2044 ± 1198 and 192 ± 165 , respectively.

Seeds may persist in the soil for 5–6 yr before germinating (Andersen 1994) and can remain viable in the soil for up to 15 yr (Andersen and Calov 1996). However, Otte and Franke (1998) found that seed-banks were minimal for populations in Germany. Morton (1978) found that seeds from Ontario plants stored at room temperature were still viable after 7 yr, although Lundström (1990) stated that seeds may remain viable for as much as 15 yr. Germination success of older seeds was tested on seed obtained from herbarium specimens by Hallam and Dodd (1996). Seeds ranging from 2 to 67 yr old were placed on moistened filter paper for 16 wk and then transferred outdoors for 1 mo. Two-year old seeds germinated at a rate of 78%, but all older seeds failed to germinate.

In British Columbia, germination usually occurs during late winter and early spring (Wall, personal observation). In Ontario and Québec, seeds are often seen on dead stems from the previous year. In Quebec, seeds collected from dead stems of the previous year showed 50–80% germination at room temperature in laboratory conditions (Darbyshire, unpublished data). In coastal British Columbia, seeds collected the previous autumn, stored over winter in an unheated shed and planted in late March or early April in potting soil, germinated between April and June, ceased germination during late June and July, and resumed the following spring after dry storage (Wall, unpublished data). A period of cold temperature of 2–3 mo is required for optimal physiological development and embryo maturation in H. sphondylium (Stokes 1952), and although definitive experiments have not been done with H. mantegazzianum, similar processes are likely present in that species. Results of germination tests in H. mantegazzianum have varied considerably but general conclusions are that seeds are dormant or require a long after-ripening period after being shed. Krinke et al. (2005) identified dormant seeds in Czech populations by testing the viability of non-germinating seeds with tetrazolium. Seeds that were artificially dried and stored indoors often failed to germinate, but seed stored outdoors throughout the winter germinated well (Tiley et al. 1996). Cold stratification at 0-5°C for 6-12 wk improved germination (Grime et al. 1981; Baskin and Baskin 1998). In germination tests of 28 d duration by Andersen and Calov (1996), germination averaged 25% in seeds that were subjected to a temperature of -18°C for 3 wk, which was higher than seeds stored at room temperature. In central Germany, germination occurred in early spring only after seeds were exposed to 2-3 mo of cold temperatures (Otte and Franke 1998). Although no light requirements have been demonstrated for germination (Moravcová et al. 2005), best emergence in the field has been observed in the open or under light vegetative cover in the United Kingdom (Tiley et al. 1996). Most seeds geminate from a depth of less than 5 cm, although emergence from 10 cm has been observed (Krinke et al. 2005; Moravcová et al. 2005). Seeds will rot in flooded soil.

In the Czech Republic, laboratory studies by Moravcová et al. (2005) found the mean germination rate of greater than 90% under optimal conditions. Seedling mortality is, however, also high. In Ireland, germination begins in February and peaks in April. Only 1.2% and 13.7% of seedlings present in April were extant by the end of August in the two populations studied by Caffrey (1999). Tiley et al. (1996) estimated that less than 23% of germinated seedlings survived to maturity. No study of mortality factors was reviewed but since most of the 20–100 000 seeds produced per plant fall within a few metres of the parent plant (Otte and Franke 1998), seedlings develop under very crowded conditions and mortality is expected to be high.

(d) *Vegetative Reproduction* — Although reproduction is usually considered to be entirely by seed (Tiley et al. 1996; Otte and Franke 1998), vegetative reproduction from perennating buds on tuberous rootstocks has been reported (Anonymous 2003a).

9. Hybrids

Hybridization is unusual between species in the family Apiaceae, but occasional hybrids between *H. mantegazzianum* and *H. sphondylium* have been reported in Europe where both species grow in proximity (Weimarck et al. 1979; Tutin 1980; Grace and Stewart 1982; Stewart and Grace 1984; Ochsmann 1996). Fertility of hybrids is low (seed set less than or equal to 1%; pollen stainability less than or equal to 7%) and introgression has not been detected (Weimarck et al. 1979; Stewart and Grace 1984), although one plant analysed by Weimarck et al. (1979) may have been a backcross. Stewart and Grace (1984) found that the prevalence of hybrids between *H. mantegazzianum* and *H. sphondylium* in the United Kingdom was reduced by the lack of habitats shared by the species, and by low viability (<10%) of hybrid seed. They also found that artificial F_1 hybrids were morphologically intermediate between the parents, had abnormal flower and fruit development and showed structural weakness in stems. Hybrids had a greater tendency to remain vegetative, and like *H. sphondylium*, were not monocarpic. Epidermal characteristics of the leaves, including hairiness and stomatal patterns, were intermediate between the parental species on those plants considered to be hybrids (Arora et al. 1982). Experimental crosses of *H. mantegazzianum* and *H. sphondylium* in Scotland have been successful only when the pistillate parent was *H. sphondylium* (Steward and Grace 1984).

The presence of *H. sphondylium* \times *H. mantegazzianum* hybrids in the field, the ease of artificial hybridization, and the absence of specialized pollination mechanisms suggests that *H. mantegazzianum* may hybridize with the North American *H. maximum*, which is part of the circumboreal *H. sphondylium* species complex. However, no hybrids have been reported in Canada.

10. Population Dynamics

The establishment and rapid spread of *H. mantegazzianum* depends on dispersal of seeds both locally and regionally from founder populations. Founder populations are generally very small, often a single plant in garden cultivation, and initial population increases are slowed by the requirement for 2–5 yr of growth before flowering and seed production occur. Early spread from founder populations may also be impeded by the lack of nearby routes, such as watercourses, for rapid dispersal into the surrounding landscape. As Otte and Franke (1998) documented, seed dispersal in the absence of water, wind, or soil movement is poor. However, once the population has expanded into riparian areas, regional population increase can occur rapidly through waterborne dispersal (Pyšek 1994; Wadsworth et al. 2000; Page, personal observation).

The spatial pattern of *H. mantegazzianum* in North Vancouver, BC, provides a useful model to characterize population dynamics during initial invasion. Introduction of H. mantegazzianum to this area occurred approximately 80 yr ago (Merilees 1981). A recent assessment found that the present population covered a 0.7 ha area distributed across 104 sites; only one population was larger than 250 m² in total patch size and contained approximately 450 plants (Kerr Wood Leidal Associates Ltd. 2005). The largest populations (>100 plants) were found in riparian areas and forest edges near what is believed to be the epicenter of introduction with the smallest populations occurring at the margin of range expansion (Fig. 5). Most populations were strongly connected by dispersal pathways, particularly water movement, and many small populations could be traced to the movement of seeds by water, wind, or soil from nearby populations. Very few populations were found in habitats away from dispersal routes which suggests that population development is still in the lag phase (Wade 1997). Outside of North Vancouver, populations in the Lower Fraser Valley are small and represent initial founder populations in parks and residential gardens. They range from 1 to 20 plants, although most consist of two to three plants in a small group. Isolated plants in residential gardens are increasingly common in the region (Page, personal observation).

Populations of *H. mantegazzianum* were studied in a small drainage system in Halton County, ON, by McIlveen (2001). Although population size at various sample points was affected by many variables, he found a trend in reduced population size in a downstream direction. In one stream system the change was from >2000, 2, 170, 138, 350, 11, 2, 0, 0, 0, 4 and 0 plants and in another the change was 79, 19, 32 and 0 plants. Based on the population presence within floodplains and the smaller downstream populations, McIlveen concluded that *H. mantegazzianum* was dispersed along these watercourses by water. Based on different population sizes and the timing of population discoveries, he speculated that the construction of water control structures has probably reduced the rate of spread.

In central Germany, Otte and Franke (1998) found that *H. mantegazzianum* populations were characterized by high densities of seedling germination in open areas where mature plants had flowered and died the previous year. There was competition within seedling cohorts for resources and high mortality in the first few months of growth. Plants in the vegetative growth phase that were more than 1 yr old had a maximum of 5–7 leaves in a rosette at the root crown. These plants formed a canopy 1.6 m high by mid-June. Similar observations were made on populations in Ireland by Caffrey (1999).

Pyšek (1994) and Pyšek and Pyšek (1995) reconstructed the spread of H. mantegazzianum in the Czech Republic. They documented an 80-yr lag phase between initial establishment and the onset of an exponential growth phase. During the lag phase, its spread was associated with its cultivation as a garden ornamental and subsequently along watercourses and other dispersal routes (Pyšek 1994). During the exponential phase (post-1945), populations developed away from dispersal-related habitats and populations became common throughout the general landscape. Population growth in the British Isles has followed a similar pattern (Tiley et al. 1996; Collingham et al. 2000). Wadsworth et al. (2000) modelled the rate of spread of H. mantegazzianum in a single watershed and found there was a lag phase of 10-25 yr before exponential growth in occupancy of suitable habitats occurred.

11. Response to Herbicides and Other Chemicals

No reports of herbicide tests have been found for Canada, but work in other countries indicates that *H. mantegazzianum* is sensitive to most commercial herbicides including glyphosate, imazapic, trichlopyr, dicamba, 2,4-D, and clopyralid. Treatments usually need to be repeated annually and, in some situations, within the same growing season.

In Washington State, 100% top kill was achieved with an early spring application of glyphosate at 1.7 kg a.i. ha^{-1} in single plant tests, followed in relative efficacy by imazapic at 0.22 kg a.i. ha^{-1} plus methylated seed oil at 0.6% vol/vol (97% top kill), trichlopyr at 0.86 kg a.i. ha^{-1} and 2,4-D at

 $3.05 \text{ kg a.i. } ha^{-1}$ (80% top kill), and dicamba at 1.14 kg a.i. ha^{-1} (66% top kill) (Miller and Lucero 1999).

More thorough tests on *H. mantegazzianum* were conducted by Davies and Richards (1985) in the United Kingdom, who applied various herbicides to 24-m² plots during May and documented percent mortality, emergence of new *H. mantegazzianum* seedlings, and recolonization by other species over the ensuing two growing seasons. Trichlopyr at 1.44 kg a.i. ha⁻¹ was most effective, killing the plants within 1 wk and allowing recolonization of plots with a mixture of other species with few new H. mantegazzianum seedlings. Glyphosate at 2.16 kg a.i. ha⁻¹ resulted in 100% mortality of existing plants over a 10-wk period, but many new seedlings appeared. The residual herbicides chlorsulfuron + methabenzthiazuron (GLEAN C, 70% w.p., Dupont) at 2.3 kg a.i. ha⁻¹ and metsulfuron-methyl at 0.016 kg a.i. ha⁻¹ provided 100% mortality with no seedling emergence, but recolonization by other species was sparse. Fosamine-ammonium at 4.8 kg a.i. ha⁻¹ caused chlorosis but did not kill or prevent flowering of the plants.

In Ireland, repeated glyphosate treatments on a large population over a 4-yr period almost completely eliminated H. mantegazzianum (Caffrey 2001). Glyphosate, trichlopyr, or imazapyr, applied early in the growing season, are recommended treatments in the British Isles (Wright 1984; Caffrey 1994; Dodd et al. 1994; Tiley et al. 1996). Glyphosate is widely used on H. mantegazzianum, even in countries where its general use has been restricted (Lundström and Darby 1994; Buttenschøn 2003). A 4-yr eradication protocol for H. mantegazzianum populations within a single drainage catchment using glyphosate was outlined by Caffrey (1999). As with most plants, the effects of glyphosate may appear slowly, often beginning about a month after application as a yellowing of newer leaves, followed by a complete yellowing (Stensones and Garnett 1994).

12. Response to Other Human Manipulations

Various means have been used to control H. mantegazzianum including root cutting, mowing, severing of the flowering stem or umbels, grazing, trampling and soil tilling. Severing of the roots 8–12 cm below the soil surface is usually very effective in killing the plant (Tiley et al. 1996; Buttenschøn 2003; Nielsen et al. 2005). This should be done early in the spring and again in the summer to catch escapes and the plants either removed or left to dry. Hand pulling is effective only with very young seedlings. Mowing or scything should be repeated several times during the growing season in order to be effective, but even a single spring cutting can reduce the number and size of seeds (Tiley et al. 1996). Care must be taken not to spread seeds during mowing operations. Removal of umbels during early flowering stages can result in considerable reduction in seed production, but new umbels, usually with fewer flowers and less viable seed, will form on lower branches (Pyšek et al. 1998). Removal of umbels when seeds are formed but have not yet matured is recommended by Buttenschøn (2003); however, in order to avoid the possibility of seeds maturing on the severed umbels, they should be removed from the site and destroyed.

Tiley et al. (1996) noted that tilling is effective for controlling infestations on agricultural land. While this may not appear to be applicable under most Canadian conditions, particularly riparian areas, it is a consideration near residential areas. Grazing, especially by sheep, has also been found to be an effective control (Andersen 1994), although part of this effectiveness may be due to trampling (see also Morton 1978).

No references regarding the effectiveness of fire or flame treatments have been found. However, heat treatment of *H. mantegazzianum* using the "Waipuna" system has been suggested as an effective control method (Sanh 2003). It has been tried in the Nanaimo–Parksville area of British Columbia with varying results (Wall, personal observation).

Biological control agents are also under investigation (Fowler et al. 1991; Seier 2003; Wittenberg et al. 2003; Seier et al. 2004). Indigenous pathogens and foraging insects of Heracleum spp. have been observed and catalogued in Europe (Bem and Murant 1979; Sampson 1994; Bürki and Nentwig 1997; Jakob et al. 1998; see Section 13), but possibilities of enhancing the effectiveness of these natural enemies in integrated weed control strategies are only beginning to be explored (Erneberg et al. 2003; de Voogd et al. 2003). Erneberg et al. (2003) and de Voogd et al. (2003) have conducted preliminary tests on the fungus Sclerotinia sclerotiorum (Lib.) de Bary as a potential bioherbicide. Seier (2003, 2005) has screened numerous fungi collected from H. mantegazzianum in its native range and found three promising candidates for biological control: Phloeospora heraclei (Lib.) Petr., Ramulariopsis sp. and Septoria heracleicola Kabat & Bubak.

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) *Herbivory* — Herbivory by mammals, insects and other organisms does occur in *H. mantegazzianum*, but it does not appear to be a limiting factor for populations in Canada. The production of furanocoumarins and lignans in many species of Apiaceae, including *H. mantegazzianum*, confers a degree of protection from herbivory by many insects (Berenbaum 1981; Klocke et al. 1989; Zangerl and Nitao 1998; Harmatha and Nawrot 2002). Also, much of the vegetative growth of *H. mantegazzianum* occurs in the winter and early spring, especially in maritime climates, when there is limited activity by herbivorous species.

(i) *Mammals* — Some farmers near Parksville, BC have indicated that their livestock (cattle, goats, hogs) have helped to suppress *H. mantegazzianum* in pastures. Browsing injury has been observed in areas frequented by deer on Vancouver Island, BC (Wall, personal observation). In the United Kingdom, cattle, sheep, goats and hogs are allowed to pasture on *H. mantegazzianum* but plants that escape the effects of grazing can flower and produce seed (Wright 1984; Tiley et al. 1996). In an experimental study in Denmark, 7 yr of grazing by 5–10 sheep per hectare eradicated *H. mantegazzianum* (Andersen and Calov 1996).

Sheep grazing is considered the most promising of nonchemical control method on suitable sites with dense populations.

(ii) *Birds and/or other vertebrates* — Clegg and Grace (1974) report that, in Scotland, seeds left in areas baited for birds were uneaten. No other information has been found.

(iii) Insects — No published records of specific insects on H. mantegazzianum have been found for Canada, although Alex (1992) noted that inflorescences in Ontario were often heavily infested with aphids. Plants in the Royal Botanic Garden in Hamilton, ON, were damaged by an aphid species (Hemiptera: Issidae) in 2004 (Hamilton and Rothfels, personal communication). On Vancouver Island, BC, leaf miner damage is frequently observed during the summer months (Wall, personal observation). Young plants cultivated at Ottawa, ON, in 2004 were attacked and heavily damaged by larvae of the butterfly Papilio polyxenes Farbicus (Darbyshire, personal observation). The insects Cavariella pastinacae (Linn.) (Hemiptera: Aphididae) and Phytomyza sphondylii Goureau (Diptera: Agromyzidae) have been studied on H. maximum in Canada with respect to furanocoumarin resistance (Camm et al. 1976b; Ashwood-Smith et al. 1984). Likewise, Berenbaum (1981) studied furanocoumarin resistance in several insect species found on H. mantegazzianum in New York State and found that species with resistance to both linear and angular furanocoumarins are likely to have a restricted host range, mainly Heracleum, Angelica and Pastinaca, while there were a few other insects, largely restricted to Apiaciae, that were resistant only to linear furanocoumarins.

In Europe, many insect species have been recorded on *H. mantegazzianum*. Jakob et al. (1998) recorded 55 species on *H. mantegazzianum* in Switzerland, mainly in sunny, low-land sites but none appeared to significantly affect plant health. Hendrix (1984) found that floral herbivory of *H. maximum* in Iowa by the parsnip webworm *Depressaria pastinacella* (Duponchel) (Lepidoptera: Oecophoridae) resulted in some losses in number and viability of seed, but much of these losses were offset by an increase in seed set by the normally sterile secondary umbels. The following paragraphs provide a summary of insect taxa recorded from *H. mantegazzianum*, mainly from Europe.

Coleoptera: the weevils (Curculionidae) Apion apricans Herbst (Bürki and Nentwig 1997), Apion flavipes (Payk.) (Jakob et al. 1998), Apion gibbirostre (Gyllenhal) (Gassmann and Kok 2002), Barypeithes pellucidus Boheman (Jakob et al. 1998), Euthron fagi Linn. (Bürki and Nentwig 1997; Jakob et al. 1998), Liparus germanus (Linn.) (Jakob et al. 1998), Lixus iridis Ol. (Wittenberg et al. 2003), Phyllobius calcaratus Fabricius (Jakob et al. 1998), Liophloeus tessulatus (Müller) (Bürki and Nentwig 1997; Jakob et al. 1998); the scarab beetles (Scarabidae) Hoplia farinosa (Linn.) (Jakob et al. 1998) and Trichius fasciatus (Linn.) (Jakob et al. 1998); the long-jointed beetle (Lagriidae) Lagria hirta (Linn.) (Bürki and Nentwig 1997; Jakob et al. 1998); the long-horned beetles (Cerambycidae) Leptura rubra (Linn.) (Jakob et al. 1998) and Strangalia melanura (Linn.) (Jakob et al. 1998); and, the pollen beetle (Nitulidae) Meligethes aeneus (Stephens) (Bürki and Nentwig 1997; Jakob et al. 1998).

Diptera: the leaf miners (Agromyzidae) *Euleia fratria* (Loew) (Berenbaum 1981), *Euleia heraclei* (Linn.) (Sampson 1994), *Melanogromyza angeliciphaga* (Spencer) (Bürki and Nentwig 1997; Jakob et al. 1998), *Phytomyza sphondylii* (Ashwood-Smith et al. 1984; Sampson 1994, Bürki and Nentwig 1997; Jakob et al. 1998), and the carrot fly (Psilidae) *Psila rosae* (Fabricius) (Hardman and Ellis 1982; Degen et al. 1999).

Hemiptera: the aphids (Aphididae) Anuraphis subterranea (Walker) (Bürki and Nentwig 1997), Aphis fabae Scopoli (Bürki and Nentwig 1997), Cavariella aegopodii (Scopoli) (Sampson 1994), Cavariella pastinacae (Sampson 1994; Bürki and Nentwig 1997), Cavariella theobaldi (Gillette and Bragg) (Sampson 1994). Paramyzus heraclei Börner (Sampson 1994); the plant bugs (Miridae) Calocoris affinis (Herrich-Schäeffer) (Bürki and Nentwig 1997; Jakob et al. 1998), Calocoris sexguttatus (Fabricius) (Bürki and Nentwig 1997; Jakob et al. 1998), Dicyphus errans (Wlff.) (Bürki and Nentwig 1997; Jakob et al. 1998), Orthops basilis Costa (Sampson 1994), Orthops campestris (Linn.) (Anonymous 2003b; Collins 2003), Orthops kalmii (Linn.) (Bürki and Nentwig 1997; Jakob et al. 1998), Orthops scutellatus Uhler (Berenbaum 1981); the leafhoppers (Cicadellidae) Eupteryx atropunctata (Goeze) (Jakob et al. 1998), Idiocerus populi (Linn.) (Jakob et al. 1998), Eupteryx aurata (Linn.) (Sampson 1994; Bürki and Nentwig 1997; Jakob et al. 1998), Aphrodes bicincta (Schrank) (Bürki and Nentwig 1997; Jakob et al. 1998); as well as Graphosoma italicum (Linn.) (Pentatomidae) (Jakob et al. 1998), Philaenus spumaris (Linn.) (Cercopidae) (Berenbaum 1981; Sampson 1994; Jakob et al. 1998), and Trioza apicalis (Förster) (Psyllidae) (Sampson 1994).

Lepidoptera: the leafrollers (Oecophoridae) Agonopterix clemensella Chambers (Berenbaum 1981), Agonopterix heracleana (Linn.) (Sampson 1994), and Depressaria pastinacella (Duponchel) (Berenbaum 1981; Sampson 1994; Bürki and Nentwig 1997; Jakob et al. 1998); and Cydia aurana (Fabricius) (Tortricidae) (Sampson 1994), Epermenia chaerophyllella (Goeze) (Epermeniidae) (Sampson 1994), and Mamestra brassicae (L.) Barathra (Noctuidae) (Seier et al. 2004).

Thysanoptera: the thrips *Thrips atratus* Haliday and *Thrips vulgatissimus* Haliday (Sampson 1994).

(iv) Nematodes and/or other non-vertebrates — No information has been found on nematodes. Slugs have been observed feeding on *H. mantegazzianum* stems during late summer on Vancouver Island, BC (Wall, personal observation). In Switzerland, Bürki and Nentwig (1997) noticed slugs and snails causing considerable damage to *H. sphondylium*, but rarely attacking *H. mantegazzianum*.

(b) Diseases

(i) Fungi — No records of fungi on H. mantegazzianum in North America have been found, although there are numerous records for H. maximum (Savile 1965; Conners 1967; Ginns 1986; Farr et al. 2005). Worldwide, the following fungi have been documented: Erysiphe heraclei DC. (Ascomycota: Erysiphales) (Farr et al. 2005); Peronospora heraclei Rabenh. (Oomycota: Peronosporales) (Farr et al. 2005); Phloeospora heraclei (Lib.) Petr. (Deuteromycetes: Coelomycetes) (Farr et al. 2005; Seier 2003); Phoma complanata (Tode: Fr.) Desm. (Deuteromycetes: Coelomycetes) (Sampson 1994; Farr et al. 2005); Phoma sp. (Deuteromycetes: Coelomycetes) (Seier et al. 2004); Ramulariopsis sp. (Deuteromycetes: Hyphomycetes) (Seier 2003); Ramularia heraclei (Oudem.) Sacc. (Deuteromycetes: Hyphomycetes) (Seier et al. 2004); Sclerotinia sclerotiorum (Ascomycetes: Helotiales) (Gray and Noble 1965; Farr et al. 2005; Erneberg et al. 2003); and Septoria heracleicola Kabát & Bubák (Deuteromycetes: Coelomycetes) (Farr et al. 2005; Seier 2003).

The fungi *Phloeospora heraclei, Ramulariopsis* sp., *Sclerotinia sclerotiorum* and *Septoria heracleicola* are under investigation as potential biological control agents for *H. mantegazzianum* (Seier 2003; Erneberg et al. 2003; de Voogd et al. 2003).

(ii) *Bacteria* — Fischer et al. (1976, 1982) isolated *Pseudomonas syringae* van Hall from *H. mantegazzinum* roots with soft rot. Sampson (1994) observed soft rots of roots and lower stems of both *H. mantegazzianum and H. sphondylium* in the United Kingdom but did not determine the causal agents.

(iii) Viruses — No records of virus diseases in *H. man*tegazzianum have been found in Canada. Zitter (2001) lists *H. mantegazzianum* as a host of celery mosaic virus in the United States. In the United Kingdom, Sampson (1994) detected aphid-transmitted agents that caused yellow mottling but made no identifications. Viruses from symptomless *H. sphondylium* have been identified as celery mosaic virus, cow-parsnip mosaic virus, parsnip yellow fleck virus, carrot red leaf virus, carrot mottle virus, heracleum latent virus, anthriscus yellows virus, and heracleum viruses 3–6 (Bem and Murant 1979; Brunt et al. 1996).

(c) Higher Plant Parasites - No records found.

14. Prognosis

The spread of *H. mantegazzianum* is likely to continue through much of southern Canada over the next 25–100 yr with worsening ecological, economic, and health effects. Its range expansion will likely follow a pattern similar to other temperate regions with initial establishment in urban gardens followed by escape and increasingly rapid spread into riparian areas, forest margins, and unmanaged urban areas in the broader landscape. It is unclear how far north it will spread in Canada and whether it will disperse into natural areas, particularly forested areas away from human settlements. Its occurrence in Kapuskasing, ON, indicates it is tolerant of cold, continental climates. Its wide establishment across the country and continued sale as an ornamental plant suggest that even the implementation of a coordinated and comprehensive management strategy is unlikely to eradicate the species.

A variety of control measures are available for H. mantegazzianum with the most efficacious strategy depending on the habitat and landscape in which the population occurs, as well as the population size and growth stage of the plants (Dodd et al. 1994). Reduction of seed production is an important part of any control strategy since the plant is a prolific seed producer and the seeds may remain viable in the soil for many years (Caffrey 1999). Because of its perennial habit and the persistent seed bank, eradication of established H. mantegazzianum populations may require annual treatments for as long as 10 yr (Andersen and Calov 1996; Buttenschøn 2003). The monocarpic perennial habit of H. mantegazzianum includes several years of vegetative growth during which there is opportunity for control. Similarly, the removal of seed heads prevents dispersal and provides an interim measure during which time more comprehensive control measures can be developed. Herbicides, animal grazing and mechanical methods are all successful; however, the toxic nature of the sap requires that precautions must be taken by those using manual methods. In addition, the prevalence of *H. mantegazzianum* populations along steep embankments, in deep ravines and other inaccessible places, makes manual treatments difficult. To reduce damage to surrounding vegetation, herbicide applications, particularly glyphosate, are best done as spot spraying or swiping early in the growing season.

A longer-term but widely accepted approach to management of invasive plants is through the deployment of biological controls (Huffaker and Caltagirone 1986; Bellows 2001) and this approach is underway in Europe as part of an international effort to manage H. mantegazzianum (Nielsen et al. 2005). Although much of the ground-breaking research may take place outside Canada, we have numerous essential roles, including support and cooperation for this research, testing of new control methods, and monitoring populations of natural enemies. As with most weeds, success of biological controls will likely depend on the number of natural enemies affecting the plant (Memmott et al. 2000; Denoth et al. 2002) and on an integrated approach to control (Henne et al. 2005). There appear to be many possibilities for using both classical and inundative biological controls as part of integrated management strategies for H. mantegazzianum. Some ecological advantages of H. mantegazzianum over other species, such as early spring growth, could provide opportunities for biological controls that exploit cold tolerant agents. The toxic nature of furanocoumarins to most herbivores also suggests a potential for highly specialized biological control agents. Biological controls cannot be viewed in isolation or to the exclusion of manual or chemical control methods but need to be integrated into the total management scenario.

We recommend that three strategies be used to control range expansion and population growth of *H. mantegazzianum* in Canada. First, we stress that prevention of introductions into new regions is more effective than large-scale control programs later in the invasion process. Canada has an opportunity to learn from the invasion dynamics in Europe and focus management attention on H. mantegazzianum before it reaches the exponential growth phase and populations begin to spread into the broader landscape. Where most populations are small but widespread in a region like the Lower Fraser Valley or southeastern Vancouver Island, invasion ecology theory recommends that control efforts focus on populations on the margin of range expansion as the most effective method for slowing or preventing further invasion (Moody and Mack 1988). This strategy may be particularly effective for controlling H. mantegazzianum in recently invaded regions because it targets small and young populations that may not have reached flowering age and established seed banks. However, large populations should not be neglected because they are the primary source of seeds for dispersal, particularly along rivers and streams (Wadsworth et al. 2000). Second, while the initial spread of *H. mantegazzianum* into new sites or regions is likely because of human transport (cf. Case and Beaman 1992; Pyšek et al. 1998), subsequent dispersal is primarily by water or the movement of soil contaminated with seed. This suggests that control focusing on large, flowering populations along streams or urban stormwater systems, as well as managing the movement of soil contaminated with seed, can also reduce local population spread. Since the primary non-human dispersal mechanism is water, management strategies must be coordinated throughout an entire drainage system if control is to be effective (Tiley and Philp 1992; Caffrey 2001). Finally, public education is critical for effective management. The close association of H. mantegazzianum with urban and suburban areas in Canada increases opportunities for landowners, stewardship groups, and park users to participate in control programs. Public education can be particularly effective in reducing the transport of seeds or plants for horticultural plantings, and identifying new populations before they expand. As well, regulation of horticultural propagation and sale should be used to reduce range expansion in Canada.

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