The biology of Canadian weeds. 103. *Vallisneria americana* Michx.

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Catling, P. M., Spicer, K. W., Biernacki, M. and Lovett Doust, J. 1994. **The biology of Canadian weeds. 103. *Vallisneria americana* Michx.** Can. J. Plant Sci. **74**: 883–897. American wild celery (*Vallisneria americana* Michx.) is a native submerged aquatic plant that differs from other ribbon-leaved aquatics in having leaves with a well-defined midvein and paler zones on either side of a central dark band. In southern Ontario and Québec the dense leaf growth, and in particular the floating plants dislodged from the sediment, impede water traffic and restrict water-based recreation. Mechanical harvesting may be the best method of control in most situations. American wild celery is beneficial as an important food source for waterfowl and other wildlife, as cover and spawning area for fish, and may also be used as fertilizer and to feed livestock. There is also potential for increased use in biomonitoring. Widespread in eastern North America, it reaches its northern limit in southeastern Canada. It is introduced in British Columbia and the northwestern United States, and has also recently been reported from the southwestern United States, Mexico, the Carribean islands, northern Central America, southeast Asia and Australia. American wild celery occurs in alkaline to slightly saline waters with pH > 6, at depths of 0.3–7 m, and in a variety of sediment types. Clonal growth is extensive. Parent rosettes can each produce 20 or more new shoots within a season. These develop from buds at the tip of stolons, some of which overwinter as turions. Pollination takes place on the surface of the water with free-floating male flowers tipping into the surface depression created by the larger, attached female flowers. Fruits mature under the water.

Key words: *Vallisneria americana*, American wild celery, weed biology, aquatic macrophyte, Canada, distribution

Catling, P. M., Spicer, K. W., Biernacki, M. et Lovett Doust, J. 1994. **Biologie des mauvaises herbes canadiennes. 103. *Vallisneria americana* Michx.** Can. J. Plant Sci. **74**: 883–897. La Vallisnérie d'Amérique (*Vallisneria americana* Michx.) est une plante aquatique submergée indigène qui diffère des autres plantes aquatiques à feuilles rubanées en cela que la feuille a une nervure médiane bien nette et des zones pâles de chaque côté de la zone centrale foncée. Dans le sud de l'Ontario et du Québec, l'abondance du feuillage de cette espèce et surtout les plantes flottantes détachées du fond de l'eau entravent la navigation et restreignent les loisirs aquatiques. La récolte mécanique est probablement la meilleure méthode de maîtrise dans la plupart des situations. La vallisnérie constitue une importante source d'aliments pour l'avifaune et pour divers autres espèces animales. Elle sert également d'abri et de zone de frai pour les poissons et elle peut aussi être utilisée comme engrais ou comme nourriture pour le bétail. Elle aurait de plus en plus de possibilités pour la surveillance biologique. Largement répandue dans l'est de l'Amérique du Nord, la limite septentrionale de son aire d'adaptation dans le sud-est du Canada. Elle a été introduite en Colombie-Britannique ainsi que dans le nord-ouest des États-Unis. On a récemment signalé sa présence dans le sud-ouest des États-Unis, au Mexique, dans les Antilles, dans le nord de l'Amérique centrale, dans le sud-est asiatique et même en Australie. La vallisnérie d'Amérique vit dans les eaux alcalines à légèrement saumâtres, de pH supérieur à 6, à des profondeurs de 0,3 à 7 m et s'accomode d'un large éventail de types de fonds. La reproduction végétative est importante, chaque rosette parentale pouvant produire une bonne vingtaine de nouvelles pousses, ou même davantage, dans une même saison de végétation. Ces pousses se forment à partir de boutons situés à l'extrémité de stolons, dont quelques-uns hivernent sous forme de turions. La pollinisation se fait à la surface de l'eau: les petites fleurs mâles flottant librement basculent dans la légère cavité formée par l'ouverture des fleurs pistillées, plus grandes, qui, elles, demeurent attachées à leur pédicelle. La maturation du fruit se fait sous l'eau.

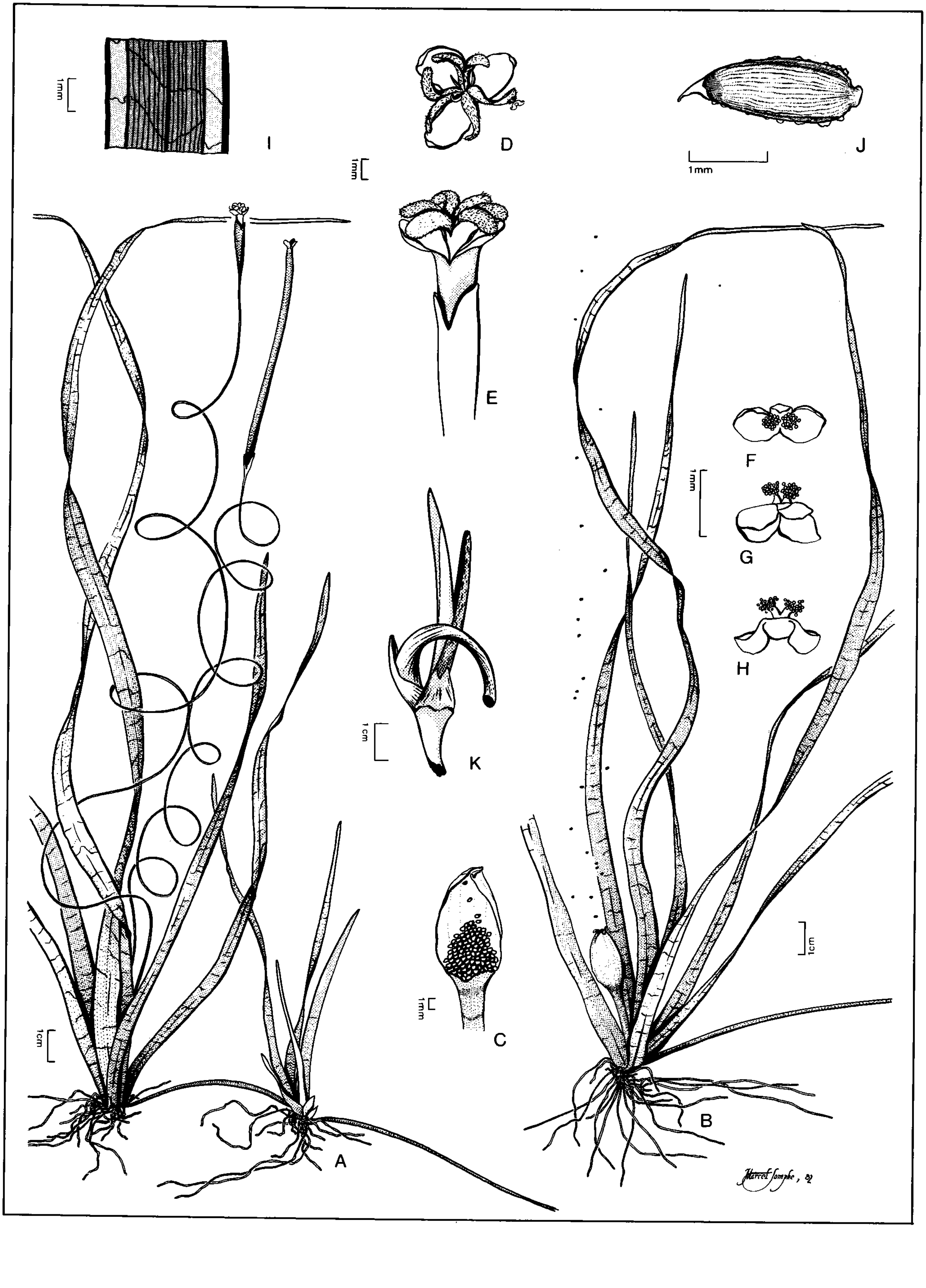
Mots clés: *Vallisneria americana*, vallisnérie d'Amérique, biologie des mauvaises herbes, macrophyte aquatique, Canada, répartition

1. Name

Vallisneria americana Michx., **American wild celery**, vallisnérie d'Amérique, tape-grass (Alex et al. 1980); tape grass, wild celery, Vallisnèria (Fassett 1957); céleri d'eau, herbe à la barbotte, herbe aux anguilles, vallisnérie américaine (Ferron et Cayouette 1975); American eel-grass (Marie-Victorin 1947); wildcelery (Martin and Uhler 1939); tapegrass, canvasback grass, celery grass, duck celery, oxtongue, plantain (McAtee 1939); Hydrocharitaceae, Frog's-bit family, Hydrocharitacées.

2. Description and Account of Variation

Vallisneria americana, American wild celery (Fig. 1) is a dioecious perennial, submerged aquatic of fresh or slightly brackish water. **Roots** unbranched and fibrous, 20–80 in number. **Leaves** ribbon-like, 1–18 in number, 8–100 (up to 300) cm long and 3–18 mm wide with serrated margins, a darkened central stripe and transverse pigmented striations; borne on short vertical stems arising from nodes of horizontal rhizomes; the internodes 3–20 (28) cm long. **Pistillate flowers** solitary, 4–8 mm across, sessile, contained in a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tubular spathe and extending on an elongate and eventually coiling scape 19–300 cm long to the surface of the water (Schloesser and Manny 1990; Titus and Hoover 1991); sepal lobes 3, 2.5–3(5) mm long, staminodia 3, linear; petals 3, rudimentary, and stigmatic branches 3, 2–4 (5) mm long. **Staminate flowers** numerous (a few to several hundred), 1–1.5 mm across; enclosed in an ovoid, 3-valved spathe 11–14 (23) mm long and 7–10 mm wide with a stalk 1.5–5.2 cm long and 1.5–3 mm wide, separating from their pedicels and floating to the surface; sepals 3, transparent spoon-shaped, 2 are 0.5–0.7 mm long and larger than the third; petals vestigial, the larger opposite the smaller sepal, and fertile stamens 2, 0.2–0.4 mm long, with filaments united and with transparent hairs at the base. **Fruit** elongate, cylindrical, 1-locular, 3–12 cm long, 3–5 mm wide, containing 160–300 seeds, dehiscing longitudinally by one valve. **Seeds** cylindrical or ellipsoid, striate, 1.8–2.6 mm long, 0.6–1 mm wide, shed in a mass of gelatinous material.

The preceding description is based exclusively on Canadian material. An extensive synonymy for *V. americana* var. *americana* is provided by Lowden (1982). A point of particular relevance to North America is that *V. neotropicalis* Marie-Victorin is placed in synonymy.

Both narrow and broad-leaved variants of American wild celery are discussed by Lowden (1982), but without suggesting taxonomic recognition. Leaves of *V. americana* var. *americana* are mostly less than 12 mm wide with 3–5 prominent longitudinal veins and margins entire to finely toothed. The blade has faint pigmented striations. This variant inhabits freshwater inland waterways, lakes and lagoons. The broad-leaved variant is identified by leaves 10–25 mm wide with 5–9 veins and conspicuously toothed margins. The many transverse pigmented striations are more visible. The broad-leaved variant is common in coastal freshwater inlets and waterways, sometimes subject to invasion of brackish water at high tide, but it does not occur in Canada.

Occasionally specimens determined as *Vallisneria spiralis* L., a European species, are seen in Canadian collections. The earlier literature (prior to 1918) treated the European and North American plants as conspecific. The name *americana* was narrowly applied to robust plants of the southeastern United States. Fernald (1918) pointed out that the type of *V. americana* is from Illinois so that the latter name does not apply to the southern plant. Recent authors have supported Fernald's (1918) and Marie-Victorin's (1943) conclusion that North American and European plants are different and have called the widespread North American plant *V. americana*. Fernald was apparently unaware of Wylie's (1917) observations of differences between European and North American plants involving the union of stamens in male flowers of the North American plant. However, both Wylie's and Fernald's work was taken into account in a more detailed study by Marie-Victorin (1943), which includes several points of comparison. According to Fernald (1918) and Marie-Victorin (1943) *V. americana* has staminate spathes 1–2.3 cm long and they usually have short thick scapes up to 4.5 cm long and 1.5–3.0 mm in diameter, while *V. spiralis* has staminate spathes less than 0.9 cm long with long filiform scapes up to 7 cm long and 0.5–1.2 mm in diameter. Marie-Victorin (1943) conducted a careful comparative study, including pigments and leaf serrations, but regarded the size of the staminate spathe as the only reliable distinguishing feature. Recently Lowden (1982) has provided a key that distinguishes the European *V. spiralis* var. *spiralis* and the Asian *V. spiralis* var. *denseserrulata* Makino from *V. americana* var. *americana* in the following manner:

a. Staminate flowers with free, divergent stamens, and without hairs at the base of the stamens; pistillate flowers with deepest incision of pistil between sepals .... *V. spiralis* (both varieties)
b. Staminate flowers with stamens partially or totally united by their filaments, and with hairs at the base of the stamens; pistillate flowers with deepest incision of pistil opposite sepals .... *V. americana* var. *americana*

The only other taxon recognized in the genus *Vallisneria* by Lowden (1982) is *V. americana* var. *biwaensis* (Miki) Lowden, which has a tropical and subtropical distribution.

There has been no reliable record of *V. spiralis* in North America (e.g. Fernald 1918, 1950; Marie-Victorin 1943; and Scoggan 1978) and no plants definitely referable to *V. spiralis* from Canada were seen during the present study. Although many plants have scapes longer than the limits of *V. americana* reported by Fernald (1918), the spathes are too large for *V. spiralis*.

Wild celery can be distinguished from other submerged aquatics with long strap-like basal leaves by its well-defined midvein which is not evident in the bur-reeds (*Sparganium* spp.) and by its long, limp leaves (more than 20 cm long) that are three-zoned with a vascularized central portion 1/3 or more the width of the leaf and bounded by broad clear zones with little vascular tissue (Thieret 1971; Hotchkiss 1972; Voss 1972). Wild celery is easily confused with Arrowhead (*Sagittaria*) but leaves of the latter are not three-zoned and exude a milky juice when broken. Also rhizomes of the former consist of a single internode between rosettes and lack leaf scales (Thieret 1971; Crow and Hellquist 1982). McAtee (1939) suggests that Arrowhead leaves have more numerous and prominent longitudinal veins and usually the ends of the leaves are expanded into a proper leaf blade or quite pointed, unlike wild celery. Northern mannagrass (*Glyceria borealis* (Nash) Batch.) and wild-rice (*Zizania* spp.) may also be distinguished from wild celery by lack of leaf zonation (Hotchkiss 1972). In slightly brackish water American wild celery may be distinguished

Fig. 1. *Vallisneria americana*: A, pistillate plant with pistillate flower and a young fruit; B, staminate plant with a spathe; C, dissected spathe showing the numerous staminate flowers; D–E, top and side view of the pistillate flower, showing the slender tube, three petals, three divided stigmas and a small staminate flower attached on a stigma; F–G–H, top and side views of the staminate flower showing calyx three-parted and the two stamens; I, portion of leaf showing venation; J, detached overwintering stolon bud. Drawings by Marcel Jomphe based on material at DAO (Catling 3 August 1981 (fresh material), Dore et al. 16305, Dore & Dore 16157, Spicer 11 August 1963, Cody & Dore 6547, Dore & Dore 24834, Bragg & Dalzell 267).

from eelgrass (*Zostera marina* L.) by the leaves: the former having leaves in bundles from the rootstalk while leaves of eelgrass rise singly and alternately on opposite sides of the stem and are generally less than 7 mm wide. Eelgrass leaves are also firmer with fibers showing at the broken ends (McAtee 1939).

The chromosome number of $2n = 20$ was reported by Löve (1981) from material collected in Manitoba. Jorgensen (1927) reported the chromosome number of *V. americana* var. *biwaensis* to be $2n = 40$. For comparison, the chromosome number of $2n = 24$, 30, 40 and aneuploids from 16 to 28 were reported by Chaudhuri and Sharma (1978) for *V. spiralis*, collected in India.

3. Economic Importance

(a) Detrimental — Wild celery contributes to aquatic weed problems in southern Ontario and Québec. The rooted plants impede water traffic and restrict water-based recreation including fishing and swimming, but plants dislodged by turbulence from propellers and wave action are particularly troublesome in this respect. In Ontario, weed problems are especially evident in the Trent–Severn Waterway, the Kawartha Lakes and Bay of Quinte (pers. obs., P. Catling, K. Spicer). Along the Rideau Canal, Ontario, wild celery is more of a problem later in the season after mechanical harvesting has effectively controlled other nuisance species (Spicer and Catling 1990).

Wild celery is involved in the uptake, movement (from water and sediment) and redistribution of heavy metals (Adams et al. 1973; Schloesser and Manny 1990; Manny et al. 1991; Manny and Kenaga 1991), and of organic contaminants (Biernacki et al. 1994; Lovett Doust et al. 1994a,b). This can cause difficulty in the containment of these pollutants to a localized area.

(b) Beneficial — Aquatic plants, including American wild celery, have been effectively used as a mulch and fertilizer for croplands and as feed for livestock (e.g. Bailey 1965; Timmons 1970). Various studies have found wild celery to be potentially valuable as food for livestock (Burton et al. 1975), and wild celery proved to be above-average for the aquatic species tested (Boyd and McGinty 1981). In leaves of *Vallisneria* the ash content was reported to be 25–28%, crude protein 11–16%, crude fiber 14–36%, ether extract >1%, and N-free extract >36% (Schuette and Alder 1927; Gortner 1934). Analysis of winter buds and fruits collected in Lake Onalaska, Wisconsin revealed a mean crude protein value of 11%, ash 4.6%, crude fiber 2.8%, crude fat 0.8% and nitrogen-free extract 80.8% (Korschgen and Green 1988). Donnermeyer and Smart (1985) state that submergent macrophytes including wild celery are similar in crude protein but lower in fiber when compared to forage crops. They reported that crude protein in wild celery was 12.2–15.2% and fiber 15.5–36.2% compared with 16.9% crude protein and 40.2% fiber for alfalfa (Linn et al. 1975). Fruits and winter buds were high in dry matter, low in ash and fiber, and also possessed greater caloric values than most other organs, thus having the greatest nutritive potential.

Among the obstacles to using harvested material of aquatic plants (including *Vallisneria*) on a large scale as feed for livestock (Holm et al. 1969), is the 90% water content. Another obstacle is actual digestibility. In a study of the nutritive value and chemical composition of some aquatic plants in Minnesota (Nelson et al. 1939), wild celery was found to contain proteins that were of such poor quality that rats tested lacked nitrogen balance. It was concluded that despite high protein, high carbohydrate and low fiber, there was also a low digestibility factor. In an experiment comparing dehydrated freshwater plants and dehydrated alfalfa as feed for chickens and ducks, Muztar et al. (1977) found that apparent metabolizable energy and dry matter digestibility values measured in a rooster diet were lower in the freshwater plants. Ash content reduced potential energy, perhaps adversely affecting the birds ability to utilize energy. It was suggested that soft water and consequent reduction in ash content might produce feed comparable to alfalfa and other forage plants. Minerals and nutrients present in leaves of wild celery are similar to those of land forages in the United States (Hentges et el 1973; Easley and Shirley 1974). Linn et al. (1975) showed that the undigestible ash content of a mixture of aquatic plant species (5% wild celery) resulted in an unpalatable diet for sheep but this was alleviated when the feed was mixed 50 : 50 with dehydrated alfalfa. The high nutritive value might be best exploited by using the plants as fertilizer in fields (Nelson et al. 1939).

Wild celery is a valuable component of the aquatic ecosystem, providing shade, shelter and food for fish, insects and other invertebrates (Titcomb 1909; Muttkowski 1918; Terrell 1930; Hubbs and Eschmeyer 1938; Bordner et al. 1939; Barnett and Schneider 1974; Andres and Bennett 1975; Heberger 1978; Keast 1984). Sculthorpe (1967) lists many types of birds seeking it as a food source and adds that it provides a spawning medium for fish. Eight times as many panfish were found in mixed *Vallisneria* communities than in *Myriophyllum spicatum* L. beds (Keast 1984). *Vallisneria* has been noted as yielding high-quality detritus that is very important for benthic food webs (Bianchi et al. 1991).

Although numerous invertebrates have been reported on wild celery (Krecker 1939; Cyr and Downing 1988), they generally exist in greater numbers on other aquatic plants (Andrews and Hasler 1942). Invertebrates are important as food for fish (Gerking 1962; Fryer 1963; Fairchild 1983; Mittelbach 1984) and ducks (Moyle 1961; Danell and Sjoberg 1980; Drobney and Fredrickson 1985). Wild celery often grows in sites subjected to strong current or wave action and in nutrient-poor sites where other species are apparently unable to grow. Thus it may not always be competing with those species which contain larger numbers of invertebrates. If it is the only species that can grow in a particular area, its vertebrate population, although relatively small, must be considered as a beneficial aspect.

Wild celery is an important source of food for many species of game birds. In North America it is the seventh most popular food of game ducks (Martin and Uhler 1939). Leaves, pod-like fruits and underground parts were identified in the stomachs of the ducks examined. Approximately 75% of North American canvasback ducks (*Aythya valisineria*) feed primarily on winter buds of wild celery on the upper Mississippi river while in migration (Donnermeyer and Smart 1985; Korschgen and Green 1988). Cottam (1939) and Perry (1982) further document the reliance of the canvasback on wild celery (and sago pondweed) during fall migration and Korschgen and Green (1988) add 16 ducks, geese and the whistling swan to the list of waterfowl feeding on all parts of the plant but especially favoring winter buds and rootstocks. As many as 25 winter buds have been found in a single stomach of the lesser scaup and the baldpate ducks, and biological survey records indicate that the plant has been found in the stomachs of 19 wild duck species and one swan (McAtee 1939). Fassett (1957) reported 24 species of ducks, at least 2 geese, 2 swans, 3 shorebirds, 3 rails, grebes and other wildfowl as feeding on various parts of the plant. Wild celery is also utilized by muskrats. A recent U.S. Fish and Wildlife Service report (Korschgen and Green 1988) recognizes the value of wild celery to wildlife and summarizes ecological information to serve as a guide for potential wetland restoration projects.

Ample oxygen production, attractive appearance and ease of cultivation and propagation make wild celery a popular aquarium plant (Titcomb 1909).

Vallisneria significantly increases rates of sedimentation, in areas where this plant is well-established (Petticrew and Kalff 1992) thereby increasing available nutrients and water clarity. This facilitates the establishment of plants in deeper water, increasing overall primary productivity. Wild celery is an important component in macro- and micro-element cycling in aquatic environments, in particular in the littoral zone, linking sediments and water column, and supplying food and habitat for epiphytes and associated algae (Adams et al. 1973; Barko et al. 1991; Nichols 1991; Guilizzoni 1991).

Aquatic macrophytes including *Vallisneria americana* have recently been shown to be involved in the uptake and movement of contaminants in aquatic ecosystems. Manny et al. (1991) reported an array of heavy metals in *V. americana*. This raises the possibility of its use as a contaminant 'sink' in wetlands. American wild celery has been used as a biomonitor of organochlorine contamination in natural aquatic ecosystems (Lovett Doust et al. 1994a,b). In a field survey, *Vallisneria* plants in the St. Clair and Detroit Rivers were found to accumulate significant amounts of organochlorine contaminant, and the concentraion increased over the growing season. Root tissue contained the highest concentrations. A significant relationship between exposure to the natural suite of organic contaminants and effect upon plant performance (measured as leaf and shoot production, and reproductive activity) was documented in a factorial experiment carried out at two stations in the channel connecting Lakes Huron and Erie (Lovett Doust et al. 1994a,b).

4. Geographical Distribution

Vallisneria americana is a common aquatic plant in quiet waters across much of eastern North America from southern Canada and the Dakotas south to Florida and Texas (Fernald 1918, 1950; Fassett 1957; Thieret 1971; Haynes 1980; Crow and Hellquist 1982). It is apparently a recent introduction in the Pacific Northwest including Washington, Oregon and British Columbia (Hitchcock and Cronquist 1973). The northern part of its range extends from Nova Scotia west across southern Québec (Duarte and Kalff 1990; Lalonde and Downing 1992) and northern Ontario (Dale 1986) to southeastern Manitoba (Fig. 2; Scoggan 1978). *Vallisneria americana* is the most abundant submersed macrophyte in the Lake Huron–Lake Erie corridor (including the St. Clair River, Lake St. Clair and Detroit River: Schloesser et al. 1985; Schloesser and Manny 1986; Schloesser and Manny 1990). Although absent from Saskatchewan and Alberta, it occurs in southern British Columbia including Vancouver Island (Fig. 2). Wild celery was recently reported from Arizona, Nebraska, and New Mexico (Lowden 1982). Stodola (1967) includes Cuba and Jamaica in its range. There is one recent report from central Mexico (Gomez-Monterrubio and Arrequin-Sanchez 1985). Korschgen and Green (1988) show a distribution which includes Mexico, Cuba, Guatemala and Honduras. Lowden (1982) who places *V. gigantea* in synonymy with *V. americana* reports the latter additionally from east and southeast Asia, Oceania and Australia.

5. Habitat

(a) *Climatic requirements* — The geographical distribution suggests that wild celery can thrive in temperate and subtropical climates. Stodola (1967) describes it as a very hardy aquarium plant requiring 18°C temeratures during vegetative growth and about 15°C winter temperatures. Titus and Adams (1979) found that the optimum temperature for photosynthesis to be 32.6°C. In the Detroit River it grew at water temperatures from 19 to 31.5°C (Hunt 1963) and from 22.7 to 26.3°C in Lake Erie (Meyer et al. 1943). Wilkinson (1963) cultivated wild celery in the laboratory and observed optimum growth at 30 to 36°C with very limited growth below 19°C and severe deterioration above 50°C. Barko et al. (1981) observed severe restriction in growth of wild celery at temperatures below 20°C but overall biomass production and shoot density generally increased with higher temperatures and increasing light.

(b) *Substratum* — Wild celery is commonly found in water at a depth from about 0.3 m, submerged or with the upper portion of leaves floating (Martin and Uhler 1939). Davis and Brinson (1980) give 6–7 m as the maximum depth for wild celery. McAtee (1939), however, noted that it has been recorded growing 5.3–6.6 m deep in Wisconsin and 7 m deep in Indiana (McAtee 1939). In Lake Opinicon (eastern Ontario) it grew at depths of 2–3 m (Crowder et al. 1977b), and was locally abundant in Douglas Lake, Michigan in water to 3 m deep (Haynes and Hellquist 1978). Lovett Doust and Laporte (1991) reported mean shoot densities of 82–170 shoots m^{-2} at sites located in the St. Clair and Detroit Rivers, at shallow depths to 1.8 m. At deeper sites in the Detroit River (3–3.5 m) the density of shoots may be as great as 1000 plants m^{-2} (M. Biernacki, pers. obs.). The greatest density of wild celery in Lake George, New York is at a depth of 1–5 m (100–1000 plants m^{-2}), but colonies of 16–400 plants m^{-2} occurred as deep as 7 m where light was estimated at nearly 25% surface intensity (Sheldon and Boylen 1977).

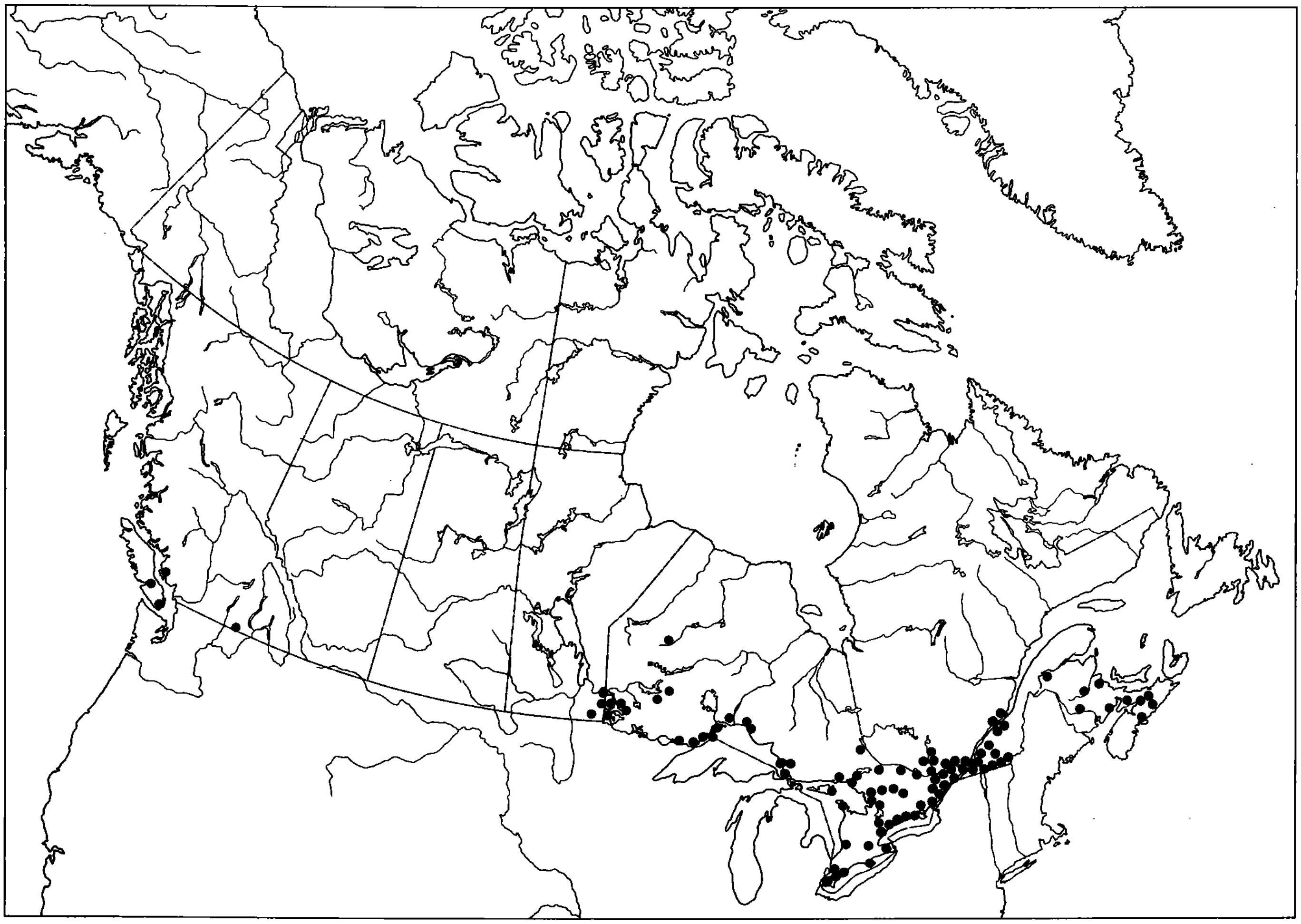

Fig. 2. Distribution of American wild celery (*Vallisneria americana*) in Canada based on specimens in ACAD, ALTA, CAN, DAO, MT, QFA, SFS, TRT, UBC, UWO and V (acronyms from Holmgren et al. (1981)).

Wild celery grows in a variety of substrates and where water turbulence ranges from high to very low (Korschgen and Green 1988; pers. obs.). Schuette and Alder (1927) reported it growing on sandy or muddy substrates, along shorelines or quiet waters like ponds, canals or shallow inlets. Pip (1979) found it mostly in open water of lakes of 10 ha or more on predominantly sand/gravel substrates. Martin and Uhler (1939) and Hunt (1963) observed best growth on bottoms having large amounts of sand or coarse silt. Lovett Doust and Laporte (1991) reported high-density populations in clay sediment. McAtee (1939) saw a preference for firm but fertile bottoms although it occurs in mud (Fassett 1957) or sand and a sluggish current suits it better than either stagnant or rapidly moving water. Waters may be calcareous, fresh or brackish; along the Atlantic coast it tolerates a degree of salinity up to one-fifth that of sea water (McAtee 1939).

The greatest beds of wild celery in the United States occur in the freshwater sections of tidal streams along the Atlantic coastal plain (Martin and Uhler 1939). In Chesapeake Bay, wild celery can be found at salinity levels from 3000 to 5000 ppm (Steenis 1970) and Bourn (1934) noted that it survived in concentrations to 7000 ppm, thriving at 4200 ppm. It is reported to grow in the Potomac River in water with salinity up to 10 000 ppm but died at 13 500 ppm (Haramis and Carter 1983; Carter et al. 1985). While studying the effects of salinity on growth of several aquatic macrophytes, Haller et al. (1974) observed that growth of wild celery gradually declined as salinity increased. It failed to grow in salt solutions of 6600 ppm. In this study, plants were transferred directly from nature to the laboratory saline solutions but there is some evidence that gradual change might result in increased tolerance (Slayter 1961). There may be differences in salinity tolerance among geographic races.

Titus (1992) gave the range of pH of water where *V. americana* is found as 5.1–7.2. In an experiment to illustrate the significant influence of pH, wild celery survived 60 d at pH 5 but with 76% reduced dry matter accumulation, 79% reduced leaf area and lower rosette and winter bud production compared with plants maintained at pH 7.5 (Grisé et al. 1985). Dissolved inorganic carbon uptake decreases with increasing pH (Titus and Stone 1982). Crowder et al. (1977b) provide water chemistry data for Lake Opinicon, Ontario, where wild celery was one of the most frequent plants. Here and in other eastern Ontario lakes, pH ranged from

7.7 to 8.5 and conductivity ranged from 182 to 316 (Crowder et al. 1977a,b). Wild celery occurs in mesotrophic and eutrophic rather than oligotrophic waters (pers. obs.).

(c) *Communities in which the species occurs* — *Vallisneria americana* is essentially the dominant macrophyte in the St. Clair River, Lake St. Clair and the Detroit River, though it has experienced some decline of late (Schloesser et al. 1985; Schloesser and Manny 1986, 1989, 1990). At 13 sites along the Rideau River in southern Ontario, Spicer and Catling (1990) observed wild celery growing in 1–3.9 m water with *Acorus calamus* L., *Amblystegium riparium* (Hedw.) B.S.G., *Ceratophyllum demersum* L., *Chara globularis* Thuill. var. *globularis*, *C. vulgaris* L. var. cf. *vulgaris*, *Elodea canadensis* Rich. ex Michx., *E. nuttallii* (Planch.) St. John, *Hydrocharis morsus-ranae* L., *Lemna minor* L., *L. trisulca* L., *Myriophyllum alternifolium* D.C., *M. sibiricum* Komarov, *M. spicatum* L., *Najas flexilis* (Willd.) Rostk. and Schmidt, *Nitella flexilis* (L.) Agardh., *Nuphar variegata* Engelm., *Nymphaea odorata* Ait., *Potamogeton crispus* L., *P. epihydrus* Raf. var. *epihydrus*, *P. gramineus* L., *P. illinoensis* Morong, *P. natans* L., *P. pectinatus* L., *P. praelongus* Wulf., *P. pusillus* L. var. *tenuissimus*, *P. richardsonii* (Benn.) Rydb., *P. robbinsii* Oakes, *P. strictifolius* Benn., *P. vaseyi* Robbins., *P. zosteriformis* Fern., *Ranunculus longirostis* Godron, *Spirodela polyrhiza* (L.) Schleiden, *Wolffia borealis* (Engelm.) Landolt and *W. columbiana* Karst. These data were collected in late June and early July. However, observations in the latter part of August and early September after weeds had been cut to a depth of 2.3–2.7 m below the surface, revealed that wild celery had become a dominant species in several locations.

In studying the aquatic macrophytes in Lake Opinicon (eastern Ontario) Crowder et al. (1977b) observed positive associations between wild celery and *Chara globularis*, *Myriophyllum* ssp., *Najas flexilis*, *N. guadalupensis* (Spreng.) Magnus, *Potamogeton friesii* Rupr., *P. robbinsii*, and *Zosterella dubia* (Jacq.) MacMillan. An earlier study by the same authors (Crowder et al. 1977a) in several southeastern Ontario lakes, revealed that wild celery and 17 of the 36 named species had a remarkably similar distribution pattern. The 17 species associated with wild celery were *Chara* ssp., *Elodea canadensis*, *Isoetes echinospora* Durieu, *Lobelia dortmanna* L., *Myriophyllum spicatum* (including *M. exalbescens*), *Najas flexilis*, *Nymphaea odorata*, *Potamogeton amplifolius* Tuckerman, *P. crispa*, *P. friesii*, *P. gramineus*, *P. illinoensis*, *P. robbinsii*, *P. zosteriformis*, *Utricularia vulgaris* L., *Zannichellia palustris* L. and *Zosterella dubia*. Studies at 305 sites in southern Manitoba and adjacent regions revealed that *Vallisneria americana*, *Potamogeton praelongus*, *P. richardsonii*, *P. zosteriformis*, *Najas flexilis*, *Elodea canadensis*, *Nuphar variegatum*, *Megalodonta beckii* (Torr. ex Spreng.) Greene and *Zizania aquatica* L. were significantly correlated with each other and showed affinities for lower values of total filtrable residue and total alkalinity (Pip 1979). Titus and Stephens (1983) observed that wild celery commonly occurred as scattered plants within dense populations of *Chara vulgaris* and *Potamogeton amplifolius* in a New York lake but was a dominant submersed macrophyte in the lake with some nearly monospecific stands.

In slightly eutrophic waters (Bazin and Saunders 1971) of Douglas Lake in Michigan, Haynes and Hellquist (1978) found wild celery along the drop-offs at 24 locations around the lake with *Ceratophyllum demersum*, *Elodea canadensis*, *Myriophyllum sibiricum*, *Najas flexilis*, *N. guadalupensis*, *Potamogeton friesii*, *P. gramineus*, *P. illinoensis*, *P. natans*, *P. pectinatus*, *P. praelongus*, *P. richardsonii*, *P. zosteriformis* and *Utricularia vulgaris*.

In the St. Clair River, Lake St. Clair and Detroit River, *Vallisneria* is the dominant macrophyte. It is associated with *Elodea canadensis*, *Myriophyllum* spp., *Najas flexilis*, and *Potamogeton* spp. (Schloesser et al. 1985; Schloesser and Manny 1986). *Vallisneria* is a strong competitor with other submersed macrophytes, especially at lower light levels (McCreary 1991).

6. History

Wild celery is native to eastern North America. It was collected by Michaux along the Mississippi as far south as the mouth of the Ohio in 1795–1796 (Fernald 1918). No detailed studies are available concerning the timing of its probable introduction into northwestern North America. Its status and history outside North America also has not been investigated and improvements to the classification of the species of *Vallisneria* which make comprehensive studies of history possible are very recent (Lowden 1982) and not yet complete.

7. Growth and Development

(a) *Morphology* — New rosettes develop from buds at the tip of stolons; they may also develop from seeds though this is infrequent (Titus and Hoover 1991). The overwintering buds are referred to as turions, or dormant apices. Parent rosettes may produce 20 or more buds within one season (M. Biernacki, pers. obs.)

(b) *Perennation* — Stolon buds produced at the end of the growing season remain dormant through the winter and resume growth the following spring (Bellrose Jr. 1941; Wilder 1974; Donnermeyer and Smart 1985). Similar methods of perrenation are apparent in other genera in the family Hydrocharitaceae, such as *Hydrocharis morsus-ranae* and *Limnobium spongia* (Bosc.) Steud. (Cutter 1964; Catling and Dore 1982; Catling et al. 1989).

(c) *Physiological data* — Titus and Adams (1979) found that wild celery had a greater physiological adaptability to low light than Eurasian watermilfoil (*Myriophyllum spicatum* L.) with a midsummer light extinction coefficient of 0.013–0.019 $m^2\ g^{-1}$, generally twice as high as Eurasian watermilfoil. At a rooting depth of 80–90 cm the former had 62% of leaf biomass within 30 cm of the bottom while the latter had 68% of its shoot biomass within 30 cm of the surface. Meyer et al. (1943) also found wild celery to be the most shade adapted of five submersed macrophytes. Titus and Adams (1979) discovered that it was an efficient fixer of carbon at low light intensities but was also able to acclimate very rapidly to increasing light.

In experiments by Manning et al. (1938), Meyer and Armitage (1941) and Meyer et al. (1943), the rate of apparent photosynthesis of species of *Vallisneria*, *Ceratophyllum*, *Elodea*, *Heteranthera*, *Najas* and *Potamogeton* increased with stronger illumination up to surface intensities which varied from 0.3 to about 1.1 g cal cm^{-2} min.

The coiling of the peduncle after fertilization is stimulated by the natural auxin IAA when applied in concentrations of 3 or 7.5 ppm to the water. Funke (1938, 1939) and Sculthorpe (1967) suggest that this coiling may be regulated by auxin released by germinating microspores or developing embryos.

Wild celery presented a heavier drain upon the soil and waters of Lake Mendota in Wisconsin than *Potamogeton* ssp., removing more silica, phosphorus, iron, aluminum, manganese, lime, potassium and sodium, but less nitrogen, sulphur and magnesium (Schuette and Alder 1927). Chemical composition of wild celery is discussed under 3(b).

(d) *Phenology* — In New York, rosettes of ribbon-like leaves emerged from winter buds buried in the sediment in late May (Titus and Stephens 1983). Peak plant biomass (76%) was reached in early August, rising steadily from early June. Twenty-four percent of plants sampled in August were in flower or fruit and winter buds were visible in late August, just prior to senescence. In a Wisconsin lake, Witmer (1937) observed plants flowering from 29 June to 3 August with mature fruit formed by 25 August. In the tidal zone of the Potomac River in Maryland, the growing period for wild celery begins in late April or May from buds or seeds with flowering beginning in early July, continuing through early September, and final die-back in November (Carter and Rybicki 1985). Crowder et al. (1977b) noted that first flowering in Lake Opinicon (eastern Ontario) occurred in late July with large floating mats forming after flowering. In the Rideau River (southern Ontario) we observed wild celery at peak flowering and fruiting stage in late August and early September with large beds of floating plants anchored on the female flowers. Plants are known to decompose rapidly in September (Harman 1974).

In southern Ontario (Lake Huron–Lake Erie corridor), *Vallisneria* plants emerge in May; flowering begins in July and flowers are present until mid-September. Peak biomass is present in mid-August. Fruits develop until about October. Plants form turions beginning in mid-September and they are mature and ready for overwintering by the time of plant senescence, in late October (M. Biernacki, pers. obs.).

In a study of biomass and nutritive potential of wild celery, Donnermeyer and Smart (1985) observed plants in a navigation pool of the upper Mississippi River. Net primary productivity attained a high of 3.2 g m^{-2} d^{-1} by late July and on 1 September, a maximum seasonal biomass of 217.3 g dry wt. m^{-2} (SE = 2.0) was reached. Senescence and death occurred between 1 September and 9 November with maximum fruit biomass at the beginning of that period, coincident with maximum rootstock biomass. Peak winter bud production occurred 14 August–6 October and maximum bud biomass (30.1 g dry wt. m^{-2}) was on 6 October.

Titus and Stephens (1983) studied seasonal growth patterns of wild celery and influences of neighboring plants in a lake in New York. Plants emerged in late spring from winter buds buried in the sediment. Early June to late September was the approximate growing season. In a nearly monospecific stand of wild celery, randomly chosen 0.25-m^2 quadrats were sampled for biomass. An initial low biomass of 2.4 g m^{-2} was recorded in early June, increasing slowly through June then rapidly in late July to 50.1 g m^{-2} in early August. Biomass declined significantly with the onset of senescence in September to 25.3 g m^{-2}. There was one rosette per plant in early June, again becoming more prolific through July and August (3.4, 18 July and 4.8, 8 August), rising to a peak 7.1 rosettes per plant by the end of August. By 23 September, plants had died back.

8. Reproduction

(a) *Floral biology* — *Vallisneria americana* is dioecious. Staminate flowers and pistillate flowers are borne on genetically distinct individuals. Pistillate flowers are borne on elongating scapes which raise the maturing flower to the surface of the water. Although the staminate flowers are borne on a short basal scape, they develop an abscission zone, detach and float to the surface (Sculthorpe 1967) where both sexes come into contact. The free-floating staminate flowers originate from a globose spathe on a short stalk. When the stigma of the long-stalked pistillate flower is ready to receive pollen, the ovary emerges from the bladder and upon reaching the surface, the flower creates a slight depression on the surface. The staminate flowers float about pushed by current and wind (Schuette and Alder 1927; Kaul 1970), and some may eventually slip into the depression created by a female flower at the same time tipping to deposit pollen on the stigma (Wylie 1917; Kausik 1939). The pistillate flowers also form a bubble including male flowers when they are submerged by a wave, and during this process there may be a tipping of the smaller staminate flowers on top of the pistillate flower, thus effectively transferring pollen to the stigma (Wylie 1917; Kausik 1939; Den Hartog 1970; Cook 1982; Cox 1993).

(b) *Seed production and dispersal* — The scape of the pistillate flower begins to coil after pollination and/or fertilization, pulling the flower below the surface. This probably serves to protect the developing seeds from foraging animals. Few of the ovules fail to develop into seeds (Wylie 1917, pers. obs.). The cylindrical fruit contains small dark seeds embedded in a clear jelly-like mucilaginous substance. Lovett Doust and Laporte (1991) reported mean seed number per fruit ranging from 167 to 288 in natural populations. Viability ranged from 93 to 98%. The seeds of species of *Vallisneria* have been found in the stomachs of ducks (e.g. Ridley 1930) and may be dispersed by waterfowl ingesting them. However, it seems more likely that they are routinely dispersed by adhesion to animals (facilitated by the gelatinous mass which surrounds them). Water currents and sediment movement are likely responsible for significant seed and fruit movement.

(c) *Viability of seeds and germination* — Seeds of *Vallisneria spiralis* in India required an optimum germination temperature of 30–35°C (Choudhuri 1966). Shortened days were beneficial but light intensity was not a factor. However, Muenscher (1936) found germination of *V. americana* seed was adversely affected by strong light, diffuse light being more beneficial. Dried seeds proved difficult to germinate. Seeds appear to germinate 2–5 wk later on more organic sediments (Hoover 1984). Ferasol (1993) showed that scarification of the seed coat significantly enhanced germination, the scarified seeds having up to 80% germination after 30 d, whereas fewer than 20% of non-scarified seeds germinated. These workers also reported that germination of seeds of *Vallisneria americana* collected from two PCB-contaminated sites in the Lake Huron–Lake Erie basin was enhanced by exposure to concentrations of the PCB mixture Aroclor 1260, whereas germination of seeds from two other sites was reduced by the highest PCB treatment. There is no record of any establishment of populations from seed (Titus and Hoover 1991).

(d) *Vegetative reproduction* — Clonal growth is extensive in this species. During the season, stolon buds give rise to many new ramets. Under experimental conditions, one overwintering bud may produce 20–40 rosettes within a growing season (Korschgen and Green 1988; M. Biernacki, pers. obs.). Towards the end of the growing season, overwintering buds are produced on the ends of stolons (McAtee 1939; Wilder 1974; Donnermeyer and Smart 1985). These buds lay dormant in the sediment throughout the winter, and initiate growth in the following spring or summer to become new rosettes. The winter buds frequently become detatched and float in late fall or spring (pers. obs.). The extent to which this is a natural process or a result of disturbance to the sediments is unknown. Detached buds can be transported great distances by currents and wave action. Limited transport of buds may also occur on boats and on waterfowl.

9. Hybrids

There are no species of wild celery in Canada other than the native Vallisneria americana Michaux and no hybrids have been reported.

10. Population Dynamics

Lovett Doust and Laporte (1991) investigated population sex ratios and plant densities for three populations of *V. americana* in the Detroit River–St Clair River system. The majority of shoots (58–72%) did not flower. The flowering ramets were significantly male-biased in their sex ratio, ranging from a male:female ratio of 9.9:1 at the northernmost, upstream site, to 3.2:1 at the southernmost site. Sites differed in the density of shoots present.

The population genetic structure of *Vallisneria americana* was investigated at a natural population in the Detroit River (Lokker et al. 1994). The density and distribution of male, female, and vegetative (non-flowering) ramets was determined along six transects at water depths ranging from 38 to 306 cm. Plant densities ranged from 233 to 677 ramets m^{-2}. At the time of peak flowering, only 5–30% of shoots were flowering. A strong male-biased sex ratio was observed in shallow water while sex ratios became increasingly female-biased, and plant density increased, at greater water depths. Cellulose acetate gel electrophoresis (using seven enzyme systems) indicated that polymorphism did not differ between transects, with 62.5% of loci being polymorphic. Overall, 91 allozyme phenotypes were identified. A single allozyme phenotype accounted for 33–55% of all ramets (depending upon the transect), indicating extensive regional clonal growth (Lokker et al. 1994).

In *Vallisneria*, gene flow may occur via pollen, seeds, turions or stolon fragments (Korschgen and Green 1988; Titus and Hoover 1991). The significant sub-structuring observed by Lokker et al. (1994) may be attributable to strong downstream gene flow by any of these structures.

Laushman (1993) excavated plants in a large patch and reported mean clone size for *Vallisneria* at Put-in-Bay, Ohio, to be 1.66 m (SE 1.42). Since *V. americana* senesces to turions every year in late fall, and connections between ramets therefore degenerate, such a sampling strategy can of course only represent the current year's clonal growth.

Wild celery is commonly found in 1–5 m in Lake George, New York with densities of 100–1000 rosettes per m^2 and at maximum depth of 7 m, rosettes per m^2 were 16–400 (Sheldon and Boylen 1977). In the Pamlico River Estuary, North Carolina, Zamuda (1976) reported a maximum density of 280 rosettes per m^2 in August with a seasonal mean of 200 per m^2. Donnermeyer (1982) recorded a maximum density of 214 rosettes per m^2 in the upper Mississippi River and Korschgen and Green (1988) determined densities of 50–250 rosettes m^{-2}. Populations of wild celery are sometimes eliminated by prolonged suspension of clayey silt in moving water (Martin and Uhler 1939) and by fungi (see Section 13, below), but effective dispersal and rapid vegetative reproduction may promote quick re-establishment.

Titus and Stephens (1983) note that wild celery grew and produced winter buds while growing in mixtures of *Chara* and *Potamogeton* but when in monospecific beds, mean values were higher for leaf length, stolon length, rosette number per plant, winter bud number per rosette, winter bud number per plant and winter bud weight. Shading of floating species such as *Hydrilla verticillata* (L. f.) Caspary in Florida (Barko et al. 1984) and *Hydrocharis morsus-ranae* (Catling et al. 1989) may result in dramatic decline of rooted aquatic species that have submersed photosynthetic parts. Wild celery competes unsuccessfully with *Hydrilla* because the higher vegetative growth level of the latter effectively blocks sunlight (Sutton 1983). Vigorous taller growth of neighbors such as *Myriophyllum spicatum* sometimes crowd out shorter rosette plants like wild celery (Titus and Adams 1979; Carpenter 1980; Orth and Moore 1981; Titus and Stephens 1983).

11. Response to Chemicals

No chemicals are available that are specific enough in their inhibiting effect to be used with impunity. Chemically destroyed plants remain in the water, decomposing and releasing nutrients to assist new growth, and therefore a greater cost is incurred despite the expensive application of herbicides as a control measure. Even harvester-cut plants that evade collection are less serious than the addition of chemicals in the ecosystem. Additional general information on the control of aquatic plants with chemicals is provided by Catling and Dobson (1985) and Spicer and Catling (1988).

Sodium arsenite, used at rates of 2–5 ppm has been widely used to control submerged species in static water (MacKenthun 1950, 1955, 1960; Hooper and Cook 1957). It is cheap, simple to apply and successful against wild celery and several other submerged macrophytes, but there are no completely satisfactory herbicides for submerged macrophytes in flowing water (Sculthorpe 1967). Little (1968a) considered it potent and cheap, but its toxicity greatly restricts its use. In 1955 by special permit, sodium arsenite was used in a lake in Wisconsin with devastating results, killing millions of fish, particularly four inch fingerlings (Grinwald 1968). Woodford and Evans (1965) also refer to the chemical as toxic and dangerous to an inexperienced applicator. It is toxic to fish above recommended levels (Gilderhus 1966) and to fish food organisms at and below recommended application levels (Ball and Hooper 1966).

A laboratory evaluation of the effect of fluridane (an herbicide introduced in 1979 for aquatic plant management) on wild celery revealed that 100% control was achieved at a dosage of 0.3 ppm 6 wk after application. There was no visible harm to other forms of aquatic fauna including bluegills, bass, catfish, crayfish, frogs and water snakes (McCowen et al. 1979).

Acrolein is widely used to control submersed aquatic plants in flowing water in Australia but the general biocide is toxic to fish. Eighty percent control of wild celery was possible in tank experiments at a dosage of 3.7 ppm for 1 h (Bowmer and Sainty 1977).

In Winter Park, Florida, wild celery proved resistant to most herbicides and aquatic harvesting methods were favored (Blanchard 1966). *Vallisneria* has been reported as resistant to most of the widely-used herbicides, including 2,4-D, diquat, and Aquatol-K (Nichols 1991).

Herbicide runoff from treated agricultural land in the Chesapeake Bay area has been suggested as a factor in the loss of submersed vegetation which included extensive beds of wild celery (Correll and Pierce 1978; Correll et al. 1978; Environmental Protection Agency 1978; Stevenson and Confer 1978; Stevenson et al. 1979). This was associated with an overall decline in fish and wildfowl. The possibility of a decline in populations of *Vallisneria americana* due to pollution in the Lake Huron–Lake Erie Corridor was reported by Schloesser and Manny (1990), and Manny and Kenaga (1991).

12. Response to other Manipulations

Attempts to eradicate or control nuisance aquatic vegetation are best planned in terms of an overall consideration of restoration and management of an aquatic system (Cooke et al. 1986; Spicer and Catling 1988).

Mechanical control of aquatic weeds continues to be the most popular method and several types of machinery are used (Livermore and Wunderlich 1969; Dunst et al. 1974; Nichols 1974; Maxnuk 1979; Newroth 1979; Armour et al. 1980; Bryan and Armour 1982). Cutting and harvesting machines usually have cutting depths from 1.5 to 2.5 m, with widths ranging from 2.0 to 3.7 m (Cooke et al. 1986). Utilization of harvested material for animal feed or feed supplements (Little 1968a,b), soil conditioners and fertilizers (Timmons 1970), or mulch and compost (Wile et al. 1978) may reduce cutting and harvesting expenses.

The importance of *V. americana* in the aquatic ecosystem is widely recognized, and aspects of the restoration of wild celery to promote wildlife habitat are discussed by Korschgen and Green (1988).

13. Response to Parasites

Grass Carp (*Ctenopharyngodon idella* Val.) is a phytophagous (plant-eating) fish that feeds on a variety of aquatic plants including wild celery (Chokder 1967; Yeo and Fisher 1970; Anonymous 1971; Sutton and Blackburn 1973; Davis and Brinson 1980: Cooke et al. 1986). Its growth rate may be higher than other fish of comparable size (Smith and Shireman 1983) and daily consumption may equal the fish's body weight under warm water conditions (Fischer and Lyakhnovich 1973). The carp is able to withstand a wide temperature range (1–39°C) and very low dissolved oxygen (lethal level for fry is 0.32–0.60 mg O_2 L^{-1}) (Opuszynski 1972). There are, however, potential problems to consider such as degree of host preference, impact on other fauna, introduction of parasites and stimulation of algal blooms, before introducing grass carp or any other fish into an area where they are not native (Stott et al. 1971; Michewicz et al. 1972; Van Zon 1974; Andres and Bennett 1975; Cooke et al. 1986). A major concern is the possible interference of grass carp with spawning and cover of game fish (Vinogradov and Zolotova 1974; Ware et al. 1975; Merkowsky and Avault 1976; Ball 1977; Bailey 1978; Forester and Lawrence 1978). For additional information on grass carp, see Spicer and Catling (1988). It is possible that the subterranean location of the reproductive structures (buds and overwintering buds) of wild celery would limit the effectiveness of control by phytophagous fish.

In the Potomac River, Maryland, Carter and Rybicki (1985) suspect that wild celery was grazed by waterfowl such as red-head ducks, muskrats (Chapman and Feldhaver 1982) and the red-bellied turtle. Grazed plants became denser and shorter, developing multiple new leaves and failing to reproduce by flowering.

Other parasites include the crayfish (Orconectes causeyi Jester) which has been used to control excessive aquatic vegetation and is known to feed on wild celery (Dean 1969), as well as fly larvae (Martin and Uhler 1939).

In a very extensive survey of the fauna of Lake Mendota (southern Wisconsin), Muttkowski (1918) observed large numbers of larvae of two species of Lepidoptera on *Potamogeton* and *Vallisneria*. Wild celery and other aquatic plant species provide food and shelter to the caddis worm and the very small oligochaets. Other Trichoptera were found on submerged leaves, petioles and stems of wild celery in the Ann Arbor, Michigan area (McGaha 1952).

In 1928 about 300 square miles (768 km^2) of aquatic macrophytes including wild celery, *Potamogeton pectinatus*, *P. perfoliatus*, *Najas flexilis* and *Ruppia maritima* were destroyed by a physiological strain of *Rhizoctonia solani* in

North Carolina and Virginia (Bourn and Jenkins 1928). This disease affects a wide range of host plants.

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