Exhibit AB

Article Biology of Canadian Weeds

THE BIOLOGY OF CANADIAN WEEDS. 34. *Myriophyllum spicatum* L.

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A review and information from recent research are provided on the biology of Eurasian watermilfoil, a weed species introduced from Eurasia, that occurs in lakes in British Columbia and in lakes and rivers of Eastern Canada, especially those close to the St. Lawrence Seaway. A table of characteristics that distinguish this species from *M. exalbescens* and *M. verticillatum* is provided. No single method of control offers the possibility of complete eradication; but the best ones include mechanical harvesting, the use of the selective herbicide 2,4-d, contact herbicides Diquat and Paraquat, rototilling and diver-operated dredges.

Cette monographie présente une mise à jour de la bibliographie ainsi que des recherches récentes concernant la biologie du Myriophylle à épi (*Myriophyllum spicatum* L.), espèce adventice introduite d'Eurasie et qui colonise les lacs de la Colombie-Britannique de même que les lacs et les cours d'eau de l'est du Canada, en particulier au voisinage immédiat du Saint-Laurent. Une clef d'identification sert à distinguer cette espèce de ses proches parents *M. exalbescens* et *M. verticillatum*. Si aucune méthode de lutte n'assure à elle seule la destruction totale de la mauvaise herbe, il reste que les meilleures comprennent la récolte mécanique de la végétation aquatique, l'emploi de l'herbicide sélectif 2,4-D ou des herbicides de contact Diquat ou Paraquat, le bêchage rotatif et le dragage commandé par plongeurs.

1. Name

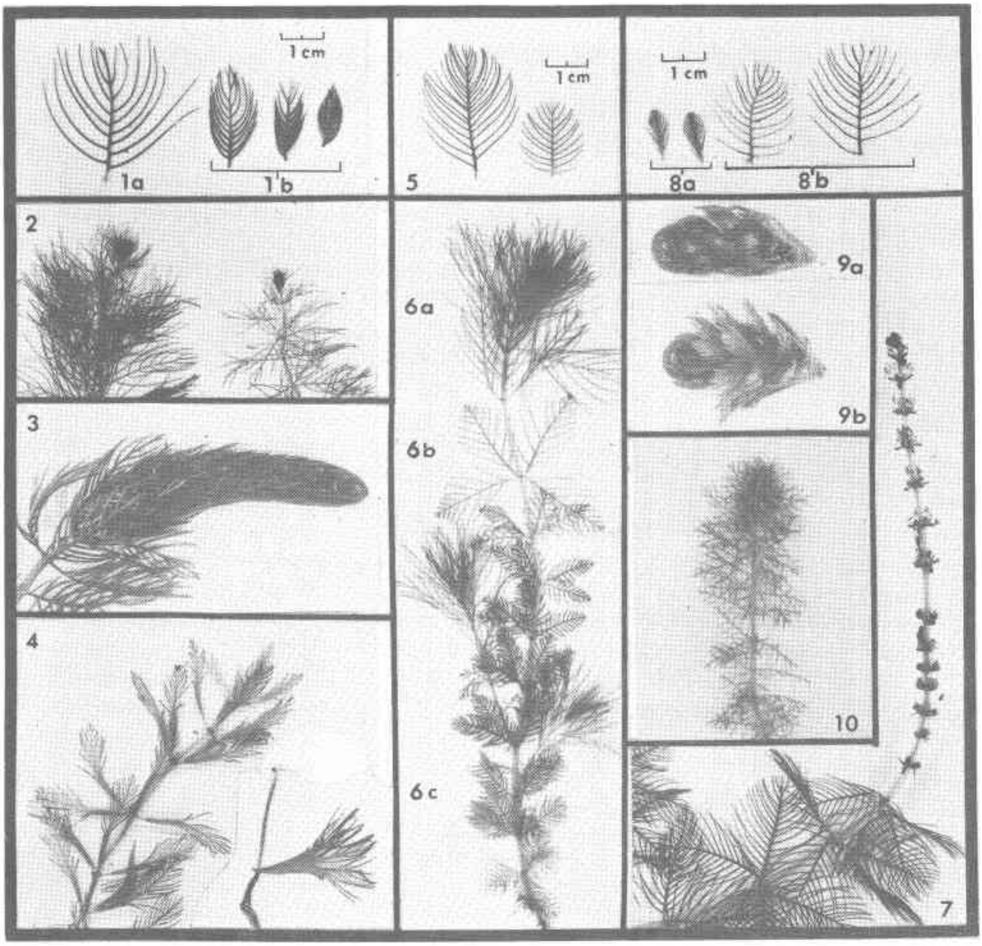
Myriophyllum spicatum L. — **Eurasian watermilfoil** (Hyacinth Control Journal 1975), **myriophylle en epi** (Van Wijk 1911). Haloragaceae, watermilfoil family, Haloragacées.

2. Description and Account of Variation

Submersed aquatic herb with branching leafy shoot, 0.5–7 m long, most commonly in water 1–3 m deep. Stem glabrous, becoming leafless toward the base by release or decay of leaves, branched near the water surface; growing apices tassel-like and often red, especially early in the growing season. Leaves whorled, 1.5–4.0 cm long, usually 4 in a whorl, most often with 14–24 pairs of filiform divisions; leaf outline feather-like, with basal division often about half the length of the leaf in Canadian material, more variable in European samples. Inflorescence a terminal spike, 5–20 cm long, often pink. The stem 5–20 nodes below the spike is almost double the rest of the stem in width, very rigid, characteristically curved so that this portion lies parallel to the water surface. Spike erect at anthesis, parallel to the water surface at fruit set. Flowers verticillate in 4's, the whorls 2-ranked, adjacent whorls rotated 45°, lower flowers pistillate, upper flowers staminate; occasionally hermaphrodite flowers occur in the transition zone. Lower 2–4 whorls of floral bracts usually pectinate and often longer than the flowers; upper bracts entire, broader than long and shorter than the flowers. Female flowers lack perianth; gynoecium 4-lobed with pink,

Table 1. A comparison of *Myriophyllum spicatum* L. with *M. exalbescens* Fern. and *M. verticillatum* L.

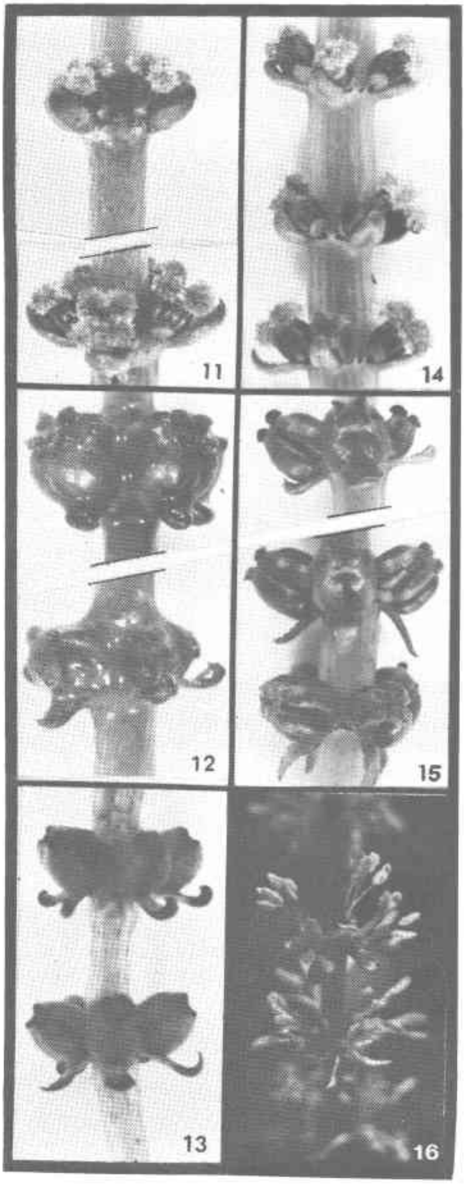
Character	*M. exalbescens*	*M. spicatum*	*M. verticillatum*
Summer leaf length	(1) 1.5–3 (4) cm (Fig. 1a)	2–4 cm (Fig. 5)	2–4.5 cm (Fig. 7)
Leaves per node	4, less frequently 5	4, very rarely 5	4 or 5
Number of pairs of leaf divisions	Variable, 4–14	Very variable, 5–24, occasionally undivided leaves	9–17
Branching near the water surface	Sparse in water more than 1 m deep	Abundant in water 1–3 m deep	Sparse in water more than 1 m deep
Land phase plants	Rare	Common Leaf divisions 4–12 pairs, mainly opposite (Fig. 6a)	Common Leaves 0.75–1.5 cm long. Leaf division 4–10 pairs, mainly alternate (Fig. 10)
Perennation	Cylindrical turions that taper to a point. Turion leaves smaller, thicker, greener than summer leaves. Dark turion leaves conspicuous at base of developing plants (Fig. 3)	No turions. Plants die back to propagating root crowns. Small buds unlike turions may be present	Clavate turions with leaves similar to normal summer leaves and not distinctive after the turion breaks dormancy (Fig. 9)
Fragmentation from specialized layers of cells	Does not occur. Free floating plants result from damage to or decay of parent. Turions released by decay; occurs in spring	Occurs frequently throughout the growing season from a "spurious separation zone of partially lignified cells" (Patten 1956)	Turions are released from an abscission layer. This occurs before the end of December
Physiology in January	Turions attached to parent plant, until April. Turions can be made to break dormancy at 15°C but new turions develop in 4–6 wk	Propagating root crowns may break dormancy and begin new seasons growth. Plants well established by April	Detached turions dormant until April. Parent plant decaying. Turions can be made to break dormancy at 15°C but new turions slowly develop
Stem width below the inflorescence	No conspicuous change in width	Stem width almost doubles in a characteristic curve below the inflorescence (Fig. 7)	No conspicuous change in width
Floral bracts	Shorter than or rarely equaling fruits in length. Lower bracts serrate, upper bracts spathulate-ovate or oblong-cochloform (Figs. 11–12)	Floral bracts equal to or longer than fruits. Lower bracts lanceolate, pectinate; upper bracts entire, rhomic to elongate (Figs. 14–15)	Very variable; from 1–10× length of the fruits, even at the tip of the spike; pinnate or pectinate, never entire
Bracteoles	Entire, ovate, longer than broad or of equal dimensions 0.7–1 mm	Entire, reniform or suborbicular, broader than long 0.5–0.8 mm long	Pectinate or absent. Minute (0.2 mm)
Perianth in female flowers	Absent	Absent	Present, 1 mm long
Petals of male flowers	Pinkish	Pinkish	Greenish-yellow
Pollen	Apertures round or only slightly elongate; circular annulus thickening present. Pollen very similar even under SEM, in these two species (Aiken 1978)		Apertures colpate; margo thickening oval or absent
Chromosome number	42	42	28
Water *p*H	Wide *p*H tolerance, common in alkaline waters	Wide *p*H tolerance *p*H 5.4–11	Acidic to circum-neutral waters
Water depths	0.5–2.5 m	1–10 m	1–3 m



Figs. 1–3. *Myriophyllum exalbescens*. 1. (a) Left, summer leaf, divisions mostly alternate, basal leaf divisions, almost as long as the midrib, × 0.5. (b) Right, three turion leaves. Extreme right a leaf from near the apex of the turion; left, a leaf from near the base. Turion leaves are thicker, stiffer and much darker in color. When the turion germinates they retain their characteristic shape at the base of the plant and are an excellent diagnostic character, × 0.5. 2. Apices that have a compact knob-like appearance, × 0.6. This character is not always present, but it is diagnostic when it is. It is never found in *M. spicatum*. 3. Overwintering turion, × 0.8. In this species the turions taper to a pointed apex. There is a gradual transition between the compact turion and the previous season's growth.

Figs. 4–7. *Myriophyllum spicatum*. 4. Distorted leaves formed on plants adjacent to a lake area treated with 2,4-D, × 0.8. 5. Summer leaves, with a feather-like cast, × 0.5. Leaf divisions are mostly opposite; there are no turion leaves. 6. (a) Fan-shaped apex typical of this species. It is commonly reddish in color, × 0.6. (b) The first whorl of leaves formed after the plant was submersed. The number of leaf divisions is low, × 0.6. (c) Land form leaves shorter and stiffer than aquatic leaves. Emergent plants develop when aquatic plants are stranded on damp mud, × 0.6. 7. Inflorescence, × 0.5. The stem below the inflorescence is wider and is characteristically curved so that this portion lies parallel to the water surface. Lower flowers pistillate; upper flowers staminate.

Figs. 8–10. *Myriophyllum verticillatum*. 8. Leaves × 0.5. (a) Two leaves removed from a turion. They are similar in color to summer leaves, and expand to be indistinguishable from summer leaves when the turion grows. Mature turions often dry brown in herbarium specimens. (b) Summer leaves. 9. (a) Compact turion, club-shaped, × 0.8. (b) Turion beginning to germinate, × 0.8. 10.Land form leaves, × 0.8. Emergent plants develop very easily in this species and they are commonly found among herbarium specimens.



Figs. 11–13. *Myriophyllum exalbescens*, × 3. 11. Pistillate flowers. Lower bracts serrate, upper bracts spathulate–ovate, entire. No scales present at the nodes. 12. Fruits. Lower fruits have bracts as long as the fruits; upper fruits have bracts shorter than the fruits. 13. Fruit set after a cross using *M. exalbescens* pistillate flowers and dusting with *M. spicatum* pollen.
Figs. 14–16. *Myriophyllum spicatum* × 3. 14. Pistillate flowers. Lower bracts lanceolate serrate, upper bracts entire, rhombic to elongate. Black or dark brown scales occur at the nodes between the flowers. These are very obvious in fresh material but not as clear in herbarium specimens. 15. Fruits 4-sulcate with 2 ridges adjacent to the lines of dehiscence. 16. Staminate flowers.

tufted, recurved, sessile stigmas. Male flowers with 4, pink, cauducous petals; stamens 8. Fruit subglobose, 2–3 mm long, 4-sulcate with two somewhat wrinkled ridges adjacent to the lines of dehiscence.

The chromosome number $2n = 42$ is here reported for plants from Guntersville Reservoir, Alabama. The same number was found in plants from Okanagan and Kalamalka Lakes, British Columbia (C. Marchant, unpublished). Löve (1961) reported $2n = 42$ for material from Iceland. The report of $2n = 28$ by Taylor and Mulligan (1968) is erroneous as the voucher specimen is *M. verticillatum* L.

Myriophyllum spicatum is frequently confused with the native species *M. verticillatum* and *M. exalbescens* Fern. and indeed some authors (Jepson 1925: Nichols 1975) consider the latter to be distinguishable only as a variety, *M. spicatum* var. *exalbescens* (Fern.) Jepson, while others (Patten 1954) recognize it as a subspecies, *M. spicatum* subsp. *exalbescens* (Fern.) Hultén. While the status of the taxon may be debatable, it is recognized that introduced weed populations are present and spreading in Canada and that these plants are much more aggressive than any of the native watermilfoils. It is more convenient to retain the two groups of plants at species level unless and until more detailed studies indicate that this is inappropriate.

Table 1 and Figs. 1–16 give morphological and ecological characters by which *M. spicatum* can be distinguished from the other two species. The table contrasts the major differences in life history and ecological range of the three species. Some of the characters used by Fernald (1919) to distinguish *M. spicatum* and *M. exalbescens* show a continuous spectrum of variation and Nichols (1975) has analyzed these using numerical taxonomic techniques. In addition Fernald claimed that in *M. exalbescens* "the dried stems very strongly tend to become white although this change is not always noted." In *M. spicatum*, herbarium specimens were said to retain a "fulvous or olivaceous tone in the stems." This character has been found to be inconsistent (Aiken, unpublished). Eurasian watermilfoil may be distinguished from *M. exalbescens* and other North American species by chromatographic separation of flavonoid pigments (Ceska 1977).

Plants of Eurasian watermilfoil from Quebec, Ontario, British Columbia as well as from Wisconsin, Tennessee, Alabama, Michigan and Washington have been grown side by side in a greenhouse in Minnesota. Their responses to growth conditions appear identical whereas plants from England and the Netherlands growing in the same situation have a slightly different cast. This may be evidence for a common clonal origin for the North American material.

A land form of Eurasian watermilfoil occurs in situations where water evaporates slowly and plants gradually become stranded. The leaves are smaller, stiffer and have fewer divisions (Fig. 6c). If such plants are submerged, new growth with aquatic leaves develops in 7–10 days but the first leaves formed have relatively few divisions (Fig. 6b) and only later does the number of divisions increase to more than 14 pairs. Young plants and free floating plant fragments often develop leaves with fewer than 14 divisions. Thus, the number of divisions is a very plastic and variable character in this species. This feature could be used 70% of the time to distinguish *M. spicatum* from other species (Nichols 1975).

Plants that receive low doses of 2,4-D develop thicker leaves, often with a much wider midrib and with relatively few leaflets (Fig. 4). Plants infected with Northeast disease (Elser 1969) also undergo morphological changes (described in section 13).

3. Economic Importance

(a) Detrimental — Where Eurasian watermilfoil occurs in Canada it is a vigorous plant that shades out other species including the large leaf pondweed, *Potamogeton amplifolius* Tuck., and the naturalized European *P. crispus* L. Stands become so dense that the tangle of branches near the surface can support the weight of frogs and wading birds. The unusual growth feature of *M. spicatum*, compared with native aquatic plants, is that it invades water from 1 to 10 m deep and regularly reaches the surface while growing in water 3½–5 m deep. In the shallow Kawartha Lakes of Ontario, aquatic plants, primarily *M. spicatum*, have covered 80% of the water surface of some lakes. Such dense stands curtail recreational activities, create habitats favorable for the production of blood-sucking insects and clog industrial and potable water supply systems. Dense Eurasian watermilfoil stands may restrict the operation of flow metering devices in flood control channels, and alter temperature profiles in a lake by as much as 10 Celsius degrees/m in shallow water (Dale and Gillespie 1977). Beach quality is substantially degraded by piles of decaying vegetation and this may add to the cost of beach maintenance. Eurasian watermilfoil is considered to have little value as a waterfowl food (Elser 1969) and furthermore, through competition it can reduce the quantities of desirable duck food species. This information is challenged by observations made in the Tennessee Valley Authority lakes (Bates, personal communication) but confirmed by observations made in British Columbia (Newroth, personal communication).

In British Columbia a multimillion dollar program attempting eradication of this weed from the Okanagan Valley was initiated in 1977 and will proceed until 1980 at least (Newroth 1977). This Provincial Government program was initiated because of the high water-based recreational value of the Okanagan lakes. Since 1973 the Ontario Ministry of the environment has budgeted $150,000 per year for the harvesting of aquatic weeds, predominantly Eurasian watermilfoil, in the Kawartha Lakes. An estimated $60,000 per year has been spent privately on the chemical control of weeds in these lakes. Between 1961 and 1977 over $4 million was expended in direct field costs for the control of Eurasian watermilfoil in the Tennessee Valley Authority reservoirs (Bates, personal communication).

(b) Beneficial — Fishermen often consider watermilfoil beds prime locations for bass fishing. Weed beds provide spawning areas and are a habitat for freshwater crustaceans. They also provide areas of calm water for waterfowl to rest. Aquatic plants compete with algae for chemicals in the water and may greatly improve water clarity by preventing dense algal blooms (Davis et al. 1973). Where Eurasian watermilfoil is removed by harvesting, attempts have been made to use it as a fertilizer (Anderson et al. 1965), as an animal feed (Muztar et al. 1976; Muztar 1976) and as a soil conditioner (Wile et al. 1978) with limited success.

(c) Legislation — In February 1978, the Canadian Nuisance Aquatic Plant Committee (IWD) recommended that the importation of *Myriophyllum* into Canada should be banned. *Myriophyllum spicatum* was not included in the recent United States Federal list of Noxious Aquatic Weeds. However, some states including Florida and Louisiana have legislation concerning the propagation, possession and transportation of Eurasian watermilfoil.

4. Geographic Distribution

Myriophyllum spicatum is ubiquitous in Eurasia and also occurs in Greenland (van der Meijden and Caspers 1971). The distribution of Eurasian watermilfoil in Canada, as known early in 1978, is recorded in Fig. 18. The plant has been spreading very rapidly and may be much more widespread in Ontario and Quebec than is shown. The distribution of the species in the United

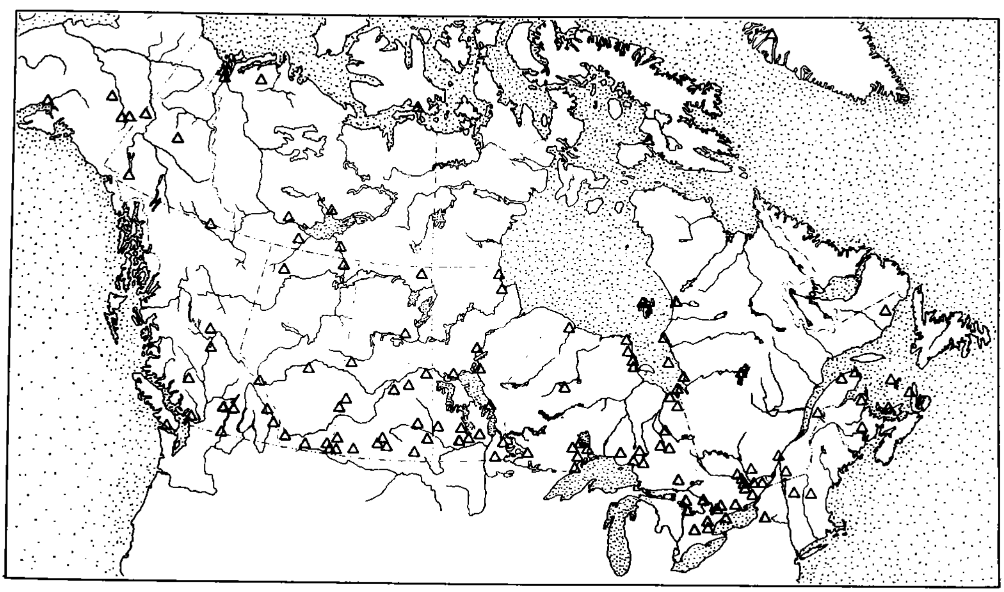


Fig. 17. Distribution of *Myriophyllum exalbescens* species in Canada and Alaska from herbarium specimens.

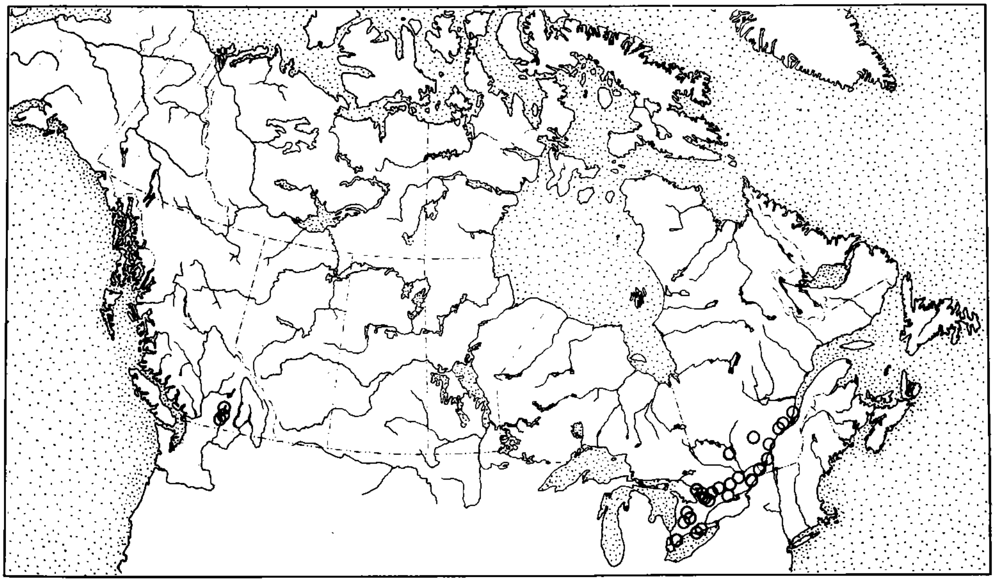


Fig. 18. Distribution of *Myriophyllum spicatum* in Canada and Alaska from herbarium specimens.

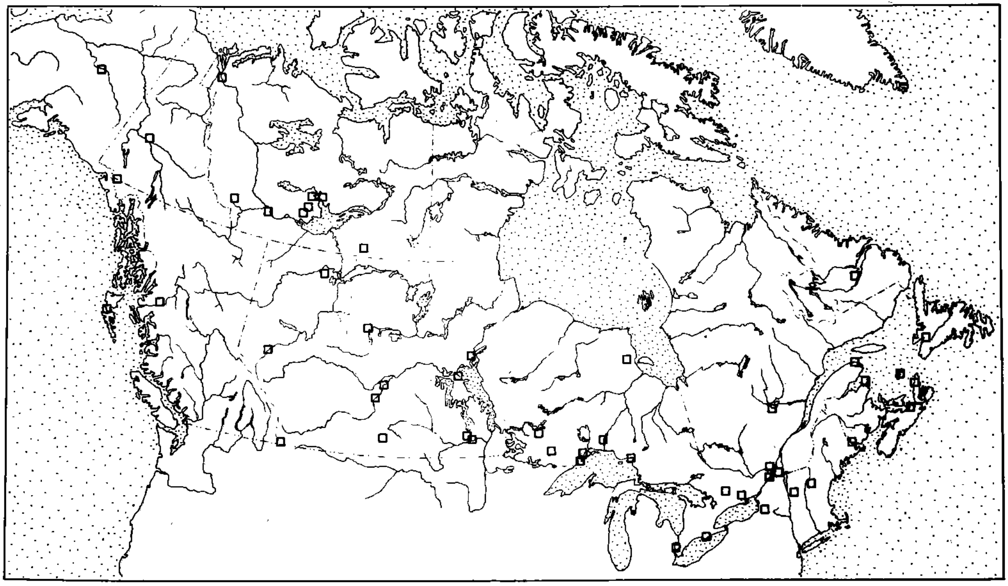


Fig. 19. Distribution of *Myriophyllum verticillatum* in Canada and Alaska from herbarium specimens.

States has been mapped by Reed (1977). Other locations include Arizona and New Mexico (Correll and Correll 1972) and Washington State (Ruthford, personal communication). *Myriophyllum exalbescens* and *M. verticillatum* are common throughout Canada (Figs. 17 and 19.).

5. Habitat

(a) Climatic requirements — The maximum depth at which rooted plants are found is at the plant's compensation point. This will vary from lake to lake with the depth of light penetration. In the clear waters of Okanagan Lake, British Columbia it has been observed in water 8 m deep (Newroth 1975). Plants become established in water 2–3 m deep, and later invade shallower and deeper water. In Ontario, most plants occur in water 0.5–3.5 m deep with less than 25% of the community in depths 0–0.5 m and 3.5–7 m. Substrate, water chemistry, water movement and other environmental factors such as the depth and duration of snow cover on a lake probably also affect the distribution of this species, but no published information is available for Canadian environments.

(b) Substratum — Eurasian watermilfoil flourishes in eutrophic lakes and in situations where waterways are enriched with nutrients. It has been found in Georgian Bay, Ontario, where phosphorus is relatively low (total P = 3 $\mu g/l$) (Wile, personal observation), and in oligotrophic lakes in British Columbia (Nijman 1976). It will also grow in sand, acidic peat (pH = 5.4) (Giesey, personal communication) and in highly alkaline water (pH = 9–10). It thrives in water with a salinity of up to 10 parts per thousand, but grows more slowly at a salinity of 15 parts per thousand (Beaven 1960). In Maryland it readily withstands 1-m tides (Steenis and Stotts 1961).

(c) Communities in which the species occurs — Eurasian watermilfoil invades communities of submerged aquatic plants and within 2–3 yr competitively displaces most other plants, forming a weed bed that may cover a larger area than was originally present. The only submerged aquatic plant in North America that competes successfully with Eurasian watermilfoil, except in slightly saline situations, is *Hydrilla verticillata* (L.f.) Royle; the latter is better adapted to low light intensities (Bowes et al. 1977). While the current distribution of this species is limited to the Southern United States, the possibility of it growing successfully in Canada cannot at present be discounted, and efforts should be made to prevent its introduction.

6. History

In the late nineteenth century, Eurasian watermilfoil was introduced into North America in the Chesapeake Bay area, possibly in shipping ballast. The early spread of this species and a list of annotated herbarium specimens have been recorded by Reed (1977). Eurasian watermilfoil was not considered a weed species until the late 1930's (Springer and Stewart 1959) but it gradually increased in the Chesapeake Bay area to a peak, in 1963, of approximately 80,000 ha (Steenis and King 1964). It was introduced in the Tennessee Valley Authority system in 1953 by a resort owner and reached a peak infestation of 10,000 ha in 1968–1969 (Bates, personal communication).

The distribution of this species in the United States, by 1970, was given in a map by Reed (1970). Records of the spread of the plant in Michigan are given by Coffey and McNabb (1974) and the plant has since spread to every county in Southern Michigan (Payne, personal communication). The history of the invasion in Wisconsin is recorded by Nichols and Mori (1971).

The first record of *M. spicatum* in Canada is probably a herbarium specimen collected in 1961 from Rondeau Provincial Park, Lake Erie: DAO 156348. Eurasian watermilfoil was collected from several sites along the St. Lawrence Seaway during the 1960's. It was not widely recognized as a nuisance until the early 1970's when it became troublesome in the Kawartha Lakes, Ontario, Gatineau Park, Quebec, and the Man and His World site, Montreal, Quebec. It was first observed in the Vernon Arm of Okanagan Lake, British Columbia, in 1970.

7. Growth and Development

(a) Morphology — Colonization of new sites is mainly by vegetative fragments. During the late winter and early spring the plants develop axillary buds that differ from normal vegetative buds in their size and in the ease with which they are detached. During the growing season the plant undergoes autofragmentation. The abscissing fragments often develop roots at the nodes before separation from the parent plant (Grace and Wetzel 1978).The abscission of buds and stems throughout the year is affected by the formation of a "spurious separation zone of partially lignified cells" (Patten 1956). The small buds found in *M. spicatum* are unlike the prominent winter bud turions found in *M. exalbescens* and *M. verticillatum* (Weber 1972; Weber and Nooden 1974).

(b) Perennation — During the fall, plants typically die back to propagating root crowns, often with unexpanded shoots attached (Grace and Wetzel 1978). In the Tennessee Valley, Eurasian watermilfoil frequently overwinters in an evergreen form and may maintain considerable winter biomass (Stanley et al. 1976). In a greenhouse pool where water was 10°C or warmer, relatively little die-back occurred (Aiken, unpublished). The longevity of root crowns is unknown. Titus (1977) speculated that they may be biennial. He found that the overwintering root crowns store nonstructural carbohydrates sometimes making up as much as 20–25% of their dry weight.

(c) Physiology — Eurasian watermilfoil has a C_3 pathway for carbon fixation but it has a low CO_2 compensation point and a high temperature optimum, both characteristics of C_4 plants (Stanley and Naylor 1972, 1973). This may be associated with C_4-like characteristics in the epidermal chloroplasts (Lunney et al. 1975). Grace and Wetzel (1978) have reviewed a growing literature on photosynthesis, respiration, and mineral nutrition in a paper on the production biology of *M. spicatum*. The nitrogen nutrition of living plants and the nitrogen and phosphorus released from plant material decaying after herbicide treatment have been discussed (Nichols and Keeney 1973, 1976a,b).

(d) Phenology — Eurasian watermilfoil root crowns have been observed to start growing in January in Tennessee. They typically begin growth in the spring when temperatures are rapidly increasing. Growth in height is often limited by water depth, and stem length seldom exceeds the water depth by more than 50 cm. When the stems reach the surface, canopy formation occurs by the profuse branching of shoots near the surface while lower leaves and branches tend to slough. This process appears to enable the plant to achieve optimal growth form relative to available light (Grace and Wetzel 1978).

Young (1973) claimed that plant growth and the time of flowering are directly related to water temperature, but this has not been substantiated at multiple locations (Bates, personal communication). Flowering may occur from June to September, with most flowering in Canada between late July and early August. Sloughing of plant parts is common following periods of flowering and spikes with mature fruits are often released in this way. Seeds exhibit prolonged dormancy and seedlings are very rare in nature.

(e) Mycorrhiza — No mycorrhizal associations have been reported for *M. spicatum*.

8. Reproduction

(a) Floral biology — The stigmas ripen as the spikes emerge, well in advance of the stamens, thereby favoring cross-pollination. There are contradictory views on the mode of pollination; these are reviewed by Patten (1956), who concludes that wind pollination is of major importance, though entomophily may be of some significance. It is not known whether the plants are self-compatible.

(b) Seed production and dispersal — Spikes produce 3–10 whorls of pistillate flowers, resulting in a potential 12–40 seeds per spike under favorable conditions. Sometimes the lowermost whorls of pistillate flowers sink below the water surface or are so washed by wave action that they are not successfully pollinated and they fail to set seed. Usually the first pistillate flowers of the summer set relatively few seeds. After flowering, spikes lie parallel to the water surface as fruits mature. The fruits float for a few hours or a day, sufficient to allow for some dispersal in moving water.

(c) Viability of seeds and germination — Seeds of Eurasian watermilfoil, like those of the overwhelming majority of aquatic angiosperms, exhibit prolonged dormancy and germination tends to be extremely erratic (Sculthorpe 1967). The fruits of *Myriophyllum* are indehiscent and have a stony sclerified endocarp. The micropyle of the seed is tightly sealed with a plug formed from the integument. Germination does not occur until this plug is dislodged or the endocarp is ruptured or has decayed.

Patten (1955) claimed that seeds of *M. spicatum* collected from Lake Musconetcong, New Jersey did not germinate immediately after formation unless they were treated to overcome pericarp inhibition. He found treatments that enhance seed germination in approximate decreasing order of effectiveness to be: (1) partial removal of the stony endocarp, (2) scarifying, (3) freezing, (4) alternate freezing and drying, (5) drying, (6) exposure to relatively high H-ion concentration and (7) prolonged exposure to low temperatures. Seeds that had been dried for periods of up to 7 yr and then placed in Petri dishes with distilled water showed 30% or better germination (Davis et al. 1973). Seeds collected in Tennessee Valley Authority reservoirs have germinated readily in the laboratory as soon as picked (Stanley, personal communication).

Seedlings have not been found in lakes, even where, as in Tennessee, the seed set is approximately 4 million seeds per hectare (Stanley, personal communication). A similar observation has been made in Currituck Sound (Davis et al. 1974), in Lake Musconetcong, New Jersey (Patten 1956) and in Okanagan Lake, British Columbia.

(d) Vegetative reproduction — For Eurasian watermilfoil, asexual reproduction is far more important than sexual reproduction. Small axillary buds detach from the root crowns at the end of winter and may establish new plants early in the growing season. During the summer, stems release numerous fragments 10–20 cm long. These float, developing roots and new more compact stems and leaves, before sinking and establishing new plants. Fragments that are formed naturally, and those formed if the plants are broken by wave action or man's activities, such as boating, are usually viable, and have been responsible for the very rapid spread of this weed in North America.

9. Hybrids

Patten (1954) claimed that in New Jersey *M. exalbescens* and *M. spicatum* intergrade, but this was challenged by Löve (1961) because no cytological studies were made and the pollen and seed fertility were not observed. So far, no intergrading or ''hybrid'' chromatograms have been found in the chromatographic identification research being done on these two species in British Columbia (O. Ceska and P. Warrington, personal communication). Fruit set in an artificial cross between *M. exalbescens* and *M. spicatum* was obtained in 1977 (Fig. 13), and more than 30% of the seeds have germinated.

10. Population Dynamics

Eurasian watermilfoil becomes established from fragments. Patten (1956) reports denuding a 1 × 4-m quadrat in a heavily vegetated area of Lake Musconetcong, New Jersey, on 11 July 1953. A buffer zone about 1 m in width was also cleared. Twenty days later, 15 rooted individuals were present.

Fifty-eight individuals were recorded on 18 Aug. and more than eighty on 2 Sept. By the following April, the quadrat was indistinguishable, and not a single specimen of another species became established (17 other aquatic species were in the lake.)

In Currituck Sound, North Carolina, Eurasian watermilfoil was first reported in 1965 when approximately 40 ha were heavily infested and there were 200–400 ha of initial establishment. A year later 3,200 ha were heavily infested and 26,800 ha had some watermilfoil plants (Crowell et al. 1967). By 1974, in this area over 32,000 ha were infested (Spencer and Lekic 1974). Similar data on the rapid spread of Eurasian watermilfoil in the Chesapeake Bay area and in the Tennessee Valley Authority reservoirs are given in the history section. In British Columbia, *M. spicatum* was first observed in the Vernon Arm of Okanagan Lake in 1970 when it occupied 20 ha. In 1977, the weed was found in small lakes and ponds in the Vancouver area and occupied about 600 ha in the mainstream Okanagan Valley Lakes.

11. Response to Herbicides and Other Chemicals

Eurasian watermilfoil is highly susceptible to 2,4-D (2,4-dichlorophenoxy acetic acid) but if it is applied in moving water the contact time of the treatment may mean the difference between extended control and fast regrowth. Provided there is no water movement, control is expected with a 1.0 ppm water concentration of 2,4-D at a minimum exposure time of 48 h and all plants are killed when exposed to 5 ppm treatments for only a 1-h period (Elliston and Steward 1972). The effect of the controlled release of PVC (polyvinyl chloride) and attaclay pellet formulations containing the butoxyethanol ester of 2,4-D on Eurasian watermilfoil has been evaluated (Steward and Nelson 1972). It was found that attaclay granules at 2 ppmw (parts per million water) dose rates of 2,4-D produced greater herbicidal injury, longer control, and higher concentrations of 2,4-D released in water than did PVC pellets at 4 ppmw dose rates. Regrowth was not controlled for more than 6 wk after application because neither formulation was able to maintain phytotoxic herbicide levels (0.25 ppmw 2,4-D). In British Columbia, field trials using granular 2,4-D showed that good control could be achieved for 1 yr, before reinfection occurred (Lim and Lozoway 1978).

Calcium at levels equivalent to that of the natural environment in which Eurasian watermilfoil plants were growing has been found to alter the effectiveness of 2,4-D in laboratory treatments (Stanley 1975). He calculated that in the Tennessee Valley, 2,4-D could be 48% more effective at the highest natural concentration than at the lowest concentration of calcium.

In Canada the only 2,4-D registered for use in treating Eurasian watermilfoil is Aqua Kleen (2,4-D butoxyethanol ester, 20% attaclay), but other formulations are being treated and evaluated (Donna MacKenzie, personal communication). Broadspectrum contact herbicides registered for use in aquatic sites are Diquat (Reglone A) (1,1′ ethylene-2-2′dipyridium cation or 6,7-dihydrodipyrido (1,2-a: 2′1′-C) pyrazidinium cation) and Paraquat (Gramoxone from Chipman Chemicals Ltd., Box 9100, Stoney Creek, Ontario). These are used alone or in 1:1 mixtures and their effectiveness in controlling watermilfoil appears to vary with the water chemistry of the site. Plants die soon after exposure to contact herbicides, but effectiveness is reduced in muddy water, at temperatures below 6°C and if cloudy overcast conditions exist. In British Columbia, field tests with Diquat, Paraquat, Dichlobenil and 2,4-D are being evaluated (Bryan et al. 1977; Lim and Lozoway 1978).

High rates of application of 2,4-D for watermilfoil control on Tennessee Valley Authority reservoirs have not produced direct adverse effects on aquatic fauna or water quality (Smith and Isom 1967; Wojtalik et al. 1971). However, there may be indirect effects such as fish kills due to depletion of oxygen by decaying plants

(Brooker and Edwards 1975) and an increased algal problem following the loss of macrophytes (Nichols 1973).

12. Response to Other Human Manipulations

In the Kawartha Lakes region, an experimental harvesting program was begun in southern Chemung Lake in 1973 (Wile 1978). Harvesting operations in 1975 resulted in the removal of 3.0×10^6 kg of plant material, containing 560 kg of phosphorus. This value was equivalent to 47% of the gross and 92% of the net annual phosphorus loading into Southern Chemung Lake. A natural reduction in algal biomass coincided with the harvesting program. In experimental plots, repeated harvests effectively reduced stem densities of Eurasian watermilfoil. In Lake Mendota, Wisconsin, a significant increase in algal biomass was found 1 yr after 2 yr of harvesting Eurasian watermilfoil in shallow water areas (depth 1 m). This increase was concomitant with a decrease in macrophytes. In the deeper water (average depth 1.3 m) a drop in macrophyte biomass was accompanied by a drop of algal biomass (Nichols 1973).

In the Okanagan Valley, 11 methods of control are being tested and evaluated. The most promising are mechanical harvesting, rototilling, diver-operated dredges, the use of fragment barriers around machine operations to prevent downstream spread, and the use of selective herbicides (Newroth 1977).

In Tennessee Valley Authority reservoirs, water level drawdown has been used to kill Eurasian watermilfoil. Stanley (1976) found that plants were killed when exposed to below freezing temperatures for 96 h after water drawdown. Goldsby et al. (1978) found that in Tennessee Valley Authority reservoirs, drawdowns of short duration during cold weather effectively reduced infested areas and did not proportionally increase infestations at deeper depths. They obtained effective control of Eurasian watermilfoil by integrating physical and chemical techniques.

The use of an early fall water level drawdown in the Kawartha Lakes as a means of controlling Eurasian watermilfoil was considered of little value because (1) it did not significantly curtail the weed in two test lakes, (2) re-infestation from adjacent areas was rapid, and (3) there was the possibility of detrimental side effects including fish kills and damage to private docks and boat houses (Wile and Hitchin 1977).

13. Response to Parasites

(a) Insects and other nondomestic animals — No insect parasites have been reported in North America. In Yugoslavia and Pakistan, entomologists have found 25 insect species feeding on Eurasian watermilfoil (Spencer and Lekic 1974). These species are potentially useful for the biological control of the weed in the United States and they are currently being investigated in research projects by the Army Corps of Engineers, Vicksburg, Mississippi and the Biocontrol Laboratory, ARS, Gainsville, Florida.

Schuytema (1977) reviewed the literature on many other organisms that have been considered in the biocontrol of macrophytes and these include snails, crayfish, several species of fish, swans and ducks, nutria, fungi and viruses. These organisms have been tested in small experiments, sometimes specifically with Eurasian watermilfoil, but none is currently in wide scale use. Fertilizing water to induce such phytoplankton turbidity that macrophytes are shaded out has also been considered.

(b) Microorganisms and viruses — Lake Venice disease, described as a "severe pathological condition" was discovered during 1962, in Eurasian watermilfoil populations of Maryland (Elser 1969). This disease first appears as a light brownish coating on the leaves, a coating that becomes thicker until it entirely obscures the leaf divisions. The watermilfoil does not flower but gradually becomes weaker and dies. Under a microscope the brown coating shows an amazing variety and quantity of diatoms, sessile protozoans, epiphytic algae

and fungi. No pathogen has been found for this disease; but under stress conditions plants become more susceptible to attack by microorganisms (Beau et al. 1973).

Northeast disease was first observed in 1964 (Elser 1969). It was thought that the primary pathogen was probably a virus, and gram negative bacilli obtained from diseased milfoil probably represented secondary infections (Bayley et al. 1968). The earliest symptoms seen with the naked eye are broken leaf divisions, and entire leaves reduced in size. The stem and leaves become stiff and remain rigid even when the plant is taken from the water. The petiole flattens and develops wings which fuse outward into flattened and often enlarged basal leaf divisions. Black spots occur along the leaves and stem before the entire plant regresses, and usually fails to flower. Subsequent studies in 1969 failed to show the presence of a virus, and transmission of the disease in the laboratory was not achieved (Bayley 1970).

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