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Rare species of dodder (*Cuscuta* L.; Convolvulaceae) in Quebec and a plea for their search in the wild

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Abstract

We report three rare dodders (*Cuscuta* L.) from Quebec: Buttonbush Dodder (*Cuscuta cephalanthi* Engelmann), Hazel Dodder (*Cuscuta coryli* Engelmann), and Smartweed Dodder (*Cuscuta polygonorum* Engelmann). Detailed descriptions of their morphological characteristics, ecology, and host range are discussed. The genus *Cuscuta* is severely under-collected in Quebec and elsewhere, and targetted fieldwork is needed to better assess the distribution and conservation status of the three rare (or overlooked) species reported here. An identification key to all *Cuscuta* species from Quebec is provided to aid botanists in accurately identifying these challenging species.

Key words: Dodder; Convolvulaceae; Cuscuta; parasitic plants; phytogeography; Quebec; species of conservation concern

Résumé

La présence de trois cuscutes rares (*Cuscuta* L.) est confirmée au Québec: la cuscute du céphalanthe (*Cuscuta cephalanthi* Engelmann), la cuscute du noisetier (*Cuscuta coryli* Engelmann) et la cuscute des renouées (*Cuscuta polygonorum* Engelmann). Une description détaillée de leurs caractéristiques morphologiques et écologiques, ainsi qu'une liste de leurs hôtes sont incluses. Le genre *Cuscuta* est gravement sous-représenté dans les collections québécoises. Des inventaires ciblés sur le terrain sont nécessaires pour mieux évaluer la répartition et le statut de conservation des trois espèces rares (ou négligé) signalées ici. Une clef d'identification de toutes les espèces de *Cuscuta* du Québec est présentée pour faciliter l'identification de ce genre difficile.

Mots clés: convolvulacées; cuscute; Cuscuta; espèce susceptible d'être désignée; plantes parasites; phytogéographie; Québec

Introduction

Dodders (*Cuscuta* L.; Convolvulaceae) are a group of obligate stem parasitic plants with enormous economic and ecological significance. The genus is nearly cosmopolitan and includes close to 200 species, about 70% of which have evolved in the Americas (Yuncker 1932; Stefanović *et al.* 2007; García *et al.* 2014). Some *Cuscuta* species are well-known agricultural pests, and 15–20 species are capable of causing major yield losses in numerous crops worldwide (Parker and Riches 1993; Dawson *et al.* 1994; Costea and Tardif 2006). Non-native species of *Cuscuta* are federally legislated as agricultural/horticultural pests in Canada, the United States, and other countries (e.g., Costea and Tardif 2006), and commercial seed crops (especially legumes) contaminated

with *Cuscuta* seeds (Knepper *et al.* 1990; Olszewski *et al.* 2020) discovered at the border are quarantined (Costea and Tardif 2006). However, some native *Cuscuta* are keystone species and, as ecosystem engineers in their natural habitats, can increase plant community diversity (Callaway and Pennings 1998; Press and Phoenix 2005). Other *Cuscuta* species are rare or at-risk worldwide (Costea and Stefanović 2009), but their conservation is challenging because of the stigma created by noxious dodder species.

Herbarium specimens from Canada and the United States were studied and annotated by M.C. during preparation of the taxonomic treatment of *Cuscuta* for Flora of North America. Annotated specimens in the holdings of larger Canadian herbaria have been digitized; the data are mediated by Canadensys

(canadensys.net) and the Global Biodiversity Information Facility (gbif.org), and taxonomic and floristic updates resulting from these data are incorporated into VASCAN, an online database of vascular plants in Canada (Brouillet *et al.* 2010+).

During the process of examining previously collected specimens, we identified three Cuscuta species from Quebec: Knotweed Dodder (Cuscuta polygonorum Engelmann), Buttonbush Dodder (Cuscuta cephalanthi Engelmann), and Hazel Dodder (Cuscuta coryli Engelmann). The presence of C. polygonorum in Quebec is mentioned in Flore laurentienne (Marie-Victorin 1964, 1995), but we were unable to find a herbarium voucher. Scoggan (1979) also referred to a specimen of C. polygonorum from "Lachine, near Montreal" (probably the same one as in Flore laurentienne), supposedly deposited in the Gray Herbarium, Harvard University, and identified by T.G. Yuncker, but we were unable to locate this collection in the Gray Herbarium, the William and Lynda Steere Herbarium-New York Botanical Garden (where Yuncker's collections are held)-or other North American herbaria. However, M.C. recently annotated several specimens of C. polygonorum collected in the Montréal, Quebec, area that had been previously misidentified, and É.L.-B. recently discovered a new site for C. polygonorum in the same area. Cuscuta cephalanthi and C. corvli are known from other Canadian provinces (e.g., Crins and Ford 1988), but no specimens from Quebec have been previously identified.

Our objectives were to provide information about *C. cephalanthi*, *C. coryli*, and *C. polygonorum* in Quebec; to illustrate the morphological traits useful for their identification; to elaborate on their ecology and host range; and to emphasize their rarity in the province. Ultimately, our aim is to stimulate field searches for these species to better assess their distribution, rarity, and conservation status in Quebec.

Methods

Cuscuta specimens from the herbaria listed in Appendix 1 have been analyzed and annotated and their hosts recorded if they had been identified by the collector on the herbarium label or when verifiable host material was attached to the herbarium specimen. Flowering times reported in the results section are based on Ontario and Quebec herbarium specimen phenology.

The species can be separated using qualitative and quantitative characters of the calyx, corolla, infrastaminal scale, gynoecium, and capsule. These characters are based on Yuncker (1932, 1965), three specieslevel taxonomic studies (Costea *et al.* 2006a,b,c), and several character evolution studies for *Cuscuta* (Wright *et al.* 2011, 2012; Riviere *et al.* 2013; Ho and Costea 2018). Stereomicroscopy images were taken from rehydrated flowers and fruits of herbarium specimens using a Nikon SMZ1500 stereomicroscope (Nikon Corporation, Tokyo, Kantō, Japan), equipped with a PaxCam Arc digital camera (MIS Inc., Villa Park, Illinois, USA) and Pax-it 7.5 software (MIS Inc.). Rehydration was done by steeping the dry plant material in 50% ethanol, which was gradually warmed up to boiling point. Rehydration in a solution of ethanol hardens the tissues, thus protecting the very delicate corolla and infrastaminal scales from disintegration during dissection.

Results

Identification key for Cuscuta species in Quebec

At the vegetative stage, all Cuscuta species that occur in Quebec are morphologically indistinguishable, with trailing or twining, yellow or orange filiform stems 0.2-0.4 mm wide. Accurate species identification based on morphology is only possible when flowers are present, from late summer to early fall. With experience, some species may be distinguished in the field using a strong magnifier. However, accurate identification of most species requires dissecting the flowers using a stereomicroscope. If fresh material is unavailable, dried flowers can be easily rehydrated (see Methods). All species included in the following taxonomic key have been recorded in Quebec, except for Large Alfalfa Dodder (Cuscuta indecora Choisy var. indecora), which we included because it is morphologically similar to C. coryli and has been recorded in neighbouring states in the United States. Figures 1-3 compare flower and fruit morphology of C. cephalanthi, C. coryli, and C. polygonorum with morphologically similar species with which they may be easily confused.

2a. Calyces and stems often reddish-purple (calyces sometimes creamy white); styles equal or longer than ovary; growing on Fabaceae, especially Medicago and Trifolium C. epithymum **2b.** Calyces and stems not purple (often yellow to orange); styles shorter than ovary; growing primarily on Linum usitatissimum (Linaceae)C. epilinum 1b. Stigmas capitate, globose, wider than the styles; 3a. Corolla lobe apices acute to acuminate, in-4a. Calyx lobes more or less carinate, acute; papillae or dome-shaped epidermal cells present on calyx and corolla lobes (requires rehydration of



FIGURE 1. Flowers and fruits of Buttonbush Dodder (*Cuscuta cephalanthi*; a–g) and Swamp Dodder (*Cuscuta gronovii*; h–m). *Cuscuta cephalanthi*. a. Flowers. b and c. Variation of calyx (dissected). d. Corolla dissected and opened to show infrastaminal scales (IFS). e. Infrastaminal scales removed from flower to show fimbriae details. Note the 3- or 4-merous, smaller flowers. f. Early stage in development of the capsule capped by persistent corolla (white arrow). g. Mature capsules (corolla was lost because of rehydration in boiling ethanol). *Cuscuta gronovii*. h. Flower. i and j. Variation of calyx (dissected). k. Corolla dissected and opened to show IFSs. 1. Note the 5-merous, larger flowers. Detail of IFSs removed from the corolla tube. m. Mature capsules surrounded by persistent corolla (white arrow). Scale bars = 1 mm. Colours as resulted after rehydration. Photos: Mihai Costea.

3b. Corolla lobe apices rounded or obtuse, straight

Cuscuta cephalanthi Engelmann

Buttonbush Dodder; Cuscute du Céphalanthe

Type—USA, Missouri, St. Louis County, on the margins of ponds and swamps near St. Louis, 1841, *Engelmann s.n.* (lectotype: MO, designated by Yuncker 1932).

Description—Inflorescences dense to loose, spiciform or paniculiform; pedicels 0.2-1 mm. Flowers 3-4(-5)-merous, 2-3 mm long; dome-like cells on calyx and corolla absent; calyx campanulate to shallowly cupulate, $\frac{1}{2}$ length of corolla tube, divided $\frac{2}{3}$ its length, lobes not carinate, oblong-ovate, bases slightly overlapping, margins entire or serrulate, apex obtuse; corolla white when fresh, becoming creamy to light brown when dry, cylindric-campanulate to cylindric, 1.8-2.8 mm long, lobes spreading to reflexed, ovate, $\frac{1}{3}-\frac{1}{2}$ the tube length, apex obtuse, straight; infrastaminal scales oblong, 0.9-1.7 mm long, shorter than or equalling corolla tube length, sparsely fimbriate laterally, more densely fimbriate distally; **styles** (0.6–) 1–2 mm, equalling or longer than ovary; stigmas capitate. **Capsules** depressed-globose to globose, 2.5– $3.2(-4) \times 2-4$ mm, not thickened or raised around relatively small interstylar aperture, capped by the withered corolla. **Seeds** 1–2/capsule, 1.4–2 × 1.3–1.4 mm. **2***n* = 60.

Distribution in Canada—British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, and Quebec. In Quebec, it is known from only one herbarium specimen collected in 1950 on the rocky margins of Saint François River in Drummondville.

Ecology and host range-In Ontario and Quebec, it flowers between July and September. It usually grows in wet habitats, such as lake shores, river, or stream banks, marshes, alluvial or periodically inundated woods, and wet meadows. The most common hosts throughout its range are Eastern Buttonbush (Cephalanthus occidentalis L.), willows (Salix L., including Sandbar Willow [Salix interior Rowlee], Almond Willow [Salix triandra L.], and Black Willow [Salix nigra Marshall]), goldenrods (Solidago L., including Giant Goldenrod [Solidago gigantea Aiton] and Spreading Goldenrod [Solidago patula Muhlenberg ex Willdenow]), and asters (Symphyotrichum Nees, including Heart-leaved Aster [Symphyotrichum cordifolium (L.) G.L. Nesom], Calico Aster [Symphyotrichum lateriflorum (L.) A. Löve & D. Löve], Ontario Aster [Symphyotrichum ontarionis (Wiegand) G.L. Nesom], and Willow-leaved Aster [Symphyotrichum praealtum (Poiret) G.L. Nesom]). It also grows on numerous other woody and herbaceous genera and species, such as yarrow (Achillea L.), alder (Alnus Miller), Shrubby False Indigo (Amorpha fruticosa L.), American Hog Peanut (Amphicarpaea bracteata (L.) Fernald), Small-spike False Nettle (Boehmeria cylindrica (L.) Swartz), bindweed (Calystegia R. Brown), Trumpet Creeper (Campsis radicans (L.) Seeman ex Bureau), thistle (Cirsium Miller), tickseed (Coreopsis L.), Purple-veined Willowherb (Epilobium coloratum Biehler), Spotted Joe Pye Weed (Eutrochium maculatum (L.) E.E. Lamont), White Wood Aster (Eurybia divaricata (L.) G.L. Nesom), Common Sneezeweed (Helenium autumnale L.), St. John's Wort (Hypericum L.), touch-me-not (Impatiens L.), American Water-willow (Justicia americana (L.) Vahl), sweet pea (Lathyrus L.), water-horehound (Lycopus L., including American Water-horehound [Lycopus americanus Muhlenberg ex W.P.C. Barton]), loosestrife (Lysimachia L., including Lowland Yellow Loosestrife [Lysimachia hybrida Michaux]), holly (Ilex L.), mints (Mentha L., including Peppermint [Mentha × piperita L.] and Spearmint [Mentha spicata L.]), forget-me-not (Myosotis L.), smartweed (Persicaria Scopoli, including Dotted Smartweed

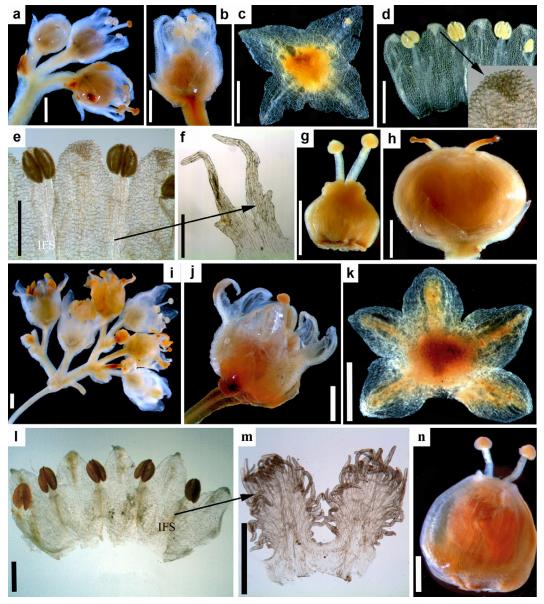


FIGURE 2. Flowers and fruits of Hazel Dodder (*Cuscuta coryli*; a–h) and Large Alfalfa Dodder (*Cuscuta indecora*; i–n). *Cuscuta coryli*. a. Fragment of inflorescence. b. Flower. c. Dissected calyx. d and e. Dissected corolla. f. Infrastaminal scale (IFS) detail. Note the 4-merous flowers with dome-like cells in the calyx and especially the corolla lobes and comparatively reduced scales. g. Gynoecium. h. Mature capsule. *Cuscuta indecora*. i. Inflorescence fragment. j. Flower. k. Dissected calyx. l. Dissected corolla. m. Detail of IFSs. Note the 6-merous, larger flowers with dome-like cells or papillae in the calyx and especially the corolla lobes and large IFSs with numerous fimbriae. n. Mature capsule. Scales bars = 1 mm, except f = 0.25 mm. Photos: Mihai Costea.

[Persicaria punctata (Elliott) Small]), American False Turtlehead (Physostegia americana (L.) Bentham), currant (Ribes L.), elderberry (Sambucus L.), Marshy Hedge-nettle (Stachys palustris L.), Bittersweet Nightshade (Solanum dulcamara L.), skullcaps (Scutellaria L., including Marsh Skullcap [Scutellaria galericulata L.] and Mad-dog Skullcap [Scutellaria lateriflora L.]), Steeplebush (Spiraea tomentosa L.), Canada Germander (Teucrium canadense L.), Poison Ivy (Toxicodendron radicans (L.), Kuntze),

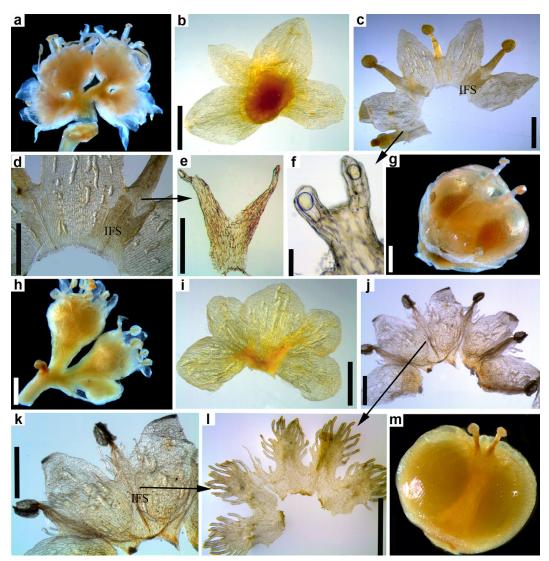


FIGURE 3. Flowers and fruits of Smartweed Dodder (*Cuscuta polygonorum*; a–g) and Field Dodder (*Cuscuta campestris*; h–m). *Cuscuta polygonorum*: a. Inflorescence fragment. b. Dissected calyx. c. Dissected corolla. d and e. Variation of infrastaminal scales (IFSs). Note the 4-merous flowers with non-overlapping calyx lobes and relatively reduced IFSs. g. Mature capsule. *Cuscuta campestris*: h. Inflorescence fragment. i. Dissected calyx. j–l. Dissected corolla and detail of IFSs. Note 5-merous flowers (larger than in *C. polygonorum*) with overlapping calyx lobes, and well-developed IFSs with numerous fimbriae. m. Mature capsule. Scale bars = 1 mm, except e and f = 0.5 mm. Photos: Mihai Costea.

ironweed (Vernonia Schreber), vetch (Vicia L.), and elm (Ulmus L.).

Conservation status—The species is Unrankable (SU) in British Columbia, Critically Imperilled in Manitoba (S1), Vulnerable–Critically Imperilled (S1S3) in New Brunswick, Imperilled (S2) in Ontario, and considered an inexact rank (S2?) in Nova Scotia (NatureServe 2021). In the United States, it is Presumed Extirpated (SX) from the District of Columbia;

Critically Imperilled (S1) in New Hampshire, New Jersey, New York, North Carolina, South Carolina, Utah, Vermont, and Virginia; Imperilled (S2) in Pennsylvania and Kansas; and not yet evaluated in the other states where it occurs (NatureServe 2021).

Herbarium voucher—Canada, Quebec, Drummond County, Drummondville, Bords rocheux du Saint-François, 5 September 1950, L. Cinq-Mars (QFA 0145549, QUE 0005442).

Cuscuta coryli Engelmann

Hazel Dodder; Cuscute du Noisetier

Type—USA, Missouri: St. Louis County, on hazelnut (*Corylus*) near St. Louis, September 1841, *Engelmann s.n.* (holotype: MO 2524873, isotype: GH 00054310).

Description-Inflorescences paniculate-corymbiform to glomerulate; pedicels 0.5-3 mm long. Flowers 4-merous (sometimes 3- to 5-merous within the same inflorescence), fleshy, with epidermal cells of calyx and especially of corolla lobes dome-like (if herbarium specimens are examined, flowers need rehydration and at least 40× to discern this trait); calyx cupulate, equalling or somewhat longer than corolla tube, divided $\frac{1}{2}-\frac{2}{3}$ of the length, lobes carinate, not or only slightly overlapping at the base, triangular-ovate, margins entire, apex acute; corolla white when fresh, becoming dark brown when dry, campanulate to suburceolate, 1.5-2.5 mm long, lobes erect to slightly spreading, triangular-ovate, 1/3 to equalling corolla tube, apex acute, inflexed; infrastaminal scales reaching the filament bases, oblong, bifid, with short dentate wings or 1-3 fimbria on each side of filament attachment, rarely truncate with 3-6 fimbriae; styles 0.7-1.5 mm long; stigmas capitate. Capsules initially globose later becoming depressed, $1.8-2.5 \times 3.5-5$ mm raised, around relatively large interstylar aperture, usually surrounded by the withered corolla. Seeds $1.3-1.6 \times 1.2-1.4$ mm. 2n = 30.

Distribution in Canada—Saskatchewan, Manitoba, Ontario, and Quebec. In Quebec, it is known only from one herbarium specimen collected from St. Lambert, Chambly County (now Montérégie).

Ecology and host range-In Ontario and Quebec, it flowers between July and September. Found in terrestrial, wetland, and anthropogenic habitats throughout its range. Terrestrial habitats include dry, rocky, upland, hardwood dominated and lowland forest types, wooded ravines, open woodlands, savannahs, thickets, forest clearings, prairies, rocky ground, and sandy old fields. Wet habitats include bottomlands, marshes, sedge marshes, salt marshes, meadow marshes, wet meadows, calcareous mixed swamps, interdunal wetlands, lake shores, pond shores, river, stream, and creek banks, and swales. Also found in agricultural fields of Alfalfa (Medicago sativa L.) and occasionally Common Flax (Linum usitatissimum L.), cutovers (lands harvested for timber), roadsides, and cemeteries. Parasitizes many herbaceous and woody species, frequently found on ceanothus (including Narrow-leaved New Jersey Tea [Ceanothus herbaceous Rafinesque]), hazelnut (Corylus L., including American Hazelnut [Corylus americana Water]), tick trefoil (Desmodium Desvaux, including Paniculate Desmody [Desmodium paniculatum (L.)

de Candolle]), goldentops (Euthamia (Nuttall) Cassini, including Grass-leaved Goldenrod [Euthamia graminifolia (L.) Nuttall] and Slender Fragrant Goldenrod [Euthamia caroliniana (L.) Greene ex Porter & Britton]), sunflowers (Helianthus L., including Woodland Sunflower [Helianthus divaricatus L.]), goldenrods (including Canada Goldenrod [Solidago canadensis L.], Giant Goldenrod, Grey-stemmed Goldenrod [Solidago nemoralis Aiton], and Roughstemmed Goldenrod [Solidago rugosa Miller]), and asters (including Heart-leaved Aster, Calico Aster, Smooth Aster [Symphyotrichum laeve (L.) A. Löve & D. Löve], and White Heath Aster [Symphyotrichum ericoides (L.) G.L. Nesom]). It has also been found on Indian mallow (Abutilon Miller), ragweed (Ambrosia L., including Great Ragweed [Ambrosia trifida L.]), goosefoot (Chenopodium L.), ash (Fraxinus L.), Sweet Pea (Lathyrus odoratus L.), pinweed (Lechea L.), Rough Water Horehound (Lycopus asper L.), Alfalfa, beebalm (Monarda L.), White Rattlesnakeroot (Nabalus albus (L.) Hooker), sumac (Rhus L.), raspberry (Rubus L.), willows, Sassafras (Sassafras albidum (Nuttall) Nees), sanicle (Sanicula L.), snowberry (Symphoricarpos Duhamel), germander (Teucrium L.), and Stinging Nettle (Urtica dioica L.).

Conservation status-The species is Unrankable (SU) in Quebec, Critically Imperilled (S1) in Ontario, Imperilled-Critically Imperilled (S1S2) in Manitoba, and Possibly Extirpated (SH) in Saskatchewan (Argus and Pryer 1990; NatureServe 2021). In the United States, it is Unrankable (SU) in Delaware and Iowa; Critically Imperilled (S1) in Kansas, Maryland, and Wisconsin; Imperilled (S2) in New Jersey and Virginia; Apparently Secure (S4) in New York; Possibly Extirpated (SH) in Ohio, Pennsylvania, Rhode Island, and West Virginia; Presumed Extirpated in the District of Columbia; and considered an inexact rank (S1?) in Massachusetts, Maryland, and North Carolina (NatureServe 2021). In the remaining states where it is present, conservation status has not been determined.

Herbarium voucher—Canada, Quebec, Chambly County, St. Lambert, 9 August 1935, *L.M. Terrill et al.* 884 (MT 00070338).

Cuscuta polygonorum Engelmann

Smartweed Dodder, Cuscute des Renouées

Type—USA, Missouri: West of St. Louis, August 1839, *Lindheimer s.n.* (holotype: MO).

Description—**Inflorescences** glomerulate; pedicels 0.2–1 mm long. **Flowers** 4-merous, 2–2.7 mm; dome-like cells absent; **calyx** cupulate, ca. equalling the corolla tube, divided $\frac{1}{2}-\frac{2}{3}$ to the base, lobes not carinate or basally overlapping, triangular-ovate, margins entire, apex obtuse to rounded; **corolla** white when fresh, becoming creamy to light brown when dry, cupulate to shallowly campanulate, 1.8-2.4 mm, lobes erect or spreading, 1.1-1.6 mm long, triangular, apex acute, usually inflexed; **infrastaminal scales** reaching the filament bases, bifid or with 2–3 irregular distal segments each bearing 1–2 fimbriae; **styles** 0.4-0.9 mm; stigmas capitate. **Capsules** depressedglobose, $1.6-3 \times 2.5-5$ mm, not thickened or raised around the large interstylar aperture, not translucent, withered corolla persistent around the capsule base. **Seeds** $1.1-1.4 \times 0.9-1.3$ mm. **2**n = ?

Distribution in Canada—Ontario and Quebec. In Quebec it has been found in three locations within the Montréal area (see below).

Ecology and host range-In Ontario and Quebec, it flowers between July and September. Mostly found in wet places including swamps, sloughs, wooded floodplains, moist thickets, dried ponds, pond edges, lake shores, low plains, marshes, wet meadows, gravel bars, riverbanks, rocky river shores, and other riparian habitats. Occasionally recorded in upland habitats, including forests and open lands and wet anthropogenic habitats, including canals. The most common hosts are knotweed, including Emerged Knotweed (Persicaria amphibia var. emersa (Michaux) JC Hickman), Red Knotweed (Persicaria hydropiperoides (Michaux) Small), Pale Knotweed (Persicaria lapathifolia (L.) Delarbre), and Dotted Smartweed. The genus Persicaria (L.) Miller was formerly included in the genus Polygonum L., which gave the specific epithet of the species. It is occasionally found on beggarticks (Bidens L., including Nodding Beggarticks [Bidens cernua L.], Purple-stemmed Beggarticks [Bidens connata Muhlenberg ex Willdenow], Devil's Beggarticks [Bidens frondosa L.], and Tall Beggarticks [Bidens vulgata Greene]), Spotted Water-hemlock (Cicuta maculata L.), Large St. John's Wort (Hypericum majus (A. Gray) Britton), touch-me-not, morning glory (Ipomoea L.), American Water-willow, Canada Wood Nettle (Laportea canadensis (L.) Weddell), waterhorehound, Ditch Stonecrop (Penthorum sedoides L.), Beefsteak Plant (Perilla frutescens (L.) Britton), dock (Rumex L.), asters, and Rough Cocklebur (Xanthium strumarium L.). Cuscuta polygonorum is exclusively annual and its hosts are always herbaceous.

Conservation status—Cuscuta polygonorum is Unrankable (SU) in Quebec and considered Critically Imperilled (S1) in Ontario (NatureServe 2021). In the United States, it is Unrankable (SU) in Delaware and Iowa; Critically Imperilled (S1) in the District of Columbia, Maryland, New York, Virginia, West Virginia, and Wisconsin; Imperilled (S2) in Kansas, Michigan, New Jersey, and Pennsylvania; Vulnerable–Apparently Secure (S3S4) in Massachusetts; and Possibly Extirpated (SH) in North Dakota (NatureServe 2021). In the remaining states where it is present, conservation status has not been determined.

Herbarium vouchers-Canada, Quebec, MRC Beauharnois-Salaberry, Îles de la Paix, Île à Tambault (Station 2): berge, 4 September 1965, M. Morency 1651 (MT 00070339). Vaudreuil-Soulanges, Île-Perrot, près de la Pointe-du-Moulin. Rivages graveleux et rocheux, 05 September 2005, S.H. Hay, C. Morisset SH05-189 (MT), SH05-190 (MT), SH05-191 (MT), SH05-192 (MT). MRC Deux-Montagnes (WGS84), 45.59833°N 73.83303°W, Baie des Grandes Largeurs, rivière des Milles-Îles, Boisbriand. Grimpant sur Persicaria amphibia et Xanthium strumarium. Haut rivage limoneux. Dominé par Persicaria amphibia, Lythrum salicaria, Carex vesicaria, Echinochloa muricata, Eragrostis hypnoides, Acalypha rhomboidea, Bidens spp., 27 October 2016, É. Léveillé-Bourret et al. 1040 (MT).

Discussion

Taxonomy

All Cuscuta species native to Quebec (C. coryli, C. cephalanthi, Field Dodder [Cuscuta campestris Yuncker], Swamp Dodder [Cuscuta gronovii Willdenow ex Roemer & Schultes], and C. polygonorum) belong to Cuscuta subgenus Grammica (Loureiro) Engelmann ex Yuncker, characterized by having two unequal styles, globose stigmas, and alveolate seed coats when dry (papillate when rehydrated). Translucent laticifers are often visible in the calyx, corolla, and ovary. They also have indehiscent capsules enclosing two to four seeds. The three Cuscuta species newly identified for Quebec have evolved in different major clades of subgenus Grammica (Stefanović et al. 2007; García et al. 2014). Two species introduced to Quebec from Europe (Costea and Tardif 2006), Flax Dodder (Cuscuta epilinum Weihe) and Clover Dodder (Cuscuta epithymum (L.) L., have not been collected in the province in the last 50 years. They both belong to Cuscuta subgenus Cuscuta and can be easily distinguished from native dodders by their stigmas, which are elongated and linear.

Cuscuta cephalanthi is closely related to Swamp Dodder (*Cuscuta gronovii* Willdenow ex Roemer & Schultes), both belonging to *Cuscuta* section *Oxycarpae* (Engelmann ex Yuncker) Costea & Stefanović (Costea *et al.* 2015a). *Cuscuta gronovii* is the most common native dodder in Canada and North America (Yuncker 1932; Costea *et al.* 2006a). These two species occur in the same types of riparian habitats, but *C. cephalanthi* can be recognized by its smaller, 4-merous flowers and persistent corolla capping the capsule (see identification key and Figure 1). The presence of *C. cephalanthi* in Quebec was to be expected because it is reported from neighbouring geographic areas in Canada and the United States: Ontario (Crins and Ford 1988), New York, Vermont, New Hampshire, and Maine (NatureServe 2021).

Cuscuta coryli has strong evolutionary affinity with *C. indecora* (*Cuscuta* section *Indecorae* (Yuncker) Costea & Stefanović; Yuncker 1932; Costea *et al.* 2006b, 2015a). *Cuscuta indecora* var. *indecora* has been reported in Canada only from Saskatchewan (Costea *et al.* 2004), but may be expected in the southern areas of Ontario and Quebec, as it is present in the neighbouring states (Crins and Ford 1988; Costea *et al.* 2006b). *Cuscuta indecora* var. *indecora* differs from *C. coryli* in the 5-merous, larger flowers, with abundantly fringed infrastaminal scales (see identification key and Figure 2).

Cuscuta polygonorum is classified in Cuscuta section Cleistogrammica Engelmann (Costea et al. 2015a), which also includes Field Dodder (Cuscuta campestris Yunker), the most widespread weedy species of Cuscuta worldwide (Yuncker 1932: Parker and Riches 1993; Costea and Tardif 2006; Costea et al. 2006c). Cuscuta polygonorum is similar to C. campestris in fruit and identification errors are possible if only capsules are present. However, even at this stage, C. polygonorum can be recognized by the persistent calyx at the base of capsules, which has four non-overlapping lobes (Figure 3b,g). Cuscuta campestris has 5-merous flowers and calyx lobes that overlap at the base; if flowers are present, its corolla is larger, with well-developed infrastaminal scales that protrude from the corolla tube (Figure 3).

Biology, ecology, and conservation

Cuscuta cephalanthi and C. corvli are annuals, but, when parasitizing woody plants, they can behave as perennials, overwintering as a haustorial endophyte inside the host and regenerating vegetatively in the spring (Yuncker 1932; Costea and Tardif 2006; Meulebrouck et al. 2009). In contrast, C. polygonorum is exclusively annual, growing on herbaceous and often annual hosts. This biological information is important when considering population genetics and population dynamics, as Cuscuta species perennating inside the host tend to reproduce vegetatively and have a high degree of clonality (Meulebrouck et al. 2009), while annual ones are necessarily more diverse genetically. These life-history aspects are virtually unstudied in these species and in Cuscuta more broadly. Dispersal of the three species has not been studied. However, similar to other Cuscuta, seed dispersal is likely accomplished by water or via bird endozoochory (Costea et al. 2016, 2019; Ho and Costea 2018). The indehiscent capsules can float for more than two weeks (Ho and Costea 2018).

Based on the few herbarium collections available for these three species in Quebec, and in Canada more broadly, they are likely rare, or overlooked, or both, and may require protection if threats exist. Unfortunately, conservation of Cuscuta species is challenging because, historically, most research and management efforts have focussed on the control and eradication of weedy Cuscuta, while rare or overlooked species have been neglected (Costea and Stefanović 2009). We do not know why species, such as C. gronovii, C. indecora, and C. campestris, can become aggressive pests (Parker and Riches 1993; Costea and Tardif 2006), whereas some of their closest relatives, such as C. cephalanthi (a close relative of C. gronovii), C. coryli (a close relative of C. indecora), and C. polygonorum (a close relative of C. campestris), are rare. Several studies have suggested that the size of the host range plays a decisive role in determining the success or rarity of Cuscuta species (Costea and Stefanović 2009; García et al. 2018; Costea et al. 2020). However, the three species discussed here seem capable of parasitizing numerous hosts and it is unknown why they are not as widespread (or, at least, not as frequently collected) as their weedy relatives. Cuscuta seedlings must survive while searching the plant community for a compatible host (Behdarvandi et al. 2015). Once they locate a host, they must establish haustorial contact with it (Dawson et al. 1994). Little is known about the impact of biotic and abiotic factors during the search and attack of the hosts, but they likely modulate the population dynamics of Cuscuta species. For these reasons, the traditional focus on pest-control methods must be complemented with targetted biological and ecological studies in natural plant communities to understand the underlying factors explaining rarity versus invasiveness.

Cuscuta are generally less collected than other plants (Austin 1979; Stefanović *et al.* 2007), and we hope this article will stimulate the search for rare species in Quebec and elsewhere in Canada. Species conservation measures cannot be taken without a species conservation status, and the latter cannot be assessed without extensive fieldwork to determine the distribution, threats, size, and dynamics of populations in the wild.

Author Contributions

Conceptualization: É.L.-B. and M.C.; Data Curation: C.W.B.; Investigation: M.C. and C.W.B.; Methodology: M.C.; Resources: É.L.-B. and M.C.; Visualization: M.C.; Writing – First Draft: M.C. and C.W.B.; Writing – Review and Editing: É.L.-B., M.C., and C.W.B.

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APPENDIX 1. Herbaria from which *Cuscuta* specimens were examined.

Abbre- viation	Herbarium	Location
ACAD	E.C. Smith Herbarium, Acadia University	Wolfville, Nova Scotia, Canada
ALTA	University of Alberta	Edmonton, Alberta, Canada
ARIZ	University of Arizona	Tucson, Arizona, USA
ASU	Arizona State University	Tempe, Arizona, USA
BM	The Natural History Museum	London, United Kingdom
BRIT	BRIT Philecology Herbarium, Botanical Research Institute of Texas	Fort Worth, Texas, USA
CAS	California Academy of Sciences	San Francisco, California, USA
CHSC	The Chico State Herbarium, California State University, Chico	Chico, California, USA
CONN	George Safford Torrey Herbarium, University of Connecticut	Storrs, Connecticut, USA
DAO	National Collection of Vascular Plants, Agriculture and Agri-Food Canada	Ottawa, Ontario, Canada
DUKE	Duke University	Durham, North Carolina, USA
F	Field Museum of Natural History	Chicago, Illinois, USA
G	Conservatoire et Jardin botaniques de la Ville de Genève	Geneva, Switzerland
GH	Harvard University	Cambridge, Massachusetts, USA
HAM	Royal Botanical Gardens	Burlington, Ontario, Canada
IND	Indiana University	Bloomington, Indiana, USA
JEPS	Jepson Herbarium, University of California	Berkeley, California, USA
Κ	Royal Botanic Gardens	Richmond, United Kingdom
LSU	Shirley C. Tucker Herbarium, Louisiana State University	Baton Rouge, Louisiana, USA
MICH	University of Michigan	Ann Arbor, Michigan, USA
MT	Herbier Marie-Victorin, Université de Montréal	Montréal, Quebec, Canada
MTMG	McGill University	Sainte-Anne-de-Bellevue, Quebec, Canada

Abbre- viation	Herbarium	Location
MO	Missouri Botanical Garden	Saint Louis, Missouri, USA
NCSC	North Carolina State University	Raleigh, North Carolina, USA
NFLD	Ayre Herbarium, Memorial University of Newfoundland	St. John's, Newfoundland, Canada
NHIC	Natural Heritage Information Centre, Ontario Ministry of Natural Resources and Forestry	Peterborough, Ontario, Canada
NMC	New Mexico State University	Las Cruces, New Mexico, USA
NSPM	The Nova Scotia Museum of Natural History, Collections	Halifax, Nova Scotia, Canada
NY	William and Lynda Steere Herbarium, The New York Botanical Garden	Bronx, New York, USA
OAC	University of Guelph	Guelph, Ontario, Canada
OKLA	Oklahoma State University	Stillwater, Oklahoma, USA
OSC	Oregon State University	Corvallis, Oregon, USA
Р	Muséum National d'Histoire Naturelle	Paris, Île-de-France, France
QFA	Herbier Louis-Marie, Université Laval	Québec, Quebec, Canada
QUE	Herbier du Québec, Complexe scientifique	Sainte-Foy, Quebec, Canada
RSA	California Botanic Garden	Claremont, California, USA
SD	San Diego Natural History Museum	San Diego, California, USA
SASK	W.P. Fraser Herbarium, University of Saskatchewan	Saskatoon, Saskatchewan, Canada
SFS	Herbier Rolland-Germain, Université de Sherbrooke	Sherbrooke, Quebec, Canada
TEX	Billie L. Turner Plant Resources Center, University of Texas at Austin	Austin, Texas, USA
TRT	Green Plant Herbarium, Royal Ontario Museum	Toronto, Ontario, Canada
TRTE	Erindale College, University of Toronto	Mississauga, Ontario, Canada
TUP	Trent University	Peterborough, Ontario, Canada
UBC	Beaty Biodiversity Museum, University of British Columbia	Vancouver, British Columbia, Canada
UC	University Herbarium, University of California	Berkeley, California, USA
UCR	University of California, Riverside	Riverside, California, USA
UNB	Connell Memorial Herbarium, University of New Brunswick	Fredericton, New Brunswick, Canada
UNM	University of New Mexico	Albuquerque, New Mexico, USA
US	United States National Herbarium, Smithsonian Institution	Washington, District of Columbia, USA
USAS	George F. Ledingham Herbarium, University of Regina	Regina, Saskatchewan, Canada
UWO	Dr. Laurie L. Consaul Herbarium, Western University	London, Ontario, Canada
UWPG	University of Winnipeg	Winnipeg, Manitoba, Canada
WAT	University of Waterloo	Waterloo, Ontario, Canada
WIN	University of Manitoba	Winnipeg, Manitoba, Canada
WIS	University of Wisconsin	Madison, Wisconsin, USA
WLU	Wilfrid Laurier University	Waterloo, Ontario, Canada