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The Biology of Canadian Weeds. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe

Mihai Costea
Wilfrid Laurier University, mcostea@wlu.ca

François J. Tardif
University of Guelph

The biology of Canadian weeds. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe.

Mihai Costea[1] and François J. Tardif[2]

Department of Plant Agriculture, Crop Science Building, University of Guelph, Guelph, Ontario, Canada N1G 2W1 (e-mail: mcostea@wlu.ca and [2]ftardif@uoguelph.ca).
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Costea, M. and Tardif, F. J. 2006. **The biology of Canadian weeds. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe.** Can. J. Plant Sci. **86**: 293–316. *Cuscuta* spp. (dodders) are rootless, holoparasitic herbs with filiform stems attached to the host by numerous haustoria. In Canada, *Cuscuta gronovii* is the most common native species of the genus followed by *Cuscuta campestris* and *C. umbrosa. Cuscuta epithymum* and *C. epilinum*, both introduced species in Canada, occur occasionally. Infestation by *Cuscuta* spp. can result in serious yield losses and dodders are listed as noxious weeds in British Columbia, Ontario and Québec, and as restricted weeds in Alberta. These plants have evolved special adaptations to ensure their success: germination occurs late in the season when potential hosts are already established; seedlings selectively forage in plant communities and they may survive relatively long periods during the autotrophic stage. Invasion occurs via extremely elaborate mechanisms designed to match the biological processes of their host and bypass defense mechanisms. The principal means of dispersal of *Cuscuta* weeds world-wide (including Canada) has been through contaminated seeds of previously infested forage legumes. In other areas (e.g., Israel), *C. campestris* has developed resistance to ALS inhibitors (chlorsulfuron, and sulfometuron-methyl) and AABI herbicides. Complete descriptions and illustrations are provided for discussed species.

Key words: *Cuscuta campestris*, *C. gronovii*, *C. umbrosa*, *C. epithymum*, *C. epilinum*, parasitism, growth, development, physiology, reproduction, control, diseases

Costea, M. et Tardif, F. J. 2006. **La biologie des mauvaises herbes au Canada. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. et *C. epilinum* Weihe**. Can. J. Plant Sci. **86**: 293–316. Les plantes du genre *Cuscuta* (cuscutes) sont des herbacées holoparasites sans racines dont la tige filiforme se fixe à l'hôte par de nombreux haustoria. Au Canada, *Cuscuta gronovii* est l'espèce indigène la plus courante, suivie de *Cuscuta campestris* et de *C. umbrosa*. On rencontre à l'occasion *Cuscuta epithymum* et *C. epilinum*, deux espèces introduites. Les infestations par *Cuscuta* sp. peuvent entraîner d'importantes pertes de rendement et les cuscutes figurent parmi les plantes nuisibles en Colombie-Britannique, en Ontario et au Québec, ainsi que parmi les adventices réglementées en Alberta. La plante s'est adaptée pour mieux prospérer : germination tardive quand les hôtes potentiels se sont déjà établis; plantules exploitant sélectivement les communautés végétales et pouvant survivre relativement longtemps pendant le stade autotrophe. L'invasion survient grâce à des moyens extrêmement élaborés, adaptés aux processus biologiques de l'hôte et qui court-circuitent ses mécanismes de défense. Le principal moyen de dispersion des cuscutes, partout dans le monde (y compris au Canada), est la contamination des semences de légumineuses fourragères antérieurement infestées. Dans certains pays (en Israël notamment), *C. campestris* a développé une résistance aux herbicides inhibant l'ALS (chlorsulfuron et méthyle de sulfométuron) et aux désherbants AABI. Suit une description complète et des illustrations des différentes espèces.

Mots clés: *Cuscuta campestris, C. gronovii, C. umbrosa, C. epithymum, C. epilinum*, parasitisme, croissance, développement, physiologie, reproduction, lutte, maladies

1. Names

I. *Cuscuta campestris* Yuncker—**field dodder** (Darbyshire 2003), cuscute des champs (Darbyshire 2003). Bayer code: CVCCA.

II. *C. gronovii* Willd. ex Schult.—**swamp dodder** (Darbyshire 2003), cuscute de Gronovius (Darbyshire 2003). Bayer code: CVCGR.

III. *Cuscuta umbrosa* Beyr. ex Hook. (*C. megalocarpa* Rydberg; *C. curta* (Engelm.) Rydberg)—**large-fruited dodder** (Darbyshire 2003), cuscute à gros fruits (Darbyshire 2003). Bayer code: CVCUB.

IV. *C. epithymum* (L.)L.—c**lover dodder** (Darbyshire 2003), cuscute du thym (Darbyshire 2003). Bayer code: CVCEY.

V. *C. epilinum* Weihe.—**flax dodder** (Darbyshire 2003), cuscute du lin (Darbyshire 2003). Bayer code: CVCEP.

The etymology of the generic name is Aramaic and/or Hebrew. The triradical root of the verb K-S-Y (Kaph, Shin, Yodh) means "to cover". Based on this root, a verbal noun that signifies "cover," "clothing" or "garment" is constructed in both languages: K-S-W-T (in Hebrew) and K-S-W-T-A (Kaph, Shin, Waw, Tav, Aleph) in Aramaic (Costea and Tardif 2004). "Campestris" in Latin means "that grows in

the field". The specific epithet "gronovii" commemorates the Dutch botanist Gronovius, who apparently was the first who referred to the species; "epi" from "epithymum" and "epilinum" means "on" or "over" (*Thymus* and *Linum*, respectively). Dawson et al. (1994) suggested that the vernacular name, "dodder," may come from an old German word, "dotter," used to describe the yolk of an egg. Other vernacular names generally used in North America for *Cuscuta* spp. are "love vine," "tangle gut," "strangle vine," "devil's gut," and "witches shoelaces" (Yuncker 1965).

Convolvulaceae, Convolvulacées. Major synoptic works of angiosperms have treated dodders within a separate family of a single genus (*Cuscutaceae*) (e.g., Takhtajan 1997; Cronquist 1988). Although preliminary results from mitochondrial gene and intron sequences have suggested a sister relationship with Convolvulaceae (McNeal and DePamphilis 2000), more recent phylogenetic studies indicate that *Cuscuta* belongs within Convolvulaceae (Stefanovic et al. 2002; Stefanovic and Olmstead 2004).

2. Description and Account of Variation

(a) *Description* (Yuncker 1921, 1932, 1965) — All *Cuscuta* spp. are rootless parasitic herbs, annual or sometimes perennial. Stems are filiform, yellow, orange, or reddish, glabrous, trailing or dextrorsely twining and attached to the host by numerous small haustoria. Leaves are reduced to alternate, minute scales. Inflorescences are cymose. Flowers are bisexual, regular, sessile or short-pedicellate, mostly 4- or 5-merous, thickened-fleshy to thin-membranous; calyx is fused at the base; corolla is gamopetalous, campanulate to tubular, with small, fringed or fimbriate-margined scale-like appendages (infrastaminal scales) adnate to the corolla tube and alternating with the corolla lobes. Stamens are (3–)5, alternating with the corolla lobes; styles 2, terminal with stigmas capitate or linear. Fruit is a capsule, indehiscent, irregularly dehiscent, or circumscissile by a more or less regular line near the base. There are 1–4 seeds per capsule.

I. *Cuscuta campestris* (Figs. 1A, 2C)—Stems are slender to medium (0.40–0.60 mm thick), yellow to orange. Inflorescences are dense, corymbiform or glomerulate of (3–)6–25 (–30) subsessile to short pedicellate flowers (pedicels 0.3–2.5 mm long). Flowers are (4–)5-merous, 2.1–4.6(–5) mm long, white, membranous, with pellucid, gland-like laticiferous cells evident in the calyx and less obvious in the corolla, ovary and capsule. Calyx is cupulate, ca. as long as the corolla tube, divided 2/5–3/5 the length, calyx lobes are ovate-triangular, obtuse, basally overlapping. Corolla tube is campanulate, ca. 1.5–1.9 mm long, corolla lobes are triangular-lanceolate, acute, inflexed at the tip, ca. as long as the tube, spreading to reflexed. Stamens are exserted; anthers are broadly elliptic, 0.3–0.5 mm long; filaments are 0.4–0.7 mm long. Infrastaminal scales are oblong-ovate, fringed, reaching the filament bases and often exerted. Styles are filiform, 0.8–1.6 mm, ca. as long as the ovary; stigmas are capitate, globose. Capsules are indehiscent or irregularly dehiscent, depressed-globose to depressed, 1.3–3 × 1.9–3.5 mm, with a large and conspicuous interstylar aperture, with the withered corolla surrounding the lower part. Seeds are 4 per capsule. **Chromosome numbers.** No chromosome counts are available from Canada. A chromosome number of $n = 28$ chromosomes was reported from the United States (Fogelberg 1938); $2n = 56$ was reported from New Mexico (Ward 1984), Israel (as "*C. pentagona*", Pazy and Plitmann 1995) and Iran (Aryavand 1987).

II. *Cuscuta gronovii* (Fig. 1B, 2A, D)—Stems are medium to coarse (0.40–0.80 mm thick), yellow to orange. Inflorescence is loose or dense, paniculiform of 7–40 subsessile to pedicellate flowers (pedicels 1–4.5 mm long), sometimes originating endogenously. Flowers are (4–)5-merous, 2–4(–4.7) mm, white, membranous, with a few to many pellucid, gland-like laticiferous cells evident in the calyx, corolla, ovary and capsule. Calyx is cupulate to short-campanulate, commonly reaching to ca. the middle of the corolla tube, divided 1/2–2/3 the calyx length; calyx lobes are ovate to suborbicular or oblong, obtuse, basally overlapping. Corolla tube is campanulate, (1–)1.5–2.5(–3) mm long; corolla lobes are mostly ovate, rounded-obtuse, 1/2–1/3 the length of the corolla tube, spreading. Stamens are exserted; anthers are ovate to oblong, 0.3–0.6 mm long; filaments are 0.4–0.7(–1) mm long. Infrastaminal scales are oblong, deeply fringed distally, reaching the filament bases. Styles are slender or occasionally slightly subulate, (0.6–)1.2–2.2 mm long, shorter than- to equaling the ovary; stigmas are capitate, globose. Capsules are indehiscent to irregularly dehiscent, ovoid to globose-conic or subobpyriform, 2.5–4.5 (–5.2) × 2–4 (–5) mm, surrounded or capped by the withered corolla. Seeds are 2–4 per capsule. **Chromosome numbers—**available from Madison, Wisconsin, $n = 30$ (Fogelberg 1938).

III. *Cuscuta umbrosa* (Fig. 1C)—Stems are medium to coarse (0.40–0.80 mm thick), yellow to orange. Inflorescences are dense, paniculiform of 5–30 subsessile to pedicellate flowers (pedicels 1–7 mm long), becoming globular through the growth and crowding of the capsules. Flowers are (4–)5-merous, 2–3.5(–4.4) mm long, membranous, white, with a few to many pellucid, gland-like laticiferous cells evident in the calyx, corolla, ovary and capsule. Calyx is campanulate reaching to ca. the middle of the corolla tube, divided 1/2–2/3 the calyx length; lobes are ovate, rounded or obtuse, basally overlapping. Corolla tube is campanulate, 1.7–2.3(–2.7) mm long; corolla lobes are mostly ovate to broadly triangular ovate, rounded-obtuse, 1/3–1/4 the length of the tube corolla tube, spreading or reflexed. Stamens are exserted; anthers are ovate to oblong, 0.3–0.6 mm long; filaments are 0.4–0.7 mm long. Infrastaminal scales are broadly oblong, and apically truncate to slightly bilobed, fringed, 1/2(–1/3) as long as the tube. Styles are slender, thickened at the base 0.3–0.7(–0.9) mm long, ca. 1/4 as long as the ovary; stigmas are capitate, globose. Capsules are indehiscent or irregularly dehiscent, subglobose, ovoid to globose-conic, 3.5–6.5(–7) × 3–5(–6) mm, surrounded or capped by the withered corolla. Seeds are 3–4 per capsule. **Chromosome numbers—**not available.

IV. *Cuscuta epithymum* (Figs. 1D, 2E)—Stems are slender (0.25–0.40 mm thick), yellow or often reddish or purplish.

Inflorescences are compact, glomerulate of 7 to 25 sessile flowers. Flowers are 5-merous, 3–4(–5) mm long, fleshy, white-creamy and sometimes reddish-tinged, laticiferous cells are visible in corolla and the midveins of calyx lobes. Calyx is cupulate, 1/2–2/3 as long as the corolla tube, divided 1/2–2/3 the length; calyx lobes are ovate-triangular, acute, sometimes purplish, basally overlapping. Corolla tube is campanulate-cylindrical, 2–3 mm long; corolla lobes are triangular, acute, 3/4–1/2 as long as the corolla tube, spreading. Stamens are exserted; anthers are ovate, 0.3–0.5 mm long; filaments are 0.4–0.7 mm long. Infrastaminal scales are oblong-spathulate, distally fringed, ca. 4/5 as long as the corolla tube. Styles are terete, stigma plus style 1.2–2.2 mm long, ca. two times longer than the ovary; stigmas are filiform-elongate, appearing as a continuation of the style. Capsules are circumscissile, globose, 1.6–2.2 × 1.6–2.3 mm, capped by the withered corolla. Seeds are 4 per capsule. **Chromosome numbers**—n =7; $2n$ = 14 available only from Europe and Asia (Pazy and Plitmann 1995).

V. *Cuscuta epilinum* (Figs. 1E, 2F)—Stems are slender to medium (0.30–0.60 mm thick), yellow to orange. Inflorescences compact, glomerulate of 4 to 15 sessile flowers. Flowers are 5-merous, 3–4 mm long, membranous, white-creamy, without laticiferous cells. Calyx is cupulate, nearly as long as the corolla tube and enclosing it, divided ca. 1/2 the length; calyx lobes are broadly ovate, bluntly acute, often mucronate, basally overlapping. Corolla tube is urceolate, 2.5–3 mm long; corolla lobes are ovate-triangular, obtuse to acute, 1/4–1/3(–1/2) as long as the corolla tube, erect. Stamens are included or barely exerted; anthers are ovate, 0.3–0.5 mm long; filaments are 0.2–0.4 mm long. Infrastaminal scales are spatulate, truncate, entire or bifid, apically short-fimbriate, sometimes reduced to short wings, 3/4–4/5 of the corolla tube. Styles are terete, stigma plus style 0.5–1.1 mm long, shorter than the ovary; stigmas are terete-elongate, appearing as a continuation of the style. Capsules are circumscissile depressed-globose, angular around the seeds, 2.8–3.5 × 3–4.2 mm, capped by the withered corolla. Seeds are 4 per capsule, usually connate in pairs. **Chromosome numbers**—$2n$ = 42 recorded from Russia (Pazy and Plitmann 1995).

(b) *Distinguishing features—Cuscuta* spp. cannot be confused with any other plants. The genus *Cassytha* from Lauraceae (or sometimes Cassythaceae) superficially resembles *Cuscuta*, but it has not been reported from Canada. Identification of *Cuscuta* species requires the rehydration of flowers in boiled water for 10–30 min, if plants are dry, and their dissection and examination under a microscope. Identification keys for *Cuscuta* are available for species occurring throughout the world (Yuncker 1932), North America (Yuncker 1965), Canada (Scoggan 1979) and Ontario (Crins and Ford 1988).

(c) *Intraspecific variation*

I. *Cuscuta campestris* — This species is part of a controversially taxonomic complex of selfing annuals. Yuncker (1932, 1965) accepted *C. campestris* as a separate species, distinct from *C. pentagona* Engelm. Engelmann (1859) previously treated these two species as varieties: *C. pentagona* var. *pentagona* and *C. pentagona* var. *calycina* Engelm., respectively. More recently, the two related taxa have been considered conspecific, and were given no infraspecific rank (e.g., Beliz 1986; Kartesz 1998). This creates problems because although in most of the cases the two taxa are distinguishable, many recent references to "*C. pentagona*" actually apply to *C. campestris*, which is more common and more aggressive as a weed. *Cuscuta campestris* is accepted as a species in the forthcoming treatment of the genus in Flora of North America (Costea et al. unpublished). The two taxa can be recognized as follows:

1. Flowers 1.4–2.1(–2.5) mm long; calyx angled, lobes broadly-ovate rhombic, forming prominent angles at sinuses; corolla tube 0.7–1.2 mm long; anthers 0.2–0.30 mm long; capsules 1.9–2.4 × 1.6–2.5 mm . . . . . .*Cuscuta pentagona*
1. Flowers 2.1–4.6(–5) mm long; calyx not angled (rounded), lobes ovate-triangular, not forming prominent angles at sinuses; corolla tube 1.1–2.5 mm long; anthers 0.4–0.7 mm long; capsules 1.3–3 × 1.9–3.5 mm . .*Cuscuta campestris*

Cuscuta campestris is also related to *C. glabrior* (Engelm.) Yuncker, *C. runyonii* Yuncker, *C. harperi* Small and *C. plattensis* Nelson, taxa that do not grow in Canada (Yuncker 1965).

II. *Cuscuta gronovii* is morphologically variable and several varieties have been described (e.g., Engelmann 1859). *Cuscuta gronovii* var. *calyptrata* Engelm. has corollas that cape the capsules. Variety *latiflora* Engelm. has a corolla tube that is short and campanulate, equaling the calyx lobes.

III. *Cuscuta umbrosa*—Described originally as a variety, *C. gronovii* var. *curta* Engelm., has been accepted as a distinct species in the forthcoming treatment of the genus for Flora of North America (Costea et al. unpublished). At the other extreme, Crins and Ford (1988) did not recognize this taxon at any rank, considering it conspecific with *C. gronovii*. This taxon is fairly homogenous.

IV. *Cuscuta epithymum* exhibits considerable variation in Europe, where two subspecies and several varieties have been described (Feinbrun 1970). The North American material belongs to *C. epithymum* subsp. *epithymum*.

V. *Cuscuta epilinum* is fairly homogenous.

(d) *Illustrations* — Line drawings of flowers, capsules, opened corollas and calyces for the five species are presented in Fig.1. Additional images can be found in Yuncker (1932). Scanning electron microscope pictures of the seeds, as well as of a flower and pollen of *C. gronovii* can be seen in Fig. 2.

3. Economic Importance

(a) *Detrimental — Cuscuta campestris* is a weed of at least 25 crops in 55 countries, while *C. epithymum* is a weed of 25 crops in 13 countries (Holm et al. 1997). Crops infested by *C. campestris* include: alfalfa (*Medicago sativa* L.),

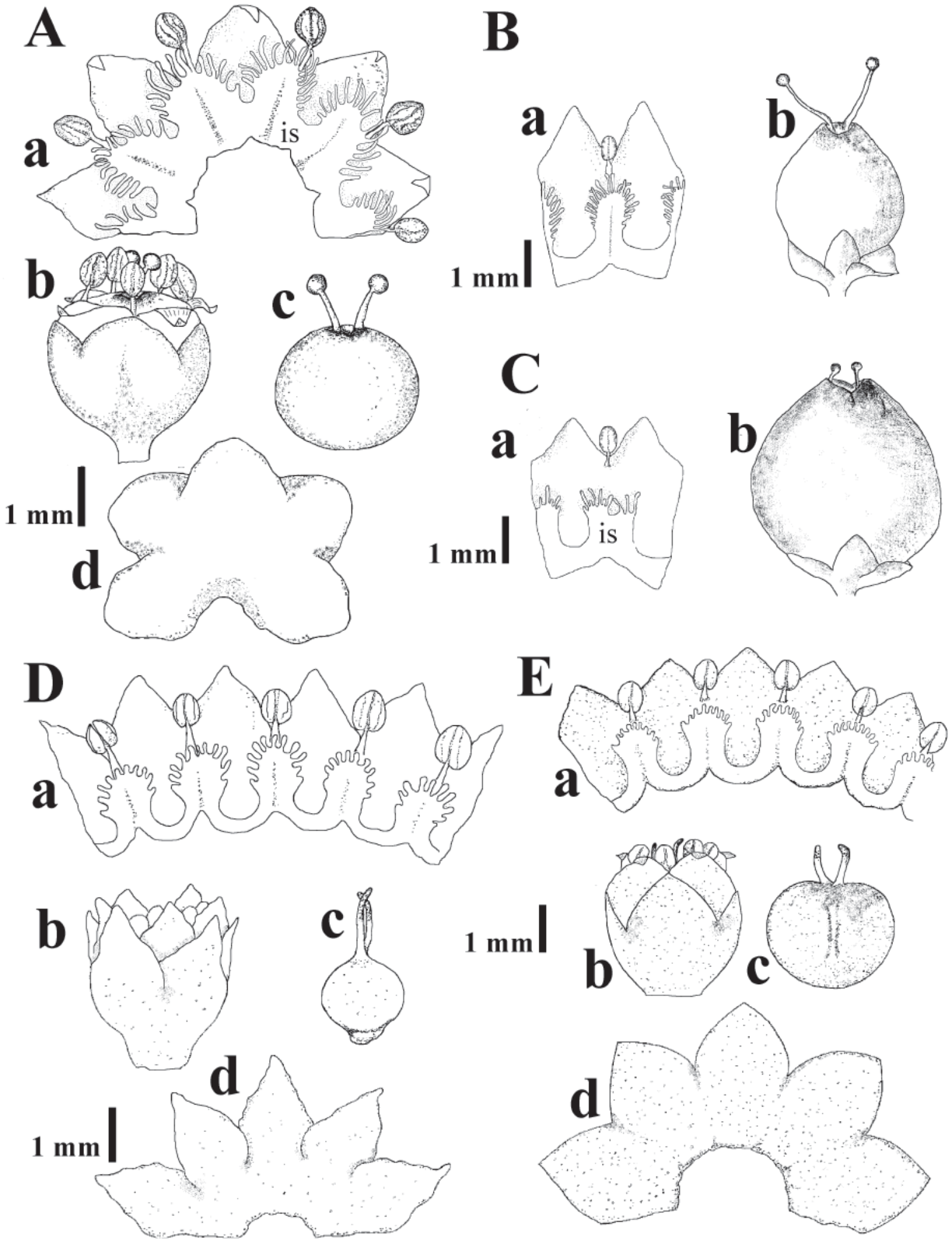

Fig. 1. A. *Cuscuta campestris*: a. opened corolla, b. flower, c. capsule, d. opened calyx., B. *C. gronovii*: a. opened corolla, b. capsule. C. *C. umbrosa*: a. opened corolla, b. capsule. D. *C. epiphytum*: a. opened corolla, b. flower, c. capsule, d. opened calyx. E. *C. epilinum*: a. opened corolla, b. flower, c. capsule, d. opened calyx. is = infrastaminal scales.

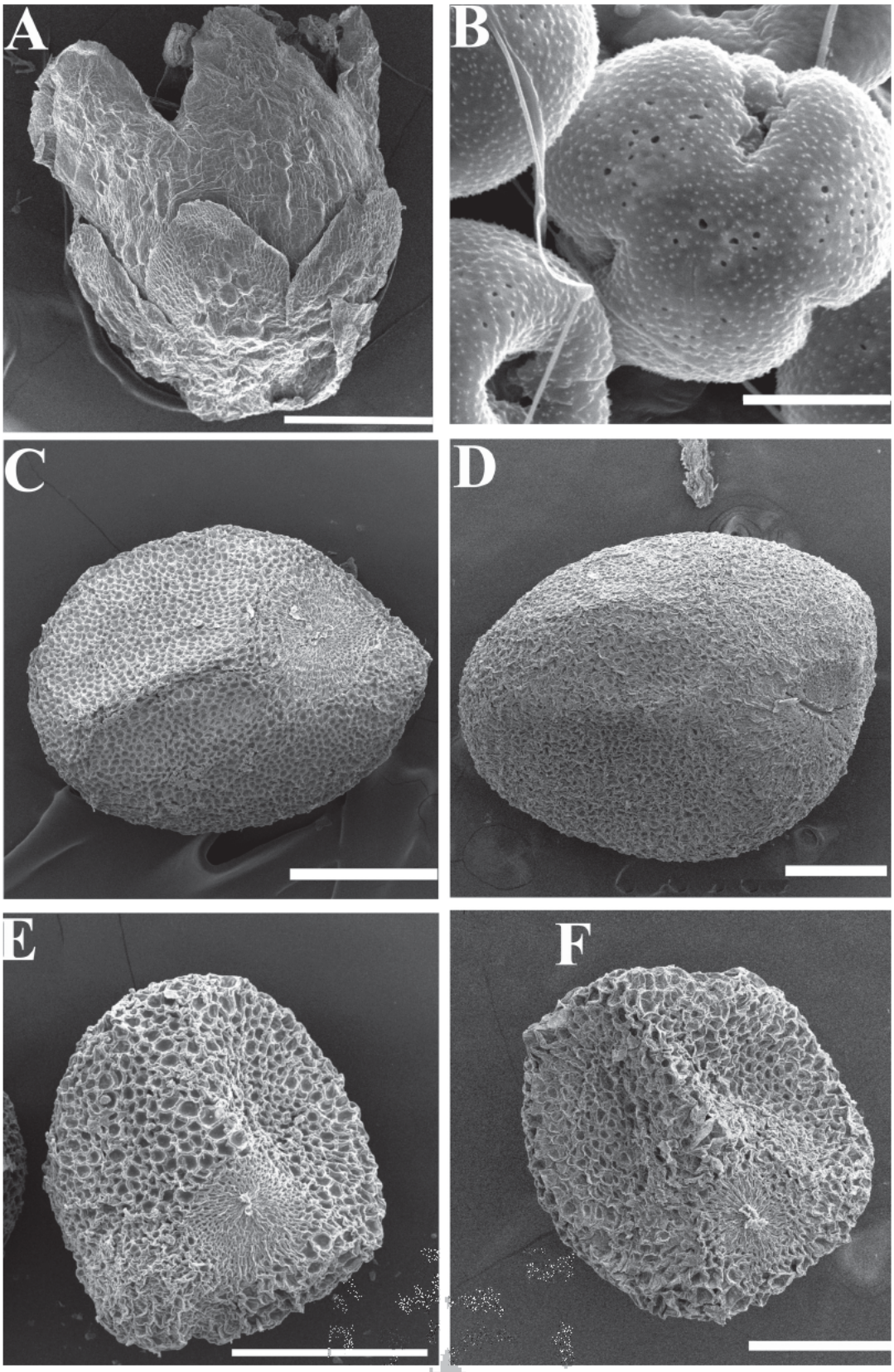

Fig. 2. A. Flower of *Cuscuta gronovii* (scale bar = 1 mm), B. Pollen of *C. gronovii* (scale bar = 7.5 µm), C–F. Seeds of: C. *C. campestris*, D. *C. gronovii*, E. *C. epiphytum*, F. *C. epilinum*. Scale bar = 0.5 mm.

clover (*Trifolium* spp.), fababean (*Vicia faba* L.), beets (*Beta vulgaris* L.), carrots (*Daucus carota* L.), and to lesser extent asparagus (*Asparagus officinalis* L.), chickpeas (*Cicer arietinum* L.), grapevine (*Vitis vinifera* L.), honeydew melon (*Cucumis melo* L.), onions (*Allium cepa* L.), potatoes (*Solanum tuberosum* L.), tomatoes (*Lycopersicon esculentum* Mill.), eggplants (*Solanum melongena* L.) and some ornamental plants (e.g., *Tanacetum* spp.) (Cooke and Black 1987; Parker and Riches 1993; Dawson et al. 1994; Kroschel 2001). *Cuscuta epithymum* is an economically important weed mainly in clover (Kroschel 2001); *C. epilinum* in flax (*Linum usitatissimum* L.), and *C. gronovii* in cranberry (*Vaccinium macrocarpon* Ait.), grapevine and *Citrus* spp. (Parker and Riches 1993; Kroschel 2001).

Infestation by *Cuscuta* can result in serious yield losses. Dawson (1989) reported a 57% reduction in forage yield of alfalfa in Prosser, Washington following an artificial infestation with *C. campestris* over a 2-yr period. In Idaho, potatoes planted after an infested alfalfa crop were completely destroyed (Dawson et al. 1994). *Cuscuta gronovii* infesting cranberry fields in Wisconsin reduced the yield by at least 50% (Bewick et al. 1988b). In Kirgizia, *C. campestris* infestation caused a reduction in sugarbeet yield and sugar content by 3.54 t ha^{-1} and 1.5–1.9%, respectively (Belyaeva et al. 1978). In Yugoslavia, over 80% of the alfalfa and red clover (*Trifolium pratense* L.) fields were infested with *C. campestris*, and 20% of these crops had to be abandoned (Stojanovic and Mijatovic 1973). Sugarbeet plants infested with *C. campestris* had the root weight and sugar content decreased by 23–41% and 1.3–2.6%, respectively (Stojsin et al. 1991).

Cuscuta spp. seeds are important contaminants, especially of small-seeded forage legumes (Knepper et al. 1990; Dawson et al. 1994). Seed contamination represents the main way the parasite spreads, and infested seed lots are denied entry at the border of most countries including Canada and United States. Cleaning of infested seed lots requires significant additional costs (Dawson et al. 1994) and reduces the quality of cleaned seeds (Caji and Stjepanovi 1995).

Although *Cuscuta* spp. are usually not mentioned among toxic plants in North America (e.g., Evers and Link 1972; Stephens 1980; Lampe and McCann 1985; Mulligan and Munro 1990), dodders have been suspected to be toxic to humans (Perkins and Payne 1978) and livestock (Kingsbury 1964). Movsesyan and Azaryan (1974) reported that *C. campestris* can be poisonous to animals if it exceeds 5% of the total roughage. Ingestion of this species by rabbits, horses and cattle caused a toxicosis characterized by anorexia, increased peristalsis followed by atonia, diarrhea, vomiting, increased pulse and respiration rates (Movsesyan and Azaryan 1974).

(b) *Beneficial* — *Cuscuta* spp. have long been used in folk medicine (Blatter et al. 1988; Bork et al. 1996; Srivastava 2002) and they have been extensively investigated as medicinal plants. *Cuscuta* spp. is an ingredient in a Chinese herbal mixture (*Zuo-gui-wan*), which was reported to restore ovarian function in women with premature ovarian failure (POF) and secondary amenorrhea (Chao et al. 2003). A different herbal mixture containing *Cuscuta chinensis* Lam. was suggested as a new approach in the treatment and prevention of postmenopausal osteoporosis (Xu et al. 2003). Flavonoids extracted from the seeds of *C. chinensis* stimulated the reproductive system and reproductive endocrine function in male rats (Qin et al. 2003). Water extract of *C. chinensis* reduced the incidence of skin carcinoma in mice, and had anti-inflammatory activity (Nisa et al. 1985, 1986). The anti-inflammatory effect was confirmed in *C. campestris* (Agha et al. 1996) and *C. tinctoria* Mart. ex Engelm. (Bork et al. 1996). A commercial herbal mixture, Equiguard™, which contains *C. chinensis* was reported to prevent or correct dysfunctional mechanisms that accompany prostate carcinogenesis by modulating prostate growth and gene expression (Hsieh et al. 2002). *Cuscuta reflexa* Roxb. contains α-glucosidase inhibitory constituents and is a potential therapeutic source against diabetes (Anis et al. 2002). *Cuscuta pentagona* can be used as a dye for wool (Dawson et al. 1994). Some species, e.g., *C. reflexa*, have antifungal (Mohammad. et al. 1984) and insecticidal effects (Chavan et al. 1982). In India, *Cuscuta santapaui* Banerji & Das has been successfully tested as a biocontrol agent against *Lantana camara* L. (Pundir 1985).

(c) *Legislation* — In Canada, *Cuscuta* spp. are listed as noxious weeds in British Columbia, Manitoba, Ontario and Québec, and as restricted weeds (destroyed when found) in Alberta (Invaders Database System 2004). In the United States, *Cuscuta* spp. are listed in the Federal Noxious Weed List and on the State lists of 20 states (Invaders Database System 2004). Seeds of *Cuscuta* spp. are prohibited by the Canada Weed Seeds Order (Anonymous 1986) and by the laws of all states in the United States (Dawson et al. 1994; Holm et al. 1997). Commercial seed/crop shipments found to contain *Cuscuta* seeds at the border of Canada and the United States are denied entry.

4. Geographical Distribution

I. *Cuscuta campestris* — This apparently native species occurs sporadically in British Columbia, Alberta, Saskatchewan, Ontario and Québec (Fig. 3). *Cuscuta pentagona* s.tr., often synonymized with *C. campestris*, was collected only on one occasion by Macoun at 1872 from Manitoba (collection in MTMG). *Cuscuta campestris* is perhaps the most widely distributed world-wide species of the genus. Although it originated in North America, the species is now semicosmopolitan being recorded from South America, Europe, Asia, Africa and Australia (Holm et al. 1997).

II. *Cuscuta gronovii*—As a native species, it is the most common dodder in Canada and occurs mostly in Ontario, Québec, New Brunswick and Nova Scotia (Fig. 4). Originally from North America, this species has also spread in Europe, especially along water courses (Parker and Riches 1993).

III. *Cuscuta umbrosa*—This native species grows in Eastern Alberta, Saskatchewan and Manitoba (Fig. 4).

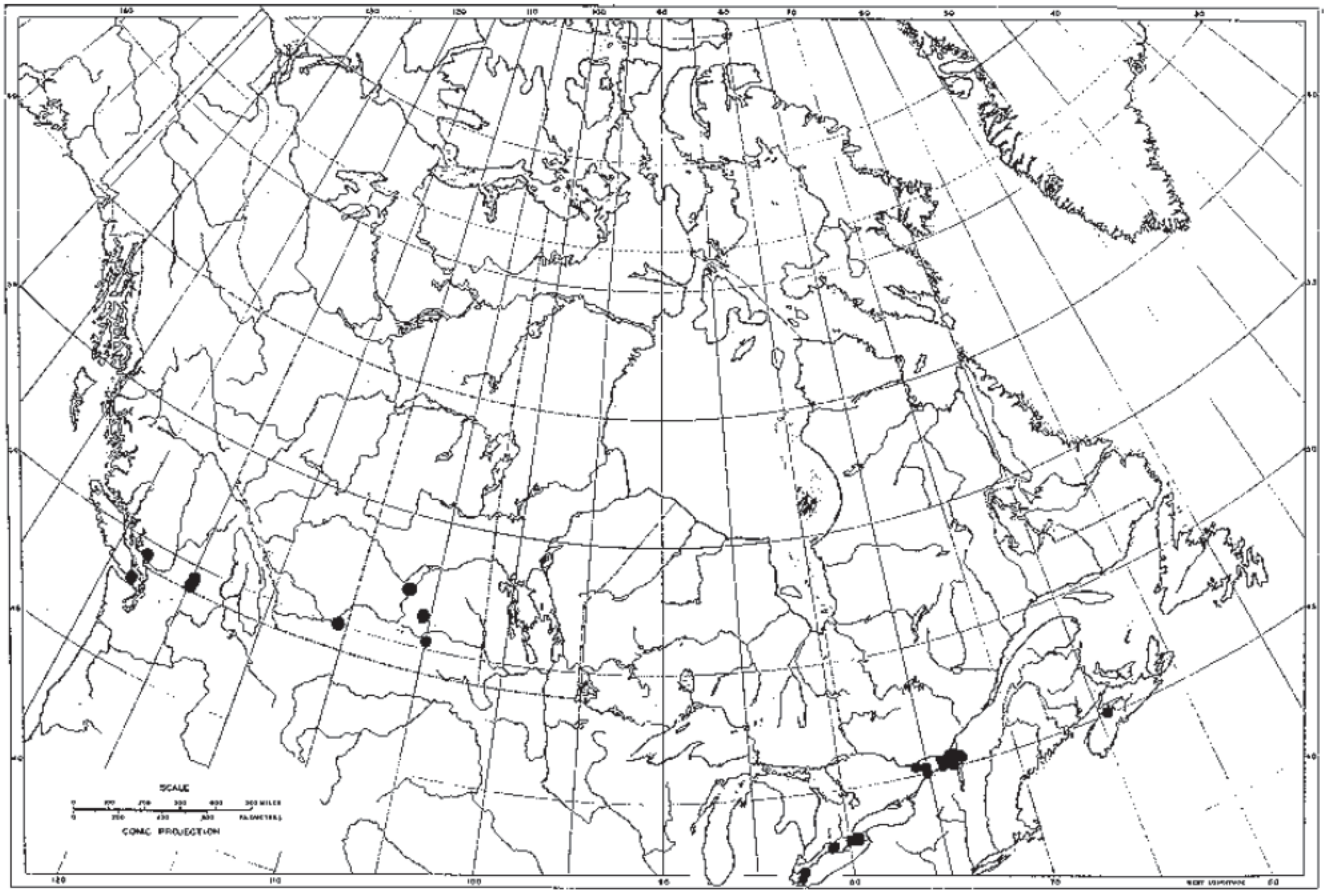

Fig. 3. Distribution of *Cuscuta campestris* in Canada. [ACAD, ALTA, DAO, HAM, MT, MTMG, NFLD, NSPM, NY, OAC, QFA, QUE, RBG, SASK, SFS, TUP, UBC, UNB, USAS, UWO, UWPG, WAT, WIN and WIS; herbarium abbreviations according to Holmgren et al. (1990)].

IV. *C. epithymum*—This species occurs sporadically in British Columbia, Ontario, Québec and New Brunswick (Fig. 5). This European and western Asian species has introduced to North America, eastern Asia (e.g., Japan), Africa, South America and Australia (Holm et al. 1997).

V. *C. epilinum*—This species originated from Europe and western Asia but may occur sporadically in North America and Africa (Parker and Riches 1993). In Canada, it has been found in Québec (Fig. 5) and there is a specimen collected by Pringle from "Lower Canada" at 1880 (deposited in MTMG).

5. Habitat

(a) *Climatic requirements* — The four species can be considered temperate to subtropical, with *C. campestris* exhibiting the widest climatic range. The preference towards a temperate climate is probably related to the cycle of dormancy undergone by the seeds in the soil (see Section 7). The ecological preferences for temperature and light are known only for the germination and seedling phases (see Section 7), and are virtually unknown for the parasitizing stage. Water is necessary for the imbibition of seeds during germination (see Section 7). Parker and Riches (1993) mentioned that *C. campestris* in Ethiopia grows poorly in humid seasons and Stojsin et al. (1991) reported that the attack of this species on sugarbeet was more intense in dry summers.

(b) *Substratum* — The influence of substratum during the autotrophic stage is poorly known (see Section 8c). If substratum has any direct effect during the parasitic stage, it is unknown. However, substratum influences *Cuscuta* spp. indirectly through the host.

(c) *Communities in which the species occur* — *Cuscuta* spp. occur in the communities of their hosts.

Gaertner (1950) reviewed the literature on host range of *Cuscuta* spp.: *C. campestris*, *C. epithymum*, and *C. gronovii* were reported to parasitize 116, 147, and 175 species, respectively. However, the number is certainly much higher. Interestingly, some species have a narrow host range (e.g., *C. epilinum*), while others are capable of parasitizing numerous species from various families. Even species with a wide host range may show a preference toward certain species, and exhibit a partial or total incompatibility with other species, or only with certain populations or cultivars of

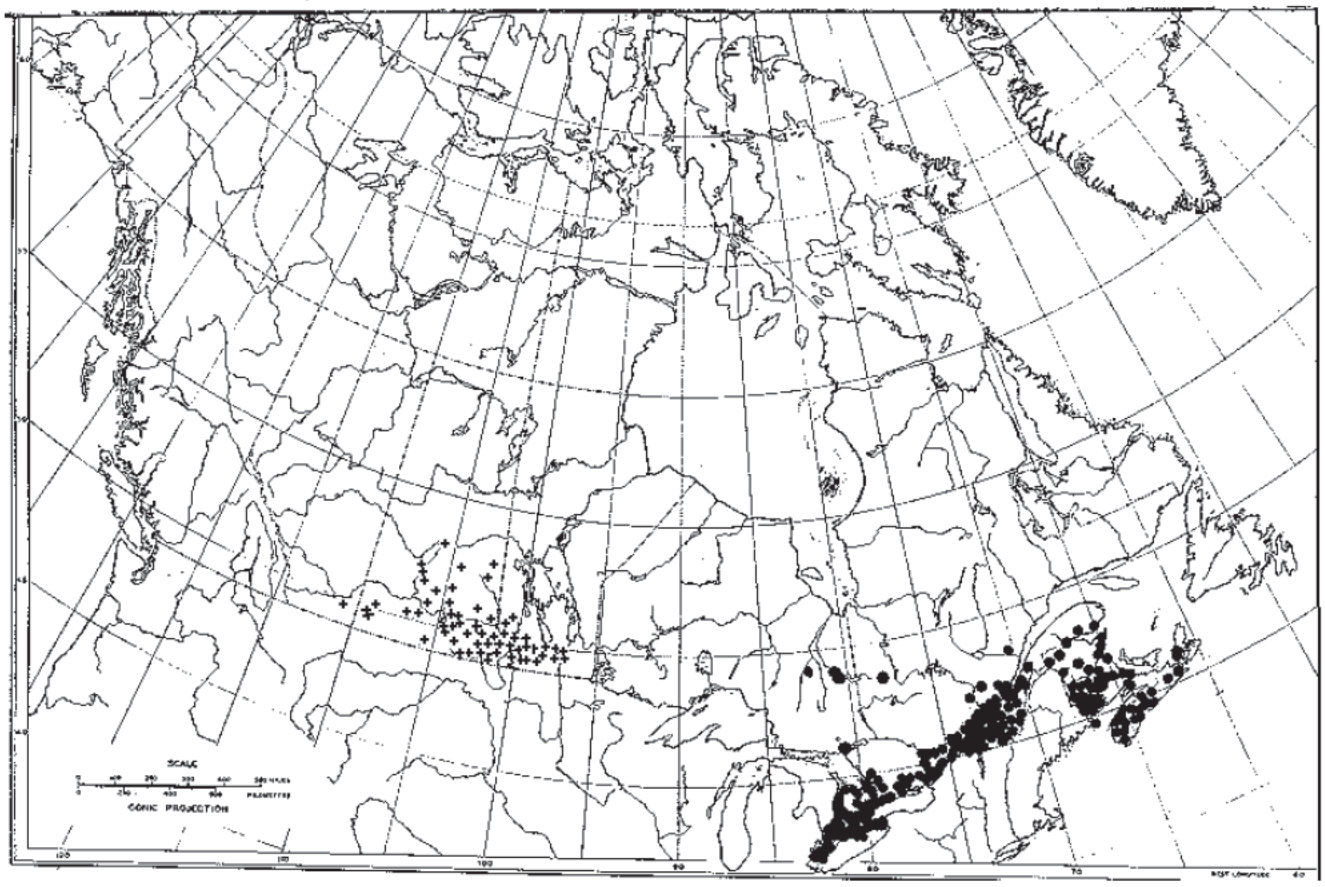

Fig. 4. Distribution of *Cuscuta gronovii* (dots) and *C. umbrosa* in Canada (crosses). [ACAD, ALTA, DAO, HAM, MT, MTMG, NFLD, NSPM, NY, OAC, QFA, QUE, RBG, SASK, SFS, TUP, UBC, UNB, USAS, UWO, UWPG, WAT, WIN and WIS; herbarium abbreviations according to Holmgren et al. (1990)].

these (see also Section 7a). *Cuscuta campestris* could not survive on *Azolla caroliniana* Willd., *Equisetum arvense* L., *Elaeocharis rostellata* Torr., *Atriplex* spp., *Amaranthus retroflexus* L., *Portulaca oleracea* L., *Brassica nigra* Koch., *Glycine max* (L.) Merr., *Vicia villosa* Roth., *Lycopersicon esculentum*, *Arctium lappa* L. or *Tanacetum vulgare* L. (Gaertner 1950).

Parker and Riches (1993) distinguished primary and secondary hosts. Primary hosts are those plants on which *Cuscuta* spp. can establish from the seedling stage. Secondary hosts are those plants on which the seedling parasite cannot establish, but with which they can connect once the parasite has established itself on a primary host. For example, the primary host range of *C. epilinum* is limited to *Linum* spp., but once established on the latter, it can attach on other dicotyledonous species as well (e.g., *Impatiens* spp., Gaertner 1950). Plants from Poaceae and Cyperaceae are incompatible as primary hosts (Dawson et al. 1994), but Parker and Riches (1993) hypothesized that some monocot species may act as secondary hosts, at least for some *Cuscuta* spp. However, although *Cuscuta* spp. may twine around grasses, no haustorial connections were observed (Rath and Mohanty 1988; Dawson et al. 1994).

6. History

The history of *Cuscuta* parasitism during ancient and medieval times has been investigated by Costea and Tardif (2004). Several *Cuscuta* spp. (*C. tinctoria* L., *C. americana* L., *C. odontolepis* Engelm.) were used by the Aztecs to produce a yellow dye called "Zacatlaxcalli" (Sahagún 1950–1982). Apparently, different hues of yellow were obtained from plants of different ages: younger stems gave lighter hues while older stems produced bright yellows. Navajo Indians of the Southwestern United States gathered seeds of *C. umbrosa* and made them into soup or stew (Castetter 1935). Paiute Indians used *Cuscuta* spp. as a contraceptive, the plant being known as "woman without children" (Moerman 1977). Maidens of Pawnee Indians used *C. gronovii* to determine the seriousness of a suitor: "A girl having plucked a vine, with the thought of the young man in mind tossed the vine over her shoulder, into the weeds of host species of this dodder […]. The second day after she would return to see whether the dodder had attached itself and was growing on the host. If so, she went away content with full assurance of her lover's sincerity and faithfulness" (Gilmore 1914).

Gronovius (1762) mentioned first from Virginia a *Cuscuta* species with "floribus pedunculatis" and stems

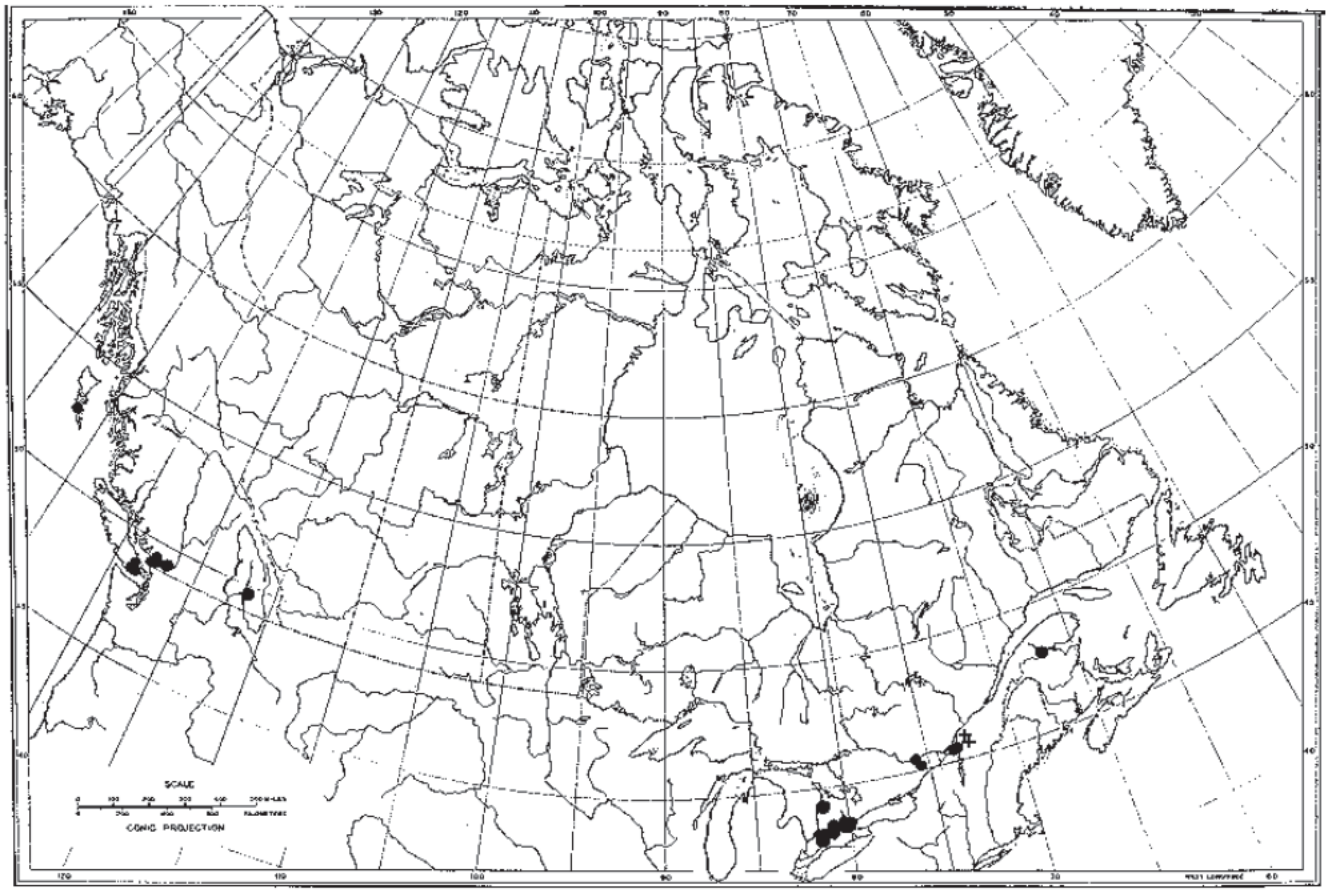

Fig. 5. Distribution of *Cuscuta epithymum* (dots) and *C. epilinum* in Canada (crosses). [ACAD, ALTA, DAO, HAM, MT, MTMG, NFLD, NSPM, NY, OAC, QFA, QUE, RBG, SASK, SFS, TUP, UBC, UNB, USAS, UWO, UWPG, WAT, WIN and WIS; herbarium abbreviations according to Holmgren et al. (1990)].

"longis & fortibus latissime super arbores vel campos se extendes." Later the species was named *C. gronovii* by Willdenow (Roemer and Schultes 1820).

7. Growth and Development

(a) *Morphology* — *Cuscuta* spp. embryos and seedlings have no cotyledons. Seedlings have a small, swollen root-like organ, which persists only a few days after emergence, and a shoot. The basal swollen root-like organ is devoid of a root cap and apical meristems. In *C. gronovii* it has absorbent hairs (Haccius and Troll 1961; Truscott 1966), while in *C. campestris* it is smooth (Lyshede 1985). Although it has a transient function in absorbing- and water storage, the structure of this organ does not resemble that of a "normal" root (see below). Removal of the "root" during the germination of *C. monogyna* did not affect survival of seedlings; however, when cut 2 d after germination, growth of seedlings was significantly reduced (JianZhong and YangHan 1993). The development of the root-like organ does not involve mitotic divisions, and growth consists only of cell swelling, presumably because of the low level of microtubules present in cells (Sherman et al. 2003). These cells undergo a programmed cell death, and the root-like organ degenerates and dies after 2–5 d (Sherman and Vaughn 2003). Sherman et al. (2003) suggested that this degeneration process may contribute carbon to the continued growth of the seedling shoot. The root-like organ has a single vascular strand centrally located, surrounded by large, thin-walled and vacuolated cells (Lyshede 1985).

Mature stems have a three-layered cortex, longitudinally traversed by short rows, or isolated laticiferous cells (Lyshede 1985). The vascular tissue of stems is centrally located and consists of a few primary collateral bundles with small vessels and tube elements (Lyshede 1985). Articulated multinucleate laticifers are located at the periphery of the vascular cylinder. Rudimentary leaves have a very simple structure with no (Lyshede 1985) or very little vascular tissue (Metcalfe and Chalk 1957), and a thin homogenous mesophyll.

The growth of stems is indeterminate and the overall size of *Cuscuta* plants greatly depends on the species and the compatibility with the host and its vigor. In turn, the latter depends on the environmental conditions. Relationship with the host may vary from total incompatibility (e.g., with plants from Poaceae), to subtle degrees of tolerance. These may depend on the species, population or even the individuals that participate in the host-parasite relationship. Koch et

al. (2004) reported that the dry weight of *C. campestris* was significantly higher when parasitizing on *Trifolium resupinatum* L. than on *T. alexandrinum* L. and *Daucus carota*. A single *Cuscuta* spp. plant can simultaneously parasitize several hosts that belong to the same or different species. *Cuscuta campestris* grown on two hosts of *T. resupinatum* accumulated more dry weight, carbon and nitrogen than when parasitizing two *D. carota* plants (Koch et al. 2004). When sequentially parasitizing on *T. resupinatum* and *D. carota*, *C. campestris* grew larger when the first host was the former, rather that the latter species (Koch et al. 2004). Kelly and Horning (1999) found that *Cuscuta attenuata* Waterfall achieved a greater stem volume when infesting two hosts of differing species, than two hosts of the same species. Koskela et al. (2002) reported that individuals of *C. europaea* L. growing on female plants of *Urtica dioica* L. had a higher biomass compared with those infesting male plants. *Cuscuta campestris* grew significantly larger on older plants of *Trifolium resupinatum* than on young plants of the same species (Koch et al. 2004).

In developing seedlings, resources are allocated to the growing shoots, as well as to the process of attachment and penetration of the host. Shoots grow very rapidly, 2 mm in 1 h (Lyshede 1985), or up 8 cm in 24 h (Dawson et al. 1984; Lyshede 1985; Panda and Choudhury 1992). Total length of stems reached almost 750 m in mature plants of *C. polygonorum* Engelm. (Dean 1942).

The presence of two branching patterns of *Cuscuta* stems has been documented (Dawson 1984). In *C. campestris*, the main and secondary stems grow continuously and never twine around the host. Instead, tendril-like branches produced from buds located in the axils of the rudimentary leaf-scales, fix the parasite to the host. In *C. gronovii* the main stem twines around the host forming haustoria and no tendril-like axillary branches are generated.

The thickness of stems is variable within the same species, or even plant (Yuncker 1921), and it is an indicator of resource availability (Kelly 1994). Growing stems of different ages on the same plant interconnect between themselves through haustorial connections, a phenomenon known as self-parasitism (Dawson et al. 1994). As a result, the plant becomes a complex tri-dimensional network. Lyshede (1985) suggested that the transport distances within the same plant may be reduced in this way.

Embryological data (Johri 1987; Johri et al. 1992) — *Cuscuta* spp. pollen grains are usually 2-celled, but sometimes 3-celled. Pollen grains are spherical to ovoid, with 2 to 6 germination pores (Fig. 2B). Compound pollen grains were reported in *C. epithymum*. Placentation is basal. Ovules are two per locule, ascending, anatropous, unitegmic and tenuinucellate. Embryo-sac development is of the *Polygonum*- or *Allium* type, and both may be present in the same species. The endosperm is nuclear, and formation of walls centripetal. Embryogeny is unique among dicotyledons and results in a mature coiled embryo without a radicle and cotyledons, consisting mostly from the hypocotyl.

Mature seeds have a multi-layered seed coat consisting of an epidermis, usually with two palisade layers and 2–4 parenchimatous layers (Tiagi 1951; Lyshede 1984, 1992). A striking feature of the seed coat epidermis is that when seeds dry out, the outer cell walls cells invaginate, which cause the seed surface to become alveolate (Fig. 2 C–F) (Lyshede 1984; Knepper et al. 1990). Water uptake induces bulging of the invaginated epidermal walls, and epidermis cells become swollen, papillose (Lyshede 1984). The seed epidermis contains starch and pectic substances, the latter becoming mucilaginous as seeds absorb water (Grubert 1974; Lyshede 1984).

Growth of seedlings, contact with the host and induction of prehaustoria — The radicle-like organ emerges through the micropyle and assumes a clavate shape. Because the plumule remains enclosed in the seed, the shoot has a characteristic loop-shape when it emerges from the soil (Kuijt 1969; Dawson et al. 1994). The middle portion of the shoot continues to grow and soon the seedling straightens itself, discarding the empty seed coat. The young shoot begins to move in an ascendant and counterclockwise (dextral) direction (Kuijt 1969; Lyshede 1985; Dawson et al. 1994), describing irregular arc-shaped movements (Lyshede 1985). The apical loop of *C. gronovii* and *C. planiflora* Ten. seedlings did not open, and seedlings did not nutate in darkness (Kujawski and Truscott 1974; Orr et al. 1996b). Orr et al. (1996b) reported reversible changes from negative to positive gravitropism under cyclical treatments with red and far-red light, suggesting the involvement of phytochrome action during this phase.

Experiments have indicated that *Cuscuta* spp. seedlings have the capacity to selectively forage into plant communities. They can sense and orient themselves towards green canopies, and they can choose the most suitable host species or age (Fritsché et al. 1958; Lyshede 1985; Kelly 1990, 1992; Orr et al. 1996a; Koch et al. 2004). Compatible host species only 3 wk old were avoided by the searching shoots, which reoriented toward bigger plants (Fritsché et al. 1958; Lyshede 1985). *Cuscuta subinclusa* Dur. & Hilg. preferred healthy, green, fertilized and mature plant hosts over yellow, diseased or underdeveloped plants (Kelly 1990, 1992). This shows not only the capacity to detect nearness of other plants, but also an "intelligent choice and intention" as well (Trewavas 2003). Initially, this foraging behavior was explained as a chemotropism (Bünning and Kautt 1956) or hydrotropism reaction (Kuijt 1969). Now it is known that seedlings are phototropic toward low red/far-red ratios (Orr et al. 1996a), and that growth and coiling of *Cuscuta* spp. shoots are under phytochrome control. Seedlings moved toward unilateral white and blue light in darkness, or toward unilateral far-red light with a background of white light (Spisar 1910; Orr et al. 1996a). A negative phototropic reaction of seedlings was observed to unilateral red or far-red light in darkness (Orr et al. 1966a). If no host is present in the vicinity, seedlings will twine indiscriminately around any inanimate object (Dawson et al. 1994). In this way, there is a chance of using this support as a ramp toward a suitable host. Holm et al. (1997) noted that in field crops, *Cuscuta* spp. may use weeds as a primary host, and then move to cultivated plants. A shoot of *C. gronovii* can wind tightly up to three coils around the host within 5 h of contact

(Dean 1937). Twining can occur only around vertically oriented shapes (innate or alive) (Tsivion 1979; Dawson et al. 1994). The length of seedling shoots depends on the species, from 5–10 cm in *C. campestris* to 15–35 cm in *C. gronovii* (Parker and Riches 1993).

The mechanism of attachment and the development of haustoria have been studied in detail from a structural perspective (Kuijt and Toth 1976; Lee and Lee 1989; Dawson et al. 1994; Vaughn 2002, 2003). Haustoria develop on the inner (concave) side of the stem coils and their part that will remain external to the host is called prehaustorium ("upper haustorium"—Lee and Lee 1989; or "adhesive disk"—Dawson et al. 1994). The prehaustorium develops endogenously from a disk-like meristem located within the cortex, close to the vascular bundles (Dawson et al. 1994). Its epidermis cells dedifferentiate and become very rich in cytoplasm. Some of the epidermal cells elongate and form secretory trichome-like structures (Dawson et al. 1994; Vaughn 2002). The cell walls of these secretory trichomes are elastic and allow prehaustoria to follow closely, often through invagination, the shape of stem and micro-outgrowths of the host epidermis (e.g., hairs). Vaughn (2002) suggested that the considerable elasticity of trichome cell walls may be the result of osmiophilic particles, which form cell-wall-loosening complexes. In addition, trichomes secrete an electron-opaque cement consisting of pectins, which fills the host-parasite interface (Dawson et al. 1994; Vaughn 2002). Trichomes ensure the tight contact and adhesion of the parasite to the host but they were never observed to penetrate the tissues of the latter (Dawson et al. 1994).

The prehaustorium in *Cuscuta* spp. investigated here can reach about 1 mm long. Development of prehaustoria may occur even in the absence of a host (Tsivion 1978; Tada et al. 1996; Ihl and Wiese 2000), or in the presence of inert materials such as glass (Rath and Mohanty 1987; Tada et al. 1996), cotton strings (Tsivion 1978), filter paper (Fritché et al. 1958), sheets of plastic (Beliz 1986) or acrylic rods (Tada et al. 1996). However, twining around the host does not necessarily lead to initiation of prehaustoria (Furuhashi et al. 1995). The coiling action and the initiation of prehaustoria are suppressed under darkness, white fluorescent and red light conditions, and they are induced by far-red and/or blue light and tactile (mechanical, thigmotropic) stimuli (Zimmerman 1962; Lane and Kasperbauer 1965; Furuhashi et al. 1995, 1997; Tada et al. 1996). This would explain why seedlings of *C. campestris* that emerged under an established alfalfa crop had their attachment to host reduced by 90% (Dawson 1966). Blue light was found to be more effective in inducing coiling than far-red light (Furuhashi et al. 1995; Haidar et al. 1997). Treatments with mixtures of ultraviolet/far-red, blue/far-red, red/far-red light determined both the twining and prehaustoria initiation (Furuhashi 1995; Haidar et al. 1997). Blue light at photon fluxes lower than 1 $\mu mol\ m^{-2}\ s^{-1}$ promoted neither coiling nor initiation of prehaustoria (Haidar et al. 1997). The effect of far-red light was completely reversed by a red light treatment (Tada et al. 1996; Furuhashi et al. 1997; Haidar et al. 1997). The action spectrum for induction of prehaustoria had a pronounced peak near 740 nm and a small peak at 420 nm, while reversal of prehaustoria induction had major a peak at 660 nm and a minor peak at 380 nm (Furuhashi et al. 1997; Haidar et al. 1997).

It has been suggested that coiling and induction of prehaustoria are under the control of two classes of photoreceptors: phytochromes (photoreceptors of red/far-red light) and cryptochromes (photoreceptors of blue/ultraviolet light) (Haidar 2003). Chryptochromes interact synergistically with the Pr (red light absorbing) form of phytochrome, and antagonistically with Pfr form in mediating initiation and coiling of prehaustoria (Haidar 2003). Phytochrome B (Furuhashi et al. 1997) or phytochrome A (Haidar et al. 1998) may be involved. Tactile stimulation determined twining and prehaustoria initiation in blue and a mixture of blue/far-red light, but not in darkness or fluorescent white light (Tada et al. 1996; Haidar et al. 1997). Coiling and development of prehaustoria occurred in the presence of cytokinins or zeatin, whereas indole-3-acetic acid (IAA) and abscisic acid (ABA), or their combination, had an opposite effect (Tsivion 1978; Rajagopal et al. 1988; Haidar et al. 1998; Ramasubramanian et al. 1988). Zeatin had a synergistic effect with far-red light but not with red light (Haidar et al. 1998). Ethylene had no effect on coiling and development of prehaustoria development (Haidar et al. 1998). Mechanical stimulation induced haustoria development even in the absence the hormones (Ihl and Wiese 2000).

The molecular mechanisms that govern the development of prehaustoria require further research. Several putative parasitism-specific cDNAs were isolated (Borsics et al. 1999; Borsics and Lados 2001). Two genes from cytokinin-induced haustoria have been cloned and sequenced: a cDNA encoding a hybrid Pro-rich protein (HyPRP) (Subramaniam and Mahadevan 1994) and a cDNA coding for cytocrome b5 (Subramaniam et al. 1994). Tada et al. (2000) reported that the down regulation of a low-molecular-weight heat shock protein (CJHSP17) may be involved in the haustorium development.

Seedlings that do not attach themselves to a host during the autotrophic stage die thereafter. Survival periods reported for seedlings in the absence of a host vary from 8 d in *C. campestris* (Sitkin 1976) to 7 wk in *C. gronovii* (Spisar 1910). Taking into account that the root-like organ functions only a few days during the emergence (JianZhong and YangHan 1993), the survival of young *Cuscuta* spp. represents a remarkable adaptation. Seedlings are succulent and relatively resistant to desiccation, apparently because stomata develop only after plants reach the parasitic stage (Lyshede 1985).

Haustoria invasion and connection to the vascular system of the host — Mechanisms of connection to the host have been studied in great detail (Kuijt and Toth 1976; Lee and Lee 1989; Dawson et al. 1994; Vaughn 2002, 2003). After the successful contact and attachment of the parasite, a mass of tissue known as the "inner haustorium" penetrates and invades the host tissue. After 1 or 2 d, epidermal cells of the inner haustorium began to elongate and form the "searching hyphae." These unicellular formations advance toward the vascular bundles of the host. Within compatible hosts,

searching hyphae may extend 800 to 2000 μm before they contact phloem or xylem cells (Dawson et al. 1994; Vaughn 2003). The inter- and intracellular advance of hyphae through the host is both a mechanical and enzymatic process (Dawson et al. 1994). When intracellular, hyphae induce the host to synthesize a new cell-wall around the cells of the advancing hyphae. The result is a chimeric wall crossed by plasmodesmata, which belongs to both species. This chimeric wall is rich in pectins and has a different composition from the cell walls of both the host and the parasite (Vaughn 2003). Apparently, its role is to minimize the injury produced by invasion, since no typical wound responses (e.g., production of callose) have been observed (Vaughn 2003). Additionally, the inter-specific plasmodesmata, which were observed to be more frequent toward the tip of growing hyphae, may represent the channels of an unknown molecular communication between the host and the parasite (Vaughn 2003).

Searching hyphae connect both to the xylem and the phloem of the host, but some may end blindly in the parenchyma. The xylem connection is almost open because only a pit membrane separates the two systems. The phloem connection is more complex: searching hyphae develop terminal digitiform structures and become "absorbing hyphae". The finger-like protrusions of a single absorbing hyphae may become attached to several (phloem) sieve elements. At the host-parasite interface, the absorbing hyphae develop extensive wall-ingrowths, characteristic to transfer cells. In addition, their cytoplasm develops a smooth endoplasmic reticulum network (Dörr 1990; Dawson et al. 1994).

Total and partial incompatibility between host and parasite — Successful contact and initial penetration of haustoria does not necessarily imply a successful subsequent parasitizing process (Dawson et al. 1994; Christensen et al. 2003). *Cuscuta* spp. may develop poorly or not at all on certain host species, populations or even individuals. Different degrees of incompatibility arise when the host is capable to defend itself by preventing the haustoria either to reach vascular bundles, or to become functional. For example, layers of lignified or water-storage tissue, present outside the vascular cylinder of the host, may passively delay or prevent the advancement of searching hyphae (Dawson et al. 1994; Sahm et al. 1994). In addition, some host species are capable of actively defending themselves by developing novel barrier tissues, by deposition of newly formed wall material against advancing hyphae, or by producing phytoalexins or other inhibitors (Dawson et al. 1994; Sahm et al. 1995; Singh and Singh 1997; Dhopte 1998; Bringmann et al. 1999; Werner et al. 2001; Christensen et al. 2003).

(b) *Perennation—Cuscuta* spp. are known as annuals. However, some species when growing on perennial hosts were observed to induce formation of galls, in which parasitic tissue overwinters (e.g., *C. gronovii* and *C. epithymum*). New *Cuscuta* plants regenerate from these embedded parasitic tissues in the next spring (Dean 1937, 1954; Truscott 1958). The procambium and phloem of haustoria that remain in the host produce a "mass of callus-like tubercle parenchyma" from which news shoots will differentiate (Truscott 1958). This "tubercle parenchyma," and the subsequent steps in regeneration resemble the somatic embryogenesis in vitro from callus observed by Bakos et al. (2000) in *C. epithymum*. In such a case, the plants can be considered perennial. The phenomenon was observed as early as 1868 by Kuhn on *C. epithymum* parasitizing clover (*Trifolium* spp.) and alfalfa (*Medicago sativa*) in Germany (see also Dean 1937).

(c) *Physiological data*

Solute flux into Cuscuta *spp.*.— Assimilate transport in *Cuscuta* spp. has been reviewed by Dawson et al. (1994). In seedlings, $^{14}CO_2$-labeled assimilates and ^{32}P-isotope absorbed from soil were allocated and translocated only to the growing tips. In plants attached to the host, labeled-sucrose accumulated more in the terminal and axillary buds (Dawson et al. 1994). The haustoria create a biochemical continuum between the parasite and its host. Numerous experiments with labeled assimilates have shown an intensive transfer from the host to the parasite (Dawson et al. 1994; Jeschke et al. 1994; Jeschke and Hilpert 1997). Parasitizing plants of *Cuscuta* spp. act like a "supersink" of their host because they can overcome and redirect the normal solute flux toward other powerful sinks of the host (e.g., the fruits) (Dawson et al. 1994). This induces an increase of the photosynthetic rate in the host (Jeschke et al. 1994; Jeschke and Hilpert 1997). Although the parasite establishes both connections at phloem and xylem levels, *Cuscuta* spp. are "phloem feeders" since this route supplies the majority of nutrients (Fer 1981; Fer et al. 1987; Dawson et al. 1994; Hibberd and Jeschke 2001). In addition to the primary metabolic compounds (Dawson et al. 1994), xenobiotics (Haupt and Newmann 1996), secondary products such as alkaloids (Czygan et al. 1988; Bäumel et al. 1993, 1994) and cardenolides (Rothe et al. 1999) are also translocated via phloem from the host. The content of minerals in *Cuscuta* spp. plants and their hosts has been reviewed by Dawson et al. (1994). Heavy metals translocated, such as Hg, As, Pb, Cu, Cd and Cr, decreased the Hill reaction activity, protein content and dry mass at doses higher than 0.5 μg mL^{-1} (Jana and Bhattacharjee 1988). Herbicides are also readily translocated by the parasite (Bewick et al. 1991; Nir et al. 1996; Nadler-Hasar and Rubin 2003).

Although the transfers across haustoria are mostly unidirectional, from the host to the parasite, some biochemical messages may travel in the other direction as well. The ultrastructural interface between parasite and host (see Section 7a) suggests an active apoplastic transfer of solutes (Tsivion 1978; Wolswinkel and Ammerlaan 1983; Dawson et al. 1994; Jeschke et al. 1994). In addition, *Cuscuta* spp. are efficient vectors for viruses and mycoplasmas (see section 13b), requiring the presence of a symplastic continuum between host and parasite. Evidence of a functional symplastic route and the capacity for macromolecular exchange were provided by the transfer of green fluorescent protein from the host to the parasite (Haupt et al. 2001). Hibberd and Jeschke (2001) suggested that *Cuscuta* spp. may use both symplastic and apoplastic pathways for solutes and

macromolecular transfer, but the physiological mechanism for these processes is unknown.

Photosynthesis — *Cuscuta* spp. are considered holoparasites (Dawson et al. 1994). Jeschke et al. (1994), Jeschke and Hilpert (1997) reported that *C. reflexa* derived more than 99% of its carbon and 93% of its nitrogen from the host. However, prior to the contact with the host, seedlings of *Cuscuta* spp. are autotrophic (although requiring the resources from endosperm). Even during parasitizing stages some species possess a low photosynthetic capacity. *Cuscuta campestris* and *C. reflexa* grown in vitro were capable of flowering or even fruiting (Loo 1946; Baldev 1959; Malik and Singh 1980). Most of the *Cuscuta* spp. investigated [see the exceptions from van der Kooij et al. (2000)] possess small amounts of chlorophyll (Zimmerman 1962; Panda and Choudhury 1992; Dinelli et al. 1993; Dawson et al. 1994; Choudhury and Sahu 1999; van der Kooij et al. 2000; Sahu and Choudhury 2000). Both chlorophyll a and b are present in normal proportions, similar to those of autotrophic members of Convolvulaceae (Dinelli et al. 1993; Dawson et al. 1994; Choudhury and Sahu 1999; van der Kooij et al. 2000). The chlorophyll a:chlorophyll b ratio is higher in *Cuscuta* spp. plants grown under natural light than in plants kept under low irradiance conditions, suggesting that photodestruction of chlorophyll b occurs in the latter condition (Choudhury and Sahu 1999). The total chlorophyll content in *C. campestris* increased from germination and reached a maximum at flowering (Dinelli et al. 1993). Carotenoid pigments, such as α-, β-carotene and xanthophylls are also present in amounts that are comparable to those of autotrophic plants (MacLeod 1961a, b). Weinberg et al. (2003) studied the effect of herbicides that inhibit carotenoid biosynthesis in *C. campestris*. Because depletion of β-carotene was associated with the destruction of amyloplasts and the decline in starch content, it was suggested that carotenoids may play a role in maintaining the amyloplast membrane (Weinberg et al. 2003).

A low photosynthetic capacity was demonstrated in several *Cuscuta* spp. using chlorophyll fluorescence, light-driven electron transport and $^{14}CO_2$ (Panda and Choudhury 1992; Dawson et al. 1994; Hibberd et al. 1998; Choudhury and Sahu 1999; Sherman et al. 1999; van der Kooij et al. 2000). Different *Cuscuta* spp. exhibit a wide range of photosynthetic capacities, which suggest a gradual evolutionary reduction of the photosynthetic apparatus from hemi- to holoparasitism. Some species have intact plastids, but a low photosynthetic activity (e.g., *C. reflexa*). Some show alterations at the ultrastructural level of plastids (e.g., *C. campestris* and *C. gronovii*), others have modifications at the level of plastid transcription (e.g., *C. grandiflora* M. Bieb.), and finally, some have lost the *rbc*L gene (e.g., *C. odorata* Ruiz & Pav.) (Machado and Zetsche 1990; van der Kooij et al. 2000). The study of the sequence and promoter structure of the gene *rrn16* coding for the ribosomal 16S rRNA showed that in "green" species (e.g., *C. reflexa*) plastid transcription is initiated from a functional plastid-encoded RNA polymerase (PEP) promoter, which is missing in other species (e.g., *C. gronovii*) (Krause et al. 2003). The loss of the promoter was associated with the loss of two genes (*rpo A* and *rpoB*) that encode subunits of PEP (Krause et al. 2003).

When present (e.g., *C. reflexa*), the photosynthetic metabolism is highly localized in a layer of cells adjacent to the vascular bundles (topographically equivalent to the starch sheath present in many dicotyledons) (Hibberd et al. 1998). Since it is unlikely that external CO_2 can diffuse to this layer of cells, it was proposed that CO_2 for carbon assimilation is derived from internally respired CO_2 (Hibberd et al. 1998).

Nitrogen metabolism — Seedlings of *Cuscuta* spp. can absorb and presumably assimilate nitrogen from ammonium sulfate, potassium nitrate and ammonium nitrate (Srivastava and Chauhan 1977). However, when attached, *Cuscuta* spp. depend on the organic nitrogen that they translocate from the host (Jeschke et al. 1994; Jeschke and Hilpert 1997). Translocation of labeled amino acids and amides from the host to the parasite was recorded (Fer 1976; Wolswinkel et al. 1984). Nitrogen metabolism during parasitizing stage was studied in *C. campestris* and *C. reflexa* (MacLeod 1963; Srivastava and Dwivedi 2003). Under field conditions, ammonia is assimilated to glutamate only by glutamate dehydrogenase (GDH pathway), as evidenced by the low levels of GDH found. The study of callus cultures of *C. reflexa* revealed the presence of GDH, but also of the enzymes glutamine synthetase (GS) and glutamate oxoglutarate aminotransferase (GOGAT). The latter two enzymes realize the primary pathway for ammonia assimilation in autotrophic plants (Srivastava and Dwivedi 2003). Apparently, because of the ability to take up the reduced form of nitrogen from the host, *Cuscuta* spp. have lost the ability to assimilate inorganic forms of nitrogen (Lea and Steward 1978). It is not clear how much of this capacity is lost ontogenetically and phylogenetically. As in the case of the photosynthetic apparatus (see above), it is possible that different species may exhibit different levels of reduction in their capacity to metabolize nitrogen. The mineral nutrition of *Cuscuta* spp. has been reviewed by Dawson et al. (1994).

Transpiration of *Cuscuta* spp. is said to be reduced (Fer 1984) and is associated with a low density of stomata (e.g., 2 stomata mm^{-2} in *C. reflexa*), which differentiate after parasitic stage is reached (Lyshede 1985).

The fleshy mature stems of *Cuscuta* spp. function as storage organs. They accumulate starch, minerals and phytic acid (a reservoir of phosphate) (Dawson et al. 1994; Weinberg et al. 2003). In this way, the parasite may complete its life cycle, even if the host plant has died (Wolswinkel 1974; Singh et al. 1963; 1968).

(d) *Phenology* — Germination of *Cuscuta* spp. occurs in southern Canada from the mid-May to mid-June. Based on information collected from herbarium specimens, flowering of *C. campestris* begins around mid-July, and that of *C. gronovii*, *C. epilinum* and *C. epithymum* in August. Flowering and fruiting extend throughout the rest of the growing season, due to the indeterminate growth pattern.

(e) *Mycorrhiza* — *Cuscuta pentagona* (*C. campestris*?) parasitizing vesicular arbuscular (VAM)-symbiotic *Abutilon*

theophrasti Medic. had a growth rate 3.4 times greater than when the host was nonmycorrhizal (Sanders et al. 1993). Khalid and Iqbal (1996) reported that arbuscular mycorrhizae (AM)-inoculated seeds of *C. reflexa* produced a network of hyphae, arbuscules and vesicles on the underground parts of seedlings within only 5 d after sowing. Spores of two or three *Glomus* spp. were observed. AM seedlings had a significant increase in biomass and longevity compared to noninoculated seedlings. These results suggests that mycorrhiza may allow *Cuscuta* spp. seedlings to survive longer before establishing the haustorial connection with host. Also, the increased fitness resulting from the mycorrhizal relationship may enhance the chances of successful contact with the host.

8. Reproduction

(a) *Floral biology* — Flowers and inflorescences have been described in Section 2b. A unique feature of *Cuscuta* flowers is the presence of the infrastaminal scales (also called "hypostaminal scales" or "corolla appendages"). The origin of these formations has been diversely interpreted: as dilatations of lowermost part of staminal filaments, as staminodes or even as duplications of petals (Yuncker 1921; Musselman 1986; Gandhi et al. 1987). More-recent studies showed that infrastaminal scales are initiated at the base of stamens after the other floral organs had been initiated (Kuoh and Liao 1993; Prenner et al. 2002). Knuth (1899, cited in Yuncker 1921) suggested infrastaminal scales may have a protective role. In this respect, Musselman (1986) observed that the scales cover the ovary in young flowers of *C. campestris* and *C. gronovii* but as the flowers grow older, scales separate from the ovary. Scales may have a secretory function (Knepper unpublished, quoted by Musselman 1986) and that they may act as floral nectaries in pollinator attraction (Tiagi 1966; Kuijt 1969). Prenner et al. (2002) observed in *C. reflexa* that scales hold the nectar secreted by stomata present the base of ovary, and regarded them as secondary nectar receptacles.

Species with small flowers are apparently self-pollinating (Verdcourt 1948; Beliz 1986; Prather and Tyrl 1993; Dawson et al. 1994) and autogamous (Beliz 1986; Musselman 1986). The low pollen/ovule ratio found by Beliz (1986) in *C. pentagona* (*C. campestris* ?)(65) supports this idea (see Cruden 1977). Holm et al. (1997) reported that *C. epithymum* is "normally cross-pollinated but in the absence of insects may be self-pollinated". In Sierra Nevada, Spain, the pollinators of *C. epithymum* were the same insects (mostly *Proformica longiseta* Collingwood, Formicidae) that pollinated the flowers of the host, *Hormathophylla spinosa* (L.) Küpfer (Gómez 1994).

Most of the flowers open in the morning, and a few during the day (Beliz 1986; Prather and Tyrl 1993). Anthers dehisce longitudinally and inwardly. Pollen is transferred through direct contact between anthers and stigmas (Prather and Tyrl 1993; personal observation). Cleistogamous flowers (Yuncker 1921; Verdcourt 1948), or mixed cleistogamous and opening flowers in the same cyme, were observed in some species (e.g., in *C. pentagona*, Beliz 1986), but not in others (*C. attenuata*, Prather and Tyrl 1993).

Fratianne (1965) found that *C. campestris* flowered only on flowering hosts, synchronous with the host photoperiodical cycles. Vegetative plants of *C. campestris* did not flower when they were attached to non-flowering plants of soybeans grown under noninductive photoperiods (long-day conditions). A similar synchronicity was also observed between *C. gronovii* and several, but not all the hosts investigated (Denffer 1948). In the latter case, although *C. gronovii* flowered when parasitizing some vegetative hosts (*Phytolacca americana* L., *Oenothera biennis* L. and *Rudbeckia purpurea* L.), the process was considerably delayed (von Denffer 1948). Fratianne (1965) suggested that flowering synchronicity may be determined by an "inhibitor flowering-hormone" produced by the host and traslocated into the parasite. Nevertheless, the existence of this "hormone" has not been proved (Jacob 1966) and the flowering synchronicity was not confirmed in other *Cuscuta* spp. (e.g., *C. salina*, Beliz 1986). *Cuscuta reflexa* grown "in vitro", with no host, flowered in short-day conditions (Baldev 1959). Artificial host defoliation, or its weakening as a result of parasitism, induced flowering of *Cuscuta* spp. plants (von Denffer 1948; Fratianne 1965; Lyshede 1985). Anthesis lasts 2–7 d, after which corolla withers (Beliz 1986; Prather and Tyrl 1993).

(b) *Seed production and dispersal* — A single plant of *C. campestris* can produce 16 000 seeds (Stevens 1932). The weight of 1000 seeds is 0.775–0.87 g in *C. campestris* (Stevens 1932; Holm et al. 1997) and 0.3 g in *C. epithymum* (Kothekar 1970). The principal means of dispersal of *Cuscuta* weeds world-wide has been through contaminated seeds of forage legumes (alfalfa, clover and lespedeza—*Lespedeza cuneata* (Dumont) G. Don (Dawson et al. 1994). Other means of dispersal are less known. Kuijt (1969) remarked that seed dispersal in this genus is "unspecialized". Lyshede (1984) suggested that wind may play a significant role in dispersal because of the pits present on the seed coat when seeds are dry (see Section 7a). However, *Cuscuta* seeds do not possess "classical" adaptations for wind dispersal, and the alveolate/papillate seed coat seems more an adaptation related to the germination process. Kuijt (1969) mentioned that seeds remain viable while they pass through the digestive system of sheep. When wetted, seed coat becomes gelatinous and adheres easily to soil particles. Seeds may thus be carried by farm machinery or by birds and animals. Water could play a role in the dispersal of other species (Verdcourt 1948). For example, the seeds of *C. gronovii* and *C. attenuata* float, and these species frequently occur near water. Therefore, although there is no direct evidence of it, seeds may be dispersed in this way as well (Prather and Tyrl 1993).

(c) *Seed banks, seed viability and germination* — Seeds of *Cuscuta* may survive at least 10 yr in the field (Menke 1954) and up to 50 yr or more in dry storage depending on the species (Gaertner 1950; Dawson et al. 1984). For example, in dry storage, *C. campestris* may survive 10 to 20 yr, *C. gronovii* up to 30 yr, and *C. pentagona* up to 51 yr (Gaertner 1950). Seeds of *C. campestris* exhibited 50% germination

after being submerged in water (in a canal) for 5 yr (Comes et al. 1978). Seed longevity increased with depth of burial, with seeds buried at 50 cm surviving longer than those buried at 10 cm (Gruzdev and Prishchepo 1984). There is no information on the seed bank of *Cuscuta* spp. in agricultural fields but these seed banks are likely quite persistent. *Cuscuta gronovii* growing in freshwater marshes from Iowa and Michigan, comprised up to 79% of the seed bank (van der Valk and Davis 1976; Leck and Simpson 1995). Inputs of *C. gronovii* to the seed bank showed year-to-year fluctuations (e.g., from 4.5% in one year to 50% in another year). Such fluctuations were correlated with fluctuations in the frequency of its hosts (Leck and Simpson 1995).

Freshly harvested seeds of *C. campestris* are not dormant and may germinate when still in the capsule (Gaertner 1950). However, after a few days, 77 to 95% of seeds become "hard". Their seed coat dries, becomes hard and impermeable, with the epidermal cells invaginated (see Section 7a), and seeds become dormant (Gaertner 1950; Tingey and Allred 1961; Dawson 1965; Hutchinson and Ashton 1980; Lyshede 1984; Prather and Tyrl 1993). The proportion of "hard" seeds in *C. campestris* is variable (Parker and Riches 1993), and may reach 95% (Hutchinson and Ashton 1980). Dormancy in *C. campestris* was reportedly associated with one of the two outer palisade cell layers of the seed coat (Hutchinson and Ashton 1980; Lyshede 1984). Dormancy was broken when *C. campestris* seeds overwintered buried at various depths in the field, or when they were stored outdoors at 3 to 8°C or at –3 to 0°C (Hutchinson and Ashton 1980). This suggests that seeds of *Cuscuta* spp. from temperate regions undergo a cyclical dormancy/non-dormancy pattern in the soil similarly to other plants (Baskin and Baskin 1998). Breaking down dormancy requires mechanical or chemical scarification (Gaertner 1950; Tingey and Allred 1961; Hutchinson and Ashton 1979; Lyshede 1984). Treatments of *C. campestris* seeds with sulfuric acid for 30–80 min, or the abrasion between layers of fine sandpaper resulted in over 75% germination (Gaertner 1950; Ashton and Santana 1976; Kroschel 2001). The optimum temperature for the germination of *C. campestris* is 30–33°C, the maximum is 36–39°C, and the minimum is 10–16°C (Stojanovic and Mijatovic 1973; Allred and Tingey 1964; Hutchinson and Ashton 1980; Lados 1999; Nojavan and Montakhab 2001).

Optimum germination of *C. epithymum* is at 26°C (Lados 1999). Germination of *C. campestris* in the field occurred after the temperature reached 10°C in the soil (Allred and Tingey 1964), or after the 5-d mean temperature reached 18°C in the air (Hutchinson and Ashton 1980). The relatively high temperature requirements for germination ensure the emergence of the parasite when potential hosts are already established. Seeds germinate both in dark and light and are stimulated by ammonium sulfate, potassium nitrate and ammonium nitrate (Srivastava and Chauhan 1977). *Cuscuta epithymum* germinated better at lower pH, whereas pH had no particular effect on *C. campestris* seeds (Lados 1999). The seed coat of germinating seeds absorbs water and becomes mucilaginous, with the epidermal cells swollen (Lyshede 1985).

Most seedlings of *C. campestris* emerge from the top 3 cm of soil, with none emerging below 6.5 cm (Allred and Tingey 1964; Hutchinson and Ashton 1980). Seeds buried on the surface emerged in 3 d, while those at 4–5 cm emerged in 6 d (Stojanovic and Mijatovic 1973). Better emergence of *C. campestris* in the field was obtained when measures to prevent soil crust formation were taken (Hutchinson and Ashton 1980). Emergence of *C. epithymum* in the field was observed 2 wk after the soil temperature reached 10°C (Holm et al. 1997). Using low-temperature thresholds (LTT) of 0 and 3.3°C, the emergence of *C. gronovii* in Wisconsin was predicted after 161 and 118 growing degree days, respectively (Bewick et al. 1988a). Furthermore, it was predicted that 0.1% seedlings may emerge in any season at values between 150 and 170 GDD/0°C or 114 and 122 GDD/3.3°C (Bewick et al. 1988a). The proportion of seedlings that emerge each year is variable. Allred and Tingey (1964) in Utah found 64% emergence of *C. campestris* in the first year, and 3% in the second year. Dawson (1965) reported that only 7% of the seeds emerged over a period of 2 yr in a greenhouse experiment. Relatively similar results were obtained in California by Hutchinson and Ashton (1980): only 10% of the *C. campestris* seeds sown in the field emerged over a period of 5 yr. Most of the seedlings (3.2–5.7%) emerged in the first year. Emergence percentage declined over time and no seedling emerged in the fifth year (Hutchinson and Ashton 1980).

(d) *Vegetative reproduction* — Fragments of stem can attach themselves and regenerate whole plants (Truscott 1958). Breakage can be the result of the host's growth or it can be produced by animals, humans or farm machinery. The study of *C. corymbosa* Ruiz & Pavón in the field, showed that natural breakage levels varied between 2 and 66%, and that fragmentation did not impair growth and biomass accumulation of individual plants (Kelly et al. 2001). Another potential way of vegetative spreading of some *Cuscuta* spp. is through the haustorial tissue surviving in perennial host over the winter (see Section 7b).

9. Hybrids

Although no interspecific hybrids have been described and experimental attempts to produce hybrids have failed (Prather and Tyrl 1993), the possibility of hybridization cannot be excluded (Beliz 1986).

10. Population Dynamics

Cuscuta spp. from temperate regions have probably only one generation per year. They can rapidly colonize (see Section 8b) disturbed areas, where they grow in patches. Population dynamics of *Cuscuta* spp. depend on a series of factors: the population dynamics of their hosts; the capacity of potential hosts to defend themselves, and the environmental conditions. Leck and Simpson (1995), studying the dynamics of vegetation in a fresh water marsh, found that in general *C. gronovii* was successful in the years when its most important host, *Impatiens capensis* Meerb., was successful as well. However, in some years successful emergence of the parasite was followed by poor establishment without apparent causes (Leck and Simpson 1995). In some cases, the failure to establish of

Cuscuta spp. is the result of the total or partial incompatibility between host and parasite (see also Sections 5c, 7a). Some weed species were reported to have an allelopathic action against *Cuscuta* spp. Extracts of *Cynodon dactylon* (L.) Pers. and *Chenopodium murale* L. controlled 83–96% of the *C. campestris* infesting alfalfa (Habib and Rahman 1988). About 10 species of *Chenopodium* were observed to inhibit in various degrees the attachment and subsequent growth of *Cuscuta* spp. (Dawson et al. 1994). Symptoms exhibited by *C. campestris* after the attachment to *Chenopodium album* L. were similar to those resulted after treatments with glyphosate (Dawson et al. 1994).

11. Response to Herbicides and Other Chemicals

Chemical control methods in various crops have been reviewed in detail by Parker and Riches (1993) and Dawson et al. (1994). Diuron inhibits photosynthesis in *Cuscuta* spp. but this does not affect plant growth and development (Lane et al. 1965; Dawson 1967). Treatments with herbicides that inhibit carotenoid biosynthesis had a variable efficacy on *C. campestris* (Weinberg et al. 2003). Flurochloridone at 625 g ha^{-1} caused a rapid stem bleaching, but plants continued to grow and eventually they recovered fully. Sulcotrione and mesotrione at 250 g ha^{-1} also caused stem bleaching, but plants did not recover (Weinberg et al. 2003). The three herbicides caused an accumulation of phytoene and depletion of β-carotene, which were associated with the destruction of plastids and depletion of starch content in *C. campestris* (Weinberg et al. 2003).

No herbicide-resistant biotypes have been reported in North America for any of the four species (Heap 2002). *Cuscuta campestris* developed resistance to ALS inhibitors (chlorsulfuron, and sulfometuron-methyl) in Israel in 1994 (Rubin 1995). Resistant plants occurred in a few sites while parasitizing ALS inhibitor resistant *Amaranthus blitoides* S. Wats. plants (Rubin 1995). *Cuscuta campestris* is capable to tolerate and recover from high rates of glyphosate and sulfometuron (amino acid bio-synthesis inhibitor herbicides — AABI) (Nadler-Hassar and Rubin 2003). The species was reported to be more resistant to AABI herbicides than the transgenic resistant host crop plants, glyphosate-resistant sugarbeet and cotton, and sulfometuron-resistant tomato.

12. Response to Other Human Manipulations

Crop rotation with forage grasses or cereal grains is one of the most efficient cultural ways to control future infestations because *Cuscuta* spp. do not attack plants from Poaceae. Rotations following infestation with *C. epilinum* should avoid flax or linseed. Crops such as beans, squash, cucumber, cotton and tomato are more or less resistant to *C. campestris*, and they can be used in rotations (Parker and Riches 1993; Dawson et al. 1994). However, there is considerable variation in susceptibility to *C. campestris*. For example, some varieties of tomatoes tend to be resistant to *C. campestris*, but others are susceptible (Goldwasser et al. 2001). This would explain contradictory reports found in the literature (Dawson et al. 1994).

Planting crops after the germination flush of *Cuscuta* spp. in the spring, or if possible in autumn, achieves good results (Dawson 1971). Seedlings of *Cuscuta* spp. cannot twine and attach themselves if the crop is already well established (see Section 7a). Hand-pulling the parasite together with its host before seeds are set, and burning the plant material are effective means in controlling isolated infestations (Parker and Riches 1993). Shallow harrowing/cultivation applied during the seedling stage of the parasite can be effective in established alfalfa or in row crops such as sugarbeet, carrots and onions (Dawson et al. 1984; Dawson 1987; Dawson et al. 1994). Close mowing of alfalfa after hay harvest at 2–3 cm proved to be more effective in removing infested stubble than mowing at 10 cm (Dawson 1987). Flail-mowing and burning with a hand-held propane gas weed burner were equally effective in controlling *C. indecora* infesting alfalfa crops in California, but the latter was more expensive (Cudney et al. 1992). Fire has been commonly used in the United States to control *Cuscuta* spp. in alfalfa but this method reduces the hay yield (Parker and Riches 1993). Dry heat treatments of 15 min at 100°C were used to decontaminate niger seeds [*Guizotia abyssinica* (Lf.) Cass.] from the seeds of *C. campestris* and *C. indecora* (Strasser 1988). Mechanical methods for seed decontamination have been reviewed by Dawson et al. (1994).

Sandler et al. (1997) reported that the application of a 2.5-cm layer of sand reduced the seedling emergence of *C. gronovii* in cranberry bogs, but it did not affect the survival of the parasite. Controlled floods (24–48h) in cranberry bogs reduced the infestation of *C. gronovii* (Sandler and Mason 2004). Solarization of scarified seeds of *C. campestris* with transparent polyethylene during 10 d, resulted in a reduction of the percent of total seed germination (PTSG) by 95% (Haidar et al. 1999b). Unscarified seeds required 6 wk to obtain a reduction of PTSG by 69% (Haidar et al. 1999b). Stojsin et al. (1991) reported that the intensity of *C. campestris* damage in a sugarbeet crop depended on the level of mineral fertilization, and the highest attack occurred in non-fertilized plots.

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) *Mammals* — Gómez (1994), in Sierra Nevada, Spain reported that plants of *Hormatophylla spinosa* infested by *C. epithymum* were avoided by the Spanish ibex (*Capra pyrenaica* Schinz.), the main herbivore of the former species. If *Cuscuta* spp. are avoided by herbivores, possibly because of their color, an advantage would be conferred to their hosts, thus influencing the structure of plant communities.

(b) *Birds and/other vertebrates* — No data.

(c) *Insects* — Only a few insects attack *Cuscuta* spp., which is reflected in the scarcity of reports found in the literature. The most important insects associated with *Cuscuta* spp. are those from the genus *Smicronyx*, subgenus *Smicronyx* (Order: Curculionidae). Eleven species of *Smicronyx*, attack *Cuscuta* spp. in North America: *S. apionides* Casey, *S. atratus* Motschulsky, *S. congestus* Casey, *S. cuscutiflorae* Pierce, *S. defricans* Casey, *S. interruptus* Blatchley, *S. pacificus* Anderson, *S. posticus* Dietz, *S. quadrifer* Casey, *S.*

sculpticollis Casey, *S. tychoides* LeConte (Pierce 1939; Anderson 1962, 1970; O'Brien and Anderson 1996). Among these, only three species are known from Canada: *S. congestus* (Manitoba), *S. sculpticollis* (Ontario and New Brunswick) and *S. tychoides* (Ontario and New Brunswick) (O'Brien and Anderson 1996). Some species (e.g., *S. tychoides* and *S. sculpticollis* produce galls on the stems of *Cuscuta* spp. (Anderson 1962), while others (e.g., *S. cuscutiflorae* and *S. defricans*) lay their eggs in the ovaries, and larvae feed on the seeds producing probably considerable damage (Pierce 1939). Other insects found on *Cuscuta* spp. in North America, e.g., *Tanaops* spp. (Coleoptera: Melyridae), *Trichochrous* (Coleoptera: Melyridae) and *Bruchus* spp. (Coleoptera: Bruchidae), were considered flower visitors and pollen feeders (Pierce 1939).

Biological control with insects has been studied mostly in Europe and Asia (Parker and Riches 1993). Some of the 30 species of *Smicronyx* that infest various *Cuscuta* spp. have been reported as potential biological control agents (Parker and Riches 1993), but no control methods have been developed so far. Most commonly, adults of *Smicronyx* spp. lay their eggs in the stems of *Cuscuta* spp.; the larvae feed inside and produce galls. In Iran, a second generation was observed in *S. robustus* Faust (Shimi et al. 1995). The adults lay their eggs in the capsules, and the larvae feed on the ovules and seeds producing more damage than the first generation (Shimi et al. 1995).

(d) *Other invertebtates — Cuscuta* spp. may be attacked by nematodes only during the short seedling phase. However, studies have showed that *Cuscuta* spp. extract is toxic to nematodes (Mojumder and Goswami 1987; Robinson et al. 1990; Haidar et al. 1999a).

Diseases

(a) *Fungi — Cuscuta pentagona* and *C. epithymum* are hosts of *Colletotrichum destructivum* O'gara in Oregon (Leach 1958; Shaw 1973). In Wisconsin, *C. gronovii* is a host of *Phomopsis cuscutae* H. C. Greene (Greene 1964), *Fusarium tricinctum* (Corda) Saccardo and an *Alternaria* spp. (Bewick et al. 1986), and *Cuscuta* spp. of *Phoma* spp. (Greene 1953). *Alternaria destruens* Simmons was recently described from *C. gronovii* growing in Indiana (Simmons 1998).

Spores of *Fusarium tricinctum* and an *Alternaria* spp. isolated from *C. gronovii* in Wisconsin and applied at 380 L ha^{-1} (5×105 spores mL^{-1}) controlled this species up to 92% (Bewick et al. 1986). Carrots, cranberries, celery, potatoes and alfalfa were tolerant to both fungi species (Bewick et al. 1986). However, these promising preliminary studies have not been applied into practice. A strain of *Colleotrichum destructivum* was identified from *Cuscuta* spp. in Oregon and it was proposed as a potential biological control agent (Leach 1958), but no further research has been undertaken. A commercial product, Lubao No. 1 based on *Colletotrichum gloeosporioides* f. sp. *cuscutae* has been developed in China since 1963 to control *C. chinensis* and *C. australis* in soybeans (Zhang 1985; Wan and Wang 1991; Julien 1992). A new strain, Lubao No. 1 S22, was re-isolated to overcome the loss of virulence of the previous strain. The product has been extensively used in China and greater than 85% control was reported (Gao and Gan 1992, 1993). The fungus produces pathogenic exotoxins that cause lesions on *Cuscuta* stems (Hui and ShiBin 2002). The product was tested in Arkansas on *C. campestris* growing on a wide range of hosts (Cartwright and Templeton 1989). Except for one population from California, which was killed by the fungus, *C. campestris* was only partially controlled by the mycoherbicide, and the authors concluded that the practical potential of the mycoherbicide in the United States was relatively low under the tested conditions (Cartwright and Templeton 1989). Better results were obtained in Israel, where *Cuscuta* spp. from 35 cultivars of 19 crop species were completely destroyed by the fungus (Nof et al. unpublished, quoted by Watson et al. 2000). Other preliminary tested biocontrol agents are *Fusarium solani* (Martius) Saccardo, *F. semitectum* Berk. & Ravenel, *Alternaria tenuis* Nees and *Pestalotiopsis guepinii* (Desm.) Stey. (their pathogenity decreased in this order) isolated from *C. reflexa* in China (Guo FengGen et al. 1998; Guo FengGen and Li YangHan 2000), and *Alternaria cuscuticidae* investigated in the former USSR (Volkov 1989).

(b) *Bacteria*—In Armenia, trichothecin, a metabolite produced by *Trichothecium roseum* (Pers.:Fr.) Link inhibited the germination of *C. monogyna*, but it was ineffective against 6- to 7-d-old seedlings (Oganyan 1976).

(c) *Mycoplasma-like organisms (MLOs) — Cuscuta* spp. are a well known vector for mycoplasmas and viruses. The transfer occurs naturally when a *Cuscuta* spp. plant infests two or more plants (same or different species) and the mechanism has been extensively used for experimentation purposes (Heintz 1989; Carraro et al. 1991; Credi and Santucci 1992; Valencia et al. 1993; Maixner et al. 1994; Dawson et al. 1994; Loi et al. 1995; Marcone et al. 1995. 1997, 1999; Kamiska and Korbin 1999; Kamiska et al. 2001a, b; Scott and Zimmerman 2001). *Cuscuta* spp. may transfer macromolecular constituents to and from the host.

(d) *Viruses — Cuscuta* spp. are not mentioned as hosts for viruses in any major virus databases (Zitter 2002; Brunt et al. 2003). However, *Cuscuta* spp. are well known artificial vectors for numerous viruses (Bennet 1944; Schmelzer 1958; Hosford 1967; Roos and Aldrich 1988; Eppler 1992; Welliver and Halbrendt 1992; Bellardi and Bertaccini 1993; Kumar and Mohan 1994; Subandiyah 1994; Pozzer et al. 1995; Jordá et al. 2001).

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