Rev. Weed Sci. 1994. 6:77–101

THE BIOLOGY OF CANADA THISTLE (*CIRSIUM ARVENSE*)[1]

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INTRODUCTION

This review updates earlier brief reviews by Moore (91) and Holm et al. (65) and includes important new or recent information on the biology of Canada thistle [*Cirsium arvense* (L.) Scop. #[1] CIRAR]. Other reviews are less complete or noncritical in nature (23, 60, 62, 85). All these earlier reviews emphasized different aspects of Canada thistle biology than the present updated review which includes tabular information needed to model Canada thistle population biology. While the current review emphasizes literature published between 1975 and 1991, older literature on Canada thistle biology is extensively cited to correct omissions in earlier reviews. This review deals chiefly with scientific literature written in English from sources found in major North American universities or that can be obtained by interlibrary loan, and excludes abstracts and theses.

Some aspects of Canada thistle biology and distribution are not reviewed because the older literature is fairly complete and does not require updating now. For example, keys can be found in Moore (91) and Donald (37) for distinguishing four commonly recognized varieties of Canada thistle. Variability in growth characteristics of different ecotypes also was reviewed by Donald (37). Canada thistle distribution was adequately reviewed by Moore (91) and Holm et al. (65). They reviewed the introduction, spread, and distribution of Canada thistle in North America and the world, respectively, including information gleaned from herbarium samples. Recent ground surveys of Canada thistle in commercial farmers' fields in North America were summarized by Donald (37). Likewise, the impact of Canada thistle on crop production and its control are not covered in this review. The economic impact of Canada thistle on crop production and the yield loss assessment due to Canada thistle in various crops also have been reviewed (37, 91). Donald (37) summarized the management of Canada thistle using nonchemical methods and herbicides in various crops. Only more recent or previously unreviewed information on Canada thistle biology is included in this update, even though some literature was partially cited in earlier reviews. A conscientious attempt has been made in this review not to rehash previously reviewed information although previously reviewed references are cited.

Information on Canada thistle biology is presented in this review in two subsections based on research conducted from two different perspectives or "paradigms." In the first section, the biology of Canada thistle is reviewed from the older natural history or physiological ecology perspective, whereas the second section considers information on Canada thistle population biology. Population biology deals with changes in plant numbers for various life cycle stages of Canada thistle and the ecological reasons for those changes.

BIOLOGY IN RELATION TO PHYSIOLOGICAL ECOLOGY

Plant Description. *Vegetative morphology and anatomy*. Moore's (91) description of Canada thistle morphology and root development is complete. Line drawings are included in reviews by Holm et al. (65) and Moore (91).

Canada thistle is a perennial in the Compositae family with an extensive, spreading root system (1, 2, 56, 62, 72, 108). Adventitious root buds arise from its roots to form new adventitious shoots (52, 53, 54, 56) (Figure 1). This is the major method of vegetative propagation of Canada thistle after seedling establishment.

The terminology used to describe the root system of Canada thistle must be defined because confusing multiple terms have been used in the literature (72). Lawrence (79) defined a rhizome as "a creeping stem, not a root, growing beneath the surface, consisting of a series of nodes and internodes, with roots commonly produced from the nodes and producing buds in the leaf axils." Rhizomes are sometimes called rootstocks (72). Canada thistle does not form rhizomes[2] (53, 91), despite this assertion in some literature (6, 65, 112). Canada thistle also does not form stolons, which are similar to rhizomes, but form above ground and grow parallel to the soil surface.

Thickened, propagative Canada thistle roots with adventitious root buds grow horizontally and vertically. These thickened roots are not like the thinner, fibrous lateral roots found on most annuals (46). This distinction could be made by using classes based on root diameter (118). An adventitious root bud is a "shoot-forming bud originating on a root" which is defined as "a bud arising outside of normal morphoge-

[1]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 309 W. Clark St., Champaign, IL 61820.

[2]W. W. Donald, 1992, personal observation.

Figure 1. Electron micrographs of an adventitious root bud of Canada thistle emerging through the root surface (top and middle) and an emerged adventitious root bud of Canada thistle on the root surface (bottom). Note the lateral root associated with the adventitious root bud (bottom). The bars correspond to 1 mm in all micrographs (micrographs prepared by and used with the approval of Dr. Steven Carlson, 1991.).

netic sequence, and lacking connection with the shoot or root poles. (It) may give rise to an adventitious shoot." (118). Root buds form adventitiously on Canada thistle roots (52, 53, 54).

The terminology for adventitious shoots of Canada thistle arising after adventitious root buds emerge through the soil surface is quite confusing and includes "daughter shoot", "secondary shoot", "regrowth shoot", "root shoot", "rosette", "root sucker", or "root sprout." The term "root shoot" should be abandoned because it is contradictory, ambiguous, and confusing. The term "adventitious shoot" will be used in this review for shoots arising above ground from adventitious root buds.

Canada thistle shoots can arise from lateral buds on the underground portion of the vertical stem of parent shoots following mowing or when stem segments are buried (83). Such shoots correspond to lateral branches when they arise above ground and are "nonadventitious" because they form at predetermined sites at shoot nodes. The proportion of emerged shoots arising from adventitious root buds or arising nonadventitiously from nodes on buried stems in the field has not been reported. Adventitious shoots probably far outnumber nonadventitious shoots arising from buried stems except, perhaps, following mowing of Canada thistle on undisturbed soil. The relative contribution of nonadventitious and adventitious shoots to vegetative propagation of Canada thistle requires further study, especially following different management strategies, such as mowing.

Unelongated adventitious shoots have sometimes been called "rosettes" which the American Heritage Dictionary defines as "a circular cluster of leaves or other plant parts." However, the stem of adventitious shoots of Canada thistle can emerge and elongate without having a rosette growth habit. In the author's experience, Canada thistle emerging in fall tends to form rosettes whose stems do not elongate prior to killing frosts, whereas shoots that emerge in spring tend to elongate without forming extensive rosettes.

Two methods are commonly used to identify adventitious root buds: 1) direct observation of emerged adventitious root buds, and 2) lactic acid clearing of roots for revealing unemerged adventitious root buds (86, 88). Plant anatomists commonly use concentrated lactic acid to dissolve soft or immature plant tissue to make plant structures translucent, except those that are highly dense or lignified. In the latter method roots are incubated in 80% lactic acid at 60 C for 3 to 6 d in order to clear them for adventitious root bud counts. Lactic acid clearing has two problems: 1) Identification of adventitious root buds is subjective; and 2) it does not adequately clear thickened, darkened, partially decayed, field-grown roots although it clears healthy white roots of greenhouse-grown plants well.

Hamdoun (53) recognized four types of underground structures produced by Canada thistle: 1) long thick horizontal roots, 2) long thick vertical roots, 3) short fine shoots (adventitious shoots), and 4) vertical underground stems. Horizontal and vertical thickened roots from greenhouse- and field-grown plants were similar in anatomical structure. Exarch xylem was prominent with diarch structure (two protoxylem poles), although a four-pole structure was observed in seedlings and mature plants.

Lateral roots develop centripetally on the root (toward the root apex) and arise from the pericycle over protoxylem poles (53). Metaphloem and metaxylem develop about 30 cm from the root tip. Secondary xylem and phloem develop as fan-shaped masses in cross section, separated by rays of parenchyma. Rogers (108) published line drawings of mature root cross sections. The root cortex had 30% intercellular space, and cortical cells became enlarged toward the root surface (53). The root epidermis and cortex persist for the life of the root (94), but cork development is incomplete in older roots. The root cortex consists of 20 or more layers in thickened roots (94) and is not shed as a result of the lateral root growth (53). It is unknown whether these cortical layers correspond to years of growth, like rings on a tree.

Adventitious root buds and roots arise over protoxylem poles in the root pericycle (53) in association with lateral roots (88) (Figure 1). The first leaves of adventitious shoots persist as scale leaves. Horizontal roots produce more adventitious root buds than do vertical roots in the field (85). Once adventitious root buds reach the soil surface, additional lateral roots form near the soil surface aside from those that had formed near where the adventitious root buds emerged through the root surface.

Probably the chief limitation of most anatomical and morphological research on Canada thistle is that it has not been conducted on plants that have grown for several years in the field. Young, greenhouse-grown plants have been studied instead. Anatomists have not referred to the varieties of Canada thistle that they studied. In addition, the impact of site-specific soil type or horizonation on the anatomy, morphology, and distribution of Canada thistle roots require more study. In the author's experience, thickened propagative Canada thistle roots commonly grow along ped faces in structured subsoils. Stress conditions, such as drought or flooding, may impact Canada thistle root structure and development in relation to soil structure, but anatomical or morphological development under these conditions has not been studied.

Sexual reproductive morphology. Information on floret and fruit dimensions and weight has been summarized (71, 81) and line drawings of florets can be found in Hodgson (60). The sexual reproductive system of Canada thistle was reviewed by Kay (71).

Moore (91) stated that Canada thistle was classified by plant taxonomists as dioecious (i.e. separate male and female plants exclusively produce male and female flowers, respectively). However, Hodgson (60) observed that male plants of Canada thistle occasionally produce achenes (termed "seed" throughout this review), making the species "imperfectly dioecious." Lloyd and Mayall (81) and Delannay (29, 30) verified Hodgson's (60) observations but classified the species as "near-dioecious" or "subdioecious." Seed produced by male plants were smaller and percent germination was less than for seed formed by female plants. Based on these data, Canada thistle clearly should no longer be classified as "dioecious", and authors should define the terms that they use to describe Canada thistle's breeding system because there is no commonly accepted terminology for it.

Delannay (29, 30) reviewed the history of research on dioecism in the genus *Cirsium* and suggested a scheme for the evolution of gynodioecy to dioecy in Canada thistle. Male plants are hermaphroditic (i.e., they contain both female and male parts) with heteromorphic sterility (i.e., female floral parts do not form normally). Thus, most flowers on male plants are not fertilized because pollen fails to adhere to the poorly developed papillae on stigmas of male flowers, even though male flowers produce well-formed egg cells. In female plants, anthers prematurely abort due to degeneration of the tapetum before the onset of meiosis.

Floral insect attractants. Canada thistle flowers on capitula (termed "seedheads" throughout this review) are insect pollinated (91). Five major volatile fragrances, benzaldehyde, phenylacetaldehyde, phenethylalcohol, methyl salicylate, and methyl 2-methoxybenzoate, from Canada thistle flowers were identified by capillary gas chromatography-mass spectrometry (GC/MS) after desorption from Tenax GC traps (26). Phenylacetaldehyde was the most concentrated of these five volatiles. The known insect-attracting properties of these volatile compounds may aid cross-fertilization of flowers (26), although this suggestion was not rigorously proven. Flowers infected with Canada thistle rust [*Puccinia punctiformis* (Strauss) Roehl.] produced benzaldehyde, phenylacetaldehyde, phenethylalcohol, and indole, but neither methyl salicylate nor methyl 2-methoxybenzoate. The impact of rust infection on successful pollination was not studied, but probably decreases it.

Chemical composition. Because little new information has been published on seasonal changes in root carbohydrate content since earlier reviews were published (91), this topic will not be covered in this review. Several researchers have studied foliar waxes from Canada thistle leaves because of the significance of these waxes for herbicide uptake. Hodgson (63) found quantitative differences in foliar "lipid" extracts from nine Canada thistle ecotypes. The amount of lipid extract increased from the floral bud stage to full bloom. Foliar lipid quantity of two selections was inversely related to survival following 2,4-D [(2,4-dichlorophenoxy)acetic acid] treatment. However, correlation coefficients were not provided, and Canada thistle growth stage at treatment, percent plant survival, and the rate and formulation of 2,4-D were not reported.

Foliar epicuticular waxes of Canada thistle were chemically characterized by GC/MS as follows: 12% hydrocarbons, 35% esters, 3% free acids, 10% free alcohols, and 8% triterpene acetates (125). C_{24} free acids predominated, although C_{26} and C_{28} free acids were present. Free alcohols varied in chain length from C_{24} to C_{30}. Esters varied in chain length from C_{40} to C_{50}. Esters of this length make leaves of other species appear glossy (125).

Habitat. *Climatic and substratum requirements.* Climatic requirements for Canada thistle have not been rigorously characterized, although Moore (91) summarized what can be surmised, based on Canada thistle's distribution in North America. Soil requirements for growth of Canada thistle also are not well characterized (91), although its distribution suggests that it is widely adapted over a broad range of soils. Alkaline or high calcium soil horizons can limit root development of Canada thistle (108). Although Canada thistle grew in 40% of saline sites surveyed in Alberta, it was absent in saline areas of Saskatchewan and Manitoba (16). Overall, Canada thistle was a minor component of the flora associated with saline seeps in the three Prairie Provinces of Canada.

Communities. The occurrence of Canada thistle in agricultural crops in North America has been reviewed (37, 39, 45, 70), updating Moore's earlier review (91). In a survey of 502 grassland farms in England and Wales from 1974 to 1977, Canada thistle "seriously" infested 8% of pastures (98). Older livestock operations ($\geq$ 20 yr) had a greater Canada thistle problem (7 to 15% of fields) than younger operations ($\leq$ 4 yr) (2 to 5% of fields). Canada thistle was more prevalent on beef than dairy farms.

In Colorado, the following species were frequently associated with dense Canada thistle stands: American bullrush (*Scirpus americanus* Pers.), creeping bentgrass (*Agrostis palustris* Huds.), longstem spikerush (*Eleocharis macrostachys* Britt.), and saltgrass [*Distichlis stricta* (Torr.) Rybd.] (115). The following species were found in moderately dense Canada thistle patches: giant ragweed (*Ambrosia trifida* L.), horseweed [*Conyza canadensis* (L.) Cronq.], common lambsquarters (*Chenopodium album* L.), redroot pigweed (*Amaranthus retroflexus* L.), prairie sunflower (*Helianthus petiolaris* Nutt.), smooth dock (*Rumex altissimus* Wood), and foxtail barley (*Hordeum jubatum* L.).

Surveys of weed species associated with Canada thistle patches in Nebraska established that kochia [*Kochia scoparia* (L.) Scrad.], marshelder (*Iva xanthifolia* Nutt.), and foxtail barley densities were inversely related to distance from the center of three separate Canada thistle patches, respectively (131). Elsewhere, the transition from monospecific stands of Canada thistle to mixed stands with other species occurred over only 2 m from the patch border (12). Transects across patches showed that species diversity increased near patch borders (115). Hume (67) suggested that Canada thistle reduced the growth of green foxtail [*Setaria viridis* (L.) Beauv.] and redroot pigweed in a 21-yr-long crop rotation study in Saskatchewan.

Allelopathy. Canada thistle has been assumed to inhibit the growth of neighboring plants by releasing allelochemicals (12). According to Fuerst and Putnam (49), the minimum proof that a weed reduces the growth of crops or susceptible plants by allelopathic interference requires four elements: 1) Quantitatively measure the symptoms of interference on susceptible plants; 2) extract, bioassay, chemically characterize, and synthesize the presumed allelochemical(s); 3) reproduce the symptoms of interference by applying the isolated, purified allelochemical(s) at rates present in nature at the appropriate growth stage of susceptible plants; and 4) quantitatively measure the release, movement, and uptake of the allelochemical(s) from the weed to the susceptible plant to show that enough allelochemical is transferred to account for reduced growth of susceptible plants. The literature reviewed below demonstrates that allelopathy has not been conclusively proven for Canada thistle.

Canada thistle shoot litter inhibited growth of redroot pigweed, green foxtail, and barley (*Hordeum vulgare* L.) (115). Amending soil with either dried, ground shoots or roots of Canada thistle (3% by weight of soil) also inhibited growth of other species (12, 131). Root tissue-amended soil was more phytotoxic than shoot tissue-amended soil, as observed for water or ethanol extracts (see below). Soil amended with as little as 0.4% (by weight) of dried shoots or roots inhibited the growth of certain plants.

Water extracts of Canada thistle roots inhibited the germination of alfalfa (*Medicago sativa* L.), flax (*Linum usitatissimum* L.), oat (*Avena sativa* L.), and wheat (*Triticum aestivum* L.) seed (57). In contrast, water extracts of Canada thistle shoots were phytotoxic only to flax and wheat. Root extracts were more inhibitory than shoot extracts to seed germination or vegetative growth, but the relative phytotoxicity of root or shoot extracts varied with test species. Other research verified that water extracts of dried Canada thistle roots, but not of foliage, inhibited seed germination of other species (e.g., subterranean clover [*Trifolium subterraneum* (L.)] (12).

Ethanol extracts of dried Canada thistle shoots or roots reduced germination of subterranean clover and Canada thistle seed (12), as well as shoot and root growth. Root extracts inhibited germination more than did shoot extracts. The significance of organic solvent-extracted residues to allelopathy in the field is problematic and may not be related to the natural release of allelochemicals in the field (115).

Alternative explanations, other than allelopathy, have been suggested to explain the inhibitory effects by Canada thistle on other species. Disease microorganisms on Canada thistle residue were demonstrated to not be responsible for reduced germination with water extracts of Canada thistle roots and shoots because sterilized water extracts were just as phytotoxic to test species as unsterilized extracts (12). Wilson (131) verified Bendall's observation (12) that microorganisms were not responsible for Canada thistle-induced growth inhibition by showing that sterilized and unsterilized Canada thistle residues were equally phytotoxic to test species. Extremes of pH or osmotic potential of the water extracts of Canada thistle residues also were eliminated as causative factors (115). Because adding nitrogen (as urea at 482 kg nitrogen ha^{-1}) (131) or Hoagland's solution (115) to Canada thistle-amended soil did not reduce the phytotoxicity of dried root or shoot tissue, residue-induced immobilization of nitrogen or other nutrients apparently was not responsible for the growth inhibition of susceptible plants. In the field, Canada thistle's extensive perennial root system may allow it to extract water from greater depths in the soil profile than annual species can, and this may give Canada thistle a competitive advantage over other species, especially under drought conditions.

Canada thistle residues were autotoxic to Canada thistle seedlings (12, 115, 131). Both water extracts of roots or shoots of Canada thistle or soil amended with dried Canada thistle roots or shoots reduced Canada thistle seed germination, establishment, and seedling growth. Soil from Canada thistle patches did not inhibit Canada thistle seedling growth.

Floral Reproductive Biology. Canada thistle is a long-day plant (60, 91, 116). Canada thistle grown over winter in greenhouses required supplemental artificial lighting (incandescent and fluorescent) for best shoot growth and flowering (25). Foliar-applied gibberellin $GA_{4/7}$ (100 mg L^{-1} to runoff) stimulated bolting of shoots grown under noninductive short photoperiods (116).

Canada thistle seedlings do not immediately flower after germination but have a juvenile vegetative period before established plants can flower in response to light (9). Canada thistle can flower in the same growing season that seedlings emerge. It has not been established whether shoots arising from adventitious root buds on established root systems have a similar juvenile period before flowering. More research is needed to better quantify this juvenile period for both shoots arising from seedlings and established root systems in relation to the timing of control measures, such as mowing.

Canada thistle ecotype, temperature (constant 16, 21, and 27 C), and photoperiod (8, 12, 14, and 16 h) modified flowering behavior, shoot and root biomass production, and the root-to-shoot ratio of potted greenhouse-grown plants (68). Seven ecotypes flowered under 16-h photoperiods at all temperatures tested. When the photoperiod was 14 h or less, three of the seven ecotypes tested exhibited temperature-dependent flowering.

Seed germination. *Seed viability during maturation.* Seed germination was used to measure the viability of Canada thistle seed harvested at various times during maturation (51). Seed germinated 0, 0, and 38% when seedheads were cut when flowering, in flower bud, and when fully mature, respectively (31, 74) (Figure 2).

Germination in relation to seed dormancy. Seed dormancy terminology summarized by Lang et al. (77) will be used in this review. Moore (91) summarized research indicating that almost all Canada thistle seed can germinate upon dispersal. Additional recent information confirms this conclusion (Table 1), demonstrating that a high proportion of Canada thistle seed were capable of germinating at maturity. Fresh mature seed germinated well within 2 to 4 d after being excised from the pericarp (seed coverings) (71),

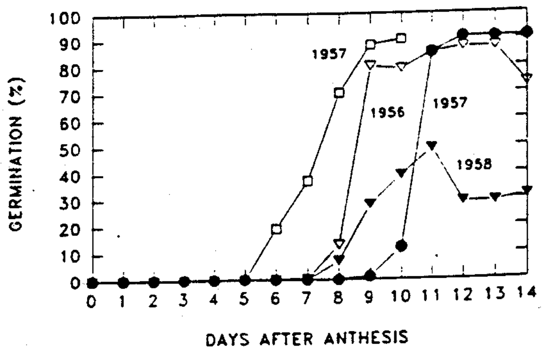

Figure 2. The development of germination ability of Canada thistle seed as a function of days after anthesis [1957 = open squares by Kinch and Termunde (74), redrawn from tabular data by permission of the Assoc. Off. Seed Anal.; other data by Derscheid and Schultz (31), redrawn from tabular data by permission of *Weed Science*].

Table 1. Percent germination of recently dispersed, mature Canada thistle seed.

Type of plant	Germination (%)	Reference
Male	19	81
Male	55	71
Subhermaphrodite	86	71
Hermaphrodite	73	71
Female	88	1
Female	53 to 96	9
Female	88 (range: 81-97)	14
Female	78	56
Female	66	71

suggesting that the pericarp restricted germination of freshly shed seed. Germination rates of seed produced on male plants were lower for seed from female plants (81). The viability of seed formed on predominantly male plants was positively correlated with seed weight (71).

Environmental effects on germination. Germination requirements of Canada thistle seed were investigated using seed brought in from the field and incubated under controlled environmental conditions. Temperature requirements for germination have been summarized (91). Chilling freshly harvested seed or seed recovered from soil enhanced dark germination under alternating temperatures (14, 128), suggesting that environmentally imposed dormancy was involved (77). Chilling freshly mature seed at 4 to 7 C for up to 24 d also enhanced germination (76). However, chilling was not absolutely required for germination since there was always some germination without chilling.

Light (2150 lux) stimulated germination of Canada thistle seed (76), especially freshly harvested seed (32). Germination was greater under an alternating 8- or 16-h photoperiod than in continuous darkness or continuous light (14, 76). Canada thistle seed germinated 80 and 62% in an 8-h photoperiod (8L:16D) and complete darkness, respectively (128). Gibberellic acid (GA_3) at 30 ppm stimulated germination of dark-incubated seed so that it equaled that of seed exposed to an 8-h photoperiod. However, gibberellic acid did not increase germination of seed incubated under an 8-h photoperiod.

In petri dishes, the pH range for optimum germination of Canada thistle is broad (5.8 to 7) although germination rate was reduced below or above this pH range (2.5 to 9) (128).

Canada thistle seed germination was relatively salt-tolerant in petri dishes (128). Percent germination was not reduced when exposed to 5000 ppm (weight basis) NaCl. This may partially explain the occurrence of Canada thistle near saline areas (16). Seed germination and seedling emergence may impact the population biology of Canada thistle establishing along waterways and near saline seeps and may differ from the establishment process on farmland.

Seed recovered from irrigation water germinated 52% (129) and 65% (18, 19). The period of immersion influenced percent germination. Seed in mesh packets suspended in flowing irrigation water germinated 54 to 92% and 19% 2 and 22 mo after immersion, respectively (18, 19). Earlier, Hope (66) reported that seed submerged in running water for 55 d germinated

26%. Thus, suspension in water did not kill all of the Canada thistle seed, even after months of immersion.

Incorporation of seed into soil clods can reduce germination of some species (119). Canada thistle seed incorporated into soft clods (compressed to 0.3 MPa) that were 1.5 to 5.3 cm in diameter germinated normally (93 to 100% germination), but germination was slightly lower (87 to 97% of controls) when the clods were hard (compressed to 2.2 MPa).

Most studies of Canada thistle seed germination have been conducted from a strictly physiological perspective (i.e., seed have been brought indoors and treated in various ways under controlled environmental conditions). Other research approaches are needed to better understand the germination and emergence behavior of this weed in the field. The impact of the natural microclimate, crop residue, or soil type on seed germination and seedling emergence deserves further study in the field. The ability of Canada thistle seed to germinate and emerge along waterways after months of immersion in water, near saline seeps, under drought conditions, under different plant residue levels, or under different tillage conditions needs to be studied in the field if the population biology of this species is to be better understood.

Vegetative growth. Vegetative (asexual) reproduction has been reviewed and compared for several perennial weeds (72). Canada thistle seedling establishment and development of roots also have been reviewed (65, 91).

The extent of physiological interconnection between separate Canada thistle shoots arising from common roots on the same plant and the sharing of photoassimilates between shoots connected by common roots has not been measured directly. However, when Canada thistle infesting an untilled nursery was sprayed with glyphosate (*N*-phosphonomethyl glycine) at 2.2 to 4.4 kg ae ha^{-1}, untreated shoots were damaged 122 cm away from glyphosate-treated shoots (13), suggesting some interconnection for movement of this phloem-mobile herbicide by translocation between shoots interconnected by common roots.

The growth response of Canada thistle shoots and roots to temperature and photoperiod has been reviewed (91). The root-to-shoot ratio of potted greenhouse-grown plants was inversely related to temperature (16, 21, and 27 C) and photoperiod (8, 12, 14, and 16 h per 24 h) (68). Fewer adventitious root buds per plant formed as temperature was increased (16, 21, 27 C) under a given photoperiod (8, 12, and 16 h per 24 h). In general, low temperature and short photoperiods, like those experienced in fall, favored root growth more than shoot growth. Reproductive-to-vegetative allocation of resources in potted plants grown outdoors in England was summarized by Bostock and Benton (15). McAllister and Haderlie (87) examined the impact of temperature and photoperiod (13 and 15 h per 24 h) on Canada thistle cuttings grown hydroponically in the growth chamber. Roots and shoots were exposed to constant temperatures (10, 20, and 30 C) and diurnally varying day/night temperature cycles (15/5, 25/15, and 30/22 C), respectively. Under both photoperiods, numbers of adventitious root buds per plant increased as root temperatures were increased from 10 to 20 C, but decreased at 30 C. Elongation rates of adventitious root buds increased as root temperatures increased from 10 to 30 C, except for the low shoot temperature cycle of 15/5 C under the 13-h photoperiod. Adventitious root bud elongation was minimal at 10 C. When root temperatures were maintained at 10 C, total dry matter per plant also decreased. These studies suggest that fall temperatures and photoperiods favor increased adventitious root bud formation while inhibiting adventitious root bud elongation.

The terminology for describing the dormancy of asexual vegetative plant organs summarized by Lang et al. (77) will be used in this review. Dormancy (i.e., correlative inhibition or paradormancy) (77) of adventitious root buds on the root system is poorly characterized for Canada thistle. Correlative inhibition of adventitious root buds on perennial roots has been reviewed in general (72) and for Canada thistle (91). Canada thistle adventitious root buds lack a long internally controlled dormancy period in fall and adventitious root bud growth is limited by low temperature in winter (86).

Recently it was proposed that correlative inhibition (paradormancy) of adventitious root bud growth on actively growing plants was due to competition for water between plant organs (69). Adventitious root bud elongation was reduced when plants were grown under low relative humidity (30 to 50%) compared to high (90 to 100%) relative humidity. When plants were decapitated, adventitious shoots from high-humidity plants grew more than those from low-humidity plants. Growth of mature stems and leaves reduced adventitious root bud growth at low relative humidity.

Environmental conditions did not appear to induce Canada thistle adventitious root bud dormancy (92, 93). When roots from as deep as 180 cm were unearthed, cuttings from shallow and deep levels produced equivalent numbers of adventitious roots buds per length of root. Similar observations were made on 1-, 2- (93), and 10-yr-old Canada thistle stands (92).

Nitrogen (urea) fertilization at 70 or 100 kg N ha^{-1} increased the numbers of emerged adventitious shoots m^{-2} (93). Fertilization increased adventitious shoot growth by increasing root growth within the top 20 cm of soil rather than preferentially stimulating adventitious root bud growth over total root growth. When environmental conditions increased or decreased Canada thistle shoot density, fertilized plots had greater shoot densities than unfertilized plots at most sampling times over the growing season.

Canada thistle adventitious root buds possess limited freezing tolerance, and the ability of adventitious root buds to survive freezing depends on their location in the soil profile (111). Canada thistle adventitious root buds were more susceptible to freezing damage than root buds of leafy spurge (*Euphorbia esula* L.), perennial sowthistle (*Sonchus arvensis* L.), or quackgrass [*Elytrigia repens* (L.) Nevski]. When 10- to 20-cm-long root sections were exposed to temperatures between −4 and −20 C in a freezer for various periods of time, the temperatures required to reduce survival (LT_{50}) and total dry weight (GR_{50}) of Canada thistle were −7 and −5 C, respectively.

POPULATION BIOLOGY

Population biology deals with changes in plant numbers for various life cycle stages of Canada thistle and the ecological reasons for those changes. The stages of the life cycle of Canada thistle are presented in Figure 3 (109). This flow diagram can be used to graphically summarize quantitative changes in different life history stages over time. The temporal scale of the flow diagram is in the left-hand margin of Figure 3. Changes in life history stages can be expressed over the seasons of the year or from one generation to the next. The spatial scale for studying Canada thistle population biology is defined by the researcher; in Figure 3 the study area is represented by the large box bracketing the various life history stages. Inputs of sexual and asexual propagules into the study population from the previous generation or year (i.e., buried seed bank, root bud bank, and surface-lying seed) are presented above the top horizontal line of Figure 3. Inputs and outputs of Canada thistle seed to and from the study area are presented to the right of Figure 3. Man's actions can affect the Canada thistle life history in different ways at different life cycle stages. Some of man's actions impact certain life history stages more than others, as indicated by the numbers in circles next to each life history stage in Figure 3. (See the legend for more description.) The impact of control measures on Canada thistle was reviewed previously (37).

Neither the population biology nor demography of Canada thistle has been described completely, although certain stages of the Canada thistle life cycle have been quantified (Tables 2 and 3). This section summarizes what is known about the number and phenology of the life cycle components of Canada thistle populations and highlights data gaps.

Reproduction. *Floral biology and phenology.* Quantitative information on the reproductive organs of male and female plants growing in fields is summarized in Table 2 (81) and in Kay (71) for seed formed on male plants. The position of shoots within patches influences the extent of flowering. Smaller stems at the patch periphery failed to flower, in contrast to shoots arising within the patch (15).

Most information on Canada thistle flowering phenology is more anecdotal than quantitative, with one exception (43) (Figure 4). Moore's (91) assertion that flowering in Canada begins in mid-June or early July and continues into September was verified elsewhere in northern latitudes (14, 15). However, flowering began in late May and ended in August in Montana (59). In Idaho (43) and Colorado (108), flowering extended from mid-June to August. In Nebraska (64), flowering extended from early June to mid-July, with only occasional flowers forming in September. Comparative observations on the impact of environmental factors (e.g., photoperiod, light intensity or quality, or air temperature) in controlling the onset and cessation of flowering of the same ecotypes at different latitudes may improve understanding of the reasons for this species' distribution in North America (37).

Canada thistle flowering phenology is important to understanding the population biology and dispersal of this weed in relation in many cropping systems. The timing of crop management, like mowing in pastures, may limit the contribution of seed to local Canada thistle population biology if flowering shoots are cut before seed mature. Likewise, Canada thistle seed maturing during grain harvesting may contaminate grain and be transported with it from re-

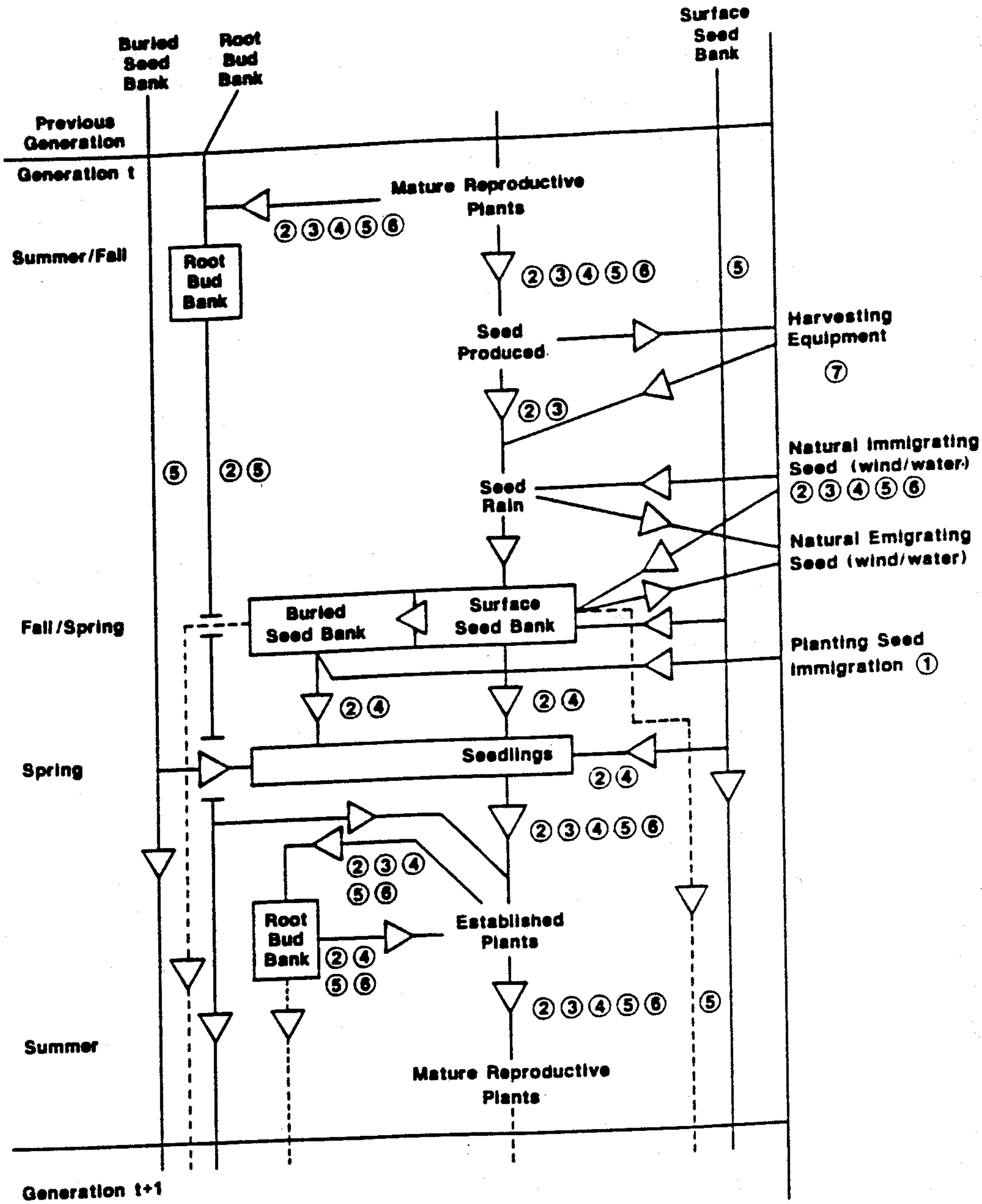

Figure 3. Linear flow chart of the life history stages of Canada thistle over two generations. The life history stages that can be manipulated by man are indicated by: *1* plant weed-free crop seed, *2* tillage, *3* mowing or grazing, *4* herbicide application, *5* biological control, *6* planting competitive crops, and *7* cleaning combines [modified after Sagar & Mortimer (109), redrawn by permission of Academic Press, Inc.]

gion to region. It can be argued that Canada thistle seed moved by man in contaminated commercial crop seed, hay, or combines are responsible for spreading Canada thistle between different regions, but vegetative propagation is probably more important for local spread after initial establishment. (See seed dispersal below.)

Seed production. Moore (91) summarized early research information on seed production of Canada thistle. More recent additional information on the yield components and reproductive output of Canada thistle is tabulated in Table 2. Seed position within the seedhead influenced seed maturation (23). Seed formed near the edge of open heads matured earlier than those formed

Table 2. Quantitative information on sexual reproduction of *Cirsium arvense*.

Reproductive parameters	Measurement	Environment	Country	Reference
Ovules per capitulum (seedhead)	61.2 ± 5.4 (mean ± 95% C.I.)	Field	England	15
	103.4 (male plants)		England	81
	104.3 (female plants)		U.S.	34
	100		U.S.	56
	32 to 69		Denmark	9
Ovules developing	39.9 % (29.1 to 53.8)	Field	England	15
	22.4 % (male plants)	Field	England	81
	100 % (female plants)			
Predispersal predation of seed	1.6 %	Field	England	15
Percentage success of ovules including predation	39.3 %	Field	England	15
	16.7 % (male plants)	Field	England	81
	100.0 % (female plants)			
Achenes produced per capitulum	26.6 ± 6.0 seed per seedhead	Field	England	15
	98 seed per seedhead	Field	U.S.	56
	83 seed per seedhead			31
	26.2 seed per seedhead	Field	England	15
	2.9 (male plants) seed per seedhead	Field	England	81
	79.3 (female) seed per seedhead	Pasture	Australia	1
	0.22 (± 0.09) (male) seed per seedhead	Field	Denmark	9
	50.6 (± 7.9) (female) seed per seedhead			
	0.3-103 seed per seedhead			
	59 (0-93) seed per seedhead			
Capitula per stem	24-85	Field	Australia	1
	23.2 ± 8.4	Field	England	15
	41 (32-69)	Field	Denmark	9
	24.3 (male plants)	Field	England	81
	18.3 (female plants)			
Capitula per stem of largest plants	100	Field	England	15
Achenes per stem, including predation	600	Field	England	15
	2.64 (male plants)	Field	England	81
	1451.2 (female plants)			
Achenes per flowering plant	1530 (high of 5300)	Field	Montana	55
	4500	Field	Denmark	42
Achenes per flowering shoot	70.5 ± 50.8	Pots outdoors	England	15
	0.1-49	Pasture	Australia	1
Achenes per m^{-2}	1-775 achenes m^{-2}	Pasture	Australia	1
Dry weight per embryo (mg)	0.67 ± 0.075 mg	Pots outdoors	England	15
Dry weight per achene (mg)	1.820 mg (± 0.107) (95% C.I.)	Field	England	14
	1.575 mg	Field	U.S.	117
Seed per m^{-2}	30,189 seed m^{-2}	Field	Denmark	9
	100-64,300 seed m^{-2}	Pasture	Australia	1

in the middle. Average seed weights are also summarized in Table 2 and vary between ecotypes (59, 60). In pot-grown plants, there was no simple relationship between seed weight and numbers of seed produced (15).

Predispersal seed predation. Information on seed predation is largely observational rather than quantitative. The extent of seed predation is greater if seed fail to disperse from the seedhead (15). Seed that remain attached to the seedhead can suffer high predation rates by insects. In October in England, 43% of Canada thistle seedheads contained insect larvae. In one study in Canada, 20 to 85% of seedheads were attacked by *Orellia ruficauda* (F.) (47). Seed predation varied from 20 to 80%. Grazed pasture, right-of-ways, and ungrazed pasture in Canada experienced 32, 44, and 63% predation, respectively, by this insect seed feeder. A brief overview of the use of insects in biological control programs for Canada thistle is included later in this review.

Seed Biology. *Seed dispersal.* Most information on seed dispersal deals with qualitative descriptions of transport mechanisms, rather than quantitative descriptions, with some exceptions. The relative importance of different routes of seed transport undoubtedly differs depending

Table 3. Typical Canada thistle shoot densities.

Country	Type of study	Crop	Shoot density[a] (no. m^{-2})	Reference
Australia	Survey	Pasture	6 to 21	1
Canada	Research	10-yr fallow	40	92
Canada	Research	Artificial stands	16 to 23 (400)	93
Denmark	Research	Noncropped	63	42
England	Research	Noncropped	3.4	80
Finland	Survey	Cereals	1 to 4	44
United States (Minnesota)	Survey	Spring wheat	0.7 to 2 (9)	11
		Barley	3 (19)	
		Oats	3 (13)	
United States (Nebraska)	Survey	Patches 4 to 5 m across	28 ± 9 (mean ± standard deviation)	130
			43 ± 20	
			17 ± 8	
United States (North Dakota)	Survey	Spring wheat	2 to 4 (16 to 23)	36
		Barley	2 to 4 (22 to 30)	
		Oats	3 to 4 (5 to 21)	
		Flax	1 to 2 (5)	
		Sunflower	2 (14)	
United States (South Dakota)	Survey	Spring wheat	5 (24)	7
		Flax	7 (25)	
		Oats	6 (42)	
		Barley	6 (24)	

[a]Means ± standard deviations presented. Maximum observed densities are presented in parentheses.

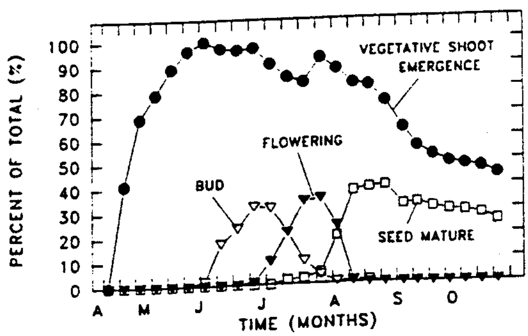

Figure 4. Phenological development of Canada thistle shoots during a growing season in Montana, Unites States. The proportion of shoots that emerged, elongated, formed floral buds, flowered, and formed mature seed is graphed over time [redrawn from tabular data by Erickson and Erickson (43) with the permission of the Western Society of Weed Science].

upon scale, and it ranges from local to international. Reportedly, Canada thistle seed are dispersed by transport in contaminated crop seed, feed, manure, and irrigation water, and by wind (89). Moore (91) mentioned only seed dispersal by irrigation water and wind, and Holm et al. (65) added transport in packing straw, as suggested earlier (28). Early agriculturalists reported that grain threshing was believed to remove most Canada thistle seed from harvested grain, although additional seed cleaning was recommended. However, Dewey (35) reported that Canada thistle seed contaminated threshing machines and also was transported with hay.

In 1913, Canada thistle seed contaminating grass and clover seed was viewed as a major avenue of spread (28). In the 1930s, 0.4% of 19,324 seed samples contained Canada thistle seed and included samples of alfalfa, alsike clover (*Trifolium hybridum* L.), barley, oat, red clover (*Trifolium pratense* L.), sweet clover (*Melilotus albus* L.), timothy (*Pleum pratense* L.), and wheat seed (55). In 1973, less than 1% of seed samples, chiefly barley, taken from grain drills in England and Wales were contaminated with Canada thistle seed (120). Similar levels of grain drill contamination (1%) were reported in wheat in the early 1980s in North Dakota (10). Despite advances in seed cleaning technology, Canada thistle seed likely continues to be spread in crop seed, especially between neighboring farms with grain moved outside of commercial seed channels.

Early agriculturalists assumed that seed dispersal by wind was a major method for local spread of Canada thistle between farms (28). However, Moore (91) questioned the role of the pappus in wind dispersal of Canada thistle seed. Bostock and Benton (15) verified Bakker's (9) observation that some seedheads do not open enough to allow the pappus to spread seed. In other cases, the pappus plume became detached from the seed, leaving the seed within the seedhead. The physics and aerodynamics of wind dispersal of Canada thistle seed attached to the pappus have been studied (20, 113). When released 30 cm above the soil, seed with attached pappus traveled 3.8, 7.6, and 11.4 m in winds of 5.5, 10.9, and 16.4 km h^{-1}, respectively. The terminal velocities of seed attached to the pappus of 18 composites ranged from 19 to 220 cm s^{-1}; that of Canada thistle seed was 22 cm s^{-1}. In turn, the aerodynamic resistance coefficients[3] of seed of these same 18 species ranged from 2.66 to 0.02 cm^{-1}, with that of Canada thistle seed being 2.1 cm^{-1}. When seed traps were used to measure movement of weed seed onto unvegetated strip mine spoils from border areas, less than 1% of the total seed captured consisted of Canada thistle seed (5). Seed were recovered in greater numbers from downslope positions than from the spoil summit. Unfortunately, the authors (5) did not characterize the relative sizes of the sources of weed seed or their distance or distribution in relation to spoil topography and capture sites.

Hope (66) was credited in Moore's (91) review with observing that Canada thistle seed were transported in irrigation water. However, Dewey (35) provided the first quantitative data on this subject at the turn of the century and asserted that irrigation ditches were recognized as major avenues of spread. More recently, irrigation water was verified to transport Canada thistle seed (18, 19, 129). Floating seed and seed at the bottom of irrigation channels comprised 78 and 22% of all Canada thistle seed recovered, respectively (129). Entrapped air between the embryo and the pericarp of the relatively water-tight achene may be responsible for seed buoyancy, but this remains to be proven. Canada thistle often flourishes along the banks of drainage channels or streams in arid states, like Nebraska (129).

Seed bank levels and seed persistence. Canada thistle shoots contributed significantly to perennial weed vegetation cover in faba bean (*Vicia faba* L.) or winter wheat in a four-crop rotation of oats, clover, winter wheat, and faba beans in Canada (58). Nevertheless, Canada thistle seed were not well represented in the soil seed bank (surface to 7.6 cm and 7.6 to 15.2 cm); no Canada thistle seed could be recovered from the seed bank (58). There are few estimates of the numbers of Canada thistle seed in the soil seed bank in fields (Table 2).

Early field research indicated that Canada thistle seed could be persistent in soil (75, 82, 91). Usually, persistence was assessed by exhuming buried seed from the field and germinating the seed under greenhouse conditions (82, 121) (Figure 5), rather than estimating total seed loss as a percent of the number initially buried. For example, some Canada thistle seed germinated 22 yr after burial 20 cm deep in the field (82). Seed germinated 45 to 55% when unearthed after burial 25 cm deep for 5 yr in the field (75) and 52% after burial 20 cm deep for 3 yr (42). Thus, if Canada thistle seed were buried ≥ 20 cm deep by moldboard plowing, a small proportion of seed would persist to reinfest soil if seed were subsequently unearthed by later tillage. However, these early seed persistence studies can be criticized because Canada thistle seed were buried well below the depth of normal emergence [25 cm in (75); 20 cm in (42, 82, 121)], and thus seed were not exposed to the seasonally changing germination environment of the soil surface. Weed seed lie close to the soil surface in most currently used crop production systems, which generally either dispense with primary tillage or employ reduced primary tillage, such as chisel plowing, rather than soil inversion, as by moldboard plowing. Early Canada thistle seed persistence studies were also somewhat artificial in that either the soil was not disturbed by tillage (75, 82, 121) or seed were not exposed to normal changes in soil moisture in response to rainfall (75). In contrast to these early field studies, Canada thistle seed germination dropped from 86 to 92% initially to 0% within 5 yr when stored under dry laboratory conditions (75).

In more recent research on Canada thistle seed persistence, which simulated more realistic field conditions, Canada thistle seed were short lived

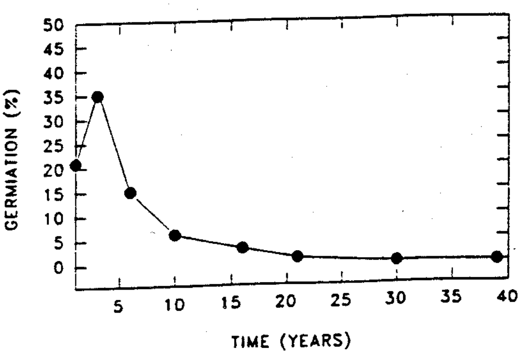

Figure 5. Persistence of undisturbed Canada thistle seed buried 20 cm deep as measured by germination of unearthed seed over time [redrawn from tabular data by Toole and Brown (121) with the permission of Cambridge University Press].

in the soil. These studies employed shallow burial (2.5 to 7.5 cm deep) and periodic soil disturbance (107), which are more typical of agricultural fields. Less than 1% of the total number sown remained after 2.5 yr in Denmark (9) (Figure 6) and 5 yr in England (107) (Figure 7). Most seed were lost from the soil seed bank by germination during the first year after burial at 7.5 cm (48 to 58%) or 2.5 cm (60%). Soil disturbance is known to speed the rate of loss of other weed seed from the soil seed bank (105, 106). When emergence alone was used to assess seed persistence of undisturbed seed in Canada, no seedlings emerged 3 yr after burial (24).

Seedling Germination, Emergence, and Phenology in the Field. Some Canada thistle seed can germinate on the soil surface, making the species "preadapted" to reduced or zero tillage (128). However, no Canada thistle seedlings became established from seed spread on the soil surface of a mixed pasture in Australia (2). However, when seed were buried 0.5 to 1.0 cm deep, 6.8 to 12.6% of seed emerged and 78 and 93% of the emerged seedlings survived to maturity, respectively (2).

With monthly soil disturbance, Canada thistle seedlings emerged from 68% of shallowly buried (2.5 cm deep) seed over 3 yr (107), with periodic soil disturbance. As planting depth increased, seedling emergence decreased and seedlings from deeper planted seed emerged later than more shallowly buried seed (132). In contrast, Derscheid et al. (33) reported that seed planted deeper than 1.3 cm failed to germinate, while soil type did not greatly influence emergence down to 2 cm (9). When seed were buried at various depths as low as 6 cm in two sandy loam soils, emergence was greatest from 0.5 to 1.5 cm (128).

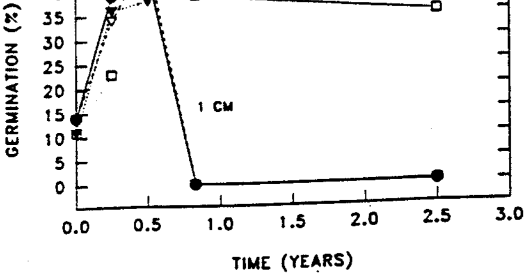

Figure 6. Persistence of undisturbed Canada thistle seed buried either 1 or 40 cm deep in Denmark. Persistence was measured by unearthing seed and germinating them under standard conditions [redrawn from tabular data by Bakker (9) by permission of Blackwell Scientific Publications, Ltd.].

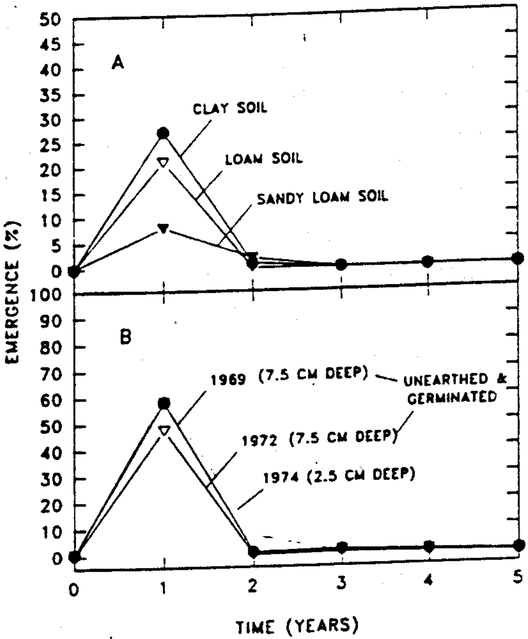

Figure 7. Persistence of periodically tilled Canada thistle seed as measured by seedling emergence over time. (A) Seedling emergence in three soil types in the field in Canada [redrawn from tabular data by Chepil (24) redrawn with permission of Agric. Inst. Canada] (B) Seedling emergence from seed buried either 2.5 or 7.5 cm deep in England. Persistence was measured as either emergence (2.5-cm depth) in the field or by unearthing seed and germinating them under standard conditions (7.5-cm depth) [redrawn from tabular data by Roberts and Chancellor (107) with permission of Blackwell Scientific Publications, Ltd.].

In fields in England, few seedlings emerged in the first fall after seed were sown in September (107) (Figure 8). Only 3 to 6 mo were required for seed to become fully capable of germinating in the field. Winter environments usually prevent Canada thistle seed germination. After seed maturation, primary dormancy was short lived but was followed by longer term, environmentally enforced (secondary) dormancy. Environmentally enforced dormancy develops if seed experience environmental conditions that prevent germination (9).

Most seedlings emerged in April and May following burial in the previous fall, but a small number persisted longer (9). In Denmark, Canada thistle seed were able to germinate 88% in the spring after fall burial (42). In England, 60% of seed planted 2.5 cm and 48 to 58% of seed planted 7.3 cm emerged in the spring after fall planting (107).

Canada thistle seedlings grow slowly at first, are poor competitors (65), and do not tolerate shade well (9). Shading at 60 to 70% of full sunlight severely restricted shoot growth, and seedlings died at 80% shade (9). Plants growing in forests were tall, spindly, and flowered less than plants growing in the open (34).

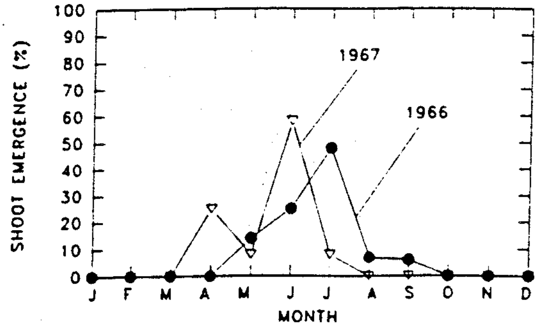

Figure 9. Seasonal cycles of adventitious shoot emergence of Canada thistle on an undisturbed site in England [redrawn from tabular data by Lawson et al. (80) with permission of the Br. Crop Prot. Counc.].

Vegetative Growth of Established Shoots. *Emergence phenology of adventitious shoots.* Cox (28) observed that more Canada thistle adventitious shoots emerged just after corn (*Zea mays* L.) planting than later in the season. The temperature requirements for adventitious shoot emergence were summarized by Moore (91). Adventitious root buds elongated in fall and winter following shoot death in fall in Nebraska (86). When roots were periodically unearthed, brought indoors, and grown in a high-humidity incubator at 15 C for 2 wk, there were no seasonal cycles of adventitious root bud elongation or numbers of adventitious root buds per unit of root length over the year. This observation suggests that the seasonal environment may restrict adventitious root bud elongation of Canada thistle, rather than endogenous physiological dormancy.

Hodgson (60) observed that rosettes of Canada thistle enlarge horizontally to cover the ground before shoots began to grow vertically about 3 wk after initial emergence. Later emerging shoots during the growing season may elongate without significant rosette formation. Seasonal emergence of adventitious shoots in England (80) and North America (91) is summarized in Figure 9. Shoot emergence from adventitious root buds can occur over an extended 6-mo period and is probably limited by low temperature in fall and winter.

Canada thistle shoots can be propagated from lateral buds at internodes on stem segments (83) and adventitious root buds arising on root segments (91). Shoots derived from stem sections survived better when partially buried than if totally buried in soil (83). Shoots derived from stem sections of postbloom plants survived better than those from stem sections derived from plants that were vegetative in spring or fall or in the floral bud stage. Only stem sections that formed adventitious roots survived winter in Minnesota. Adventitious roots formed above the axils of scale leaves on the stem and later formed at stem internodes. Earlier, Parker (95) had observed that 2.5- to 5-cm-long stem segments were able to form shoots, but these died later because of poor root development. The relative contribution of shoots arising from buried vertical stems versus adventitious shoots arising from adventitious root buds to total Canada thistle shoot populations has not been determined in the field, although it probably is minor. Shoot regrowth following mowing may be from buried stem segments (buried lateral branches with stem internodes), although this possibility requires confirmation in the field.

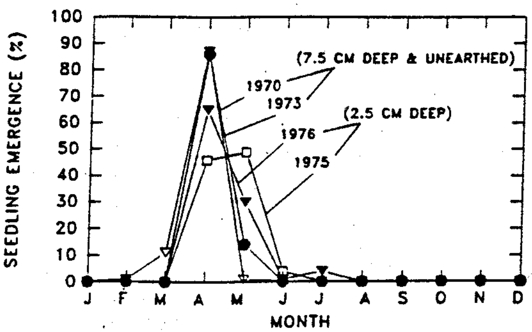

Figure 8. Seasonal cycles of seedling emergence of periodically disturbed Canada thistle buried 2.5 or 7.5 cm deep in England [redrawn from tabular data by Roberts and Chancellor (107) with permission of Blackwell Scientific Publications, Ltd.].

Adventitious shoot density. Information on Canada thistle densities in surveys of cereal fields is summarized in Table 3. Each study employed different methods, and the experimental design for sampling was usually not provided. The sampling experimental design for estimating shoot density undoubtedly influenced measurement accuracy because Canada thistle grows in patches in the field. Canada thistle shoot density across patches also varies, probably as a result of differences in position within the patch, age, management, and/or response to weather (3). Thus, the estimates of shoot density in Ta-

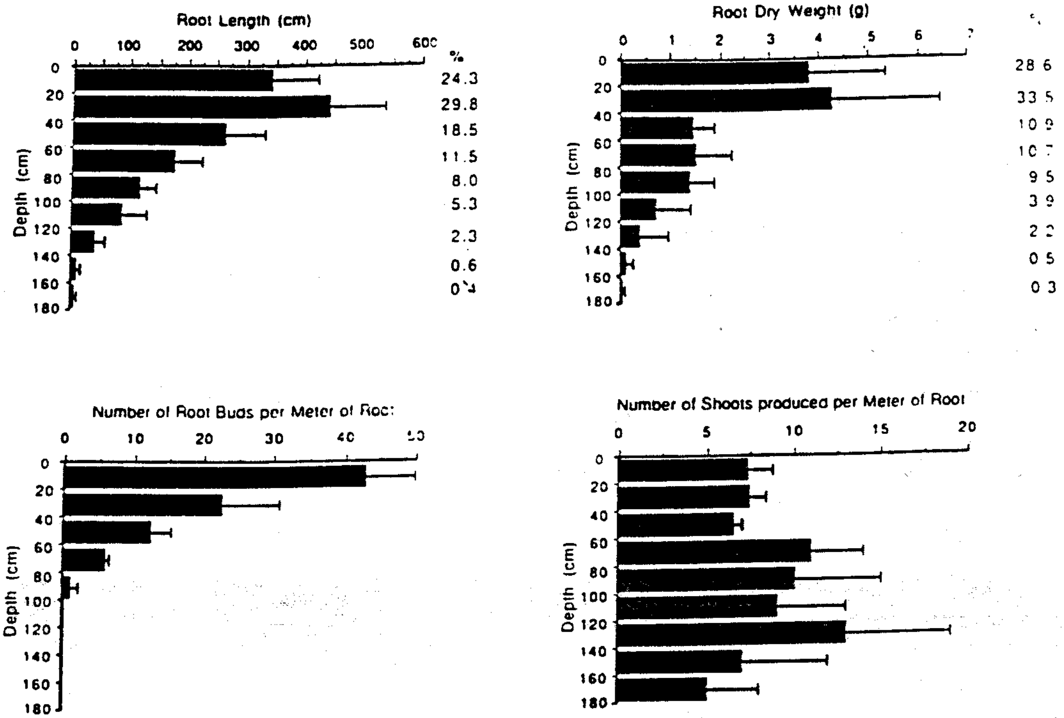

Figure 10. Average total root length, average root dry weight, average number of adventitious root buds per meter of root, and average shoot production per meter of root of Canada thistle down the soil profile from a 10-yr-old patch. Means ± standard errors are presented for roots taken in 12 soil bands (2-m-wide by 10-cm-thick by 20-cm-deep soil bands) [Nadeau and Vanden Born (92) by permission of the authors and the *Canadian Journal of Plant Science*].

ble 3 cannot be compared with one another statistically.

Shoot densities vary across patches (131). Lower shoot densities near patch borders of most expanding patches may be due to nonuniform root distribution at the leading edge of patch expansion. Densities declined in the centers of 4- to 5-m-wide patches in Nebraska. In Australia, plant density and height also were reduced near the center of a 28-m-wide patch from the patch borders, suggesting senescence (2). Earlier, Pavlychenko (96) had observed that during a prolonged drought, dense patches of Canada thistle became ring-like. Shoots emerged on the periphery of such patches much more than in the center of patches. Perhaps environmental stress rather than autotoxicity may limit the emergence of Canada thistle adventitious shoots from adventitious root buds in well-established patches, especially when patches are drought stressed. Others observed that areas of greatest density shifted from year to year within patch borders (101). Although shoot density and biomass are not likely to be directly related, the shoot biomass of Canada thistle exhibited a bell-shaped distribution across a 35-m-wide patch in Colorado (115).

Under favorable conditions, a Canada thistle patch can spread rapidly by vegetative means. One 7.5-cm-long cutting formed a solid patch 7.2 m wide after 3 yr of uninterrupted growth (97). Patches spread laterally 0.8 to 1.6 m per year in Australian pastures, depending upon site and year (2), 6 m per year in the U.S. (56), and 0.8 to 1.3 m per year in Europe (9), depending upon site and year.

Crop and land management can reduce the rate of Canada thistle patch growth (37). For example, Canada thistle did not spread as rapidly in grazed as in ungrazed pastures in Australia (2).

Roots. After shallowly buried seed germinated, seedling roots penetrated 5 to 10 cm before shoots emerged (9). Horizontal roots developed and adventitious shoots emerged within 6 to 8 wk after establishment. In Canada, the first lateral roots were initiated at the two-leaf stage when seedings were 4 to 5 wk old (48). Adventitious root buds formed on the taproot (48, 110), but the depth of adventitious root bud formation varied. After new Canada thistle seedlings became established, their ability to survive clipping by sending up adventitious shoots increased

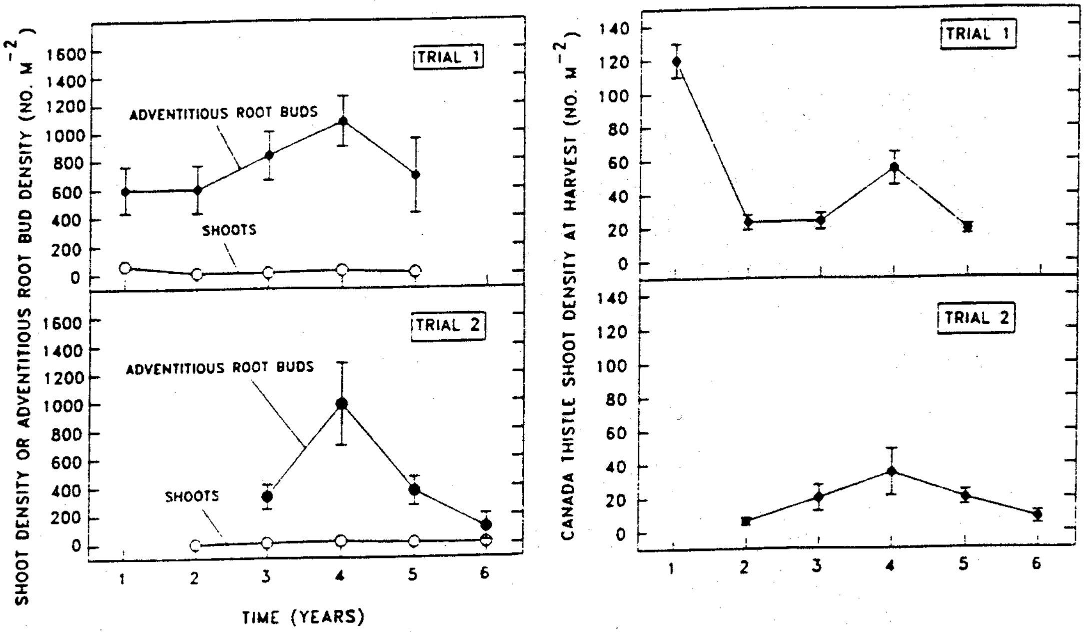

Figure 11. Changes in numbers of adventitious root buds (left) and emerged shoots (right) of Canada thistle over time. Means ± standard errors are presented. An established Canada thistle stand was growing in continuous spring wheat for 4 yr followed by mechanical fallow in the fifth year of observation. A fall chisel plow tillage regime was employed. [Donald (38), reproduced by permission of *Weed Science*; Donald and Prato (41), redrawn by permission of the *Canadian Journal of Plant Science*].

as plants aged (128). Seedlings produced adventitious shoots in response to clipping 16 to 78 d following planting, presumably because new adventitious root buds formed (128). However, propagation of new shoots arising from vertical underground stems was not determined.

The depth distribution of Canada thistle roots in the soil profile is controversial. In Montana, most roots of 2-yr-old plants were found 7.5 to 30 cm deep (60). Fifty-four, 30, and 16% of the roots extracted were found at depths of 7.5 to 22.5, 22.5 to 37.5, and 37.5 to 52.5 cm, respectively. Estimates of the maximum depths to which roots extend also vary. Arny (8) observed that most roots grew no deeper than 40 cm while most horizontal roots were found 20 to 30 cm deep. Vertical roots grew 1.8 to 3 m deep in Minnesota (8) and 1.5 to 1.8 m deep in Iowa (56). Soil type influenced rooting depth. Maximum depths of 1, 1.8, 3.8, and 4.5 m were observed in sand or gravel, limestone, muck soil, and clay soils, respectively (34). Maximum depths of 2.4 to 2.7 m were reported elsewhere (73). A 10-yr-old undisturbed stand in Canada had roots extending down 2 m, but most roots were in the top 20 cm (92) (Figure 10). Restrictive soil conditions, such as hard pans, gravel or sand layers, alkaline or high calcium soil horizons, and high water tables, may restrict the maximum depth of root penetration (108). Roots can grow along ped faces in the subsoil[3].

There are few estimates of the numbers of adventitious root buds formed by Canada thistle plants over time. One example is presented in Figure 11. Canada thistle adventitious root bud densities are three to five times greater in late summer than in spring. Additional adventitious buds are formed as the growing season progresses but winterkill in a seasonally varying, cyclical fashion (22). The development of a washer for extracting Canada thistle roots from soil may facilitate further quantitative research on Canada thistle roots and adventitious root buds (21).

There are no commonly accepted standards for presenting quantitative data on adventitious root buds. Adventitious root bud numbers have been expressed: 1) per plant, but for plants must be grown in isolation, 2) per unit volume of soil, 3) per unit area of soil surface for a standard depth, and 4) per unit root length. Expressing both numbers of emerged adventitious shoots and adventitious root buds per unit area of soil surface (for a common sampling depth) provides a common basis for comparison for

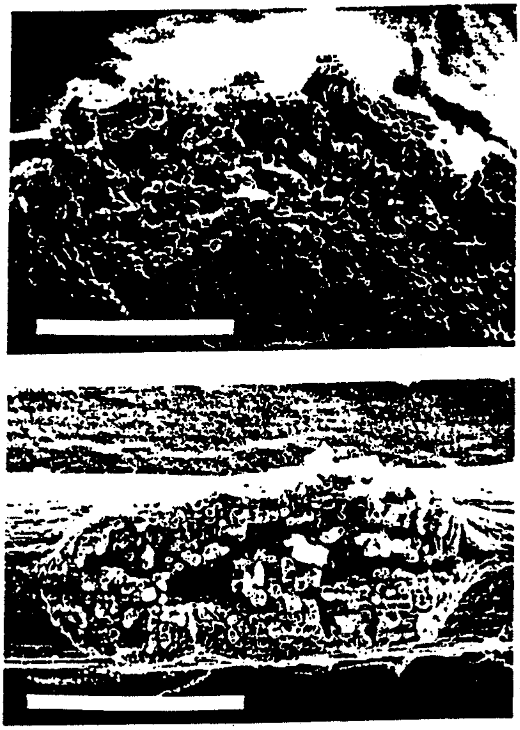

Figure 12. Scanning electron micrographs of callus and aerenchyma formation on the root surface (top) and in cross section (bottom) of hydroponically grown Canada thistle. Bars correspond to 1 mm in both micrographs (micrograph prepared by and used with the approval of Dr. Steven Carlson, 1991).

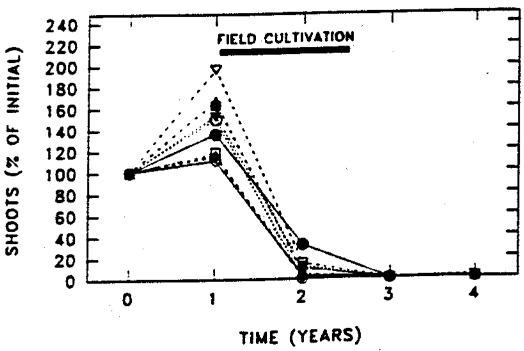

Figure 13. Changes in adventitious shoot emergence in mid-July of 10 ecotypes of Canada thistle over time. Established patches were field cultivated (solid black bar in figure) every 3 wk during the growing season for 1.5 yr between year 1 and 3 [Hodgson (61), redrawn by permission of *Weed Science*].

demographic research. Presenting adventitious root bud numbers per unit root length, without providing root length data, is misleading and precludes use of the data for other purposes.

The maximum depth of emergence of adventitious shoots from adventitious root buds was reported as 0.9 m in Canada (48). Adventitious shoots often emerged where horizontally growing roots extended downward (96). More adventitious root buds arose from horizontal than from vertical roots.

When left undisturbed, a single Canada thistle plant produced 26 emerged adventitious shoots, 154 underground adventitious root buds, and 111 m of roots ($\geq$ 0.5-mm diam) after 18 wk of growth outdoors in boxes (92). Year-to-year variation in root growth was observed (39, 93). Roots sampled down to 1.8 m produced an equivalent number of adventitious shoots compared to shallower sampling depths from a 10-yr-old undisturbed stand (92).

The drought tolerance of Canada thistle has not been compared with that of other species in the field. Although Canada thistle's perennial root system probably allows it to survive drought years better than annuals, its perennial root's biomass and numbers of adventitious root buds decrease after several years of drought (38). Drought influenced the relative distribution of Canada thistle roots in the soil profile by reducing the relative number of roots near the soil surface compared to well-watered plants (78). Drought can suppress subsequent shoot growth for 12 mo (3) by reducing root biomass and adventitious root bud numbers in the soil profile (38). Canada thistle patch thinning during dry weather has been attributed to autotoxicity (6), without experimental proof. When 10-cm-long root cuttings were dried to 20% moisture content or less, subsequent growth was severely reduced (46). In the greenhouse, 50-mm-long root cuttings, which were drought stressed by being placed in soil of moisture contents between 10 and 35%, did not differ in their ability to form roots, but formed progressively fewer shoots as moisture stress increased (54). A proportion of fragments under the greatest moisture stress formed either shoots or roots, but not both, suggesting to Hamdoun that drier conditions might limit adventitious shoot establishment. Shoot and adventitious root bud density of Canada thistle growing in continuous spring wheat decreased in the year following drought years (39, 40, 41) (Figure 11).

Canada thistle can survive flooding, but this stress reduced subsequent shoot and root growth. Plants growing in wet soil with a high water table had poorly formed and shallow roots (108). Flooding prevented flowering and reduced plant survival due to damping-off diseases (9). Roots of 10-wk-old seedlings grew abnormally in hydroponics (110). The root tips died, new lateral roots developed along the root, and adventitious

Table 4. Insects and nematodes found on Canada thistle.

Insect or nematode	Taxonomy	Damage	Origin	Limitations to adaptation	Reference
Altica carduorum Geurin-Meneville	Coleoptera: Chrysomelidae	Defoliates and feeds on floral buds	Europe	Failed to overwinter in northern U.S. & Canada	124, 99
Anuraphis cardui L.	Homoptera: Aphididae	Feeds on floral buds	United States	Not thought to be a good biological control agent	34
Capitophorus carduinus Walker	Homoptera: Aphididae	Not described	United States		34
Cassida rubiginosa Muller	Coleoptera: Chrysomelidae	Defoliator	Europe	Young plants defoliated ≥ 50% whereas old plants were not damaged Naturalized in eastern Canada Slow to establish in Montana	47, 90, 99, 127
Ceuthorhynchus litura (Fab.)	Coleoptera: Curculionidae	Stem boring beetle; mines leaf veins and root crown	Europe	Limited dispersal ability; transmits Canada thistle rust fungus *Puccinia punctiformis*	100, 104, 124
Cleonus piger Scop.	Coleoptera: Carculionidae	Root crown feeder; gall former at crown	Europe	Does not control Canada thistle; death of infected shoots is limited	47, 127
Ditylenchus dipsaci (Kuhn) Filipjev	Nematode	Root feeder	Canada		114, 127
Haetica cardurorum Guer.	Coleoptera: Chrysomelidae	Beetle	United States		60
Meloidogyne incognita var. *acrita*	Nematode	Root feeder	Indiana	Host	50
Meloidogyne hapla	Nematode	Root feeder	Canada	Root feeder	123
Orellia ruficauda (Fab.)	Diptera: Tephritidae	Seed feeder	Canada	Little effects on established stands in pastures	114, 127
Pratylenchus penetrans	Nematode	Root feeder	Canada	Root feeder	122
Urophora cardi (L.)	Diptera: Tephritidae	Stem gall former	Europe	Release in Canada and the United States; only slight impact on Canada thistle (reduce shoot height)	102, 127

shoots formed where lateral roots emerged. When 50-mm-long root cuttings were submerged for various periods of time, subsequent rates of adventitious shoot production were progressively reduced in less than 2 d. If cuttings were flooded for 0, 10, 20, or 30 d, shoots formed on 90, 50, 20, and 0% of cuttings, respectively. Canada thistle roots formed callus in hydroponics (Figure 12).

Tillage influenced the depth distribution of roots (34). In untilled grassland, horizontal roots extended from just below the soil surface to a depth of 75 cm, whereas horizontal roots formed only below the tillage zone in moldboard plowed fields. Tillage also breaks up the root system of Canada thistle, although it is not the only mechanism of subdividing and spreading Canada thistle roots. When limited sections or portions of roots die overwinter (22), surviving root systems with adventitious root buds (i.e., ramets) may be physiologically separated from one another, even though they were formed by a single parent plant (i.e., genet).

There are no estimates of root system persistence for established patches of Canada thistle. Hodgson (61) cultivated fields every 3 wk over 1.5 yr, to deplete the root biomass of 10 ecotypes of Canada thistle (Figure 13). He observed no regrowth in the year following the end of cultivation (year 3), which may provide

Table 5. Fungi found on Canada thistle.

Fungus	Damage	Comments	Reference
Puccinia obtegens (Link) Tul.	Foliar disease	Ecotype dependent infection	126
Puccinia punctiformis (Str.) Rohl.	Foliar disease which reduces flowering and seed production	Widespread in Canada; Transmitted by *Ceuthorhynchus litura*	100, 124, 127
Sclerotinia sclerotiorum (Lib.) de Bay	Crown and root disease leading to shoot death	Native to United State, found in Montana to cause 20 to 80% death of shoots	17
Septoria cirsii Niesl.	Foliar disease	Ohio	34

Table 6. Canada thistle mortality observed in July and August after *Sclerotinia sclerotiorum* treatment in early to mid-June in Montana (17) (reproduced by permission of *Weed Science*).

Location	Land use	Observation date	Dead shoots* Treated	Dead shoots* Untreated
			(%)	
Havre	Pasture	July 7	44 (± 6)	4 (± 3)
Moccasin	Cultivated	Aug. 28	79 (± 4)	50 (± 11)
Benchland	Pasture	Aug. 28	80 (± 7)	31 (± 4)
Corvallis	Cultivated	July 7	61 (± 7)	5 (± 2)
Huntley	Cultivated	Aug. 25	19 (± 1)	2 (± 1)

*Means (± standard errors) are presented.

Table 7. The residual effect of *Sclerotinia sclerotiorum* treatment on shoot density at two sites in Montana (17) (reproduced by permission of *Weed Science*).

Site	Treatment	Shoot density* Year 1	Shoot density* Year 2
		(no. m^{-2})	
Benchland	Treated	105 (± 26)	4 (± 1)
	Untreated	93 (± 24)	60 (± 9)
Corvallis	Treated	15 (± 2)	2 (± 1)
	Untreated	14 (± 2)	5 (± 1)

*Means (± standard errors) are presented. Observations were made in early to mid-July.

a preliminary estimate of root persistence until a more suitable experiment is performed.

Impact of parasites and microorganisms on survival. Seed predation prior to seed dispersal from the parent plant, on the soil surface after dispersal, and in the soil seed bank were discussed in earlier sections. Maw (84) and Moore (91) summarized information on insects found on shoots and roots of Canada thistle. Additional information on insects and nematodes found on Canada thistle is summarized in Table 4. Survey work continues to identify potential native biological control agents for Canada thistle (127). Biological agents for controlling Canada thistle have been reviewed (4, 90, 103, 124). Widespread adoption of foreign biological control agents is unlikely because of public concern for native thistles (99) and the general lack of effectiveness of currently available biological control agents. Unfortunately, many of the insects and nematodes listed in Table 4 are often widespread, persistent pests of important crop species, limiting their use on commercial farms.

The weevil *Ceutorhynchus litura* (F.) severely reduced overwinter survival of below ground adventitious shoots of Canada thistle to as little as 3% of that of uninfested shoots in Canada (100). In a 3-yr study in Montana, 8 to 12% of weevil-infested shoots survived from one year to the next compared with 94 to 99% of uninfested shoots (104). This stem feeder was not nearly as devastating in spring as in fall. Weevil damage also promoted the invasion of damaged shoots by other arthropods (mites, spiders, springtails), nematodes, and fungi, although the role of these organisms in plant death was not determined. The insect may have assisted in spreading the rust fungus, *Puccinia punctiformis* (Str.) Rohl. (100), although this assertion was not substantiated later (101). *C. litura* were released 18 times in the United States in California, Colorado, Idaho, Montana, New Jersey, South Dakota, and Washington between 1971 and 1975. In Montana, *C. litura* spread 9 km in 10 yr and the proportion of infested plants increased from 11 to 29% in 1977 to over 80% after 10 yr. In Canada, this insect did not greatly or consistently increase mortality of Canada thistle shoots (101).

Fungi and higher plant parasites found on Canada thistle have been reviewed (91). Most pathogenic viruses or bacteria reported on Canada thistle are diseases of crops, such as the tobacco rattle virus (27), limiting their potential for biological control of Canada thistle. Recent information concerning fungi found on Canada thistle is summarized in Table 5. Canada thistle is an alternate host for diseases and nematodes of crops (Table 4). The fungus *Sclerotinia sclerotiorum* applied to Canada thistle patches as a biological control agent killed 20 to 80%

of shoots in Montana (17) (Tables 6 and 7). Shoot emergence also was severely reduced in the growing season following treatment. However, *Sclerotinia sclerotiorum* is an aggressive, persistent pathogen on many broadleaf crop species, limiting its use on commercial farms.

OVERVIEW

The biology of Canada thistle has been studied chiefly because it is a persistent, hard-to-control perennial weed in many crops and it has a wide geographic range. Two different research approaches have been taken in studying its biology: life history studies in relation to its physiological ecology and population biology studies which attempt to quantitatively measure life cycle components of this weed. No eclectic, comprehensive model of its population biology has been put forward, although most elements for a matrix model of its life cycle are available in the scientific literature. Such a model might be useful in predicting the outcome of control measures (37).

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