

Review

## Managing *Cuscuta gronovii* (Swamp Dodder) in Cranberry Requires an Integrated Approach

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**Abstract:** Dodders (*Cuscuta* spp.) are parasitic plants that threaten the sustainability of many crops. Because this parasite is very adept and successful from biological and ecological perspectives, a single control strategy is unlikely to provide sufficient economic control. Dodder (*C. gronovii*) is a particularly serious pest in commercial cranberry (*Vaccinium macrocarpon*) production. Multiple viable strategies must be integrated and tailored into a weed management plan to provide acceptable control. The key to sustainable management of this serious pest will require a combination of chemical and cultural approaches, supported by understanding the complicated nature of dodder biology. Research from small fruit production systems like cranberry into the biology of dodder (e.g., germination patterns, host preference, use of plant growth regulators) may provide insights that could ultimately be useful for other crop system management plans. This paper will present the current knowledge base for integrated management of dodder in cranberry as well as highlight relevant research from other crops and potential topics for future research.

**Keywords:** parasitic plants; *Cuscuta*; weed management; IPM; *Vaccinium macrocarpon*

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### 1. Introduction

Dodders are obligate parasitic plants consisting of yellow twining stems that produce small clusters of white flowers [1]. The stems will wrap around the host (Figure 1) and insert specialized structures (haustoria) into the vascular system of the host and become a strong sink for photosynthates. Although several species of dodder are considered to be pests in certain agricultural contexts, the parasite is also

noted for its potential for biological control for other weeds [2,3] and serves as an important species in various ecosystems [4,5].

**Figure 1.** Dodder climbing and encircling a cranberry stem.



Although typically considered an annual, overwintering of dodder haustoria can occur [6,7], enabling the parasite to produce shoots in the spring without relying on seed germination. Prodigious numbers of seeds are produced by *C. gronovii* in a given year [8]. Its seed is very long-lived and germinates over many years [9], increasing the probability that its progeny will encounter suitable environmental conditions for growth and reproduction. Emerging independent of a host, a seedling can search (circumnutate) for several days for a suitable host [10]. In cranberry, *C. gronovii* parasitizes the vine to the extent needed to ensure its own survival; it weakens, but rarely kills its host. An infected crop plant can survive but is deprived of enough nutrients and carbohydrates to greatly diminish its ability to produce viable commercial yields [11].

Dodder has other characteristics that enable it to establish in many types of agroecosystems. Haustoria of *C. gronovii* present within the host tissues may regenerate new stems [12], potentially negating control efforts from mechanical removal of exterior stems. Though generally thought to be devoid of chlorophyll, some species do have the ability to photosynthesize even if in a limited fashion [13-15]. Dodder seed can successfully survive ingestion and processing in an animal rumen [16], adding another layer of concern for those who raise livestock and crops. Typical horticultural practices, such as harvesting, can facilitate the dispersal of seeds if dodder seeds are not easily separated from crop plants [17]. When cranberries are harvested, fruit are usually removed in shallow flood waters that are recycled from bed to bed during the harvest season. Since swamp dodder seeds are borne in capsules that can float in water and are logistically difficult to completely separate from the cranberry fruit, dodder seeds can be readily distributed from bed to bed and from farm to farm.

Swamp dodder is a serious threat to the sustainable production of cranberries in Southeastern Massachusetts [18,19] and other cranberry production areas including New Jersey and Wisconsin. In commercial production areas, dodder spreads rapidly, damages cranberry vines significantly and can reduce yields 80% to 100% [18-20]. Many management options available to growers of annuals crops

(e.g., altering time of planting, crop rotation, resistant varieties, *etc.*) are not possible in cranberry. Loss of control options for this one weed pest would seriously jeopardize the economic sustainability of Massachusetts cranberry farms. The key to sustainable management of this serious pest will require a combination of chemical and cultural approaches, supported by understanding the complicated nature of dodder biology. The objectives herein are to review the current knowledge of IPM for dodder in cranberry, to highlight related management research from other crops and suggest potential topics for future research.

## 2. Cranberry and Dodder Phenology

Cranberries are perennial plants and produce a single crop each year. The plant has short (ca. 10 cm) vertical stems (uprights) that grow from buds produced on stolons (runners), which can be 1 to 2 m in length. A stand of cranberry vines is a mixture of vegetative and reproductive uprights as well as runners (Figure 2) and forms a continuous mat of vegetation on the production area. A system of ditches, to facilitate movement of water for flooding and improve drainage, typically bounds the bed on all sides; additional ditches may also be placed in the center of the bed [21].

**Figure 2.** Schematic of cranberry uprights (vegetative and reproductive) and stolon growth [24].



Flower buds are initiated in the year before the crop is harvested, beginning in mid-summer. The buds, present at the same time as expanding fruit, develop through the fall, eventually becoming dormant. The dormant state lasts until the plant has been exposed to sufficient chilling hours. In response to increased temperature and day length, the terminal bud begins to lose dormant color and swells (April). This corresponds to the time at which initial dodder seedlings may be germinating in warm areas of the bog or in nearby stockpiles of leaves dislodged by harvest operations. By late May, buds have begun to expand and lengthen, and new leaves and flower buds are visible. If dodder seedlings are present, they can parasitize the expanding new growth. Pre-emergence herbicides are usually timed to impact the greatest number of emerging seedlings [9] but before extensive cranberry

shoot expansion has occurred (to minimize crop injury). This would also correspond to the time at which short-term floods could be used to control dodder as well as other insect pests [22,23].

It had been observed that herbaceous weeds on cranberry bogs may serve as initial hosts during the early spring (M.J. Else, unpublished data). Although recent research has shown that older plants of *Calluna vulgaris* limit the establishment of *Cuscuta epithymum* [25], the relationship of cranberry vine age and the establishment of *C. gronovii* has not been documented. Field observations by the author indicate that as the cranberry uprights expand with new succulent growth, dodder parasitizes the elongating cranberry stems (see Figure 1) in preference to the older woody stems. Substantial dodder growth can be easily noticed by late May-early June. In early June, the uprights continue to increase in length (new leaves formed) and the first flowers open. The flowering period begins during the middle of June and lasts three to six weeks, with the first berries visible in late June or early July. *C. gronovii* stems will continue to grow and form a mat on the top of the vine canopy during the bloom and fruit set periods of the cranberry.

Dodder flowers in July and August in Massachusetts and seeds are set prior to the cranberry harvest, which occurs from mid-September through early November. Most cranberries in Massachusetts are harvested in shallow floods using mechanical water reels (rotating heads with slats that dislodge the fruit from the pedicel). The movement of the water harvesters through the beds may also dislodge the dodder seed capsules, produced on weeds and cranberry uprights, into the water. Some seed capsules are removed when leaf debris is separated from the cranberry fruit, but much of the dodder seed remains on the bed or may be transferred to another location on the farm when the floodwaters are re-used for more harvesting activities.

After harvest, the beds are flooded again for several days to remove more of the detached leaves generated during harvest, but there is no practice that removes all cranberry leaves and/or dodder seed capsules. These plant parts are then deposited on the floor of the bog when the flood is withdrawn. By the end of December, many beds will be flooded from several weeks to several months to prevent desiccation of the plants [26]. Another horticultural practice is to apply thin layers of sand during the winter or early spring to help anchor runners and encourage upright growth [27]. Thus, dodder seed present on the ground may be covered (to varying degrees depending on the season) with leaf debris and/or sand. The seeds represent a robust seedbank capable of germinating the following season [9]. It is also possible that additional dodder seed may be deposited onto the bog when the sand is applied [28].

### 3. Host Preference, Seeds, and Taxonomy

#### 3.1. Host Choice and Preferences for Dodder

Categorized as a generalist since it is known to parasitize many plant species [1,29-32], *Cuscuta* species do vary in their degree of host specificity [29,33]. *C. gronovii* has a wide host range [30,34] and has been observed by the author to parasitize a broad range of hosts including species of *Euthamia*, *Cyperus*, *Aster*, *Rubus*, *Lysmachia*, *Panicum*, *Poa*, *Acer*, *Smilax*, and *Vaccinium*. Survey

data indicated that seed production of *C. gronovii* is greater on certain weed hosts (e.g., *Euthamia* sp.) in commercial cranberry (H. Sandler and J. O'Connell, unpublished data).

Host choice by *Cuscuta* species may be influenced by many factors. Kelly (1990) reported the association of host secondary metabolites (e.g., flavonoids) and successful growth of *C. subinclusa*. Cytokinins have been implicated in haustorial development of *C. campestris* [35]. An Italian group reported on the importance of phototropism for host selection for *C. campestris* [36]. In addition, a report on the role of volatiles and host selection for parasitic plants [37] broadens the thesis that dodder is discriminating among hosts and “making choices”. Jasmonic acid (JA) and salicylic acid (SA), plant hormones positively associated with the expression of induced plant defenses, may affect host selection; a review of relevant work with regards to JA- and SA-mediated defense responses was recently published [38]. Host vigor or quality may also play a role in determining the choice of resource acquisition for *C. subinclusa* and *C. europaea* [39,40]. Tall plants have been shown to be a preferential trait in host choice for *C. gronovii* [41].

### 3.2. Seed Longevity and Factors Affecting Emergence

The seeds of *C. gronovii* are known to survive for up to 30 years in dry storage [30]. The emergence and viability of Massachusetts dodder seed have been monitored for 12 years utilizing a system of simulated bogs maintained in an outdoor environment; collected data support the longevity of the seedbank of *C. gronovii* [9]. The highest germination percentage occurred from seeds that were most recently deposited into the seedbank; subsequent generations had declining germination percentages. Over the course of this 12-year study, the peak germination period was delayed relative to the first year, occurring later each year. Thus, overlapping generations may exist in an infested cranberry farm. The delay of peak germination from resident populations in the seedbank extends the potential germination period of dodder. These factors likely contribute to the difficulties with managing dodder in cranberry. Since most herbicides targeting dodder can only be efficacious for a specific window of time, a portion of the population may always escape preemergence control and provide enough viable seedlings to cause substantial infestations in the vine canopy.

Many control strategies for dodder target newly emerged seedlings [42]. However, it is not a simple task to predict the emergence of dodder seedlings in Massachusetts. The starting point for accrual of growing degree days (GDD) for Massachusetts has been difficult to identify since winter and spring conditions on the farm are highly variable. Although the emergence of dodder in Wisconsin was predicted by using a low temperature threshold model [43], despite attempts to create one, a working model has not been developed for Massachusetts conditions [44]. Wisconsin farms experience definitive demarcations of conditions (*i.e.*, the farms are flooded and the waters stay frozen for several successive months) by which one can accurately initiate the accrual of GDD. Currently, warm areas, bare areas, or piles of abscised leaves that contain dodder seed capsules are inspected for newly emerged seedlings and management decisions in Massachusetts are based on those observations.

Cultural practices and environmental conditions can affect dodder germination and emergence in cranberry. In Massachusetts, application of thin (1.5–5 cm) layers of sand is a common cultural practice that buries stolons and encourages upright production [27]. Burial of seeds under sand depths of at least 2.5 cm can inhibit *C. gronovii* emergence, though seedlings did emerge from burial

under 5 cm of sand [10]. Similarly, germination of *C. approximata*, *C. campetris*, and *C. monogyna* also decreased with increasing depth of burial, although some emergence was reported from seeds buried under 4 to 8 cm of light clay [45]. Germination is increased when the seeds of *C. gronovii* are scarified [30,46]; however weather conditions in Massachusetts usually provide appropriate temperatures to physically break dormancy. Since the farms are flooded during the winter, water that is needed for imbibition during germination [47] is adequately available. As mentioned above, harvesting is a cultural practice that facilitates dispersal of seed capsules. The redistribution of capsules in the flood waters is usually patchy, and predicting exactly where successful infestations might appear is difficult. Since seedling emergence may occur at different times and in different locations on the farm in any given year, control efforts with localized applications of preemergence herbicides is severely limited.

### 3.3. Taxonomy of Dodder Species in Cranberry

In Massachusetts, the dodder that parasitizes cranberry has been assumed to be the single species, *C. gronovii*. However, a sample collected from a cranberry farm in Marion (Plymouth County), MA in 2006 was identified to be *C. cephalanthi* Engelm. The specimen was collected on 22 September 2006 (J. Cascino, Sylvan BioProducts, Kittaning, PA) and identified on 4 October 2006 (B. Davis, University of Florida Herbarium (FLAS), Florida Museum of Natural History, Gainesville, FL 32611). Phenotypic differences of various infestations observed by the author in the field may represent species other than *C. gronovii*. Although management strategies would likely not differ for different dodder species, it would be interesting to catalog which species are present and capable of infecting cranberry. Future work could involve collection of dodder samples from various farms in Massachusetts, Wisconsin, and New Jersey, which could then be identified. Surveys of this nature could provide important information about the distribution and characteristics of *Cuscuta* species in cranberry production in the United States.

## 4. Current Chemical Options

When chemical recommendations were first initiated in the 1960's, dodder was not considered to be a serious pest for cranberry production. In 1966, only 1% of surveyed cranberry operators classified dodder as first in importance for weeds needing control. Using a scale where 100 equated to most important, dodder was given a very low composite score of nine [48]. The importance of dodder as a pest has grown over the past 40 years. It is believed that the increase is related to the large-scale adoption of water harvesting (which facilitates seed capsule dispersal) by the industry. Dodder is now considered a Priority One weed, which indicates that it spreads quickly, is hard to control, and severely reduces yield [20]; it is considered to have a zero threshold [42]. Chemical control has been the primary tool for dodder control, but nonchemical methods, such as short-term floods [49,50] and flame cultivation (K. Ghantous, unpublished data), hold promise and are discussed below.

### 4.1. Preemergence Options

Recommendations for dodder control in Massachusetts were first published in 1962. In that year, iron sulfate was the only recommended control. Chloropropham (CIPC) appeared on the recommendation charts in 1963 and was actively recommended through 1990, the year EPA announced its intention to revoke the tolerance for the herbicide (the tolerance was revoked in January 1999). Dichlobenil (Casoron, Norosac) was first recommended for use against dodder (and broadleaved weeds) in cranberry in 1965; low-rate applications in mid-May are still recommended for dodder control in 2009 [42]. The first emergency exemption (Section 18) permit for the use of pronamide (Kerb) for dodder control was granted in 1998. This very effective compound was permitted on an annual basis until 2008 when the Section 18 request was denied by EPA; full label registration seems highly unlikely.

Preemergence herbicides are typically applied to the soil to stunt early dodder growth such that attachments to a susceptible host are unsuccessful. Many compounds are currently listed for control of dodder in crops other than cranberry (Table 1). A recent paper gives a review of herbicide usage at the turn of the 21st century [32]. Although the present article is written only four years hence, changes have already occurred as some uses have been dropped from labels and others added. Although pronamide is no longer used in cranberry, it is used on alfalfa against dodder [51] and on sugar beets in Oregon. Dichlobenil is still recommended in blueberry production. No preemergence herbicide is 100% effective, so escapes can occur and postemergence options must be employed in most situations.

**Table 1.** Herbicides currently available for dodder control in various crops.

Host	Herbicide
alfalfa	trifluralin, pronamide, pendimethalin, ethalfluralin, glyphosate, N-phuric acid
onion	DCPA
tomatoes	DCPA, rimsulfuron (suppression); glyphosate.
sugar beets	glyphosate, ethofumesate, metolachlor, trifluralin, pronamide
carrot	pendimethalin, paraquat dichloride
blueberry	dichlobenil
cranberry	dichlobenil, mesotrione

Some herbicides are available on a limited basis (e.g., *via* Section 18 permit or special local needs permit).

Dichlobenil is the only preemergence herbicide currently recommended in cranberry and its use can be particularly challenging. Currently, dichlobenil is available only as a granular material and must be applied by a drop spreader. A skilled operator working on a regularly shaped continuous bog can treat about 5 ha per day (B. Gilmore, personal communication). The window of opportunity to apply a granular material during a typical New England spring can be limited. Conditions can be rainy (which preempts application) or cold (which means vines will be wet from many hours of frost protection). To avoid injury to new cranberry growth, low rates (<67 kg/ha) are recommended [42]. Dichlobenil quickly dissipates when temperatures exceed 15 C and the maintenance of an effective dose level may be quickly lost. For dichlobenil to be most effective, it must be applied prior to germination. To determine this biofix, one must scout areas that are likely to have dodder seeds (e.g., areas where the fruit is removed during harvest) or bare areas (which warm faster) for newly emerged seedlings; the

seedlings can be very difficult to find (Figure 3). Due to these logistical constraints, applications are frequently made too early or too late and control is often less than satisfactory [52].

**Figure 3.** Newly emerged dodder seedlings, which are used as a biofix for timing preemergence herbicide and short-term flooding control strategies.



Dichlobenil primarily affects seed germination and seedling emergence and has some effect on emerged seedlings that have begun to attach to a host [53]. In Dawson's work, injury to attached seedlings was only temporary and shoot development from haustoria occurred as described by Truscott (1958). It is not known if seedlings that successfully emerge from dichlobenil applications on cranberry farms are similarly proficient in seed production as untreated seedlings, but this could be an area of future research. Anecdotal observations indicate that dichlobenil applications do not substantially decrease dodder seed production unless the majority of seedlings are controlled. Repeated annual dichlobenil applications do not impact yield of cranberry [54].

#### 4.2. Postemergence Herbicides

In cranberry, emergent dodder infestations coincide with cranberry bloom and fruit set periods. Since cranberry is a low-growing trailing perennial that is horticulturally managed to form and sustain a continuous canopy across the production area, control methods that require walking or riding on the vines during bloom and fruit set are not readily embraced. Thus, herbicides that can be applied *via* the irrigation systems (chemigation) or *via* ground applicators that ride on the dike are favored.

In terms of herbicides, the greatest challenge is to find a compound that will kill the parasite but not kill or severely injure the host. Spray solutions of nitrate of soda were recommended from 1973 to 1978 for postemergence dodder control. Mesotrione (Callisto) was first used for postemergence control of dodder and other weeds in Massachusetts in 2008. Mesotrione was applied postemergence at 140 and 280 g a.i./ha (either once or twice before or once after the dodder flowered) at two commercial Massachusetts farms in 2008 and 2009 [55]. In the first year (2009 samples are being processed), the production of seeds visually assessed as healthy (*i.e.*, good color and appearance with uniform shape) was reduced by at least 66% when mesotrione was applied at any tested timing or rate compared to the control except one application of the low rate before flowering (BF). Percentage

germination of healthy seeds was lower in most treatments compared to the untreated and low-rate-BF single application treatments. Cranberry is known to be quite tolerant to mesotrione [56] and yields are not reduced [55], though temporary discoloration of uprights has been observed by the author. Mesotrione can be chemigated (*i.e.*, applied through the irrigation system) in Massachusetts, which means the herbicide can be applied without walking or riding on the vines.

Quinclorac is another herbicide that may offer good control in cranberry and potentially other crops. A small data set collected from Wisconsin in 2008 indicated that 420 g a.i./ha of quinclorac (dry flowable formulation) applied at the end of June (early postemergence) was extremely effective for control of dodder (J. Colquhoun and J. Perry, unpublished data). A single application made in mid-July was not as effective. Based on these preliminary data, an emergency exemption permit (Section 18) was granted to Massachusetts by EPA in 2009 for the use of quinclorac. Results from Wisconsin indicated that earlier applications of the dry flowable formulation are more efficacious than later applications. A liquid quinclorac formulation was used in Massachusetts and control was poor. However, applications were made in mid-June to mid-July, which may be too late. More studies are planned to determine why the two states had different results with the same active ingredient.

Glyphosate-resistant crops, such as sugar beets and alfalfa, offer another means of controlling dodder with postemergence chemical applications. *C. gronovii* and *C. monogyna* are reported to be susceptible to glyphosate [57,58] and growers have reported excellent dodder control on their farms using the herbicide in conjunction with glyphosate-resistant crops (T. Lanini, personal communication). Although ornamental plants differ in their sensitivity to glyphosate, low rate applications to multiple species adequately controlled *C. campestris* [59]. Injury to the host plant is of primary consideration if utilizing glyphosate in a dodder management program. In cranberry production, the use of herbicide-resistant varieties is not available and the prospect of developing the technology for this perennial crop is unlikely.

#### 4.3. Plant Growth Regulators (PGRs) and Other Products

Dodder is a prolific seed producer; a major goal for management of this parasitic plant for the long term is to reduce the seedbank [42]. If flowering and/or seed production could be retarded or aborted through the applications of PGRs or other chemicals, significant progress could be made towards controlling this weed.

Ethylene is involved with fruit ripening, leaf and flower senescence, and leaf and fruit abscission [60]. Cranberry researchers studied the impact of ethephon (an ethylene inducer) for postemergence control of *C. gronovii* in field experiments in 1992–1994 [61]. They applied ethephon at 2,500, 5,000, 7,500, and 10,000 ppm in 40 GPA water and found partial control at all rates, with increasing control at the highest rates. Some negative yield effects were noted, but not greater than those caused by dodder infestations. Unfortunately, additional work with this compound for dodder control was not pursued.

Cytokinins, produced primarily in root tips, are involved in cell division, promotion of shoot formation in tissue culture, the delay of leaf senescence and the release of apical dominance [60]. Cytokinins have been associated with the promotion of haustorial development of *C. campestris* [35]. Evaluation of various phytohormones indicated that zeatin (a natural cytokinin isolated from maize,

*Zea mays*) induced coiling and prehaustorial formation in *Cuscuta* [62]. Auxins or indole acetic acid (IAA) are hormones involved with apical dominance, vascular tissue differentiation and the inhibition or promotion of flowering and abscisic acid (ABA) is involved with stomatal closure, stress response, and inhibiting gibberellin signaling [60]. The inhibition of cytokinin-induced haustorial formation of *C. reflexa* has been associated with IAA, ethylene, and ABA [63]. 2,4-D caused abnormal stem growth of *C. gronovii* [64], but was not as effective as other herbicides for inhibiting germination of *C. campetris* and *C. trifolii* [65].

Gibberellins are associated with hyperelongation of shoots, induction of seed germination, and stimulation of flowering [60]. Gibberellic acid (GA3) is important for the growth of shoot tips of *C. chinensis* and the lack of GA3 reduces the transports of auxin [66]. Gibberellins and similar substances have multiple growth effects in cranberry including increased shoot growth in cranberry [67], increased fruit set, and decreased bud set in cranberry [68], which impact sustainable fruit production.

Other products have been evaluated for their impact on flower removal of cranberry and might be used for removal of dodder flowers. Paclobutrazol is a triazole-type plant growth retardant that blocks gibberellin biosynthesis and is involved in reducing ABA, ethylene and IAA while increasing cytokinin levels [69]. It has been reported to induce flowering and retard vegetative growth in microcultured cranberry plants [70]. Ammonium thiosulfate (ATS) is a liquid fertilizer (12-0-0) and has been reported to injure cranberry flowers by chemically burning them (J. Polashock, personal communication).

Common nontoxic, biodegradable household products may have beneficial applications in dodder management. The efficacy of three nontoxic household cleaners (white vinegar, liquid dish detergent, and butyl cellosolve (Simple Green®), were tested for control of post-attachment dodder in greenhouse and field conditions on cranberry farms [71]. Two subsequent studies evaluated the impact of four sprays of glyphosate, neem oil, and butyl cellosolve applied weekly to dodder parasitized to alfalfa in the greenhouse and to cranberry in the field. Butyl cellosolve (20% solution) was the most effective treatment for increasing dodder necrosis without harming the cranberry vines.

Foliar applications of an effective PGR or flower-burn material would provide a low-labor, low-cost method to remove or inhibit flower development in dodder. To explore this potential, a project was initiated in 2009 in Massachusetts to evaluate the use of PGRs for dodder control. The impact of these compounds on the health and fecundity of the cranberry vines is critically important. In a nonreplicated, demonstration study, low and high rates of ATS, ethephon, ABA, and GA were applied before and after the flowering period of dodder to determine the effect of PGRs on cranberry and dodder. Dodder had higher injury ratings with post-flowering applications of ethephon, ABA, and GA; rate of the compound did not seem to impact injury rating [72]. Since cranberry injury appeared to be very minor, the utility of these compounds for dodder control in cranberry will be pursued.

#### 4.4. Phenolics and Metabolites

Phenolics and metabolites are not actively used for dodder management in cranberry, but could be areas of future research. Several phenolic compounds derived from weed extracts that were phytotoxic against *C. campetris* on alfalfa have been identified [73]. Concentrations of aqueous extract of every

tested weed showed significant effectiveness against dodder compared to the untreated control in both greenhouse and field conditions. The content of phenolics varied by weed species with Bermuda grass (*Cynodon dactylon*) having the highest content. Alternatives to traditional approaches for dodder management in alfalfa and potentially other crops as well could be further explored.

The use of natural metabolites as potential inhibitors against parasitic plants (primarily *Orobanche* species) has been recently reviewed [74]. The review also includes the authors' data that indicated that the 10 tested fungal phytotoxins were not inhibitory to seed germination of *C. campestris*. However, several compounds (including ophiobolin A and fusicoccin at concentrations below 1 mM) inhibited seedling growth; inhibition decreased as concentration of the phytotoxin decreased. Preliminary studies with *Striga* and *Orobanche* species indicated that certain amino acids can have an inhibitory effect on seed germination [75]. Future research could certainly include evaluation of amino acids and other natural compounds as possible inhibitors of *Cuscuta* seed germination and seedling growth.

## 5. Current Nonchemical Methods

Nonchemical control methods are desirable for many reasons including potentially lower environmental impact, improved public relations, and increased interest for organic farm products. Preventing initial and sustained movement of seed into the farm area is the best nonchemical approach. Equipment should be cleaned when moving between infested and clean farms. Efforts should be made to minimize movement of seed capsules in harvest waters. Application of thin layers of sand to the cranberry vines [10] and short-term floods [50] can control a portion of early emerging dodder population in cranberry production and will be discussed below. Control of early season weed hosts have been observed to diminish dodder infestations in alfalfa [53] and cranberry (M. Else, unpublished data), but these observations should be validated in a replicated study.

### 5.1. Mechanical or Hand Removal

Mechanical or nonchemical removal of infestations can be used for dodder control [42,76]. The removal of stems has many benefits, including increased sunlight penetration into the canopy, reduction of photosynthate loss in the host plant, and the potential to reduce the number of seeds produced by the parasite by reducing overall biomass [77]. Any practice that leads to decreased seed production should aid in the reduction of future dodder infestations on the production area. In cranberry production, mowing around ditches and reservoirs to reduce the number of weed hosts for dodder is a recommended practice [42]. The removal of the parasite early in the season by hand (very labor-intensive) or during the postharvest (de-trashing) flood helps to minimize the spread of dodder within the farm. Hand-held bamboo rakes are also used to break the mat of dodder stems that have twined around cranberry uprights during mid-summer when dodder is flowering. Raking dodder infestations is beneficial if the infestations are severe [77]; no additional benefits were obtained by raking more than once. Raking is normally conducted when cranberry fruit are present and may detach fruit from the pedicel. Multiple rakings may dislodge many more fruit, making treated areas as low-yielding as the infested areas.

### 5.2. Flooding

Often used for cranberry pest management in the early to middle decades of the 20th century [78], flooding fell out of favor during the 1950's–1980's with the development of inexpensive pesticides. Recent research showing that spring (late water) re-floods [79] and fall floods (floods held for several weeks after fruit are removed) reduce weed and insect populations in cranberry farms [50,80] has supported a resurgence of flooding for pest management. Late water floods (typically 30-day floods) are effective enough to reduce pesticide (usually insecticide and fungicide) inputs during the year of implementation and sometimes, for the subsequent year as well [79]. Holding a flood is typically inexpensive, and late water and fall floods can be readily incorporated into IPM programs [81].

At the onset of the cranberry economic crisis that occurred in 1999–2000, one large-scale cranberry operation in Massachusetts opted to hold several 18- to 30-hour floods during May to control dodder. Data from this company indicated a 65 to 89% reduction in pesticide use for dodder management when short-term spring floods were implemented during 2001–2003 compared to the previous three-year period. Using the lack of dodder growth as an indicator, the company felt the floods were successful. A two-year demonstration project was initiated in 2002 that documented intermittent efficacy of short-term floods [50]. Subsequent studies indicated flooding four weeks after the first seedling emergence (biofix) resulted in the lowest mean attachment ratings in both years [49] compared to floods initiated one, two, or three weeks after the biofix. Further studies on the effect of water temperature and flood duration indicated that although germination decreased as water temperature increased, percent germination was never reduced enough to make a practical management impact [72]. If spring flooding is used in lieu of herbicide application for dodder control, this cultural practice could save money and provide environmental benefits due to overall lowered pesticide inputs.

Post-harvest floods are used in cranberry production as a sanitation measure to remove abscised leaves, stems, and fruit from the production surface. These plant parts float on the surface of the water and are wind-driven to an edge where the debris can be collected for disposal. A post-harvest flood can remove a portion of dodder seed capsules from the bog and is a recommended practice [42]. If all capsules are not removed (a likely event), floods can spread seed when the water resource is pumped from farm to farm. Cranberries are at risk for carbohydrate reduction with fall floods [82,83] so care must be taken when utilizing this cultural practice. Although flooding is used for weed management in rice cultivation [84,85], *Cuscuta* spp. are not considered pests.

### 5.3. Sanding

The periodic application of a thin layer (1 to 5 cm) of sand over cranberry vines during the dormant season is primarily used to stimulate rooting and production of uprights [27]. Other than its use in turf as a dressing [86] and for pest management [87], the application of sand is a specialized cultural practice linked to cranberry production. Sand can be applied directly onto dry vines by ground rigs that ride on the vines (dry sanding) or on rails (rail sanding), applied during the winter on top of frozen flood waters (ice sanding), or delivered *via* a floating barge in shallow flood waters (barge sanding) during the spring or fall [88]. The application of at least 1.3 cm of sand on top of dodder seeds was needed to reduce seedling emergence in greenhouse tests; seedling emergence decreased more

than 66% with 2.5 cm of sand [10]. Sand has additional pest management benefits including burial of cranberry girdler (*Chrysoteuchia topiaria*) pupae and reduced fruit rot inoculum survival [89].

Pest control often depends on the deposition of uniform layers of sand. Recent research reported that the majority of measurements of sand depths actually deposited to the bog floor were much lower than the target depth [90]. In fact, deposition patterns were very irregular and would reduce the expectation of pest suppression that requires a uniform layer of sand, such as dodder. To achieve consistent pest management benefits from sanding, improved technology is needed to deposit uniform layers of sand to the production surface.

#### 5.4. Flame Cultivation and Solarization

Flame cultivation has been used in agriculture for decades and dodder has been the target pest in several studies. Exposure to the intense heat generated by a propane-butane flame cultivator in July effectively reduced *C. campestris* infestation in sugar beet (*Beta vulgaris*) and did not allow sufficient time for the dodder to set seed [91]. Flaming also controlled dodder (*Cuscuta* spp.) and burned stubble of lucerne (*Medicago sativa*) [92]. A combination of chlorpropham and flame cultivation was needed to control *C. arvensis* and *C. epithimum* in lucerne [93].

A new research project in Massachusetts, supported by Pesticide Environmental Stewardship Program funds, is exploring the efficacy of flame cultivation to control dodder in cranberry [94]. In 2008, dodder was exposed to various durations of infrared (IR) or open flame (OF) cultivators at three timings: after dodder flowering (AF) but before seed formation, during seed formation (SF), and at seed set (SS). Preliminary results from the SF treatment show that areas treated with all exposures of the OF had significantly less dodder cover than the untreated areas, while dodder cover did not appear to be reduced by the IR (K. Ghantous and H. Sandler, unpublished data). In addition, data indicate that exposure to OF and IR may reduce viable dodder seed number, and that the effect may be more pronounced for treatments conducted during SF than those conducted during SS. Germination viability may be related to the interaction of flame cultivation, length of exposure, and treatment timing. Negative impacts on cranberry growth seem to be minimal and short-lived [94,95]. The use of flame cultivation may provide a nonchemical option that could be easily incorporated into an integrated program for dodder and general weed management, providing that the crop is not irreparably injured.

Solarization has been used to reduce weed seed germination for many years. However, the effect of solarization on dodder seed is not well studied. Work from Lebanon indicated that scarified seed of *C. campestris* needed 10 days of solarization for significant reduction of germination; unscarified seed required six weeks of solarization for significant reduction [96]. Though not practical for cranberry farming, further investigation into applying solarization as an additional management strategy for dodder control in other crops seems warranted.

#### 5.5. Dodder Resistant Varieties

Resistant varieties are not currently available in cranberry production. Research has been proposed to examine cranberry cultivar resistance to *C. gronovii* using both no-choice and choice assays in the greenhouse and field (L. Adler, personal communication). Data collection will also quantify volatiles,

JA, SA, flavonols, and phenolics in leaves, flowers and fruit of plants with and without swamp dodder. It is anticipated that the results will enhance our basic understanding of the physiological response of different cranberry cultivars to infestation by *C. gronovii*.

Resistant varieties are employed in other crops and several examples are listed here. Several varieties of processing tomatoes have been observed to be either totally resistant or tolerant to dodder [97,98]. In greenhouse tests, lespedeza dodder (*C. pentagona*) germinated, made contact, twined around tomato stems, and adhered to them. In most cases, however, haustoria failed to penetrate into the stem, eventually leading to the death of the parasite. In field studies, lespedeza dodder attachments were 75% less on tolerant varieties, and dodder growth was reduced by more than 70%. In addition, larger stem diameters seem to be parasitized less than stems with smaller diameters. Greenhouse studies on black gram (*Vigna mungo*) and green gram (*V. radiata*) have also indicated varietal differences to *C. chinensis* attachment [99] that could be potentially exploited in agricultural systems. Several varieties of green gram showed considerable resistance while only two varieties of black gram showed some tolerance. A varietal response to dodder parasitism has been recently reported in carrot [100].

Vascular connections were not well established in kidney bean (*Phaseolus vulgaris*) due to increased cellular proliferation and an accumulation of polyphenolic compounds in and around haustoria attachments generated from *C. reflexa* [101]. Other legumes exhibited variation in their susceptibility to dodder parasitism [102,103]. Kidney bean and vetch (*Lathyrus sativus*) were among the most resistant and lentil, chickpea and alfalfa were among the most susceptible [33]. Parasitism of *C. chinensis* on cluster bean (*Cyamopsis tetragonoloba*) was stunted and abnormal and the authors suggest the investigation of the active compound related to this host resistance as a potential bioherbicide [104]. External application of a propeptide could lower infection rates of *C. reflexa*; the propeptide and its associated promoter might be useful in the development of resistant plants [105]. Host resistance could be integrated into a sustainable management program for some annual crops and is a good area for further research.

## 6. Biological Control with Fungi, Insects, and Bacteria

*Alternaria destruens* has been identified as a pathogen of dodder [106,107]. The commercial availability of the mycoherbicide has been hampered by many production problems over the past 20 years. However in 2006, a manufacturer in Pennsylvania (Sylvan BioProducts) registered the product, Smolder®, for dodder control on cranberries in Massachusetts. Two formulations were registered: a preemergence granular and a postemergence wettable powder. Supported in part by the IR-4 Biopesticide Program, scientists from Massachusetts, Wisconsin, and Sylvan collaborated to conduct field trials. Results from 2006 indicated that timing and application procedures needed to be more clearly defined to maximize the performance of Smolder [108]. However, results from replicated trials conducted in 2007 in both Wisconsin and Massachusetts indicated that Smolder did not perform reliably in the field [109] and further development of a commercial product is not being pursued at this moment.

Combinations of *A. destruens*, glyphosate, and ammonium sulfate and have been evaluated for control of dodder (*C. pentagona*) on citrus [110]. In many of the tested combinations, the host and the

parasite were adversely affected. In greenhouse studies, the highest disease or damage severity rating was obtained with a mixture treatment (*A. destruens* + oil + glyphosate + ammonium sulfate). By 35 days after treatment, all field dodder plants that received the mixture treatment were dead but the host plant, citrus, was not.

Several strains of *Colletotrichum* have been noted as potential components for development as commercial mycoherbicides [111,112]. As early as 1958, *C. destructivum* was noted as a possible dodder pathogen for alfalfa but further development was not pursued [113]. Another strain, identified from infected soybean in China in the 1960s, was named Lubao 1; research on this bioherbicide was reviewed in 1992 [114]. In 1989, preliminary tests conducted on several North American dodder species with cultures of *C. gloeosporioides* f. sp. *cuscuta* reported that only *Cuscuta campestris* was affected [115]. *C. gloeosporioides* has also been identified as a pathogen of dodder in cranberry [116], but no attempts have been made to commercialize this fungus. It is not known if the pathogen is host-specific.

Insects have been investigated for their role as potential control agents of dodder in crops other than cranberry and several examples are noted. In the 1960s, several reports indicated that weevils, flies, and caterpillars might be utilized to manage dodder [117-119]. The gall beetle, *Smicronyx jungermanniae*, was associated with the stunting, inhibition, and death of *C. campestris* in Kazakhstan [120]. Subsequent work from the USSR (at the time) provided further information on the habit and relationships of *S. jungermanniae* and a fly (*Melanagromyza cuscutae*) with five species of dodder [121]. More recently, *S. jungermanniae* and additional species of *Smicronyx* continue to be associated with causing detrimental effects on dodder in Slovakia and Iran, respectively [122,123]. In South Africa, eriophyid mites were investigated as potential biocontrol agents for *C. epithimum* [124].

Recent work from Serbia has demonstrated that several species of *Bacillus*, plant-growth promoting rhizobacteria, had inhibitory effect on the germination of *C. campestris* [125]. Tomato spotted wilt virus and cucumber mosaic virus were reported to be capable of infecting *Cuscuta* sp. [126]. These findings could certainly open up additional fields of inquiry for new biological control options.

## 7. Conclusions

Dodder is a complex organism from both biological and management perspectives. Its long-lived seedbank, tremendous growth potential, wide host range, robust seed production, and ability to regenerate from haustoria embedded in host tissues make management very challenging. The cranberry production system has unique characteristics that permit the development of management strategies that may not be easily transferred to other crops (e.g., flooding, sanding). On the other hand, cranberry farmers can not use resistant varieties or other options available to farmers of annual crops. An integrated plan offers a solution for managing *C. gronovii* in cranberry production while sustaining the economic viability of the industry in Massachusetts. IPM for swamp dodder in cranberry could combine methods such as preemergence herbicides, hand removal of dodder seedlings, maintaining vigorous crop growth, raking or mowing infestations, sanding, use of postemergence herbicides, flame cultivation, and flooding (Boxes 1 and 2). Research from small fruit production systems, like cranberry, into the biology and management of *C. gronovii* (e.g., germination patterns, host preference,

use of plant growth regulators) may provide insights that could ultimately be useful for managing problematic *Cuscuta* species in other agricultural systems.

**Box 1.** Current strategies for integrated management of dodder in cranberry.

Prevent movement of seeds onto farm.  
 Scout for newly emerged seedlings.  
 Use preemergence herbicides.  
 Manage early season weed hosts.  
 Use short-term spring floods.  
 Remove seedlings and infected hosts by hand.  
 Apply postemergence herbicides.  
 Rake heavy dodder infestations.  
 Remove seed pods in harvest floods.  
 Clean equipment between infested and clean farms.  
 Apply uniform applications of sand.  
Future additions:  
 Use of plant growth regulators? New herbicides? Flame cultivation?  
 Unconventional (household) products? Biological control products?

**Box 2.** Options that do not control dodder in cranberry.

*Late water floods* have not proven effective against dodder.

The efficacy of *fall floods* has not been tested but the general inclination is that they would not be effective at all. The seed is already formed (by late August-September) and is quite capable of surviving winter floods.

Smolder, a mycoherbicide formulated with the fungus, *Alternaria destruens*, performed poorly in 2 years of field tests conducted in both Wisconsin and in Massachusetts and is not being pursued as a viable option.

*Napropamide* and *norflurazon* are not effective preemergence herbicides.

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