Infection by the Fungal Pathogen Colletotrichum coccodes Affects Velvetleaf (Abutilon theophrasti)-Soybean Competition in the Field

ANTONIO DITOMMASO, ALAN K. WATSON, and STEVE G. HALLETT

Abstract. Field research was conducted from 1990 through 1992 to evaluate the effect of the fungal pathogen, Colletotrichum coccodes, on velvetleaf intra- and interspecific (with soybean) competition across a range of monoculture and 1:1 mixture densities. In pure stand, application of this velvetleaf foliar pathogen had little impact on seed yield of the weed. In these plots, velvetleaf interspecific competition stimulated vertical growth and favored the rapid replacement of diseased leaf tissue that had prematurely senesced. In mixtures, however, C. coccodes inoculation differentially influenced the yield of both species. In two of three years, C. coccodes inoculation reduced velvetleaf seed yields by an average, 60% compared with yields for control (uninoculated) plants. Velvetleaf suffered greater yield losses from soybean interspecific competition in the presence of C. coccodes, especially at the lower planting densities. The decline in velvetleaf yield was primarily attributed to the stunting effect of the pathogen, which allowed soybean plants to grow above the weed. Consequently, soybean yield losses within inoculated mixture plots were generally lower than for control plots, although significant increases (23%) in soybean yield were recorded only in 1992. The inoculation treatment had relatively little impact on the number of seeds produced per fruit or seed unit weight in both species regardless of whether plants were grown in monocultures or in mixtures. The finding that C. coccodes has only a limited effect on velvetleaf performance in pure stand, while having a significantly greater effect in a competitive environment with a soybean crop, has important ramifications as to the value and accuracy of initial efficacy testing that rates potential biocontrol agents based solely on their effect within pure stands of the target weed. Nomenclature: Colletotrichum coccodes (Wallr.) Hughes; velvetleaf, Abutilon theophrasti Medik. #3 ABUTH; soybeans, Glycine max (L.) Merr. ‘Maple Arrow.’

Additional index words. Biological weed control, disease, interspecific competition, interspecific competition, mycoherbicide, weed/crop interference, ABUTH.

INTRODUCTION

Velvetleaf is a major annual weed in soybean and corn (Zea mays L.) in the midwestern United States, southern Ontario and is increasing in Quebec (3). Within the last few years, velvetleaf has also been reported for the first time in several Canadian maritime provinces (9). Important crop yield losses caused by velvetleaf competition have been well documented (1, 2, 5, 10, 12, 13, 19, 20). The effect of soybean interference and velvetleaf interspecific competition on growth and reproduction of this weed have not, however, received a great deal of attention (1, 2, 10, 14, 24).

Velvetleaf is difficult to control because of its rapid growth rate and prolific production of seed with extended dormancy. The high competitiveness of velvetleaf in soybean and corn is partly attributed to its capacity to establish a height differential with the crop, especially when both crop and weed emerge at the same time (1, 5, 27). Moreover, this robust weed is tolerant to many soybean and corn herbicides (12). Hence, weed control strategies in soybean and corn have been largely inadequate against velvetleaf (26).

The prospect of controlling velvetleaf with the fungal pathogen Colletotrichum coccodes has been investigated within the last decade (15, 23, 32, 33, 34, 35). Typically, the velvetleaf isolate of C. coccodes causes gray-brown foliar lesions on infected velvetleaf. Initially, lesions appear as small flecks but later become large and necrotic (35). The areas surrounding lesions become desiccated, and diseased leaves are shed prematurely. In general, velvetleaf plants are killed only when inoculated at a relatively young age (i.e., cotyledon stage) (35). When C. coccodes is applied at later growth stages, the pathogen causes extensive necrotic lesions on inoculated leaves, but although infected plants are stunted, and development is delayed, velvetleaf recovers.

A substantial part of the velvetleaf-C. coccodes biocontrol research has focused on laboratory and field experiments that have attempted to optimize inoculum production and application as well as to elucidate environmental conditions under which this pathogen provides better control (23, 35). An integral component of the C. coccodes-velvetleaf biocontrol research also has been to determine the effect of this selective pathogen on velvetleaf-soybean interspecific and velvetleaf intraspecific competitive interactions under laboratory and field conditions (11). This research is critical in light of the growing body of research demonstrating the mediating effect of host-specific disease on intra- and interspecific competitive interactions (4, 17, 21, 22). For example, Burdon et al. (7) were able to quantify the effect of the rust, Puccinia chondrillina Bubak & Syd., on competition between resistant and susceptible forms of skeleton weed (Chondrilla juncea L.) in Australia. In the absence of the rust, the two
weed forms had similar competitive abilities. However, the presence of the rust resulted in greater competitive ability of the resistant weed form (i.e., the dry weight of the resistant form increased by at least 10%, while that of the susceptible form decreased substantially). Paul and Ayres (22) found that the competitive ability of common groundsel (Senecio vulgaris L.) grown in mixture with lettuce (Lactuca sativa L.) decreased significantly following inoculation with a rust fungus. Interestingly, the pathogen had little effect on common groundsel interspecific interactions. Hence, a more in depth understanding of the way in which disease caused by C. coccodes is likely to mediate velvetleaf intraspecific and interspecific (with soybean) competitive interactions is an important prerequisite for the establishment of a successful biological control strategy. This research is crucial given that weed species may not respond in the same way to disease when growing in pure stands as opposed to mixed stands. Moreover, this work also will have important implications for initial biocontrol efficacy testing that has often been restricted to trials using weed populations grown only in pure stand (6, 18, 31, 35). Hence, using a modified replacement series design, the specific objective of this field study was to determine the effect of C. coccodes inoculation on velvetleaf intra- and interspecific (with soybean) competition based primarily on the reproductive performance of each species.

MATERIALS AND METHODS

Study site and experimental procedure. Field experiments were conducted at the Emile Lods Agronomy Research Centre, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, Quebec, Canada, from 1990 through 1992. The soil type was a St. Bernard fine sandy-loam (orthic melanic brunisol) with a pH of 6.8 and 3% organic matter. Rainfall and temperature varied between years, however, rainfall was generally lowest and temperatures were highest in 1991 compared with either 1990 or 1992 (Figure 1).

During each of the three years, both monocultures and 1:1 mixtures of soybean [var. 'Maple Arrow'] and velvetleaf were established within 1 m² plots arranged in a randomized complete block design. Each plot was 2 m from any adjacent plot. In 1990, a total of five monoculture planting densities (80, 160, 240, 320, 480 plants m⁻²) and three 1:1 mixture planting densities (i.e., total densities of 160, 320, 480 plants m⁻²) were used. In 1991, the experiment was expanded to include seven monoculture density levels of each species (1, 10, 20, 40, 80, 160, 320 plants m⁻²) and six mixture density levels (10, 20, 40, 80, 160, 320 plants m⁻²). In 1992, one additional monoculture density (5 plants m⁻²) was also established. There were three replicates of each density treatment in 1990 and four replicates in 1991 and 1992. The experimental design was expanded to include lower planting densities that more closely reflected actual field weed densities as well as to allow a more accurate calculation of competitive indices.

Establishment of planting densities. For all three years, soybean and velvetleaf seedling densities were established within the 1 m² plots from 26 to 28 May. The top 3 cm of soil within each plot was removed with a shovel and seeds of both species were broadcast as evenly as possible over the 1 m² plots by hand. The top soil initially removed was then used to cover the seeds. Before field seeding, velvetleaf seeds collected from Macdonald Campus agricultural field populations in previous years were germinated by incubation in distilled water in a plastic bag for 48 h at 3 C and 24 h at 30 C. Prior to seeding, soybean seeds were inoculated with Bradyrhizobium japonicum⁴. Crop and weed emerged simultaneously approximately 6 d following planting. Soon after emergence, soybean and velvetleaf seedlings were thinned to desired density levels. Within each 1 m² plot, the number of soybean and velvetleaf seedlings within a central 0.25 m² (50 cm by 50 cm) sub-plot were counted and recorded. Throughout the growing season, all other weed species were removed from the 1 m² plots by hand.

Inoculum production and application. A stock culture of Colletotrichum coccodes (DAOM 182826 deposited in the Biosystematics Research Institute, Ottawa, Ontario, Canada) was established from diseased velvetleaf collected in Vermont, USA and maintained on potato-dextrose agar (PDA) slants under mineral oil at 3 C. Mycelium from the stock culture was transferred to PDA plates and incubated for 10 d at 24 C. Mycelial plugs were removed and transferred to 100 ml of a modified Richards' liquid medium (10 g sucrose, 10 g KNO₃, 2.5 g MgSO₄, 5 g KH₂PO₄, 0.02 g FeCl₃, 6H₂O, 150 ml V-8 juice⁵ and H₂O per L) in 250 ml Erlenmeyer flasks (35). Cultures were

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⁴Nitragin, The Nitragin Company, Milwaukee, WI.
⁵Campbell Soup Co. Ltd., Toronto, Ontario, Canada.
incubated for 7 d on a rotary shaker (250 rpm) and conidia harvested and washed by filtering through four layers of cheesecloth and centrifuging (6500 g). The spore pellet was resuspended in distilled water and the inoculum density adjusted using a haemocytometer.

In all three years, C. coccodes application was carried out c. 21 d post-seeding when velvetleaf plants were at the two-leaf stage and soybean plants were at the first trifoliate leaf stage. Plants were sprayed at dusk at a rate of 1 × 10⁶ conidia m⁻² (with a 1% w/v gelatin adjuvant)⁶ using a hand-held pressurized sprayer equipped with a Teejet full cone nozzle 7, operating at 200 kPa air pressure and a spray volume of 500 L ha⁻¹. Control plots were sprayed with distilled water + 1% w/v gelatin adjuvant. During spraying, plots were protected on three sides with a plastic screen to minimize spray drift.

Harvest procedure. In each year, all soybean and velvetleaf plants within a central 0.25 m² sub-plot of each plot were harvested by hand 120 d following seeding (September 22 to 23). For both species, all aboveground tissue was cut at the soil line. Velvetleaf height was determined by measuring each live plant from the soil surface to the terminal shoot apex to the nearest 0.5 cm. Mature, entirely blackened velvetleaf capsules were collected by hand and counted every 3 d from all plants within the 0.25 m² sub-plots from mid-August until harvest. Mature capsules were air dried for at least 4 wk and then weighed. Capsules were subsequently mechanically crushed, winnowed and the seed separated from pod chaff with an air blower cleaner. All seed were then counted using an electronic seed counter and weighed. The number of pods from mature, fully senesced soybean plants harvested within sub-plots was also recorded. Seeds were counted and weighed after being air dried for at least 6 wk following harvest.

Measuring intra- and interspecific competitive effects. Intraspecific competitive effects (for 1991 and 1992 field trials only) were distinguished from overall competitive effects (i.e., intraplus interspecific competition) by using an analytical technique described by Jolliffe et al. (16).

Using this technique, the effects of intraspecific competition on a particular species is defined by the relative monoculture response (Rₘ):

\[ R_m = \frac{Y_p - Y_m}{Y_p} \]

where \( Y_p \) is the projected yield (e.g., seed yield) in the absence of competition (and is determined from the initial slope of the yield density curve) and \( Y_m \) is the measured monoculture yield at a given density. \( R_m \) values can range between 0 (no intraspecific competition) and 1.0 (maximum intraspecific competition). \( R_m \) values were determined for both soybean and velvetleaf within control and inoculated plots for all four replicates at each planting density.

The magnitude of the overall effects of competition (i.e., intra- plus interspecific competition) on a particular species is defined by the relative mixture response (\( R_x \)):

\[ R_x = \frac{Y_m - Y_x}{Y_m} \]

where \( Y_m \) is the measured monoculture yield and \( Y_x \) is the measured yield in mixture (i.e., at a total density twice that in monoculture). As with \( R_m \), \( R_x \) values can range between 0 and 1.0. The greater the \( R_x \) value, the more important is the loss in yield due to the effects of interspecific competition. For both species, \( R_x \) values were determined in each of three years for all replicates of the control and inoculated treatments within each mixture planting density. Note that \( R_m \) and \( R_x \) values do not change whether yields are expressed on a per plant or per unit area basis (16).

Environmental data. Daily precipitation and daily maximum/minimum temperatures for May through September of 1990, 1991, and 1992 were obtained from Environment Canada for the Ste-Anne-de-Bellevue Station, located approximately 1 km from the field site. For each year, leaf wetness within the plant canopy was recorded² for the 3-d period following spraying. The leaf wetness sensor (a printed circuit board measuring 5.8 by 7.7 cm and painted off-white) was placed at the height of the velvetleaf leaves at the time of inoculation. Leaf wetness periods were considered to occur when resistance measurements were ≥2.14 × 10⁴ ohms.

Statistical analysis. Due to variations in weather and because of significant year by treatment and year by species interactions, data from each year were analyzed separately. For each year and each species, data were subjected to an ANOVA (25) to evaluate the main effects and interactions of competition (i.e., intraspecific and interspecific), C. coccodes inoculation, and planting density on all reproductive variables, both on a per plant and per unit area basis. Where significant interactions were detected, simple effects of each of the main factors were considered. Where appropriate, data were log₁₀ or square-root transformed to homogenize variances and treatment means were separated using Duncan’s Multiple Range test (P < 0.05).

For each species, an ANOVA was used to determine the effect of C. coccodes inoculation and planting density on the relative monoculture response (\( R_m \)) for 1991 and 1992. However, Bartlett’s test showed significant heteroscedasticity in \( R_m \) values despite arcsine-transformation. Homoscedasticity was restored by dividing the monoculture planting density treatment into a ‘low’ density (1, 5, 10, 20, 40 plants m⁻²) and a ‘high’ density (80, 160, 320 plants m⁻²) treatment. Hence, the effect of the ‘low’ and ‘high’ planting density factor on \( R_m \) was determined separately. An ANOVA was also used to determine the effect of C. coccodes inoculation, and planting density on the relative mixture response (\( R_x \)) for 1990, 1991 and 1992. \( R_x \) values were arcsine-transformed before analysis to homogenize variances. For each year and for each species, best fitting regressions describing the relationship between seed yield and planting

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⁶Gelatin, BDH Inc., Toronto, Ontario, Canada.
⁷Teejet GTO.7 Spraying Systems Co., Wheaton, IL.
⁸Leaf wetness digital recorder, Model DP223 and leaf wetness sensor LWS 223, Omnidata Int., Inc., Logan, UT.
density were determined in pure stand and mixtures using the regression analysis procedure in SAS (25).

RESULTS AND DISCUSSION

Soybean reproduction. The form of competition (i.e., intra-versus interspecific) and planting density had a highly significant effect ($P < 0.001$) on most soybean reproductive variables measured in all three years (Table 1). Soybean yield per unit area varied depending on the year and on whether soybean was grown in pure stand or in mixture with velvetleaf (Figure 2). Soybean yield remained relatively stable across most of the mixture planting density range in both 1990 and 1991 (Figure 2d, e) and generally increased with planting density in 1992 (Figure 2f). Soybean yields per unit area in mixtures were substantially lower than in pure stand across the entire density range in all three years. This was not surprising given that yields per unit area in the 1:1 mixtures were based on only half the number of soybean plants found in monocultures.

The significant ($P < 0.05$) competition by inoculation interactions observed in 1990 and 1992 suggest that the effect of *C. coccodes* inoculation on yield varied depending on whether soybean plants were grown in pure stand or in mixtures with velvetleaf (Table 1). In monocultures, inoculation had no significant effect on soybean yield (Figure 2a–c). This is consistent with previous studies showing that *C. coccodes* is a selective foliar pathogen of velvetleaf, and soybean is immune to the disease (35). However, soybean yields in 1990, 1991, and 1992 mixtures were, on average, 39, 6, and 23% greater, respectively, for plants grown in the presence of inoculated velvetleaf than for plants grown with uninoculated velvetleaf (Figure 2d–f). Increases in soybean yield typically observed for inoculated plots in 1990 and 1992 were coupled with significant height reductions in velvetleaf (data not shown). Velvetleaf height for inoculated plants was reduced, on average, 28.5 cm in 1990 and 20.0 cm in 1992 compared with heights for uninoculated plants. *C. coccodes* application in mixtures typically resulted in short velvetleaf plants that were unable to grow above soybean and effectively compete for available light (1, 5, 24, 27).

Growth chamber studies have shown that *C. coccodes* disease development in velvetleaf can be severely limited with dew periods of less than 8 h (35). Leaf wetness readings within the plant canopy for three successive nights following *C. coccodes* application in 1991 confirmed the absence of an adequate dew period for disease development and may explain the relatively lower increases in soybean yield obtained within inoculated mixture plots. The longest leaf wetness period recorded during any of the three nights was only 6 h. In contrast, continuous leaf wetness periods of 10, 7, 10 h and 10, 12, and 9 h were obtained in 1990 and 1992, respectively. Also, total precipitation for the 5 d period after inoculation in 1991 was only 2.2 mm compared with 30 mm and 15.4 mm received over the same period in 1990 and 1992, respectively. Although leaf lesions were observed on all inoculated velvetleaf plants within 10 d of *C. coccodes* application in 1991, lesions were generally infrequent and failed to enlarge sufficiently to cause premature leaf abscission in most plants.

In all three years, *C. coccodes* inoculation had little effect on the number of soybean seeds produced per pod and seed unit weight (Table 1). In 1990 and 1991 however, the presence of velvetleaf typically resulted in a lower number of soybean seeds

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**Table 1. Summary of ANOVA for the effect of form of competition, Colletotrichum coccodes inoculation, planting density, and treatment interactions on soybean seed yield, number of pods, seeds per pod, and weight per seed in each of three years both on a per plant and per unit area basis.**

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<th>Source of variation</th>
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* *, **, ***Denotes significance at the 0.05, 0.01, 0.001 probability levels, respectively; ns = not significant; — = not applicable.
produced per pod and a lower seed unit weight compared with plants grown in pure stand. Eaton et al. (12) also found that the presence of velvetleaf at densities of 130 to 204 plants m\(^{-2}\) reduced the number of soybean seeds produced per pod, but increased seed unit weight compared with weed-free soybean.  

**Velvetleaf reproduction.** All velvetleaf reproductive variables were significantly affected (P < 0.001) by planting density (Table 2). Velvetleaf unit area seed yields generally peaked at the lower planting densities (i.e., 10, 20 plants m\(^{-2}\)) and then declined steadily with increasing density, regardless of inoculation treatment (Figure 3). *C. coccodes* inoculation had little influence on velvetleaf seed yield in pure stand (Figure 3a–c), on the number of seeds produced per capsule and on seed unit weight in both monocultures and in mixtures (Table 2). In general, the number

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*Figure 2.* Soybean yield (Kg ha\(^{-1}\)) within control (○–○) and *Colletotrichum coccodes* inoculated (●–●) plots, as a function of monoculture planting density in (a) 1990, (b) 1991, and (c) 1992 and 1:1 mixture planting density with velvetleaf in (d) 1990, (e) 1991, and (f) 1992.
of seeds produced per capsule remained relatively constant (37 to 40) at or below the 80 plants m⁻² density in both monocultures and mixtures. At higher planting densities, significant declines were commonly observed. The limited effect of C. coccodes application on velvetleaf seed yield in pure stand was in sharp contrast to the 62 and 52% average reduction in seed yield observed in 1990 and 1992 mixture plots, respectively (Figure 3d, f).

Although the presence of C. coccodes resulted in significant decreases in velvetleaf yield only in mixtures, there were no visible differences in disease severity between plants grown in monocultures compared with plants grown in mixtures. Hence, the response of velvetleaf, as measured by reproductive output, was affected differently by C. coccodes depending on the identity of neighbouring plants. In pure stand, intense intraspecific competition resulted in tall, spindly velvetleaf individuals with a more or less uniform height hierarchy (pers. obs.). This general growth habit allowed most plants to obtain a share of available light. Consequently, the rapid increase in height exhibited by most velvetleaf individuals in pure stand favored the quick replacement of diseased leaves that had been prematurely shed. In mixtures, however, the stunting effect of C. coccodes on velvetleaf provided enough of a delay to allow soybean with its large trifoliate leaves to shade velvetleaf effectively. This delay in growth permitted soybean to rapidly overtop the shorter, diseased velvetleaf plants, which then remained within the canopy and appeared to have little competitive influence on soybean (24). These findings support the call by several workers that potential biocontrol agents need not completely eradicate a host weed species to be considered effective (22, 28, 29). This contrasts with the generally accepted view that rapid and complete weed control is required within intensively managed agroecosystems (8). Unlike most chemical herbicide treatments that attempt to eradicate a weed species completely, very few biological weed control agents (including many fungi being evaluated as bioherbicides) cause the direct mortality of mature hosts. Paul and Ayres (22) found that inoculation of common groundsel with the rust Puccinia lagenophorae (Cook), reduced the impact of this weed on lettuce yield without causing a significant increase in common groundsel mortality. This effect was attributed to a decrease in competitive ability of infected common groundsel plants. Field evaluations of other biocontrol agents have also shown that effective weed control (i.e., significant increases in crop yields) can be achieved even if they do not cause high levels of mortality (30, 33).
interspecific competition on velvetleaf increased with increasing mixture density (Figure 5d–f). At the lower mixture densities, the presence of soybean had little negative effect on the seed yield of uninoculated velvetleaf. Several workers have also observed that velvetleaf growth and reproduction may be limited more by the presence of conspecifics than by that of soybean (2, 10).

*C. coccodes* inoculation significantly reduced (22%) soybean $R_s$ only in 1992 (Table 3 and Figure 5). A lower soybean $R_s$ for the inoculation treatment indicates that the negative effect of velvetleaf interspecific competition on soybean yield was reduced in the presence of *C. coccodes*.

In two of the three years, *C. coccodes* application resulted in significant increases in velvetleaf $R_s$ (Table 3 and Figure 5d–f).
In 1990 and 1992, the intensity of soybean interspecific competition on velvetleaf seed yield increased 22 and 44%, respectively, within inoculated plots compared with uninoculated plots. In both years, the deleterious effects of *C. coccodes* inoculation on velvetleaf competitive ability were most evident at the lower mixture planting densities (Figure 5d, f). Although not significant, the 41% increase in velvetleaf $R_v$ in 1991 was surprising given the suboptimal environmental conditions for disease development.

This field study demonstrated that soybean and velvetleaf responded differently to the presence of *C. coccodes* in mixtures. When an appropriate dew period was provided, *C. coccodes* infection substantially reduced velvetleaf reproductive output in two of three years, especially at lower mixture densities. From a weed management perspective, any reduction in the seed output of velvetleaf should have a beneficial effect on lowering future weed populations. Equally important was the finding that under favorable field conditions for fungal development (i.e., adequate dew period and moisture), inoculation of velvetleaf plants with *C. coccodes* can result in significant increases in soybean reproductive output. Given that velvetleaf competition has a substantial negative impact on soybean yield at relatively low infestation levels, increasing the efficacy of this potential bioherbicide at the lower velvetleaf densities commonly found in agricultural systems would be most beneficial. Future field research into more effective *C. coccodes* suppression of velvetleaf should continue.

![Figure 4. Relative monoculture response ($R_m$) for (a, b) soybean and (c, d) velvetleaf seed yield in 1991 and 1992, respectively, for plants subjected to an uninoculated control (O—O) and *Colletotrichum coccodes* inoculated (●—●) treatment across a range of monoculture planting densities.](image-url)
Figure 5. Relative mixture response (Rx) for (a, b, c) soybean and (d, e, f) velvetleaf seed yield in 1991 and 1992, respectively, for plants subjected to an uninoculated control (O—O) and Colletotrichum coccodes inoculated (●—●) treatment across a range of mixture planting densities.

The limited impact of *C. coccodes* on velvetleaf grown in monocultures as opposed to the notable effects on plants grown in mixtures with soybean suggests that the establishment of future biocontrol strategies will necessitate a better understanding of the way in which foliar disease and a competing crop’s morphological characteristics interact to reduce light availability and ultimately lower the performance of the target weed. As was shown in this study, the effect of disease on a target weed in the presence of a crop may be very different from that...
observed in pure stand largely because of morphological differences (e.g., leaf shape and size, canopy architecture) between the competing species. These findings also highlight a possible critical shortcoming of previous biological control efficacy testing procedures. That is, potentially effective biological control candidates may have been mistakenly characterized as being inefficient agents, and were likely discarded, because initial efficacy tests were carried out using target plants grown only in pure stand. Hence, to assess accurately the full potential of future biocontrol agents, initial efficacy testing should also include trials examining the impact of the biocontrol candidate on the host weed in the presence of the crop.

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LITERATURE CITED


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