Biological control in the management and spread of invasive weed species

D.L. ISAACSON, D.B. SHARRATT and E.M. COOMBS

Oregon Department of Agriculture, 635 Capitol Street, N.E., Salem, Oregon 97310-0110, USA

Abstract. Biological control of weeds has traditionally been judged successful if target weed densities decline to acceptable levels. However, biological control agents may also influence invasion processes by reducing seed production and dispersal and thus limit establishment of the weed in distant foci. Three lines of empirical evidence suggest that classical biological control agents have impeded the dispersal of tansy ragwort in Oregon in this way. Firstly, agents reduced seed production in western Oregon and the numbers of new infestations many miles away in eastern Oregon dropped correspondingly. Secondly, ragwort is usually most abundant in older disturbances and is less likely to be found within recently-disturbed areas at the margins of its current distribution. Thirdly, the occurrence of the ragwort seedfly on remote, recently-established infestations of the weed, and the occurrence of the ragwort flea beetle on isolated plants, suggests that both these agents have efficient host-finding abilities. Most evaluation studies to quantify the influences of classical biological control agents have been conducted at one or a few points and often focus on temporal effects to the exclusion of spatial effects. Simulations of spatial dynamics of invasions suggest biological control agents may exert influence on both the rate of invasion and ultimate target weed distribution, both important factors in management of weed invasions.

Introduction

Successful classical biological control of weeds, and even successful weed control by other methods, is usually thought to involve reduction of densities of target weeds to below economic threshold levels (see for example Messersmith and Adkins 1995). This view of biological control assumes target species have already reached or exceeded acceptable densities. In most cases, biological control is initiated after a weed species has invaded and become problematic over large areas. On a continental scale, an alien weed may take many years to occupy its potential range and the weed may become a legitimate target of biological control long before the invasion process is complete.

Leafy spurge, *Euphorbia esula* L. (Euphorbiaceae), purple loosestrife, *Lythrum salicaria* L. (Lythraceae), spotted knapweed, *Centaurea maculosa* Lam. (Asteraceae) and yellow starthistle, *Centaurea solstitialis* L. (Asteraceae) are all alien weeds in North America that are problematic enough to be targets for biological control, but have not yet realized the full extent of their invasion. Several biological control agents have been successfully introduced against these weeds, and the numbers of many of these agents have increased sufficiently for them to be collected for redistribution. This invites consideration of whether biological control agents should be employed solely to reduce densities within infestations of the weed, or whether they should also be used to slow or prevent invasions of new areas.

We have evidence that the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), tansy ragwort flea beetle, *Longitarsus jacobaeae* L. (Coleoptera: Chrysomelidae) and the ragwort seedfly, *Botanophila seneciella* (Meade) (Diptera: Anthomyiidae), have combined to limit the invasion of tansy ragwort, *Senecio jacobaea* L. (Asteraceae) in Oregon. This evidence is supported by alien weed invasion simulations. Our paper presents the evidence that the agents have limited the spread of ragwort and shows the results of the simulations.

The tansy ragwort problem

Tansy ragwort was first detected in Oregon in 1922 (Isaacson 1973) and, by the mid-1950s, had become recognized as an important pest, causing poisoning of

livestock and competing with desirable forages in 16 counties in western Oregon. In 1974 the Oregon Department of Agriculture (ODA) initiated an interim control programme, and in 1975 the Oregon Legislature passed a law formalizing the programme and provided supporting funds.

Control in western Oregon originally relied on the distribution of cinnabar moth and ragwort flea beetle, aiming to distribute both agents over the entire range of ragwort as quickly as possible (Isaacson 1976). By 1978, cinnabar moth populations had been established in 350 of approximately 400 townships (approximately 10x10 km) by releasing larvae at approximately 5580 different sites. By the early 1980s redistribution of flea beetles was also nearly complete. The ragwort seedfly dispersed throughout western Oregon with limited intervention.

Field monitoring and experimentation showed marked reductions in ragwort densities due to the cinnabar moth and the flea beetle (Coombs *et al.* 1991; McEvoy *et al.* 1991; McEvoy *et al.* 1993). The incidence of livestock losses was reduced (Coombs *et al.* this Volume) and economic benefits of ragwort control in western Oregon were estimated at US$4-5 million annually (Burrill *et al.* 1995).

In eastern Oregon, pioneering infestations of ragwort were discovered in the late 1970s with increasing frequency, with 10 discovered in 1975. In 1979 an employee was reassigned to eastern Oregon with the primary responsibility of detecting and treating new infestations of ragwort east of the Cascade Mountains. The goals of the tansy ragwort programme in Oregon are twofold. West of the Cascade Mountains, biological, chemical and cultural control methods are combined to reduce ragwort densities to acceptable levels, while east of the Cascade Mountains, efforts focus on preventing the movement of propagules from west to east, and on the detection and eradication of new infestations as early as possible.

Reductions of tansy ragwort infestations in eastern Oregon

The first record of tansy ragwort east of the Cascade mountains in Oregon was from Baker County in 1936. Few further sightings were recorded until 1974 when the numbers of new sightings began to increase (Fig. 1), reaching a peak at 102 new sightings in 1983, after which new sightings subsided to nearly zero in recent years. These changes corresponded with
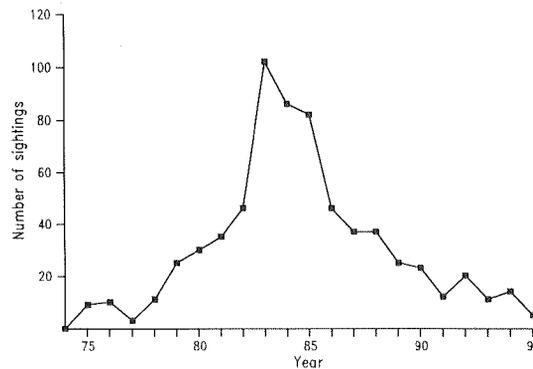

Fig 1. The number of new infestations of tansy ragwort detected east of the Cascade Mountains from 1974 to 1995.

dynamics of ragwort west of the Cascade Mountains. Ragwort expanded its range and increased in density in the 1960s and early 1970s so that by the mid-1970s the weed had occupied all of its potential range in the west.

Before biological control agents reduced the density of infestations of the weed, contaminated crop-seed and hay from western Oregon, and ragwort seeds dispersed on westerly winds, were the main source for new infestations. The marked decrease in the number of eastern Oregon sightings in 1984 and afterwards coincided with reductions of ragwort in the west (Coombs *et al.* 1991). This suggests that successful biological control of ragwort resulted in suppression of the weed well beyond the areas of implementation because fewer seeds dispersed away from the infested regions.

Limitations on tansy ragwort dispersal at the margins of its current range

Early in the 1970s, it was assumed that tansy ragwort was mainly a maritime plant that could not survive above about 3000 ft (914 m) or in continental areas east of the Cascade Mountains (Isaacson 1976). This assumption proved to be incorrect and, with time, many tansy ragwort plants became established above 3000 feet and on the east side of the mountains.

County noxious-weed control programmes, land managers from the Mt. Hood and Willamette National Forests and the ODA began to tackle the tansy ragwort problem on its eastern margins during the late 1970s, intending to prevent seeding by ragwort in the area east of the Cascade Mountains. These efforts continue.

Clearcuts in forests cause disturbances which create ideal conditions for invasion by several ruderal plant species, including ragwort (McEvoy *et al.* 1993). Tansy ragwort typically establishes in the second and third years after trees are felled, increases in abundance

for two to three years, and then gradually becomes less abundant with the development of competing perennial herbs and shrubs. The role of cinnabar moth and ragwort seedfly in reducing or preventing dispersion of ragwort from these areas into adjacent infestations needed to be evaluated.

From 30 July to 2 August 1991, ragwort infestations and the biological control agents were surveyed within forest clearcuts of various ages in the Bear Springs and Clackamas Ranger Districts of the Mt. Hood National Forest above 3000 ft west of the Cascade Divide. Discrete clearcuts three years of age and older without adjacent harvested areas were monitored by walking straight-line transects through the centre, where practical, of the clearcuts. Numbers of ragwort stems and the presence or absence of cinnabar moth larvae and of ragwort seedfly, or of their feeding damage, was recorded over one metre on either side of the transect, every 10 m.

Of 113 clearcuts, 25 (22.1%) had ragwort. Ragwort seedfly attacks were observed on 23 of the 25 clearcuts with ragwort, and cinnabar larvae were observed in seven of the clearcuts. Ragwort flea beetles were not active at the time of the observations, and beetles were not generally detectable in the area.

Clearcuts infested with ragwort were significantly older (on average 22.9 years of age) than uninfested clearcuts (on average 16.7 years) (P < 0.05), the reverse of what would be expected under the usual conditions of succession in disturbed areas. Of clearcuts older than 10 years, 28.2% had ragwort, while 9.7% of clearcuts 10 years of age or younger had ragwort (PGV < 0.06). All clearcuts that exceeded a ragwort density of 50-100 stems/acre (125-250 stems/ha) and which thus exceeded an arbitrary economic threshold were older than 10 years. Six clearcuts with estimated ragwort densities that exceeded the threshold by > 50x were on average 27.5 years of age and were all heavily grazed by cattle. Ragwort plants in five of these were attacked by cinnabar moth, and plants in all six of the clearcuts were attacked by seedflies.

Ragwort is less likely to invade disturbances at the margins of its current range than before the widespread dispersal of biological control agents. Lower seed production, in nearby areas at lower elevations, caused by the flea beetle and the cinnabar moth reduce the amount of seed dispersed into new sites. Ragwort seedflies find plants in outlying areas and limit seed-dispersal by both direct destruction of seeds and webbing of flowerheads. While high densities of ragwort persist in some clearcuts, seed production is often reduced because of seedfly attack and defoliation by cinnabar larvae before flower production.

Simulations of invasions

The process of invasions by weedy alien species can be modelled as a combination of a process of diffusion along margins of established infestations, and 'jumps' from these core infestations that result in satellite infestations (Fig. 2). Moody and Mack (1988) simulated invasions of this sort and determined that eliminating new foci usually provided more effective control than tackling the core infestation. Attack efficiency (the proportion of new foci eliminated), the age of new foci at detection and the rate of generation of new foci are all variables included in their simulations. Each of these variables can be influenced by one or more of the biological control agents used against tansy ragwort.

Using a raster geographic information system, we simulated spatial patterns of invasions using parameters derived from empirical data or from our experience with tansy ragwort. The assumptions and conditions for two sets of simulations, one examining the effects of the efficiency of detection, and the other the possible effects of biological control agents, are listed in Table 1. The results of the simulations are shown in Figs 3 and 4. Unchecked invasions occupied 100% of the universe in less than 40 years (a year is one cycle or time unit for these simulations). At 50% detection efficiency, the universe was approximately 75% occupied in 40 years, and at 90% efficiency the universe was approximately 10% occupied (Fig. 3).
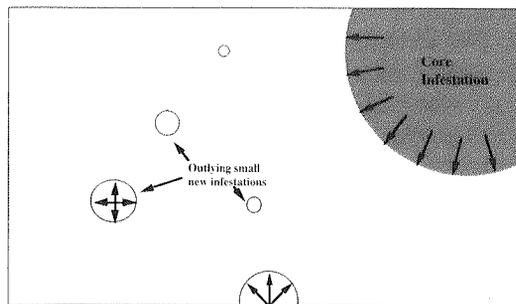

Fig. 2. A graphic representation of an invasion by an alien weed species. A large 'core' infestation expands along its periphery while satellite infestations, founded by dispersing propagules, establish and expand and, in turn, become a source of propagules.
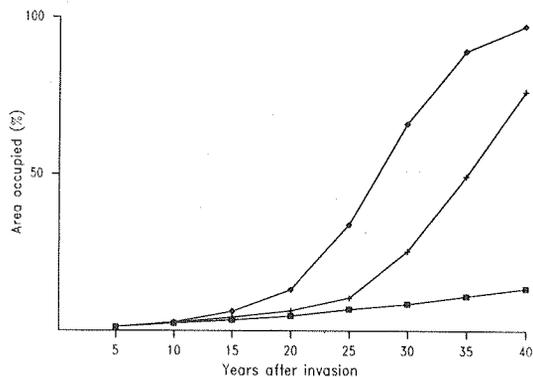
Fig. 3. Raster geographic information simulations: the area occupied by an invading weed through time when 10%, 50% and 90% (upper, middle and lower graphs respectively) of the satellite infestations are detected and eliminated.

Assuming that either agents could find outlying foci themselves, or that releases of agents were made when foci were detected, 10%, 50% and 90% 'efficiencies' of biological control agents were examined (Fig. 4). At the 10% level of 'efficiency', agent effects were little different from the 10% levels in Fig. 3. At the higher levels of 'efficiency', initial rates of invasion turned from positive to negative and greatly extended the time until the potential range of the weed was fully occupied. The rates of invasion approached, but did not reach, zero. A zero rate of increase would describe a new asymptote, suggesting agent ability to limit potential range of the target weed.

Discussion

We conclude that the insect agents introduced for control of tansy ragwort have influenced the course of invasion of this weed by helping to reduce the rate of spread from western Oregon to eastern Oregon and along the margins of its current distribution. The biological control agents have reduced the spread of ragwort to new areas and, thus, there has been a savings on other control measures.

Given that biological control agents have the potential to alter the course of invasion of weeds, we have initiated efforts against target weeds other than ragwort. Coombs *et al.* (1995) describe a plan to limit the rate of yellow starthistle by releasing agents on new foci of the weed. Agents against purple loosestrife, a weed which is in the very early stages of invasion into Oregon, will also be released on small populations of this weed to reduce its rate of spread and prevent it from dominating ecosystems as it has in other areas of

Table 1. Initial conditions and assumptions used in simulations of weed invasion, detection and control. * Spread is to adjacent cells, not including those at corner of source cell: ** "yr" is one iteration time unit: *** perimeter unit is one edge of cell.

A. Simulation universe - 100x100 cells, uniform with no barriers except at edge of universe.

B. Weed parameters:

    1) initial conditions
        - one infestation centrally located
        - extent = 37 cells
    2) spread
        - without agents: spread = one cell* / 2 yrs**
        - with agents (< 5 yrs on site);
        spread = 1 cell / 4 yrs
        - with agents (5+ yrs on site):
        spread = 1 cell / 20 yrs
    3) if satellite > 69 cells, becomes 'supersatellite'
    4) satellite generation
        - satellites and supersatellites generate satellites
        - satellite locations determined randomly within
          whole universe
        - generation rates:
        a. without agents:
        rate = 1/10 perimeter units*** / 5yr
        b. with agents (< 5 yrs on site):
        rate = 1/20 perimeter units
        c. with agents (5+ yrs on site):
        rate = 1/100 perimeter units
    5) detection of satellites is random
    6) supersatellites all detected
    7) maximum of 15 supersatellites controllable
    8) simulation series with three sets of detection efficiency:
        10%, 50%, 90%.

C. Agent parameters:

    1) initial conditions
        - 1 cell in extent
        - centrally located in universe
    2) spread
        - 1 cell / yr
        - radially from agent origin to weed cells

the United States of America (Thompson *et al.* 1987).

Field observations lead us to suspect that biological control agents may be impeding invasions of other weeds. *Urophora quadrifasciata* (Meig.) and *Urophora affinis* (Frld.) (Diptera: Tephritidae), released onto diffuse and spotted knapweed in Oregon in 1975, were observed in 1988 to attack most of the seed heads of the only known Oregon population of squarrose knapweed, *Centaurea virgata* (Lam.) ssp. *squarrosa* (Gugl.) (Roche and Roche 1989). Neither spotted nor diffuse knapweed are common in the area around the squarrose knapweed infestation. The *Urophora* species dispersed rapidly throughout Oregon
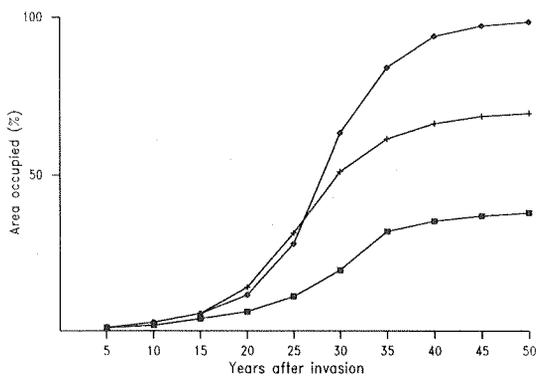
Fig. 4. Raster geographic information simulations: the area occupied by an invading weed when biological control agents disperse and, after five years, control production of propagules in the core area and in 10%, 50% and 90% (upper, middle and lower graphs respectively) of the satellite infestations.

after their introduction in 1975, and thus demonstrated efficient host location capabilities. This ability, coupled with the suitability of squarrose knapweed as an alternate host, may reduce the probability of establishment of new squarrose knapweed infestations and reduce the seed production of those plants that escape detection during alternate control treatments.

Exapion (Apion) ulicis (Forster) (Coleoptera: Apionidae), a seed-feeding weevil widely established in Oregon on gorse, *Ulex europaeus* L. (Fabaceae), has been observed on outlying small populations of the target weed more than 40 miles (64 km) from the nearest other-known infestations of gorse. Observations such as these remind us that we know relatively little about the searching or host-finding capacity of many of the agents we use. In general, post-introduction observations and research efforts focus on assessments of proximal impacts, and field-management usually deals with the artificial dispersal and establishment of agent populations.

To what extent might biological control agents be influencing the invasions of weeds? An answer to this question for tansy ragwort can be advanced because location-specific records for a large area were kept over a period of 21 years, and detailed experiments were conducted which quantified agent-host interactions. For each weed species, an understanding will depend upon thorough, long-term observations over large areas on the invasion dynamics of the weed. Such studies are rare and a neglected aspect of biological control of weeds.

Acknowledgements

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