Scentless chamomile, a target weed for biological control in Canada: factors influencing seedling establishment

H.L. HINZ

CAB International Institute of Biological Control, European Station, CH - 2800 Delémont, Switzerland

Abstract. Scentless chamomile, Tripleurospermum perforatum, is a plant of European origin that had been a noxious weed in North America. As chemical and mechanical control often prove unsuccessful or uneconomic, a project aiming at the biological control of scentless chamomile was started in 1990. Since the plant relies entirely upon seeds for reproduction and dispersal, the emphasis was put on seed-feeding insects. Whether a reduction in seed output will lead to a decrease in plant density depends largely on the plant’s demography, i.e. whether the plant is seed-limited or not. Forty plots (0.5x0.5 m) were set up in October 1994 in the German Rhine Valley on a fallow field dominated by perennial grasses (about 90% cover). The following treatment factors were assigned in a two-factorial design: (i) disturbance, i.e. total removal of vegetation and hoeing; and (ii) additional seeds sown, i.e. 3500 seeds per plot in autumn 1994 and spring 1995. Disturbance was the prerequisite for seedling emergence, explaining nearly 50% of the variance in the number of seedlings. Additional seed input had an effect on seedling establishment only in combination with disturbance, whereas disturbance alone resulted in a significant three-fold increase in seedling emergence compared to undisturbed plots. However, hardly any rosettes established, and no flowering plants developed. Apparently other biotic and abiotic factors limited plant population development. It is concluded that scentless chamomile is seed-limited on disturbed sites, where microsites for germination are numerous, such as in most of the target areas in North America. However, since seeds can stay viable in the soil for up to 20 years, large seed-banks can build up, meaning that seed feeders will have a long term effect by decreasing the number of seeds added to the seed-bank, and reducing the spread of scentless chamomile. Agents attacking earlier plant phenostages, reducing resource allocation to seed production, as well as a change in management practices will be useful for supplementing the impact of seed feeders.

Introduction

Scentless chamomile, Tripleurospermum perforatum (Mérat) Wagenitz, is a plant of European origin that had been introduced into North America by the end of the 19th century (Woo et al. 1991). The plant first spread slowly, but in recent decades has spread at an increasing rate and has become a noxious weed primarily in the prairie provinces of western Canada (Douglas 1989). Tripleurospermum perforatum is a winter or summer annual, sometimes a short-lived perennial (Hegi 1987; Woo et al. 1991), which can form dense, semi-permanent stands in periodically disturbed moist sites (Peschken et al. 1989; Bowes et al. 1994; Cole 1994), from where it spreads onto cultivated fields, causing considerable losses in the yield of various crops (Douglas et al. 1991, 1992). A detailed account of the biology and ecology of T. perforatum in Europe is given by Kay (1994), and in Canada by Woo et al. (1991).

As chemical and mechanical control often prove unsuccessful or uneconomic (Stahlman and Hong 1974; Douglas 1989; Peschken et al. 1989), a project aiming at the biological control of scentless chamomile was initiated in 1990. Since the plant relies entirely upon seeds for reproduction and dispersal, the emphasis was put on seed feeding insects (Peschken and Sawchyn 1993). However, whether a reduction in seed output will inevitably lead to a reduction in plant density largely depends on the plant’s demography, i.e. whether its population is seed-limited or not. For Eucalyptus sp. in Australia it has been shown that artificially increased seed output led to an increase in seedling establishment through predator satiation
(Wellington and Noble 1985; Andersen 1987). In studies conducted by Louda (1982) and Louda et al. (1990), a reduction of pre- and post-dispersal seed predation in Haplopappus squarrosus and Cirsium canescens also resulted in an increase in seedling densities. On the other hand it has been stated that the establishment and density of seedlings will most often be determined by the number of microsites available (Crawley 1983; Andersen 1989).

The present study investigated the importance of disturbance and additional seed input on seedling establishment of scentless chamomile. The relevance of the results for the biological control of scentless chamomile will be discussed.

Materials and methods

The experiment was carried out on a fallow field in the German Rhine Valley (47°48’N 7°37’E). The field was dominated by perennial grasses (Poa trivialis, Festuca pratensis and Lolium perenne), interspersed with small patches of T. perforatum. The soil is a nutrient-poor sandy loam.

Ten blocks (1.5x3 m) and one permanent quadrat (0.5x0.5 m) per block were established in spring 1994, using the stratified unaligned square sampling method (Greig-Smith 1983). All plants in each quadrat were labelled individually and their fate was followed until summer, when plants reproduced and died. The results of these investigations will be published elsewhere. In autumn 1994, three more quadrats, also 0.5x0.5 m, were established per block, and the following treatment factors assigned at random within each block in a two-factorial design: (i) disturbance (D+) or no disturbance (D-); and (ii) additional seeds sown (S+) or not (S-).

The initial permanent plot was used as a control (D-/S-). Between 7-11 October 1994, grasses in the D+ plots were clipped at ground level, and the soil disturbed using a hoe and spade. Soil clinging to the grass roots was carefully shaken off in order not to remove scentless chamomile seeds together with the vegetation. On the S+ plots, 3500 seeds were sown that had been collected from plants on a nearby field in September 1994. Subsequently, all emerging seedlings were counted in the plots on seven occasions; twice in autumn 1994, and five times during the growing period in 1995, and labelled individually with coloured toothpicks. Rosettes were defined as being ≥3.5 cm high and, or, having ≥ five leaves.

In a parallel experiment, germination rates, removal by herbivores and immigration of seeds were estimated by burying four plastic pots (15 cm diameter) filled with soil, free of T. perforatum seeds, into the soil in each block. In three of the four pots, 250 seeds each were sown, and one was left without seeds. One of the pots that received seeds was covered with gauze (0.2 mm mesh size) to exclude herbivores. Seedlings that emerged in the pots were counted and removed. As hardly any seeds germinated in autumn, an additional 3500 seeds were sown on each S+ plot, and 100 seeds in the pots without gauze cover on 13 February 1995. The percentage vegetation cover was recorded three times in all plots during the 1995 growing period. In March 1995, one soil core (2.5 cm diameter and 15 cm deep) was taken in each D+ and D- plot to check for possible changes in nutrient contents, as an effect of disturbance.

The results were analysed as a randomized complete block design, using ANOVAS in SPSS 6.0, with the ten blocks as a blocking factor, and disturbance (D) and additional seed input (S) as two treatment factors, with two levels each. Means were separated using the Scheffé test. The number of seedlings and rosettes were square-root transformed to satisfy statistical assumptions. In the text, means are followed by standard errors.

Results

Treatment factors

Both treatment factors explained a significant proportion (P < 0.001) of the variation in seedling emergence (Table 1). However, whereas disturbance explained nearly 50% of the variance, additional seeds sown explained only 15%. The interaction term (D+S) was also significant (P < 0.01), i.e. treatment effects were multiplicative rather than additive (Crawley 1993). This is reflected by the fact that additional seed input only had an effect on seedling establishment in combination with disturbance (Table 2). In contrast, disturbance alone (D+/S-) caused a significant three-fold increase (P < 0.05) and, together with additional seeds sown, a nine-fold increase (P < 0.001) in seedling emergence compared to undisturbed plots (D-/S-).

Although disturbance also explained a significant amount (P < 0.01) of the variation in the number of rosettes developing, no differences could be detected between treatment means (Scheffé test, P < 0.05) (Table 2).
Table 1. ANOVA table on the effect of disturbance and additional seeds sown on the total number of scentless chamomile seedlings and rosettes established per plot. Number of seedlings and rosettes were square-root transformed; \( ** = P < 0.01; \*** = P < 0.001 \).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>Total no. seedlings</th>
<th>Total no. rosettes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>9.00</td>
<td>36.50</td>
<td>7.07</td>
</tr>
<tr>
<td>Disturbance (D)</td>
<td>1.00</td>
<td>220.58***</td>
<td>7.74**</td>
</tr>
<tr>
<td>Seeds added (S)</td>
<td>1.00</td>
<td>68.12***</td>
<td>0.49</td>
</tr>
<tr>
<td>D x S</td>
<td>1.00</td>
<td>35.46***</td>
<td>0.88</td>
</tr>
<tr>
<td>Error</td>
<td>27.00</td>
<td>87.32</td>
<td>26.08</td>
</tr>
<tr>
<td>Total</td>
<td>39.00</td>
<td>447.98</td>
<td>42.26</td>
</tr>
</tbody>
</table>

On the disturbed plots, plant available nitrogen and phosphorus were slightly increased, from 2-3 kg/ha NO\(_3\)-N, and from 25-32 mg/100g soil P\(_2\)O\(_5\), respectively. The pH decreased slightly from 5.6-5.1.

Germination rate

Hardly any seeds germinated on the plots in autumn, irrespective of treatment (Fig. 1). Similarly, only three seedlings emerged from the 250 seeds sown in uncovered pots in October and November, whereas an average of 132.9 ± 5.3 seeds germinated during the same time period in the pots covered with gauze, i.e. 53.16%. This compares well with germination rates of 54.6% of seeds from the same source in Petri dishes (n = 20) under controlled conditions in a greenhouse. Between April and June, a mean number of 6.05 ± 1.04 (n = 20) seedlings emerged in the uncovered pots, i.e. a germination rate of 6.0%, assuming that only the 100 additional seeds sown in February germinated, or 1.7%, assuming that autumn-sown seeds were still present (350 seeds). No seedlings emerged in pots without seeds being sown, indicating that no seeds immigrated. By subtracting the average number of seedlings establishing in the D+/S- plots (43.6) from the seedlings emerging in the D+/S+ plots (120.5) the average number of seedlings that germinated from the additional seeds sown can be estimated, i.e. as 1%, assuming all 7000 seeds sown contributed to germination. On D- plots between 0.12% and 0.06% of the additional seeds sown germinated.

Seedling mortality

Most seedlings emerged in April (Fig. 1). However, most of these died between May and August. Only a small percentage of seedlings developed to rosettes (Table 2), and even these died during summer, so no flowering plants developed. One cause of mortality that could be ascertained was earthworm activity, i.e.

![Graph showing average number of seedlings per plot](image-url)

Table 2. Number of seedlings and rosettes of scentless chamomile established per plot in different treatment combinations (mean ± SE; n = 10). Homogeneous groups are followed by the same letter (Scheffé test, \( P < 0.05 \) and \( P < 0.001 \), see text for details).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number of seedlings</th>
<th>Number of rosettes</th>
</tr>
</thead>
<tbody>
<tr>
<td>D+/S+</td>
<td>120.50 ± 14.66 a</td>
<td>3.80 ± 1.04</td>
</tr>
<tr>
<td>D+/S-</td>
<td>43.60 ± 8.26 b</td>
<td>2.30 ± 0.70</td>
</tr>
<tr>
<td>D-/S+</td>
<td>19.00 ± 3.68 bc</td>
<td>0.80 ± 0.36</td>
</tr>
<tr>
<td>D-/S-</td>
<td>14.80 ± 4.26 c</td>
<td>1.60 ± 1.12</td>
</tr>
</tbody>
</table>

Fig. 1. Mean number (±SE) of scentless chamomile seedlings present per plot in different treatments during the experimental period. Closed circles - D+/S+; closed squares - D+/S-; closed triangles - D-/S+; inverted, closed triangles - D-/S-.
seedlings were buried under earthworm casts. This amounted to nearly one quarter of the total seedling mortality occurring in May and June. Slugs (Arion spp.) were observed rasping off leaves, but apparently are also capable of consuming entire seedlings, and are common agricultural pests in this region (H. Schmidt personal communication).

Since the percentage vegetation cover was always low in the disturbed plots (Table 3), mortality due to interspecific competition is considered unlikely. The rise in vegetation cover in May to 25% was mainly due to perennial grasses over-hanging the plots. In the undisturbed plots the percentage cover was always high, ranging from 85% in April to 94% in May.

Discussion

Treatment factors

When microwebs are numerous (disturbance), scentless chamomile is seed-limited, as shown by the significant difference in the number of seedlings on D+/S- and D+/S+ plots (Table 2). However, the magnitude of this difference depends upon the number of seeds present in the seedbank, i.e. small seedbanks will result in a bigger difference, thus increasing the effect of additional seed input. This is supported by previous experiments carried out by Klinkhamer and De Jong (1988) with Cirsium vulgare, where seed input (not disturbance) was the primary prerequisite for seedling emergence, because this species has practically no seed-bank. In contrast, scentless chamomile seeds can stay viable in the soil for at least 10 years (Kay 1994), and up to a maximum of 20 years (Anonymous 1988).

Douglas (1989) found mean seed densities of 100 000 per square metre within a source of infestation. Thus, additional seed input will presumably not be of great importance for seedling establishment of scentless chamomile in Canada, except for newly-infested areas, distant from a source of infestation and where no seedbanks had accumulated.

The increase in nutrient contents on disturbed plots might have resulted from the decomposition of left-over organic material (e.g. grass roots) and, or, by increased oxygen entry, and thus enhanced activity of microorganisms. Although the slight increase in nitrogen might have enhanced germination (Mekki and Leroux 1991), it is assumed that the higher numbers of seedlings on the disturbed plots were mainly due to an increase in available light and space through removal of other vegetation. Scentless chamomile seeds have a high light requirement for germination, i.e. only very few seeds germinated when buried 5 cm deep (Mekki and Leroux 1991).

Biotic and abiotic factors

As scentless chamomile seeds lack primary dormancy and can germinate all-year-round, given appropriate conditions (Thomas et al. 1994), it is assumed that the minimal germination rates in autumn were mostly due to warm and exceptionally dry weather conditions, i.e. 44 mm and 14 mm rainfall in October and November, respectively. Only in pots covered with gauze did a considerable number of seeds germinate in autumn. Whether the gauze had an effect on the microclimate, i.e. increased humidity, or prevented seed removal or translocation by herbivores, could not be ascertained. Earthworms have been reported to transport seeds from the soil surface to a depth below 4 cm (Reest and Rogaar 1988, in Silvertown and Lovett Doust 1993). Seeds might also get lost through earthworm digestion (McRill and Sagar 1973), ant removal (Andersen 1987) or predation by voles (Borchert and Jull 1978). Earthworms and ants were mainly present on disturbed plots. Vole paths were observed in undisturbed plots.

Additional data (Hinz unpublished) indicate that the time of germination also plays a crucial role in the survival of scentless chamomile in the Rhine Valley. All plants that were still in the seedling stage at the end of April 1993 on D-/S- plots died during the following weeks, whereas 61% of all plants that had already started to shoot at that time reached the reproductive stage. As winter rosettes are already bigger than summer rosettes in late spring, they can presumably withstand adverse weather conditions, competition and herbivore attack.

Several studies have revealed the importance of abiotic factors for seedling survival and plant recruitment (e.g. Mack and Pyke 1984; De Jong and Klinkhamer 1988; Crawley and Gillman 1989), as well as the effect of polyphagous seed- and seedling-predators (e.g. Rice 1987; Crawley and Long 1995;
Paynter this Volume). Further experiments quantifying the importance of herbivores, water supply and germination time for seedling establishment and survival of scentless chamomile would be worth doing.

Relevance for biocontrol

It is concluded that scentless chamomile is seed-limited on disturbed sites, where microsites for germination are numerous, such as in most of the target areas in North America. However, as scentless chamomile can build up large seed-banks, it is assumed that seed-limitation will rarely be the case in the target area, i.e. high seed-banks will buffer years with low or no seed input. Thus, seed feeders will probably have a long-term effect by decreasing the number of seeds added to the seed-bank, and reduce the spread of scentless chamomile, instead of directly influencing plant density. Insects that reduce resource allocation to seed production (e.g. stem- or root-feeders) should supplement the impact of seed feeders. Studies on the population biology of scentless chamomile in Canada indicate that rosettes establishing in autumn contribute disproportionately more to seed output than summer rosettes (A. McClay personal communication). Thus, agents attacking winter rosettes would be useful. In addition, a change in management practices, i.e. reduced disturbance, especially in low-lying areas and sloughs in Canada, could prevent the establishment of scentless chamomile monocultures, and thus reduce sources for further spread.

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References


