Impact of seed reducing natural enemies on weediness of thistles

A.W. Sheppard, CSIRO Division of Entomology, Co-operative Research Centre for Weed Management Systems, GPO Box 1700, Canberra, ACT 2601, Australia.

Summary

The impact of biological control agents introduced around the world to control thistles has resulted in some success with seed-reducing agents contributing to this process. This short paper reviews the knowledge on seed-losses to endophagous insects for Australian thistles in an attempt to suggest where such insects may have a role in future biological control programs. It also illustrates how, in addition to direct seed losses, natural enemies can affect the spread and long-term viability of seeds that escape destruction, thereby reducing regrowth potential of declining thistle infestations.

Introduction

Causing high seed loss is the dominant strategy of most thistle control, as thistles tend to reproduce only by seed, generating soil seed banks that generally determine the outbreak potential of these weeds (Sindel 1991). Biological control applies this strategy by attempting to duplicate in Australia the seed losses to natural enemies found in the native range. This strategy is built on the assumption that control agents, if similarly destructive, should reduce a thistle's status in Australia to at least that found in the native range. This assumption is supported by example: the successful control of nodding thistle (*Carduus nutans*) in parts of North America (Harris 1984, Kok and Surles 1975), where seed losses to the control agent (approximately 50%) were comparable with the native range. This case history however belies explanation on two counts. First, simple models (Lashley 1969, Shea 1996) fail to explain how control was achieved, and second, control has not been replicated in other countries despite similar seed predation levels (Woodburn and Cullen 1993, Kelly and McCallum 1995).

This paper explores the general applicability of the seed loss strategy in biological control of Australian thistles described above by reviewing the potential for seed loss to candidate control agents. It then explains how direct seed-losses to biological control agents can have non-linear effects on both short and long distance seed dispersal capability. This is used, together with other ways that seed-reducing agents may indirectly reduce the growth rate of thistle infestations, to suggest why some such agents may contribute more to thistle control than is at first apparent.

Seed predation

If the introduction into Australia of seed-reducing insects on thistles is going to contribute to thistle control, then it is important to know their likely destructive capacity. Figure 1 shows the levels of seed-loss per plant recorded for thistles known to occur in Australia from both inside and outside (not necessarily Australia) the native range. The data from the native range have been collected from a number of studies (Sheppard 1996). Information is still unavailable for several thistles in regions where agents have been only recently or have never been introduced. However two features come out of this figure. Firstly, general seed losses in the native range are far less than 50% for most species; nodding thistle, Illyrian thistle (*Onopordum illyricum*) and artichoke thistle (*Cynara cardunculus*) being the exceptions. This begs the question as to whether releasing seed-reducing biological control agents against thistles other than on these three will be of any value. Secondly, in four out of five cases where data are available, insects released as biological control agents have caused more seed loss outside their native ranges; nodding thistle being the exception. While acknowledging the first feature, this is in general encouraging for biological control and probably results from relative differences in the ease with which capitula are located between the native and introduced regions (thistle abundance) and the fact that most biological control agents are released without any of their parasites/predators (Sheppard and Woodburn 1996).

Mathematical models used to predict the likely impact of seed reducing agents in biological control usually indicate that very high levels of seed loss (>90%) are necessary to cause weed populations to become sufficiently seed limited to force the net growth rate below 1 (Lashley 1969, Forrester 1995, Paynter *et al.* 1996). Only one nodding thistle model suggests that observed seed losses (at least those in the native range, Figure 1) might be sufficient (65%, Shea 1996). None would have successfully predicted the control of nodding thistle achieved in North America. This leads to two questions addressed in the remainder of this paper:

i. what features not included in these models might explain why lower levels of seed loss can contribute to thistle control (e.g. the case of nodding thistle)? and
ii. is the strategy of introducing seed-reducing biological control agents against thistles still justified in most cases?

Seed dispersal

Thistles depend on three general types of dispersal for invasion and the establishment of new infestations:

i. local dispersal, where seeds are dropped directly from or remain in the capitulum,
ii. wind-born dispersal involving a pappus that varies in effectiveness between species, and
iii. long distance dispersal, where seeds are fortuitously carried a greater distance by some vector (animal, man or vehicle).

In some species, dispersal types one and two are associated with different seed morphs (Olivieri *et al.* 1983). In all types, the slope of the seed dispersal profile (any relationship of seed rain (y, usually log transformed) against distance (x)) will be shallower the further the seed are

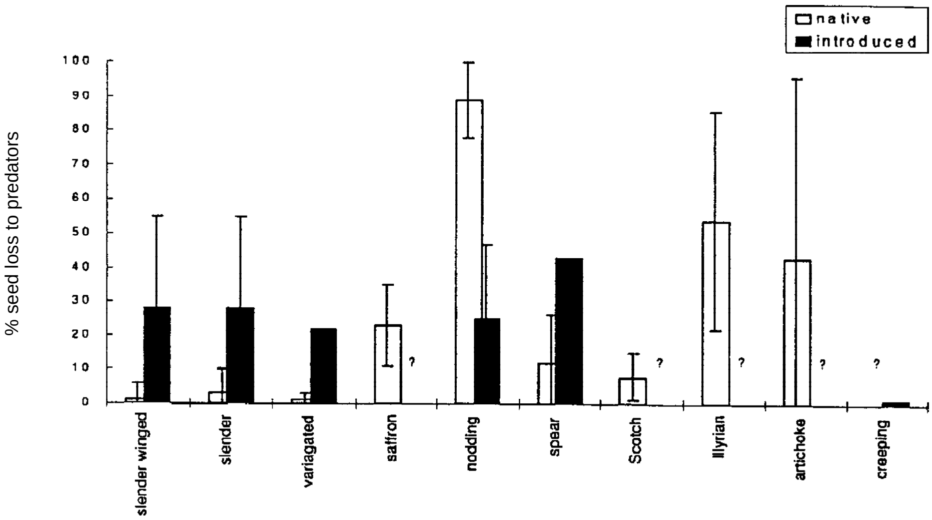

Figure 1. Seed loss (mean ± range) to seed reducing insects for ten Australian thistles both in the native range (white) and elsewhere where they have been introduced and subjected to biological control programs (black).

dispersed. There are two conceivable ways that seed predators can affect such relationships and thus influence the ability of a thistle to spread.

Firstly, direct seed losses will have a greater impact on long distance spread than they will on local dispersal because of the slope of the dispersal profile (Figure 2, Lonsdale 1993). This is because seed loss will affect the intercept, but not the slope of the profile and with a lower profile there will be a greater reduction in distance dispersed. To expand this, a thistle species with a well developed pappus will have a greater dispersal capability, but it will also be more prone to having that capability curtailed through seed-loss, assuming equal levels of seed production. This is the simple way seed-reducing insects can limit the invasibility of a thistle species.

Secondly, seed-reducing insects may be able to steepen the slope of the seed dispersal profile, particularly for wind-born dispersal, by reducing the proportion of viable seed leaving a capitulum with an intact pappus as a result of their disruptive feeding activities in the capitulum. While this has never been tested, seed dispersal profiles generated, for example, from data collected by Kelly *et al.* (1988) for nodding thistle appear to have a steeper profile in a year when the receptacle weevil was more abundant (these data were too few and unsuitable to test such a hypothesis).

Seed longevity

The activities of seed reducing agents in capitula may also reduce long-term viability of seeds that escape destruction and thereby reduce regrowth potential of declining thistle infestations. Viable seeds that drop from capitula that have had their receptacles bored out by insects are less likely to be either the same mean weight or as perfectly formed as seeds from undamaged capitula. Such seed may well be shorter-lived than normal seed and as such may contribute little to a long-lived seed bank. This hypothesis was tested when seed from damaged capitula of nodding thistle were sown into both a cultivated pasture (5000 m^{-2}) and buried in muslin bags (100 seeds per bag) at different depths in the native range. Seeds of similar weight from unattacked capitula imported from Australia (as nearly all capitula in the native range are attacked by insects), were buried in identical muslin bags as part of the same experiment (Meyer 1991). The Australian seed also had the same viability and germinability (results from tetrazolium and germination tests) as the seed from attacked heads (Meyer 1991). The sown seed bank in cultivated pasture had disappeared within 12 months of sowing (Sheppard unpublished data), whereas a seed bank of this size in Australia has much greater longevity (T. L. Woodburn personal communication). After 120 days, the seeds in the muslin bags from damaged heads had significantly lost viability by 15% while the seeds from intact heads were all recovered and viable (Meyer 1991).

Conclusions

In the last two sections of this paper I have attempted to outline subtle and rarely considered ways in which seed-reducing biological control agents can reduce the invasive ability of their host thistles. Such effects may partially explain the differences between successes worldwide in the biological control of thistles and the predictions of ecological models designed to explain them. Together with the observations that seed-losses are often greater following biological control attempts than in the native range (Figure 1), these effects offer optimism for the continued use of such insects as agents against thistles as yet untested. The equal success of other sorts of insects as biological control agents should also not go ignored and careful ecological consideration should take place before any agent type is introduced against thistles.

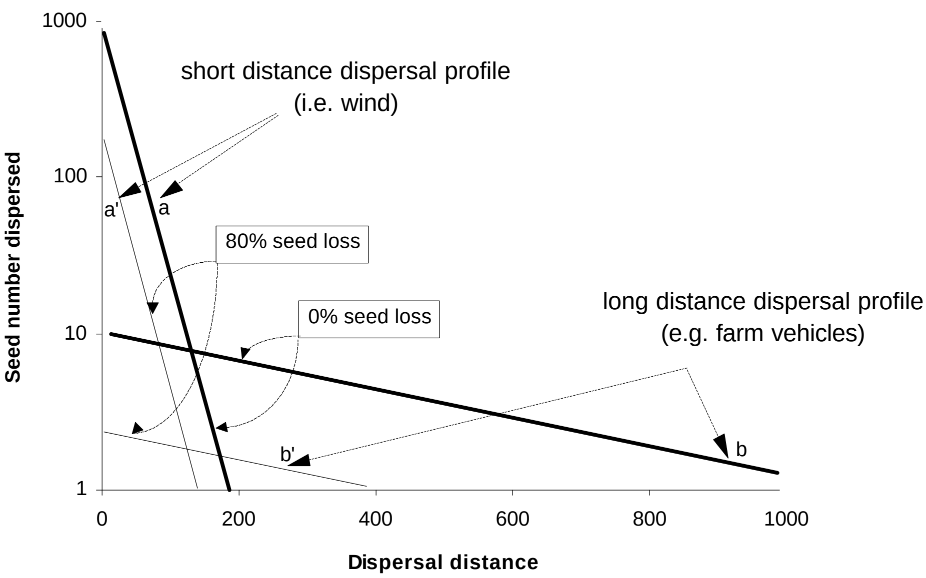

Figure 2. Effect of seed losses on potential dispersal distance. Given two types of dispersal (short and long distance), a similar percentage of seed loss will cause a much greater reduction in dispersal distance for long distance dispersal strategy (b → b') than for a short distance dispersal strategy (a → a'), because of the lower seed dispersal profile (adapted from Lonsdale 1993, Figure 9).

References

Forrester G.J. (1995). Persistent seed banks, plant fitness and their importance in the control of annual weeds: A study of *Echium plantagineum*, a winter annual weed of Mediterranean pasture. Proceedings of the VIII International Symposium on Biological Control of Weeds, pp. 339-46.

Harris, P. (1984). *Carduus nutans* L., nodding thistle and *C. acanthoides* L., plumeless thistle (Compositae). *In* 'Biological Control Programmes against Insects and Weeds in Canada 1969–80', eds. J.S. Kelleher and M.A. Hulme, pp. 115-26. (CAB, Slough, UK).

Kelly, D. and McCallum, K. (1995). Evaluating the impact of *Rhinocyllus conicus* on *Carduus nutans* in New Zealand. Proceedings of the VIII International Symposium on Biological Control of Weeds, pp. 205-12.

Kelly, D., Cameron, H. and Alex J. (1988). Wind dispersal of nodding thistle seeds and pappi. Proceedings of the 41st New Zealand Weed and Pest Control Conference, pp. 207-9.

Kok, L.T. and Surles, W.W. (1975). Successful biocontrol of musk thistle by an introduced weevil *Rhinocyllus conicus. Environmental Entomology* 4, 1025-27.

Lashley, R. (1969). Musk thistle control. Proceedings of the 24th North Central Weed Control Conference, pp. 99-100.

Lonsdale, W.M. (1993). Rates of spread of an invading species—*Mimosa pigra* in northern Australia. *Journal of Ecology* 81, 513-21.

Meyer, J.-Y. (1991). Taille et longevité de la banque de graines de deux chardons: *Carduus nutans* L. et *Carduus pycnocephalus* L. Diplôme d'Etudes Approfondies en Sciences de l'Evolution et Ecologie, Academie de Montpellier, France.

Paynter, Q., Fowler, S., Hinz, H., Memmott, J., Shaw, R., Sheppard, A. and Syrett, P. (1996). Seed predation, seed banks and seed-limitation: are seed-feeding insects of use for the biological control of broom? Proceedings of the IX

International Symposium on Biological Control of Weeds, pp. 495-501.

Olivieri, I., Swan, M. and Gouyon, P.H. (1983). Reproductive system and colonizing strategy of two species of *Carduus* (Compositae). *Oecologia* 60, 114-7.

Shea, K. (1996). Estimating the impact of control efforts: models of population dynamics. *Plant Protection Quarterly* 11, 263-5.

Sheppard A.W. (1996) Weeds in the Cardueae: Biological control and patterns of herbivory. Proceedings of the International Compositae Conference, Kew, 1994, Volume 2 Biology and Utilization, pp. 291-306.

Sheppard, A.W. and Woodburn, T.L. (1996). Population regulation in insects used to control thistles: can we predict effectiveness? *In* 'Frontiers of Population Ecology', eds. R.B. Floyd, A.W. Sheppard and P. J. Debarro, p. 227. (CSIRO Publications, Melbourne).

Sindel, B.M. (1991). A review of the ecology and control of thistles in Australia. *Weed Research* 31, 189-201.

Woodburn, T.L. and Cullen, J.M. (1993). Effectiveness of *Rhinocyllus conicus* as a biological control agent for nodding thistle, *Carduus nutans*, in Australia. Proceedings of the 10th Australian and 14th Asian-Pacific Weed Conference, pp. 99-103.

Ecology of *Cirsium vulgare* and *Silybum marianum* in relation to biological control

E. Bruzzese, Keith Turnbull Research Institute, Co-operative Research Centre for Weed Management Systems, PO Box 48, Frankston, Victoria 3199, Australia.

Summary

Spear thistle (*Cirsium vulgare*) and variegated thistle (*Silybum marianum*) are two of the most widespread thistles which infest pastures in temperate southern Australia. A biological control program targeting these thistles was commenced in 1985. No specific ecological studies of these thistles and their predators in the area of origin aimed at the selection of insects for release in Australia, have been carried out. Insects have been released in Australia, based on data from biocontrol programs against these thistles elsewhere in the world. This paper reviews the literature on ecological studies of these thistles and the effects of their predators. Additional studies from Victoria are summarized. Progress towards the classical biological control of these weeds in Australia is outlined and conclusions are drawn on the chances of success using the agents currently available.

Introduction

Spear and variegated thistles (*Silybum marianum* and *Cirsium vulgare* respectively) are two of the most widespread thistles in temperate eastern Australia (Briese 1988, Parsons and Cuthbertson 1992). In an extensive review of the ecology and control of thistles in Australia no comment was made on the implications of this information for their successful biological control (Sindel 1991). Biological control programs, commenced in Australia in 1986, are opportunistic in that they utilize insect species already introduced into other countries. There are considerable European ecological data on spear thistle and the effects of general predation on population dynamics (van Leeuwen 1983, de Jong and Klinkhamer 1988a,b, Klinkhamer *et al.* 1988, Klinkhamer and de Jong 1993) as well as the insect fauna associated with spear thistle (Redfern 1968, Zwölfer 1965, 1972). Detailed European ecological data are lacking for variegated thistle, but its insect fauna has been documented (Zwölfer 1965, Goeden 1976). This paper compares European and Australian information on plant population dynamics of spear and variegated thistle, outlines progress in the biological control of these two weeds in Australia and elsewhere and discusses this information in relation to successful biological control.

The ecology of spear thistle

Spear thistle is an annual or biennial herb, depending on its time of germination. Although seed can germinate at any time of the year, there are two main germination times in late-summer to autumn and late winter to spring (Bruzzese and Heap unpublished). Because of this, infestations can consist of plants of different size and ages. Seedlings develop into rosettes, up to 60 cm diameter, which generally require vernalizing before flowering can occur. Plants resulting from autumn germination become winter annuals and flower the following summer (6–9 month life-cycle). Plants that germinated in late winter-spring act as biennials, growing as rosettes through summer, autumn and winter and flowering the following summer (12–15 month life-cycle). A small percentage of plants which germinate in summer become summer annuals, flowering in autumn. Flowers appear in December to February and later in higher rainfall areas. Plants die after flowering and dead plants can remain standing for one or two years.

Seed production

Three populations of spear thistle were studied at grazed sites in Victoria in 1986–87. Seed production per plant (Table 1) at the three sites (2668, 4207 and 19 343) was much higher than that recorded in coastal sand dunes in Holland (246–2500 over a five year period on plants undamaged by predation (Klinkhamer and de Jong 1993)). It was however comparable to Australian values reported by Forcella and Wood (1986).

Soil seed bank

Soil seed banks in Victoria (Table 1) show a yearly pattern of replenishment after seed dispersal, followed by a marked decrease throughout the following year. The most important decrease, which ranged between 83 and 99%, was caused by germinations following the autumn rains. From the results, seed input occurs from December to March indicating a very long flowering and seed set period for spear thistle. Seed banks were lower during the second year of monitoring.

Victorian results are comparable to those obtained by Roberts and Chancellor (1979) in England who found that more than 90% of all seeds germinated within one year after production. Klinkhamer and de Jong (1993) estimated that less than