

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

1% of seed produced is still viable the following winter and suggested that there is no persistent seed bank. Victorian studies did not include observations on seed

longevity in the soil but Roberts and Chancellor (1979) found a few seeds dormant after five years. Extrapolations on our seed bank indicated that without seed

replenishment only one to two viable seeds 100 m² would remain after five years.

Table 1. Spear thistle seed production, soil seed bank and plant density over time at three sites in Victoria.

Site	Lang Lang	Derrinallum	Wodonga
Seed production January 1986			
Flowering plants m ⁻²	2.8	6.1	2.6
Heads per plant	53.8	9.3	115.9
Seeds per head	78.2	286.9	166.9
Seeds per plant	4207	2668	19343
Seeds m ⁻²	11779	16274	50291
Soil seed bank (viable seeds m ⁻²)			
March 1986	4260	3496	2355
May 1986	716	302	37
September 1986	180	175	35
April 1987	647	1389	–
October 1987	21	748	42
Plant density (plants m ⁻²)			
March 1986	2.2	2	4.7
May 1986	33.6	390.5	68
August 1986	24.8	27.5	11.2
November 1986	2	11.2	0.2
January 1987	0.5	6.2	0.5
April 1987	12.1	6.7	–

Table 2. Insect/mite predators and fungal pathogens of spear and variegated thistles in Victoria.

Name	Plant part	Host
Insects and mites		
Hemiptera:		
<i>Nysius cleveandensis</i>	flowers	<i>Silybum marianum</i>
<i>Capitophorus elaeagni</i>	leaves	<i>Silybum marianum</i> <i>Cirsium vulgare</i>
<i>Brachycaudus helichrysi</i>	leaves	<i>Cirsium vulgare</i>
<i>Myzus persicae</i>	leaves	<i>Silybum marianum</i>
Coleoptera:		
<i>Arsipoda chrysis</i>	leaves	<i>Cirsium vulgare</i>
<i>Stegobium paniceum</i>	dry seedhead	<i>Silybum marianum</i>
<i>Lasioderma</i> sp.	dry seedhead	<i>Silybum marianum</i>
<i>Corticaria hirtalis</i>	dry seedhead	<i>Silybum marianum</i>
<i>Edusella lineata</i>	leaves	<i>Cirsium vulgare</i>
<i>Corticaria japonica</i>	dry seedhead	<i>Silybum marianum</i>
<i>Teretrius</i> sp.	flowers	<i>Cirsium vulgare</i>
<i>Desiantha caudata</i>	leaves	<i>Silybum marianum</i>
<i>Phlyctinus callosus</i>	leaves, stems	<i>Cirsium vulgare</i>
<i>Melanophthalma</i> sp.	leaves	<i>Cirsium vulgare</i>
<i>Sericoderus</i> sp.	leaves	<i>Cirsium vulgare</i>
Lepidoptera:		
<i>Tebenna bradleyi</i>	leaves	<i>Cirsium vulgare</i>
<i>Epiphyas postvittana</i>	leaves	<i>Silybum marianum</i>
<i>Heliothis punctigera</i>	leaves	<i>Cirsium vulgare</i>
<i>Vanessa kershawi</i>	leaves	<i>Cirsium vulgare</i> <i>Silybum marianum</i>
Acarina		
<i>Tetranychus urticae</i>	leaves, stem	<i>Cirsium vulgare</i>
<i>Halotydeus destructor</i>	leaves	<i>Cirsium vulgare</i>
Fungal pathogens		
<i>Alternaria</i> sp.	leaf spot	<i>Silybum marianum</i>
<i>Ulocladium</i> sp.	leaf spot	<i>Silybum marianum</i>
<i>Trichoderma piluliferum</i>	stem rot	<i>Silybum marianum</i>
<i>Septoria silybi</i>	leaf spot	<i>Silybum marianum</i>
<i>Puccinia cnici</i>	rust	<i>Cirsium vulgare</i>

Seed, seedling and plant survival to flowering

In Holland, losses in the seed stages were severe (97%), with losses in the seedling stage accounting for 67% of seedlings (Klinkhamer and de Jong 1993). When seed production was compared to the seed banks in Victoria (Table 1), losses between 64 and 95% were found to occur between January to March 1986. In the ACT, Forcella and Wood (1986) found average losses in the seed stage ranged between 85 and 90% while losses in the seedling stage were extremely high ranging between 99 and 99.8%. Losses in the rosette stage were 49% in grazed and 51% in ungrazed pastures.

In Victoria the major increase in thistle density in 1986 occurred in May at all sites (Table 1). The decrease in thistle density from May to November ranged between 94 and 99% indicating that survival from seedling to flowering ranged between 1 and 6%. Although individual plants were not tagged, observations at the three Victorian sites indicate that the proportions of plants is winter annual > biennial > summer annual.

The natural enemies of spear and variegated thistle in Victoria

Before a biological control program against thistles commenced, a survey of the natural enemies of thistles was undertaken to establish if specific natural enemies of thistles were present in Victoria. Table 2 lists insects, mites and fungal pathogens collected and identified on spear and variegated thistle. Inspections were carried out during the seedling (autumn), rosette (winter), cabbage (spring) and flowering/seeding (summer) stages of the thistles' life-cycle. Of the insect predators collected on spear and variegated thistle, only the larvae of the moth *Tebenna bradleyi* was considered damaging. It was found to skeletonize leaves of spear thistle at all sites during the flowering period.

Of the fungal pathogens collected, further studies were carried out on the spear thistle rust *Puccinia cnici* (Bruzzese *et al.* 1988) and the variegated thistle leaf spot fungus *Septoria silybi* (Bruzzese and Predebon 1987). Both fungi are specific to their host and very widespread. *Puccinia cnici* was found to have little effect on above ground biomass of spear thistle in the laboratory (Bruzzese *et al.* 1988) and has little effect in the field. *Septoria silybi*, which is highly virulent to variegated thistle, causes considerable foliar damage in the field and has potential for development as a mycoherbicide.

Table 3. Variegated thistle seed production, soil seed bank and plant density over time at four sites in Victoria.

Site	Euroa	Penshurst	Omeo	Maryborough
Seed production December 1985				
Flowering plants m ⁻²	27	5	40.5	134
Heads per plant	2.1	8.8	1.5	1.2
Seeds per head	76.9	100	65.5	35.9
Seeds per plant	160	876	100	42
Seeds m ⁻²	4329	4382	4060	5664
Soil seed bank (viable seeds m ⁻²)				
February 1986	2191	2662.7	6058.4	2111.4
April 1986	509.2	1236.1	4970.9	318.3
July 1986	355.4	933.7	4090.2	620.7
October 1986	376.6	880.6	4334.3	578.2
December 1986	286.4	822.3	3368.7	275.8
March 1987	530.5	1331.5	4058.4	748.0
June 1987	53	1082.2	4286.5	212.2
Plant density (plants m ⁻²)				
February 1986	53.2	3	77.2	6.5
April 1986	475.7	382	153.5	2136
July 1986	144.5	1.7	247.7	450
October 1986	64.7	1.2	65.2	347
December 1986	49.7	0.5	2.5	178.5
March 1987	2.9	21	259.2	39
June 1987	7	1.3	48	10.4

Importation of natural enemies from the area of origin of spear thistle

Spear thistle has been the subject of biological control programs in Canada, USA, South Africa and New Zealand (Julien 1992). The insects which attack the weed in its area of origin are known (Zwölfer 1965). No specific ecological studies of the weed and its predators in the area of origin, with regard to with potential impact in Australia, have been carried out. Based on evidence of establishment in other countries, three insects are currently being released on spear thistle in Australia. These are the spear thistle gall fly (*Urophora stylata*), the thistle receptacle weevil (*Rhinocyllus conicus*) and the thistle crown weevil (*Trichosiromus horridus*).

The spear thistle gall fly

In Europe the gall fly attacks between 20 and 60% of flower heads resulting in seed destruction of between 10 and 60% (Zwölfer 1972). The larvae induce the plant to form woody galls in the flower heads which become physiological sinks for plant nutrients, thus redirecting plant resources from seed production. This insect has been successfully released in Canada, USA and South Africa (Julien 1992). *U. stylata* from south western France was released in southern Victoria in December 1994 in the high rainfall, temperate coastal area. Gall formation occurred at all release sites and the insect successfully overwintered, emerging as adults in early December 1995. At this stage it is too early to confirm establishment. An additional 11 releases were carried out in December 1995, extending releases into drier, Mediterranean type climates.

The thistle receptacle weevil—spear thistle strain

Larvae of *R. conicus* destroy the receptacle of a number of thistle species in Europe. It has been released in a number of countries, including Australia (Woodburn and Cullen 1995) for the control of *Carduus* thistles and in Canada and South Africa for the control of spear thistle (Julien 1992). Zwölfer and Preiss (1983) suggested that an ecotype of *R. conicus*, known to attack 80–100% of spear thistle flowerheads in western France, could be a successful biological control agent. Based on this information, insects from western France are established in South Africa (Zimmermann 1991).

Adults collected in south western France were screened for the debilitating microsporidian disease *Nosema* (Woodburn and Cullen 1995) which commonly attacks *R. conicus* in France. Their progeny were first released at a coastal site near Geelong in 1990 but establishment failed. A release in 1994 at a coastal site in Victoria resulted in recoveries of ovipositing adults in 1995. Releases at an additional five sites occurred in December 1995 increasing the climatic range of releases to colder and drier areas. At this stage it is too early to confirm establishment.

The thistle crown weevil

Larvae of *T. horridus* are known to attack the crowns of rosettes of spear thistle during the winter months (Kok 1975, Jessep 1989). This insect, used for the control of *Carduus nutans* in New Zealand (originally from Germany), is now well established at *C. nutans* sites in New South

Wales (Woodburn and Briese 1996). It was first released on spear thistle in Victoria and New South Wales in March 1996. This insect has the potential to reduce the vigour of the weed in the rosette stage.

The ecology of variegated thistle

Variegated thistle is predominantly an annual herb which reproduces by seed and therefore relies on a soil seed bank for population survival. The main germination in temperate, predominantly winter rainfall climate of southern Australia occurs after the first autumn rains, with some emergence in late winter-spring and after summer storms (Bruzzese and Heap unpublished). The majority of plants behave as winter annuals with some plants acting as summer annuals and (rarely) as biennials. Infestations can therefore consist of plants of different sizes and ages. Seedlings develop into rosettes and 'cabbage like' plants which can grow to 1 m diameter before flowering stems develop in spring. Flowering commences in October and is normally finished by early summer, continuing into summer and early autumn in wetter, more temperate areas. Plants die after flowering and dead stems can remain standing for several months.

Seed production

Four populations of variegated thistle were studied in grazed sites in 1986–87. Head and seed production per plant (Table 3) was variable between sites and ranged from 1.2 heads producing 42 seeds to 8.8 heads producing 876 seeds. This is much lower than the per plant estimate recorded in Western Australia of 55 heads producing 6390 seeds (Dodd 1988).

Seed bank

Soil seed banks (Table 3) show a yearly pattern of replenishment in the summer period from December to March followed by a steady decrease in autumn, winter and spring. At all sites, the highest seed levels were in February 1986 and these levels were not reached again during the study. Seed banks ranged from 2111 to 6058 seeds m⁻². When seed production was compared to the seed bank, losses of between 39 and 62% were found from December to February. The reduction from February to December 1996 ranged between 44 and 87%. These differences are due to seed predation and seed germination in autumn. Variegated thistle seeds are large and palatable and are eaten by birds and rodents. Evidence of this was observed at all sites. In spite of these losses, large seed banks were maintained at all sites. Michael (1968) found that the soil seed bank decreased by 85% over nine years, from 351 to 48 m⁻². In contrast, at a site in central eastern Spain over a two year period, Groves (personal communication) found a seed bank of 25 and 0 m⁻².

Seedling survival to flowering

In Victoria, thistle density at all sites increased markedly in March 1986, coinciding with the autumn rains. There was great variability in seedling numbers between sites, ranging from 153 to 2136 m⁻² (Table 3). From April to December 1986, thistle density decreased between 89 and 99% indicating that only 1–11% of seedlings reach flowering stage. The decrease is due mainly to intra and interspecific competition plus factors such as the presence of red legged earth mites and *Septoria* leaf spot during the seedling stage.

Seedlings were found at all sites in spring and at three sites in summer. The former is contrary to findings by Michael (1968) who found no spring germination. Spring seedlings usually survive but result in small flowering plants in early summer. Summer seedlings survive only if sufficient moisture is available and result in large rosettes which overwinter and flower the following spring, usually having multiple flower stems. In contrast, at a site in central eastern Spain in 1992–95 Groves (personal communication) found an average range of 2.5 to 12.9 seedlings m⁻² in autumn resulting in 1.6 and 0.5 flowering plants m⁻² in spring.

Importation of natural enemies from the area of origin of variegated thistle

Variegated thistle has been the subject of a biological control program in the USA (Julien 1992). As with spear thistle, no specific ecological studies were carried out in the area of origin to select agents with the potential to have the maximum impact in Australia. Based on evidence of establishment in the USA, the thistle receptacle weevil, *R. conicus*, is currently being released on variegated thistle in Australia. Two defoliating European rust fungi, *Puccinia mariana* and *P. cruchetiana*, were considered, but not introduced into quarantine because the funding organization recommended that the project concentrate on the field release and establishment of insects already approved for release. Recently, Groves (personal communication) concluded that *P. mariana* was not a strong candidate as a biological control agent, based on his observations in Mediterranean Europe.

The thistle receptacle weevil, variegated thistle strain

Goeden (1976) suggested that an Italian strain of *R. conicus* was the only promising insect candidate for the biological control of variegated thistle in California. It was released in 1972, attacking up to 94% of heads after three years (Goeden and Ricker 1977). This strain was transferred to Texas in 1978 and where it became established (Boldt and DeLoach 1985). Zwölfer and Preiss (1983) suggested that an

ecotype of *R. conicus* from southern France had a preference for variegated thistle, and after being screened for *Nosema*, this strain was released at two sites in 1988–89, Omeo in December 1988 but did not establish. Releases in 1994 at Maryborough and Peshurst resulted in recoveries of ovipositing adults in 1995. Four extra release sites were seeded in November 1995. At this stage it is too early to confirm establishment.

Conclusions

Spear and variegated thistles rely on seed production, adequate autumn/winter soil moisture and lack of competition from other vegetation to maintain populations from one season to the next. A soil seed bank is also important to both species to re-infest areas after soil disturbance. Both species can be managed with appropriate cultural practices; pasture competition during the main germination periods; grazing management to increase competition at critical times; chemical control to reduce dense infestations (Sindel 1991). The aim of biological control of annual and biennial thistles is to reduce seed production either by direct destruction in the flower head or by weakening the plant so that it dies before flowering or produces less seed. European data available on the plant population dynamics and the effects of general predation on spear thistle (van Leeuwen 1983, de Jong and Klinkhamer 1988a,b, Klinkhamer *et al.* 1988, Klinkhamer and de Jong 1993) are of little use in trying to predict which predators will be the most effective in the control of spear thistle in temperate Australia, as they were not collected in comparable climates and grazing regimes which result in the dense Australian infestations. European data on the insects associated with spear and variegated thistle (Goeden 1976, Redfern 1968, Zwölfer 1965, 1972), give an indication of which insects may be of use in Australia, but again were not collected with the aim of predicting which agents may have the greatest impact on plant populations in another part of the world.

Populations of these weeds can be diminished if seed production is reduced from the current level to well below the soil seed bank level just before the main autumn germination period, and preferably to the level after the autumn germination. From Victorian data, spear thistle seed reduction would have to be at least 78% and preferably 96% while variegated thistle seed reduction would have to be at least 50% and preferably 84%.

There is no information on either the impact of *U. stylata* and *R. conicus* on spear thistle in South Africa, or the impact of *T. horridus* in Canada and New Zealand. However, *U. stylata* is capable of reducing seed production in Canada by between 57–62% (Harris and Wilkinson 1981).

Assuming that *U. stylata* will result in a similar reduction in southern Australia, *R. conicus* and *T. horridus* will need to reduce seed production by at least an additional 18% to achieve a reduction in plant populations. Establishment and evaluation of the impact of these three insects in Australia is recommended before considering the search for additional agents for spear thistle in its area of origin.

Variegated thistle results from USA indicate that *R. conicus* cannot achieve successful biological control alone. In a personal communication to R. Amor in 1978, Goeden reported that '*Rhinocyllus* is all that we have on *Silybum*, and it is not all that effective here' while Boldt and DeLoach (1985) state that while it caused significant damage to flowerheads in Texas, it did not appear to reduce the weed population. While it is too early to determine the impact of *R. conicus* on seed production in Victoria, the USA experience leads to the conclusion that, although a different ecotype free of *Nosema* was released in Victoria, it is unlikely to achieve successful biological control by itself and additional natural enemies will have to be found. Goeden (1976) concluded from southern European surveys that *R. conicus* was the only promising agent and suggested south western Spain and north west Africa as suitable locations for exploration for additional candidate agents. The fungal pathogens of variegated thistle in Europe have not been carefully surveyed for potential biological control agents and recent observations of the rust fungus *P. mariana* have discounted it as a candidate (Groves personal communication). Another defoliating rust fungus (*Puccinia cruchetiana*) is mentioned by Wapshere (1984) and may be worth investigating. Detailed plant population studies coupled with predator/pathogen impact studies in suitable climatic areas of Europe/North Africa are suggested to maximize the chances of finding candidate agents for Australia.

Acknowledgments

The national program on biological control of spear and variegated thistles is funded by the International Wool Secretariat and the Victorian Department of Natural Resources and Environment. Jacqueline Heap, Kate Blood, Dale Stephenson, Peter Stevens and Brad Roberts are thanked for technical assistance. Dr. Jean-Paul Aeschlimann of CSIRO Montpellier collected numerous shipments of *R. conicus* and *U. stylata* in France, while Tim Woodburn of CSIRO Entomology Canberra tested *R. conicus* for *Nosema* and supplied *T. horridus*. Dr. Richard Groves of CSIRO Plant Industry kindly provided unpublished data on variegated thistle in Spain.

References

- Briese, D.T. (1988). Weed status of twelve thistle species in New South Wales. *Plant Protection Quarterly* 3, 135-41
- Boldt, P.E. and DeLoach, C.J. (1985). Evaluating *Rhinocyllus conicus* (Coleoptera: Curculionidae) on *Silybum marianum* (Compositae) in Texas. Proceedings of the VI International Symposium on the Biological Control of Weeds, pp. 417-22.
- Bruzzese, E., Buxton, R.J. and Heap, J. (1988). Aspects of the biology of the spear thistle rust fungus in Victoria, Australia. Proceedings of the VII International Symposium on Biological Control of Weeds, pp. 449-54.
- Bruzzese, E. and Predebon, S. (1987). Septoria leaf spot on variegated thistle in Victoria. Proceedings VI Conference Australasian Plant Pathology Society, (abstract only).
- Dodd, J. (1988). Seed production and phenology of variegated thistle (*Silybum marianum* (L.) Gaertn.). *Australian Weed Research Newsletter* 37, 17-21.
- Forcella, F. and Wood, H. (1986). Demography and control of *Cirsium vulgare* Savi (Ten.) in relation to grazing. *Weed Research* 26, 199-206.
- Goeden, R.D. (1976). The Palaearctic insect fauna of milk thistle, *Silybum marianum*, as a source for biological control agents for California. *Environmental Entomology* 5, 345-53.
- Goeden, R.D. and Ricker, D.W. (1977). Establishment of *Rhinocyllus conicus* on milk thistle in Southern California. *Weed Science* 25, 288-92.
- Harris, P. and Wilkinson, A.T.S. (1981). *Cirsium vulgare* (Savi) Ten., Bull Thistle (Compositae). In 'Biological Control Programmes against Insects and Weeds in Canada 1969-80', eds. J.S. Kelleher and M.A. Hulme, p. 147 (CAB, Slough).
- Jessep, C.T. (1989). Introduction of the crown weevil (*Trichosirocalus horridus*) as an additional biocontrol agent against nodding thistle. Proceedings 42nd New Zealand Weed and Pest Control Conference, pp. 52-4.
- de Jong, T.J. and Klinkhamer, P.L.G. (1988a). Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand-dune area. *Journal of Ecology* 76, 366-82.
- de Jong, T.J. and Klinkhamer, P.L.G. (1988b). Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand dune area: the importance of water for differential survival of growth. *Journal of Ecology* 76, 393-402.
- Julien, M.H. (ed.) (1992). 'Biological control of weeds: a world catalogue of agents and their target weeds', 3rd edition. (CAB International, Oxon, UK).
- Klinkhamer, P.G.L. and de Jong, T.J. (1993). Biological flora of the British Isles. *Cirsium vulgare* (Savi) Ten. *Journal of Ecology* 81, 177-91.
- Klinkhamer, P.G.L., de Jong, T.J. and Van der Meijden, E. (1988). Production, dispersal and predation in the biennial *Cirsium vulgare*. *Journal of Ecology* 76, 403-14.
- Kok, L.T. (1975). Host specificity studies on *Ceuthorrhynchidius horridus* (Panzer) (Coleoptera: Curculionidae) for the biocontrol of musk and plumeless thistles. *Weed Research* 15, 21-6.
- van Leeuwen, B.H. (1983). The consequences of predation in the population biology of the monocarpic species *Cirsium palustre* and *Cirsium vulgare*. *Oecologia* 58, 178-87.
- Michael, P.W. (1968). Perennial and annual pasture species in the control of *Silybum marianum*. *Australian Journal of Experimental Agriculture and Animal Husbandry* 8, 101-5.
- Parsons, W.T. and Cuthbertson, E.G. (1992). 'Noxious weeds of Australia', p. 94. (Inkata Press, Melbourne).
- Redfern, M. (1968). The natural history of spear thistle heads. *Field Studies* 2, 669-717.
- Roberts, H.A. and Chancellor, R.J. (1979). Periodicity of seedling emergence and achene survival in some species of *Carduus*, *Cirsium* and *Onopordum*. *Journal of Applied Ecology* 16, 641-7.
- Sindel, B.M. (1991). A review of the ecology and control of thistles in Australia. *Weed Research* 31, 189-201.
- Wapshere, A.J. (1984). The possibilities of biological control of thistles in Australia. Proceedings of the IV Australian Applied Entomological Research Conference, pp. 324-32.
- Woodburn, T.L. and Briese, D.T. (1996). The contribution of biological control to the management of thistles. *Plant Protection Quarterly* 11, 250-3.
- Woodburn, T.L. and Cullen, J.M. (1995). Release and establishment of the thistle head-weevil, *Rhinocyllus conicus*, in Australia. Proceedings of the VIII International Symposium on the Biological Control of Weeds, pp. 411-14.
- Zimmermann, H.G. (1991). Biological control of spear thistle, *Cirsium vulgare* (Asteraceae) in South Africa. *Agriculture, Ecosystems and Environment* 37, 199-205.
- Zwölfer, H. (1965). Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) species in Europe. *CIBC Technical Bulletin* 6, 81-154.
- Zwölfer, H. (1972). Investigations on *Urophora stylata* Fabr., a possible agent for the biological control of *Cirsium vulgare* in Canada. *CIBC Progress Report* 29, 1-20.
- Zwölfer, H. and Preiss, M. (1983). Host selection and oviposition behaviour in West-European ecotypes of *Rhinocyllus conicus* Froel. (Col., Curculionidae). *Zeitschrift für Angewandte Entomologie* 95, 113-22.