
The Future of Biological Control of Weeds with Insects: No More 'Paranoia', No More 'Honeymoon'

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Abstract

To meet the future challenges facing biological control of weeds, two issues are considered: first the 'paranoia' about the threat of biocontrol agents to non-target plant species, and second, the 'honeymoon' regarding the lack of accountability for projects that failed to achieve their desired objectives. With a suggested new mindset on these issues, proposals are made to deal with five current pressures that biological control of weeds is facing: (i) the image of the discipline, (ii) host specificity verification, (iii) selection of candidates, (iv) funding and (v) regulatory requirements.

Keywords: biocontrol, weeds, insects, host specificity, effectiveness

Introduction

Biocontrol of weeds with insects aims to control the target weed by the introduction of host specific insects which contribute to the suppression the plant in its country of origin. Classical biocontrol of weeds is principally restricted to monophagous species, i.e. those that can feed and survive only on a single host plant species in the field, although there have been a few notable exceptions as, for example, with some of the oligophagous cactus biocontrol agents (Dodd, 1940). Variations such as inundative release (Wapshere, 1982), the biocontrol of native weeds (Pemberton, 1985) and the 'new association' of Hokkanen and Pimentel (1984), are not considered in this paper. Unless otherwise stated the term 'biocontrol' refers exclusively to the biocontrol of weeds by insects.

There are two main risks in biocontrol of weeds. First, that the introduced insects pose a threat to non-target plants. Second, that the biocontrol agent will not effectively control the target plant and be a poor investment of resources. The former risk has given rise to the 'paranoia' and the latter to the 'honeymoon.' The aim of this paper is to consider the 'paranoia' and 'honeymoon' with regard to the current pressures and suggest pointers for the future. Borne out a South African experience, the paper does not presume to have universal application, although there are certain to be common points of interest.

'PARANOIA'

Since early on in its history, there has been an element of 'paranoia' regarding the first risk i.e. that the biocontrol agent itself will become a pest or a threat to non-target plants 'after it has destroyed the weed'. There is little doubt this has been due to the notoriety of insects as pests in agriculture, disastrous biocontrol programs especially using vertebrates such as the giant toad (*Bufo marinus*) in Australia (Simberloff, 1991) and the criticism of biocontrol of pest insects using polyphagous insects by Howarth (1983; 1991). In this climate, early biocontrol practitioners, with little previous experience to draw on, were understandably cautious and adopted the 'seeing is believing' approach by 'demon-

strating' (Wapshere, 1982; Wapshere, 1985) behaviour of insects under artificial conditions in cages. This legacy from the past is still prevalent in host specificity verification today, and seems to have stifled reason and imagination in affirming host specificity of biocontrol candidates. Consequently biocontrol has been landed in the dilemma where potentially effective candidates have to be rejected because they feed and develop on non-target species in the laboratory, even if it is known that they will probably not do so in the field.

After nearly 100 years, and after approximately 1049 deliberate releases resulting in 603 successful establishments of 259 insect species on 111 weed species in over 70 countries, the 'paranoia' has not materialized. The same is also true for approximately 169 records of 63 insect species on 45 weed species in 51 countries where no deliberate release was recorded i.e. there was no prior testing or permission for release (Julien and Griffiths, 1999). (These figures include the tribes Cynareae and Heliantheae in the Asteraceae, and the Boraginaceae and Cactaceae where some oligophages have been used.) No biocontrol agents have become commercially important pests (Cruttwell-McFadyen, 1998). There have also been no host shifts, here defined as the preference of the adopted host over the original host. According to the recent survey by Cruttwell-McFadyen (1998), there are only eight records of damage to non-target plants. So far none of these have been shown to have negative impacts on non-target species (Cruttwell-McFadyen, 1998), although this is being challenged for some oligophagous species such as the weevil, *Rhinocyllus conicus*, on indigenous thistles (Louda *et al.*, 1997). In spite of his criticism regarding the dangers of biocontrol, Howarth (1991) has concluded that 'no plant species appear to have been driven to extinction by biological control introductions'.

This good record is not entirely attributable to the testing methods or the expertise of the biocontrol practitioners. The first introductions in Hawaii up until the 1920's were done without any testing (Harris, 1998), and quarantine studies and procedures for the release of biocontrol organisms during the earlier introduction programs were not as intensive and restrictive as they are to-day (Funasaki *et al.*, 1988). Even though host specificity methods have been evolving since then, they are still imperfect (Cullen, 1990). Furthermore, there are great discrepancies in regulatory standards for obtaining permission to release biocontrol agents in the different countries. In countries where biocontrol is infrequently practiced there is a lack of protocols for introducing biocontrol agents (Cruttwell-McFadyen, 1998). It seems that the host specificity, i.e. monophagy itself, has been a significant factor in the good record of biocontrol.

In retrospect, it would seem that the 'paranoia' about the danger of biocontrol of weeds may have been unwarranted, and was an attitude understandably arising out of the ignorance of the time. With this impeccable safety record, a growing understanding of the sophistication of insect behaviour in host specialisation (Wan and Harris, 1996) and with accumulated experience, the probability of the feared disaster seems more unlikely now than ever before, decreasing rather than increasing. Is it not time to resign this 'paranoia' with its 'seeing is believing' or 'demonstration' mentality to the past and to replace it with more rational approaches suggested below?

HONEYMOON

Since its inception, biocontrol of weeds has enjoyed a 'honeymoon' with regard to the second risk i.e. the effectiveness of biocontrol agents. This lack of accountability for failures may have understandably been caused by the 'paranoia' described above, which

resulted in a pre-occupation with 'safety' (Harris, 1974). Furthermore, initially biocontrol was mainly funded by governmental bodies, for whom it was politically more expedient to stress safety than effectiveness.

However, the climate in which biocontrol of weeds is operating has changed. Currently this is characterized by research contracts with specified goals, strict fiscal discipline and deadlines. Biocontrol of weeds is being expected to justify itself in the face of other options such as chemical control. The new breed of client is funding biocontrol for its potential as an environment-friendly control option and not just as an opportunity to fund research *per se*. Furthermore, these clients now tend to take the safety aspect for granted and want to see visible results of control in return for their investment. Is the 'honeymoon' not maybe over?

SOME CURRENT PRESSURES FACING BIOCONTROL AND POINTERS FOR THE FUTURE

With a new mindset freed from the 'paranoia' of the past and mindful that 'honeymoon' maybe over, some suggestions are made with a view to the future.

Image of the discipline

Biocontrol of weeds is still to-day considered with mistrust in some quarters because of ignorance and 'paranoia' it started with. To counteract this there is a need to improve the image of the biocontrol of weeds by giving it its own unique identity which would clearly distinguish it from other forms of biocontrol that do not place a premium on monophagy. This identity will become more important in future, to prevent biocontrol of weeds being lumped together with biologically engineered organisms and the possible danger of biocontrol insects being treated as imported germplasm and subject to the same restrictions as recombinant DNA (Waage and Greathead, 1988) for the sake of standardisation and simplification of regulations.

The integrity of the phenomenon of monophagy on which biocontrol of weeds is based should be stressed. As suggested above, there is good reason to believe that the good safety record may well be attributable to the phenomena of monophagy, more so than to traditional flawed host specificity testing (Cullen, 1990) or the greatly varying standards for obtaining permission to release biological control agents found in the different countries (Cruttwell-McFadyen, 1998).

Attention should be given to the terminology used in biocontrol of weeds. For example, a word such as 'attack' is widely used in biocontrol literature without qualification. The fact that it is a mildly emotive word may have contributed to 'paranoia' mentality. The word 'attack' is more suited to predator/prey relationships than to insect/plant relationships. 'Attack' should be outlawed and qualified by terms of degree such as 'exploratory feeding', 'restrained feeding' or 'normal feeding', and where there is 'normal feeding,' by 'completed development' or measurements of viability. Consensus has been expressed by biocontrol practitioners that the term 'attack' 'referred to cases where agents could complete their development (or at least a considerable portion of their life cycle) on non-target species and would cause enough damage to routinely reduce the vigour and/or fecundity of the plants' (Moran and Hoffmann, 1995).

Host specificity verification

Host specificity verification normally takes up to two years and requires 52% of pre-

release costs (Harris, 1979). This, together with the fact that it is the stage of the biocontrol program over which biocontrol practitioners have the most control, identifies it as the phase with the greatest potential for saving time and resources, mindful however of not compromising safety.

Harris (1998) has divided the evolution of host specificity verification into four eras. To begin with, insects were released without prior testing, relying entirely on the intuition of the biocontrol practitioners. The second era started in the 1920's, prompted by the first fears about safety which led to no-choice starvation tests in cages. During the third era, a biologically relevant approach was introduced (Harris and Zwolfer, 1968). The host tests, still in cages, were broadened to include congeneric plants thereby introducing an element of predictability. This era ended with doubts about the adequacy of these tests, and the problem, mentioned before, that many insects developed on congenics even if they do not feed on or colonise them in nature. This resolution of this dilemma is a characteristic of current era e.g. Balciunas *et al.* (1996) and Wan and Harris (1996).

So, for most its history, safety or host specificity verification in biocontrol has principally been based on host specificity testing done by no-choice and choice testing in cages in the quarantine laboratory. Marohasy (1998) has concluded that host specificity testing reflects the attitude and experience of the time, and is a product of the political and community pressures, rather than scientific considerations or perceived needs and knowledge. In essence, traditional host specificity testing has persisted until now, without being seriously challenged, despite the fact that it has known flaws (Dunn, 1978; Cullen 1990). Even though attempts have been made to improve host specificity testing procedures (Dunn, 1978) none have convincingly solved the fundamental problem of artefacts intrinsic to caging and laboratory research (Dunn, 1978), or succeeded in reducing the two years it normally takes for traditional testing (Harris, 1979).

Furthermore, it is now evident how erroneous and misleading larval feeding and development, the emphasis of traditional testing, can be in predicting host range. Host finding is a catenary process of opportunités and constraints, with host finding near the beginning of the process and suitability for larval development near the end (Wapshere, 1989; Harris and McEnvoy, 1995; Marohasy, 1996; Wan *et al.*, 1996).

Relieved from the anxieties of the past, there should now be a move away from the heavy reliance on this 'seeing is believing' and 'demonstration' mentality of host range cage testing in the laboratory to a more rational approach. Dodd (1940) advocated field studies in the country of origin as the most reliable method of determining host specificity. The recent return to this approach (Balciunas, *et al.*, 1994), open-field testing (Clement and Cristofaro, 1995) and the suggested immunological techniques to identify proteins in the gut content of field-collected candidates (McClay, 1996) should be encouraged and pursued. Ultimately these methods could prove to be more convincing and cost-effective than traditional methods.

With the development and adoption of these new methods, the monopoly of the stereotypic approach of the past can be broken. The various methods can be flexibly and imaginatively combined, as with the reverse testing sequence of Wapshere (1989) and the six-factor risk assessment approach (Harris and McEnvoy, 1995) to build up a convincing, rational case for host specificity dictated by the particular circumstances of each case.

There is still an important place for no-choice cage testing, by using it to disqualify obvious non-hosts, and to thereby reduce the number of species that need to be subjected to closer scrutiny (Wapshere, 1989; Harris and McEnvoy, 1995; Wan *et al.*, 1996). In

cases where the candidate is rare in its native country, field surveys of Balciunas *et al.* (1994; 1996) will not be practical and laboratory testing may be the only option. Traditional tests can also be improved by, for example, making them more quantitative and objective with innovations such as risk assessment proposed by Wan and Harris (1997). The results of no-choice tests also can be more constructively used because they no longer have to be taken at face value but can now be interpreted in the context of the concept of the 'physiological host range' and 'realised host range' (Balciunas *et al.*, 1996).

Selection of candidates

Although the importance of predicting the effectiveness of biocontrol agents was recognized in early proposals for developing a 'rational and methodical approach for biocontrol' (Wapshere, 1974; 1985) and even though various attempts have been made (Harris, 1974; Goeden, 1983; Cullen, 1995), it is still poor compared to that of safety. This again is probably attributable to the 'paranoia.' With the current pressure for funding, the selection of candidates for effectiveness has now become just as important as selecting for safety.

Without the pre-occupation with safety, more attention can be given to making the predictability of establishment and effectiveness of an agent as good as that of safety. Oligophages should be avoided if at all possible as they carry an extra cost as a public relations risk and also in the more extensive host testing that is required. There is no longer any place for the past 'try and see' approach. Although the ideal of a predictive theory for biocontrol (Ehler 1991) seems unlikely in the short-term (Lawton, 1984), there are trends (Crawley, 1989) that have emerged from case histories that are helpful in making specific decisions. For example, higher number of generations per year and higher fecundity are associated with higher probabilities of establishment and control (Crawley, 1989). Certain genera, such as *Longitarsus* and *Apion*, have such good track records (Julien and Griffiths, 1999) that they should be given priority.

There should be a move away from the opportunistic way in which candidates have been obtained in the past, to a more disciplined and rational selection using the methods available as reviewed by Harris (1991) and by weighing up the 'attractiveness' versus 'feasibility' of the available options (Scott 1996). There must be a greater focus on 'effective' than on 'cosmetic' damage or 'virulence' (Wapshere, 1982) and on relating damage to control.

The importance is emerging of the contribution that post-evaluation studies can make to the future selection of candidates. Until now, these studies have been overshadowed by host specificity testing. In their evaluation of *Sesbania punicea* biocontrol program, Hoffmann and Moran (1998) were able to separate out the contributions of the impact of the damage on the plant population for each of the three agents used. They were even able to make recommendations on the order in which the agents should be introduced. This is further motivation for the necessity of post release evaluations.

A practical suggestion to promote progress in the selection of biocontrol candidates, is to challenge biocontrol practitioners to publish, prior to release, a prioritized list of candidates together with predictions for the establishment and effectiveness of each one, based on whatever preliminary studies have been done, as Blossey (1995) has done for purple loosestrife, *Lythrum salicaria*. Comparison of predictions and post-release results would contribute to the improvement of the methods used. Published predictions would also foster accountability to peers and clients.

Funding

A complete biocontrol program is likely to require 20 scientist years (Harris, 1979) and the cost of screening one candidate has been estimated to cost \$400,000 (Canadian) (Harris, 1991). In the current climate, the trend is to fund short-term, applied research which guarantees results. The characteristically long-term nature of biocontrol programs (minimum of ten years) and the introduction of a single agent (minimum three years) does not make it attractive to potential funders.

Biocontrol programs have to be made more attractive to prospective clients and to retain current clients. Freed from the the past fears, it may now be possible to speed up biocontrol programs without compromising safety as discussed above. Biocontrol programs could also be speeded up by increasing research efficiency. For example, by adopting a multidisciplinary team approach (Harris, 1989; Julien, 1989) with specialization in pre-release (primarily entomological) and post-release (primarily plant ecological) studies. Available resources may also be optimized by paying attention to non-biological aspects such as project management and the morale of researchers.

Regulatory requirements

Many countries have two separate sets of regulations pertaining to the introduction of organisms: one to prevent the importation of new pests and another to protect indigenous species i.e. biodiversity (Harris, 1991). Some of the current regulatory requirements still tend to reflect the 'paranoia' of the time when they were first drawn up. Ironically, biocontrol practitioners to-day are frustrated by regulations that were originally drawn up by their predecessors at that time. In the context of present knowledge and experience, current regulations make unnecessary and unrealistic demands for assuring safety, which are wasting scarce research resources without increasing safety.

The regulations should be up-dated, by re-stating the criteria needed to obtain permission for release agents, to incorporate the scientific progress made in biocontrol. For example, the misleading and outdated emphasis on no-choice testing which has now been shown to give a wider physiological host range than the realized host range (Balciunas, *et al.*, 1996) should be reconsidered.

Unfortunately there is some resistance to the decrease in the use of no-choice tests (Harris and McEnvoy, 1995). This makes it imperative that biocontrol practitioners should be pro-active. Attention should be given to assisting the regulators and those who oppose the release of biocontrol agents, with education regarding biocontrol (Julien, 1989). The interpretation of regulations by regulators would also be easier and more consistent if they had guidelines based on precedents. Such guidelines should be prepared jointly by regulators and biocontrol practitioners (Harris, 1989).

Conclusion

No more 'paranoia.' Despite the initial fears, biocontrol has an excellent track record of safety (Cruttwell-McFadyen, 1998). This, it seems, is not entirely attributable to the discipline of biocontrol with its imperfect testing procedures (Dunn, 1978), but also, arguably even more so, to the nature and integrity of monophagy. Grounded on this sound foundation, together with the increased knowledge and experience, the perceived risks of biocontrol can be addressed with greater confidence to develop more rational, imaginative, cost-effective testing methods than in the past. These new approaches should be less time-consuming to allow practitioners to attend to other neglected aspects such as post-

release evaluation.

No more honeymoon. Freed of the 'paranoia' and mindful that the 'honeymoon' is over, biocontrol practitioners may now focus their attention on increasing the cost-effectiveness of biocontrol programs by concentrating on the aspects that best contribute to the reduction of the density of the target plant i.e. effectiveness. The romance of biocontrol of weeds must give way to hard realities in which it finds itself to assure its future. The emphasis on safety has successfully served to establish biocontrol of weeds, but now more emphasis on 'effectiveness' is needed to assure its future.

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References

- Balcianas, J.K., D.W. Burrows, and M.F. Purcell. 1994. Field and laboratory host ranges of the Australian weevil, *Oxyops vitiosa* (Coleoptera: Curculionidae), a potential biological control agent for the paperbark tree, *Melaleuca quinquenervia*. Biol. Control 4: 351-360.
- Balcianas, J.K., D.W. Burrows, and M.F. Purcell. 1996. Comparison of the physiological and realized host-ranges of a biological control agent from Australia for the control of the aquatic weed, *Hydrilla verticillata*. Biol. Control 7: 148-168.
- Blossey, B. 1995. A comparison of various approaches for evaluating potential biological control agents using insects on *Lythrum salicaria*. Biol. Control 5: 113 - 122.
- Crawley, M.J. 1989. The success and failures of weed biocontrol using insects. Biocontrol News and Inform. 10: 213-223.
- Clement, S.L., and M. Cristofaro. 1995. Open-field tests in host specificity determination of insects for biological control of weeds. Biocontrol Sc.Tech. 5: 395-406.
- Crutwell-McFadyen, R.E. 1998. Biological control of weeds. Annu. Rev. Entomol. 43: 369-393.
- Cullen, J.M. 1990. Current problems in host specificity screening. pp. 27-36. In Proceedings of the 7th International Symposium on the Biological Control of Weeds, 6-11 March 1988, Rome, Italy. Istituto Sperimentale per la Patologia Vegetale, Rome, Italy.
- Cullen, J.M. 1995. Predicting effectiveness: fact or fantasy. pp. 103-110. In Proceedings of the 8th International Symposium on the Biological Control of Weeds, 2-7 February, 1992, Canterbury, New Zealand. Lincoln University, Canterbury, New Zealand.
- Dodd, A.P. 1940. The biological control campaign against prickly pear. Commonwealth Prickly Pear Board, Brisbane, Australia.
- Dunn, P.H. 1978. Shortcomings in the classic tests of candidate insects for the biocontrol of weeds. pp. 51-56. In Proceedings of the 4th International Symposium on the Biological Control of Weeds. 30 August - 2 September 1976, Gainesville, Florida. Center Environmental Programs, Institute Food and Agricultural Sciences, University of Florida, Florida, U.S.A.
- Ehler, L.E. 1991. Planned introductions in biological control. pp. 21-39. In Assessing Ecological Risks of Biotechnology. L.R. Ginzburg [ed.], Butterworth-Heinemann, London.
- Funasaki, G.Y., P.-Y. Lai, L.M. Nakahara, J.W. Beardsley, and A.K. Ota. 1988. A review of biological control introductions in Hawaii: 1890 to 1985. Proc. Hawaiian Entomol. Soc. 28: 105-160.

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- Goeden, R.D. 1983.** Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Prot. Ecol* 5: 287-301.
- Harris, P. 1974.** The selection of effective agents for the biological control of weeds. pp. 75-85. *In* Proceedings of the 3rd International Symposium on the Biological Control of Weeds. 10-14 September 1973, Montpellier, France. CAB, Slough, England.
- Harris, P. 1979.** Cost of biological control of weeds by insects in Canada. *Weed Sc.* 27: 242-250.
- Harris, P. 1989.** Practical considerations in a classical biocontrol of weeds program. pp. 23-31. *In* Proceedings International Symposium on Biological Control Implementation. 4-6 April, McAllen, Texas.
- Harris, P. 1991.** Classical biocontrol of weeds: its definition, selection of effective agents, and administrative-political problems. *Can. Entomol.* 123: 827-849.
- Harris, P. 1998.** Evolution of classical weed bio-control: meeting survival challenges. *Bull. Ent. Soc. Canada.* 30: 134-143.
- Harris, P., and P. McEvoy. 1995.** The predictability of insect host plant utilization from feeding tests and suggested improvements for screening weed biological control agents. p. 125-132. *In* Proceedings of the 8th International Symposium on the Biological Control of Weeds, 2-7 February, 1992, Canterbury, New Zealand. Lincoln University, Canterbury, New Zealand.
- Harris, P., and H. Zwolfer. 1968.** Screening of phytophagous insects for biological control of weeds. *Can. Entomol.* 100: 295-300.
- Hoffmann, J.H., and V.C. Moran. 1998.** The population dynamics of an introduced tree, *Sesbania punicea*, in South Africa, in response to long-term damage caused by different combinations of three species of biological control agents. *Oecologia* 114: 343-348.
- Hokkanen, H., and D. Pimentel. 1984.** New approach for selecting biological control agents. *Can. Entomol.* 116: 1109-1121.
- Howarth, F.G. 1983.** Classical biological control: Panacea or Pandora's box? *Proc. Hawaiian Entomol. Soc.* 24: 239-244.
- Howarth, F.G. 1991.** Environmental impacts of classical biological control. *Ann. Rev. Entomol.* 36: 485-509.
- Julien, M.H. 1989.** Biological control of weeds worldwide: trends, rates of success and the future. *Biocontrol News Inform.* 10: 299-305.
- Julien, M.H., and M.W. Griffiths. 1999.** Biological control of weeds - a world catalogue of agents and their target weeds. CAB Publishing, Wallingford.
- Lawton, J.H. 1984.** Ecological theory and choice of biological control agents. pp. 13-26. *In* Proceedings of the 6th International Symposium on the Biological Control of Weeds, 19-25 August, 1984, Vancouver, Canada. Agriculture Canada, Ottawa, Canada.
- Louda, S.M., D. Kendall, J. Connor, and D. Simberloff. 1997.** Ecological effects of an insect introduced for the biological control of weeds. *Science* 277: 1088-1090.
- Marohasy, J. 1996.** Host shifts in biological weed control: real problems, semantic difficulties or poor science? *International J. Pest Manag.* 42: 71-75.
- Marohasy, J. 1998.** The design and interpretation of host-specificity tests for weed biological control with particular reference to insect behaviour. *Biocontrol News Infor.* 19: 13-20.
- McClay, A.S. 1996.** Host range, specificity and recruitment: synthesis of session 2. pp. 105-112. *In* Proceedings, 9th International Symposium on the Biological Control of Weeds, 19-26 January 1996, Stellenbosch, South Africa. University of Cape Town, Cape Town, South Africa.
- Moran, V.C., and J.H. Hoffmann. 1995.** Should agents that attack native or other target plants be used in biological weed control? pp. 13-15. *In* Proceedings of the 8th International Symposium on the Biological Control of Weeds, 2-7 February, 1992, Canterbury, New Zealand. Lincoln University, Canterbury, New Zealand.
- Pemberton, R.W. 1985.** Native weeds for candidates of biological control research. pp. 869-877.

- In Proceedings of the 6th International Symposium on the Biological Control of Weeds, 19-25 August, 1984, Vancouver, Canada. Agriculture Canada, Ottawa, Canada.
- Scott, J.K., and D.G. Bowran. 1996.** Workshop to identify research priorities for *Emex* species. Plant Prot. Quart. 11:175-176.
- Simberloff, D. 1991.** Keystone species and community effects of biological introductions. pp. 1-20. In Assessing ecological risks of biotechnology. L.R. Ginsberg [ed.], Butterworth-Hieneman, London.
- Waage, J.K., and D.J. Greathead. 1988.** Biological control: challenges and opportunities. Phil. Trans. R. Soc. Lond. B 318:111-128.
- Wan, F.H., and P. Harris. 1996.** Host finding and recognition by *Altica carduorum*, a defoliator of *Cirsium arvense*. Entomol. Exp. Applic. 80: 491-496.
- Wan, F.-H., P. Harris, L.-M. Cai, and M.-X. Zhang. 1996.** Host specificity of *Altica carduorum* Guer. (Chrysomelidae: Coleoptera), a defoliator of *Cirsium arvense* (L.) Scop. (Asteraceae) from north-western China. Biocontrol Sc.Tech. 6: 521-530.
- Wan, F.-H., and P. Harris. 1997.** Use of risk analysis for screening weed biocontrol agents: *Altica carduorum* Guer. (Coleoptera: Chrysomelidae) from China as a biocontrol agent of *Cirsium arvense* (L.) Scop. In North America. Biocontrol Sc.Tech. 7: 299-308
- Wapshere, A.J. 1974.** Towards a science of biological control of weeds. pp. 3-12. In Proceedings of the 3rd International Symposium on the Biological Control of Weeds. 10-14 September 1973, Montpellier, France. CAB, Slough, England.
- Wapshere, A.J. 1982.** Biological control of weeds. pp. 47-56. In Biology and Ecology of Weeds. W. Holzner and N. Numata [eds.], Dr W. Junk Publishers, The Hague.
- Wapshere, A.J. 1985.** Effectiveness of biological control agents for weeds: present quandaries. Agric. Ecosyst. Environ. 13: 261-280.
- Wapshere, A.J. 1989.** A testing sequence for reducing rejection of potential biological control agents for weeds. Ann. Appl. Biol.: 114, 515-526.