Fungal pathogens as classical biological control agents for invasive alien weeds – are they a viable concept for Europe?

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Summary

In the majority of cases neophytes arrive in new, adventive ranges free from most, if not all of their associated co-evolved arthropods and pathogens. Based on the theory that the impact of invasive plant species is linked to a reduced attack by natural enemies, classical biological control (CBC) aims to redress this imbalance by deliberately introducing highly-specific natural enemies from the centre of origin of the target weed into its exotic range. Traditionally the domain of invertebrate natural enemies, fungal pathogens have only recently been considered and exploited as classical biological agents for invasive alien plant species. However, their potential has already been well-documented following their successful use against invasive neophytes in countries such as South Africa and Australia with a tradition of using CBC to manage alien weeds. Based on well-established scientific principles and protocols CBC follows defined steps to ensure a thorough evaluation of the potential and safety of any exotic agent. Two European research projects are currently underway to assess the potential of fungal pathogens as classical biocontrol agents for giant hogweed (*Heracleum mantegazzianum*) and Japanese knotweed (*Fallopia japonica*) in their introduced ranges. Although Europe has not yet employed CBC as a method to manage invasive alien weeds, the prospects to implement this strategy successfully against neophytes are considered to be high, given an estimated minimum 80 % success rate of weed CBC worldwide. However, in contrast to countries such as Australia and New Zealand, current European legislation governed by the EU directive 91/414 assigns pesticide status to the use of micro-organisms as classical biocontrol agents for weeds; hereby implying a lengthy registration process with considerable costs involved. In order to make the strategy of using fungal pathogens in weed CBC a viable concept for Europe, it is argued that applications for import and release of such organisms should be dealt with under a different non-pesticide legislation enforced by appropriate national bodies.

Key words: EU directive 91/414, giant hogweed, Japanese knotweed, neophytes

1. Introduction

The threat posed by invasive alien species to the native biota and ecosystems as well as to local economies has risen dramatically in recent years as a result of the growth in world trade and transport. Increasing globalization and the associated translocation of animals, plants and microorganisms has left hardly any part of the planet earth unaffected. Today, biological invasions are considered second only to habitat destruction and landscape fragmentation with respect to their devastating impact on global biodiversity (Vitousek et al. 1997). The ecological and economic costs resulting from these invasions can be extremely high and have been widely documented (Pimentel 2002). In contrast to invasive vertebrates or invertebrates, alien plant invaders (neophytes) have often received less attention due to their impact being frequently more cryptic and hence less well documented. Their potential to endanger native species and to cause substantial ecological as well as economic damage often becomes apparent only after a considerable lagphase following the initial introduction and establishment, but matches, nevertheless, that of more high-profile invasive animal species (Adair & Groves 1998; Reinhardt et al. 2003).

Introductions of non-native plant species can occur either deliberately – as a result of global trade in exotic ornamentals or species with a perceived economic value – or accidentally, e.g. as seed contaminants. Either way, the majority of neophytes usually arrive in their new, adventive ranges free from most, if not all of their associated co-evolved natural enemies. According to the enemy release theory, exotic plant species should experience "a decrease in regulation by herbivores and other natural enemies, resulting in an increase in distribution and abundance" in their introduced range (Keane & Crawley 2002). In other words, the impact of invasive plant species is strongly linked to a reduced attack by both specialist and generalist natural enemies (Mitchell & Power 2003). Based on this theory, classical biological control (CBC) aims to redress this imbalance between invasive alien plants and their natural enemies through the intentional introduction of co-evolved, highly-specific arthropods and pathogens, from the centre of origin of the target weed into its new exotic range. While the potential of non-coevolved natural enemies, or new associations, as biological control agents for invasive alien species has been highlighted (Hokkanen & Pimentel 1984), CBC is considered to be the most effective approach for the control of invasive neophytes, particularly when using fungal pathogens (Greathead 1995; Evans & Ellison 2004). The long history of CBC has shown it to be a highly successful method which, if carried out scientifically, provides a safe, environmentally sustainable and cost effective strategy for long-term weed control (Julien & Griffiths 1998; McFadyen 1998). Countries such as Australia, South Africa, New Zealand, Canada and the USA have a long-standing experience using CBC as part of an integrated weed management plan. Thus their national legal frameworks regulating the import and release of exotic biological control agents have been well-established and tested. Europe, in contrast, has little experience with CBC and has, so far, never implemented this strategy for the management of invasive alien weeds. Consequently, any legislation dealing with the implementation of this method and the associated issues is also lagging behind.

The aim of this paper is to highlight the potential of fungal pathogens as classical control agents for invasive neophytes and to outline the principles and protocols followed to ensure their safe use in CBC. The prospects and constraints facing classical weed biocontrol with fungal pathogens in Europe will be discussed using two current European research projects as case studies which are assessing the options for biological control of giant hogweed *(Heracleum mantegazzianum)* and Japanese knotweed *(Fallopia japonica)*.

2. The potential of fungal pathogens as classical control agents

Biological control has been defined as the "use of living organisms to control pest species" (Waage & Greathead 1988; Watson 1991). CBC of weeds, exploiting natural enemies from the centre of origin of a target neophyte in order to control it in its adventive range, has traditionally been the domain of entomologists. The most famous early success story is undoubtedly the control of *Opuntia* spp. or prickly pear in Australia using the pyralid moth *Cactoblastis cactorum*. Following the importation and release of this neotropical insect into Australia in 1926, the invasive cacti, affecting at that time around 50 million hectares of rangeland in New South Wales, were brought under control within a few years (Dodd 1936; Julien & Griffiths 1998).

The potential of fungal pathogens to have a severe impact on plant populations has manifested itself in serious outbreaks of plant diseases during history such as potato blight resulting in the Irish potato famine in the 19th century, chestnut blight and Dutch Elm disease altering the species composition of forest ecosystems in North America and Europe respectively, coffee rust severely affecting coffee-producing countries around the world and, most recently, the spread of Sudden Oak Death in the USA and Europe. Such epidemics can be the result of new associations, i.e. where the plant host has not been previously exposed to the causal fungal pathogen, as has been documented for a number of diseases affecting tropical crop plants outside their native ranges (Hokkanen 1985). In many cases, however, disease outbreaks have been particularly devastating in situations where coevolved pathogens, such as the causal agent of potato blight *Phytophthora infestans*, have eventually caught up with their crop hosts cultivated in exotic situations (Evans 2000). Despite, or most likely because of the fear of this documented potential of plant pathogens, fungal pathogens have only recently been exploited for classical weed biocontrol. The first intentional release of an exotic fungal agent was undertaken in 1971, when the rust *Puccinia chondrillina* was imported from Italy into Australia against skeleton weed (*Chondrilla juncea*), at that time a serious problem in wheat (Cullen et al. 1973, Julien & Griffiths 1998). Regarded as one of the most successful biological control examples using a fungal pathogen, the release of this rust resulted in a reduction of skeleton weed infestation levels by more than 99 % and annual returns calculated at around AU$ 18 million (Burdon et al. 1981; Cullen & Hasan 1988). Since *P. chondrillina* was first released, 25 fungal species have been used as agents for classical biological control of weeds in seven countries, all of which are outside Europe (Barton 2004). Two more recent examples highlighting the potential of fungal pathogens as classical weed biocontrol agents are the use of the Australian gall rust, *Uromycladium tepperianum,* against the invasive Port Jackson willow (*Acacia saligna)* in South Africa (Morris 1997) and the release of the rust *Maravalia cryptostegiae* from Madagascar to target rubbervine weed (*Cryptostegia grandiflora*) in Queensland, Australia (Evans et al. 2001; Tomley & Evans 2004). The gall rust, first introduced into South Africa in 1987, has by now brought the invasive Australian *Acacia* species almost under complete control reducing its population levels by up to 95 % (Morris 1991, 1997). Following its initial introduction in 1994, *M. cryptostegia* has spread up to 550 km from original release sites in Queensland severely damaging existing rubbervine weed populations and preventing new invasions as seedling recruitment has been reduced to zero. According to Tomley & Evans (2004) complete control of the Madagascan invader could be achieved within 4-6 years.

Limitations to the successful use of fungal pathogens, as well as of arthropods, in weed CBC can arise due to various factors. Differences in the climatic and ecological conditions between native and introduced ranges of alien weeds can effect the establishment, survival and propagation of a particular classical agent (Harley & Forno 1992). Given the potential existence of fungal pathogen strains specific to individual host plant genotypes, a pathogen strain adapted to target weed populations in the centre of origin not matching populations in the adventive range can prove to be ineffective in controlling the invasive neophyte. On the other hand, the particular good match, both with respect to virulence and host specificity, between the Italian *P. chondrillina* strain and the skeleton weed biotype most dominant in Australia at the time of its release, left two less common biotypes of the weed unaffected in the field, thus potentially favouring their spread. This issue was subsequently addressed through the introduction of additional *P. chondrillina* strains from Italy as well as from Turkey capable to attack these two other biotypes (Evans et al. 2001; Barton 2004).

3. Protocols for the use of fungal pathogen in weed CBC

Whilst the protocols for CBC have originally been devised and subsequently refined over more than a century by entomologists in order to evaluate the potential of invertebrates as control agents (Huffaker 1959; McFadyen 1998), the fundamental principles and procedures of the strategy apply to fungal pathogens alike (Evans 2000; Evans et al. 2001). The steps followed by a typical classical biocontrol programme – foreign exploration, agent selection and screening, introduction and release, monitoring – are, therefore, universally valid (McFadyen 1998; Evans et al. 2001). McFadyen (1998) and Evans et al. (2001) have published comprehensive reviews addressing these issues and only a brief summary of the procedures will be given here.

Based on the theory that in its native range the population of a plant species is, to a certain extent, controlled by its associated natural enemies (Evans et al. 2001), the centre of origin of an invasive neophyte needs to be established correctly in order to direct the survey work for coevolved fungal pathogens to the most promising regions. Climatic and ecological conditions need to be taken into account when selecting survey areas and populations of the weed in the introduced range should be matched with those in its native range. Based on the preliminary information gathered during field surveys about the mycobiota of the target weed in its centre of origin – especially abundance and distribution of associated fungal pathogens, damage and apparent host specificity of potential agents, as well as initial data on their biology and life cycle – various strains of the most promising pathogens are selected for further testing. Typically any search will concentrate on biotrophic fungal pathogens, since over time these have evolved closely with their hosts and, therefore, are generally highly host specific (Evans et al. 2001). Rusts in particular combine all the traits required for safe and effective weed control, such as high impact on the host, characteristically narrow host ranges, substantial reproductive capacity and efficient long-distance aerial dispersal (Adams 1988; Evans & Ellison 1990, TeBeest 1991; Watson 1991). Evaluating the potential of different strains of one or more selected pathogens as classical agents, and especially assessing their host specificity, constitutes the most time-consuming part of any biocontrol project and, if conducted outside the area of origin, has to be undertaken under quarantine conditions. Since the introduction and release of an exotic organism into a new environment inevitably carries a risk, host-range screening of fungal agents provides crucial data for a risk assessment on which to base any further decisions about their potential use for classical weed biocontrol (McClay 1996). Host-specificity testing, typically conducted under optimum conditions for fungal infection (Barton 2004), generally follows the centrifugal phylogenetic method, which was initially devised by Wapshere (1974) for arthropod agents, and subsequently refined for fungi by Watson (1985) and Weidemann (1991). Based on the assumption that plant species more closely related to the target weed are also more likely to be attacked by any potential classical agent, test plant lists are devised according to the phylogenetic relationship to the target weed. Additionally, plant species likely to be attacked by a particular agent because they are either hosts of a species closely related to the control agent or similar in morphological or biochemical properties to the target weed, will be included. Based on the data obtained, scientific dossiers are prepared for fungal pathogens considered to have high potential as classical control agents for the target weed and are then submitted to the relevant national authorities responsible for the approval of importation and release of exotic biocontrol agents. If approved for introduction, a classical agent will ideally be monitored and assessed following its release with respect to its impact on the invasive neophyte and to ensure the absence of negative side effects on non-target species.

4. Europe's experience

While not exempt from the threat posed by invasive neophytes, Europe has been slow in the uptake of CBC as a potential strategy for dealing with this problem. So far over 1000 releases of weed biocontrol agents have been made around the globe with EU member states being the source of 381 of these, but, ironically, the recipients of none (Shaw 2003). The only documented releases of classical biocontrol arthropod agents against alien weeds in Europe took place in the former USSR (Reznik 1996; Julien & Griffiths 1998). Exotic fungal pathogens have so far not been exploited. While the rust *Puccinia canaliculata* was undergoing initial evaluations as a classical agent for the introduced weed *Cyperus esculentus* in the Netherlands the pathogen was subsequently rejected due to lack of host specificity (Scheepens & Hoogerbrugge 1991). Europe's poor experience in this field stands in sharp contrast to its use of CBC against arthropod pests with, according to the Biocat database as of April 2004, 276 releases of invertebrate agents (comprising 137 species) being made in EU member states since 1901 (R.H. Shaw, pers. comm. 2004). However, the relatively recent success in obtaining funding for two research projects evaluating the options for CBC of two invasive alien weeds, giant hogweed and Japanese knotweed, clearly reflects a change in European policy. Within the framework of both projects, fungal pathogens, as well as arthropods, are being assessed for their potential as classical agents. The current status of the pathogen work together with a brief summary of the history of the individual projects is given below.

4.1 Giant hogweed *(Heracleum mantegazzianum)*

Giant hogweed, a member of the Apiaceae, is native to the western part of the Caucasus, the mountain range stretching from the Black Sea to the Caspian Sea. First introduced into botanical gardens in central and northern Europe in the late 19th century (Briggs 1979), this impressive plant was actively planted as an ornamental curiosity in gardens and parks. Now an invasive in most of its introduced range in western Europe, giant hogweed not only poses a threat to the local biodiversity (Pyšek & Pyšek 1995; Otte & Franke 1998) but also constitutes a health hazard causing phytophotodermatitis following contact with its sap (Dodd et al. 1994).

In January 2002, the multidisciplinary research programme "Giant Alien" commenced looking at an integrated management strategy for the invasive neophyte with a strong emphasis on CBC. Funded by the European Commission under the 5th framework programme the project is led by the Danish Forest and Landscape Research Institute and involves altogether eight partners from six European countries as well as one Russian subcontractor. The evaluation of fungal pathogens as classical agents for giant hogweed is being undertaken by CABI Bioscience UK Centre.

Following the steps of a classical biocontrol programme, a number of surveys have been undertaken in the Caucasus region to assess the composition and the impact of the mycobiota associated with the weed in its centre of origin. Out of the list of fungal species recorded on giant hogweed during these field surveys (Seier et al. 2004), the following four pathogens, considered to have high potential as classical agents, were selected for further evaluation under quarantine conditions in the UK: the coelomycetes *Phloeospora heraclei, Septoria heracleicola* and *Phomopsis* sp., and the cercosporoid fungus *Ramulariopsis* sp. nov.. Initial host range testing of *P. heraclei, S. heracleicola* and *Ramulariopsis* sp. nov. revealed that all three species are able to attack and reproduce on parsnip (*Pastinaca sativa*), a close relative of the target weed (Seier et al. 2004). Coriander (*Coriandrum sativum*), another test plant species, showed symptoms in the form of necrosis after inoculation with *Ramulariopsis* sp. nov. and *P. heraclei,* but only the latter pathogen was able to sporulate and complete its life cycle on the non-target species. The results suggest that none of the fungal pathogens assessed to date exhibits sufficient host specificity to be considered for introduction as a classical agent for giant hogweed in its introduced European range. The fungal species *Phomopsis* sp., observed to attack the umbels of giant hogweed in the field thereby preventing seed set, is still undergoing evaluation and the results are pending.

4.2 Japanese knotweed *(Fallopia japonica)*

Japanese knotweed, a herbaceous, rhizomatous perennial belonging to the Polygonaceae, was introduced as an ornamental from eastern Asia into Europe during the 1800s (Child & Wade 2000). Relatively uncommon in its native range in Japan (Evans 2003), the plant is an aggressive invader in its exotic situations displacing the native flora and causing substantial environmental as well as physical damage e.g. to tarmac and concrete (Child & Wade 2000; Shaw 2003). By now the neophyte is considered to be the most pernicious weed in the UK (Mabey 1998), if not in many parts of Europe.

Attempts by CABI Bioscience to obtain funding in the UK for research into biological control of Japanese knotweed were first made in 1989. However, it took 11 years for start-up funding to be secured. The initial phase (Phase 1) involved a feasibility study and encompassed a literature review and a set-up mission to Japan (Shaw & Djeddour 2004). Field surveys revealed that in contrast to its introduced range, Japanese knotweed is heavily attacked by both pathogens and insects in its native range. Based on the preliminary results obtained during Phase 1, a case for further funding was prepared which, following a successful bid for the project tender, was obtained by CABI Bioscience UK under Phase 2 in 2003. This second phase comprises a four-year research programme funded by a consortium of organisations, coordinated by Cornwall County Council (D.H. Djeddour, pers. comm. 2004). Further field surveys for natural enemies have been restricted to Kyushu Island/Japan following identification of this region as the origin of plants with the closest match to the single UK knotweed clone. Preliminary host-range testing carried out under quarantine conditions in the UK has shown two rusts, *Puccinia polygoni-amphibii* var. *tovariae* and *Aecidium polygoni-cuspdati,* as well as a damaging *Mycosphaerella* leafspot, to be the most promising fungal pathogens as classical biocontrol agents. Apart from comprehensive host range screening, a number of questions concerning the biology of the three potential agents still need to be addressed and evaluations are ongoing (D.H. Djeddour, pers. comm. 2004).

5. Prospects and constraints

When considering the prospects and constraints for CBC of weeds using fungal pathogens in Europe a clear distinction needs to be made between issues of scientific nature and those concerning politics, legislation and public awareness. From a scientific point of view the opportunities and challenges faced by Europe do not differ significantly from those in other regions of the world. As outlined in this paper, the principles and protocols on which CBC is based are scientifically sound, well-established and tested. Europe is in the fortunate position to benefit greatly from the experiences and scientific advances made in researching and implementing weed CBC over a considerable period of time by pioneering countries such as Australia and South Africa. Inherent to the science involved, constraints in a biocontrol programme can arise at any time, e.g. due to the nature of individual fungal agents under evaluation. As happened during the course of the giant hogweed project, the options to use fungal pathogens as classical control agents became more and more restricted when initially promising candidates failed to show sufficient host specificity. Research into pathogens for classical control of Japanese knotweed is confronted with the challenge to elucidate the life cycles of two rusts, a group of pathogens regarded to have the highest potential for weed CBC, but which can exhibit extremely complex life cycles (Petersen 1974). Despite such problems, the overall success rate of weed CBC is considered to be at least 80 % (McFadyen 2000) with fungal agents showing an impeccable safety record (Barton 2004) and achieving high returns, both in monetary and ecological terms (Burdon et al. 1981; Tomley & Evans 2004).

The real challenges for Europe regarding the use of exotic fungal pathogens to control invasive neophytes do not lie in the science but in the public perception and the existing legal framework. Having virtually no experience in classical weed biocontrol, Europe also lacks any specific legislation regulating the import and release of classical fungal agents and the concept of this control strategy constitutes a novel idea for the general public (Evans 2003; Shaw 2003). Taking also into account that there is a common fear of plant pathogens based on well-known devastating disease outbreaks, as well as concerns about spontaneous mutations and a frequent confusion with GMOs

(Evans et al 2001; Shaw 2003; Barton 2004), it becomes apparent that intensive educational work needs to be undertaken if exotic fungal agents are to become a commonly accepted method for the control of invasive alien weeds. This European situation stands in stark contrast to the public awareness and acceptance of weed CBC in countries such as Australia, South Africa, New Zealand, Canada and the USA which have been active and successful in using this method for many years. These countries have also developed legal frameworks and protocols regulating the import and release of classical biocontrol agents and have defined the relevant authorities implementing these regulations, generally as part of legal acts addressing plant quarantine or plant health issues (Sheppard et al. 2003). In Australia, the only country with biological control legislation, the legal basis for the classical introduction is provided by the Biological Control Act of 1984 (Cullen & Delfosse 1985). In New Zealand, a specific semi-judicial body, the Environmental Risk Management Authority (ERMA), appointed by the Minister for Environment, assesses and decides on import and release applications for classical agents (Sheppard et al. 2003). For Europe, the European and Mediterranean Plant Protection Organization (EPPO) has developed standards for the "safe use of biological control" (EPPO 2001) based on the IPPC Code of Conduct for the import and release of exotic biological control agents (IPPC 1996). However, neither the code nor the EPPO standards are legally binding and the latter also explicitly exclude microorganisms. Within the EU the legal document which currently covers potential introductions of fungal pathogens for weed CBC is the EU directive 91/414 (1991). This directive deals with the "placing of plant protection products on the market" and classifies microorganisms as "active substances of plant protection products". Switzerland, not a member of the EU, will, nevertheless, follow the EU directive closely when addressing the issue of pathogens as classical agents during the current revision of its legislation for plant protection products (H. Dreyer, pers. comm. 2004). Initially developed to protect humans and the environment from harmful chemicals, these regulations assign microbial agents a pesticide status with immense registration costs and "product" efficacy paramount for registration. They are, therefore, totally inadequate when dealing with fungal agents as classical agents for weed control, which generally carry no human health risk and, in contrast to a marketable product, are not for sale and are meant to establish permanently in the environment after initial releases for "the public good" (Harley & Forno 1992). As a direct result of the EU directive, in the UK the approval of any potential application for the importation and release of exotic fungal pathogens falls within the responsibilities of the Pesticide Safety Directorate (PSD). Despite a recent PSD pilot scheme offering a free pre-consultation and reduced registration fees for applications dealing with alternative control measures at around Euro 33.000 (R.H. Shaw, pers. comm. 2004), the cost to register a fungal pathogen as a classical agent for control of giant hogweed or Japanese knotweed, for example, would still be out of reach for most project budgets. In sharp contrast, applications for the release of arthropods as classical biocontrol agents (or "Beneficial Pests") are dealt with in the UK free of charge by the Department of Environment, Food and Rural Affairs (DEFRA) Biotechnology Unit supported by the Advisory Committee on Releases into the Environment (ACRE), an institution much better placed to take such decisions.

Much can be learnt from countries such as Australia, New Zealand and South Africa if CBC of invasive alien weeds using fungal pathogens is to become a viable concept for Europe. Most of all, the problems in the current legislation dealing with microbial classical agents need to be addressed and, ideally, these organisms would be dealt with under a different non-pesticide legislation. Appropriate national bodies such as DEFRA and ACRE in the UK, should be tasked with the evaluation of applications for the import and release of classical fungal agents and with granting approval for the implementation. Agreements need to be in place between European states governing the introduction of fungal classical agents as their spread is not halted by national borders. If the use of classical fungal agents requires registration, then ideally this needs to be reflected in increased funding allocated to individual biocontrol projects. Alternatively, such costs should be borne by the national governments. Once the potential of exotic fungal pathogens to control invasive neophytes becomes widely realized and valued, the current prohibitive legislation and unaffordable costs may encourage illegal introductions, as has been well-documented in Australia (McFadyen 1998; Evans 2000), with potentially disastrous consequences. Fortunately, due to various recent initiatives the dialogue with the European authorities concerning these problems has started with the objective of revising components of the current directive 91/414 in order to better accommodate the needs for the use of classical agents in weed biocontrol.

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References

Adair, R.J. & Groves, R.H. (1998): Impact of Environmental Weeds on Biodiversity: A Review and Development of a Methodology. – National Weeds Programme, Biodiversity Group, Environment Australia: Canberra, Australia, 56pp.

Adams, E.B. (1988): Fungi in classical biocontrol of weeds. – In: Burge, M.N. (Ed.): Fungi in Biological Control Systems, pp. 111-124, Manchester University Press: Manchester, UK.

Barton, J. (née Fröhlich) (2004): How good are we at predicting the field host-range of fungal pathogens used for classical biological control of weeds? – Biol. Control 31: 99-122.

Briggs, M. (1979): Giant hogweed – a poisonous plant. - BSBI News 21: 27-28.

Burdon, J.J.; Groves, R.H. & Cullen, J.M. (1981): The impact of biological control on the distribution and abundance of *Chondrilla juncea* in south-eastern Australia. – J. Appl. Ecol. 8: 957-966.

Child, L.E. & Wade, P.M. (2000): The Japanese Knotweed Manual. – Packard Publishing Ltd: Chichester, UK, 123pp.

Cullen, J.M. & Delfosse, E.S. (1985): *Echium plantagineum*: catalyst for conflict and change in Australia. – In: Delfosse, E.D. (Ed.): Proceedings of the VI International Symposium on Biological Control of Weeds, Ottawa, Canada, pp. 249-292: Agriculture Canada.

Cullen, J.M. & Hasan, S. (1988): Pathogens for the control of weeds. – Phil. Trans. R. Soc. 318: 213-224.

Cullen, J.M.; Kable, P.F. & Catt, M. (1973): Epidemic spread of a rust imported for biological control. – Nature 224: 462-464.

Dodd, A.P. (1936): The control and eradication of prickly-pear in Australia. – Bull. ent. Res. 27: 503-533.

Dodd, F.S.; de Waal, L.C.; Wade, P.M. & Tiley, G.E.D. (1994): Control and management of *Heracleum mantegazzianum* (giant hogweed). – In: de Waal, L.C.; Child, L.E.; Wade, P.M. & Brock, J.H. (Eds.): Ecology and Management of Invasive Riverside Plants, pp. 111-126, John Wiley & Sons Ltd.: Chichester, UK.

EPPO (2001): EPPO Standards: Safe use of biological control. Import and release of exotic biological control agents. – EPPO Bull. 31: 29-35.

Evans, H.C. (2000): Evaluating plant pathogens for biological control of weeds: an alternative view of pest risk assessment. – Australas. Plant Pathol. 29 (1): 1-14.

Evans, H.C. (2003): Biological control of invasive alien weeds using fungi, with particular reference to *Rhododendron ponticum* in the British Isles. – In: Argent, G. & McFarlane, M. (Eds.): Rhododendrons in Horticulture & Science, pp. 8-19, Royal Botanic Garden Edinburgh: Edinburgh, UK.

Evans, H.C. & Ellison, C.A. (1990): Classical biological control of weeds with microorganisms. Past, present, prospects. – Aspects appl. Biol. 24: 38-49.

Evans, H.C. & Ellison, C.A. (2004): The new encounter concept: centres of origin, host specificity and plant pathogens. – In: Cullen; J.M.; Briese, D.T.; Kriticos, D.J.; Lonsdale, W.M.; Morin, L. & Scott, J.K. (Eds.): Proceedings of the XI International Symposium on Biological Control of Weeds, Canberra, Australia, pp.42-47, CSIRO Entomology: Canberra, Australia.

Evans, H.C.; Fröhlich J. & Shamoun, S.F. (2001): Biological control of weeds. – In: Pointing, S.B. & Hyde, K.D. (Eds.): Bio-Exploitation of Filamentous Fungi, pp. 349-401, Fungal Diversity Press: Hong Kong.

Greathead, D.J: (1995): Benefits and risks of classical biological control. – In: Hokkanen, H.M.T. & Lynch, J.M. (Eds.): Biological Control: Benefits and Risks, pp. 53-63, Cambridge University Press: Cambridge, UK.

Harley, K.L.S. & Forno, I.W. (1992): Biological control of weeds – a handbook for practitioners and students. – Inkata Press: Melbourne & Sidney, Australia, 74pp.

Hokkanen, H. (1985): Exploiter-victim relationships of major plant diseases: implications for biological weed control. – Agr. Ecosyst. Environ. 14: 63-76.

Hokkanen, H. & Pimentel, D. (1984): New approach for selecting biological control agents. – Can. Entomol. 166: 1109-1121.

Huffaker, C.B. (1959): Biological control of weeds with insects. – Annu. Rev. Entomol. 4: 251-276.

IPPC (1996): Code of Conduct for the import and release of exotic biological control agents. International Standards for Phytosanitary Measures Publication No.3. – FAO: Rome, Italy, 23pp.

Julien, M.H. & Griffiths, M.W. (1998): Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds. – fourth ed., CABI Publishing: Wallingford, UK, 223pp.

Keane, R.M. & Crawley, M.J. (2002): Exotic plant invasions and the enemy release hypothesis. – Trends Ecol. Evol. 17 (4): 164-170.

Mabey, R. (1998): Flora Britannica. – Chatto & Windus: London, UK, 271pp.

McClay, A.S. (1996): Host range, specificity and recruitment: synthesis of session 2. - In: Moran, V.C. & Hoffmann, J.H. (Eds.): Proceedings of the IX International Symposium on Biological Control of Weeds, Stellenbosch, South Africa, pp. 105-112, University of Cape Town Press: Cape Town, South Africa.

McFadyen, R.E. Crutwell (1998): Biological control of weeds. – Annu. Rev. Entomol. 43: 369-393.

McFadyen, R.E. Crutwell (2000): Successes in biological control of weeds. - In: Spencer, N.R. (Ed.): Proceedings of the X International Symposium on Biological Control of Weeds, Bozeman, Montana, USA, pp. 3-14, Montana State University: Bozeman, Montana, USA.

Mitchell, C.E. & Power, A.G. (2003): Release of invasive plants from fungal and viral pathogens. – Nature 421: 625-627.

Morris, M.J. (1991): The use of plant pathogens for biological weed control in South Africa. – Agr. Ecosyst. Environ. 37: 239-255.

Morris, M.J. (1997): Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa. – Biol. Control 10: 75-82.

Otte, A. & Franke, R. (1998): The ecology of the Caucasian herbaceous perennial *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in cultural ecosystems of Central Europe. - Phytocoenologia 28 (2): 205-232.

Petersen, R.H. (1974): The rust fungus life

cycle. – Bot. Rev. 40: 453-513.
Pimentel, D. (Ed.) (2002): Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. – CRC Press: Boca Raton, Florida, USA, 384pp.
Pyšek, P & Pyšek, A (1995): Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. – J. Veg. Sci. 6: 711-718.
Reinhardt, F., Herle, M., Bastiansen, F. & Streit, B. (2003): Economic Impact of the Spread of Alien Species in Germany. - R+D project 201 86 211 report for the Federal Environmental Agency, Berlin, Germany; undertaken by the Biological and Computer Science Division, Dep. Ecology and Evolution, J.W. Goethe University, Frankfurt/Main, Germany, 190pp.
Reznik, S.Ya. (1996): Classical biocontrol of weeds in crop rotation: a story of failure and prospect for success. - In: Moran, V.C. & Hoffmann, J.H. (Eds.): Proceedings of the IX International Symposium on Biological Control of Weeds, Stellenbosch, South Africa, pp. 503-506, University of Cape Town Press: Cape Town, South Africa.
Scheepens, P.C. & Hoggerbrugge, A. (1991): Host specificity of *Puccinia canaliculata*, a potential biocontrol agent for *Cyperus esculentus*. – Neth. J. Pl. Path. 97: 245-250.
Seier, M.K.; Wittenberg, R.; Ellison, C.A.; Djeddour, D.H. & Evans, H.C. (2004): Surveys for natural enemies of giant hogweed (*Heracleum mantegazzianum*) in the Caucasus region and assessment for their classical biological control potential in Europe. – In: Cullen; J.M.; Briese, D.T.; Kriticos, D.J.; Lonsdale, W.M.; Morin, L. & Scott, J.K. (Eds.): Proceedings of the XI International Symposium on Biological Control of Weeds, Canberra, Australia, pp. 149-154, CSIRO Entomology: Canberra, Australia.
Shaw, R.H. (2003): Biological control of invasive weeds in the UK: opportunities and challenges. – In: Child, L.E.; Brock, J.H.; Brundu, G.; Prach, K.; Pyšek, P.; Wade, P.M. & Williamson, M. (Eds.): Plant Invasions: Ecological Threats and Management Solutions, pp. 337-354, Backhuys Publishers: Leiden, The Netherlands.
Shaw, R.H. & Djeddour, D.H. (2004): Progress with the biological control program for Japanese knotweed. – In: Cullen; J.M.; Briese, D.T.; Kriticos, D.J.; Lonsdale, W.M.; Morin, L. & Scott, J.K. (Eds.): Proceedings of the XI International Symposium on Biological Control of Weeds, Canberra, Australia, p. 230, CSIRO Entomology: Canberra, Australia.
Sheppard, A.W.; Hill, R.; DeClerck-Floate, R.A., McClay, A.; Olckers, T.; Quimby Jr., P.C. & Zimmermann, H.G. (2003): A global review of risk-benefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? – Biocontrol News Inf. 24 (4): 91N-108N.
TeBeest, D.O. (1991): Ecology and epidemiology of fungal plant pathogens studied as biological control agents of weeds. – In: TeBeest, D.O. (Ed.): Microbial Control of Weeds, pp. 97-114, Chapman & Hall: New York, USA.
Tomley, A.J. & Evans, H.C. (2004): Establishment of, and preliminary impact studies on, the rust, *Maravalia cryptostegiae*, of the invasive alien weed, *Cryptostegia grandiflora* in Queensland, Australia. – Plant Pathol. 53: 475-484.
Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M. & Westbrooks, R. (1997): Introduced species: A significant component of human-caused global change. – New Zealand J. Ecol. 21(1): 1-16.
Waage, J.K. & Greathead, D.J. (1988): Biological control: Challenges and opportunities. – Phil. Trans. R. Soc. B 318: 111-128.
Wapshere, A.J. (1974): A strategy for evaluating the safety of organisms for biological weed control. – Ann. App. Biol. 77: 201-211.
Watson, A.K. (1985): Host specificity of plant pathogens in biological weed control. – In: Delfosse, E.S. (Ed.): Proceedings of the XI International Symposium on Biological Control of Weeds, pp. 577-586, Agriculture Canada: Ottawa, Canada.
Watson, A.K. (1991): The classical approach with plant pathogens. – In: TeBeest, D.O. (Ed.): Microbial Control of Weeds, pp. 3-23, Chapman & Hall: New York, USA.
Weidemann, G.J. (1991): Host-range testing: safety and science. – In: TeBeest, D.O. (Ed.): Microbial Control of Weeds, pp. 83-96, Chapman & Hall: New York, USA.