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Plant pathogen eradication: determinants of successful programs

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Abstract Data from 190 plant pathogen eradication programs in the Global Eradication and Response Database (GERDA) were reviewed to identify characteristics that contributed to successful programs in 45 countries between 1912 and 2013. The most successful treatment (94%) was tissue culture, often in combination with thermotherapy to eradicate viral or bacterial pathogens from plants held in in germplasm collections. Whilst 6% of these programs had no reported outcome, there were no recorded failures of this strategy. Host removal and/or destruction was successful in 55% of the programs and was used against all the pathogen groups. The analysis was limited by the high percentage of unknown outcome results across the pathogen groups. A quarter (49 of 190) of the records contained no indication of the eradication treatment: in 43% of these cases an unknown treatment resulted in successful eradication. There were no obvious correlations between the characteristics of a pathogen (viral/viroid, bacterial/phytoplasma, fungal/oomycete or nematode) and the outcome of the eradication program. For many species there is only one record, or the taxa records were dominated by a few genera that do not represent the biological diversity of the pathogen group. No economic or other analysis was possible due to the large number of unknown result/ongoing programs and the lack of common data. Despite these limitations, GERDA

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is an important record of the outcomes of worldwide plant pathogen eradication programs since the second decade of the twentieth century. However, care should be exercised when extrapolating from these records to formulating responses to new taxa as pathogens emerge and/or adapt to new plant hosts as the biology of plant pathogens is extremely variable and this diversity is not represented by the records in the database.

Keywords Eradication · Tissue culture · Thermotherapy · Host removal · Host destruction

Introduction

Any species, strain or biotype of plant, animal, or pathogenic agent, injurious to plants or plant products is a pest (FAO Corporate Document Repository 2017). Agents that are pathogenic to plants range in scale from the nanometre size of viroids and viruses to a single Armillaria ostoyae (causal agent of Armillaria root disease of conifer) clone ranging over 10 km^2 in the USA (Casselman 2007). This trillion (10^{12})-fold (nm to km) scale and the range of diversity that includes abiotic viroids and viruses, the prokaryotic bacteria, rickettsia, mollicutes and the eukaryotic fungi, algae, oomycetes and nematodes, presents a significant challenge to the development of tools and strategies for effective response, including eradication, to plant pathogen incursions. Worldwide, the combined plant pests (pathogen, arthropod and weed) cause pre-harvest yield loss of 42%: plant pathogens are responsible for almost a third of this pre-harvest loss (Fletcher et al. 2006).

Human activities are now the most important determinant of biological invasions (Essl et al. 2011) with the rate of biological incursions by pests increasing via the world-wide movement of people and goods (Essl et al. 2015). The number

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of invasive species in ten taxonomic groups in 28 European countries was found to be closely related to the socioeconomic activity from 1900 to 2000 with taxa with natural dispersal capability (insects, birds) more closely linked with socioeconomic criteria (Essl et al. 2011). Thus, the relative importance of natural pathways has decreased as various human-assisted pathways and activities facilitate the movement of pests across biogeographic barriers.

Detection of a pest incursion, an isolated, recently detected population, which is not known to be established but is expected to survive for the medium future (Anon 2007), results in consideration of a range of response actions, some of which have been predetermined in biosecurity response plans. Options include no response, management of the incursion including containment, or initiating an eradication. An eradication response seeks to permanently extirpate the pest from the locality. The likelihood of success of the response is dependent on a number of criteria including appropriate tools, the extent of its dispersal, the biology of the pest, the availability of fiscal and physical resources, economic justification (e.g. cost/benefit) and the probability of additional incursions.

GERDA, the Global Eradication and Response DAtabase (Kean et al. 2017) is a web-based (http://b3.net.nz/gerda/ index.php) compilation of worldwide incursion response and eradication programs. The database contains information on almost 1100 incursion responses including 972 eradication programs from over 100 countries against over 300 taxa from 1890 to the present. In 2013, an analysis of 672 arthropod eradication programs was undertaken to define the determinants of successful programs (Tobin et al. 2014). Other taxa, including plant pathogens were not included in this analysis 'to avoid comparing taxa that differ vastly in their respective biology and invasion ecology' (Tobin et al. 2014). As noted above, there is extensive variability in biology and invasion ecology both between and within plant pathogen taxa. The aim of this analysis was to identify determinants associated with successful plant pathogen eradication programs by subcategorising the plant pathogens into four groups (bacteria/ phytoplasma, fungi/oomycete, nematode, virus/viroid) and assessing the treatments successfully used to effect eradication of invasive species in these significantly different subcategories. For completeness, the mollusc (which are neither arthropods nor plant pathogens) eradication programs in GERDA were also evaluated.

Materials and methods

A process similar to that described by Tobin et al. (2014), was used. Four taxonomic groupings of non-arthropod organisms were defined: bacteria/phytoplasma (B), fungi/oomycete (F), nematode (N), virus/viroid (V) and information available from published and unpublished sources was entered into the database. Protist and algae options were available in GERDA, however as no incursions or responses were found for either of these taxa, they are not included in our analysis. The plant pathogen groupings reflect important physical and genomic differences as outlined in Table 1. An additional taxa mollusc, not included in the arthropod analysis by Tobin et al. (2014), was included in this analysis for completeness of assessment of the different taxa groups in GERDA. Some species of molluscs are vectors of oomycete plant pathogens (Alvarez et al. 2009). For example, *Achatina fulica* vectors in its faeces the spores of *Phytophthora palmivora*, the cause of black pod disease of cacao (Evans 1973).

The viroid/virus group are nanometre scale pathogens with relatively small genomes that require the host cell metabolic process to reproduce both the genome and any structural components such as the proteins that form the virion. Bacteria and the cell-wall deficient Phytoplasma (sometimes referred to as BLOs (bacterium-like organisms)) are prokaryotes with relatively small genomes. The fungi (a taxa that has substantial variation in reproductive systems and process, nuclear status and infection processes) and the oomycetes are often grouped together, despite being phylogenetically distant (Beakes et al. 2012). The oomycetes are most closely related to the brown algae and, like fungi, obtain nutrients via absorption, and many species produce mycelium, a structure found in many fungal species. However they differ significantly in composition of the cell wall, nuclear state and sexual reproduction process (Rossman and Palm 2006). Nematodes are roundworm animals that exhibit substantial diversity in reproductive strategy, feeding process and ecological niche.

Seven control and treatment options were initially identified from the literature as plant pathogen eradication options (Table 2). In a number of programs, combinations of options (e.g. tissue culture and replacement, chemotherapy and thermotherapy (Ram et al. 2005)) were used to effect successful eradication. The outcome of each program was assigned a letter to indicate the most probable outcome. In the absence of a stated eradication outcome (E, confirmed eradicated; P, in progress; F, failed eradication), two options were used (L, likely eradicated; U, uncertain status).

Results

As at 22 November 2016, 1345 NZDST, GERDA contained 190 plant pathogen and 14 mollusc eradication program entries as part of a total of 972 eradication programs (Table 3). Since the analysis of Tobin et al. (2014) a further 96 arthropod programs have been entered into the database. These additional programs were not analysed for differences or similarities to the 672 arthropod eradication programs assessed in 2014. There were about four-fold more arthropod eradication programs in GERDA than those for plant pathogens, however **Table 1** Physical characteristicsof the four plant pathogengroupings in GERDA

GERDA grouping	Code	Typical physical size/ scale range	Genome type and size range
Virus/Viroid	V	2–600 nm (10 ⁻⁹ m)	DNA or RNA 250 b-1.3 Mbp
Bacteria/Phytoplasma	В	100–300 μm (10 ⁻⁶ m)	Prokaryote 0.6-14 Mbp
Fungi/Oomycete	F	5 µm (spore)-10 km ² (colony)	Eukaryote 14-900 Mbp
Nematode	Ν	$0.2-5 \text{ mm} (10^{-3}) \text{ m} (\text{non-cyst forms})$	Eukaryote 54–100 Mbp

only about two-fold more genera, reflecting that initiation of eradication programs against incursions by arthropod pests are dominated by a small number of taxa. In 2014, Tobin et al. noted that there were 73 entries for *Lymantria dispar dispar* (European Gypsy Moth), 56 for *Ceratitis capitata* (Mediterranean fruit fly), and 40 for *Bactrocera dorsalis* (oriental fruit fly). Only two pathogen species, *Plum pox virus* (PPV) (19) and *Xanthomonas smithii* pv. *citri* (15) (currently one of seven synonyms of *X. citri*, subsp. *citri* (Anon 2014)) were targeted by more than 10 eradication campaigns.

Plant pathogen eradication programs often have only one example against a species or genus

The plant pathogen eradication programs have largely targeted the bacteria/phytoplasma (B), fungi/ oomycete (F) and viroid/virus (V) groups. Both the fungi/ oomycete and viroid/virus groups had similar numbers of eradication programs against genera (63 programs / 21 genera and 61 programs /16 genera respectively). Many of these programs targeted incursions by different species (e.g. 21 genera/ 28 species and 16 genera/ 29 species respectively). There were 22 unique programs against a single species in a genus with representatives within all four plant pathogen groups (Fig. 1). In particular, the fungal/oomycete and virus/viroid groups had significant numbers of single programs against a single species in a genus (53% and 56% respectively). The largest number of eradication programs initiated against a plant pathogen genus was 27 (potyvirus) followed by

 Table 2
 Control and treatment code and tools for plant pathogens available in GERDA

Code	Control/ treatment
С	Tissue culture and replacement
Н	Host removal/destruction
М	Quarantine/ movement control
0	Other e.g. Ribavirin/6-benzylaminopurine
Р	Pesticide/antibiotic
R	Removal by hand (roguing)
Ζ	Thermotherapy

21 against the bacterial genus *Xanthomonas*. The number of programs (at 22 November 2016) for these two genera were the sixth and eighth most frequent eradication programs in GERDA: a list dominated by programs against the arthropod genera *Bactrocera* (101), *Ceratitis* (100) and *Lymantria* (93). Plum pox potyvirus was the most targeted pathogen species with 19 programs recorded in GERDA (ninth on the overall list with *Ceratitis capitata*, Mediterranean fruit fly, first with 100 programs).

Plant pathogen eradication programs have a high level of unknown outcome

Overall, the plant pathogen eradication programs had a lower success rate (confirmed (E) or likely (L) eradication) than the arthropod eradication programs reported previously by Tobin et al. 2014 (Table 4). As the eradication failure (F) rate was similar, this lower level of success was the consequence of programs either still in progress (P), or with unknown (U) outcomes. Some plant pathogens can take years or decades to successfully eradicate, especially those present in soil. For example, *Synchytrium endobioticum*, the causal agent of potato wart, produces sporangi, resting spores that can persist for over 30 years in soil (Hooker 1981).

Specific biological treatments were the most successful tools for eradicating plant pathogens

Sixteen combinations of plant pathogen treatments were reported (Table 5). As many combinations were used only once, for analysis the combinations were grouped into three major classes: biological, tissue culture and replacement/ thermotherapy; physical, host removal/destruction/rouging/ quarantine/movement control; and chemical, pesticide/antibiotic/other chemical.

The biological-based tissue culture and replacement/ thermotherapy treatments were very successful with no known failures and a small percentage of unknown outcomes (Table 6). This specialised and limited eradication treatment, used in 18 of the 190 plant pathogen programs, can only be applied where tissue culture systems are available and/or the plant germplasm can withstand the thermotherapy (including cryotherapy) **Table 3**Summary of plant pesteradication programs in GERDA(22 November 2016, 1345NZDST)

GERDA grouping	No. of programs	No. of genera	No. of families	No. of orders	
Arthropod	768	109	53	14	
Bacteria/Phytoplasma	51	7	7	7	
Fungi/ Oomycete	63	21	17	13	
Mollusc	14	3	3	1	
Nematode	15	5	5	4	
Viroid/Virus	61	16	12 ^a	2 ^b	
Totals	972	161	97	41	

^a 48 of the 61 species are not assigned to a family; ^b Currently only two orders exist in viral taxonomy

necessary to kill the bacterial/phytoplasma pathogen (Wang and Valkonen 2008; Ding et al. 2008). This approach was also used successfully to eradicate viruses: a regime of alternating temperature (38 and 30 °C every 4 h) and apical meristem culture was used to eliminate *American hop latent virus* (AHLV), *Hop latent virus* (HpLV) and *Hop mosaic virus virus* (HpMV) from infected plants (Postman et al. 2005).

The physical-based host removal/destruction/rouging, sometimes combined with another treatment (e.g. quarantine/movement control or pesticide/antibiotic application) was the most widely applied treatment (110 of the 190 programs) across all four pathogen groups. This treatment was considered successful in 55% of the programs and failed 17% of the time (Table 6). Successes and failures were found in all four pathogen groups, with no apparent taxonomic bias within any group (Table 7). For example GERDA contains records of two failures and three successes using this treatment against *Erwinia amylovora* incursions.

Only 13 of the 190 plant pathogen eradication programs were chemically based. This dataset was too small to undertake any meaningful analysis. The number of cases in which treatments and control measures were not stated or were not apparent in the source documents was high (49 of 190). In many instances these references are a brief EPPO report where 'phytosanitary measures' were being applied and the incursion was 'under eradication' (e.g. Anon 2011). No further records could be found indicating the outcome of the program.



Fig. 1 Number of eradication program entries in GERDA for each of the four plant pathogen groupings and number of species per plant pathogen genus against which an eradication program was undertaken

Table 4Summary of outcomesof plant pathogen, mollusc andarthropod eradication programsavailable in GERDA (22November 2016, 1345 NZDST)

GERDA groups	No of programs	% of total programs	% Success (E, L)	% Unknown (P, U)	% Failure (F)
Plant Pathogen All	190	100	55.3	31.1	13.7
Bacteria/Phytoplasma	51	26.8	49.0	41.2	9.8
Fungi/Oomycete	63	33.2	52.4	30.2	17.5
Nematode	15	7.9	40.0	26.7	33.3
Viroid/Virus	61	32.1	67.2	24.6	8.2
Mollusc	14	100	50.0	42.9	7.1
Arthropod	768	100	66.9	17.4	15.6
All eradication programs	972	100	64.4	20.5	15.1

E, confirmed eradicated; L, likely eradicated; P, in progress; U, uncertain status; F, failed eradication

There are insufficient data to undertake economic analyses

There are limited data on the cost of the plant pathogen eradication programs. For example there are data for only four of the 27 potyvirus programs and five of the 21 *Xanthomonas* programs. Combined with the high level of unique response against single species in unique genera, a meaningful analysis of costs and other determinants such as size of incursion could not be undertaken.

Mollusc eradication programs

Three species in different genera were the targets of 14 eradication programs. Half of these programs were successful: the only noted method for one of these programs was lure and kill using metaldehyde baits against the giant African snail, *A. fulica* (Anon 2003). Only one program was considered a failure whilst six had unknown outcomes or were in progress. This 43% unknown/in progress is higher than the value for the plant pathogen or arthropod programs. Also, there was a high proportion of programs (71%) for which the control tool was not reported. Metaldehyde baits, hand removal of snails and host destruction were noted as treatments in the unsuccessful

 Table 5
 Plant pathogen control combinations in GERDA allocated to major treatment class

Class	Treatment Codes
Biological	C, CZ, Z
Physical	H, HM, HMO, HO, HMO, HP, HR, R, M, MOP
Chemical	O, OP, P

C, Tissue culture and replacement; H, Host removal/ destruction; M Quarantine/ movement control;

Z, Thermotherapy

programs. No meaningful conclusions can be synthesised from this small dataset on mollusc eradication.

Discussion

GERDA contains entries obtained from a wide variety of sources including published science (e.g. peer-reviewed journal), official announcements (e.g. EPPO) and other literature (organisation reports, media and official letters). These records cover only a small fraction of potential invasive plant pathogens in the world: in the USA alone plants are attacked by over 50,000 different pathogens (Fletcher et al. 2006). It is not obvious why there are fewer plant pathogen entries in the database than those for arthropods, given the level of production loss due to pathogens. Arthropods include taxa with natural dispersal capability closely linked with socioeconomic activity (Essl et al. 2011), whilst pathogens, in general, have dispersal mechanisms (e.g. rain splash, wind, waterways) that are associated with natural pathways. Thus efforts to control pathogens may be regarded as routine pest management rather than as a biosecurity incursion necessitating consideration of an eradication response (e.g. breeding programs to maintain resistance to evolving cereal rust pathogens).

Similar to the arthropods, however on a smaller scale, a small number of genera dominate the plant pathogen eradication response records in GERDA that originate from these diverse sources. The bacteria/phytoplasma group (seven genera /11 species) records of 51 eradication programs were dominated by over 30 eradication programs against two γ -proteobacteria genera: 21 against three *Xanthomonas* species and 12 against *Erwinia amylovora*. A further eight programs were against the β -proteobacteria *Ralstonia solanacearum*. Thus 80% of the bacteria/phytoplasma responses recorded in GERDA are to three bacteria species. There is a similar situation in the virus/viroid group as 44% of the records are responses to incursions by potyviruses, with 31% of the records to one potyvirus species, plum pox. Six of the 15 nematode

O, Other (e.g. Ribavirin/ 6-benzylaminopurine; P, Pesticide/ antibiotic; R, Removal by hand (roguing);

Smith G.R. et al.

Table 6 Summary of plant pathogen eradication treatments Instant	Treatment	Success (E, L)	Unknown (P, U)	Failure (F)
and outcomes as percent of programs available in GERDA (22 November 2016, 1345 NZDST)	Biological: Tissue culture and replacement	94.4	5.6	0.0
	Physical: Host removal/ destruction	55.5	28.2	16.4
	Chemical: e.g. Ribavirin/6-benzylaminopurine	46.2	23.1	30.8
	Not stated	42.9	49.0	8.2
	Overall	55.3	31.1	13.7

E confirmed eradicated, L likely eradicated, P in progress, U uncertain status, F failed eradication

eradication programs targeted two Globodera species (G. pallida and G. rostochiensis) with outcomes evenly distributed between success, unknown and failure. In contrast, while 16% of the responses to fungal/oomycete pathogens where against three Phytophthora species, 39% (11 of 28) of the fungal/oomycete species were targeted by a single program.

Tobin et al. (2014) noted that for the 672 arthropod eradication programs analysed in 2012 there were 112 species for which the number of programs was less than 10(17%), and 51species were targeted by a single program (7.6%). Of the programs targeting eradication of the 74 plant pathogen species, 57 species (77%) were targeted by less than 10 programs, whilst 22 species were targeted by a single program (30%). Thus there were proportionally more single eradication programs targeting a single plant pathogen species with just two pathogen species, *Plum pox virus* (19) and *X. smithii* pv. *citri* (15) targeted by more than 10 eradication programs.

The most successful control technology for plant pathogen eradication was tissue culture, often in combination with other treatments such as thermotherapy. Temperature-based therapies included both cold- and heat-based regimes (e.g. Postman et al. 2005; Wang and Valkonen 2008; Ding et al. 2008). This approach has been used successfully to eradicate bacterial, phytoplasma and viral pathogens. These biological treatments require tissue culture facilities, previous knowledge on the most appropriate system and a serological or molecular assay to determine efficacy and outcome. As such these very successful protocols have been applied to rescue valuable germplasm held in small germplasm repositories. For example, Postman et al. (2005) noted that a Humulus germplasm collection contained '...267 clonal accessions and seedlings... maintained as potted plants in a screen house' and the '... 'core' subset of 84 genotypes is also maintained in vitro under cold storage'. This strategy however is not applicable to large-scale eradication programs, unless the pathogen-free tissue cultured plants can be used to initiate replacement of infected plants after the pathogen has been eradicated by a physical or chemical treatment.

Physical removal and/or destruction of the plant host was recorded as successful in 55% of the programs that were recorded in GERDA. This strategy has been used on a large scale including the 2004–2009 program to eradicate X. smithii pv. citri from 800,000 ha in the Emerald shire in Queensland, Australia. The program was declared successful in January 2009 after approximately 500,000 trees had been destroyed. Conversely, physical removal and destruction of the plant host to eradicate this pathogen from Florida between 1995 and 2006 was a failure as the spores were widely dispersed during the 2004 hurricane season. After approximately USD1.5B (2015 equivalent) had been spent eradication was deemed infeasible (Connor 2006). Thus, in this program, failure to eradicate was not due to the control/treatment strategy, and illustrates the difficulties of delimiting and extirpating a pest with propagules that are easily dispersed by wind and/or rain.

Interestingly, with the ongoing concern of a Myrtle rust, Puccinia psidii, incursion into New Zealand (http:// www.biosecurity.govt.nz/pests/guava-rust), the only successful eradication in the database of a rust pathogen of a myrtaceous species was in New Zealand. Puccinia

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Outcomes and pathogen groups		Success (E,L) %			Unknown (P,U) %			Failure (F) %				
Treatments	В	F	Ν	V	В	F	Ν	V	В	F	N	V
Biological: Tissue culture and replacement	11			83				6				
Physical: Host removal/destruction	16	19	3	17	10	11	1	6	5	7	2	3
Chemical: e.g. Ribavirin/6-benzylaminopurine		38		8	23					8	15	8
Not stated	10	14	6	12	14	14	6	14		4	2	2

39

36

32

7

25

19

42

19

19

6

Table 7 Summary of plant pathogen eradication treatments available in GERDA and program outcomes (in percentage) against the four pathogen groups

E confirmed eradicated, L likely eradicated, P in progress, U uncertain status, F failed eradication

24

31

B bacteria/phytoplasma, F fungi/oomycete, N nematode, V virus/viroid

Totals for pathogen group outcomes

cvgnorum is one of the two native Australian rust fungi found on plants in the family Myrtaceae (Makinson and Butcher 2014). In Australia, the host plant is Kunzea glabrescens (Makinson and Butcher 2014), which was originally identified as K. ericifolia (Shivas and Walker 1994), whilst K. vestita, which was also identified as a host for this pathogen is now considered to be a synonym of K. ericifolia subsp. ericifolia (Makinson and Butcher 2014). In New Zealand this pathogen was found on Astartea fascicularis (Myrtaceae) in the Australian section of the Napier Botanic Gardens in 2006 (Dick and Inglis 2011). Prompt action by Biosecurity New Zealand resulted in immediate removal of the plants, followed by an intensive survey of the other myrtaceous plants in the gardens. In 2011, P. cygnorum was declared eradicated from New Zealand (Dick and Inglis 2011). Myrtle rust, caused by P. psidii, has been spreading throughout Australia, causing significant damage and death to numerous host plants in the Myrtaceae (Carnegie et al. 2016 and references within). New Zealand has a small number of unique Myrtaceae species including the culturally and economically important Pohutukawa, Metrosideros excelsa and Mānuka, Leptospermum scoparium. Whilst noting the differences in biology, in particular host range, of these two Puccinia species, host destruction after early detection of P. psidii may be possible based on the previous experience with P. cygnorum. However should Myrtle rust be found in New Zealand, host destruction as part of an eradication program will have significant cultural, social, environmental and economic consequences. Many New Zealand Myrtaceae species are known to be susceptible (http://www.anbg.gov.au/anpc/resources/Myrtle Rust.html), so there will also be substantial consequences if an incursion cannot be extirpated, as evidenced by the current Australian situation (Carnegie et al. 2016 and references within).

Chemical technologies have also been successfully applied to eradicate plant pathogens. *Mycosphaerella fijiensis* was successfully eradicated from banana plantations near Tully (Queensland, Australia) using multiple fungicide applications rotated weekly for six months (Sosnowski et al. 2009). Early detection of the pathogen, the approaching dry season (resulting in reduced ascospore production) and pathogen biology (no alternative hosts/no long-term resting spores) also contributed to this successful eradication (Sosnowski et al. 2009).

GERDA is a very important collection of programs spanning over 100 years of plant pathogen eradication programs in 45 countries. It provides a unique resource enabling biosecurity practitioners to learn from the past experiences of their international counterparts. However, care should be exercised in extrapolating from these plant pathogen eradication records when considering responses to incursions by new taxa. The biology of plant pathogens is extremely variable and is not represented by the records currently in the database. We encourage our worldwide colleagues to register (for free), agree to the terms of use and create a new user account at GERDA (http://b3.net.nz/gerda) to contribute both new entries, and data missing from current entries, to increase the value of this important resource for future plant pathogen eradication efforts.

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